



UNIVERSITY OF  
**LINCOLN**

# **THE EVOLUTION OF VIOLENCE IN PRIMATES**

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Doctor of Psychology

School of Psychology  
College of Social Science

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## ABSTRACT

Violence is a widely studied trait across the social and biological sciences due to its social, economic, and political significance. Understanding the emergence, triggers, and expression of violence through evolved psychological processes is a principal goal of conflict research. Violence can be observed in many social species and may be considered as a uniform or pluriform phenomenon. Recently work has provided evidence of violence having an evolutionary basis when considering the single facet of lethal violence as a pooled measure. However, to understand the ultimate and proximate causes of violence it is critical to determine if violence is a single trait or in fact composed of different traits, each with their own evolutionary history. Moreover, violence has been associated with specific socioecological variables which have impacts on individual fitness. However, it is unclear how they predict a range of violence types. Furthermore, it has been suggested that prosocial behaviours may have co-evolved with certain violence types. Consequently, in a series of four research studies this thesis explored the evolution of five violence types to determine if they were unique traits. Investigated, the socioecological factors impacting on the emergence and activations of each violence type, including sex differences on adulticide, and explored the relationship between prosocial behaviours and violence.

An extensive species level primate comparative dataset was created containing data on five violence types and a range of socioecological and prosocial variables. Data were obtained through a systematic review of the primatological literature and through a survey distributed to specialist researchers, resulting in data on up to 104 primate species. Analysis was carried out using Bayesian multivariate modelling, with phylogenetic control, within the ‘brms’ R package.

There were strong/moderate correlations found between the three lethal violence types with adulticide types producing the strongest phylogenetic signal and intergroup aggression the lowest. Several socioecological variables were associated with specific violence types; coalition formation, a positive predictor of intra/intergroup adulticide; territoriality, a positive predictor of intergroup aggression; and diet type, a negative predictor of intragroup aggression. Sex specific violence data retained a strong phylogenetic signal with strong/moderate correlations between male/female adulticide. Prosocial behaviours indicated differential effects on coalition formation and each violence type.

This thesis has determined that violence is not a single trait but that the five violence types are distinct. Phylogeny explains a substantial amount of variance in lethal violence with strongly correlated adulticide types, though they have different phylogenetic signals and are not always observed in the same set of species. Furthermore, the different violence types are modulated by different socioecological and prosocial factors. Sex specific data indicated importance of intergroup adulticide for males which reinforces that killing is frequently committed by males towards intergroup males, often driven by sexual motives. Coalition formation was important to both sexes in adulticide, reducing potential costs to the attackers, and may be driven by factors other than prosocial behaviours. Overall, it is recommended that research be conducted on specific violence types and, unless pertinent to the study, should not amalgamate into a single measure.



## ACKNOWLEDGEMENTS

I must confess to experiencing some trepidation in writing this section. I wanted to be able to write eloquently enough to truly express my thanks to all concerned, but also share a little of what this journey has meant to me. As it happens this is merely my heartfelt thanks to those that have gotten me to the point of writing this, and perhaps a little gentle advice added for good measure.

I'll start first of course with my director of studies, Bonaventura (Bino) Majolo who has provided calm and consistent guidance as well as helping me improve my grammar! I cannot say how much your encouragement has helped me on this journey, thank you. Also, my second supervisor Marcello Ruta who was helpful when chatting about stats and phylogenetic stuff and managed to make me laugh with his wonderful jokes. I would also like to thank Erik Willems whose insight on the brms package has been invaluable. Also, all the kind researchers who gave their time to complete my survey and shared their knowledge and experience of primate behaviour. Lastly to the admin team in the psychology office who over the years have patiently answered all my questions.

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All this support has been so important. Doing a PhD is hard work and there have been challenges, mentally, physically, and practically. Despite my best efforts at staggering out the work it still came in waves, and there were times when I felt I might drown, but here I am writing this final part. What I would like to say is that as a writer and researcher you are never alone, if you feel like you are drowning someone can always throw you a lifeline, be that a supportive word or a cooked meal! So, despite the challenges both spoken, unspoken, or merely alluded to, I would like to say one very simple thing to those that follow, you can do it!

You might notice as you go through this thesis that I have quoted one of my favourite authors, Sir Terry Pratchett when introducing each new chapter. Well one reason is that he has the ability to say something quite profound about human nature in only a few simple, funny words. This unfortunately is about as far removed from me as it is possible to get. If something can be written in 100 words, I will endeavour to write it in 1000 (if you are still reading this then you may be getting the point!). To my defence, the comparative study of primates in illuminating our own behaviour is a fascinating subject and there is so much to say! On that note...enjoy!!!!



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## **CHAPTER ONE - STUDYING THE EVOLUTION OF VIOLENCE**

*“It is important that we know where we come from, because if you do not know where you come from, then you don’t know where you are, and if you don’t know where you are, you don’t know where you’re going. And if you don’t know where you’re going, you’re probably going wrong.”*

(I Shall Wear Midnight - Pratchett, 2010, p.477)



## 1(A) Introduction

Violence is a widely studied trait across the social and biological sciences due to its social, economic, and political significance, and seeking to understand it at ultimate and proximate levels continues to drive further research. It has been described in social psychology as “*any behaviour directed toward another individual that is carried out with the proximate intent to cause harm*” (Anderson and Bushman, 2002, p.28). Violent behaviour operates within a cost-benefit trade-off. There are potential fitness costs, including injuries and death, to be balanced against the fitness-related benefits a winning combatant gains, including dominance, access to territory, food sources, and mating opportunities (Maynard Smith and Price, 1973). Yet, despite the potential risks, throughout the natural world violence is widespread (Broom, 2009). Understanding the emergence, causal triggers, and expression of violence through evolved psychological processes that depend on internal and environmental factors is one of the principal goals of evolutionary psychology (Confer *et al.*, 2010).

### 1(A).1 Comparative methods and the importance of primates

A frequently employed tool in evolutionary psychology is that of comparative methods. They are powerful means for clarifying and illuminating the roots of psychological, behavioural, and cognitive adaptations in both human and nonhuman species (Alcock, 2009; Buss, 2015). These comparative methods may incorporate phylogenetic analysis which is a rapidly growing area of comparative behavioural research (Maestripieri and Roney, 2006). The phylogenetic comparative approach studies variation in traits of different species (or higher/lower taxonomic level) which are used to test specific hypotheses or to generate new hypotheses about evolutionary phenomena (MacLean and Nunn, 2017). However, species do not represent statistically independent data points due to their shared phylogeny, therefore comparative analyses need to control for this non-independence (Stone, Nee and Felsenstein, 2011). Accordingly, it is possible through phylogenetic comparative studies, which control for non-independence, to address a wide range of questions regarding trait co-evolution, such as potentially different violence types.

While comparative studies can explore species that are not genetically closely related, because they may have evolved a trait under similar selective pressures, many studies are conducted using closely related species. Humans (*Homo sapiens*) sit within the primate order and specifically within the family Hominidae and therefore share a close genetic relationship

with other species of great ape such as bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), and gorillas (*Gorilla sp.*). These species also share some comparable traits; for example, Pliocene human ancestors had social structures that were similar to those observed in extant social primates (Foley and Gamble, 2009). Indeed, the closer the species phylogenetic relationship the higher the probability that these species share comparable behaviours, and as such, non-human comparative research has a valuable role to play in understanding human behaviour (Maestriperi and Roney, 2006). Comparison between human and non-human primates can reveal homologies, where inheritance is through a common ancestor, and also analogies, where the behaviour has a similar function but occurs via independent evolution (Maestriperi and Roney, 2006). Additionally, primates also show a high degree of intra- and inter-species diversity in several anatomical, behavioural, and cognitive traits (Snaith and Chapman, 2007). Such diversity makes this taxon particularly useful to explore the impact of socioecological factors on behaviour, while controlling for phylogenetic non-independence due to common ancestry. Further expansion can later be undertaken into other taxa as data becomes available as comparative studies have progressively shown that other species, even distant ones, can show similarities with humans. For example, Common ravens' (*Corvus corax*) cognitive performance was comparable to adult apes in physical and social cognition tasks despite not having a similar cortical architecture (Pika *et al.*, 2020).

Historically evolutionary approaches have been questioned. In 1986 UNESCO commissioned twenty scientists to make a platform statement, the “Seville Statement on Violence” to condemn the notion that human beings have a biological, genetically determined basis for violence and aggression (Adams, 1989). Beroldi (1994) described the statement as giving an incorrect portrayal of evolutionary scientists, as providers of inaccurate information, as generating public pessimism, and implied there was a belief in genetic determinism. Despite this statement occurring nearly 40 years ago concern is still expressed about the role of evolutionary psychology (Smith, S. E., 2020) Even some evolutionary psychologists hold the view that comparative data are of limited use in understanding human psychological adaptations (Maestriperi and Roney, 2006). For example, cognitive differences between humans and non-human primates limit the latter's ability to express and develop group cultures through normative conformity and cumulative behaviour limitations (Gruber *et al.*, 2015). Additionally, there can be wide variations in the extent to which traits are associated with phylogeny, as cognitive, behavioural, and ecological variables show lower phylogenetic

signals than morphological traits (Blomberg, Garland Jr and Ives, 2003; MacLean *et al.*, 2012; Kamilar and Cooper, 2013). Furthermore, when developing a comparative dataset, methodological differences between studies can require careful handling.

Psychological adaptations, such as violence traits, have evolved due to their benefits in enhancing reproductive fitness and survival (Confer *et al.*, 2010). Evolutionary biologist E.O Wilson (1975, p. 577) incorporated fitness into his definition of aggression as “*one animal’s physical act or threat of action that reduces the freedom or genetic fitness of another*”. For example, Wrangham (1999) concluded that selection has favoured a hunt and kill tendency, and also stated the importance of coalitionary killing for chimpanzees and humans. The role of coalitions thereby acting to reduce the risks associated with conspecific killing.

Understanding the ultimate explanations of why a behaviour may be selected for is essential if a behaviour is to be properly understood. However, while genetics may give rise to behavioural traits, they do not determine the specific expression of those behaviours (Pratarelli and Mize, 2002). Therefore, an understanding of the function of a behaviour, the proximate/causal triggers that control the behaviour, should also be examined. Thus, in opposition to a determinist view, ultimate and proximate explanations are not dichotomous positions but distinct yet complementary accounts which must both be obtained to fully understand the behaviour (Scott-Phillips, Dickins and West, 2011).

Comparative analysis can therefore be a valuable method to analyse these potential evolutionary forces and is meaningful and robust to different formulations (Freckleton, 2009), especially when using high quality studies within a largescale dataset (MacLean and Nunn, 2017). The study of primate violent behaviour within the context of a phylogenetic comparative method is therefore essential in understanding the basis of human evolved violence traits.

#### 1(A).2 The evolution of violence types

An aid in understanding the ultimate and proximate causes of violence is through creating more specific violence/aggression definitions. Psychological, and biological research create sub-divisions of more specific violence types depending on the target of the attack, the aggressor/s, mode of delivery, state of arousal, or level of violence involved (Table 1.1). For the purposes of this thesis violence is considered as an umbrella term for all sub-types of

violence and also individually applies to lethal violence types, whereas non-lethal sub-types are termed aggression.

### *1(A).2.1 Intra and intergroup aggression*

In group-living species aggression may be defined based on whether it occurs within the group (intragroup aggression exchanged between group members) or between members of distinct groups (intergroup aggression). Both intergroup and intragroup aggression have been frequently researched, though the latter in more detail due to the methodological constraints of observing intergroup interactions. Both forms of aggression are often non-lethal aggression and linked to sexual dominance and resource acquisition/defence (Wrangham, 2018).

Non-lethal intergroup aggression has been observed frequently in social species such as birds, humans, and primates (Radford, 2003; Bowles, 2009; Crofoot and Wrangham, 2010).

Aggression is common during take-over attempts by rival males from other groups where aggressive dominance provides potential reproductive fitness benefits for the aggressor and possible heritability of the trait through sexual selection (e.g., *Alouatta palliata* - Dias *et al.*, 2010, *Alouatta pigra* - Van Belle, Estrada and Strier, 2008, *Propithecus verreauxi* - Brockman, Cobden and Whitten, 2009). Intergroup aggression also commonly occurs at territorial boundaries, as part of territorial defence or expansion with both males and females acting individually and occasionally as coalitions (Kitchen and Beehner, 2007).

Intragroup aggression may operate as mate competition within the group from males attempting to gain access to females. For example, mate competition has been observed to play an important role leading to elevated levels of aggression and testosterone in chimpanzees (Muller and Wrangham, 2004; Muehlenbein, Watts and Whitten, 2004).

However, bonobos do not show the same levels of aggression, as male-male competition may be less beneficial due to female dominance and their key role in mate choice (Surbeck *et al.*, 2012). In these situations, females can also be involved in mate competition, especially where mating opportunities are in short supply, when female bonobos harass others during mating (Fruth and Hohmann, 2003). Additionally, it may serve a protective purpose, operating as either punishment or coercion to prevent costly interactions during current or future intergroup encounters (Arseneau-Robar *et al.*, 2018), or through resource competition for physical resources, such as food or nest sites (Hrdy, 1979).

*Table 1(A).1: Violence has been sub-divided into several violence and aggression types within biological and psychological research based on both intrinsic and extrinsic factors.*

	Sub-division	Definition and context
<u>Mode of delivery</u>	Verbal aggression Physical aggression Indirect aggression	Kaukiainen, <i>et al.</i> , (1999) explored aggression in relation to social intelligence and specified three aggression types: Indirect aggression targeted indirectly through social manipulation, physical attacks and/or aggression directed through verbal intimidation. Indirect aggression was positively correlated with social intelligence, while both physical and verbal aggression had negligible correlation to social intelligence.
<u>Functional</u>	Competitive Protective Parental	Archer (1988) sub-divided aggression into three functional types: Competitive aggression involves competition for resources e.g., space, food, territories. Protective aggression incorporates protection from a conspecific attack, individual distance intrusion, and sudden pain. Parental aggression functions to protect offspring or eggs
<u>Relationship to the victim</u>	Domestic violence Intimate partner violence (IPV) Non-intimate partner violence (non-IPV) Unknown victim offender	Domestic violence involves threatening, controlling or coercive behaviour by intimate partners (IPV) or any family member (non-IPV) Turner, Brown and Medina (2021). Stöckl <i>et al.</i> , (2013) identified utilising data for 66 countries identified that 13.5% of homicides were committed by an intimate partner (rate six times higher for female victims than male). Mulder <i>et al.</i> , (2012) identified that having a previously committed a violent act against an unknown victim was one of the predictors of serious recidivism
<u>Psychological state</u>	Proactive aggression Reactive aggression  Frustration induced Instrumental aggression	Wrangham (2018) sub-dividing aggression into proactive (premeditated) and reactive aggression (impulsive) and concluded that humans had a high tendency to proactive aggression in similarity to chimpanzees but a low frequency of reactive aggression in similarity to bonobos. Frustration induced (impulsive) occurs with the delay or inaccessibility of reinforcement. Instrumental aggression (premeditated) defines aggression which previously resulted in reinforcement (see: Bushman and Anderson, 2001 for review of the dichotomy).
<u>Social division</u>	Intragroup violence/aggression Intergroup violence/aggression <sup>b</sup>	Hipp <i>et al.</i> , (2009) used the terms intra- and intergroup violence to specify violence within the same racial/ethnic group or between different ones. Several primate comparative studies have used the terms intra and intergroup aggression to describe aggression between and within social groups (e.g. Majolo, de Bortoli Vizioli and Lehmann, 2016; Van Belle, Grueter and Furuichi, 2020; Glowacki and McDermott, 2022).
<u>Level of aggression</u>	Lethal violence Non-lethal violence	Lethal violence (as opposed to non-lethal) broadly covers the killing of another individual/s. There are more specific definitions that may incorporate “intentional”, “unlawful” etc. (see: Oberwittler, 2019 for review).
<u>Age of the victim</u>	Adulticide Infanticide	Adulticide is a form of lethal violence that occurs by an adult actor/s to an adult victim. Infanticide is a form of lethal violence that occurs when an adult actor/s carryout a behaviour that causes a conspecific infant’s death, either immediately or shortly afterwards (Digby, 2000)

a Definitions can also be combined, for example, lethal intragroup or lethal intergroup; lethal adulticide or lethal infanticide.

b The terms within- and between groups can also be utilised.

### 1(A).2.2 Lethal violence

Violence can be described according to its intensity, the maximum extent of which is lethal violence. Violence occurs both within and between groups, though intragroup lethal violence is less frequent, and with infants or adults as the victim. When lethal violence is directed to a conspecific adult it is termed adulticide (Gómez, Verdú and González-Megías, 2021). Despite being relatively rare there are several studies giving examples across the primate order (see: Gros-Louis, Perry and Manson, 2003 (*Cebus capucinus*); Campbell, 2006 and Valero *et al.*, 2006 (*Ateles geoffroyi*); Talebi, Beltrão-Mendes and Lee, 2009 (*Brachyteles arachnoides*); Dias *et al.*, 2010 (*Alouatta palliata*); Wilson, M. L. *et al.*, 2014 (*Pan spp.*). Intergroup adulticide is more common than intragroup and similarly male adulticide occurs more frequently than female killing (Gómez, Verdú and González-Megías, 2021).

While primate conspecific adulticide has received limited attention, in contrast infanticide has been widely studied (Fossey, 1984; Jolly *et al.*, 2000; Ramírez-Llorens *et al.*, 2008; Pavé *et al.*, 2012). Infanticide involves a group or individual carrying out a behaviour that causes a conspecific infant's death, either immediately or shortly afterwards (Digby, 2000). Unlike adulticide, infanticide has been reported in numerous primate species (Hrdy, 1979; Valderrama, Srikosamatara and Robinson, 1990) and may be viewed as a common social behaviour (Hausfater, 1984). It has been proposed that this type of lethal aggression may in part be explained by sexual selection (Hrdy, 1974; Hrdy, 1979; van Schaik, 2000), where it would be beneficial for a male to kill an unrelated infant to gain reproductive access to the females (Digby, 2000). Resource competition has also been suggested as a possible cause of infanticide by both males and females (Hrdy, 1979; Lukas and Huchard, 2019).

It has been suggested that some violence types (e.g., infanticide) may occur during a state of generalised aggression and so be part of a generalised aggressive profile (Bartlett, Sussman and Cheverud, 1993), where aggression can be considered a single trait rather than distinct types. However, in primate males there is evidence that indicates that it is not simply non-lethal aggression progressing to lethal violence (Dobash *et al.*, 2007; Gómez, Verdú and González-Megías, 2021). Different types of violence show differences in terms of frequency, mode of delivery and importance for different species. Humans have been shown to display generalised violence, but also specific forms are expressed in isolation (Holtzworth-Munroe and Stuart, 1994). Early indications based on presentation in the literature indicate that primates also show propensity to specific types of violence rather than a generalised violent profile (Dobash *et al.*, 2007; Gómez, Verdú and González-Megías, 2021). Therefore, what is

required, but has yet to be established, is whether these five violence types (1. intragroup aggression, 2. intergroup aggression, 3. intra adulticide; 4. intergroup adulticide, 5. infanticide) show a similar and correlated evolutionary history or whether they are in fact distinct. Furthermore, to identify if similar evolutionary trends are detected when using sex specific adulticide data.

### 1(A).3 The drivers of violence

Human violence, specifically homicide, attracts a great deal of attention both generally and scientifically (Daly and Wilson, 2017). However, an understanding of who may kill and why remains elusive. Several factors have been suggested as having an impact, including biological, psychological and sociological explanations (Brookman, 2005). Research can focus not just on these explanations in isolation but on their interplay, such as the relationship between evolution, socio-ecological factors, group norms, and cultural behaviour. Specific factors which have been studied include parental affection or rejection, rivalry between siblings, sex differences (interests and inclination), social comparison, and justice/morality/fairness (Daly and Wilson, 2017). Evolutionary models consider natural and sexual selection mechanisms (Daly and Wilson, 1997). As such it has been suggested that the strength of the genetic relationship may inversely affect the degree of conflict between victim and perpetrator (Daly and Wilson, 1988). Furthermore, family homicides most often occur between spouses and are driven by male sexual motives. Infanticidal conflict varies based on the ages, sexes, and other characteristics of protagonists (Daly and Wilson, 1988). However, evolutionary psychologists do not hold a deterministic view but consider human behaviour to be due to present environmental and social influences acting on ancestral tendencies or ‘mental hardware’ (Cartwright, 2017).

The role of group norms and cultural diversity on the occurrence of violence is significant, particularly in human studies, due to the extent of cultural diversity demonstrated (Mace *et al.*, 2016). Human cultural transmission largely operates through cumulative inheritance allowing group members to incorporate behavioural traits that may have positive, neutral, or potentially negative biological value (Castro and Toro, 2004). Humans are a relatively young species, which shows little genetic variation (Mace *et al.*, 2016) and much lower levels of genetic variation than other great apes (Kaessmann *et al.*, 2001). This has traditionally been

explained by a relatively recent demographic bottleneck; however, selection can suppress neutral genetic diversity via culturally mediated migration (Premo and Hublin, 2009).

Humans do demonstrate great cultural diversity (Mace *et al.*, 2016) and differential cultural evolution between groups may lead to conflict, driven by cultural norms, political exclusion, socioeconomic deprivation and cultural status inequalities impacting on group identity (Langer and Brown, 2008). However, conflict is not certain as groups may adopt alternative strategies to maximise their fitness. For example, the Amazonian polygynous Yānomamö adopt aggressive strategies including coalitionary lethal raiding parties and fighting over women, where fighting improves social status which in turn may increase the male's number of wives (Macfarlan *et al.*, 2014). Conversely, the egalitarian monogamous !Kung hunter-gatherers of the Kalahari generally frown upon violence and employ within-group cooperative sharing (Fog, 2017). These cultural differences may have arisen because both groups experience different social hierarchies and environmental challenges.

Cultural and genetic evolution interact with the environment to allow for rapid adaptation (Creanza, Kolodny and Feldman, 2017), with both human and nonhuman primates modifying culturally copied behaviours to suit current and successive environments (Castro and Toro, 2004). The role of socio-ecological factors within the environment can impact on human and non-human primates in terms of accessing resources and developing cultural norms to distribute these resources. This may then be connected to moral systems that for example reward or punish free-riding individuals, potentially impacting on reproductive success and trait transmission (Boyd and Richerson, 2009).

### *1(A).3.1 The role of socio-ecological factors*

It has been stated that notwithstanding the impact of pathological factors most cases of violence are driven by the acquisition of resources (Barrett, Dunbar and Lycett, 2002). Resource availability may be dictated by socio-ecological variables such as food/diet type, group size, population density, climate and seasonality (Hanya and Chapman, 2013; Hatfield and Prueger, 2015).

Research has been conducted on these specific variables. For example, higher levels of aggression have been observed in frugivores due to the potential monopolisation of the resource (Isbell, 1991; Snaith and Chapman, 2007; Klass and Cords, 2015, but see: Wheeler,



Scarry and Koenig, 2013). Primate species also vary in their home-range usage and home-range overlaps could lead to increased intergroup aggression especially over resource defence or acquisition (Cheney, 1987). Resource availability may be limited by environmental conditions such as temperature, humidity and rainfall. Controversially, climatic differences have been suggested as an explanation for human increased aggressive tendencies towards the equator (Rushton, 1996; Van Lange, Rinderu and Bushman, 2017). Group size has been positively related to the number of aggressive intergroup encounters (Willems and van Schaik, 2015), and coalition formation may be more likely in larger groups with more males (Henzi, Weingrill and Barrett, 1999). However, the physical environment may place constraints on the formation of coalitions, specifically the degree of terrestriality (Bissonnette *et al.*, 2014).

Research has fed into human conflict strategy where it is believed that ensuring access to resources may increase competition, acting as a driver for conflict within and between states (Ministry of Defence, 2014). Nevertheless, it is acknowledged that further work is needed exploring the variation between ecology, group size, and other variables in group functional behaviours (Boyd and Richerson, 2009). Consequently, with the ecological differences that exist between primate species it is essential to explore their potential impacts on violence types and so understand if different ecological and social systems can explain different types of violence. Furthermore, it is important to understand if these socio-ecological factors have similar impacts when using sex specific data.

### *1(A).3.2 The potential importance of prosocial behaviours*

Humans often act as part of a group (Böhm, Thielmann and Hilbig, 2018; Böhm, Rockenbach and Zimmermann, 2018) which may be defined as “...two or more individuals who are connected by and within social relationships” (Forsyth, 2018, p.4). Human psychology is adapted to group living (Cosmides and Tooby, 2013) and the trait of group living is present in many primate species. There are distinct advantages to living in a group (Brewer and Caporael, 2006; Wilson, M. L. *et al.*, 2012), including hunting, protection from predators or enemies, and task sharing such as raising young individuals. Prosocial behaviour is a key component of group-living, which includes instrumental helping, where an individual needs support in achieving a goal, cooperation, sharing of resources, comforting, or informing others (Eisenberg, Eggum-Wilkens and Spinrad, 2015). Examples of primate prosocial

behaviours include food sharing, mutual grooming and the provision of coalitionary support (Silk, 2007).

Coalitionary support is a form of cooperative behaviour which provides several benefits, such as reducing costs that can be associated with agonistic actions and potentially improving reproductive fitness for the winning combatants (Wrangham, 2006). Kin selection theory has been posited as an explanation for these potentially cooperative actions, as while individual fitness will be diminished there are benefits for genetic relatives (Maynard-Smith, 1964; Hames, 2015). However, altruistic behaviours are also carried out between unrelated individuals (Workman and Reader, 2021) where there is no inclusive fitness advantage. For example, human foraging societies have demonstrated frequent cooperation with unrelated individuals (Boyd and Richerson, 2009). Reciprocal altruism may explain sharing and cooperation, not only with kin but also non-kin (Feistner and McGrew, 1989; Brown, G. R., Almond and van Bergen, 2004), where there is an exchange of acts between individuals such that it results in a net benefit to both parties.

Two of the most well observed affiliative behaviours are grooming and food sharing. Allogrooming, or social grooming, is common in social species (Mooring, Blumstein and Stoner, 2004; Kutsukake and Clutton-Brock, 2006), including humans and non-human primates (Nelson and Geher, 2007; Thompson, K. P., 2010). Active food sharing involves food solicitation by a recipient and offering behaviour from the possessor (Feistner and McGrew, 1989). Several functions have been proposed for these affiliative behaviours, which may be coarsely divided into two groups, maintenance functions and social functions. For example, grooming may improve hygiene (Seyfarth, 1977; Barton, 1985; Grueter *et al.*, 2013), reduce psychological stress (Terry, 1970; Schino *et al.*, 1988; Radford, Majolo and Aureli, 2016), and aid social bonding (Dunbar, 2013; Radford, Majolo and Aureli, 2016) which may support coalition formation.

While intragroup cooperation is relatively common, outgroup cooperation is frequently limited by prejudice, spite and discrimination which can escalate into intergroup conflicts (Langer and Brown, 2008). Groups may function through comparison with each other and, as such, it is proposed that cooperation within-group and aggression to out-groups may have co-evolved, as promoting in-group efficiency has the same result as damaging out-group efficiency (De Dreu, Balliet and Halevy, 2014). Abbink *et al.*, (2012) observed a positive correlation between individual pro-sociality benefiting the in-group and participation in

intergroup conflict that harms the out-group. However, Thielmann and Böhm, (2016) found that prosocial individuals were ready to encourage intergroup cooperation rather than generate intergroup conflict.

While there appears to be a link between cooperation and intergroup aggression, the latter's role as an evolutionary driver of within-group social behaviour remains unclear (Bowles, 2009). Therefore, the question remains if there is any evolutionary correlation between aggression types and prosocial behaviours in primate species.

#### 1(A).4 Thesis aims

No one ultimate and proximate mechanism is solely responsible for violent behaviour, and therefore understanding how aggression may be driven through the inter-play between evolution, group norms, values and cultural behaviours is deemed central to research on social evolution (Davidheiser and Treitler, 2007). Furthermore, activation of evolved mechanisms requires some environmental input (Confer *et al.*, 2010) therefore the role of socioecological conditions must be explored. Lastly, traits do not always evolve independently, and there are some compelling arguments that violence may be directly and indirectly influenced by prosocial acts, for example via coalition formation or through increasing social tolerance (Seyfarth and Cheney, 1984; Watts and Mitani, 2001; Jäggi, 2010; De Dreu, Balliet and Halevy, 2014). Therefore, the relationship between prosocial behaviours, which may be defined as helping, sharing and cooperating (Bandon and Scrimgeour, 2015) and violence warrants further analysis.

Consequently, this thesis will address four research topics.

**Chapter two** - Aims to explore the different type of aggression (intergroup aggression, intragroup aggression, intergroup adulticide, intragroup adulticide and infanticide) present in primates and determine if they are each unique, following their own evolutionary history or if they are in fact the same behaviour.

**Chapter three** - Aims to investigate the socioecological factors that may impact on the emergence and activations of each violence type.

**Chapter four** - Aims to consider any differences with regards to sex on intragroup and intergroup adulticide through phylogeny and key socio-ecological variables.

**Chapter five** - Aims to consider the potential relationship between intragroup prosocial behaviours (including allogrooming, adult food-sharing and coalitionary support) and intergroup aggressive interactions.

**Chapter six** – Aims to discuss the implications of this study when applied to existing research on human violence.

This chapter has provided an overview of the ultimate and proximate mechanisms at play. The following chapters will delve deeper into the literature, to explore each of the variables to be analysed, and allow the chapters findings to be placed within the context of the wider literature.

#### 1(A).5 Ethics statement

Ethical approval for this study was granted by the University of Lincoln Ethics Committee (ref. no. 2019-0885) before the start of the project.

## **1(B) Methods Overview**

This section provides a detailed overview of the methods used across this thesis. These are then summarised within the subsequent chapter's methods sections with additional descriptions specific to that chapter. Links are made to those chapters throughout this overview.

### **1(B).1 Dataset construction**

An existing species level comparative dataset containing intergroup aggression and socio-ecological data in non-human primates (Willems, Hellriegel and van Schaik, 2013; Majolo *et al.*, 2020) was expanded to include a wider range of primate species and four further distinct violence variables; intra-group aggression, inter-group adulticide; intra-group adulticide, and infanticide. This first stage dataset expansion provided the data required for the analysis conducted in chapter two and four (research questions 1 and 3). The dataset was then further expanded to include data on a range of socioecological factors including, but not limited to group size, territoriality, proportion of leaves in the diet, dimorphism, and social system. This expansion provided the data required for the analysis in chapter three (research question 2). Finally, the dataset was again built upon this time with the inclusion of data on the following prosocial behaviours; food-sharing, grooming, 'time-social' (chapter 5 – research question 4).

Data were obtained through a systematic review conducted on the primatological literature published up to June 2020. Sources included: Google Scholar (<http://scholar.google.com>), ProQuest Dissertations & Theses Global, academic books and websites such as 'All the World's Primates' (<https://alltheworldsprimates.org/> - Rowe and Myers, 2016), and the Animal Diversity Web (<http://www.animaldiversity.org> – Myers *et al.*, 2006). To narrow the search, specific keyword searches were conducted (Table 1(B).1). These were applied in various combinations to specific species and taxonomic families in an effort to fully review the primatological literature. Some existing datasets were also utilised. Specifically, food-sharing data were primarily obtained from Jaeggi and van Schaik (2011) and grooming data from Grueter *et al.*, (2013). Further, a survey was produced utilising Qualtrics software [version: April 2020 – July 2020] (<https://www.qualtrics.com>) and distributed via social media channels and emailed to various primatological societies and specialist researchers (Appendix 1(B)A – Survey design). It was anticipated that this would add further data that was, as yet, unpublished or had not been detected through the literature review. Part one of

the survey requested demographic and study details for the specified species, followed by questions related to any lethal violence incidents, including sex of the victim and perpetrator. Part two asked for socioecological and prosocial data, which potentially required respondents to extract data from their own records. While there was a relatively high response rate to the survey, part two received fewer responses than part one.

*Table 1(B).1 Keyword searches used to obtain data for each chapter/research question.*

<b>Chapter</b>	<b>Keywords</b>
Chapter 2 and 4 - Violence data	“kill”; “violence”; “death”; “died”; “fatal”; “attack”, “lethal”, “infanticide”, “aggression” “intra-group”, “inter-group”, “between-groups”, “within-groups”; “competition” and, “activity budget”.
Chapter 3 - Socioecological data	Keywords were used that represented the ecological variable e.g., “group size”, “diet”.
Chapter 5 - Prosocial data	"food", “sharing”, “food sharing" and "food-sharing”, “grooming” and “allo-grooming”, “time social”, “social time”, “time-budget” and “activity-budget”.

As studies can vary in their terminology, specific spatial and behavioural criteria were assigned to each variable to allow for comparison between studies (see chapters 2, 3 and 5: Table 2.1 – five violence types; Table 3.3 – socioecological variables; Table 5.2 – prosocial behaviours). *A priori* exclusion criteria were also established; specifically excluding studies conducted on captive, semi-free-ranging or provisioned groups as behaviour patterns can differ to wild counterparts (Hosey, 2005; Birkett and Newton-Fisher, 2011). Furthermore, species not clearly defined as ‘social’ were also excluded, using the Dunbar *et al.*, (2018) definition of social species, that is, species living in groups that have a stable composition through time while sharing a common ranging area, rather than a loose association around resources. This resulted in the exclusion of several nocturnal species that while displaying some social grouping did not appear to form clear long-term social relationships. Where possible, data for each species were taken from the same population or within a close geographic location. However, this become more problematic as additional variables were

included in the analysis. The resultant species lists utilised for each analysis, and a list of species-specific sources are available in Appendix 1(B)B and 1(B)C.

### 1(B).2 Tree construction

A set of 1000 Bayesian mammal phylogenies were extracted at random from the data repository at Vertlife.org (Upham, Esselstyn and Jetz, 2019). The trees were subsequently loaded into R version 4.0.2 (R Core Team, 2020) as an object of class *multiphylo*.

Package ‘ape’ version 5.4.1 (Paradis and Schliep, 2019) was installed to assemble a tabulation of pair-wise distance, using the Kuhner-Felsenstein distance (Kuhner and Felsenstein, 1994). There are numerous methods available to compare trees (Kuhner and Yamoto, 2015), including Rooted Branch Score (RBS), Maximal Clade Credibility (MCC), and Common Ancestor Trees (CAT). Each has specific advantages, so the chosen methods must depend on the purpose of the tree (Heled and Bouckaert, 2013) and the similarity of the trees being compared (Kuhner and Yamoto, 2015). For example, when trees are similar, measures using branch lengths are superior (Kuhner and Yamoto, 2015), e.g., Kuhner-Felsenstein distance which utilises branch lengths along with topography (Kuhner and Felsenstein, 1994). A single tree was chosen based upon the criteria that the tree should have the smallest sum of distance values from the remaining trees, therefore being the tree closest to the centroid of a multidimensional tree space.

The selected tree was further pruned to include only the 104 extant primate species and sub-species from the dataset (Appendix 1(B)D – script), then inspected to ensure a fully bifurcated topology. Taxa not available in Vertlife.org (e.g., chimpanzee subspecies) were added to the topology and their position relative to their immediate sister taxon was estimated at 0.5 million years divergence from the present (Caswell *et al.*, 2008) to create the final tree (chapter 2, Figure 2.1).

This study utilised the current names as listed on the National Center for Biotechnology Information (NCBI) taxonomy database. Where previous names may have been used in a study an assessment was made as to the exact species based on study location.

## 1(B).3 Principal component analysis (PCA) and congruence testing

Principal component analysis (PCA) is a statistical method primarily used to reduce the dimensionality of large datasets without losing too much information/accuracy. In the case of this thesis chapter two utilised PCA to determine any differences between the five datasets that had been subject to qualitative/quantitative conversion and sensitivity adjustment (see chapter 2, section 2.2.4). This was accomplished by firstly undertaking a phylogenetic principal component analysis (PCA) using the phytools package in R (Revell, 2009) followed by a test of congruence using the R psych package (Revelle, 2010). An assessment was made of the congruence between pairs of datasets taken from the five datasets to be compared. The ‘psych’ package uses the ‘factor.congruence’ function to find the coefficient of factor congruence (vector cosine) between two sets of factor loadings (Revelle, 2009) (Figure 1(b).1).



Figure 1(B).1: Determining congruence between two datasets using the psych package and factor.congruence function (Revelle, 2009).

## 1(B).4 Factor Analysis of Mixed Data (FAMD)

While PCA is a powerful tool it does have some limitations when analysing complex data sets as it generally only analyses quantitative variables. Factor analysis of mixed data (FAMD) is methods that allows the analysis of a range of principal component types; PCA for quantitative data, component analysis (CA) and multiple correspondence analysis (MCA) when variables are qualitative, and Multiple Factor Analysis for grouped variables, and hierarchical cluster analysis (Husson and Pages, 2011). FAMD can be calculated in R using the ‘FactoMiner’ (Husson *et al.*, 2014) and ‘factoextra’ packages to extract and visualise results (Kassambara and Mundt, 2017). When employing FAMD to analyse both quantitative and qualitative variables within a dataset these are normalised during the analysis to balance the effect of each variable type (Kassambara and Mundt, 2017).

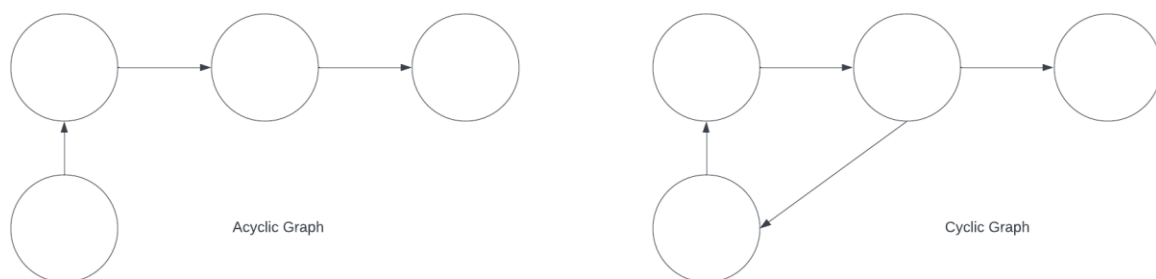


### 1(B).5 Structural Models

A key aim of social research is to understand social systems through illumination of their intricate causal relationships (Lleras, 2005). It is important to understand these relationships to assist in building models that address specific research question and identify any pathways that may need adjusting for. Structural causal models (SCMs), which utilise elements of structural equation models (SEMs), are frequently utilised in causal modelling (Pearl, 2009). They are usually composed of outcome (observed), predictor (observed), and latent (unobserved) variables. Structural models are associated with a graphical model (Glymour, Pearl, and Jewell, 2016) such as Directed Acyclic Graphs (DAGs).

#### 1(B).5.1 Directed Acyclic Graphs

Directed Acyclic Graph's (DAGs) display assumptions about the relationship between variables. It is composed of nodes (variables) and directed edges, represented by single headed arrows (Barrett, 2022). It is essential for a DAG that the pathways are acyclic, therefore containing no feedback loops (Figure 1(B).2).



*Figure 1(B).2: Acyclic and cyclic pathway diagrams. DAGs must be acyclic.*

DAGs prove useful in identifying confounders, selection bias, errors (Brophy, 2021), and providing graphical visualisation of the theoretical foundations of a system which can assist in hypothesis formation. A useful browser-based environment to create and edit DAGs, and to analyse any modelling issues is DAGitty ([www.dagitty.net](http://www.dagitty.net)) (see chapter 3, section 3.2.4, Figure 3.2 – *DAG output from DAGitty*).

*1(B).5.2 Path analysis*

Path analysis is a methodological approach to aid in defining a set of causal assumptions imposed on a system of relationships (Nie *et al.*, 1975) and was originally developed in the 1920s by Sewall Wright. Path analysis is a development of multiple regression analysis (Stage, Carter and Nora, 2004; Lleras, 2005) where multiple direct and indirect relationships can be analysed simultaneously (Valenzuela and Bachmann, 2017). A direct relationship occurs when one variable is associated directly to another (Lleras, 2005; Valenzuela and Bachmann, 2017). Whereas an indirect relationship occurs when one variable is connected to another variable but via a third, which itself is directly connected to the outcome variable (Valenzuela and Bachmann, 2017). The sum of these direct and indirect associations provides the variables total association (Valenzuela and Bachmann, 2017) (see: chapter 5). Path analysis, is a technique that comes under the umbrella of structural equation modelling (SEM), does not incorporate latent variables (Valenzuela and Bachmann, 2017).

To develop a model (or series of models) path analysis requires the generation of a path diagram, similar to a DAG (see: chapter 5 - figure 5.1 and 5.2). The path diagram contains the variables linked directly or indirectly by arrows. The arrows are mostly single headed pointing from cause to effect (Stage, Carter and Nora, 2004). However, unlike a DAG, arrows can be double-headed, though in this instance they represent a correlation rather than any assumed causality (Valenzuela and Bachmann, 2017). There are two types of variables within the model. Firstly, exogenous which are predictor (or independent) variables that are not influenced themselves by other variables (Stage, Carter and Nora, 2004; Lleras, 2005; Streiner, 2005; Valenzuela and Bachmann, 2017). Secondly, endogenous variables which are influenced by variables and may also influence other variables (Lleras, 2005; Valenzuela and Bachmann, 2017), these may then be classified as outcome variables (Stage, Carter and Nora, 2004) or intervening variables respectively (Lleras, 2005). Traditionally variables would be continuous however they may now also employ a combination of binary, ordinal, counts or censored (Valenzuela and Bachmann, 2017). Path models are built on current theories (Stage, Carter and Nora, 2004; Lleras, 2005) therefore the researcher's theoretical knowledge is critical to the effective use of path analysis (Valenzuela and Bachmann, 2017).

### 1(B).6 Bayesian analysis

Bayesian analysis, founded on Bayes theorem, determines the degree of belief (conditional probability) in an event based on prior knowledge and data. Bayesian approaches differ from frequentist ones due to their epistemological assumptions (Ellison, 2004; Vallverdú, 2015).

For example, Bayesian inference considers data points to be variable with a fixed interval, whereas the frequentist view holds that data points are fixed with a variable interval.

Bayesian methods can be considered to have several advantages over frequentist approaches including the ability to incorporate into the model prior knowledge about the data parameters (Bürkner, 2017). Historically, Bayesian approaches were limited because the posterior distributions of complex models, for instance multi-level models (MLMs), could not be found analytically (Bürkner, 2017). However, the development of Markov chain Monte Carlo (MCMC) algorithms and expanding computing power has increased the used of Bayesian approaches (Bürkner, 2017; Carlin and Chib, 1995). MCMC sampling algorithms allow the drawing of random samples from the posterior distribution (Bürkner, 2017) which allows the analysis of large hierarchical models with thousands of unknown parameters.

### 1(B).7 brms package

The brms package (Bayesian Regression Models using 'Stan') uses the probabilistic programming language Stan to run Bayesian multivariate multilevel models in R. There are other similar packages, such as the frequentist framework lme4 package, that offers multilevel model analytic possibilities. However, models in brms, while constructed using lme4 syntax, are extended to accommodate additional functionality (Bürkner, 2017). This includes supporting a wide range of link functions and distributions in a multilevel context, autocorrelation of the response variable, and user defined covariance structures (Bürkner *et al.*, 2022a). Furthermore, non-linear relationships may be specified (Bürkner, 2017). For Bayesian approaches prior specifications (prior probability distributions) are required. With brms these are flexible and promote the application of prior distributions that reflect the user's beliefs. As there is no frequentist alternative able to offer this degree of model flexibility and complexity, brms was the logical choice for this studies analyses.

### 1(B).7.1 Phylogenetic and multivariate models

Multilevel models (MLMs) allow data measured on different levels at the same time to be modelled, thereby taking complex dependencies into account (Bürkner, 2017). A form of MLM is a phylogenetic model, which can be modelled within the brms package. These models are relevant in evolutionary biology when data of many species are analysed at the same time. One approach would be to model species as a grouping factor in a multilevel model and estimate varying intercepts (and possibly also varying slopes) over species. However, species are not independent as they come from the same phylogenetic tree and the model needs to be adjusted to incorporate this dependency (Bürkner, 2022a). The model construction outline (Figure 1(B).3) is reflective of the phylogenetic models utilised within this study (chapters 2,3,4 and 5). However, the vignette accompanying the brms package provides detailed information on how to specify a range of phylogenetic multilevel models using brms (Bürkner, 2022a).

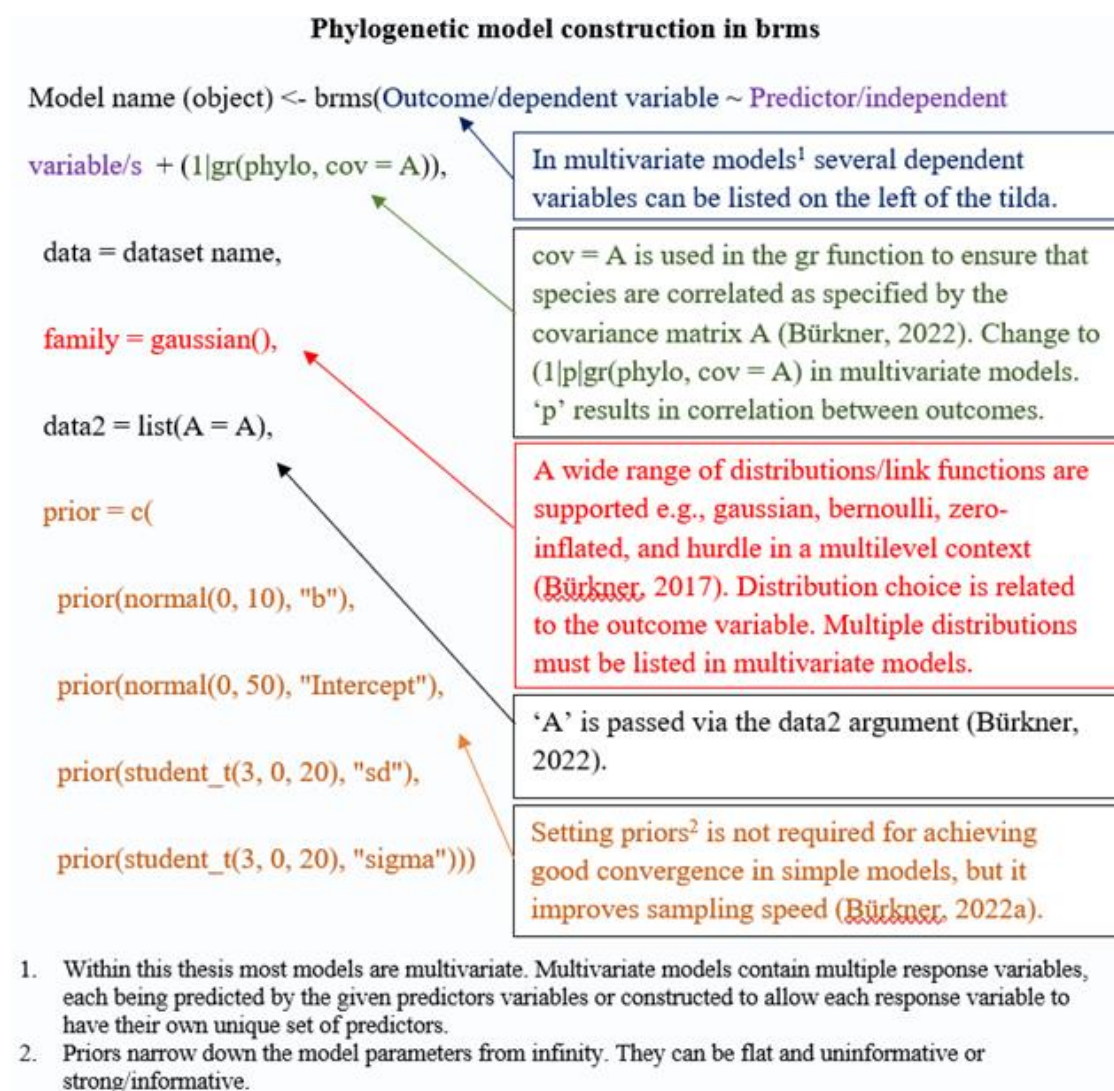


Figure 1(B).3: An annotated example of phylogenetic model construction in brms.

Throughout this thesis multivariate models are predominantly specified. Multivariate models contain multiple response variables that are predicted by their own set of predictors (Bürkner, 2022b). When multivariate models are specified in brms the required response variables are listed on the left side of tilde in the model (Figure 1(B).3) and the ‘mvbind’ notation is added to tell brms that the listed response variables are separate (Bürkner, 2022b). Correlations can be determined between the separate outcome/response variables through a slight alteration to the model code (Figure 1(B).3 – green text box) (Bürkner, 2022b). Coefficients for each predictor variable are estimated for each of the response variables separately.

### 1(B).7.2 Exploring model fit and results

An early impression of model fit can be found by exploring the posterior predictive checks (pp checks). The plots indicate if the fitted model is successful in explaining the observed data (Figure 1(b).4).

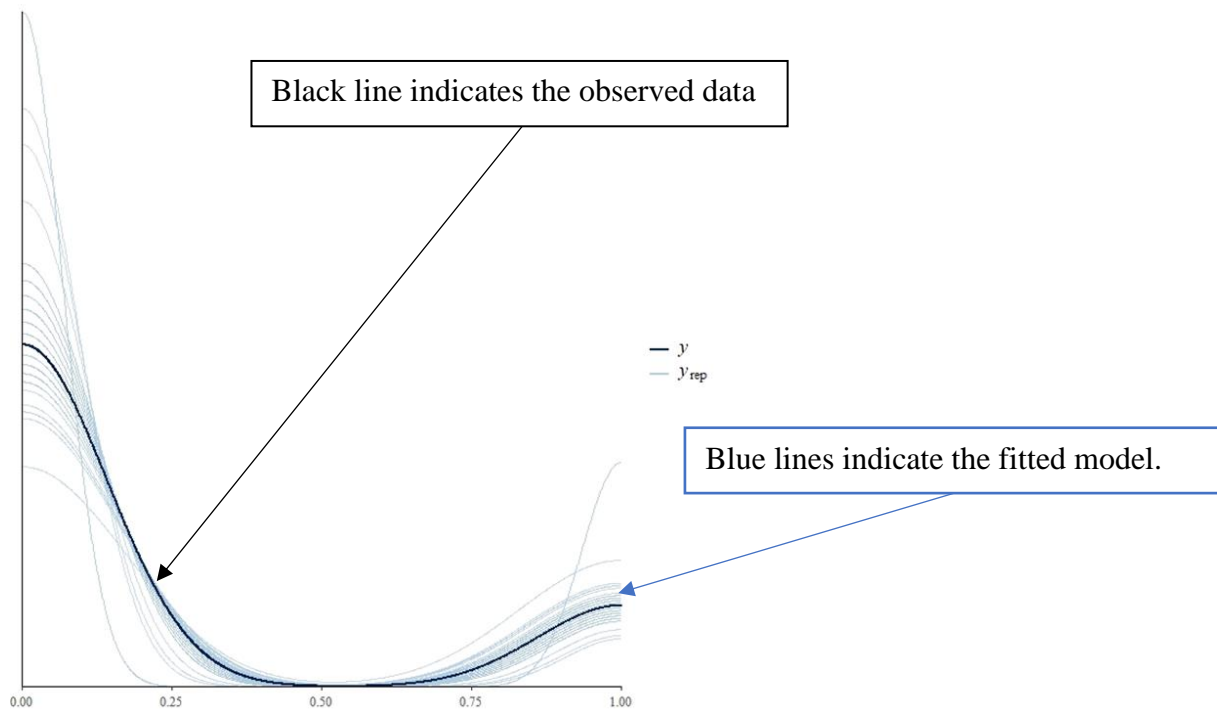


Figure 1(B).4: Posterior predictive check plot

It is also essential to check the Rhat value. Rhat is the ‘Potential scale reduction factor’ which measures between chain variability. There are usually four chains, and these should have minimal variability between them. Chain convergence is indicated at Rhat=1 therefore, Rhat must be  $\leq 1.01$ . If Rhat is greater than this then the chains will not have converged, and the

model should be run again with priors (or stronger priors) and for more iterations (Bürkner, 2017).

The next stage is to assess the trace and density plots of all relevant parameters. Trace plots can sometimes be referred to as caterpillar plots due to their resemblance of a ‘fuzzy caterpillar’ (Figure 1(B).4). These plots allow the user to assess that the model has explored all possible options/values and converged well. The plots should not have flat sections or slopes as this would indicate that the chains had stayed in the same state for too long. Density plots are provided alongside the trace plots. Density plots are a distribution of means. The means and the number of times they occur. The mean that occurs most frequently is likely to be the correct mean.

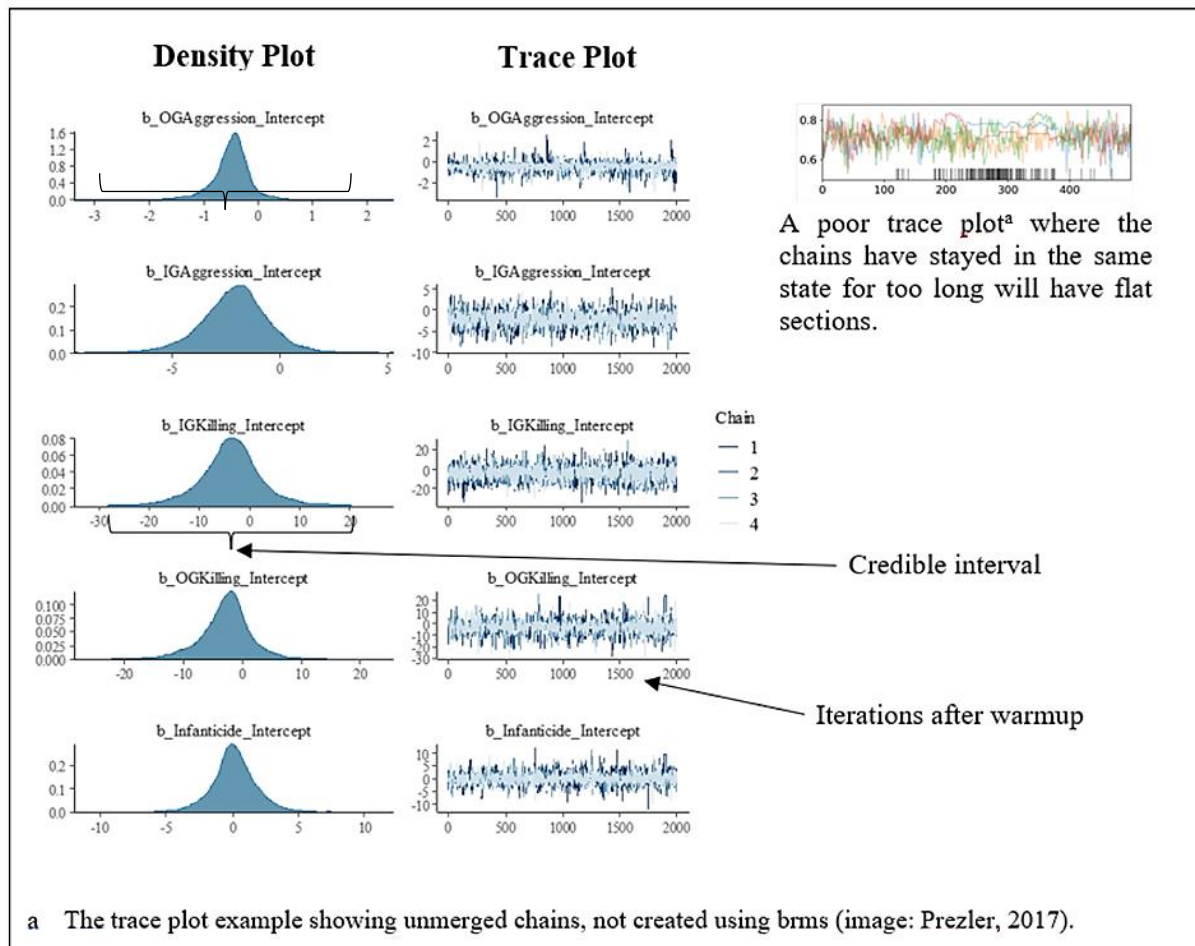


Figure 1(B).5: Trace and density plots used for assessing the fit of the model.

There are three types of results to be read from the model summary. The effects (regression coefficients) identified by the predictors on the outcome variables. The correlations (correlation coefficients) identified between outcome variables in a specified multivariate

model, measured as a degree of association between -1 and +1. Finally, the overall model fit,  $R^2$ .

The effects of a predictors on the outcome variable (as reported in chapters 3,4,5) are described through the credible interval (CI). CI is an interval within which an unobserved parameter value falls within a particular probability. While significance in the frequentist way is not used in Bayesian terminology, effects can be considered ‘significant’ if the CI does not pass through zero. This classically is based on a 95% credible interval e.g., subjective probability that the parameter lies between 25-38 is 95% CI.

$R^2$  values are reported as a goodness of fit measure for the models.  $R^2$  is displayed as a value between 0 and 1 but can be interpreted as the percentage of variance in the response variable explained by the model. This interpretation has been used in this thesis. With the multivariate models brms generates  $R^2$  values for each response variable separately. In chapter two  $R^2$  is taken to be a proxy for the phylogenetic signal because the multivariate model contains no predictor variables only the phylogenetic group level random effect. It is more traditional to express phylogenetic signal via Pagels Lambda, however this could not be calculated with the data used in this thesis as no sigma value can be calculated for Bernoulli families (lethal violence data).

#### 1(B).8 K-Fold Cross-Validation

Within the brms package it is possible to perform several types of cross-validation which are used to estimate how well the model could perform when used on data not within the current dataset. One method available within brms is exact K-fold cross-validation (Bürkner, 2023a). The ‘kfold’ function returns an object that in structure is like the objects returned by the leave-one-out cross validation (LOOCv) and widely applicable information criterion (WAIC) methods (Bürkner, 2023a). However, while LOOCv is useful when data size is small it can become increasingly computationally expensive on larger datasets, whereas K-fold can be more computationally efficient. Furthermore, LOOCv can be subject to high variance or overfitting as the model is feed almost all the training data to learn and just a single observation to evaluate (Bürkner, 2023a).

K-fold cross validation involves partitioning the data into equal sized subsets ( $k$  folds) then the refitting of the model  $k$  times, each leaving out one of the  $k$  subsets (James *et al.*, 2013). K

value must be carefully chosen in order to accurately represent the success of the model. Frequently selected  $k$  values are five and 10 because these produce relatively low bias and modest variance (Kuhn and Johnson, 2013). As  $k$  gets larger the bias reduces however if  $k$  increases such that it is equal to the number of entries ( $n$ ), then LOOCv should be performed (Kuhn and Johnson, 2013). This thesis employed a  $k$  value of 10 where dataset entries ranged between 46-77 species (see chapter 5).

In addition to assessing model fit, brms enables models to be compared using the widely applicable information criterion and leave-one-out cross-validation (Bürkner, 2017). To compare models the `loo_compare()` function is used (see chapter 5). The comparisons are made between objects of class `loo`. A class `loo` object is generated using the `add_criterion(x, criterion, ...)` function, where `x` is a `brmsfit` object and the criterion is "loo", "waic", or "kfold" (Bürkner, 2023b), the latter of which was utilised in chapter five. After running “`loo_compare`” a matrix is returned containing “`elpd_diff` (expected log pointwise predictive density – difference between two models) and `se_diff` (the standard error of component-wise differences of `elpd_loo`) columns (Vehtari, Gelman, and Gabry, 2017). Pairwise comparisons are made between each model and the model with the largest ELPD. That latter model occupies the first row and is assigned a value of zero. The remaining models in the subsequent rows have negative values as they are compared to the preferred model (Vehtari, Gelman, and Gabry, 2017) (chapter 5, table 5.7).



## **CHAPTER TWO –THE EVOLUTION OF LETHAL AND NON-LETHAL VIOLENCE**

*“Most species do their own evolving, making it up as they go along, which is the way Nature intended. And this is all very natural and organic and in tune with mysterious cycles of the cosmos, which believes that there's nothing like millions of years of really frustrating trial and error to give a species moral fibre and, in some cases, backbone.”*

*(Reaper Man - Pratchett, 1991, p.17)*

## 2.1 Introduction

Violence has been observed frequently in social species such as birds, humans, and primates (Radford, 2003; Bowles, 2009; Crofoot and Wrangham, 2010) and is often used to defend or obtain resources, including food, territory, and mates from conspecifics (de Boer, 2018).

With a range of functions, violence can be displayed in numerous ways, affecting both young or old, from within the group or outside, with attackers operating alone or in coalitions. Due to this structural and functional variety, violent behaviour may be sub-divided into unique types i.e., intragroup, and intergroup adult lethal violence (hereafter termed adulticide), intragroup and intergroup non-lethal aggression, and infanticide. These violent behaviours may be adaptive (Wilson, M. L. *et al.*, 2014) or as has been suggested, may occur through non-adaptive drivers such as anthropogenic impacts (Bruitjes and Radford, 2013). However, support for this latter argument is weak (Moore, J., 1992; Wilson, M. L. *et al.*, 2014).

Considerable efforts have been made to determine the evolutionary roots of certain types of violence (see: infanticide (Lukas and Huchard, 2014); lethal violence (Gómez *et al.*, 2016); intergroup lethal violence (Wrangham and Peterson, 1996)). Nevertheless, the evolutionary origins continue to be vigorously debated. This is in part due to the cost-benefit pay-off that may exist when considering violence within an economic model (Treisman, 1975). A successful aggressor for example may gain fitness-related benefits, including dominance, access to territory, food sources, and mating opportunities (Maynard Smith and Price, 1973). However, they face potential fitness costs including injuries and death (Piper *et al.*, 2008). Additionally, selection acts on functional consequences (Arnold, 1983) such as enhanced capabilities, but these are only transferred through natural selection if they confer improved survival or reproductive success (Losos, 2011). As there is structural and functional multiplicity of violent behaviour seen across different species and populations this can question the adaptive and non-adaptive pressures.

Comparative methods may be utilised to explore evolutionary history or to determine how traits affect patterns of diversification (Nunn, 2011). Therefore, to understand the basis of human violent behaviour a comparative analysis of not just those species which are closest phylogenetically, but also incorporating the wider primate tree is pivotal. Traits may evolve through direct selection or through selection on other traits as a correlated response (Price, Turelli and Slatkin, 1993). Consequently, this species level analysis should attempt to identify if violence is a single trait or a combination of different behaviours, each with their distinct phylogenetic history.

In the study of lethal violence by Gómez *et al.*, (2016) the authors obtained data on a wide range of lethal violence types, including infanticide, cannibalism, intergroup aggression, and accidental injury which were combined into a single violence measure. The propensity to kill in any form can certainly be a gauge of violence; however, individual violence types may have distinct functions with uniquely evolved pathways or show a pattern of correlated evolution which should be explored. The review to follow will be an overview of the key types of violence observed in primates (for in-depth reviews see: Hausfater, 1984; Crofoot and Wrangham, 2010; Lukas and Huchard, 2014; Wilson *et al.*, 2014; Gómez *et al.*, 2016; Lukas and Huchard, 2019; Lowe *et al.*, 2020).

### 2.1.1 Non-lethal inter and intragroup aggression

Intergroup aggression in primates is both substantial and common (Silk, 2014). However, when groups meet one another the behaviour they exhibit can vary between species, between groups of the same species, within a group over time (Bates, 1970) and also between individuals (Glowacki and McDermott, 2022). Aggression is commonly seen during take-over attempts by rival males from other groups (e.g., *Alouatta palliata* - Dias *et al.*, 2010, *Alouatta pigra* - Van Belle, Estrada and Strier, 2008, *Propithecus verreauxi* - Brockman, Cobden and Whitten, 2009). This aggressive dominance thereby providing potential reproductive fitness benefits for the aggressor and possible heritability of the trait through sexual selection. Intergroup aggression also commonly occurs at boundaries as part of territorial defence or expansion with both males and females acting individually and occasionally as coalitions (Kitchen and Beehner, 2007). For example, when black howler monkey (*Alouatta pigra*) groups meet, the alpha males frequently display aggression towards each other, but the participation of other members varies across groups, as well as encounters (Kitchen, 2004).

Many species engage in behaviours, such as the use of territorial calls or scent marking, that partially function to reduce the risk of aggressive encounters (Brown, R. E. and Macdonald, 1985; Cowlishaw, 1992; Roberts, 2012; Bonadonna *et al.*, 2017, but see: Lledo-Ferrer, Peláez and Heymann, 2011). Scent marking is common in numerous prosimian and New World monkeys but comparatively scarce in Old World monkeys and apes (Freeman *et al.*, 2012). Scent marking at boundaries can show the presence and potential long-term status of the marker to the receiver which can be advantageous in preventing the potential fitness costs of

aggressive fights (Hagen and Hammerstein, 2009; Roberts, 2012). Likewise, loud calls, while themselves energetically costly can reduce the potentially higher cost associated with an aggressive intergroup encounter. Encounters based on awareness of the neighbours position appear in part to be driven by resource scarcity (see: Van Belle and Estrada, 2020).

In addition to intergroup aggression species may also engage in intragroup aggression. Historically, group selection (see: Maynard-Smith, 1964; Lorenz, 1966) suggested that intragroup aggression would be selected against as the group may be weakened through intragroup conflict. Nevertheless, intragroup conflict does occur, and contemporary approaches look toward selective pressures primarily at the individual level. As such, intragroup aggression is largely a result of within-group competition for resources. For males, aggression may occur because of mate competition within the group from males wishing to gain access to females. Mate competition has been observed to play an important role leading to elevated levels of aggression and testosterone in chimpanzees (Muller and Wrangham, 2004; Muehlenbein, Watts and Whitten, 2004). However, bonobos do not show the same levels of aggression as male-male competition may be less beneficial due to female dominance and their key role in mate choice (Surbeck *et al.*, 2012).

Female intragroup aggression can also be driven by mate competition, especially where mating opportunities are in short supply (Fruth and Hohmann, 2003). For example, in the female dominated bonobos, aggression can happen as harassment during mating, with the mating pair splitting up after the attack (Fruth and Hohmann, 2003). Further, female intragroup aggression may also be driven by competition for physical resources, such as food or nest sites (Hrdy, 1979), particularly when food may be monopolised (Isbell, 1991). Aggression associated with contest competition (Miller, 1967) over food has potentially shaped female dominance hierarchies in female philopatric species in order to limit the costs associated with aggression over food resources (Huchard and Cowlshaw, 2011). Finally, intragroup aggression may serve a protective purpose, operating as either punishment or coercion to prevent costly interactions during current or future intergroup encounters (Arseneau-Robar *et al.*, 2018).

### *2.1.2 Inter and intragroup adulticide*

There is the potential that non-lethal inter or intragroup aggression could become lethal either through accident or intention. While aggression can occur frequently in primates, conspecific

killing appears to be rare. Scarce lethal aggression is also observed in bird species (Cox and Cusick, 2018) and is attributed to the cost/benefit imbalance that the receiver needs to consider prior to engagement (Hof and Hazlett, 2012). This imbalance has also been suggested as the reason for low levels of lethal violence in primates (Silk, 2014).

Nevertheless, examples of killing are seen across primate species, such as chimpanzee (*Pan troglodytes* - Wilson, M. L. *et al.*, 2014; Nishie and Nakamura, 2018), southern muriqui (*Brachyteles arachnoides* - Talebi, Beltrão-Mendes and Lee, 2009), mantled howler (*Alouatta palliata* - Dias *et al.*, 2010), *Cebus capuchinus/imitator* - Gros-Louis, Perry and Manson, 2003), *Gorilla beringei* (Rosenbaum, Vecellio and Stoinski, 2016), ring-tailed lemur (*Lemur catta*) and, spider monkeys (*Ateles geoffroyi* - Campbell, 2006; Valero *et al.*, 2006). Data suggest that in chimpanzees, for example, certain demographic and ecological conditions can tip the cost/benefit assessment in favour of engaging in these acts of lethal violence (Silk, 2014). For example, more intercommunity killing occurred when the victims were greatly outnumbered by their attackers (Wilson, M. L. *et al.*, 2014).

As with non-lethal aggression, the participants and function of lethal violence can be diverse across species. However, some species, such as chimpanzees (*P. troglodytes*), have engaged in this behaviour on multiple occasions showing similar actors and behavioural drivers. For example, killing is frequently committed by unrelated males towards other males often from another group (Wilson, M. L. *et al.*, 2014). This can be driven by the acquisition of mates where intrasexual competition would be particularly high, for example when members of the opposite sex are limited. Lethal violence has thus been considered an adaptive strategy through natural or sexual selection as the killer obtains fitness benefits through resource acquisition (Silk, 2014). However, the cost can be high, for example, howler monkeys when entering or defending troops or engaged in status challenges can be seriously injured or die (Crockett, 2003). The individual circumstances may be assessed via inferential and simulative mechanisms (Penn and Povinelli, 2007) to determine if the costs are worth the benefits to the aggressor, or the behaviour occurs innately.

To counter potential costs, evolved strategies may be in place to minimise the risks to the aggressor such as coalition formation or at least outnumbering the opposition. For example, in chimpanzees most intergroup lethal aggression occurred when attackers substantially outnumber the defenders (Wilson, M. L. *et al.*, 2014), while in red howlers, two immigrants are often more successful at evicting the resident male than a lone individual (Crockett and Sekulic, 1984). This forms the basis of the imbalance of power hypothesis (Wrangham and

Peterson, 1996) which describes that, whenever a group outnumbers another group, a state of hostility exists, and attack may occur. These coalitions can occur through the strong bonds formed between philopatric males from the same community (Aureli *et al.*, 2006). Under these conditions, the attackers face low costs due to the dilution effects and aggression becomes beneficial for the attackers. Sustained killing also has the added benefit of reducing the power of the neighbouring group, thereby making the chances of being successful in future encounters even greater (Wrangham, 2006).

Compared to intergroup adulticide, intragroup adulticide is both more rare and less well understood (Wilson, M. L. and Wrangham, 2003; Newton-Fisher and Thompson, 2012). However, there are also likely to be intrasexual motivations. Certainly, rank instability gives higher levels of aggression as individuals seek to obtain alpha status with associated mating opportunities and coalitions can also be advantageous in these situations (see; Kaburu, Inoue and Newton-Fisher (2013)).

Despite evolutionary avenues through sexual selection, non-adaptive hypotheses have been suggested often as a response to anthropogenic impacts such as, provisioning or habitat change (see: Power, 2005; Ferguson, 2011). This may occur through behavioural plasticity that can allow the development of beneficial behavioural adaptations to changing environments to occur, therefore enabling exploitation of the resources (Van Schaik, 2013). However, stressful environments that are different to the ancestral conditions can impact on development, producing non-adaptive by-products (Ghalambor *et al.*, 2007). Human impacts such as habitat change or limiting access to food, causing stress and frustration, have been proposed to result in aggression (Power, 2005). For example, increased levels of aggression were observed as a result of provisioning in chimpanzees at Gombe National Park in Tanzania (Silk, 2014). However, the validity of the arguments made have been questioned (Moore, J., 1992) and more recently rejected by Wilson *et al.*, (2014) who found in *Pan* that their results favoured adaptive explanations for adulticide and did not support the human impact hypothesis as killing mostly occurred at a largely undisturbed, non-provisioned site.

### 2.1.3 Infanticide

A specific form of lethal violence is infanticide which involves a group or individual carrying out a behaviour that causes a conspecific infant's death, either immediately or shortly afterwards (Digby, 2000). Infanticide has received considerable attention and has been

reported in numerous primate species (Hrdy, 1979; Valderrama, Srikosamatara and Robinson, 1990) to the extent that it may be viewed as a common social behaviour (Hausfater, 1984). Prolific species appear to be the Northern plains gray langur (*Semnopithecus entellus*); Eastern chimpanzee (*P. troglodytes schweinfurthii*) (Lowe *et al.*, 2020); Eastern gorilla (*Gorilla beringei*) and red howler monkey (*Alouatta seniculus*) (Agoramoorthy and Rudran, 1995).

It has been proposed that infanticide has evolved independently on multiple occasions (Lukas and Huchard, 2014). It certainly lends itself to an evolved strategy (but see: Sussman, Cheverud and Bartlett, 1994; countered by Hrdy, Janson and van Schaik, 1994), because of the obvious costs to the victim and mother, and potential benefits to the aggressor through improved reproductive success (Crockett, 2003). It is therefore unsurprising that many theories have been posited to account for infanticidal behaviour that are constructed from an adaptive base. A primary example is the sexual selection hypothesis (Hrdy, 1974; Hrdy, 1979; van Schaik, 2000) which holds that it would be beneficial for an unrelated infant to be killed by a male to speed up reproductive access to the infant's mother (Digby, 2000; van Schaik, 2000). Indeed, a male who killed infants he sired would be selected against (Hrdy, 1974) and a DNA study of langur monkeys identified that the male attackers were not related to the victims (Borries *et al.*, 1999).

The sexual selection hypothesis requires that infanticide would lead to females being receptive quicker than would naturally occur through the premature cessation of lactational amenorrhea. However, it is not applicable to all species. While females of some species may resume cycling soon after the dependant infant's death, in others such as callitrichines, female fertility would be largely unaffected as ovulation occurs naturally in the first month postpartum, regardless of lactation status (Lunn and McNeilly, 1982). Infanticide has also been observed in an increasing number of seasonal breeding species, such as *Macaca fuscata* (Soltis *et al.*, 2000; Yamada and Nakamichi, 2006) and *Macaca mulatta* (Ciani, 1984). Palombit (2012) described two possible hypotheses; that species have an interbirth interval larger than the breeding season or, when it would be advantageous to breed early in the season to maximise infant survival. Hrdy, Janson and Van Schaik (1994), argue that in most infanticidal breeding species the males have a short tenure and so any reduction in interbirth interval would be beneficial.

Sexual selection may also occur through future male mating competition as reproductive success may be improved through the selective killing of male infants who at maturity may become rivals to the infanticidal male (Takahata, 1985). Though, this selection pressure would operate only if the reproductive male was likely to maintain an alpha position until the targeted male infants would have matured (Crockett, 2003). Furthermore, Lukas and Huchard (2014) found that male infanticide also occurs in species that maintain their dominant position for shorter periods.

Previously it has been suggested that infanticide is a by-product of sexual excitement and aggression by a new male involved in a successful takeover (Mohnot, 1971). It has also been proposed that infanticide occurs during generalised overt aggression by competing males (Bartlett, Sussman and Cheverud, 1993). If, as suggested, it is a by-product, there could potentially be a phylogenetic correlation between the evolution of non-lethal aggression and infanticide (Sussman, Cheverud and Bartlett, 1994), as the two potential traits would be observed in the same species. However, Crockett (2003), observing *Alouatta sp.*, highlights that infanticide more frequently occurred when the parental male had left the group and consequently the incoming male was no longer in a heightened aggressive state. Therefore, indicating that infanticide was a deliberate act.

The strategy of male infanticide can have significant costs on female reproductive fitness, especially those who have a slow reproductive rate (Palombit, 2012). Co-evolution of counterstrategies limit the impact of infanticide. These include adult males associating closely with offspring (van Schaik and Dunbar, 1990), females mating with multiple partners to create paternity confusion (van Schaik, van Noordwijk and Nunn, 1999; Kowalewski and Garber, 2010) or abortion or premature weaning to terminate costly investment (van Schaik, van Noordwijk and Nunn, 1999). Hrdy, Janson and Van Schaik, (1994) argue that many counterstrategies seen in primates only make sense if they have been subject to selection pressures through infanticide.

While there are significant costs to the reproductive female and potentially co-evolved strategies the female may use to reduce the infanticide risk, infanticide is still a trait also displayed by females. Despite the impact of female infanticide being outlined by Hrdy (1979) the male strategies initially received the most attention (Palombit, 2015). Digby (2000) stated that the risk of infanticide by group living females could provide a more persistent threat than other forms of infanticide. For example, in wild callitrichines only females have been



observed committing infanticide (Culot *et al.*, 2011). This is likely, in part, due to their specific breeding biology including reproductive suppression in nondominant females and cooperative breeding strategies. Understanding the direct benefits of infanticide over the indirect cost of competing with kin is a challenge and it is apparent that females compete over a wide variety of resources (Lukas and Huchard, 2019).

Hypotheses that may explain female infanticide focus on resource competition such as food or nest sites (Hrdy, 1979). Indeed, the food competition hypothesis may be applicable if food is limited (e.g., *Alouatta seniculus* (Agoramoorthy and Rudran, 1995)). Further, in times of food scarcity natural selection may even favour infanticide as a means of meat acquisition (Hrdy and Hausfater, 1984) though this hypothesis would expect complete ingestion of the victim. Examples of infant cannibalism appear more opportunistic, sporadic and/or partial (e.g., *P. troglodytes schweinfurthii* - Lowe *et al.*, 2020; *Gorilla beringei* - Fossey, 1984, *Saguinus mystax* - Culot *et al.*, 2011; *Rhinopithecus bieti* - Xiang and Grueter, 2007; *Callithrix jacchus* - Bezerra, Souto and Schiel, 2007). This may be expected because predators do not always eat whole prey as complete consumption may be energetically inefficient (Sih, 1980). Moreover, Lukas & Huchard (2019) found that carnivores were no more likely to show infanticide than non-carnivores. Additionally, females may also be involved in parental manipulation at times of limited resources to improve parental lifetime reproductive success through the termination of ill, surplus, or poorly timed infants (Hrdy, 1979; also see: *Saguinus mystax* - Culot *et al.*, 2011).

The adaptive hypothesis clearly offers an explanation for many cases of infanticide, however in some instances infanticide is committed where there is no apparent gain, and these may be assumed to be non-adaptive or potentially “pathological” (Hrdy, 1979). The social pathology hypothesis (Curtin and Dolhinow, 1978; Hausfater, 1984) argues that aberrant behaviour is likely seen as a result of animals living in high population densities potentially as the result of provisioning or anthropogenic disturbance (Hausfater, 1984; Silk, 2014). Vulnerable infants may therefore be killed by adults of either sex during aggressive events (Crockett, 2003). However, given the reproductive benefits, rather than an artifact of atypical, challenging conditions or pathology, infanticide should be viewed as an adaptive behavioural strategy in males (Palombit, 2015) and females (Lukas and Huchard, 2019).

### *2.1.4 Study direction*

Each type of violence described has several specific hypotheses ascribed to them based on the function and form of the violent act. There appears to be some similarities between hypotheses which connect the violence types, such as maintenance/survival, reproduction or social status, which facilitates access to resources and mates. Potentially this could indicate generalised ‘monolithic’ aggression in some species. However, there are also differences raising the potential of distinct violence types with manifestations based on intensity, the age of the opponents and, in group-living species, by whether the opponents belong to the same or to distinct groups. Based on current theory it is anticipated that evolution should play a key role in violence and that individual types may be identified, but with correlation between traits showing similar selection pressures.

## 2.2 Methods

### 2.2.1 Data collection

An existing species level comparative dataset (Willems, Hellriegel and van Schaik, 2013; Majolo *et al.*, 2020) containing intergroup aggression (exchange of agonistic vocalizations or facial expressions and/or agonistic physical interactions including chases, pushes, hits, or bites (Willems *et al.*, 2015), and socio-ecological data in non-human primates was expanded to include four further distinct aggression variables; intra group aggression involving chases, pushes, hits, or bites within the social group or reproductive group; intergroup and intragroup adulticide, where an adult/s kills a conspecific adult from another social group or within the social group respectively; and infanticide, where an infant is killed by either a related or unrelated adult conspecific. As studies can vary in their terminology, specific spatial and behavioural criteria were assigned to these five violence types to allow for comparison between studies (see: Table 2.1 for a detailed description of the five variables). *A priori* exclusion criteria were also established; specifically excluding studies conducted on captive, semi-free-ranging or provisioned groups as behaviour patterns can differ to wild counterparts (Hosey, 2005; Birkett and Newton-Fisher, 2011). Furthermore, species not clearly defined as ‘social’ were also excluded, using the Dunbar *et al.*, (2018) definition of social species, that is, species living in groups that have a stable composition through time while sharing a common ranging area, rather than a loose association around resources. This resulted in the exclusion of several nocturnal species that while displaying some social grouping did not appear to form clear long-term social relationships.

Utilising these criteria, data were obtained through a systematic review conducted on the primatological literature published up to June 2020. Sources included; Google Scholar (<http://scholar.google.com>), ProQuest Dissertations & Theses Global, academic books and websites such as ‘All the World’s Primates’ (<https://alltheworldsprimates.org/>) (Rowe and Myers, 2016), and the Animal Diversity Web (<http://www.animaldiversity.org>). To narrow the search, the following keywords were used; “kill”; “violence”; “death”; “died”; “fatal”; “attack”; “lethal”; “infanticide”; “aggression” “intra-group”, “inter-group”, “between-groups”, “within-groups”; “competition” and, “activity budget”. These were applied in various combinations to specific species and taxonomic families in an effort to fully review the primate literature. Further, a survey was produced utilising Qualtrics software [version: April 2020 – July 2020] (<https://www.qualtrics.com>) and distributed via social media channels and emailed to various primatological societies and specialist researchers (Appendix

2A – Survey design). It was anticipated that this would add further data that was, as yet, unpublished or had not been detected through the literature review.

### *2.2.2 Standard quantitative measures*

Inspection of published literature revealed that, alongside varying terminology for behavioural traits, sampling and aggression recording methods also varied markedly in different studies. This has been highlighted before (Sussman and Garber, 2004) and can provide a methodological challenge for comparative work. This issue became particularly notable when compiling the intra-group aggression data. Consequently, careful handling was required to ensure comparability through conversion to a single unit of measurement (Table 2.1) the feasibility of which was considered on a study-by-study basis through exploration of their individual methods. In some cases, the conversion was relatively straightforward. For example, when aggression data were recorded as per day or per group values, such values were converted by dividing the daily total by the observational hours or the group size respectively. However, in some instances, such as when a percentage was given as part of an activity budget, it was deemed appropriate to discard the relevant data, as these were not able to be converted.

At the end of the systematic review complete violence data were available for 104 species and sub-species after quantitative conversion, which were carried forward for further transformation and analysis.

### *2.2.3 Qualitative transformation and binary allocation*

The established dataset contained a combination of both qualitative and quantitative data for the intra-group and inter-group aggression variables. Both data types were required to be included to ensure a sufficient number of species could be included in the final analysis. To allow for comparison, the qualitative data required converting to the numerical unit of measurement used by the quantitative data with each variable. Assignment of qualitative values can be a subjective procedure, based on individual researchers' perception, as can numeric transformations which can create biases in comparative analysis (De Block and Vis, 2019). Therefore, cautious handling of this procedure was required. Initial baseline values were established based on the existing quantitative data by exploring species where both qualitative and quantitative options were presented from different studies. A value was given

to the qualitative descriptor based on the average of these figures (Table 2.2). The most frequently used descriptors were ‘rare’, and ‘all’ thus provided multiple opportunities for association with quantitative data; however, other descriptors (e.g., ‘fairly calm’) offered fewer opportunities for comparison.

*Table 2.1: Definitions, measurements, and coding of the first aggression types*

Aggression Type	Definition
Inter-group aggression	<p>A minimum of one of the following behaviours must be exhibited between at least one individual of each group. Either an exchange, occurring at up to 50m, of agonistic vocalizations (other than long-distance territorial advertisement) or facial expressions and/or agonistic physical interactions including chases, pushes, hits, or bites (Willems <i>et al.</i>, 2015).</p> <p><u>Unit:</u> Qualitative descriptor or the number of aggressive inter-group encounters divided by total number of inter-group encounters per day.</p>
Intra-group aggression	<p>Interaction involving chases, pushes, hits, or bites within the social group as defined by Dunbar <i>et al.</i>, (2018) or in fission-fusion societies the reproductive group.</p> <p><u>Unit:</u> Qualitative or/ number of aggressive encounters per individual per hour. (n/ind./hour).</p>
Inter-group adulticide / Intra-group adulticide	<p>The following definitions adapted from Wilson <i>et al.</i>, (2014) were utilised.</p> <p>The attack was directly witnessed (observed); the attack not directly observed but there was persuasive evidence that the victim was killed by a conspecific e.g., bite wounds (inferred); the previously healthy individual disappeared (not related to natural dispersal) or individuals died from wounds that may have been inflicted by conspecifics (suspected).</p> <p><u>Coding:</u> Observed (O); Inferred (I); Suspected (S).</p>
Infanticide	<p>The observed killing of an infant either immediately or after an attack by either a related or un-related conspecific (observed). Infants missing or died which most likely can be attributed to infanticide though has not been observed (suspected). Infant attacked but survived (attempted).</p> <p><u>Coding:</u> Observed (O); Suspected (S); Attempted (A); No record found in literature (N).</p>

<sup>a</sup> Individual cases separately compiled including sex of victim and attacker/s for separate analysis

<sup>b</sup> Individual cases separately compiled including sex/age of victim and attacker/s for separate analysis

Similar consideration needed to be applied to the binary data, specifically from the lethal violence categories. With any meta-analysis it is important to consider possible biases in the methods used to obtain the data (Hadfield and Nakagawa, 2010); for example, particularly rare species may be harder to observe (Kunin and Gaston, 2012). Consequently, where entries of zero (i.e., no lethal violence) were recorded it became important to ask whether this represented a genuine lack of adulticide or a lack of data which could potentially lead to misclassification. Therefore, while both published and non-published sources had been reviewed it potentially required the incorporation of data beyond those directly observed killings to include inferred cases, in line with the work of Wilson *et al.*, (2014).

### 2.2.4 Sensitivity checks

To consider the impact of these transformations and allocation decisions and to test the robustness of the results, several variations of the baseline dataset were created to act as sensitivity checks (Table 2.2). This was achieved by altering binary cut-off points and changing the numeric transformation values along the quantitative scale from established baselines.

Initially, all five variables were converted to binary responses ('yes', 'no'), where any level of aggression above 'absent or very rare' was treated as the specific type of aggression had occurred. This created an 'absolute' model that sought to capture any propensity for aggression. Consequently, also included were both observed and inferred cases of adulticide. To then take a more conservative approach, the binary cross-over point was allocated based on a 'half & half' approach which, for example, included inter-group aggression entries of  $\geq 0.50$  being coded as 1 and also using only observed adulticide data. Thereby, dropping some species out of the five violence categories. The continuous values obtained for the inter-group and intra-group aggression variables were then reinstated (baseline dataset) and utilised to create two further datasets. These involved altering the quantitative values that were applied to each qualitative entry by exploiting staggered higher ('upper-end') and lower ('lower-end') conversion values. This was based on the spread of quantitative data within the dataset and the inclusion or exclusion of inferred lethal adulticide data in each dataset respectively.

Table 2.2: Sensitivity testing

Dataset name	Data type	Violence variable binary coding and transformation <sup>a</sup>							
		OG Agg <sup>b</sup>		IG Agg <sup>c</sup>		OG Killing	IG Killing	Infanticide	
‘Absolute’	Binary	Any occurrence (1) / Absence (0)				Observed and inferred (1) / Absent or no record found (0)	Observed (1) / No record or absent (0)		
‘Half & half’	Binary	<0.5	}	0	<0.034	}	0	Observed (1) / Absent or no record found (0)	Observed (1) / No record or absent (0)
		‘none’			‘none/very rare’				
		‘rare’			‘rare’				
		‘some’							
		≥0.5	}	1	≥0.034	}	1		
‘most’	‘infrequent’								
‘all’	‘low’								
					‘frequent’				
‘Baseline’	Binary + continuous	‘none’	0	‘none/very rare’	0	Observed (1) / Absent or no record found (0)	Observed (1) / No record or absent (0)		
		‘rare’	0.1	‘rare’	0.005				
		‘some’	0.25	‘infrequent’	0.0275				
		‘most’	0.75	‘low’	0.05				
		‘all’	1	‘frequent’	0.5				
‘Upper-end’	Binary + continuous	‘none’	0	‘none/very rare’	0	Observed and inferred (1) / Absent or no record found (0)	Observed (1) / No record or absent (0)		
		‘rare’	0.43	‘rare’	0.034				
		‘some’	0.62	‘infrequent’	0.206				
		‘most’	0.75	‘low’	0.346				
		‘all’	1	‘frequent’	0.960				
‘Lower-end’	Binary + continuous	‘none’	0	‘none/very rare’	0	Observed (1) / Absent or no record found (0)	Observed (1) / No record or absent (0)		
		‘rare’	0.18	‘rare’	0.001				
		‘some’	0.28	‘infrequent’	0.006				
		‘most’	0.43	‘low’	0.034				
		‘all’	1	‘frequent’	0.960				

<sup>a</sup> Variables listed as intra-group aggression (IG Agg), inter-group aggression (OG Agg), intra-group adulticide (IG Killing), inter-group adulticide (OG Killing) and Infanticide.

<sup>b</sup> Inter-group aggression recorded as a fraction of encounters that were aggressive.

<sup>c</sup> Intra-group aggression measured and transformed into n/ind/hr.

### 2.2.5 Data exploration

The intergroup aggression data posed something of a challenge in that it contained a sizable mix of both qualitative and quantitative data. This required some careful handling to convert the qualitative descriptors into usable numeric data for the analysis (see section 2.2.4). Post conversion, the aggression data was explored to establish distributions prior to analysis. Exploration of the complete intergroup aggression data revealed a bimodal distribution with notable levels of either low or high aggression. Restricting analysis to only the quantitative data showed this distribution was no longer observed, instead there was a slight left skew (low aggression). It was unlikely, that this distribution change was due to the numeric

conversions carried out during the sensitivity checks as systematic alterations yielded no notable difference in results. This sensitivity testing also controlled for any potential unconscious subjective bias that may lead to the application of a particular descriptor for a behaviour. Therefore, it could be proposed that the way the source data was originally recorded and reported has impacted on the distribution.

People comprehend the world through classification and simplification (Mieda and Oshio, 2021). Human studies on violence often polarise behaviour e.g., ‘good’ or ‘evil’, ‘nature’ versus ‘nurture’ (McEllistrem, 2004). This type of dichotomous thinking may potentially lead to a stronger awareness of more extreme examples of behaviour. Consequently, it is natural to comment on that which appears noteworthy or interesting. This is particularly likely when it is an ad-hoc observation or an observer’s narrative comment on the situation. Thus, if no aggression was seen, or extreme aggression, this likely attracted attention and was recorded using dichotomous descriptors such as “rare” or “all”. This study observed that intermediate descriptors such as “sometimes” were less commonly found in the literature. Potentially, these are perceived as vague, or not noteworthy. Non-response bias can sometimes apply to information that a researcher may feel lacks interest or usefulness (Easterbrook *et al.*, 1991), especially when constrained by publication wordcounts. Notably, the same bimodal pattern was observed in the qualitative survey data utilised in this study, where no intermediate descriptors were reported. However, this is suggestive rather than definitive due to the low qualitative response rate. Nevertheless, in combination it does appear to suggest that the qualitative data operated differently to the quantitative. In the latter’s case, behavioural quantitative studies utilised precise numeric metrics and these more ‘occasional’ behaviours were more likely captured, and subsequently reported.

The differences between the data types does not mean qualitative data is less valid. This dataset was built using quantitative data as the primary information source, then further developed through the addition of qualitative data. Qualitative data having been produced in the field, often by highly experienced researchers can add colour and detail that would otherwise be lost should the focus only be on quantitative data. However, possibly violence data were only available for use on species that are showing notable/dichotomous behaviour. Other species, that were not included in this dataset, may well show ‘average’ behaviours, but these are yet to be recorded and reported. If they were, then the distribution pattern may shift from bimodal to that observed in quantitative data.



### 2.2.6 Tree construction

A single tree was selected for use in this analysis as described in section 1(b).2).

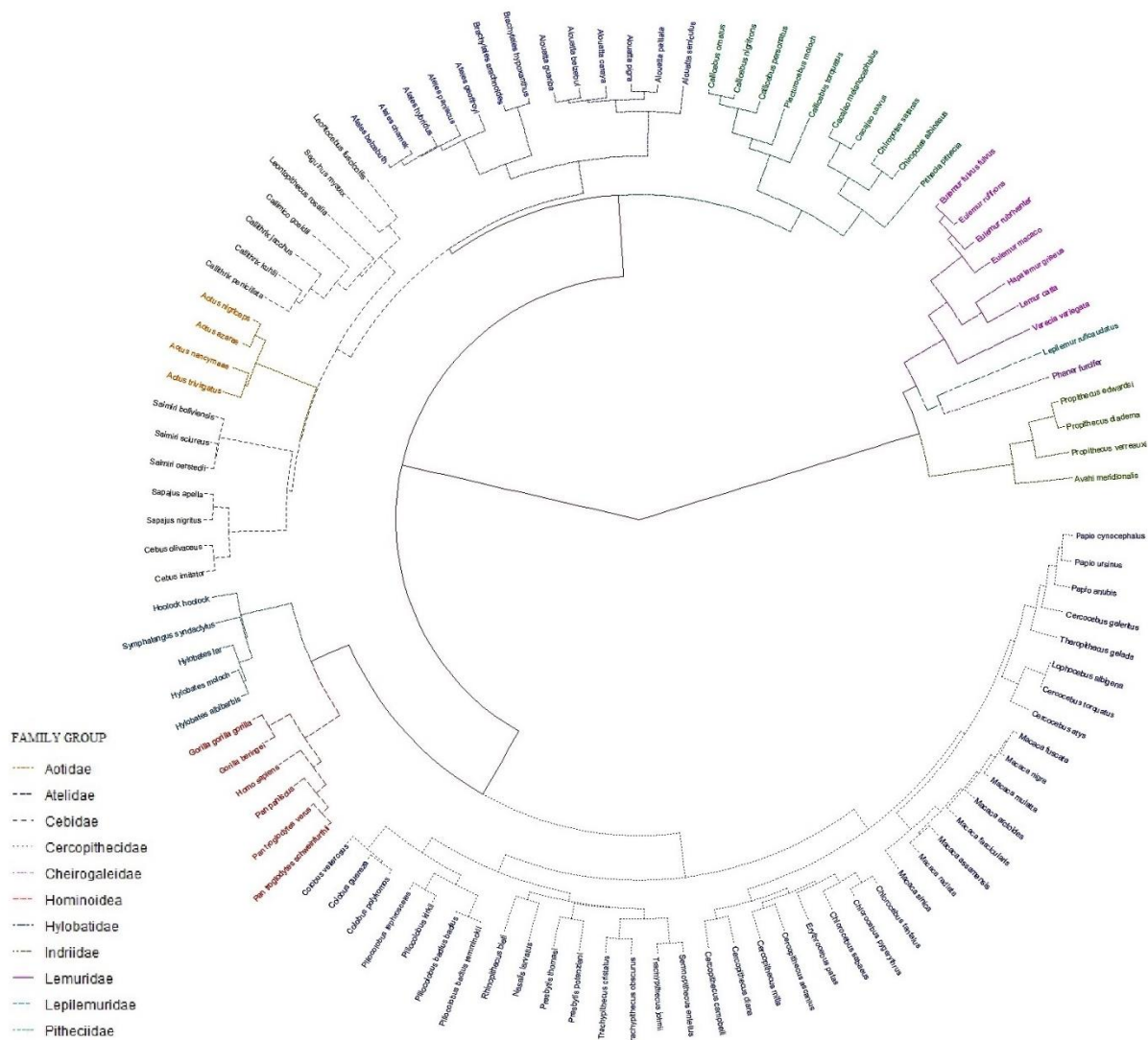


Figure 2.1: Phylogenetic tree for the 104 primate taxa used within this study. The colours allocated indicate the 11 families that were included within the scope of the study.

### 2.2.7 Statistical analysis

To control for phylogenetic relatedness and to assess for congruence between datasets, a phylogenetic principal component analysis (PCA) was conducted using the phytools package in R (Revell, 2009) followed by a test of congruence using the psych package in R (Revelle, 2009) (Appendix 2C) (see section 1(b).3 for additional details). Based on the results of the PCA and congruence analysis (Appendix 2D), the ‘baseline’ dataset was selected for further

analysis as it showed little variation from the other datasets and contained most data in its original unconverted format.

Analysis on the ‘baseline’ dataset was carried out using Bayesian multivariate modelling using the Stan probabilistic programming language (Carpenter *et al.*, 2017) and the high level interface ‘brms’ package version 2.14.0 (Bürkner, 2017) in R version 4.0.2 (R Core Team, 2020). A Bayesian multivariate Generalized Linear Mixed Model (GLMM) was fitted to the data, specifying Bernoulli distribution for the three lethal violence variables. Zero one inflated distribution (proportion data which includes zeros) for the intergroup aggression data, and hurdle gamma (data with an excess of zeros) for the intragroup aggression data. Phylogenetic relatedness was built into the model by including species ID as a random effect, weighted by the variance-covariance matrix calculated from the Bayesian consensus tree. Bayesian methods have been gaining prominence in recent years (Touchon and McCoy, 2016; Van De Schoot *et al.*, 2017) and offer several benefits over the typical frequentist approach (Gelman and Hill, 2006). In this study there was no frequentist algorithm that could model multivariant phylogenetic outputs using both binary and continuous data, so a Bayesian approach was essential.

The data were incorporated into the model and set to run for four chains, each with 4000/5000 iterations (2000 warmup, resulting in 8000/12000 posterior samples). The R-hat convergence diagnostic was reviewed on the output and found to be  $\leq 1.01$ , indicating the chains had well mixed (Bürkner, 2017). On the occasion when this was not the case, then the model was run again with increased iterations (5000) which resolved the issue. Additionally, plots were also checked to ensure the chains had converged.

## 2.3 Results

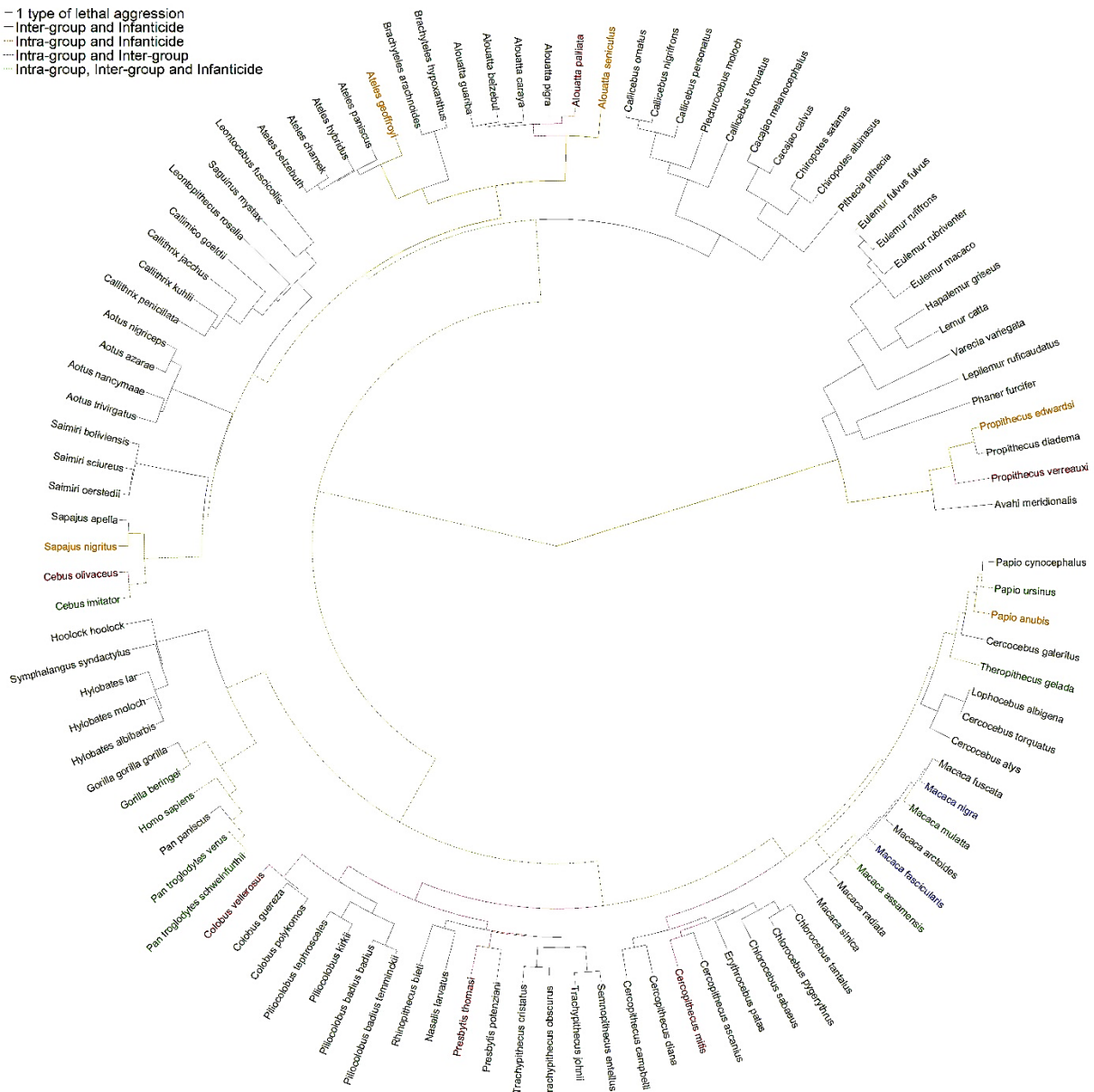
### 2.3.1 Descriptive results

Using non-lethal intergroup aggression data, it was found that when encountering another group, 47.1% of the species in the dataset would engage in aggression towards that group  $\geq 50\%$  of the time. This number reduced to 38.5% when aggression was observed to occur in  $\geq 75\%$  of encounters. Intragroup aggression occurred at a mean rate of 0.163 ( $\pm 0.407$ ) occurrences per individual per hour. While some species were observed to refrain from either non-lethal inter- or intragroup aggression, no species were observed to abstain entirely. Therefore, violence of at least one type was found to be present in all 104 species.

When reviewing all observed and inferred lethal violence cases (including infanticide), 52% of collated species committed at least one type of violence. Of the individual types of lethal violence, 46 species carried out infanticide, 19 intragroup adulticide, and 20 undertook intergroup adulticide. 32 species demonstrated a single lethal violence trait in isolation, with 84.4% of those single types being infanticide. When violence types are considered in combination, 13 species had descriptions of two types of lethal violence, with 46.2% being intergroup lethal violence and infanticide (Figure 2.2). Nine species from three families (*Cebidae* – 11%, *Hominoidea* – 44.5%, *Cercopithecidae* – 44.5%) had examples of lethal violence across all three categories.

### 2.3.2 Co-evolution of aggression types

Strong/moderate correlations were found between: intragroup adulticide and intergroup adulticide (0.67; 95% CI = 0.24-0.94), intragroup adulticide and infanticide (0.61; 95% CI = 0.08-0.93) and intergroup adulticide and infanticide (0.66; 95% CI = 0.13-0.94). A low/moderate positive correlation was found between intragroup aggression and infanticide (0.37; 95% CI = -0.24-0.85) and intragroup aggression and intergroup adulticide (0.33; 95% CI = -0.23-0.77). However, the latter two results were not statistically ‘significant’ as the credible interval transits through zero (see Table 2.3).



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Table 2.3: Correlation of the intercepts of the five violence types

Correlation Pairs	Estimate	CI	
		l – 95%	u – 95%
Intergroup Agg. – Intragroup Agg.	-0.08	-0.78	0.65
Intergroup Agg. – Intragroup Adulthood	-0.15	-0.79	0.65
Intragroup Agg. – Intragroup Adulthood	0.19	-0.35	0.72
Intergroup Agg. – Intergroup Adulthood	-0.02	-0.74	0.71
Intragroup Agg. – Intergroup Adulthood	0.33	-0.23	0.77
<b>Intragroup Adulthood – Intergroup Adulthood</b>	<b>0.67</b>	<b>0.24</b>	<b>0.94</b>
Intergroup Agg. - Infanticide	-0.15	-0.81	0.63
Intragroup Agg. - Infanticide	0.37	-0.24	0.85
<b>Intragroup Adulthood – Infanticide</b>	<b>0.61</b>	<b>0.08</b>	<b>0.93</b>
<b>Intergroup Adulthood – Infanticide</b>	<b>0.66</b>	<b>0.13</b>	<b>0.94</b>

\*Significant results, indicated by the upper and lower limits of the credibility interval not passing through zero, are highlighted in bold.

### 2.3.3 The phylogenetic signal of aggression

The  $R^2$  values are used as a proxy to indicate the strength of the phylogenetic signal as Pagel's lambda cannot be calculated when using Bernoulli distribution as no sigma value is generated. The values presented explain the variance in the occurrence of the five types of violence observed in different species. The  $R^2$  for intragroup adulthood was 60.6% along with 47.7% of intergroup adulthood. The model explained a smaller amount of variance for infanticide (25.3%) and intragroup aggression (26.9%). Only a very low amount of variance in the intergroup aggression data was explained by phylogeny (0.15%) (Table 2.4).

Table 2.4:  $R^2$  values for the five violence types

	Estimate	Est. Error	Q2.5	Q97.5
Intergroup aggression	0.015	0.018	2.538e-05	0.063
Intragroup aggression	0.269	0.148	5.542e-02	0.600
Intragroup adulthood	0.606	0.185	2.582e-01	0.940
Intergroup adulthood	0.477	0.173	1.845e-01	0.875
Infanticide	0.253	0.111	5.765e-02	0.500

### 2.4 Discussion

This analysis drew together an extensive compilation of primate species in a first attempt to uncover the phylogenetic roots of five types of violence. The exploratory approach aimed to understand if these behaviours were in fact distinct, or a single generalised violent behaviour. The analyses revealed that phylogeny explained a large amount of variance in the distribution of intergroup and intragroup adulticide, a moderate amount for infanticide and intragroup aggression, but a very limited amount for intergroup aggression. Additionally, strong/moderate correlated evolution was identified between the three types of lethal violence. Conversely, inter- and intragroup aggression showed no clear correlation with each other or with the other lethal violence types.

With strong/moderate correlations shown between lethal violence types and phylogeny explaining a notable amount of variance in intergroup and intragroup adulticide, potential exists for a singular lethal trait of ‘adulticide’, with infanticide and inter- and intragroup aggression as three further distinct traits. However, this may not unequivocally imply co-evolution (Nuismer, Gomulkiewicz and Ridenhour, 2010) and similarly a lack of correlation does not necessarily conclude an absence of co-evolution (Thompson, J. N., 1994; Thompson, J. N., 2005). Therefore, to understand these results more fully they must be considered alongside the known behavioural hypotheses previously discussed.

#### 2.4.1 *The evolution of adulticide*

Phylogeny explains high levels of variance in both intra and intergroup adulticide. The strong selection pressure for adulticide is predominately driven by males, through a sexual selection mechanism against males from other communities (Dobash *et al.*, 2007; Davidian *et al.*, 2022) and within communities in some species. Despite potential costs, such as the risk of injury or death, there are clear benefits in removing rival males by providing more assured access to females and subsequent mating opportunities. In contrast, the evolutionary benefits of intragroup adulticide are poorly understood (Wilson, M. L. and Wrangham, 2003; Newton-Fisher and Thompson, 2012) and may appear counter-intuitive to overall fitness. Attrition of intragroup males through adulticide may limit the ability to obtain coalitionary allies during intercommunity engagements, such as those observed in *P. troglodytes* (Wrangham, 1999; Newton-Fisher and Thompson, 2012). Additionally, a weakened group may result in cycling females transferring to a stronger neighbouring group (Takahata, 1985), thereby reducing the

reproductive fitness of the remaining males. This may in part explain the reduced prevalence of intragroup adulticide compared to intergroup adulticide.

In species that commit intragroup adulticide it could be anticipated that males would largely be philopatric, fighting to eliminate upcoming rivals, obtain rank reversal or access limited females. Indeed, some are, for example a *Pan troglodytes* *verus* unsupported ex-alpha male was killed within the group potentially due to the unstable hierarchy derived from low female numbers (Pruetz *et al.*, 2017). Yet, most of the species in this study's dataset showed male dispersal, though even in these species some may remain within the natal group. For example, red howlers (*A. seniculus*) exhibit fierce reproductive competition usually to enter but sometimes to remain in the troop (Crockett and Pope, 1988).

While both intra and intergroup adulticide share a similar evolutionary mechanism, the traits can present differently. This is clearly illustrated in *Pan troglodytes*, by the level of violence demonstrated with intragroup attacks in comparison to intergroup attacks, and the formers extended duration, which potentially suggests that the motivations between the attacks are different (Kaburu, Inoue and Newton-Fisher, 2013). Furthermore, the extended duration of intragroup killing is likely due to the costs to the attacker. Attacking within the group on a weakened individual may afford the opportunity for a slower kill, whereas the risks of killing an outgroup member away from the home range, who may eventually gain coalitionary support will be higher.

While adulticide is predominantly delivered by males, potentially operating through an evolved stronger drive for frequent mating due to the male's lower energetic reproductive costs (Thornhill and Palmer, 2000), females also engage in adulticide. These behaviours however present at a relatively low level and intergroup adulticide appears to mainly occur as part of a coalition with males (see: *Cebus capucinus* - Gros-Louis, Perry and Manson, 2003; *Macaca nigra* - Martínez-Íñigo, 2020). Intragroup adulticide is less frequent, though when operating without the presence of, or in support of males, females are just as likely to kill within the group as outside it. Motivation for these attacks would appear to be for intrasexual motives, or potentially to protect infants.

The analysis also revealed that intra- and intergroup adulticide traits were strongly correlated. Despite the potential disparity between the apparent benefits of each trait, both intra and intergroup adulticide are important selection pressures in some species. In other species however correlated traits can evolve that are of limited adaptive significance or even

deleterious (Price, Turelli and Slatkin, 1993). Potentially, intragroup is less advantageous but is evolving along with the more obviously beneficial intergroup adulticide where morphological and psychological changes that are of benefit to intergroup aggression may prove useful in an intragroup situation. Furthermore, intragroup may be operating through behavioural plasticity, where modification of the behaviour allows the individual to manipulate their environment and alter the selective pressures they experience (West-Eberhard, 2003). However, it is also feasible that intragroup adulticide drove the evolution of intergroup adulticide. Intergroup adulticide providing significant benefits for the attacker, particularly when combined with the ability to form coalitions.

Due to the amount of variance explained by phylogeny, the strong correlation and the similar sexual selection mechanism operating on both inter and intragroup adulticide, it is possible that they may be considered as the same behavioural trait, that of ‘adulticide’. However, intra and intergroup adulticide do have different phylogenetic signals. Furthermore, they are not always observed in the same set of species and have cost implications which may alter the lethal delivery style and frequency. Thus, caution is warranted when treating adulticide as a single trait and consequently separation in to intra and intergroup adulticide may be beneficial.

#### 2.4.2 *The co-evolution of adulticide and infanticide*

In keeping with the findings of Gómez, Verdú and González-Megías (2021), both intra- and intergroup adulticide and infanticide were strongly correlated. Males who try to violently immigrate into another group and take-over the dominant position, and those who try to mate with females from other groups, sometimes through coercion, often use infanticide to maximise their reproductive success (e.g., Takahata, 1985; Teichroeb, 2020). Infanticide can accelerate female receptivity and is therefore predominantly but not solely of benefit to species whose females are continuously receptive, and this was mirrored in the dataset.

Specifically intergroup adulticide and infanticide showed the strongest correlation, and these behaviours were largely occurring in species within the clade *Cercopithecidae* and *Hominoidea*. The strong correlation between these two types of aggression may be due to the combined effect of high levels of inter-sexual and intergroup competition. However, five species were found to show only these two lethal traits (i.e., not intragroup adulticide), and they came from four different families (*Atelidae*, *Cercopithecidae*, *Indriidae* and *Cebidae*)



indicating that the strong correlation may largely be due to species that demonstrate all three lethal violence types.

There is clearly a strong selective force on males through engaging in adulticide and infanticide, however, it is important again not to discount the role of females. Females also engage in adulticide and infanticide. However, it is rare, and the dataset compiled in this study contained examples of females observed committing both intragroup adulticide and infanticide in only two species; *Homo sapiens* and *Pan troglodytes schweinfurthii* (Fossey, 1984; Lowe *et al.*, 2020). Female adulticide can be a strategy to reduce the risk of infanticide through infant protection or as a retaliatory consequence. Whereas infanticide is likely a consequence of threats to the killer's own reproductive efforts (Lukas and Huchard, 2019). Therefore, in species where females commit adulticide and infanticide they may be acting both to protect their own offspring, and also, if necessary, remove any competition to them.

Despite the strong correlation, the results indicated a difference between the amount of variance in the adulticide and infanticide data that could be explained by phylogeny. The reduced explanatory power of the infanticidal model may in part be due to specific socio-ecological factors, or through diverse lineages potentially arriving at the same infanticidal behaviour independently. It could be speculated that adulticide may have evolved in an infanticidal species when relevant morphological or psychological changes led to a rival's death, subsequently providing a selective advantage. Adulticide may then have evolved into a distinct trait with stronger selection pressures. Certainly, the two behaviours appear different in their presentation due to the strength, and techniques that may be needed to kill an adult victim over an infant, along with the potentially different motivations (Wilson, M. L. and Wrangham, 2003).

#### 2.4.3 A generalised lethal aggressor

A small group comprising of nine of the 104 species in the dataset were identified as displaying all three lethal violence types. Gómez *et al.*, (2016) determined that humans occupied a particularly violent position in the evolutionary tree and this study adds additional evidence by identifying the propensity of humans along with three other species from the family *Hominidae* (*Pan troglodytes schweinfurthii*, *Pan troglodytes verus*, *Gorilla beringei*) to display all three types of lethal violence. Four further species were from the family *Cercopithecidae* (*Macaca mulatta*, *Papio ursinus*, *Macaca assamensis*, *Theropithecus*

*gelada*). However, these old-world monkeys diverged from apes over 25 million years ago (Stevens *et al.*, 2013).

All three lethal types involve the maximisation of reproductive fitness, largely driven by males. It may potentially suggest that these species display a generalised aggressive profile and thus would also incorporate non-lethal aggression types. However, no significant correlation was observed between non-lethal aggression types or any type of lethal violence. Nevertheless, a lack of correlation does not necessarily indicate a lack of a generalised propensity in some species. For example, in addition to displaying all three lethal violence types, high levels of non-lethal intra and intergroup aggression were recorded in *Pan troglodytes schweinfurthii*. The by-product hypothesis suggests that intergroup/community aggression in male chimpanzees has resulted in this species being able to exploit intense aggression when necessary. There is deemed to exist a psychological threshold which is triggered at a level of aggression beyond which there is a cessation of control on the level of aggressive intensity (Watts, 2004). Yet, *Homo sapiens* within the same family scored comparatively low on non-lethal aggression. Further, a study conducted on human males that have killed, found that the results did not support the hypothesis that non-lethal aggression can simply progress to lethal violence (Dobash *et al.*, 2007).

#### 2.4.4 Non-lethal aggression types

Based on the analysis non-lethal aggression appears to be two distinct types of aggression. In similarity to infanticide, phylogeny explained a moderate amount of the intragroup data variance but failed to capture the variance in the intergroup data. Furthermore, non-lethal aggression types showed no clear correlation between themselves or with any lethal violence type.

These differences between the non-lethal aggression types indicate that these distinct, uncorrelated behaviours are subject to unique socioecological controls or potentially co-evolved avoidance behaviours, such as scent marking in some primate species. A classic example of two dichotomously behaving species is that of chimpanzees (*P. troglodytes*) and bonobos (*P. paniscus*). Both sister species are territorial, but bonobos are less likely to engage in intergroup aggression and show no lethal violence traits. Lower levels of aggression may in part be due to female bonobos, in contrast to chimpanzees, having more reproductive and social control, thereby limiting male sexual competition (Davidian *et al.*,

2022). The potential benefits to the male of violence against a rival may be somewhat muted for bonobos if they were not selected by the female. Therefore, these social factors may have a strong bearing on the presentation of a trait that may be present or has simply not evolved.

### 2.5 Conclusion and next steps

The study has identified a clear phylogenetic component to intra and intergroup adulticide. Additionally, strong correlations between all lethal violence types were identified, with the strongest being between intra and intergroup adulticide. This study has shown that adulticide is more common across primates than previously thought, extending beyond chimpanzees and humans, and it has clear evolutionary roots. Almost one fifth (>18%) of the species in the dataset presented here displayed intragroup or intergroup adulticide. This is likely to be a conservative figure, because reports of adulticide are usually anecdotal and not often published. The occurrence of adulticide in a species may vary substantially across populations and groups, as observed in chimpanzees, and as it may be the case in macaques (Martínez-Íñigo *et al.*, 2021). Moreover, very few primate species, other than chimpanzees, have been subject to continuous long-term research on different populations.

Some species were identified as showing all three types of lethal violence, specifically from the families *Hominidae* and *Cercopithecidae*. Consequently, in-line with Gómez *et al.*, (2016) it can be suggested that *Homo sapiens* have an evolutionary link to aggression, and particularly multiple types of violence. While it is possible that species showing three types of lethal violence are demonstrating a single aggressive trait, there is no correlation to non-lethal violence types, and so lethal violence is unlikely to be an escalation of mild aggression. This may be because the species have not encountered socio-ecological trigger factors, or they have effective conflict management strategies (i.e., scent marking) that prevent violence escalation.

Based on existing theories sexual selection may be the overarching evolutionary driver of lethal violence traits, but they may additionally be controlled through specific socio-ecological factors. As intragroup and intergroup adulticide share some distinct commonality in terms of a strong correlation and likely similar selection pressures, they may be considered as one trait: adulticide. However, while adulticide types show correlated evolution, these types of violence have slightly different phylogenetic signals and are not always observed in the same set of species. Thus, caution should be applied when treating adulticide as a single trait. Infanticide should also remain as a separate trait due to the higher level of non-phylogenetic factors impacting on presentation and the potential morphological and psychological differences required to kill an adult in contrast to an infant. Theory suggests intragroup and intergroup non-lethal aggression generally have different impacting factors

and the results of this study suggest, certainly in the case of intergroup aggression, that these are not creating extensive evolutionary pressure. It is therefore suggested that these two non-lethal aggression traits are also distinct.

Due to the availability of data this study was conducted at species level, consequently, there will be some examples that sit outside the findings of this study based on distinct individual and population differences. Should data permit in the future, it would be desirable to carry out the analysis again at the population level. Nevertheless, this study has expanded understanding of the evolution of violence types which are of relevance for future studies. Certainly, it is clear that phylogeny plays an important, but variable role on the distribution of violence in primates, which depends on the type of violence. These findings support the importance of phylogeny for comparative analyses on violence in vertebrates, particularly for lethal violence. At the same time, these results show that additional factors need to be considered, therefore the next step is to understand which socioecological factors affect violence. This will be undertaken in chapter three and applied to the five distinct violence types identified in this chapter.

**CHAPTER THREE – THE ROLE OF SOCIO-ECOLOGICAL VARIABLES ON  
SPECIFIC VIOLENCE TYPES**

*“... so much in life revolves around food. In fact, good manners started to happen as soon as all the mammoths were killed off and there was no piece of food big enough for everyone to eat at the same time.”*

*(Nanny Ogg's Cookbook - Pratchett, 1999, p.16)*

### 3.1 Introduction

Findings from the previous chapter suggest that violence types are distinct rather than a homologous behaviour, with each form of violence appearing to follow a unique evolutionary trajectory. Furthermore, a substantial amount of the total variability for four out of the five forms of violence can be explained by phylogeny. However, there remains to be identified additional factors driving each violence type, particularly intergroup aggression, intragroup aggression, and infanticide. Early research, by Lorenz (1966), considered violence an innate trait, analogous to appetite, as an increasingly spontaneous behaviour occurring if not satiated. However, this process would potentially result in violence occurring when there was no opponent or incitement (Toates and Archer, 1978) and as such, it is unclear how it would act as a functional behaviour enhancing fitness (Archer, 1988). It is therefore likely that a range of factors interact, which may include internal motivators such as impulses, needs and drives, but also external motivators that help elucidate the variation in strength and incidence rate of violence (Bandura, 1977). This chapter will attempt to ascertain any key socioecological variables.

Many researchers have attempted to model the socio-ecological determinants of violence (Table 3.1). Some of these models consider violence, as Archer (1988) did, to be a behavioural response to difficulties the individual encounters within their environment. Consequently, they incorporate environmental triggers such as temperature (e.g., Cognitive neoassociation theory - Berkowitz, 1990; or, Anderson, 2001). Others consider social factors like social structure and population density (e.g., Social pathology hypothesis - Curtin and Dolhinow, 1978; Hausfater, 1984). While some researchers have considered violence as a whole, others have addressed specific forms of violence, such as intra and intergroup aggression, within the confines of resource acquisition (e.g., Food abundance or distribution and contest or scramble competition - Isbell, 1991).

Previous research indicates that several socio-ecological variables are likely to have an influence on the occurrence of violence. Yet, what remains unclear is their impact, on the degree of violence, specifically their influence on lethal and non-lethal types as defined by this study. Through a review of key socio-ecological variables, and their likely effects, models can be derived in an attempt to offer an improved explanation for the presentation of the five violence types, above that of their evolutionary basis.

*Table 3.1: Violence models and theories - involving socio-ecological determinants.*

<b>Model</b>	<b>Description and/or example</b>	<b>Ref.</b>
Frustration–aggression theory	When external factors limit the achievement of goals frustration will result. This leads to aggression as a form of cathartic release in the presence of particular cues e.g., weapons.	1
Motivational Models of Aggression	Interplay of motivational variables e.g., fear and aggression. These fluctuate based on factors such as body size or territory quality. Also incorporates genetic predisposition.	2
Social learning theory	Considers the reciprocal role of behaviour and controlling factors. Where aggression is not solely driven by internal forces or environmental factors.	3
Socio-Ecological models (human)	Consider the impact on the individual across four overlapping levels of society and ecology: Individual, microsystem, exosystem, macrosystem.	4
Socio-Ecological models (non-human primates)	Explores the impact of socio-ecological variables on aggression e.g., Group size/structure <sup>5a</sup> , agonistic coalitions <sup>5b</sup> , diet <sup>5c</sup> , and breeding biology <sup>5d</sup> .	5 <sup>a-d</sup>
Economic models	Considers fitness as a currency e.g., territorial defence occurring as a result of ‘economic defendability’.	6
Game theory models	Evolutionary Stable Strategy (ESS). Strategy that is most appropriate for the current conditions. The model can predict under what circumstances the behaviour will occur. Cost benefit - based on the strength of the other group and the payoff that could be expected from engaging them.	7
Social pathology hypothesis	Aberrant behaviour likely the result of animals living in high population densities e.g. may result in infanticide (Hausfater, 1984; Silk, 2014).	8
The General Aggression Model (GAM)	A biological-social-cognitive model. Describes the influence of proximate processes (personal and situational) and distal (biological and persistent environment factors) on aggression.	9
Cognitive neoassociation theory	Fight or flight events may be triggered through adverse events including uncomfortable temperatures.	10
Climate, Aggression, and Self-control in Humans (CLASH)	Lower temperatures, especially larger degrees of seasonal variation, call for individuals and groups to adopt a slower life history strategy. The resultant slow life strategy, future orientation, and strong self-control are important determinants of inhibiting aggression and violence.	11
The Routine Activity Theory	Temperature acting indirectly through changes in social behaviour resulting in a convergence in time and space.	12

1. Dollard, Doob, Miller, Mowrer, & Sears, (1939), revised by Berkowitz, (1969); (1990); 2. Maynard Smith & Riechert, (1984) 3. Bandura (1977); 4. (Heise, 1998); 5<sup>a</sup>. (Schaffner and French, 1997; Majolo, de Bortoli Vizioli and Schino, 2008; Wheeler, Scarry and Koenig, 2013; Majolo *et al.*, 2020) including humans (Faris and Ennett, 2012); 5<sup>b</sup>. Bissonnette *et al.*, (2014); 5<sup>c</sup> Isbell, 1991; 5<sup>d</sup>; 6. (Brown, 1964); 7. Kitchen and Beehner (2007); Maynard Smith and Parker (1976); Parker (1974); Wrangham (1980); Maynard Smith (1974); 8. (Curtin and Dolhinow, 1978; Hausfater, 1984); 9. Allen, Anderson and Bushman, (2018); 10. Berkowitz, (1989), (1990); 11. Van Lange, Rinderu and Bushman, (2017); 12. Cohen & Felson 1979; Rotton & Cohn 2001



### 3.1.1 Substrate type

The environment in which the primate lives may be fundamental to the occurrence of violence. Substrate forms a significant part of the environment and can be categorised as terrestrial, arboreal or a combination of the two, as some primates expand their niches vertically (Tabacow, Mendes and Strier, 2009). The limitations of these specific environments may place constraints on acts of violence in terms of presentation, frequency or magnitude. For example, it is likely that there are risks and difficulties carrying out attacks in an arboreal environment that would be less problematic in a terrestrial one. This may be due to spatial limitations, the restrictions on coalition formation (Noë and Sluijter, 1990; Bissonnette *et al.*, 2014), the increased challenge in delivering simultaneous attacks (Noë and Sluijter, 1990), and the inherent cost of accidental injury an aerial environment affords (Broom, Koenig and Borries, 2009). It is therefore more likely that violent behaviour will bias a terrestrial, rather than arboreal, environment.

### 3.1.2 Diet – proportion of leaves consumed

Species potentially evolve a diet pertinent to the environment in which they live, which may include seeds, grain, leaves, insects, gum, and/or meat, as well as specialist items such as bamboo (e.g., *Hapalemur aureus*). Associations have been suggested between diet and behaviour for decades in numerous species, including, non-human primates, humans, birds, rodents, and equines (see: D'Asaro *et al.*, 1975; Schoenthaler and Bier, 1985; Isbell, 1991; Hanstock *et al.*, 2004; Carere *et al.*, 2005; Britt *et al.*, 2015; Bulmer *et al.*, 2019). Potential links between violent behaviour and food are perhaps not surprising, not least because access to food is critical for individual survival and reproductive success. Consequently, being able to monopolise these resources may be very beneficial (Trivers, 1972; Sterck, Watts and Van Schaik, 1997; Sterck and Steenbeek, 1997). Nevertheless, debate continues around any relationship that may exist between violent behaviour and diet, notably among behavioural scientists, nutritionists, and criminologists (Fishbein and Pease, 1994). Partly this debate stems from the scope and degree of dietary manipulation that can occur. To illustrate, studies have altered the nutritional content of a diet, explored changing availability and distribution, and focused on different species, both free-ranging and in captivity (Table 3.2).

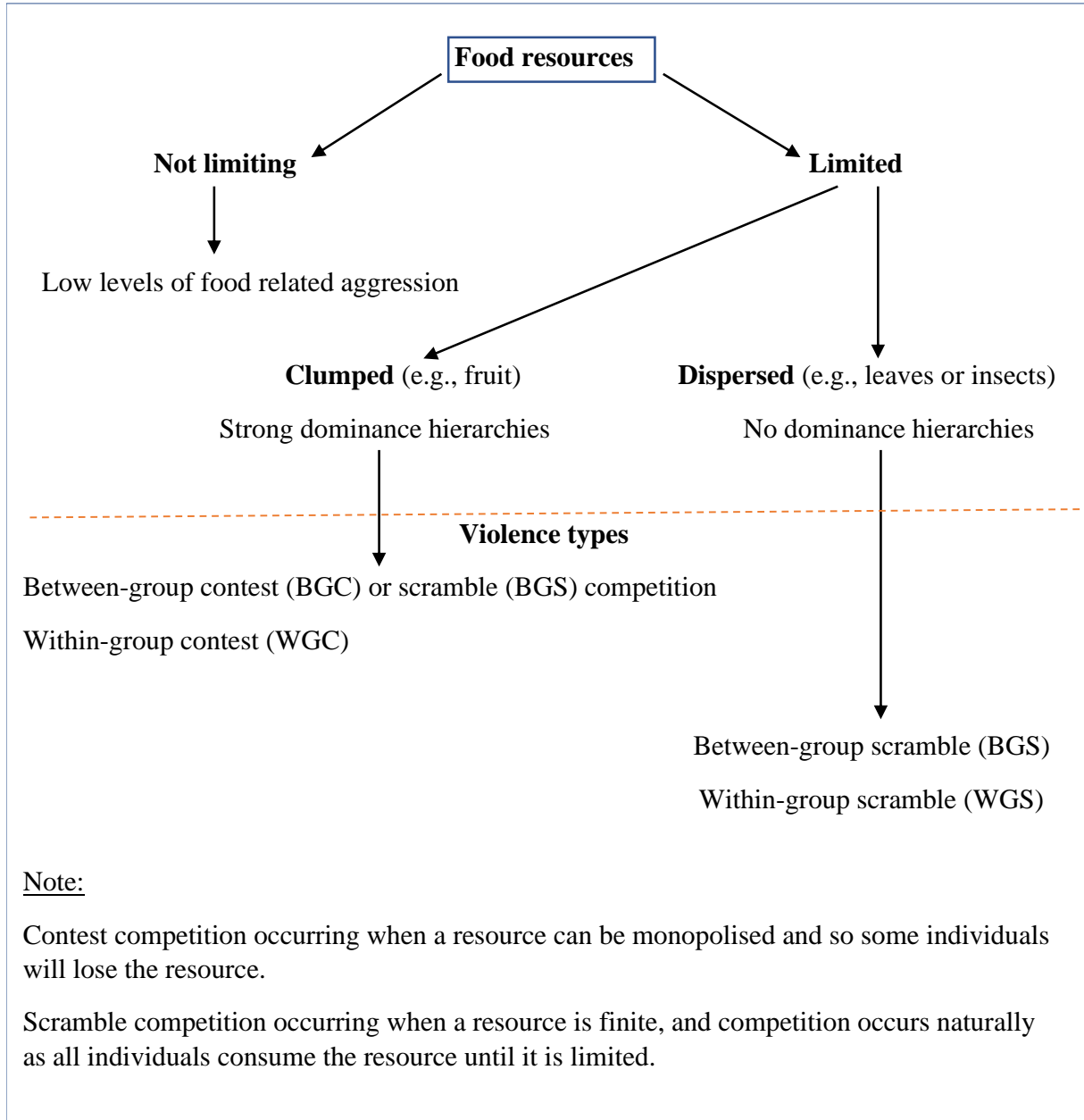
Changes in violent behaviour may therefore be related to diet change, food availability and distribution. Even supposed specialists show dietary adaptability, which in many primate

species does not appear to be influenced by factors such as seasonality, population density or habitat (Chapman and Chapman, 1990). The change in diet may lead to a change in absorbed macro and micro-nutrients (but see: Curtis, 2004) impacting on gut microbiota which are associated with health, behaviour and gut-brain axis communication (Bulmer *et al.*, 2019). For example, changes from high fibre to high sugar diets, such as leaves to fruits, could potentially result in individuals becoming less settled and more reactive. Many primate species, including *Alouatta sp.* and *Gorilla sp.*, have a folivorous and frugivorous diet.

Food shortages may occur as a result of environmental impacts such as seasonal variation in the temperature and rainfall that can lead to differing growing conditions. Resource acquisition models propose that limited resources can lead to violence in order to secure the resource. When food is scarce ranging behaviour increases and consequently so does the likelihood of encountering others. Therefore, food abundance is a determinant in intergroup competition (Isbell, 1991). However, resting time has been identified to increase in lower quality habitats, or those with food resource shortages in some species (Li and Rogers, 2004), which may reduce violent interactions. Furthermore, frugivores have been shown to adopt either a strategy of home range expansion or engage in energy saving practices (Campera *et al.*, 2014). For example, there is variation between red-bellied lemurs and rufus lemurs, the latter feeding less and resting more at times of food scarcity (Overdorff, 1996).

The significance of food distribution is explored in the ‘Food distribution’ hypothesis (Brown & Orians, 1970; Isbell, 1991; Isbell & Enstam, 2002) which theorises that food spatial distribution influences inter-individual distance. For example, the leaves of a folivore’s diet are often considered to be distributed evenly and generally abundant, therefore cannot be monopolised (Isbell, 1991) (Figure 3.1). Consequently, inter-individual distance will be greater between conspecifics than when food resources are clumped, such as fruits (Isbell, 1991) (see Table 3.2). With close interindividual distance around a clumped and contested resource between-group contest (BGC) or scramble (BGS) competition and within-group contest (WGC) may occur (Isbell, 1991) (see Figure 3.1 for definitions). The latter may in part be frustration-induced aggression when attempting to access the resources and failing to receive the expected reward (Archer, 1988). Higher levels of aggression have been observed in frugivores (Cords, 2000); Klass and Cords, 2015, but see: Wheeler, Scarry and Koenig, 2013). However, even with dispersed resources conspecifics may engage in a degree of violence, likely between-group scramble (BGS) and within-group scramble (WGS) (Isbell, 1991; Kappeler and van Schaik, 2002). Though the costs of violent behaviour under these

conditions would not generally yield sufficient benefit, so intragroup aggression would likely be low.



*Figure 3.1: Associations between food distribution/abundance and intra and intergroup aggression types. Adapted from Isbell (1991).*

Table 3:2: Overview of dietary impacts on violence across a range of species

Dietary variability	Examples of the resultant violence impact	Ref
Nutritional content – the impact of various macro and micronutrients	<ul style="list-style-type: none"> <li>Juvenile male crickets (<i>Gryllus bimaculatus</i>) that consumed high protein diets were, as adults, more aggressive and more behaviourally unstable, heavier, and were more active during mating in comparison to conspecifics fed on carbohydrate rich diets.</li> </ul>	1
	<ul style="list-style-type: none"> <li>Four species of zoo-based lemurs' diet was changed to mimic the diet of their wild counterparts more accurately, by eliminating fruit from the diet. Levels of aggression were significantly lowered in comparison to behaviour observed under the original feeding regime.</li> </ul>	2
	<ul style="list-style-type: none"> <li>Blood sugar swings and associated hormonal responses may be associated with mood and behavioural changes such as irritability, anxiety, and agitation.</li> </ul>	3
Availability	<ul style="list-style-type: none"> <li>Avian study exploring the environmental factors of food availability and sibling competition, indicated that the behavioural trait of heightened aggressiveness was potentially shaped by the food rationing availability in early life. Indicating a change in availability can lead to behavioural plasticity.</li> </ul>	4
	<ul style="list-style-type: none"> <li>Woolly monkeys had closer interindividual distances and higher rates of agonism as levels of frugivory increased during times of lower fruit availability.</li> </ul>	5
	<ul style="list-style-type: none"> <li>Females may also be involved in parental manipulation at times of limited resources to improve parental lifetime reproductive success through the termination of ill, surplus or poorly timed infants.</li> </ul>	6
Distribution	<ul style="list-style-type: none"> <li>The insectivorous redbell monkeys (<i>Cercopithecus ascanius</i>) were observed to be further away from their conspecifics when they eat both insects and leaves as opposed to clumped fruits.</li> </ul>	7
	<ul style="list-style-type: none"> <li>Where resources are limited between group competition (BGC) is important to females. If these resources are clumped, then within group competition (WGC) occurs shaping female dominance hierarchies. If dispersed resources are limited, then within group scramble can occur (BGS).</li> </ul>	8

1. Han and Dingemanse, (2017); 2. Britt *et al.*, (2015); 3. Fishbein and Pease (1994); 4. Carere *et al.*, (2005); 5. Cavalcante, Strier and Bicca-Marques, (2021); 6: Hrdy (1979); Saguinus mystax - Culot *et al.*, (2011) ;7. Bryer, Chapman and Rothman, (2013); 8. Isbell (1991).

Due to many species having dietary flexibility, the standard labels applied to dietary types are very general, as species cross dietary type boundaries to greater or lesser extents (Kay and Covert, 1984). By using qualitative values to a specific food type rather than global labels a better understanding of the majority diet type can be appreciated. However, folivores may feed selectively with resources varying in quality, distribution, and availability (Snaith and Chapman, 2007). Nevertheless, while challenging, the proportion of leaves in the diet has been anticipated to show the level of feeding competition within a group (Snaith and Chapman, 2007), it is commonly used in primate research, and is a useful metric for this study.

### 3.1.3 Seasonal breeding

Attempts may be made by some species to control for fluctuating food availability through timing birthing intervals to coincide with peak food abundance. As such, primate species display two main reproductive seasonality types; continuous breeders that give birth throughout the year and seasonal breeders that have a defined timeframe in which they breed. Though, seasonal breeding may also include opportunistic breeding where animals may breed anytime of the year but favour specific conditions (Vasanth, 2016). In many mammalian species, seasonal breeding is triggered by photoperiodic cueing (Urbanski, 1990; Revel *et al.*, 2009; Perfito and Bentley, 2009), particularly in temperate regions (Bronson, 1989, 2009). This has also been observed in primates where at latitudes of  $\geq 10^{\circ}\text{N}$  they become seasonal breeders due to the fluctuating photoperiods occurring at higher latitudes (Heldstab *et al.*, 2021). However, many primate species are concentrated in the tropics and season breeding also occurs in these species. Factors leading to seasonal breeding in lower latitude species can include gestation length, annual mean temperature, percentage of leaves in the diet and Madagascan origin (Heldstab *et al.*, 2021).

Seasonal breeding can improve fitness under some ecological conditions and aid in mitigating food resource-based violence. However, it by no means negates all violence as seasonal breeding itself could lead to elevated aggression levels. For example, infanticide has been observed in an increasing number of seasonal breeding species, such as *Macaca fuscata* (Soltis *et al.*, 2000; Yamada and Nakamichi, 2006) and *Macaca mulatta* (Ciani, 1984). Palombit (2012) described two possible situations for when infanticide should occur in species; those that have an interbirth interval larger than the breeding season, or when it

would be advantageous to breed early in the season to maximise infant survival. Infanticide may also benefit a dominant male who typically would have a short tenure (Hrdy, Janson and Van Schaik, 1994; Lukas and Huchard, 2014) where the dominant/breeding male is removed by male challengers. Therefore, lethal violence could provide some seasonal breeding species with substantial benefits, either to remove an infant, accelerating female receptivity or to kill a rival male and take their breeding status. However, infanticidal behaviour is also of benefit to non-seasonal breeders when it encourages the female to return to breeding condition more quickly.

#### *3.1.4 Group size*

The effect of group size on violence has been explored in numerous species such as, farm animals, including poultry (Estevez, Keeling and Newberry, 2003; Rodenburg and Koene, 2007), and primates (Schaffner and French, 1997; Majolo, de Bortoli Vizioli and Schino, 2008; Wheeler, Scarry and Koenig, 2013; Majolo *et al.*, 2020), including humans (Faris and Ennett, 2012). Primate studies have largely identified that violence increased with expanding group size, which has often been connected to resource defence and acquisition by influencing intraspecific competition (Gómez, Verdú and González-Megías, 2021). Group size shows considerable variation both across primate species (Kappeler and van Schaik, 2002; Campbell *et al.*, 2011; Griesser *et al.*, 2011) and within (Wrangham, 1980; Isbell, 1991; Griesser *et al.*, 2011; Campbell *et al.*, 2011). This can result in group sizes ranging from a solitary individual to several hundred (Campbell *et al.*, 2011).

As discussed in section 3.1.2 violence between groups can be linked to contest and scramble competition over food resource acquisition, determined by distribution, availability, and quality (Wrangham, 1980; Isbell, 1991). Larger sized groups may need larger home ranges to nutritionally support all group members. However, the larger group will also have a more extensive overlapping range (Willems, Hellriegel and van Schaik, 2013; Willems and van Schaik, 2015) and consequently an increased risk of intergroup encounters. Willems and van Schaik (2015) observed that the number of aggressive intergroup encounters per day is positively related to group size (but see: Majolo *et al.*, 2020). Those that engage in encounters may attempt to reduce costs through agonistic coalition formation which are more probable in larger groups (Henzi, Weingrill and Barrett, 1999).

Intragroup competition may also increase as group membership increases limiting maximum group size. This is the basis of the ecological constraints model of group size which described how intragroup competition for food resources is positively correlated to group size. The larger groups have higher energetic costs as daily travel distances and home-range also increase (review in Chapman and Chapman, 2000). Consequently, foraging efficiency, as a consequence of feeding competition, can limit group size, though this is balanced against the number of individuals needed to decrease predation risk (van Schaik and van Hooff, 1983; Romey, 1995). Several studies found that higher rates of agonism occurred between female primates that were living in larger groups (Wheeler, Scarry and Koenig, 2013; Klass and Cords, 2015; Cowl and Shultz, 2017). In addition to food resources, aggression may be related to the defence of a reproductive resource. For example, Schaffner and French, (1997) observed that the cooperative breeding primate, *Callithrix kuhlii*, were more tolerant of strangers when they lived in small groups. Intolerance increased where potential immigration of further helpers was both unnecessary and undesirable due to cost implications.

What has been termed ‘Folivore paradox’ raises the issue that group size of folivores is smaller than what would be expected based on the potentially lower feeding competition associated with this dietary type (Janson and Goldsmith, 1995; Steenbeek and van Schaik, 2001; Snaith and Chapman, 2005; Snaith and Chapman, 2007). It has been suggested that this could be connected to infanticide risk resulting in selection for smaller group sizes (Isbell, 1991; Janson and Goldsmith, 1995; Steenbeek and van Schaik, 2001). However, group size may be limited in folivores because rather than having low levels of intragroup aggression due to dispersed abundant foods, they prefer patches of high quality folivorous food and experience competition for these (Snaith and Chapman, 2005).

### *3.1.5 Territoriality – defendability index*

Like group size, home range size varies widely among primate species (Bates, 1970). Factors including population density, predators, food availability, substrate preference and topography are known to influence its extent (Mason, 1968; Bates, 1970). While core areas are usually subject to exclusive use (Jewell, 1966), home ranges frequently overlap with those of neighbouring groups (Bates, 1970). Encounters may therefore arise when groups use more space, having larger group sizes, or more overlapping areas (Hutchinson and Waser, 2007). These encounters could lead to increased inter-group aggression especially over

resource defence or acquisition (Cheney 1987). Thus, territoriality occurs when an animal defends its home range against conspecific encroachment and can be observed, as displays or physical altercations, in many animal species (Willems, Hellriegel and van Schaik, 2013). However, it is not a universal behaviour in primates (Bates, 1970).

Geographic areas can be maintained by behavioural mechanisms that partially function to reduce the risk of any physical altercations, such as scent marking (Hagen and Hammerstein, 2009; Roberts, 2012), vocalisations, long-distance calls, and dawn choruses (Brown, R. E. and Macdonald, 1985; Cowlshaw, 1992; Roberts, 2012; Bonadonna *et al.*, 2017; but see: Lledo-Ferrer, Peláez and Heymann, 2011). Species may also further try to reduce contact by crossing a territorial boundary when they know their neighbours will be in another part of the range and unaware of the intrusion (Isbell *et al.*, 2021). Consequently, they maximise the benefit of resource acquisition with minimal conflict.

When resources are scarce, seeking encounters despite being aware of the neighbours' position may occur (see: Van Belle and Estrada, 2020). The decision to engage in this potential conflict will more likely occur if the invading party has intergroup dominance. However, Bates (1970) noted that only in exceptional cases do groups progress beyond agonistic displays and threats to physical violence. The home range of the resident group may be defended by both sexes. Yet, the motivation behind these behaviours has been differently attributed. Males are considered to defend an area to increase their chances of access to mates, whereas females seek safety and resources (Trivers, 1972; Emlen and Oring, 1977; Kappeler and van Schaik, 2002). Females have higher cost implications in engaging in escalating fights as lethal violence may impact not only on the female but lead to the deaths of any dependant offspring (Jolly *et al.*, 2000). Though in certain species males may act to defend a female's concerns, such as resource defence, if reproductive output would be improved (Willems, Hellriegel and van Schaik, 2013).

Brown (1964) considered territoriality to evolve based on 'economic defendability'. To quantitatively determine this the defendability index ( $D$ ) was postulated by Mitani and Rodman (1979). They contended that defendability relies on the ability to detect possible intruders through observation of its boundaries and consequently calculated as the observed ratio of daily path length to an area equal to the diameter of a circle that encompass the same area as the home range. This  $D$ -index could subsequently be related to the level of territoriality of the assessed species, as many that are territorial have an index of 1.0 or



greater (Mitani and Rodman, 1979). However, while economic defendability can define territoriality it does not always indicate the effectiveness of territorial action. For example, the increasing number of males in a group can reduce effective range defence (van Schaik, 1996; Willems, Hellriegel and van Schaik, 2013). Furthermore, group defence cannot be monopolised and so some individuals may not face the potential costs of engaging in these behaviours yet will reap the benefits (Kitchen and Beehner, 2007). This free-riding behaviour can be observed in males and females depending on the sex of the dominant range defender and can be linked to increasing group size (Willems, Hellriegel and van Schaik, 2013).

### *3.1.6 Number of males within a group*

The typical number of males within a primate group varies across species and consequently results in several types of social system. These include a single male in a monogamous relationship or polygynous group, all male groups, and multi-male/multi-female groups, the latter of which may involve fission-fusion (Smuts *et al.*, 1987; Campbell *et al.*, 2011; Cowlshaw and Dunbar, 2021).

Richard (1992) identified that historically, the number of males within a social system has been linked to levels of male-male violence resulting from mate competition. Therefore, in monogamous systems male sexual competition will be low whereas in polygynous systems competition may be intense. Mate competition has been observed to play an important role in elevating levels of violence and testosterone in chimpanzees (Muller and Wrangham, 2004; Muehlenbein, Watts and Whitten, 2004). Furthermore, rank instability increases levels of violence as individuals seek to obtain alpha status with associated mating opportunities (see; Kaburu, Inoue and Newton-Fisher, 2013). Again, coalitions may be advantageous, potentially between philopatric males who can form strong bonds (Aureli *et al.*, 2006). This coalitionary behaviour would be higher in groups containing more males (Henzi, Weingrill and Barrett, 1999).

While an argument can be made that an increasing number of males will lead to increased violence, other factors may mitigate this behaviour. For example, the simple definition of polygyny actually contains a great deal of group diversity, furthermore, female choice can have a clear impact (e.g., Goodall, 1986; Small, 1989; Silverberg and Gray, 1992). The latter can be illustrated through the behaviours of bonobos, in contrast to chimpanzees, who do not show the same levels of violence as male-male competition may be less beneficial due to

female dominance and their key role in mate choice (Surbeck *et al.*, 2012). However, in this environment females may also be involved in aggressive interactions and engage in coalition formation (Surbeck *et al.*, 2017).

### 3.1.7 Dimorphism

In addition to elevated levels of violence, male social systems have been linked to size dimorphism. Darwin (1871) first noticed that polygynous mammals show a larger size dimorphism than monogamous mammalian species. This is due to differing selection pressures on males and females within a polygynous species (Clutton-Brock, 1985), and has been explored in several early primate studies (Kleiman, 1977; Clutton-Brock and Harvey, 1978; Leutenegger and Cheverud, 1985; Clutton-Brock, 1985). Dimorphism may also relate to weaponry, such as canine tooth size. Size dimorphism and the development of weaponry can be linked to violence levels in certain species. With a high degree of dimorphism, competition between males is frequent, furthermore the canines of both sexes are larger in species where violence often escalates (Plavcan and van Schaik, 1997).

Sexual selection is often considered the main driver of dimorphism (Cassini, 2020). However, other factors may include natural selection (Cheney and Wrangham, 1987; Demment, 1983; Milton, 1985a), phylogenetic inertia (Cheverud *et al.*, 1985, 1986), and non-selected allometric responses to evolutionary change in body size (Leutenegger and Cheverud, 1982, 1985). Though, the change in ratio may be due to a comparative reduction in female size as opposed to an increase in the male (Kappeler, 1990). In addition to mate competition within and between male social groupings, there is potentially a degree of interconnectedness between dimorphism and other socio-ecological variables. Arboreal species can show lower levels of aggression, and lower dimorphism than compared to terrestrial species (Plavcan and van Schaik, 1997). Frugivores, who engage in scramble and contest competition over clumped resources, are likely more dimorphic than folivores or insectivores, who have dispersed food sources (Plavcan and Van Schaik, 1997). However, this does not necessarily mean collinearity, with these variables becoming interchangeable. For example, it is highly unlikely that dimorphism and mating system can be used interchangeably for modelling violence, as size dimorphism does not offer unequivocal evidence of mating systems in some animals (Plavcan and Van Schaik, 1997).

### 3.1.8 Coalitions

Coalitions may be defined as a temporary alliance between at least two individuals to either carryout an aggressive combined action or, defend themselves, against a third party (Noë, 1992). Coalitions usually only involve a few individuals (Bissonnette *et al.*, 2015) and may operate against males and females of any age, except the very young (Noë, 1992). Alliances may also be created, which are long term associations involving repeated coalitions that provide mutual support between others in the coalition (Harcourt, 1992). Coalitions can be observed in several primate species including *Macaca*, *Papio* and *Pan sp.* (Smuts *et al.*, 1987; Kitchen, 2004; Olson, L. E. and Blumstein, 2009)

Coalitions are important in group living species in intra and intergroup competition (Bissonnette *et al.*, 2015). As alluded to earlier beneficial coalitionary associations can be formed for a range of reasons such as the ousting of an incumbent male/s and achieving a group take-over (Komorita and Kravitz, 1983; Noë, 1992; Harcourt, 1992; Pope, 2000; Wilson, M. L. *et al.*, 2014). Intergroup coalitions can be substantial (Bissonnette *et al.*, 2015), and the attacks may become lethal (reviewed by Wrangham, 1999). Through prolonged killing the opposing groups power is diminished, as larger groups are likely to be more successful in intergroup encounters than smaller ones (Majolo *et al.*, 2020) thereby reducing the costs of any future intergroup encounters (Wrangham, 2006) for the aggressors.

In addition to proactive attacks coalitions may have the purpose of a defensive action, such as group members forming a coalition to prevent the take-over attempt (Treves, 1998; Feh, 1999; Palombit, 2015) or defend a territorial boundary, with both males and females acting occasionally as coalitions (Kitchen and Beehner, 2007). Coalitionary support can also attempt to defend against infanticide (see: Hrdy, 1974; Struhsaker, 1977; Crockett, C. M. and Sekulic, 1984; Valderrama, Srikosamatara and Robinson, 1990). However, a review by Ebensperger (1998) identified that coalitions merely delay infanticide rather than prevent it.

It is likely that coalitions are important in all types of primate violence but particularly important in lethal forms where the costs of acting alone can be significantly higher.

## 3.2 Methods

### 3.2.1 Data collection

The dataset was expanded from the original one detailed in the previous chapter (section 2.2.1) to include further data on a range of socioecological factors including, but not limited to group size, territoriality, proportion of leaves in the diet, dimorphism, and social system.

The socioecological data were obtained through a systematic review conducted on the primatological literature published up to June 2020. Sources included; Google Scholar (<http://scholar.google.com>), ProQuest Dissertations & Theses Global, academic books and websites such as ‘All the World’s Primates’ (<https://alltheworldsprimates.org/>) (Rowe and Myers, 2016), and the Animal Diversity Web (<http://www.animaldiversity.org>). To narrow the search keywords were used that represented the ecological variable e.g., “group size”, “diet”. These keywords were applied in various combinations to specific species and taxonomic families in an effort to fully review the primate literature. Further, data were also obtained from part two of the distributed survey (see chapter 2.2.1 and appendix 2A for survey details). Where possible, data for these factors were taken from the same population, and the *A priori* data exclusion criteria established and outlined in the previous chapter were retained.

### 3.2.2 Factor analysis of mixed data (FAMD)

The expanded data set provided numerous predictors that could be employed in the model. However, too many predictors can introduce both redundancy and noise into the data increasing the variance in the model. Consequently, as part of an exploration of the data, an attempt was made to reduce the number of predictor variables and create the most parsimonious model by checking for any multicollinearity. The dataset contained both categorical and quantitative data, so a Factor analysis of mixed data (FAMD) was carried out which is a method based on principle component analysis that is designed to analyse continuous and categorical data (Pagès, 2014).

### 3.2.3 Data assignment (variables)

The full results of the FAMD are given in Appendix 3A, but in summary revealed no collinearity between variables. Consequently, the predictor variables selected for use in the

model were based on a review of the literature and specifically those found to be significant for one or more forms of violence in previous comparative studies (see section 3.1). This resulted in the selection of the eight variables. The eight variables and the specific definition applied to each variable are provided in Table 3.3.

*Table 3.3: Model predictor variables with definition and data type.*

Model variables	Definition	Data type
Number of Males	The average number of males present in the group was recorded as either single or multiple.	Categorical – sM / mM
Seasonal Breeding <sup>a</sup>	<i>Seasonal breeding species</i> – Breeding within a defined period, either single or double peak birth period, with no births for the rest of the year.	Categorical – Yes/No
Proportion of leaves in the diet	By using quantitative values to a specific food type rather than general labels a better understanding of the majority diet type can be appreciated. Consequently, the metric utilised the number of leaves consumed by the species, expressed as a percentage of the total diet.	Continuous – where 1.0 equals 100%
Defendability Index (D-Index) <sup>b</sup>	Calculated using – Defendability index = $d/(4A/\pi)^{0.5}$ where $d$ = the average daily journey/path length (km) and $(4A/\pi)^{0.5}$ = the diameter of a circle with a surface area $A$ (km <sup>2</sup> ) equal to that of the home range.	Continuous
Group Size <sup>c</sup>	Group is considered to apply to stable social groups. Defined as primates that share a ranging area and maintain a degree of compositional stability across a sustained period. This does not include foraging group size (subset that forage together) or reproductive group (subset that form a reproductive unit e.g., harem). When data has been taken from a number of groups within a study then the mean group size is reported.	Count
Substrate	The substrate is considered the primary environment in which the species lives. This was defined as arboreal or terrestrial. Where species demonstrated semi-terrestrial/arboreal tendencies these were categorised as terrestrial.	Categorical – Terrestrial / Arboreal
Dimorphism	Sexual dimorphism indicating the differences in body size (kg) between males and females. Calculated as a ratio of M/F.	Continuous – Ratio
Coalitions	A temporary alliance between male/female or mixed members to carry out a combined action.	Categorical Yes/No

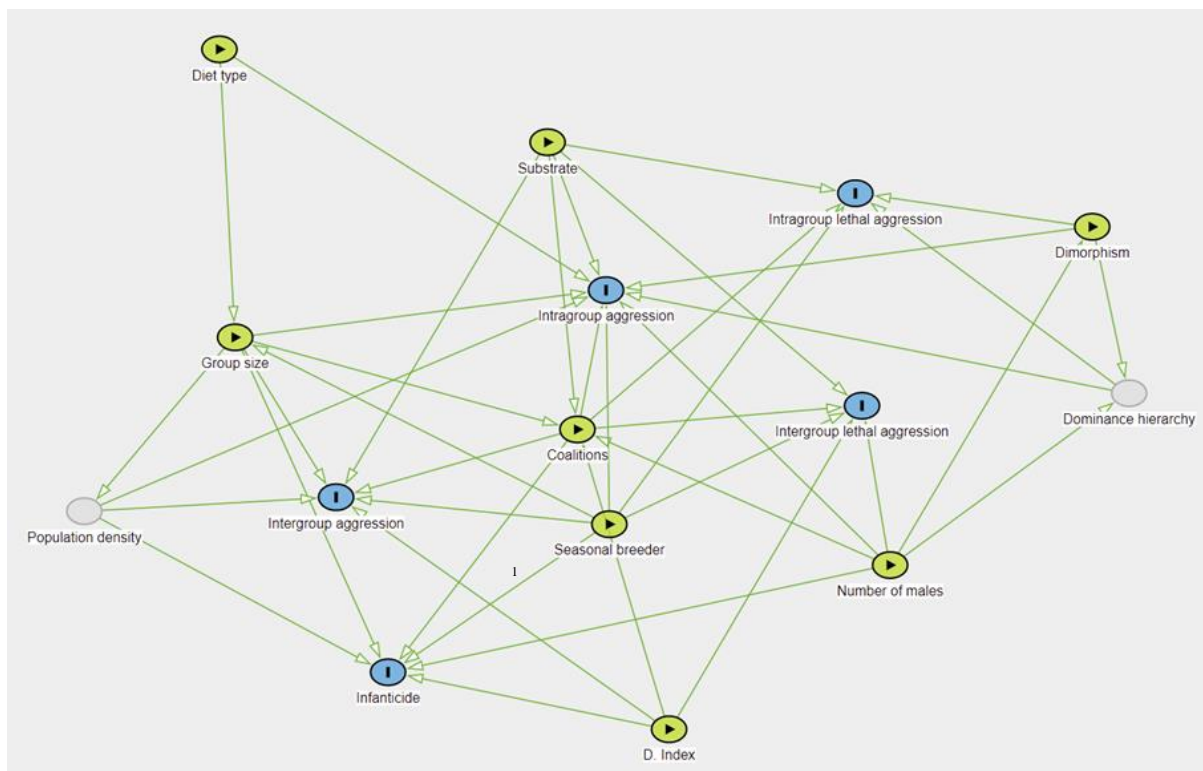
a Adapted from Heldstab *et al.*, (2018): Non-seasonal breeders based on category 1&2 / Seasonal breeders based on categories 3-5.

b In order to quantitatively determine the territoriality of a species the D-index model postulated by Mitani and Rodman (1979) was used.

c Definition of group size adapted from Dunbar, RIM, Mac Carron and Shultz (2018).

### 3.2.4 Hypothesis testing

Hypotheses were generated based on a review of the literature and by placing the main variables and their potential directed effects into a causal graph produced using DAGitty Version 3.0 (Textor *et al.*, 2016) (Figure 3.1). Causal graphs visually represent causal assumptions and can assist in determining testable hypotheses and guide the building of the model. There can be great difficulty in identifying the directionality of causal relationships which can impact on results (Terborgh and Janson, 1986; Shultz and Dunbar, 2022) however the main pathways identified in the literature were incorporated into the graph. The resultant causal graph indicated no biasing paths based on the given causal pathways, and so no adjustment was necessary to estimate the total effect. As a result, models were developed to test eight main hypotheses with associated sub-hypotheses pertinent to each violence type (Table 3.4). Furthermore, as the multivariate ‘all’ model tested all variables against all violence types, results beyond the tested hypotheses were also obtained.



\*Green nodes indicate measured predictor variables, blue nodes measured outcome variables and grey nodes are unmeasured variables not included in the modelling.

<sup>1</sup> Infanticide observed in an increasing number of seasonal breeding species but dependent on a range of factors (see section 3.1.3).

*Figure 3.2: Directed Acyclic Graph (DAG) of socio-ecological variables researched. The assumed direction of the effect is indicated by the arrowhead.*

*Table 3.4: The eight hypotheses tested and associated sub-hypotheses*

Code	Description
<b>H1 – Degree of folivory</b>	
H1 <sub>a</sub>	Due to the dispersed, potentially low nutritional value, and generally abundant nature of leaves as a food source the degree of folivory exhibited is anticipated to negatively affect intragroup aggression.
<b>H2 – Group size</b>	
H2 <sub>a</sub>	As intragroup competition intensity over food and reproductive resources may increase as group size grows. Consequently, it is anticipated group size will positively affect rates of intragroup aggression.
H2 <sub>b</sub>	As group sizes grow, ranges increase, leading to more intergroup encounters which may lead to resource competition. Therefore, group size is anticipated to positively affect rates of intergroup aggression.
H2 <sub>c</sub>	Following that group size may be limited to reduce infanticide risk and, the risk of infanticide by group living females could provide a more persistent threat than other forms, it is expected that group size will positively affect infanticide rate.
<b>H3 – Number of males</b>	
	Following that the number of males within a social system has been linked to levels of male-male aggression resulting from mate competition, it is anticipated that...
H3 <sub>a</sub>	...the number of males in the group e.g., multimale or single males, is expected to positively affect intragroup aggression.
H3 <sub>b</sub>	...the number of males in the group is expected to positively affect intergroup adulticide.
H3 <sub>c</sub>	After take-over as reproductive success may be improved through the selective killing of infants, it is expected that the number of males in the group will negatively affect levels of infanticide.
<b>H4 – Territoriality (D-Index)</b>	
	Territoriality is considered connected to resource acquisition with differing motives attributed to males and females. Consequently...
H4 <sub>a</sub>	...D-Index is anticipated to positively affect intergroup aggression.
H4 <sub>b</sub>	...D-Index is anticipated to positively affect Intergroup adulticide.
H4 <sub>c</sub>	...D-Index is anticipated to positively affect levels of infanticide.

**H5 – Seasonal breeder**

A seasonal breeder may obtain substantial benefits through the killing a rival male and taking their breeding status. However, both non-seasonal breeders and seasonal breeders, with an IBI longer than the breeding season, may benefit from infanticide. Therefore, it is anticipated that...

- H5<sub>a</sub> ...seasonal breeding will not affect levels of infanticide.
- H5<sub>b</sub> ...seasonal breeding will positively affect intragroup adulticide.
- H5<sub>c</sub> ...seasonal breeding will positively affect intergroup adulticide.

**H6 – Substrate**

Due to spatial limitations, the restrictions on coalition formation, the increased challenge in delivering simultaneous attacks, and the inherent cost of accidental injury by being in an aerial environment it anticipated that aggressive behaviour would favour a terrestrial environment. Consequently...

- H6<sub>a</sub> ...substrate (terrestrial) is anticipated to positively affect intragroup aggression.
- H6<sub>b</sub> ...substrate (terrestrial) is anticipated to positively affect intergroup aggression.

**H7 – Dimorphism**

When there is a high degree of dimorphism competition between males is frequent....

- H7<sub>a</sub> ...sexual dimorphism (body size) is anticipated to positively affect intragroup aggression.
- H7<sub>b</sub> ...sexual dimorphism (body size) is anticipated to positively affect intragroup adulticide.

**H8 – Coalition**

Coalitions are important in group living species in intra and intergroup aggression (including lethal) for a range of reasons such as, the ousting of an incumbent male/s and achieving a group take-over or as part of a defensive action. Consequently...

- H8<sub>a</sub> ...the formation of a coalition is expected to positively affect intragroup aggression.
  - H8<sub>b</sub> ...the formation of a coalition is expected to positively affect intergroup aggression.
  - H8<sub>c</sub> ...the formation of a coalition is expected to positively affect intragroup adulticide.
  - H8<sub>d</sub> ...the formation of a coalition is expected to positively affect intergroup adulticide.
  - H8<sub>e</sub> ...the formation of a coalition is expected to positively affect levels of infanticide.
-



### 3.2.5 Tree construction

The previous tree created for the first analysis (section 2.2.4) was utilised in this analysis. However, three species were removed from the tree (R code utilised - Appendix 3B) as data were not obtainable for each variable for these species. This resulted in a sample size of 101 species and subspecies.

### 3.2.6 Statistical analysis and model construction

As per the previous chapter, analysis on the selected dataset was carried out using Bayesian multivariate modelling utilising the Stan probabilistic programming language (Carpenter *et al.*, 2017) and the high-level interface ‘brms’ package version 2.14.0 (Bürkner, 2017) in R version 4.0.2 (R Core Team, 2020). Three multivariate models were developed (Figure 3.3). The ‘Basic’ model with no predictor variables to confirm the phylogenetic signal strength; The ‘All’ model where all eight predictor variables (number of males, diet, seasonal breeder, D.index, group size, substrate, dimorphism, and coalitions) were applied to all five violence outcome variables in an attempt to improve the explanation of the variance in the aggression data. Finally, the ‘Specific’ model in which five different key predictor variables from the literature were applied to each outcome variable (Figure 3.3). The ‘All model’ used the Forced-entry method, where all predictor variables are ‘forced’ into the model in one step. This method is not suitable for a large number of predictor variables (Kucuk *et al.*, 2016) but appropriate for the eight utilised in this study.

Distribution families were set for the outcome variables as per section 2.2.7. Weakly informative priors were applied to improve convergence and the models set to run for four chains, each with 4000 iterations (2000 warmup, resulting in 8000 posterior samples). The R-hat convergence diagnostic was reviewed on the output and found to be  $\leq 1.01$  indicating the chains had well mixed (Bürkner, 2017). Additionally, plots were also checked to ensure the chains had merged (Appendices 3D-F).

Once run, calculation of  $R^2_{\text{Adjusted}}$  was carried out which adjusts for the number of predictor variables in a model based on their predictive use to the model. This can control for overfitting of the model and subsequently misleadingly high  $R^2$  values. Then model comparison of the three fitted models was undertaken to estimate the difference in predictive accuracy by determining the difference in elpd\_loo (Bayesian leave one out cross validation),

in which pairwise comparisons are computed between the models (Vehtari, Gelman and Gabry, 2017).



\* Predictor variables indicated in blue text. Variables are given in full – complete script in Appendix 3C.

Figure 3.3: The three multivariate models used in the analysis – ‘Basic’, ‘All’ and ‘Specific’.

### 3.3 Results

#### 3.3.1 Descriptive results

101 species and sub-species were analysed. Descriptive results for the violence data followed those stated in section 2.3.1. Descriptive results for the eight predictor variables are as follows (Table 3.5).

*Table 3.5: Descriptive statistics for the eight predictor variables explored independently and in combination.*

Variable <sup>a</sup>	Lone statistics	Combined statistics
Substrate	74.26% of species were arboreal.	<i>Arboreal species</i> : 66.67% territorial; dimorphism 1.19 (mean); 28% leaves (mean); 46.67% form coalitions. <i>Terrestrial species</i> : 53.85% territorial; dimorphism 1.56 (mean); diet 22% leaves (mean); 76.92% form coalitions.
Group size	Group size ranged from 1.4 to 69.33 Mean group size is 20.54 (mode = 6)	<i>Group size &lt; mean</i> : 70.49% territorial; consume between 0-92% (mean 28%) of leaves and 46% were seasonal breeders. <i>Group size &gt; mean</i> : 52.5% territorial; consume between 0-94% (mean 25%) of leaves and 42.5% were seasonal breeders.
Territoriality	63.37% of were territorial.	<i>Territorial species</i> : 50% are seasonal breeders; mean group size was 17.98 (range 1.4 - 69). <i>Non-territorial</i> : 35% are seasonal breeders; mean group size 24.97 (range 2–64.5).
Number of males in the group	35.64% of species lived in single male groups.	<i>Multi male groups</i> : 58.46% were territorial; group size range in multi-male groups was 4.2–69.3. <i>Single-male groups</i> : 72.22% were territorial; group size range in single-male groups 1.4–45.
Seasonal breeders	44.55% of species were seasonal breeders.	<i>Seasonal breeders</i> : Consumed between 0-92% of leaves in their diet; 44.44% were in single-male groups; 71.11% were territorial; group size ranged from 6 to 64.5 (mean 18.07).
Diet - Proportion of leaves	Leaf consumed ranged 0-95%; 12.87% of species consumed $\leq 1\%$ ; 22.77% consumed $>50\%$ .	$\leq 1\%$ proportion of leaves in diet: Only one species ( <i>Phaner furcifer</i> ) lived in multi-male groups and were purely arboreal; $>50\%$ proportion of leaves in the diet: 43.48% single-male groups; 91.30% arboreal; 65.22% were non-territorial; however, all eight species that consumed $\geq 90\%$ of leaves were territorial.
Dimorphism <sup>b</sup>	0.84 – 2.38 (range); 1.29 (mean)	$\leq 1.2$ : 66.04% territorial; 54.71% live in multi-male groups. $> 1.2$ : 60.41% territorial; 75% live in multi-male groups.
Coalitions	54.46% form coalitions.	<i>Coalitions (yes)</i> : GS 4.25-69.33 (mean 29.89); 56.36% territorial. <i>Coalitions (no)</i> : GS 1.4-41.5 (mean 9.36); 71.74% territorial

a For variable definitions, including measure of territoriality, see section 3.2.3

b Body size (kg) calculated as a ratio of M/F.

### 3.3.2 Effects

Coalition formation was a positive predictor of intragroup adulticide (6.87; 95% CI = 1.06 - 14.26) and intergroup adulticide (5.80; 95% CI = 0.64 - 12.78). Likewise, D-Index was a positive predictor of intergroup aggression (0.40; 95% CI = 0.13 - 0.69). The proportion of leaves in the diet was a negative predictor of intragroup aggression rates (-2.32; 95% CI = -4.34 - -0.30). However, the wide credible intervals (CI) indicate a level of uncertainty. Group size was potentially a marginal negative predictor of intragroup aggression (-0.04; 95% CI = -0.07 - 0.00) but the result is not statistically 'significant' in the frequentist sense as zero is included in the CI. The brms package offers a 'hypothesis' function which computes an evidence ratio, which for a one-sided hypothesis is the posterior probability of the hypothesis against its alternative (Bürkner, 2017). Hypothesis testing conducted on the group size/intragroup aggression interaction produced a CI clear of zero (-0.04; 95% CI = -0.06 - -0.01) but with a small evidence ratio of 58.57 (appendix H). Hypothesis function requires 95% of the posterior values to fall within the credible interval, though Bürkner *et al.*, (2022) strongly argue that arbitrary cut-offs (e.g.,  $p < .05$ ) should not be applied to establish the presence of an effect. Consequently, based on the results ('specific' model) there is acceptance of four of the previously stated hypotheses (Table 3.6).

Coefficients for each predictor variable estimated for each of the five responses, across the three models are given in appendix 3d-f.

Table 3.6: Acceptance of the following hypothesis

Hypothesis	Supported
<b>H1 – Degree of folivory</b>	
<i>H1<sub>a</sub> Due to the dispersed, potentially low nutritional value, and generally abundant nature of leaves as a food source the degree of folivory exhibited is anticipated to negatively affect intragroup aggression.</i>	<i>Yes</i>
<b>H2 – Group size</b>	
<i>H2<sub>a</sub> As intragroup competition intensity over food and reproductive resources may increase as group size grows. Consequently, it is anticipated group size will positively effect rates of agonistic intragroup interactions.</i>	<i>No<sup>b</sup></i>
H2 <sub>b</sub> As group sizes grow, ranges increase, leading to more intergroup encounters which may lead to resource competition. Therefore, group size is anticipated to positively effect rates of agonistic intergroup interactions.	No
H2 <sub>c</sub> Following that group size may be limited to reduce infanticide risk and, the risk of infanticide by group living females could provide a more persistent threat than other forms, it is expected that group size will positively effect infanticide rate.	No
<b>H3 – Number of males</b>	
H3 <sub>a</sub> The number of males in the group e.g., multimale or single males, is expected to positively effect intragroup aggression.	No
H3 <sub>b</sub> The number of males in the group is expected to positively effect intergroup adulticide.	No
H3 <sub>c</sub> The number of males in the group will negatively effect levels of infanticide.	No
<b>H4 – Territoriality (D-Index)</b>	
<i>H4<sub>a</sub> D-Index is anticipated to positively effect intergroup aggression.</i>	<i>Yes</i>
H4 <sub>b</sub> D-Index is anticipated to positively effect Intergroup adulticide.	No

**H5 – Seasonal breeder**

H5 <sub>a</sub>	Seasonal breeding will not affect levels of infanticide.	Yes
H5 <sub>b</sub>	Seasonal breeding will positively affect Intragroup adulticide.	No
H5 <sub>c</sub>	Seasonal breeding will positively affect Intergroup adulticide.	No

**H6 – Substrate**

H6 <sub>a</sub>	Substrate (terrestrial) is anticipated to positively effect intragroup aggression.	No
H6 <sub>b</sub>	Substrate (terrestrial) is anticipated to positively effect intergroup aggression.	No

**H7 – Dimorphism**

H7 <sub>a</sub>	Sexual dimorphism (body size) is anticipated to positively effect intragroup aggression.	No
H7 <sub>b</sub>	Sexual dimorphism (body size) is anticipated to positively effect Intragroup adulticide.	No

**H8 – Coalition**

H8 <sub>a</sub>	The formation of a coalition is expected to positively effect intragroup aggression.	No
H8 <sub>b</sub>	The formation of a coalition is expected to positively effect intergroup aggression.	No
<b>H8<sub>c</sub></b>	<b><i>The formation of a coalition is expected to positively effect Intragroup adulticide.</i></b>	<b><i>Yes</i></b>
<b>H8<sub>d</sub></b>	<b><i>The formation of a coalition is expected to positively effect Intergroup adulticide.</i></b>	<b><i>Yes</i></b>
H8 <sub>e</sub>	The formation of a coalition is expected to positively effect levels of infanticide.	No

- 
- a Statistically ‘significant’ results are shown in bold and italics  
b A positive effect was not observed however a negative effect was identified.

### 3.3.3 Overall model impact

The ‘Basic’ model reaffirmed the strength of the phylogenetic signal ( $R^2$ ) identified in chapter two for all five individual aggression outcome variables (Table 3.7). These findings were considered against the second ‘All’ model where the  $R^2$  values indicated the strength of the phylogenetic signal plus the effect of the eight socio-ecological predictor variables. The  $R^2$  values increased for all aggression variables but specifically for the lethal aggression types e.g., infanticide increased from 25.7% to 85.4%. Finally, the third model (‘Specific’) contained a combination of unique predictor variables for each outcome aggression variable. Again, there was an increased in the amount of variance in the aggression data that was explained by the model, but the improvement was slightly smaller than that delivered by the ‘All’ model (Table 3.7). Statistical comparison of the three models indicated that the ‘All’ model was indeed the most successful at explaining the variance in the data for each aggression type (Table 3.7).

As the number of variables included in a model can impact on the  $R^2$  value,  $R^2_{\text{adjusted}}$  was calculated for each model and each violence type. Again, overall, the ‘All’ model provided the best fit. However intragroup aggression was a very poorly fitting model as indicated by the negative  $R^2$  value where the model utilised did not follow the trends in the data. Infanticide continued to provide a much-improved model fit as did intra and intergroup adulticide.

Table 3.7:  $R^2$  and  $R^2_{adj}{}^a$  values for the five violence types across the three tested models.

Model	Agg. Variable	Estimate	Est. Error	Q2.5	Q97.5
BASIC MODEL	Intergroup Aggression	0.022 (0.007)	0.023 (0.019)	4.75E-05 (-0.037)	0.084 (0.038)
	Intragroup Aggression	0.255 (0.046)	0.138 (0.090)	5.37E-02 (-0.166)	0.547 (0.178)
	Intragroup adulticide	0.592 (0.231)	0.187 (0.114)	2.30E-01 (-0.024)	0.936 (0.421)
	Intergroup adulticide	0.472 (0.215)	0.173 (0.098)	1.88E-01 (0.014)	0.874 (0.393)
	Infanticide	0.257 (0.080)	0.113 (0.063)	5.79E-02 (-0.049)	0.506 (0.196)
ALL VARIABLES (8 each)	Intergroup Aggression	0.096 (0.071)	0.030 (0.042)	0.042 (-0.011)	0.161 (0.154)
	Intragroup Aggression	0.473 (-1.000)	0.084 (0.000)	0.255 (-1.000)	0.612 (-1.000)
	Intragroup adulticide	0.811 (0.360)	0.118 (0.107)	0.539 (0.118)	0.988 (0.539)
	Intergroup adulticide	0.814 (0.360)	0.115 (0.101)	0.551 (0.130)	0.989 (0.534)
	Infanticide	0.854 (0.502)	0.078 (0.064)	0.679 (0.365)	0.977 (0.612)
SPECIFIC VARIABLES (5 each)	Intergroup Aggression	0.083 (0.079)	0.029 (0.039)	0.034 (0.004)	0.147 (0.156)
	Intragroup Aggression	0.419 (-0.912)	0.108 (0.197)	0.179 (-1.000)	0.598 (-0.286)
	Intragroup adulticide	0.712 (0.204)	0.157 (0.115)	0.340 (-0.051)	0.949 (0.398)
	Intergroup adulticide	0.679 (0.231)	0.166 (0.108)	0.298 (0.000)	0.939 (0.420)
	Infanticide	0.787 (0.346)	0.137 (0.073)	0.364 (0.191)	0.956 (0.477)
<b>Model comparison:</b>					
	elpd_diff <sup>b</sup>	se_diff			
All	0.0	0.0			
Specific	-22.1	3.8			
Basic	-47.5	5.8			

a  $R^2_{adj}$  values are given in brackets.

b The model with the largest elpd is given in the first row.



### 3.4 Discussion

This chapter identified that the model containing all eight socio-ecological variables gave a better explanation of the five types of violence than the ‘specific’ and ‘basic’ models.

Overall, four of the predicted effects, were confirmed by the analyses. These were that the degree of folivory negatively affects intragroup aggression, the D-index positively affects intergroup aggression, and coalition formation positively affects intragroup and intergroup adulticide. However, there were several results that did not appear to reflect current theories (see: Table 3.5 - hypotheses).

#### 3.4.1 The effect of the degree of folivory

The results revealed that the degree of folivory had a negative effect on intragroup aggression levels. This reinforces the earlier work by Isbell (1991) who identified that food types, such as leaves, are usually evenly distributed and generally abundant, and as such cannot be monopolised and contested. Whilst there does remain a degree of within-group scramble (WGS) aggression (Isbell, 1991; Kappeler and van Schaik, 2002), the costs of aggressive behaviour outweigh the benefits of this generally widely available food type, thus intragroup aggression is limited in folivore species. Some folivorous species (e.g., red colobus monkeys) have been observed to consume limited foods, such as young leaves, that occur in patches and so engage in higher levels of within-group scramble competition (Snaith and Chapman, 2005). However, this increased aggression is not observed in all folivorous species (Snaith and Chapman, 2007) as variation in quality and availability depends on several factors such as seasonality, size of the area, amount of disturbance and degree of deciduousness (Chapman and Chapman, 2000; Struhsaker, 2000; Struhsaker *et al.*, 2004). Furthermore, consumption of high-quality food is only necessary when food sources in the habitat have below average protein concentrations for the species needs (Ganzhorn *et al.*, 2017).

The ‘all’ model, which considered the effects of all identified socioecological variables on all five violence types, found that the remaining four types (intergroup aggression, inter and intragroup adulticide and infanticide) were not similarly lowered by the degree of folivory. For example, *Theropithecus gelada*, *Hapalemur griseus*, and *Lepilemur ruficaudatus* have the expected high degree of folivory combined with low intragroup aggression, yet *T. gelada* also displays all three lethal aggression types with low/med intergroup aggression. Whereas *H. griseus* and *L. ruficaudatus* do not carry out lethal violence but differ between each other

in their levels of intergroup aggression. These differences in violence profiles between species provides further evidence that each violence type is distinct and not a generalised aggressive or non-aggressive profile.

In the future, as a consequence of climate change, availability and quality of food items may diminish due to poor growing conditions; furthermore, leaves may become a substitute food for many frugivores increasing competition between species (Marshall and Wrangham, 2007). Currently there is a lack of research in relation to primates and the effects of climate change (Bernard and Marshall, 2020). Thus, as food quality and availability reduce, violence levels may increase in species not currently considered aggressive.

#### 3.4.2 D-index – the effect of territoriality

Territorial species engage in intergroup aggression over valuable resources (Lemoine *et al.*, 2020). The analysis strongly confirmed that intergroup aggression was positively affected by levels of territoriality, as measured by the D-index. Consequently, the increasingly territorial the species, the higher levels of intergroup aggression could be expected as the animal defends its home range against conspecific encroachment.

However, there were some species who did not show the identified effect of D-index on intergroup aggression such as, *Propithecus verreauxi*, *Propithecus diadema* and *Hapalemur griseus* which have a high D-index but low levels of intergroup aggression. Due to their relatively close taxonomic relationship, there are similarities between these Madagascan species. They are arboreal, folivorous, and engage in scent marking behaviours. For an area to be truly economically defendable requires a degree of assessment of the cost and benefits around any aggressive action (Dyson-Hudson and Smith, 1978), and these arboreal species engage in scent marking to avoid aggressive interactions. Should intergroup contact occur these species are only rarely aggressive (Mittermeier, Wilson and Rylands, 2013). However, this does not appear to reflect interactions in all scent marking species. For example, the primarily terrestrial species *Lemur catta* are territorial and scent mark to avoid intergroup interactions yet when encountering another group will demonstrate aggressive behaviour on the majority of occasions (Sauter and Sussman, 1993). Differences between species may be due to specific socioecological factors. For example, the role of substrate may be important in determining the alternative strategies used during intergroup encounters. The arboreal environment has risks of operating at height (Bissonnette *et al.*, 2015) which may make

intergroup interactions more costly. Furthermore, social structure and group sizes can affect territorial defence (van Schaik, 1996; Willems, Hellriegel and van Schaik, 2013), as well as dietary type. Resource availability may be driving more intergroup aggression in *L. catta* as the dataset indicated they consume a more seasonal and contestable food type than the forementioned species.

The effect of D-index on intergroup aggression did not extend to lethal violence. Lethal aggression is rare, as Bates (1970) noted only in exceptional cases do groups move from agonistic displays and threats to physical aggression. Dataset interrogation revealed that some species with the highest D-index did not engage in any type of lethal violence e.g., *Phaner furcifer*, *Lepilemur ruficaudatus*, *Chiropotes albinasus*, *Chlorocebus tantalus*. It is possible that this behaviour is present but has not yet been recorded in the wild. Furthermore, some species categorised as non-territorial were seemingly extremely aggressive engaging in all three types of lethal violence (e.g., *Macaca mulatta* and *Papio ursinus*). *P. ursinus* tend to avoid other groups but have extensively overlapping ranges (Wrangham, 1980). Avoidance is based on the dominance relationships between the groups that can be established through the fighting ability of the males (Wrangham, 1980) with these interactions occasionally becoming lethal. Furthermore, *P. ursinus* are also known to form coalitions (Smuts *et al.*, 1987) in contrast to the territorial species mentioned above that do not engage in lethal violence.

### 3.4.3 The effect of coalition formation

In group living species coalitions are important in intra and intergroup competition (Bissonnette *et al.*, 2015) with the attacks even becoming lethal (Wrangham, 1999). While previously connections have been made between coalitions and lethal violence (Macfarlan *et al.*, 2014) this study's analysis is believed to be the first to identify an effect of coalitions specifically on intragroup and intergroup adulticide while controlling for phylogeny. Species that displayed coalition formation and adulticide include *Ateles geoffroyi* (see: Campbell, 2006), *Gorilla beringei* (see: Rosenbaum, Vecellio and Stoinski, 2016), *Pan troglodytes schweinfurthii* (see: Watts, 2004), *Pan troglodytes verus* (see: Boesch *et al.*, 2008) and undoubtably *Homo sapiens*. Operating as a coalition reduces individual risk (Henzi, Weingrill and Barrett, 1999), and through prolonged killing diminishes the opposing groups strength (Wrangham, 2006). The reduced costs through the 'imbalance of power' between the

coalitionary attack and the victim supports selection for the trait of coalition formation in adulticide.

During a coalitionary lethal take-over infanticide may occur (Fedigan, Carnegie and Jack, 2008). However, the results of this study did not support the role of coalitions in infanticide, and this is not surprising as both the act of infanticide and the role of coalitions is multifaceted. For example, the coalition formation may be for attack, defence, or as part of a retaliatory effort. Consequently, rather than coalitions resulting in infanticide the causal direction may be reversed if infanticide leads to successful defensive or retaliatory coalitionary behaviour against the infanticidal individual (e.g., Starin, 1994). Further, while coalitions play a role in a few infanticidal attacks many are committed by both intra and intergroup members, of either sex, acting alone. Females appear to be strong drivers of infanticidal behaviour from intragroup individuals, whereas males often perform intergroup infanticide. Overall, there is unlikely to be significant evolutionary advantage to carrying out infanticide as a coalition. Following the sexual selection hypothesis which has been proposed for infanticide (Hrды, 1974; Hrды, 1979; van Schaik, 2000), it would be beneficial for a male to kill an unrelated infant to gain reproductive access to the females (Digby, 2000). Coalitions may reduce an individual's chance of mating with the infant's mother as several males may be vying for the opportunity. Furthermore, the infant could be easily killed even when defended by females from within the group as female intragroup coalitions are rarely effective against the infanticidal male (Palombit, 2012).

Levels of inter and intragroup aggression were also anticipated to be affected by coalition formation. However, this behaviour is perhaps linked to the economics (cost/benefit assessment) of engaging in aggressive acts. Lethal aggression can be costly which may be mitigated somewhat by conspecific support whereas non-lethal aggression is potentially not as risky as it can occur without physical interaction. Furthermore, there are differences in emotional arousal between lethal and non-lethal aggression types which may incorporate reactive and proactive aggression as defined by Wrangham (2018). Coalitionary attacks are largely proactive violence types, certainly in humans and chimpanzees (Martinez Inigo, 2018), whereas inter and intragroup aggression are predominantly reactive. For example, Wrangham (2018) describes how when a fight steadily escalates between two individuals over mates or food the aggression will usually be reactive. With reactive aggression there is not the time to form a coalition and therefore this combined with the lower costs associated

with non-lethal aggression may in part explain the lack of significance of coalition formation on non-lethal aggression types.

#### 3.4.4 *The effect of group size*

Contrary to the predicted effect, the results indicated that group size may negatively affects rates of agonistic intragroup aggression. This result conflicts with earlier studies (e.g., Wheeler, Scarry and Koenig, 2013; Klass and Cords, 2015; Cowl and Shultz, 2017 - but see dyadic rates). Additionally, group size was not found to statistically affect the other tested violence types.

Female-female interactions are interesting as the role of females within the group may fundamentally impact on general levels of aggression in some species, as females seek to defend resources and ensure safety (Trivers, 1972; Emlen and Oring, 1977; Kappeler and van Schaik, 2002). Depending on dietary type (i.e., frugivores clumped resources versus folivores potentially dispersed resources), food competition will occur to a greater or lesser extent both within and between social groups. In the study by Cowl and Shultz (2017) focal sampling of an individual revealed increased rates of F-F agonistic behaviours as group size grows, however, dyadic agonism reduced as group size increased. Cowl and Shultz (2017) suggest that either aggression is buffered between individuals in larger groups or large groups can only be sustained if there are low levels of dyadic conflict. Potentially this study's larger dataset has identified this dyadic reduction but through its potential effect on lowering the overall group level of aggression.

Based on previous work (e.g., Schaffner and French, 1997; Willems and van Schaik, 2015) it was anticipated that intergroup aggression would be positively affected by group size. Primarily due to home-range size increasing as group size grows and food resources become limited (Isbell, 1991), thus leading to more extensive overlapping ranges (Willems, Hellriegel and van Schaik, 2013; Willems and van Schaik, 2015) thereby increasing the risk of intergroup encounters. However, no significant relationship between group size and levels of intergroup aggression was found. Likewise, Majolo *et al.*, (2020) also identified no significant association between the tendency to engage in aggressive intergroup encounters and group size.

Majolo *et al.*, (2020) identified that relative group size was a predictor of a successful intergroup encounter in some species. The group must make a cost/benefit assessment at

some level prior to engagement yet apparent group size may be deceptive. As discussed, the effectiveness of this territorial action can vary as the intensity of intergroup competition is affected by the existence of territorial collective action problems (CAPs), with the risk of free riding increasing with group size in certain species (Willems and van Schaik, 2015). Larger groups are consequently not always functionally larger than apparent smaller groups (Majolo *et al.*, 2020). What is important is the effective group size ratio between the groups, that is the number of group members who take an active aggressive role in the between-group confrontation. Analysis of this ratio may demonstrate a more consistent effect on intergroup aggression rather than an analysis with purely group size.

Furthermore, increasing group size is deemed to expand home range size and thus the degree of intergroup encounters and possible aggression. However, Terborgh and Janson (1986) questioned the direction of the causal relationship between group size and home range whereby group size may in fact be influenced by resource size/home range. In this instance potentially high levels of intergroup aggression are determining home range size which then limits group size because of intragroup scramble costs (Snaith, 2008). However, both effect directions (i.e., home range limiting group size or group size driving home range expansion) may be true depending on the overall population/geographic conditions. The causal relationship switching directionality at a certain ecological point e.g., the group expands which drives expansion of the home range, however when overlap and aggressive intergroup encounters increase, and expansion is no longer possible the group size may need to be reduced. This perhaps reinforces the suggestion by Gómez, Verdú and González-Megías (2021) that the impact of resource competition on group size to be occurring at a population/geographic level rather than at a species level. Certainly, group size varies both between and within primate species (Campbell *et al.*, 2011) which may be due to the local ecological conditions and subsequently the cost-benefit assessment made by the animals to obtain optimal size for their specific requirements (Dunbar, 1996; Dunbar, Mac Carron and Shultz, 2018), but also by the individual groups' demographic history (Cowl and Shultz, 2017). This intraspecies variation may make comparison between groups and species problematic (Snaith, 2008).

This study did not identify a relationship between group size and lethal violence. Despite differences in group size definitions this result mirrored the findings of Gómez, Verdú and González-Megías (2021) where they identified that male and female adulticide was not connected to group size. Furthermore, Gómez, Verdú and González-Megías (2021) identified

that infanticide occurs in both group living and solitary species. While this study only considered social primates the presence of infanticide in group living and solitary species may in part explain why this study did not identify an effect of group size on infanticide. It was nevertheless an unexpected result as the ‘Folivore paradox’ suggests that the group size of folivores is smaller than would be anticipated based on lower feeding competition associated with this dietary type, and it has been suggested that could be related to the risk of infanticide (Steenbeek and van Schaik, 2001). Given the important role of females in infanticide and intragroup feeding competition, had this dataset separated male/female or intra/intergroup infanticide a significant effect of group size may have been identified. This would illuminate sex specific evolutionary pathways. For example, Lukas and Huchard (2014) found that while infanticide by males did not lead to transitions in mammalian social evolution e.g., female sociality, female infanticide is adaptive over resource competition (Lukas and Huchard, 2019).

#### *3.4.5 Variables where no effect was identified*

There were several variables where no predicted effects across any of the five violence types were observed in the analysis: substrate type, number of males and degree of dimorphism. Furthermore, as hypothesised no effect of seasonal breeding on infanticide was found. Substrate represents a key aspect of the environment and may place constraints on acts of violence in terms of the presentation, frequency, or magnitude of attacks. Arboreal species are considered to show lower levels of aggression than terrestrial ones (Plavcan and van Schaik, 1997) due to the inherent spatial limitations, the challenge in delivering simultaneous attacks, the restrictions this may have on coalition formation (Noë and Sluijter, 1990; Bissonnette *et al.*, 2014) and the inherent cost of accidental injury an aerial environment affords (Broom, Koenig and Borries, 2009). Thus, an effect was expected on intra and intergroup aggression types. Within this dataset, 46.67% of arboreal species form coalitions as opposed to 76.92% of terrestrial species. While this study identified that coalition formation does have a positive effect on inter and intragroup adulticide (see section 3.4.3), the role of coalition formation does not have an effect on non-lethal aggression. Many restrictions that an aerial environment affords which can apply to coalitions are not having a significant effect in driving the evolution of intra and intergroup aggression. Furthermore, while terrestrial environments may offer the opportunity to be more aggressive other socio-ecological factors may be limiting levels of violence in some terrestrial species.

Richard (1992) identified that the number of males within a social system has been linked to levels of male-male violence due to mate competition. However, no effect on intragroup aggression, intergroup adulticide or infanticide was identified. Potentially, multimale groups effects on lethal intergroup violence may be modulated by coalition formation, as having multiple males in a group leads to increased coalition formation (Henzi, Weingrill and Barrett, 1999) and coalition formation is a predictor of intergroup adulticide (see section 3.3.2). However, the role of non-coalitionary lethal attacks occurring in both single male and multimale units is the likely explanation for not identifying any effect. Additionally, the presence of more males within a group has been shown to lead to increased territory size in some species (Lemoine *et al.*, 2020). These larger territories have lower neighbouring pressures as measured by encounter distance occurring further from the range centre, less heavily used areas, and/or lower frequency of the encounters (Lemoine *et al.*, 2020).

Consequently, there are potentially counteracting socio-ecological factors impacting on intergroup aggression levels in multimale groups. Moreover, this study categorised groups as single-male and multi-male. If the study were to be repeated utilising quantitative number of males, or ratio between males and females, rather than the two categorical categories then an effect may have been established. Categorical classification may also explain the lack of effect of multimale groups on infanticide. Multimale groups in which females can mate with multiple males can lead to the possibility of females creating paternity confusion and consequently less infanticide from intragroup males, but this effect may be hidden by small multimale groups.

Male-male aggression can increase when there is a high degree of dimorphism between sexes, which results from sexual selection over competition for mates (Plavcan and van Schaik, 1997). As such it was anticipated that a higher dimorphic ratio would likely lead to increased intragroup aggression (including lethal), this study found no such correlation. In some dimorphic and monomorphic species there was quite a mix of violence types displayed. For example, the monomorphic *Presbytis thomasi* display high levels of intragroup aggression which would not be anticipated, yet commit intergroup adulticide and infanticide, however no intragroup adulticide was found. Additionally, the highly dimorphic *Nasalis larvatus* have low levels of intragroup aggression, no intergroup and intragroup adulticide but commit infanticide. These findings partially contradict those of Gómez, Verdú and González-Megías (2021) who identified that adult killing was significantly, positively associated with size dimorphism in males (Gómez, Verdú and González-Megías (2021) - data sub-set III -



species observed in natural conditions). However, there was a lack of any significant effect of size dimorphism for females. Due to the rarity of adulticide this study did not, at this stage, consider separating attacks by sex, especially as the adulticide data was already sub-divided into intra- and inter-group. Yet, the combining of male and females' lethal acts may have caused some effects to be neutralised as the evolutionary drivers of adulticide in males and females differ.

The role of the attacking sex is also pertinent in exploring infanticide. For example, intergroup infanticide in seasonal breeding species was expected to be affected largely by males following take-over (see: Ciani, 1984; Soltis *et al.*, 2000; Yamada and Nakamichi, 2006). Infanticide is advantageous to the incoming male if the interbirth interval (IBI) is longer than the breeding season or breeding early in the season could maximise infant survival (Palombit, 2012). As posited in section 3.1.3 the lack of effect of seasonal breeding on infanticide was anticipated. In seasonal breeding species where the IBI is shorter than the breeding season then infanticide would not be a advantageous, additionally in non-seasonally breeding species can find infanticide beneficial in hastening a females return to breeding condition. Furthermore, as Digby (2000) stated, the risk of intragroup infanticide by group living females could provide a more persistent threat than other forms of infanticide. Given the potentially different impacts of males and females it currently appears likely, as Gómez, Verdú and González-Megías (2021) state, that there are different evolutionary pathways for males and females for each violence type.

#### 3.4.6 Model discussion

The two models that incorporated the socioecological predictors were most successful at explaining the variance in the violence data. This was especially true for lethal aggression, including infanticide. Intergroup adulticide appeared to be particularly well explained by the model despite only having one significant identifiable effect from the predictor variables, coalition formation. Most of the model's explanatory power is coming from the impact of phylogeny.

There was very little improvement made to the intergroup aggression model through the addition of socioecological variables despite being the least well explained phylogenetically. The additional variables were strongly expected to show an impact based on the literature (see section 3.1). The one variable that had a strong effect was D-index as a measure of

territoriality. These results suggest that social factors are playing a more significant role in intergroup interactions than ecological factors, which has also been observed previously (see: Willems, Hellriegel and van Schaik, 2013).

Further explanations for the lack of model effectiveness can be connected to the potential difficulties with working at species level. Many species show behavioural flexibility in response to different conditions which is captured with comparative data at the population or individual level but may be obscured at the species level. Consequently, due to individual personality and group cultural variability there is likely no simple unifying model to explain the presentation of low levels of aggression. The complex and essentially unique interplay between all these variables require a more detailed models integrating factors beyond phylogeny and socioecological variables. DeWall, Anderson and Bushman, (2011), expressed concern that even a complete socioecological model does not explain the assessment and decisions involved in ultimately deciding whether groups will engage in aggressive interactions.

Unfortunately, obtaining large-scale data to conduct an analysis at the population or group level is highly challenging. For example, while an individual primate may be well known to the researcher, levels of baseline aggression, past experiences and cognitive ability are not usually recorded. These individual factors may heighten or reduce the effect of exposure to aggression on future group aggressive behaviour (DeWall, Anderson and Bushman, 2011). Thus, as Majolo *et al.*, (2020) summarised, individual decisions during intergroup encounters may involve the interaction of socioecological factors that impact on that individual based on their unique relationship within and between groups, which makes generalisation across species within a meta-analysis difficult. Furthermore, due to preferences or necessity for a particular site or group data is often disproportionately weighted towards certain populations. Species and site bias was identified in a study by Bezanson and McNamara (2019) who found research was highly clumped around certain species and locations. Between 2011-2015 the top ten studied species, in descending order, included *Pan troglodytes*, *Macaca fuscata*, *Macaca mullata*, *Alouatta palliata*, *Alouatta pigra*, *Gorilla gorilla*, *Cebus capucinus*, *Papio hamadryas*, *Ateles geoffroyi*, and *Lemur catta*. An example of site bias can be found in Madagascar where 49.4% of site visits occurred in Ranomafana National Park, Berenty Private Reserve, Kirindy Forest National Park, or Ankarafantsika National Park (see: Bezanson and McNamara, 2019 for the full review). There are many significant challenges to using other sites such as the long-term commitment required to set up a site including

administrative, and biological considerations (Struhsaker, 2008). Therefore, it is not simply a case of visiting other sites and obtaining data, so the ability to study cross-taxa at the individual or population level will take many more years of research. As and when data do become available then they should be integrated into this large-scale dataset for future analysis. In the interim, while this dataset may not completely address the questions it provides a valuable first step in addressing how socio-ecological variables impact on five specific violence types.

### 3.5 Conclusion

The analysis incorporating socioecological variables partly added to the phylogenetic understanding of violence. Consequently, the two models that incorporated the socioecological predictors were most successful at explaining the variance in the aggression data. This was especially true for lethal violence, including infanticide where a significant variable was the ability to form coalitions. However, there was very little improvement made to the intergroup aggression model through the addition of socioecological variables despite being the least well explained phylogenetically. The additional variables were strongly expected to show an impact based on the literature. The one variable that had a strong significant effect was D-index as a measure of territoriality. These results suggest that social factors are playing a more significant role in intergroup interactions than ecological factors, which has also been observed previously (see: Willems, Hellriegel and van Schaik, 2013). For non-lethal intragroup aggression, the degree of folivory had a negative effect on intragroup aggression levels, and contrary to the predicted effect potentially group size negatively affects rates of agonistic intragroup interactions. Several variables where no anticipated effects across any of the five aggression types were observed including, substrate type, number of males and degree of dimorphism.

Despite some correlations between aggression types and socio-ecological variables it remains surprising that a lot of the total variability (high  $R^2$  values) is explained for four out of five forms of aggression, without identifying many strong correlations with the socio-ecological independent variables considered. This suggests a strong phylogenetic pattern in four of the violence types, but it still is not fully clear what is driving it. It is likely there is considerable species variability that the tested models remain naïve about.

In human studies socioecological models consider the impact on the individual across four overlapping levels of society and ecology: Individual, microsystem, exosystem, macrosystem (Heise, 1998). Potentially in adopting a similar method a deeper understanding could be found. However, there are clear challenges in obtaining enough data for this type of analysis. Therefore, future work should ideally be addressed at a population/group level as and when the data becomes available. Furthermore, Gomez *et al.* (2016) identified several socioecological factors that had an impact on lethal violence and found differences between males and females. This study found similar impacts on several ecological variables but did not consider the aggression separated by sex. Therefore, the next step in this study is to

separate the adulticide data into male and female perpetrators and run the socioecological and baseline phylogenetic models again to see how this effects the findings.

**CHAPTER FOUR –SEX SPECIFIC EVOLUTION OF ADULTICIDE**

*“... the only important thing in a fight to the death is that the death should not be yours.”*

(Snuff - Pratchett, 2011, p.87)

## 4.1 Introduction

The previous chapter identified that the addition of socio-ecological variables aided in understanding the variance in the five types of violence. Four of the predicted effects from socioecological variables were confirmed by the analyses; degree of folivory negatively affected intragroup aggression, D-index positively affected intergroup aggression, and coalition formation positively affected intragroup and intergroup adulticide. However, there were several results that did not appear to reflect current theories and it was proposed that some variables may apply different evolutionary pressures on males and females. Gómez, Verdú and González-Megías, (2021) analysed sex specific adulticide in a wide range of mammals, however a study focused on primate sex specific adulticide incorporating further sub-divisions of intra/intergroup adulticide has not previously been carried out.

Adulticide has been considered a rare behaviour however, this study found it was more common in primates than previously thought by identifying that at least one form of adulticide occurs in 28 species, and both intra and intergroup adulticide have been observed in 11 species (chapter 2, section 2.3.1). Intergroup adulticide has been found to be more common (i.e., it is observed in a greater number of species) than intragroup adulticide, and male adulticide occurs more frequently than female adulticide (Wilson, M. L. *et al.*, 2014; Gómez, Verdú and González-Megías, 2021). The trend is also observed in human studies where men are more likely to be both perpetrator and victim; 90% of suspects in homicides (2014-2016 data) were male and furthermore, males were up to 11 times more likely to be victims in parts of the Americas. (UNODC, 2019).

Adulticide can be viewed as an adaptive strategy where the killer gains fitness benefits (Wilson, M. L. *et al.*, 2014) and males and females have been considered to have different drivers of aggression (van Schaik, 1996). However, Gómez, Verdú and González-Megías, (2021) argued that adulticide research was largely only focused on the male drivers, primarily male breeding competition (Clutton-Brock, 2016). Adulticide is observed in both sexes and while females do experience breeding competition in some species, females are largely considered to commit adulticide for defence of food/nest sites (Hinsch and Komdeur, 2017), to defend infants (Gómez, Verdú and González-Megías, 2021), for retaliation, and or in support of males. Furthermore, both sexes may commit adulticide when preying on conspecifics (Gómez, Verdú and González-Megías, 2021), though cannibalism is generally rare in primates, and it usually involves the ingestion of infants (e.g., *P. troglodytes*

*schweinfurthii* (Lowe *et al.*, 2020); *Gorilla beringei* (Fossey, 1984), *Saguinus mystax* (Culot *et al.*, 2011); *Rhinopithecus bieti* (Xiang and Grueter, 2007); *Callithrix jacchus* (Bezerra, Souto and Schiel, 2007)).

Chapter three identified several socioecological variables that influence specific violence types, including the effect of coalition formation on intra and intergroup adulticide. However, other variables that were predicted to have an effect were not identified in the analysis, and it was proposed that had male and female adulticide been analysed separately then further effects may have been seen. Other authors have analysed lethal violence types by sex of the perpetrator (e.g., Lukas and Huchard, 2014 - male infanticide; Lukas and Huchard, 2019 - female infanticide; Gómez, Verdú and González-Megías, 2021 - lethal violence). Sex specific differences in the levels of adulticide are due to the different fitness benefits that adulticide confers to males and females balanced against the cost of taking lethal action. As such, there are likely to be different socioecological factors that affect adulticide in males and females and some of these were elucidated in the Gómez, Verdú and González-Megías, (2021) study on sex specific mammal adulticide. Adulticide can be considered to be affected by a range of socioecological variables, such as group size, size dimorphism, and territoriality (Gómez, Verdú and González-Megías, 2021).

#### 4.1.1. Territoriality

Territoriality occurs when an animal defends its home range against conspecific encroachment and can be observed, as displays or physical altercations, in many animal species (Willems, Hellriegel and van Schaik, 2013). Often aggressive encounters between groups do not extend beyond agonistic displays and threats to physical violence (Bates, 1970) however when resources are scarce, opposing groups will enter territories despite being aware of the neighbours' position (see: Van Belle and Estrada, 2020). The decision to engage in this potential conflict will more likely occur if the invading party has intergroup dominance and so the cost of engagement is lower.

The home range/territory of the resident group may be defended by both sexes (Lemoine *et al.*, 2020). Yet, the motivation behind these behaviours has been differently attributed. Males are considered to defend an area to increase their chances of access to mates, whereas females seek safety and resources (Trivers, 1972; Emlen and Oring, 1977; Kappeler and van Schaik, 2002). Females have higher cost implications in engaging in escalating fights as lethal



violence may impact not only on the female but lead to the deaths of any dependant offspring (Jolly *et al.*, 2000). Though in certain species males may act to defend a female's interests, such as resource defence, if the male's reproductive output would be improved (Willems, Hellriegel and van Schaik, 2013). The degree of territoriality can be measured with the defendability index (D-Index) (see chapter 3, section 3.1.5 for full details). In chapter three this study found no association between D-index and adulticide however given the role of males in territorial defence and its potential impact on reproductive success it is possible that D-index may be associated with male adulticide (hypothesis H3 – Table 4.1).

#### 4.1.2 Group size

Territorial species engage in intergroup competition over resources, and the size of these groups can vary considerably both across primate species (Kappeler and van Schaik, 2002; Campbell *et al.*, 2011; Griesser *et al.*, 2011) and within (Wrangham, 1980; Isbell, 1991; Griesser *et al.*, 2011; Campbell *et al.*, 2011), resulting in group sizes ranging from a solitary individual to several hundreds (Campbell *et al.*, 2011). Lemoine *et al.*, (2020) identified that the larger the group the greater their territory but the lower amounts of neighbouring pressure that group experiences. This potentially indicates group size may negatively affect intergroup adulticide as encounters are reduced. However larger groups may also be more likely to form coalitions which can reduce cost of violent intergroup interactions which may occur during territorial expansion.

Gómez, Verdú and González-Megías, (2021) identified that foraging group size was not related to male adulticide and concluded that adulticide could not be explained by resource (including progeny) protection in males. There can be potentially different results when using foraging group sizes, which can result from temporary alliances, as opposed to the more stable social group number (Dunbar, Mac Carron and Shultz, 2018). This study used stable social grouping (Table 3.3. for definition) as recommended by Dunbar, Mac Carron and Shultz, (2018) and also found no relationship between adulticide and group size. Given that group size may have both a positive and negative effect on aggression and that in chapter three no relationship was identified on adulticide, it is anticipated that the separation into males and females will not result in a significant effect (hypothesis H4 – Table 4.1). However, as working at the species level removes variance from the data, confirming the

result when bringing back some variance through the addition of sex specific data is a useful clarification of the earlier result.

#### *4.1.3 Number of males within the group*

Differing group sizes can result in several types of social system; polyandrous, polygynous, monogamous, multimale-multifemale. Therefore, the number of males present within a group can also vary quite considerably across the primate order. Richard (1992) identified that the number of males within a social system has been linked to levels of male-male violence resulting from mate competition. Therefore, in monogamous systems male sexual competition would be low, whereas in polygynous systems competition may be intense. While an increasing number of males may lead to increased violence, other factors e.g., female mate choice, can mitigate this behaviour. For example, bonobos, in contrast to chimpanzees, do not show the same levels of violence because male-male competition is less beneficial due to female dominance and their key role in mate choice (Surbeck *et al.*, 2012). Furthermore, while in male-bonded groups males are key to territorial defence, in bisexually bonded group male number is not as relevant as adult group size as females also engage in aggressive defence (Lemoine *et al.*, 2020). Nevertheless, it is anticipated that in many multimale groups levels of aggression would be high both within and between groups and this could potentially lead to adulticide (hypothesis H5 – Table 4.1).

#### *4.1.4 Size dimorphism*

Male social systems have been linked to elevated levels of violence and size dimorphism. Darwin (1871) first noticed that polygynous mammals show a larger size dimorphism than monogamous mammalian species. This is due to differing selection pressures on males and females within a polygynous species (Clutton-Brock, 1985). In the study by Gómez, Verdú and González-Megías, (2021) it was found that male biased size dimorphism was positively associated with male, but not female, adulticide. With a high degree of dimorphism, competition between males is frequent (Plavcan and van Schaik, 1997) with sexual selection often considered the main driver of dimorphism (Cassini, 2020). Dimorphism can be seen to be affected by other socio-ecological variables such as substrate, where arboreal species demonstrate lower levels of aggression compared to terrestrial species (Plavcan and van Schaik, 1997). Given the results of Gómez, Verdú and González-Megías, (2021) and the

strong relationship between dimorphism and male sexual competition it is anticipated that dimorphism will be a positive predictor of male adulticide (hypothesis H6 – Table 4.1).

#### 4.1.5 Substrate

Substrate can be categorised as terrestrial, arboreal or a combination of the two, as some primates expand their niches vertically (Tabacow, Mendes and Strier, 2009). While an animal is adapted to its environment, aspects of that environment such as substrate can place limitations on acts of violence in terms of presentation, frequency, or magnitude. Arboreal environments can be particularly challenging as there is the inherent cost of accidental injury from falling at height (Broom, Koenig and Borries, 2009), spatial limitations, the restrictions on coalition formation (Noë and Sluijter, 1990; Bissonnette *et al.*, 2014), and the increased challenge in delivering simultaneous attacks (Noë and Sluijter, 1990). Therefore, it is more likely that violent behaviour would occur in terrestrial, rather than arboreal species. However, chapter three of this study did not find an association between substrate type or any type of violence, suggesting that there are other species-specific socioecological factors that are limiting violence in terrestrial species. Consequently, it is unlikely that utilising sex specific data will identify an effect of substrate on adulticide (hypothesis H7 – Table 4.1).

#### 4.1.6 Coalition formation

Substrate has been identified as having an effect on coalition formation where terrestrial environments create fewer restrictions (Noë and Sluijter, 1990; Bissonnette *et al.*, 2014). Coalitions may be defined as a temporary alliance between at least two individuals to either carry out an aggressive combined action or defend themselves against a third party (Noë, 1992). Coalitions are important in group living species in intra and intergroup competition (Bissonnette *et al.*, 2015) and can be formed for a variety of reasons. In males coalitionary association can assist in the ousting of an incumbent male/s and achieving a group take-over (Komorita and Kravitz, 1983; Noë, 1992; Harcourt, 1992; Pope, 2000; Wilson, M. L. *et al.*, 2014). In females coalitionary support can act to defend against infanticide (see: Hrdy, 1974; Struhsaker, 1977; Crockett, C. M., and Sekulic, 1984; Valderrama, Srikosamatara and Robinson, 1990). However, a review by Ebensperger (1998) identified that coalitions merely delay infanticide rather than prevent it. Furthermore, both sexes may benefit from coalitions when used to prevent a take-over attempt (Treves, 1998; Feh, 1999; Palombit, 2015) or

defend a territorial boundary (Kitchen and Beehner, 2007). Coalitionary attacks may become lethal (reviewed by Wrangham, 1999) whereby prolonged killing reduces the opposing groups power, as larger groups are likely to be more successful in intergroup encounters than smaller ones (Majolo *et al.*, 2020). This reduces the costs of any future intergroup encounters for the aggressors (Wrangham, 2006) and would likewise reduce immediate costs in intragroup engagements. This study identified that coalition formation was positively related in both inter and intragroup adulticide (see chapter 3 section 3.3) and so is anticipated to also be important in sex specific adulticide (hypothesis H8 – Table 4.1).

#### 4.1.7 Diet – degree of folivory

Aggression because of food competition is not rare in social mammals (Ostfeld, 1990). Potential links between violent behaviour and food are anticipated given that access to food is critical for individual survival and reproductive success. Consequently, being able to monopolise food resources may be beneficial (Trivers, 1972; Sterck, Watts and Van Schaik, 1997; Sterck and Steenbeek, 1997). The monopolisation of food resources has been linked to dietary type. For example, the ‘Food distribution’ hypothesis (Brown & Orians, 1970; Isbell, 1991; Isbell & Enstam, 2002) theorises that food spatial distribution influences inter-individual distance. Distribution of food is related to its type, whereby the leaves/grasses of a folivore’s diet, or the insects of an insectivore’s diet, may be considered to be abundant and evenly distributed (but see: Snaith and Chapman, 2005), whereas fruits, the basis of a frugivores diet, are clumped and can be monopolised (Isbell, 1991). With close interindividual distance around a clumped and contested resource between-group contest (BGC) or scramble (BGS) competition and within-group contest (WGC) may occur (Isbell, 1991). Consequently, while there will still be a degree of aggression present between folivores (Isbell, 1991; Kappeler and van Schaik, 2002), higher levels of aggression have been observed in frugivores (Cords, 2000; Klass and Cords, 2015; but see: Wheeler, Scarry and Koenig, 2013), where the higher costs would yield sufficient benefit. Frugivores are likely more dimorphic than folivores or insectivores which can aid violence (Plavcan and Van Schaik, 1997), though sexual selection is often considered the main driver of dimorphism (Cassini, 2020) rather than diet type.

Competition for food resources is considered to be more associated with female rather than male violence. Gómez, Verdú and González-Megías, (2021) considered this when analysing

whether carnivorous diets (consuming meat, insects, other invertebrates, and omnivores) versus non-carnivorous diets, were associated with adulticide. They did not identify carnivory as related to male adulticide but did find a significant effect of carnivory on female adulticide which was proposed to be related to intraspecific predation. While there are examples of intraspecific predation in primates (e.g., *P. troglodytes schweinfurthii* - Lowe *et al.*, 2020; *Gorilla beringei* - Fossey, 1984; *Saguinus mystax* - Culot *et al.*, 2011; *Rhinopithecus bieti* - Xiang and Grueter, 2007; *Callithrix jacchus* - Bezerra, Souto and Schiel, 2007), it is not common. Interestingly, both categories used in the Gómez, Verdú and González-Megías, study to separate food types contained a mixture of contestable and dispersed food types i.e., fruits and leaves, which were both be in the non-carnivorous category. This opposed the view that clumped or dispersed food sources may be related to different levels of violence. In contrast to Gómez, Verdú and González-Megías, (2021), diet within this entire study has been represented by the proportion of leaves in the diet (see Table 3.3 for rationale) which therefore considers the degree to which an individual would eat a dispersed food source. Despite the methodological differences Chapter three of study (non sex differentiated) also observed no effect of diet on adulticide. However, an effect was observed on intragroup aggression which predominantly is driven by females. Therefore, potentially an effect could be observed on female adulticide that had been masked from the earlier analysis (section 3.3.2) due to the impact of the combined male/female data (hypothesis H9 – Table 4.1).

#### 4.1.8 Seasonal breeding

There are two main reproductive seasonality types displayed by primates; continuous breeders give birth throughout the year and seasonal/opportunistic breeders have a specific timeframe in which they breed, which is triggered by daylength (Urbanski, 1990; Revel *et al.*, 2009; Perfito and Bentley, 2009) or favoured by specific conditions at points throughout the year (Vasanth, 2016).

Seasonal breeding can lead to some elevated levels of violence, for example, infanticide has been observed in an increasing number of seasonal breeding species, such as *Macaca fuscata* (Soltis *et al.*, 2000; Yamada and Nakamichi, 2006) and *Macaca mulatta* (Ciani, 1984). There are also advantages in seasonal breeding species to removing the dominant/breeding male which may occur through adulticide. Therefore, lethal violence could provide a male with substantial benefits, if they lethally remove an infant, accelerating female receptivity or kill a

rival male and take their breeding status. In contrast seasonal breeding may reduce the risk of aggression in females as a consequence of resource/feeding competition due to timing reproduction at times of peak food availability. Overall seasonal breeding may be associated with male adulticide (hypothesis H10 – Table 4.1) but is unlikely to produce a strong enough pressure to lead to the evolution of female adulticide.

In summary, therefore, the literature suggests that male and female adulticide have different evolved pathways in mammals (Gómez, Verdú and González-Megías, 2021) and consequently in primates, including humans. The purpose of this chapter is to therefore understand the sex specific evolution of adulticide by exploring the ultimate phylogenetic component and proximate socioecological drivers, thus adding to the results of chapters two and three.

#### *4.1.9 Hypotheses testing*

Based on a review of the literature and the results of chapter two and three the hypothesis outline in Table 4.1 will be tested.

*Table 4.1: The 10 hypotheses tested exploring specific male and female drivers of adulticide*

Code	Description
H <sup>1</sup>	A stronger evolutionary signal will be detected in males than females due to the higher fitness/reproductive implications of adulticide for males.
H <sup>2</sup>	The evolutionary signal will be stronger for the intergroup adulticide data and the intragroup adulticide data for both males and females.
H <sup>3</sup>	D-index will be a positive predictor of male adulticide.
H <sup>4</sup>	No effect will be identified of group size on male and female adulticide.
H <sup>5</sup>	Number of males will be a positive predictor of male adulticide.
H <sup>6</sup>	Dimorphism will be a positive predictor of male adulticide.
H <sup>7</sup>	No effect will be observed of substrate (terrestrial) on male or female adulticide.
H <sup>8</sup>	Coalition formation will be a positive predictor of male and female adulticide.
H <sup>9</sup>	Proportion of leave in the diet will be a negative predictor of female adulticide.
H <sup>10</sup>	Seasonal breeding will be a positive predictor of male adulticide.

## 4.2 Methods

### 4.2.1 Data collection

The adulticide and socio-ecological data were obtained during the systematic review of the primatological literature as detailed in sections 2.2.1 (adulticide data) and 3.2.1 (socio-ecological data) and through distribution of a survey to various primatological societies and specialist researchers (Appendix 2A and section 2.2.1). *A priori* data exclusion criteria established and outlined in section 2.2.1 were retained.

### 4.2.2 Data assignment variables

The dataset containing intra and intergroup adulticide data was sub-divided to contain data pertaining to the occurrence of adulticide by the sex of the aggressor (Figure 4.1).

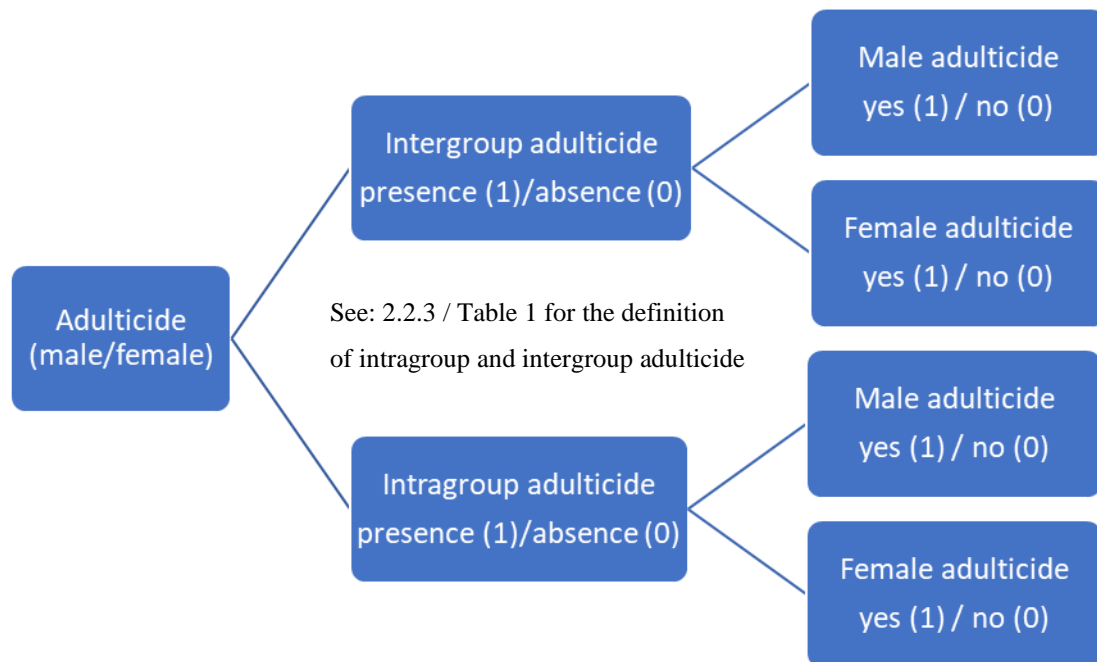


Figure 4.1: Data categorisation for the adulticide data, which were then used for analysis

### 4.2.3 Tree construction

A set of 1000 Bayesian mammal phylogenies were extracted at random from the data repository at Vertlife.org (Upham, Esselstyn and Jetz, 2019). The trees were subsequently loaded into R version 4.0.2 (R Core Team, 2020) as an object of class `multiphylo`. Package ‘ape’ version 5.4.1 (Paradis and Schliep, 2019) was installed to assemble a tabulation of pairwise distance, using the Kuhner-Felsenstein distance (Kuhner and Felsenstein, 1994), that

considers tree branch lengths as well as tree branching patterns. Next, a single tree was chosen based upon the criteria that the tree should have the smallest sum of distance values from the remaining trees. Taxa not available in Vertlife.org (e.g., subspecies) were added to the topology and their position relative to their immediate sister taxon was estimated at 0.5 million years divergence from the present (Figure 2.1 – section 2.2.6). The selected tree was pruned (see section 3.2.5) to include only the 101 extant primate species and sub-species from the dataset for which complete adulticide and socioecological data were available (Appendix 3B).

#### 4.2.4 Statistical analysis and model construction

As per the previous chapters, analysis on the selected dataset was carried out using Bayesian multivariate modelling utilising the Stan probabilistic programming language (Carpenter *et al.*, 2017) and the high-level interface ‘brms’ package version 2.14.0 (Bürkner, 2017) in R version 4.0.2 (R Core Team, 2020). Six multivariate models were developed (Table 4.1). Model one contained no predictor variables and so aimed to determine phylogenetic signal strength of adulticide when separated into intra and intergroup, and also by sex. Models two, three and four used all eight socio-ecological predictor variables (as previously used in section 3.2.6) to six different adulticide outcome variables (male/female adulticide and intra/intergroup adulticide, separated by sex), in an attempt to improve the explanation of the variance in the adulticide data. This employs the Forced-entry method, which is not suitable for a large number of predictor variables (Kucuk *et al.*, 2016) but appropriate for the number utilised in this study. Finally, models five and six employed ‘specific’ key predictor socioecological variables (see section 3.2.6) applied to the four adulticide types (adulticide separated intra/intergroup and sex (male / female)).


Families were set for Bernoulli distribution for the adulticide outcome variables (discrete data). Weakly informative priors were applied to improve convergence and the models set to run for four chains, each with 4000 iterations (2000 warmup, resulting in 8000 posterior samples). The R-hat convergence diagnostic was reviewed on the output and found to be  $\leq 1.01$  indicating the chains had well mixed (Bürkner, 2017). Additionally, plots were also checked to ensure the chains had merged (Appendix 4B-G).

Once run, calculation of  $R^2_{\text{Adjusted}}$  was carried out which adjusts for the number of predictor variables in a model based on their predictive use to the model. This can control for



overfitting of the model and subsequently misleadingly high  $R^2$  values (McCarthy, McCarthy and Ceccucci, 2022). Then model comparison of the three fitted models was undertaken to estimate the difference in predictive accuracy by determining the difference in `elpd_loo`, in which pairwise comparisons are computed between the models (Vehtari, Gelman and Gabry, 2017).

Table 4.2: The six models used in the analysis

Model Name	Variables	Model in 
<b>1</b> fitadult1phylo	Outcome: Adulticide separated by sex of attacker / adulticide separated into intra and intergroup and by sex	brm(mvbind(Male_Killing, Female_Killing, IG_Killing_M, IG_Killing_F, OG_Killing_M, OG_Killing_F) ~ 1 + (1 p gr(SpeciesTree, cov= A))
<b>2</b> fitadult2eco	Aggression separated only by sex + ‘All’ variables (see section 3.2.6)	brm(mvbind(Male_Killing, Female_Killing) ~ No_Males + Leaves + Season_Breeder + D.Index + Group_Size + Substrate_1 + Dimorphism + Coalition + (1 p gr(SpeciesTree, cov= A))
<b>3 and 4</b> fitadult3eco_ig  fitadult4eco_og	Aggression separated by type (intra and inter) and sex (male / female) – ‘All’ variables (see section 3.2.6)	brm(mvbind(IG_Killing_M, IG_Killing_F) ~ No_Males + Leaves + Season_Breeder + D.Index + Group_Size + Substrate_1 + Dimorphism + Coalition + (1 p gr(SpeciesTree, cov= A))  brm(mvbind(OG_Killing_M, OG_Killing_F) ~ No_Males + Leaves + Season_Breeder + D.Index + Group_Size + Substrate_1 + Dimorphism + Coalition + (1 p gr(SpeciesTree, cov= A))
<b>5 and 6</b> fitadult5eco_ogsp  fitadult6eco_igsp	Aggression separated by type (intra and inter) and sex (male / female) – ‘Specific’ variables (see section 3.2.6)	bf_OG_Kill_M <- bf(OG_Killing_M ~ D.Index + Season_Breeder + Coalition + No_Males + Substrate_1 + (1 p gr(SpeciesTree, cov= A)), family = bernoulli()) bf_OG_Kill_F <- bf(OG_Killing_F ~ D.Index + Season_Breeder + Coalition + No_Males + Substrate_1 + (1 p gr(SpeciesTree, cov= A)), family = bernoulli())  brm(bf_OG_Kill_M + bf_OG_Kill_F)  bf_IG_Kill_F <- bf(IG_Killing_F ~ Coalition + No_Males + Season_Breeder + Substrate_1 + Dimorphism + (1 p gr(SpeciesTree, cov= A)), family = bernoulli()) bf_IG_Kill_M <- bf(IG_Killing_M ~ Coalition + No_Males + Season_Breeder + Substrate_1 + Dimorphism + (1 p gr(SpeciesTree, cov= A)), family = bernoulli())  brm(bf_IG_Kill_M + bf_IG_Kill_F)

### 4.3 Results

#### 4.3.1 Descriptive results

The dataset revealed adulticide, of either type (intra or intergroup), occurred in 28 species. Male adulticide was present in all 28 species from six families, whereas female adulticide was present in 11 species from four families (Figure 4.2). When male/female adulticide data were then further split into inter and intragroup adulticide, intergroup adulticide was more common for both males and females (Figure 4.3). Eleven species were identified as carrying out both intra and intergroup adulticide and these came from the families *Cercopithecidae*, *Hominoidea* and *Cebidae*. The presence/absence data for the categorical socio-ecological variables identified similarities between male and female adulticide. For example, number of males i.e., multi-male was the social grouping for 80% female adulticide species and 79% of male adulticide species. Terrestrial species committed 36% of male adulticides and 40% of female adulticide. Coalitions occur in 86% of species that commit male adulticide and 100% in female adulticidal species. A larger difference was seen between seasonally breeding species where this occurred in 25% of males and 50% of females adulticidal species.

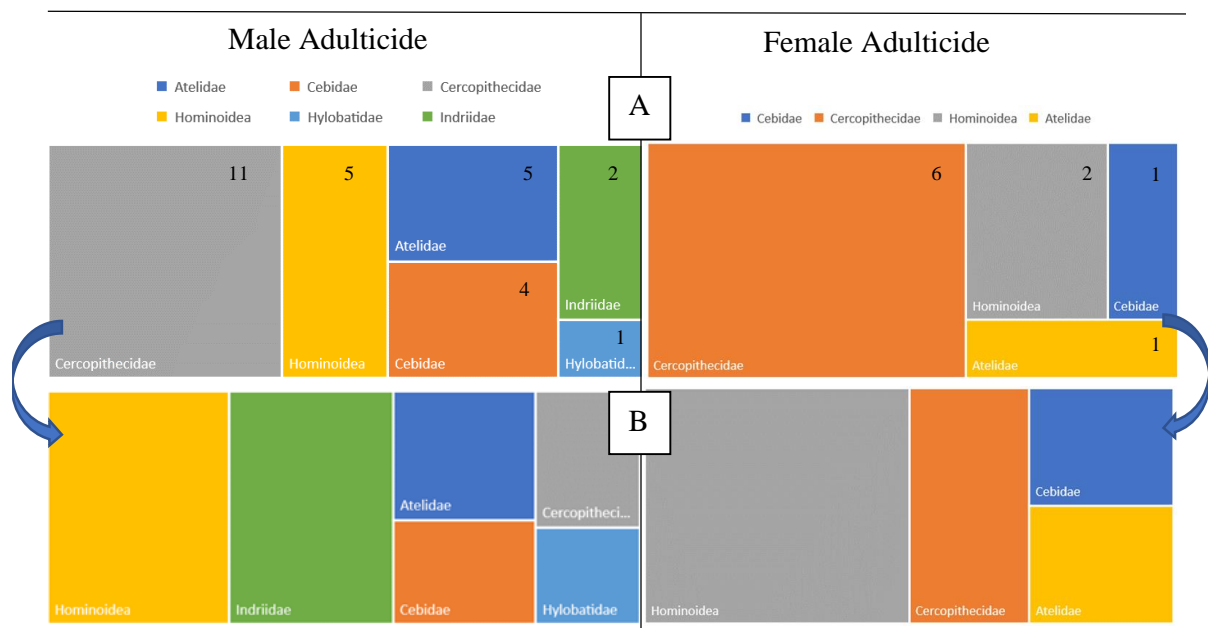


Figure 4.2: (A) The tree map indicates the families that carried out at least one type of adulticide (intra or intergroup). Block size relates to the number of species observed to commit adulticide within the family (number of species in black text). Species were scored one point for each type of adulticide they committed. (B) Value previously assigned to each family divided by the total number of species represented within the family in an attempt to control for sampling bias.

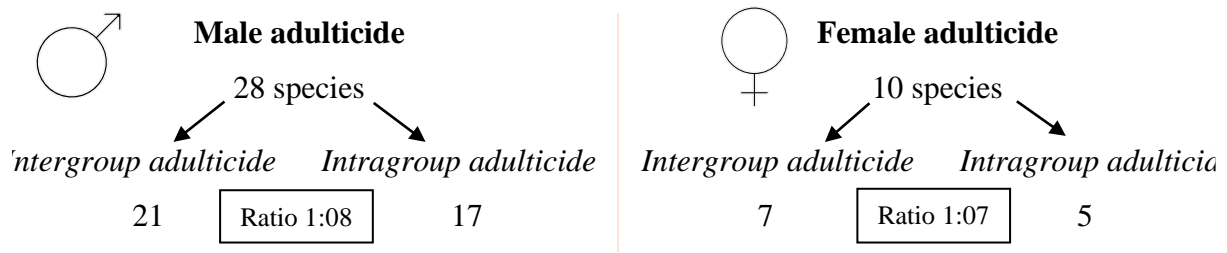


Figure 4.3: The number of species that display adulticide. First separated into male and female further by intra and intergroup adulticide.

#### 4.3.2 Phylogenetic signal based on sex and sex/type

The  $R^2$  values act as a proxy to indicate the strength of the phylogenetic signal explaining the variance in the occurrence of adulticide. When considering total adulticide separated by sex, the  $R^2$  for male killing was 92.5% and female killing 86.2%. When separating lethal adult aggression by both sex and intra/intergroup only slightly less variance was explained. For male intergroup adulticide, the model explained 88.9% and 85.1% for intragroup adulticide. Female adulticide was slightly less well explained, with the model explaining 80% of intergroup adulticide and 73.1% of intragroup adulticide (Table 4.3). Overall phylogeny explains a high proportion of the variance in the data for both males and females.

Table 4.3:  $R^2$  values for the six aggression types.

$R^2$ Variable	Estimate	Est. Error	Q2.5	Q97.5
Male adulticide	0.924	0.051	0.801	0.997
Female adulticide	0.861	0.104	0.613	0.998
Intragroup male adulticide	0.850	0.102	0.603	0.992
Intragroup female adulticide	0.731	0.195	0.242	0.996
Intergroup male adulticide	0.888	0.074	0.714	0.995
Intergroup female adulticide	0.799	0.146	0.440	0.996

#### 4.3.3 Correlations between sex engaging in adulticide

Based on the phylogenetic only model (Appendix 4B), strong/moderate correlations were found between male and female adulticide (0.65; 95% CI = 0.33 – 0.88). A strong positive correlation was found between male intergroup adulticide and female intergroup adulticide

(0.76; 95% CI = 0.43 – 0.95). A moderate positive correlation was identified between male intragroup and female intragroup adulticide (0.56; 95% CI = 0.13 – 0.86). Moderate correlations were observed between male intragroup adulticide and male intergroup adulticide (0.65; 95% CI = 0.36 – 0.86) and female intragroup adulticide and female intergroup adulticide (0.59; 95% CI = 0.20 – 0.87).

The models also tested correlations between sexes but on different types of adulticide (inter/intragroup). Intragroup male adulticide was found to be moderately positively correlated to intergroup female adulticide (0.51; 95% CI = 0.13 – 0.80). Moreover, intragroup female adulticide was potentially moderately positively correlated to intergroup male adulticide, but this result was not statistically significant due to the CI range passing through zero (0.41; 95% CI = -0.02 – 0.76) (Table 4.4).

*Table 4.4: Correlations between the adulticide sub-types (intra/intergroup and male/female)*

	Estimate	Est. Error	Credible Interval (CI)	
			Upper	Lower
<b>Correlation between male and female adulticide (combined intergroup and intragroup)</b>	0.65	0.14	0.33	0.88
<b>Correlation between adulticide types (within sex)</b>				
Intragroup male adulticide – Intergroup male adulticide	0.65	0.13	0.36	0.86
Intragroup female adulticide – Intergroup female adulticide	0.59	0.17	0.20	0.87
<b>Correlation between sex (within adulticide type)</b>				
Intragroup male adulticide – Intragroup female adulticide	0.56	0.19	0.13	0.86
Intergroup male adulticide – Intergroup female adulticide	0.76	0.13	0.43	0.95
<b>Correlation between adulticide divided by sex and type</b>				
Intragroup male adulticide – Intergroup female adulticide	0.51	0.18	0.13	0.80
Intragroup adulticide female – Intergroup male adulticide	0.41	0.20	-0.02	0.76
<b>Combined male adulticide correlations to specific adulticide types (intra/intergroup)</b>				
Male adulticide – Intragroup male adulticide	0.81	0.09	0.59	0.95
Male adulticide – Intergroup male adulticide	0.92	0.05	0.80	0.98
<b>Combined female adulticide correlations to specific adulticide types (intra/intergroup)</b>				
Combined female adulticide – Intragroup female adulticide	0.77	0.13	0.46	0.95
Combined female adulticide – Intergroup female adulticide	0.85	0.09	0.62	0.97

\* Rhat 1.00 for all results

The highlighted results indicate the correlation where the CI passed through zero and so an effect is less clear.

#### 4.3.4 Effect of socioecological variables on sex specified adulticide

The data when separated into sex specific adulticide types and by intra and intergroup identified one significant effect; Female intragroup adulticide was negatively affected by D-Index -6.28 [CI -12.22 – -1.30]. There were no ‘significant’ effects observed when data were only separated only by sex, not type, as the credible interval containing 95% of the posterior samples contained 0 (Appendix 4G). However, several variables are likely to have a positive effect as a high percentage of each of the posterior samples were to the right of zero (Table 4.5).

*Table 4.5: Regression coefficients between adulticide types and key socio-ecological variables with high % posterior samples but with a CI containing zero.*

	Estimate	Est. Error	Credible Interval (CI)*		% Posterior samples > 0
			Upper	Lower	
Male adulticide – Coalitions (yes)	6.28	3.65	-0.75	13.51	95.72
Female adulticide – Season breeder (yes)	4.77	3.18	-1.37	11.32	94.54
Female adulticide – Group size	-0.17	0.16	-0.06	0.54	92.35
Female adulticide - Coalition(yes)	6.24	4.00	-1.79	14.00	94.34

\* While passing through zero the CL's are strongly skewed to the right indicating a positive effect.

*Table 4.6: The hypotheses tested and those accepted as a result of the analysis*

Code	Description	Accepted
H1	The evolutionary signal will be stronger in males than females.	√
H2	The evolutionary signal will be stronger for the intergroup adulticide data and the intragroup adulticide data for both males and females.	√
H3	D-index will be a positive predictor of male adulticide.	x <sup>a</sup>
H4	No effect will be identified of group size on male and female adulticide.	x <sup>b</sup>
H5	Number of males will be a positive predictor of male adulticide.	x
H6	Dimorphism will be a positive predictor of male adulticide.	x
H7	No effect will be observed of substrate (terrestrial) on male or female adulticide.	√
H8	Coalition formation will be a positive predictor of male and female adulticide.	√
H9	Proportion of leave in the diet will be a negative predictor of female adulticide.	x
H10	Seasonal breeding will be a positive predictor of male adulticide.	x <sup>c</sup>

a D-Index was a negative predictor of female adulticide

b Group size was a positive predictor of female adulticide

c Seasonal breeding was a positive predictor of female adulticide

## 4.4 Discussion

### 4.4.1 *Effect of phylogeny on sex specific adulticide*

The variance in male and female adulticide data were strongly explained by phylogeny, though more so for male adulticide. This was also true when adulticide was separated by both sex and intra and intergroup types with male intergroup adulticide the most well explained. Males and females have been considered to have different drivers of aggression (van Schaik, 1996). The stronger signal for males would be expected given the strong sexual and natural selection mechanisms which act on this trait in males. Males commonly commit adulticide as a result of male breeding competition (Clutton-Brock, 2016) and have an evolved stronger drive for frequent mating due to the male's lower energetic reproductive costs (Thornhill and Palmer, 2000). Female adulticide is less common than male adulticide and while females do experience breeding competition in some species, females are largely considered to commit adulticide for defence of food/nest sites (Hinsch and Komdeur, 2017), to defend infants (Gómez, Verdú and González-Megías, 2021) and for retaliation. The results therefore indicate that in both males and females adulticide, while infrequent, has a strong evolutionary pressure.

### 4.4.2 *Correlations between adulticide types*

All variations of correlations between adulticide types were significant, except male intergroup adulticide and female intragroup adulticide. Male and female intergroup adulticide were the most strongly correlated. This was predicted given that female intergroup adulticide appears to mainly occur as part of a coalition with males (e.g., *Cebus capucinus* - Gros-Louis, Perry and Manson, 2003); *Macaca nigra* - Martínez-Íñigo, 2020). Lethal intergroup coalitionary attacks, regardless of sex combination, reduce immediate individual costs to the aggressors and provide reduced costs in any future engagements by altering the balance of power between groups (Wrangham, 2006), as larger groups are likely to be more successful in intergroup encounters than smaller ones (Majolo *et al.*, 2020).

Intragroup adulticide between males and females was not as strongly correlated. Again, this may be related to the different drivers of adulticide behaviour in males and females. Males are acting primarily in competition to gain reproductive access (e.g., *Ateles geoffroyi* - Campbell, 2006), while females defend infants or food/nest sites (Hinsch and Komdeur, 2017), though intrasexual motives can also be a cause (e.g., *Cercopithecus diana* - McGraw *et*

*al.*, 2002). Furthermore, as with intergroup adulticide, they can be operating in support of males. For example, females have been observed participating in “revolutions” against the alpha male supporting and strengthening the challenger’s position. This was observed when ten *Cebus capucinus* males and females lethally evicted the alpha male who had failed to flee. (Gros-Louis *et al.*, 2003). Intragroup adulticide in similarity to intergroup mainly occurs when females operate in the presence of, or in support of males which will lead to the significant correlation between males and females in intragroup adulticide. The slightly reduced intragroup correlation likely due to female intragroup adulticide not always occurring in male intragroup adulticidal species (80% - exception *Cercopithecus diana* - McGraw, Plavcan and Adachi-Kanazawa, 2002; Kane, 2020) in contrast to intergroup where all female adulticide occurs in males adulticidal species.

#### 4.4.3 The effect of socioecological variables on sex specific adulticide


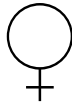
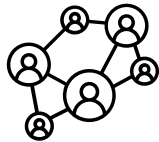

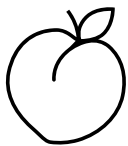
There were four potentially significant socio-ecological variables three of which impacted on female adulticide. As female adulticide was slightly less well explained by the phylogenetic model it is not surprising that there are more socio-ecological variables explaining it. These included, territoriality, seasonal breeding, group size and coalition formation. The latter of which was also important to males. The importance of coalition formation in relation to adulticide was identified in Chapter three and this analysis confirms those findings, though the effect was not as clear when separated by sex. Males had the clearer effect which likely reveals the more frequent and key part coalitions play in male fitness.

The separation of adulticide types by sex however did allow the identification of further socio-ecological variables that were hidden from the earlier models (chapter 3). Seasonal breeding was found to be a positive predictor of female intragroup adulticide where 80% of female intragroup adulticidal species were seasonal breeders. This contrasts with the 71% of female intergroup adulticidal species that were continuous breeders. Infanticide has been observed in an increasing number of seasonal breeding species, such as *Macaca fuscata* (Soltis *et al.*, 2000; Yamada and Nakamichi, 2006) and *Macaca mulatta* (Ciani, 1984). Adulticide has been considered to be a mechanism to prevent infanticide. Therefore, an evolved trait of lethal protection would be beneficial. Furthermore, females may try to prevent the immigration of new females to the group, if immigration may limit resources or



reproductive opportunities, which may be dependent on group size. Group size was identified as a positive predictor of female intergroup adulticide.

There are a few species that current evidence suggests only appear to commit intragroup adulticide. These species have some socioecological similarities, for example most live in multimale-multifemale groups, predominantly involve male-male killing, and are arboreal (Figure 4.4). It has been suggested terrestrial environments are more conducive to lethal attacks (Noë and Sluijter, 1990; Broom, Koenig and Borries, 2009; Bissonnette *et al.*, 2014).

Sex of attacker/victim		
<u><b>Male/Male</b></u> <i>Alouatta seniculus</i> <i>Ateles geoffroyi</i> <i>Brachyteles arachnoides</i> <i>Sapajus nigritus</i>		<u><b>Male/Female</b></u> <i>Papio anubis</i>
		<u><b>Female/Female</b></u> <i>Cercopithecus diana</i>
Social structure		
<u><b>Multi-male/Multi-female</b></u> <i>Alouatta seniculus</i> <i>Ateles geoffroyi</i> <i>Brachyteles arachnoides</i> <i>Sapajus nigritus</i> <i>Papio anubis</i>		<u><b>Single-male/Multi-female</b></u> <i>Cercopithecus diana</i>
Substrate		
<u><b>Arboreal</b></u> <i>Alouatta seniculus</i> <i>Ateles geoffroyi</i> <i>Brachyteles arachnoides</i> <i>Sapajus nigritus</i> <i>Cercopithecus diana</i>		<u><b>Terrestrial</b></u> <i>Papio anubis</i>
Diet		
<u><b>Frugivore<sup>a</sup></b></u> <i>Alouatta seniculus</i> <i>Brachyteles arachnoides</i> <i>Ateles geoffroyi</i> <i>Cercopithecus diana</i> <i>Sapajus nigritus</i>		<u><b>Omnivore</b></u> <i>Papio anubis</i>

<sup>a</sup> Frugivore category contains species that are categorised as frugivore or part frugivore e.g., frugivore-insectivore.

Figure 4.4: Species that only commit intragroup adulticide divided into categories based on several socioecological variables.

In Chapter three no ‘significant’ association was identified between substrate type and violence type, and in this chapter’s analysis individual adulticide types divided by sex also had not revealed an effect. However, categorisation of species that commit intergroup only, intragroup only, or both types may have identified substrate as a predictor. In ‘intragroup only’ species they are predominantly arboreal, and in these species, death may be exacerbated by falls from height, as it is an inherent risk in this environment (Bissonnette *et al.*, 2015). Interestingly the one terrestrial species to commit intragroup only adulticide *Papio anubis* did so after the female was chased into a tree, where she dropped from a branch onto the ground and was winded, whereby the male dropped onto her and delivered a fatal bite to the stomach. This was the only case in nearly 48 years of observing baboons that the researcher had seen an example of adulticide (Strum, 2020).

While some effects were identified, largely for female adulticide, it was anticipated that separating the data based on sex would provide more insight into the individual socioecological factors that influence males and females. This problem however was also observed by Gómez, Verdú, and González-Megías, (2021) in their study when exploring sex differences in lethal violence. They felt that the lack of socioecological effects may be due to resources/variables influencing adulticide at the population level rather than the species scale. It is possible that this may also explain the results of this study, however it is also suggested that further analysis should be conducted on the combined behaviours species display e.g., intragroup only adulticide, or intra and intergroup.

## 4.5 Conclusions

Male and female adulticide was very well explained by phylogeny, particularly male adulticide. Males have strong sexual and natural selection mechanisms acting on adulticide as a result of male breeding competition (Clutton-Brock, 2016) and an evolved drive for frequent mating (Thornhill and Palmer, 2000). Females are considered to have different drivers of aggression (van Schaik, 1996) and commit adulticide for defence of food/nest sites (Hinsch and Komdeur, 2017), to defend infants (Gómez, Verdú and González-Megías, 2021) and for retaliation. The results therefore indicate that in both males and females adulticide, while infrequent, has a strong evolutionary pressure.

When separated by both sex and intra and intergroup types, male intergroup adulticide was the most well explained by phylogeny. All correlations between adulticide types were significant, except male intergroup adulticide and female intragroup adulticide. Correlations between male and female adulticide types are likely due to female adulticide mainly occurring as part of a coalition with males. Coalitions regardless of sex combination, reduce immediate individual costs to the aggressors and provide reduced costs in any future engagements by altering the balance of power between groups (Wrangham, 2006).

There were four notable socio-ecological variables three of which impacted on female adulticide: territoriality, seasonal breeding, group size and coalition formation. The latter of which was also important to males. There are a few species that current evidence suggests only appear to commit intragroup adulticide and they have socioecological similarities, for example most live in multimale-multifemale groups, predominantly involve male-male killing, and are arboreal (Figure 4.4). This thesis has not identified a relationship between substrate and adulticide however, if the analysis had been conducted on the combination of adulticide types each species displayed then further effects may have been seen. A lack of correlation between socioecological factors and lethal violence was also observed by Gómez, Verdú, and González-Megías, (2021) in their study. They felt that the lack of socioecological effects may be due to resources/variables influencing adulticide at the population level rather than the species scale. It is possible that this may also explain the results of this study however, it is also suggested that further analysis should be conducted on the combined behaviours a species displays.

## CHAPTER FIVE – THE ROLE OF PROSOCIAL BEHAVIOURS ON AGGRESSION

*“...The True Human Beings. It’s what most people call themselves, to begin with. And then one day the tribe meets some other people, and gives them a name like The Other People or, if it’s not been a good day, The Enemy. If only they’d think up a name like Some More True Human Beings, it’d save a lot of trouble later on.”*

*(The Carpet People - Pratchett, 1993, p.1)*

## 5.1 Introduction

Chapter two established that there are unique forms of violence, and Chapter three showed that the five types of violence considered in this study are influenced by several socio-ecological factors, including diet type, territoriality, group size, and coalition formation. Furthermore, Chapter four identified that some ecological variables were more important than others within the context of sex specific adulticide, such as seasonal breeding, group size, D-index and coalitions. This last variable is of particular interest for this chapter, in part because coalitions are considered to form as a result of affiliative acts (Seyfarth, 1977; Muller and Mitani, 2005). Thus, prosocial cooperative interactions (Ren *et al.*, 2018) can potentially result in agonistic social exchanges. The role of cooperation and coalition formation has been significant to research on human warfare (Fry and Söderberg, 2013; Kim and Kissel, 2018) where intergroup competition and conflict is made possible via intragroup cooperation (Turchin, 2007) or at least there is a positive correlation between the two (Abbink *et al.*, 2012; but see: Thielmann and Böhm, 2016).

### 5.1.1 *The cooperative nature of humans*

Humans (*Homo sapiens*) have been suggested to be more prosocial and cooperative than any other primate (Wrangham, 2021). Human history is built on this remarkable ability to cooperate with both kin and non-kin (Feinman and Carballo, 2018) which has supported the development of intricate societies and empires over the centuries, in part through the formation of institutions or central authorities (Turchin *et al.*, 2013). The capacity to form more complex and large cooperative networks potentially evolved alongside the emergence of largescale complex warfare, because more cooperative groups are thought to have a fighting advantage over less cooperative groups (Majolo and Maréchal, 2017). Warfare between societies may operate as a potential selection mechanism that eliminate uncooperative and poorly organised societies (Turchin, 2009; Redmond and Spencer, 2012).

The development of this powerful cooperative ability has stemmed from cultural and Darwinian evolutionary pressures. Though these mechanisms are not exclusive, as a trait may evolve but culture can drive or inhibit its effect (Majolo, 2019). The evolution of cooperation is deemed to occur through mutualism (or “mutually beneficial” when describing within species cooperation – West, Griffin and Gardner, 2007), kin selection, where characteristics favour the survival of genetic relatives (Maynard-Smith, 1964), and reciprocity, involving an

exchange of benefits between non-kin, now or in the future (termed ‘reciprocal altruism’ by Trivers, 1971). All three routes could lead to a form of cooperation (Grinnell, Packer and Pusey, 1995; Nowak, 2006) and may be important in primate cooperative evolution. Certainly, cooperation observed in primates is more than kin selection or mutualism alone would anticipate (Wrangham, 2021). Reciprocal altruism can explain many costly cooperation’s between non-relatives (Watts, 2015), including human societal groups where foraging societies display frequent cooperation between unrelated group members (Boyd and Richerson, 2009). Wrangham (2021) grouped the cooperative and prosocial behaviours that seem to rise above the level of genetic self-interest under the term ‘Groupishness’. This term includes sharing resources, conforming to normative group behaviours, and paying attention to the needs of group companions (Wrangham, 2021).

Sharing of resources and support is rarely purely altruistic, whereby the act is carried out with no reciprocal reward and against genetic self-interest. Cooperative behaviours are often of benefit to each participant, for example Hemelrijk *et al.* (2015) argues that cooperative coalitions provide benefits for all members so inherently may not be altruistic. This may be due to the perceived cost/benefit shift that occurs when attacks are carried out as a group, and the resultant power and dilution effects that reduce the risk of injury and death for all within the coalition (Wrangham, 2006; Majolo *et al.*, 2020). Reciprocal altruism will result in a benefit from an action that may be delayed and so provides a direct fitness benefit (West, Griffin and Gardner, 2007), for example in non-human primates reciprocal grooming may be exchanged for coalitionary support in the future (Schino, 2007). For reciprocal altruism to evolve it must be possible to detect those that cheat or obtain benefits without reciprocity (Stephens, 1996). This results in ‘collective action’ problems which arise from the struggle between the public nature of benefits obtained through cooperation and private costs incurred (Olson, M., 1989). This is when Darwinian evolved traits may be acted on through culturally evolved mechanisms such as social norms and institutions (Pinker, 2011; Glowacki and Wrangham, 2013) thereby ensuring mutual cooperation from the group.

### *5.1.2 Non-human primate affiliative traits*

Human cooperation can be considered to share similarities with observed cooperation in other primates, particularly in regard to coalitions, conflict, and hunting (Jäggi, 2010). So, while non-human primates do not appear to display the majority of ‘groupish’ behaviours

(Wrangham, 2021) there are clear affiliative traits that can be observed in many primate species, including humans. These include acts such as allogrooming, embracing, and food sharing (Strayer and Harris 1979; Sussman et al. 2005). They are commonly observed in social species although the form and frequency of their occurrence may vary between taxa, individuals, sex, and social setting (Cheney, Seyfarth and Smuts, 1986; Sussman, Garber and Cheverud, 2005; King *et al.*, 2008; Furuichi, 2020).

Two of the most well observed affiliative behaviours are grooming and food sharing. Firstly, grooming may occur as self-grooming or allogrooming (social grooming), the latter broadly defined as an individual brushing through a conspecific's pelt (Jaeggi *et al.*, 2017) which is common in social species (Mooring, Blumstein and Stoner, 2004; Kutsukake and Clutton-Brock, 2006), including humans (Nelson and Geher, 2007; Thompson, K. P., 2010) and non-human primates (Goosen, 1987). Secondly, active food sharing has been defined as food solicitation by the recipient and offering behaviour from the possessor (Feistner and McGrew, 1989). However, the definition may also be expanded to include proactive sharing, where food is offered without solicitation, and passive food sharing where food is taken without resistance (de Waal, 1989; Wolovich *et al.*, 2006; Jaeggi and Gurven, 2013; Krupenye, Tan and Hare, 2018). This is in contrast to food transfer, when food is stolen and may be explained by agonistic rather than affiliative behaviours (Fragazy and Mason, 1983).

Several functions have been proposed for these affiliative behaviours, including hygiene (Seyfarth, 1977; Barton, 1985; Grueter *et al.*, 2013), reducing psychological stress (Terry, 1970; Schino *et al.*, 1988; Radford, Majolo and Aureli, 2016), and social bonding (Dunbar, 2013; Radford, Majolo and Aureli, 2016). These functions may be coarsely divided into two groups, maintenance functions and social functions.

### *5.1.3 The maintenance functions of affiliative behaviours*

Maintenance functions may relate to learning, nutrition, and self-comforting activities. For example, there are two key hypotheses for food sharing (the nutritional hypothesis and the informational hypothesis) which are pertinent to adult/infant exchanges, the most common type of food sharing (Feistner and McGrew, 1989). The nutritional hypothesis suggests that adults utilise food sharing to facilitate weaning and speed growth rates by sharing high quality food items with their infant (Brown *et al.* 2004, but see Jaeggi and Van Schaik, 2011 who found only limited evidence for this hypothesis). The informational hypothesis posits

that food-sharing supports infants to acquire knowledge about dietary options or food processing methods (Brown, G. R., Almond and van Bergen, 2004); (but see: Jaeggi and Van Schaik, 2011). Similarly, grooming has a clear practical function as described by the grooming-need (hygiene) hypothesis (Grueter *et al.*, 2013) in which grooming is conducted for maintenance and efficacy of the pelt (Jaeggi *et al.*, 2017). Some studies have associated grooming to terrestriality, with grooming time theoretically increasing due to the higher parasitic exposure and debris in terrestrial environments (Grueter *et al.*, 2013)

Both grooming and food-sharing behaviours have clear fitness benefits for the individual. However, there may be additional benefits to allogrooming, where operating within the context of reciprocal exchange, it may evolve a more social function in many primate species (Korstjens, Sterck and Noë, 2002; Grueter *et al.*, 2013). It is not uncommon for a behaviour, such as grooming, that evolved for one purpose e.g. hygiene, to be utilised and adapted to serve another purpose, such as social grooming (Dunbar, 1991) Similarly, food sharing may be considered to reflect a high social tolerance (Jäggi, 2010) and the affiliative behaviour of food sharing between adults evolved in species that were already sharing with infants (Jaeggi and Van Schaik, 2011). Natural selection might favour the development of these adults-adult social interactions through Trivers (1971) reciprocal altruism theory.

#### *5.1.4 The social function of affiliative behaviours – the role of reciprocity*

Reciprocal altruism is one type of return-benefit altruism that involves the exchange of acts between individuals which results in a net benefit to both parties (Trivers, 2006). This may be the basis for sharing, not only with kin but also with non-kin (Feistner and McGrew 1989; Brown *et al.*, 2004). The wider social sphere within which sharing occurs can promote group unity. For example, as group size increases, grooming time also increases with the key aim of ensuring group cohesion by addressing social demands such as forging alliances (Dunbar, 1993; but see: Grueter *et al.*, 2013). This expands grooming beyond the initial dyadic pair bonding to integration of these networks to form a larger cohesive group.

Grooming has evolved a clear social role (Dunbar and Lehmann, 2013; Grueter *et al.*, 2013) as it functions to reduce stress and to strengthen social bonds in both giver and receiver (Aureli and Yates 2009; Radford 2012; Schino *et al.* 1988). This potentially reciprocal behaviour may have been sustained through the release of the neurotransmitter oxytocin (Crockford *et al.*, 2013) or endorphins (Dunbar, 2010) during the grooming process which



inhibits pain, and stimulates ingroup bonding (Sheng *et al.*, 2013). It has been suggested that, following the evolution of reciprocal grooming, these social relationships may be maintained by exchanging allogrooming for coalitionary support or food (Watts and Mitani, 2001; Jaeggi and Gurven, 2013).

In primates, food sharing has been a primary means by which reciprocity under natural conditions has been studied in wild populations (Feistner and McGrew 1989; Brown *et al.*, 2004; Gurven 2004; de Waal 2006). Food sharing can maintain social structure and dominance hierarchies, for example, dominant males may share valuable food items, such as meat, with other group members (Knauft *et al.*, 1991). The reciprocal exchange in adults can in part take place to assist with mate choice or, in similarity to grooming, provide agonistic support, (Knauft *et al.*, 1991), which may be termed food-for-sex or food-for-support (Jäggi, 2010). The sex of the sharing dyad is relevant here as same sex sharing coevolved with coalition formation, while male–female sharing along with the opportunity for mate choice (Jaeggi and Van Schaik, 2011). Furthermore, it has been proposed that food sharing coevolved with in a foraging context with group hunting (Rose, 1997). Evolution of the group hunting behaviour would occur regardless of the level of cooperation during the hunt as long as the result was access to the kill/meat (de Waal, and Brosnan, 2006). This group cooperative action may have progressed to social coalition formation in some species depending on the level of social tolerance and the payoff structure

As discussed in previous chapters, reciprocity can be subject to collective action problems due to free riders who do not provide a cooperative share. However, it has been noted that in some species, such as chimpanzees and baboons, potential monitoring of these transactions occurs by individual members so that support may be withdrawn if an imbalance is identified (Cummins, 1998). Furthermore, rather than just ceasing the collaboration the individual may be physically punished (de Waal, 1989). However, while both direct and third-party punishment is common in human societies, non-human primates do not engage in third-party punishment (Riedl *et al.*, 2012), whereby they punish another's freeriding behaviour even when not directly harmed by that individual's actions.

### 5.1.5 *The pathways between violence and cooperation*

The reciprocal exchange of food or grooming for support and social bonding may impact on levels of violence, though the potential causal pathways may be different for different violence types.

A key aspect of lethal intra and intergroup aggression appears to be the role of coalition formation (see chapter 3, section 3.4.3). It is apparent that both food sharing and grooming may play an important role in forging social connections and may potentially be traded for social support including coalition formation. Coalitions or alliances within groups can operate proactively, for example ousting an incumbent male/s and achieving a group take-over (Komorita and Kravitz, 1983; Noë, 1992; Harcourt, 1992; Pope, 2000; Wilson, M. L. *et al.*, 2014). In addition they can have a defensive purpose, protecting members from aggression by competitors (van Schaik, 1983; Dunbar, and Lehmann, 2013) which may occur during take-over attempts (Treves, 1998; Feh, 1999; Palombit, 2015), or at territorial boundaries when defending home ranges (Kitchen and Beehner, 2007). Coalitions are not present in all social species that engage in allogrooming. The cost/benefit assessment of coalitions considers which socio-ecological conditions make coalitions advantageous (Dunbar and Lehmann, 2013). For example, the strength of affiliative associations between same sex individuals has been ascribed to the significance of intergroup competition (Strier, 1994). Under intense intergroup competition coalitions may allow the successful delivery of lethal intra and intergroup violence at potentially lower cost to the individual. Therefore, it is anticipated that both intra and intergroup adulticide will be positively, indirectly, affected by the prosocial behaviours of grooming and food sharing through their reciprocal exchange for coalitionary support (Hypothesis H<sup>1</sup>, H<sup>2</sup>, H<sup>3</sup> (grooming) and H<sup>7</sup>, H<sup>8</sup>, H<sup>9</sup> (food-sharing) – Table 5.1).

Coalitions can also be important when males and females act together to defend against infanticide (see: Hrdy, 1974; Struhsaker, 1977; Crockett, C. M. and Sekulic, 1984; Valderrama, Srikosamatara and Robinson, 1990), however this is often ineffective and only delays infanticide (Ebensperger 1998). A relationship between infanticide and coalition formation was not detected in the analysis in chapter three. Therefore, it is anticipated that food sharing and/or allogrooming will not indirectly, via coalition formation, predict infanticide (Hypothesis H<sup>6</sup>, H<sup>11</sup> – Table 5.1).

While it is likely that affiliative behaviour promotes coalitions and the escalation of aggression into lethal violence, the causal link may also operate in the opposite direction as intense levels of aggression can drive the need for coalitions. Further, it has also been suggested that primates may carry out affiliative behaviours, such as grooming, to compensate for the psychological stress endured during intergroup aggressive encounters (Terry, 1970), thereby reducing both intra and intergroup social tension after engagement (Mitani and Watts 2010). Other studies have also identified the benefits of affiliative behaviours, such as grooming and food-sharing, on intragroup aggression through establishing and maintaining social status (Surbeck, Mundry and Hohmann, 2011) and improving resource allocation (Mitani and Watts 2010). However, strong male affiliations to monopolise resources e.g., females, does not always lead to tolerant intragroup male relationships (Vehrencamp, 1983). Given the relationship between intergroup aggression and grooming to reduce tension following engagement it is anticipated there will be a correlation between intergroup aggression and allogrooming (Hypothesis H<sup>4</sup> – Table 5.1) and furthermore as grooming and food sharing has been identified to aid in social order and resource allocation these affiliative behaviours will be correlated with intragroup aggression (Hypotheses H<sup>5</sup> and H<sup>10</sup> – Table 5.1).

Brown *et al.*, (2004) argue that affiliative behaviours may simply occur between closely ranked individuals and are not causally linked in either direction with violence types. This being the case it is likely, these affiliative and violent behaviours are correlated through other socio-ecological factors as discussed in chapters three, four and earlier in this chapter, including substrate type, group size and diet (Figure 5.1). However, there is evidence to indicate a link between cooperation and intergroup violence, though the latter's role as an evolutionary driver of within-group social behaviour remains unclear (Bowles, 2009). Through a comparative analysis of specific affiliative behaviours and violence types, it is anticipated an understanding of their evolutionary roles and interplay may be identified.

### 5.1.6 Hypotheses

Based on the literature review, this research aimed to explore the potential relationships between prosocial behaviours (food-sharing, allogrooming and coalition formation), and five violence types. Thus, a series of eleven hypotheses were developed (Table 5.1).

*Table 5.1: Hypotheses proposed between prosocial behaviours and specific violence types*

No.	Hypothesis to be tested
<b>Grooming (Grooming dataset)</b>	
H <sup>1</sup>	Given that intergroup adulticide is positively affected by coalition formation, it is anticipated that allogrooming will positively affect intergroup adulticide, indirectly via its effect on coalition formation.
H <sup>2</sup>	Given that intragroup adulticide is positively affected by coalition formation, it is anticipated that allogrooming will positively affect intragroup adulticide, indirectly via its effect on coalition formation.
H <sup>3</sup>	Allogrooming time will positively affect coalition formation.
H <sup>4</sup>	As allogrooming has the proximate functions of social bonding and stress reductions it is anticipated that allogrooming and intergroup aggression will be correlated.
H <sup>5</sup>	As allogrooming has the proximate functions of social status and resource allocation it is anticipated that allogrooming and intragroup aggression will be correlated.
H <sup>6</sup>	There will be no direct effect of allogrooming on infanticide.
<b>Food sharing (food-sharing dataset)</b>	
H <sup>7</sup>	Given that intergroup adulticide is positively affected by coalition formation, it is anticipated that food-sharing will positively affect intergroup adulticide, indirectly via its effect on coalition formation.
H <sup>8</sup>	Given that intragroup adulticide is positively affected by coalition formation, it is anticipated that food-sharing will positively affect intragroup adulticide, indirectly via its effect on coalition formation.
H <sup>9</sup>	Adult food sharing will positively affect coalition formation.
H <sup>10</sup>	Adult food sharing will be negatively correlated to intragroup aggression.
H <sup>11</sup>	There will be no direct effect of food sharing on infanticide.

## 5.2 Method

### 5.2.1 Data collection

The dataset built upon the one detailed in the earlier chapter (chapter 3, section 3.2.1) to include data on the following prosocial behaviours; food-sharing, grooming, ‘time-social’. Definitions, coding, and data type utilised for each predictor variable are described in Table 5.2.

Food-sharing data (voluntary transfer by food motivated individuals of defensible food to others - Feistner and McGrew, 1989) were primarily obtained from Jaeggi and Van Schaik (2011). Additional species were added following a further systematic review of the primatological literature published up to August 2021. Sources included; Google Scholar (<http://scholar.google.com>), ProQuest Dissertations & Theses Global, academic books and websites such as ‘All the World’s Primates’ (<https://alltheworldsprimates.org/>) (Rowe and Myers, 2016), and the Animal Diversity Web (<http://www.animaldiversity.org>). To narrow the search the following keyword search terms were utilised; "food", "sharing", "food sharing" and "food-sharing". Further, data were obtained from part two of the distributed survey (see chapter 3.2.1 and Appendix 2A). Food sharing was recorded as present if conspecific transfer occurred between adults and absent if food sharing only to infants. Furthermore, in line with the methods of Jaeggi and Van Schaik (2011) food-sharing was recorded as absent if no sharing had been described despite considerable study effort (in this instance, searching with specified keywords across the range of sources).

Grooming data (time the average individual spends in conspecific social grooming) was primarily obtained from Grueter *et al.*, (2013). Further data were obtained utilising the search method stated above but using the following keyword searches “grooming” and “allogrooming”. Data were available in quantitative and qualitative form within the literature, though quantitative (percentage of individuals activity budget) was selected over qualitative where it was available to minimise subjectivity. However, qualitative data was used in five cases where the term ‘rare’ was utilised. ‘Observed’ was removed as there was no clear way to convert this into reliable quantitative data. For two species *Propithecus edwardsi* and *Varecia variegata* data was provided by sex dyad. This was combined and the mean obtained. It is possible therefore that there is an over or under representation of group grooming as equal weighting was given to each dyad.

While individual affiliative behaviours offer insights into their role on specific aggression types, arguments have been made for the benefits of considering all social behaviour as an amalgamated measure of investment in social relationships (Shultz and Dunbar, 2007). This combined ‘social activity’ may allow for better comparative analysis across taxa, beyond primates, where bondedness does not always have a clearly defined measure, as grooming does in primates (Shultz and Dunbar, 2007). Following Sussman and Chapman (2004) ‘time social’ was recorded, which only included active social interactions and excluded passive interactions such as resting in contact or social communication (Table 5.2 – detailed definition). Again, existing published datasets were utilised including Sussman and Chapman (2004) and Campbell *et al.*, (2010). This was expanded using the aforementioned literature search but using the keywords “time social”, “social time”, “time-budget” and “activity-budget”.

### 5.2.2 Dataset sub-groupings

When the data were collected for the additional variables, it was apparent that some information was not available for certain variables in some species. When species were collated where information for all variables were present this resulted in a dataset of 46 species/sub-species. This number could be greatly expanded upon if sub-datasets were created that looked at the specific affiliative variables in turn (Table 5.3).

### 5.2.3 Factor analysis of mixed data (FAMD)

To check for collinearity between variables a factor analysis of mixed data (FAMD) was carried out (Appendix 5A). This is a method based on principal component analysis that is designed to analyse qualitative and quantitative data (Pagès 2004). The analysis was carried out on the ‘combined dataset’ which incorporated all the potential variables that would be used in the analysis. Of particular relevance for the analysis was the correlation that may be present between terrestriality, grooming time and coalitions. Terrestriality was identified as a possible confounding variable on the pathway diagram (Figure 5.1). Additionally, Dunbar (2013) identified a confound between terrestriality and other aspects of sociality that may have affected previous studies.

Table 5.2: Model predictor variables with definitions, coding, and data type.

Variables	Definition and coding	Data type
Food-Sharing <sup>a</sup>	<p>Food sharing is considered to be when there is the voluntary transfer by food motivated individuals of defensible food to others (Feistner and McGrew, 1989). This did not include passive food transfer or theft.</p> <p>Initially recorded, following the work of Jaeggi and Van Schaik (2011) using their three-point coding system, then divided into two groups for this analysis as adult food sharing was of primary interest.</p> <ul style="list-style-type: none"> <li>• Food sharing with adults and infants = 1</li> <li>• No food sharing or only food sharing with infants = 0</li> </ul>	Binary 0/1
Grooming <sup>b</sup>	<p>The time the average individual spends allogrooming, considered as a percentage of their activity budget.</p> <p>A mean was taken from the data available if it did not relate to a specific population where data was already included. Where there was data from a specific study that was already being used then this was included.</p>	Continuous 100% = 1
Time-social	<p>Time-social (Social activity) has been broadly defined as all intragroup active non-maintenance affiliative and non-affiliative behaviours including, but not limited to, social grooming, social play, agonistic behaviour, territorial behaviour (Shultz and Dunbar, 2007), active alliance formation and food sharing (Sussman and Chapman, 2004). There were some descriptive differences between studies (see Sussman, 2004 regarding data reliability).</p> <p>The mean was calculated when data was available from several populations or groups due to the individual variation that may occur if data was not available for the same population/s as the aggression data.</p>	Continuous 100% = 1
Coalitions	<p>These variables are described in Table 3.3 in section 3.2 and the data was transferred from the dataset using in that part of the study.</p>	Categorical Yes/No
Group size	<p>Definition based on social grouping as per Chapter three, Table 3.3.</p>	Continuous
Frugivory	<p>A broad definition of frugivory was applied. As such when any degree of frugivory was present then the species was classified as a frugivore (“yes”). If no fruits are consumed as part of the diet, then “no”.</p>	Categorical Yes/No
Terrestriality	<p>Substrate data as described in Table 3.3 in section 3.2 was converted into Yes/No to describe whether the species was or was not terrestrial.</p>	Categorical Yes/No

a Primarily adapted from Jaeggi & Van Schaik (2011).

b Primarily obtained from Gruter *et al.*, (2013) and Campbell *et al.*, (2010).

c Largely obtained from Campbell *et al.*, (2010) and Sussman and Chapman (2004).

Table 5.3: Sub-datasets for each key variable and the combined variable dataset.

Sub-dataset	Variables <sup>ab</sup>	Number of species/sub-species (species tree)
Grooming	Grooming	68 (Appendix 5B.1)
Food-sharing	Food-sharing	61 (Appendix 5B.2)
Time social	Time social	77 (Appendix 5B.3)
Combined	Grooming, food-sharing, terrestriality, group-size, frugivory.	46 (Appendix 5B.4)

a All sub-datasets contained the five aggression variables and coalition data.

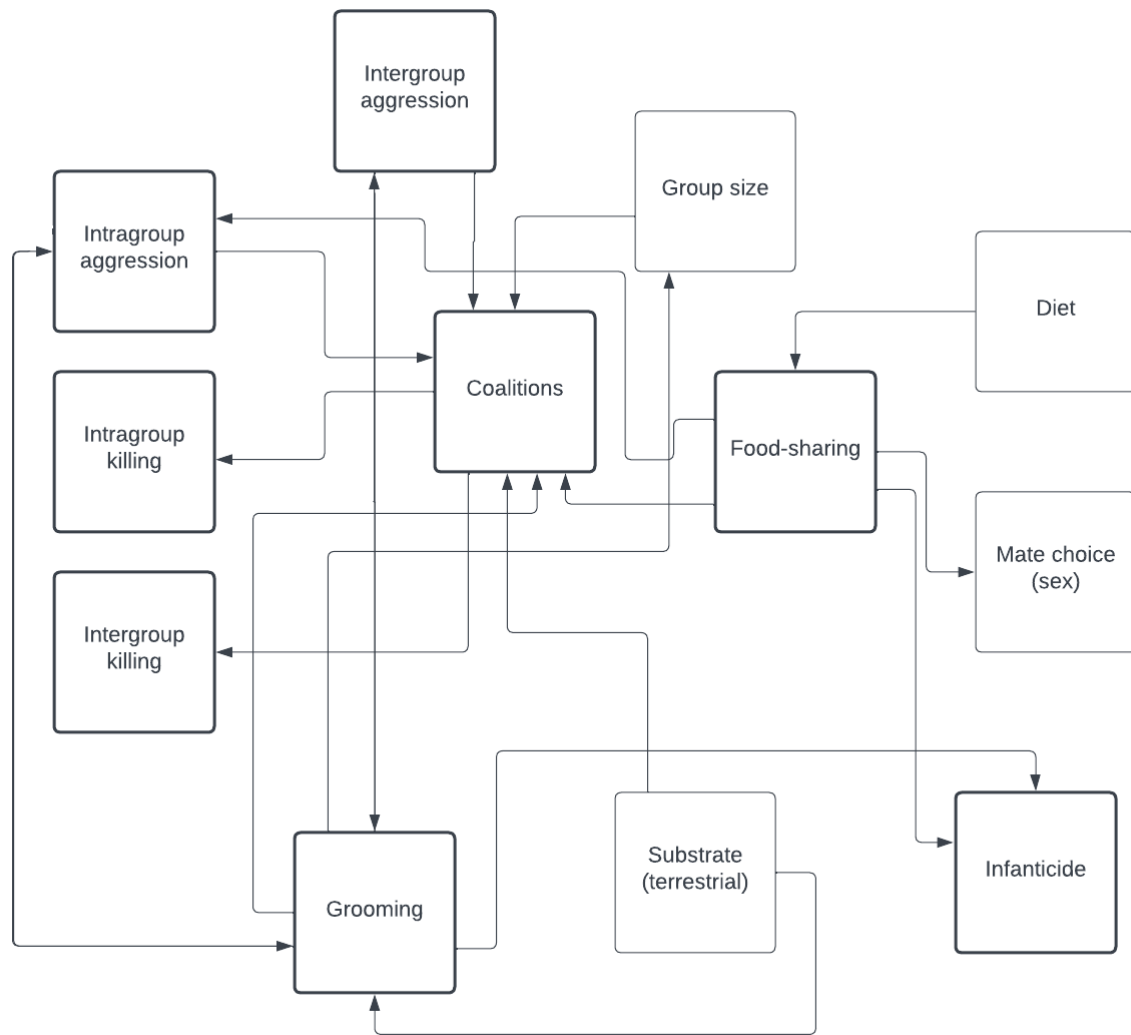
b Definitions for these variables can be found in Table 5.2.

#### 5.2.4. Statistical analysis and model construction

As per the previous chapters, analysis on the sub-datasets was carried out using Bayesian multivariate modelling utilising the Stan probabilistic programming language (Carpenter *et al.*, 2017) and the high-level interface ‘brms’ package version 2.14.0 (Bürkner, 2017) in R version 4.0.2 (R Core Team, 2020). A path diagram used to visualise the interactions between variables (Figure 5.1) was also utilised to aid in building the six models (Table 5.4).

The models were designed to test a series of hypotheses that considered the pathways (direct only, indirect only, or direct and indirect) between specific prosocial behaviours (grooming and food-sharing) and the five violence types while controlling for phylogenetic non-independence (Figure 5.2). The results of the FAMD revealed no correlation between the variables, particularly terrestriality with coalitions, lethal aggression types and grooming. Therefore, there was no requirement to control for terrestriality in the model as to be a confounding variable correlation would be required with the outcome variable and at least one predictor. Furthermore, no relationship was identified in earlier analysis between terrestriality, coalition formation or violence types (chapter 3, section 3.3.2).

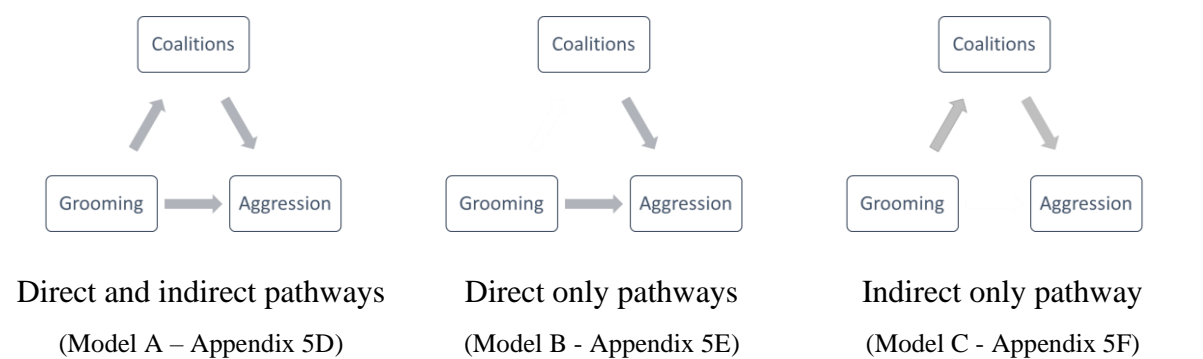




*Figure 5.1: Path diagram indicating the likely paths between variables extracted from the literature. Identifying dependent and independent variables can be difficult to untangle (Shultz and Dunbar, 2022), however the five violence types were defined as dependent/outcomes. Unlike directed acyclic graphs (DAG) this cyclical path diagram uses double headed arrows to identify when effects could go either way (correlation).*


Families were set for the outcome variables as per the previous chapter and the models set to run for four chains, each with iterations ranging from 4000-8000 iterations (2000 warmup, resulting in 8000 posterior samples) (Appendix 5C). The R-hat convergence diagnostic was reviewed on the output and found to be  $\leq 1.01$  indicating the chains had well mixed (Bürkner, 2017). Additionally, plots were also checked to ensure the chains had merged (Appendices 5E-F). The models were compared using the brms ‘Loo-Compare’ function and using k-fold cross-validation. K-fold is like loo and waic validation methods in that it produces an object with a similar structure (Bürkner, n.d.). However, the k-fold method randomly partitions the

sample into k-equal sized subsamples, which for this analysis was k-10 (ten subsamples) and then the model is fitted again with one of the sub-sets left out each time (Bürkner, n.d.).



*Figure 5.2: The three pathway models to be tested. Grooming in the model is replace for food-sharing when testing this prosocial behaviour.*

Table 5.4: The six main models and sub-models used to test variable interaction and possible pathway along with the name of the dataset used.

	Model No.	Model formula in 	Pathway	Dataset name
Adulticide	A(i)	OG_Killing ~ Grooming + Coalition + (1   gr(SpeciesTree, cov = A)) IG_Killing ~ Grooming + Coalition + (1   gr(SpeciesTree, cov = A)) Coalition ~ Grooming + (1   gr(SpeciesTree, cov = A))	Direct and indirect	Grooming
	B(i)	OG_Killing ~ Grooming + Coalition + (1   p   gr(SpeciesTree, cov = A)) IG_Killing ~ Grooming + Coalition + (1   p   gr(SpeciesTree, cov = A))	Direct only	Grooming
	C(i)	OG_Killing ~ Coalition + (1   gr(SpeciesTree, cov = A)) IG_Killing ~ Coalition + (1   gr(SpeciesTree, cov = A)) Coalition ~ Grooming + (1   gr(SpeciesTree, cov = A))	Indirect only	Grooming
	A(ii)	OG_Killing ~ Food_Sharing_AandI + Coalition + (1   gr(SpeciesTree, cov = A)) IG_Killing ~ Food_Sharing_AandI + Coalition + (1   gr(SpeciesTree, cov = A)) Coalition ~ Food_Sharing_AandI + (1   gr(SpeciesTree, cov = A))	Direct and indirect	Food-sharing
	B(ii)	<i>OG_Killing ~ Food_Sharing_AandI + Coalition + (1   p   gr(SpeciesTree, cov = A))</i> <i>IG_Killing ~ Food_Sharing_AandI + Coalition + (1   p   gr(SpeciesTree, cov = A))</i>	Direct only	Food-sharing
	C(ii)	<i>OG_Killing ~ Coalition + (1   gr(SpeciesTree, cov = A))</i> <i>IG_Killing ~ Coalition + (1   gr(SpeciesTree, cov = A))</i> <i>Coalition ~ Food_Sharing_AandI + (1   gr(SpeciesTree, cov = A))</i>	Indirect only	Food-sharing
	A(iii)	Infanticide ~ Grooming + Coalition + (1   gr(SpeciesTree, cov = A)) Coalition ~ Grooming + (1   gr(SpeciesTree, cov = A))	Direct and indirect	Grooming
	B(iii)	Infanticide ~ Grooming + Coalition + (1   p   gr(SpeciesTree, cov = A))	Direct only	Grooming
	C(iii)	Infanticide ~ Coalition + (1   gr(SpeciesTree, cov = A)) Coalition ~ Grooming + (1   gr(SpeciesTree, cov = A))	Indirect only	Grooming
	A(iv)	Infanticide ~ Food_Sharing_AandI + Coalition + (1   gr(SpeciesTree, cov = A))	Direct and indirect	Food-sharing

Non-lethal aggression		Coalition ~ Food_Sharing_AandI + (1   gr(SpeciesTree, cov = A))		
	B(iv)	Infanticide ~ Food_Sharing_AandI + Coalition + (1   p   gr(SpeciesTree, cov = A))	Direct only	Food-sharing
	C(iv)	Infanticide ~ Coalition + (1   gr(SpeciesTree, cov = A))	Indirect only	Food-sharing
		Coalition ~ Food_Sharing_AandI + (1   gr(SpeciesTree, cov = A))		
	A(v)	OG_Aggression ~ Food_Sharing_AandI + Coalition + (1   gr(SpeciesTree, cov = A))	Direct and indirect	Food-sharing
		IG_Aggression ~ Food_Sharing_AandI + Coalition + (1   gr(SpeciesTree, cov = A))		
		Coalition ~ Food_Sharing_AandI + (1   gr(SpeciesTree, cov = A))		
	B(v)	OG_Aggression ~ Food_Sharing_AandI + Coalition + (1   p   gr(SpeciesTree, cov = A))	Direct only	Food-sharing
		IG_Aggression ~ Food_Sharing_AandI + Coalition + (1   p   gr(SpeciesTree, cov = A))		
	C(v)	OG_Aggression ~ Coalition + (1   gr(SpeciesTree, cov = A))	Indirect only	Food-sharing
Cor	D(i)	OG_Aggression ~ 1 + (1   p   gr(SpeciesTree, cov = A))	Correlation	Grooming
		IG_Aggression ~ 1 + (1   p   gr(SpeciesTree, cov = A))		
		Grooming ~ 1 + (1   p   gr(SpeciesTree, cov = A))		
Time-Social	E(i)	OG_Killing ~ Time_Social + (1   p   gr(SpeciesTree, cov = A))	Direct	Time-social
		Infanticide ~ Time_Social + (1   p   gr(SpeciesTree, cov = A))		
	E(ii)	OG_Aggression ~ Time_Social + (1   p   gr(SpeciesTree, cov = A))	Direct	Time-social
Mixed	F(i)	IG_Killing ~ Grooming + Food_Sharing_AandI + Coalition + (1   p   gr(SpeciesTree, cov = A))		Complete
		OG_Killing ~ Grooming + Food_Sharing_AandI + Coalition + (1   p   gr(SpeciesTree, cov = A))		
		Infanticide ~ Grooming + Food_Sharing_AandI + Coalition + (1   p   gr(SpeciesTree, cov = A))		

a Due to the potential biasing pathway between grooming and intra and intergroup aggression as a result of the bi-directional effect  $H^4$ ,  $H^5$  and  $H^{10}$  will also be calculated within a separate correlation model 'Cor', while again controlling for phylogeny.

### 5.3 Results

#### 5.3.1 Descriptive statistics

Data were analysed for a total of 91 species distributed across three datasets containing grooming, food-sharing and ‘time-social’ data. The 68 species in the grooming dataset had a grooming range of 0-23.4%. The highest grooming species (*Macaca fuscata*, *Theropithecus gelada*, *Macaca arctoides* and *Papio ursinus*) were all terrestrial and form coalitions. The four lowest grooming species (*Alouatta palliata*, *Brachyteles arachnoides*, *Brachyteles hypoxanthus* and *Hylobates moloch*) were all primarily arboreal and all bar *H. moloch* have been known to form coalitions. The food-sharing dataset contained 61 species with 26.2% of these engaged in food sharing between adults. These included *Pithecia pithecia*, *Saguinus mystax*, *Sapajus apella* and *Varecia variegata*. The third variable/dataset ‘Time-social’, contained 77 species, and social time ranged from 0-24%. *Chlorocebus pygerythrus*, *Macaca fuscata*, *Macaca nigra* and *Pan troglodytes schweinfurthii* devoted the highest percentage of their activity budget to social activity.

#### 5.3.2 Effects and correlations

The six models (as defined in Table 5.4) tested the 11 hypotheses and obtained evidence to support three (Table 5.5 - includes signposting to the raw results). While support for a hypothesis is firstly determined by having a result where the credible interval (CI) is clear of zero, further interpretation can be obtained from the trace and density plots (Figure 5.3, and Appendices E to J for the full range) and calculating the percentage of posterior samples above and below zero, as Bürkner *et al.*, (2022) strongly argue that arbitrary cut-offs should not be applied to establish the presence of an effect. This method identified the positive effect of food sharing on intragroup adulticide (3.01; 95% CI = -0.45- 8.40) (H<sup>8</sup> – Appendix 5D.2, 5E.2, 5J.1) and grooming as a positive predictor of coalition formation (61.12; 95% CI = -105.27 – 415.06) (H<sup>3</sup> - Appendix 5D.3, 5D.5, 5F.5); Food sharing as a negative predictor of infanticide -11.53 (82.15 - -8.73) (H<sup>11</sup> - Appendix 5E.4)

While not formally tested within this chapter the models also identified coalition formation as a positive predictor of intragroup adulticide (5.84; 95% CI = 0.73 - 12.16) (Appendix 5D.1, 5D.2, 5E.1, 5E.2, 5F.1, 5F.2, 5I.1). After assessing the trace plots and posterior samples also identified coalition formation as a positive predictor of intergroup adulticide (2.73; 95% CI = 0.11-8.38) (Appendix 5D.1, 5D.2, 5E.1, 5E.2, 5F.1, 5F.2). These findings confirm the results

obtained in chapter three. Furthermore, coalition formation as a negative predictor of infanticide (2.61; 95% CI = -2.29 – 9.09) (Appendix 5D.3, 5F.3), and intergroup aggression was a positive predictor of time social (4.03; 95% CI = -1.76 – 9.74) (Appendix 5H.2).

*Table 5.5: Results of the hypothesis testing - including signposting to raw data.*

No.	Hypothesis to be tested	Output (Appendices)	Supported
Grooming (Grooming dataset)			
H <sup>1</sup>	Given that intergroup adulticide is positively affected by coalition formation, it is anticipated that allogrooming will positively affect intergroup adulticide, indirectly via its effect on coalition formation.	5E.1, 5F.1, 5G.1 5E1-6 & 5G1-6	No
H <sup>2</sup>	Given that intragroup adulticide is positively affected by coalition formation, it is anticipated that allogrooming will positively affect intragroup adulticide, indirectly via its effect on coalition formation.		No
H <sup>3</sup>	Allogrooming time will positively affect coalition formation.	5E.5, 5F.5, 5G.5, 5J.1	Yes <sup>a</sup>
H <sup>4</sup>	As allogrooming has the proximate functions of social bonding and stress reductions it is anticipated that allogrooming and intergroup aggression will be correlated.		No
H <sup>5</sup>	As allogrooming has the proximate functions of social status and resource allocation it is anticipated that allogrooming and intragroup aggression will be correlated.		No
H <sup>6</sup>	There will be no direct effect of allogrooming on infanticide.		Yes
Food sharing (food-sharing dataset)			
H <sup>7</sup>	Given that intergroup adulticide is positively affected by coalition formation, it is anticipated that food-sharing will positively affect intergroup adulticide, indirectly via its effect on coalition formation.	5E.2, 5F.2, 5G.2 5E1-6 & 5G1-3, 5J.1	No
H <sup>8</sup>	Given that intragroup adulticide is positively affected by coalition formation, it is anticipated that food-sharing will positively affect intragroup adulticide, indirectly via its effect on coalition formation.		Yes <sup>a</sup>
H <sup>9</sup>	Adult food sharing will positively affect coalition formation.	5E1-6 & 5G1-3, 5J.1	No
H <sup>10</sup>	Adult food sharing will be negatively correlated to intragroup aggression.		No <sup>b</sup>
H <sup>11</sup>	There will be no direct effect of food sharing on infanticide.		No <sup>a</sup>

a The credible interval containing 95% of the posterior samples contained 0, however, as a high percentage of the posterior sample was to the right of zero an effect can be determined (see Figure 5.3).

b A positive relationship was identified between adult food sharing and intragroup aggression (0.68; 95% CI = -0.28- 1.69) (Appendix 5D.6).

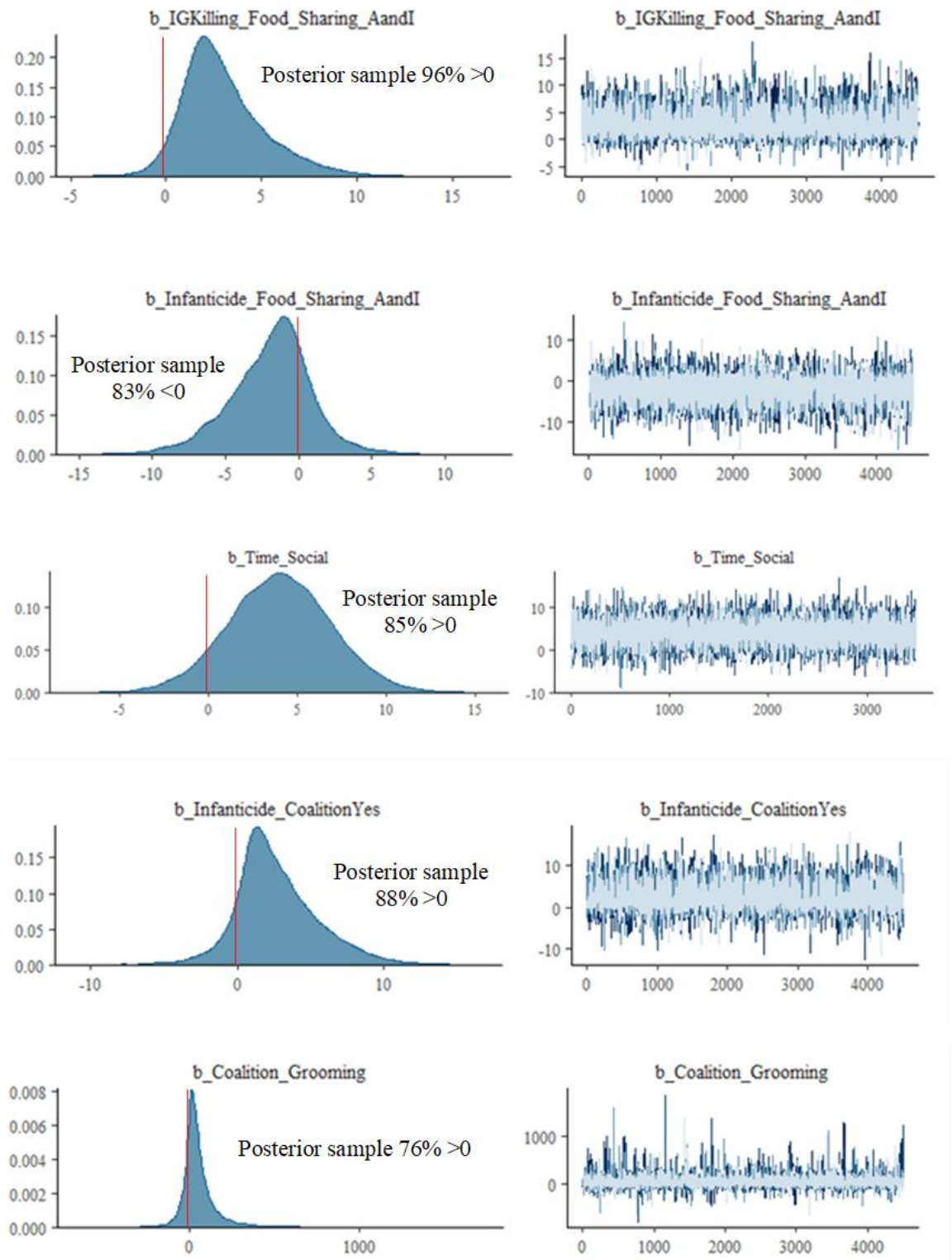


Figure 5.3: Selected trace and density plots for the  $\beta$  population level coefficients (standardized regression coefficients). While all have credible intervals that pass through zero indicating not enough evidence to support an effect following the frequentist approach, they do have a large posterior distribution to the right of the zero line as indicated by the percentage.

### 5.3.3 Model results

The six models, controlling for phylogenetic non-independence, determined how much variance could be explained by the prosocial predictor variables (Table 5.6). Additionally, through model comparison, the favoured pathway model for each violence type was identified (Table 5.7). The preferred adulticidal multivariate model for both grooming and food-sharing was Model B - two independent direct pathways (Appendix 5E.1 and 5E.2).  $R^2$  values were similar for intragroup adulticide and intergroup adulticide models at 41.1% and 45.4% respectively for grooming, and 63.3% and 46.0% respectively for food-sharing. Likewise, the preferred infanticidal model incorporating grooming or food-sharing was Model B – two independent direct pathways. High  $R^2$  values were reported for food-sharing (80.6%) and grooming (69.3%), though a slightly higher  $R^2$  value was reported for grooming's effect on infanticide via the indirect effect model (70.4%). Though model comparison did not identify this as the preferred model.

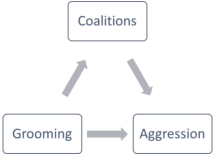
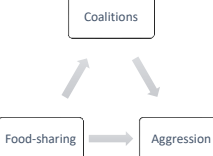
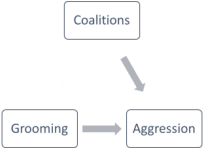
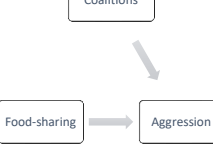
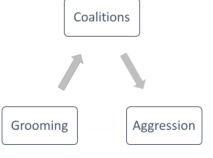
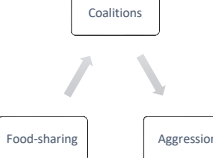
For non-lethal aggression, the favoured food-sharing model was Model B - two independent direct effects. The  $R^2$  values for this pathway model were 5.6% for the intergroup aggression data and 38.5% for intragroup aggression. The preferred multiple regression model, assessing the effect of grooming on non-lethal aggression, was also the two direct effects model, however the intergroup aggression result warrants caution due to the potential biasing path that exists between grooming and intergroup aggression (see Figure 5.1). The correlation model between grooming and intra/intergroup aggression found no 'significant' association between the grooming and aggression variables.

'Time-social' and the 'Combined' dataset both measured a combination of variables to understand any combined effect. The time-social model, which included all intragroup social behaviour as a continuous variable, explained a moderate amount of the variance in the intergroup adulticide data (32.6%) and a low/moderate amount of variance in the infanticide data (18.9%). In contrast the 'Combined' dataset, which incorporated the predictors; coalition formation (binary), food-sharing (categorical), and grooming (continuous), explained 49.8% of the variance in the intergroup adulticide data and a high proportion of the variance in the infanticide data (79.7%).

Additionally, the models identified that phylogeny explained 37% of the variance in the grooming data (Appendix 5G.1). Furthermore, variance in the coalition data explained by food-sharing was 87.3% (Appendix 5D.4) and by grooming 88.4% (Appendix 5D.3).



Table 5.6:  $R^2$  values produced by the models focusing on specific variables

Grooming Causal pathway		Grooming R <sup>2</sup> (Q2.5-Q97.5)					Food-sharing Causal pathway	Food-Sharing R <sup>2</sup> (Q2.5-Q97.5)				
		IG kill 0.606	OG kill 0.477	Infanticide 0.253	OG Agg 0.015	IG Agg 0.269		IG kill 0.606	OG kill 0.477	Infanticide 0.253	OG Agg 0.015	IG Agg 0.269
A		0.369 (0.096-0.757)	0.426 (0.070-0.895)	0.684 (0.105-0.975)	0.046 (0.002-0.194)	0.358 (0.080-0.627)		0.600 (0.197-0.924)	0.371 (0.058-0.885)	0.735 (0.250-0.967)	0.064 (0.005-0.191)	0.385 (0.110-0.679)
		0.411 (0.128-0.764)	0.454 (0.116-0.884)	0.693 (0.111-0.998)	0.040 (0.002-0.170)	0.360 (0.080-0.631)		0.633 (0.253-0.930)	0.460 (0.100-0.928)	0.806 (0.0249-1.00)	0.056 (0.004-0.171)	0.385 (0.112-0.676)
C		0.371 (0.088-0.760)	0.409 (0.064-0.887)	0.704 (0.132-0.976)	0.039 (0.001-0.161)	0.346 (0.072-0.632)		0.531 (0.121-0.908)	0.297 (0.037-0.816)	0.634 (0.113-0.950)	0.053 (0.002-0.169)	0.333 (0.094-0.620)
Model descriptor		Time-Social R <sup>2</sup>			Model descriptor	Mixed data (additional socio-ecological variables)						
		OG Kill	Infanticide	OG Agg		OG Kill	IG Kill	Infanticide				
E	Time-Social ~ Aggression	0.326 (0.016 - 0.830)	0.189 (0.012 - 0.545)	0.039 (0.002 - 0.128)	F	Combined model ~ Aggression	0.498 ( )	0.493 ( )	0.797 ( )			

a  $R^2$  in blue is the phylogenetic analysis in chapter one using a wider data set. The values are provided for information and not for comparison to these results due to sample size differences.

$R^2$  value the greatest for this aggression type across the three models.

$R^2$  greatest for this aggression type across the three models and also the phylogenetic only  $R^2$  from chapter 1.

Table 5.7: Model comparison results for adulticide, infanticide and non-lethal aggression with the alternative pathways <sup>a</sup>

Grooming					Food-sharing				
			<i>elpd_diff</i>	<i>se_diff</i>			<i>elpd_diff</i>	<i>se_diff</i>	
Adulticide	<i>loo2LG</i>	Direct effect	0.0	0.0	Adulticide	<i>loo2LF</i>	Direct effect	0.0	0.0
	<i>loo1LG</i>	Direct and indirect effect	-47.7	2.6		<i>loo3LF</i>	Indirect effect only	-42.4	3.3
	<i>loo3LG</i>	Indirect effect only	-47.8	2.7		<i>loo1LF</i>	Direct and indirect effect	-43.5	3.5
			<i>elpd_diff</i>	<i>se_diff</i>			<i>elpd_diff</i>	<i>se_diff</i>	
Infanticide	<i>Loo2infG</i>	Direct effect	0.0	0.0	Infanticide	<i>loo2infF</i>	Direct effect	0.0	0.0
	<i>Loo1infG</i>	Direct and indirect effect	-47.4	2.5		<i>loo3infF</i>	Indirect effect only	-40.1	3.1
	<i>loo3infG</i>	Indirect effect only	49.4	2.6		<i>loo1infF</i>	Direct and indirect effect	-40.4	3.0
<i>Non-lethal grooming pathway models not compared</i>							<i>elpd_diff</i>	<i>se_diff</i>	
					Non-lethal aggression	<i>loo2AGF</i>	Direct effect	0.0	0.0
						<i>loo3AGF</i>	Indirect effect only	-38.8	3.0
						<i>loo1AGF</i>	Direct and indirect effect	-40.6	2.9

<sup>a</sup> Model comparison via brms Loo-Compare using k-fold cross-validation

## 5.4 Discussion

Affiliative traits such as allogrooming and food sharing can be observed in many primate species, including humans (Strayer and Harris, 1979; Sussman, Garber and Cheverud, 2005). There are some compelling arguments that these prosocial acts may directly and indirectly influence levels of violence, for example via coalition formation or through increasing social tolerance (Seyfarth and Cheney, 1984; Watts and Mitani, 2001; Jäggi, 2010; De Dreu, Balliet and Halevy, 2014). This chapter identified that allogrooming was a positive predictor of coalition formation, whereas food sharing was a positive predictor of intragroup adulticide, but a negative predictor of infanticide. The analysis also confirmed the results obtained in Chapter three, where coalition formation was a positive predictor of intragroup and intergroup adulticide. Furthermore, when using the ‘Time Social’ dataset social time was found to be a positive predictor of intergroup aggression. The analysis also identified that the preferred pathway to each violence type was a result of two independent direct effects: that of prosocial behaviour on lethal violence/aggression, and of coalition formation on lethal violence/aggression. While the preferred pathway model was the same for each violence type, the results revealed varied effects/correlations between different prosocial behaviours and violence types resulting in several hypotheses where evidence was not found in the analysis (see: Table 5.5).

### 5.4.1 Adulticide and the importance of coalitions

It was predicted that the pathway to adulticide would predominantly operate indirectly, via a pathway from the prosocial behaviours of food-sharing and/or grooming via coalitions to adulticide. This was largely due to the role of reciprocity in coalition formation and the previously established role of coalitions on adulticide (see chapter 3, section 3.3). Theories outlining an effect of grooming on coalition formation are based on social bonding between individuals with whom, through reciprocity, coalitions may be exchanged (McGrew, Marchant and Nishida, 1996; Watts and Mitani, 2001; Jaeggi and Gurven, 2013). Coalitions can provide males with fitness benefits including increased reproductive success and rank improvement (Gilby *et al.*, 2013). Therefore, males should form coalitions that offer the greatest benefit, be that with near kin or distant relatives (Mitani, Merriwether and Zhang, 2000; Langergraber, Mitani and Vigilant, 2007) and they should focus more of their efforts on these key coalitionary partners (Kudo and Dunbar, 2001). An example may be seen in

male chimpanzees who form sustained affiliative relationships and coalitions (Nishida, 1983; Boesch *et al.*, 2008; Mitani, 2009) that are founded on reciprocity and everyday social interactions (Nishida, 1983; Hemelrijk and Ek, 1991; Watts, 2002; but see: O’Hearn *et al.*, 2022 - no evidence for reciprocity between grooming and coalitions in rhesus macaques).

This study potentially identified allogrooming time as a positive predictor of coalition formation (see section 5.3.2 – weak effect), corroborating the observations of earlier studies (e.g., Watts and Mitani, 2001; Dunbar, 2010a; Jaeggi and Gurven, 2013; but not: O’Hearn *et al.*, 2022). Furthermore, it confirmed the results of Chapter three that coalition formation was a positive predictor of inter and intragroup adulticide. However, the favoured model operated via two direct pathways, that of coalitions to adulticide, and grooming to adulticide rather than the indirect route via coalition formation. Furthermore, no significant effect was found between allogrooming and adulticide. The power of the direct model is therefore likely due to the role of coalition formation in adulticide, and that these coalitions are not always formed with individuals they frequently affiliate with (e.g., O’Hearn *et al.*, 2022). Several studies have identified that a coalition may occur with other group members (see: Tokuyama and Furuichi, 2016; Kawazoe, 2021). Tokuyama and Furuichi’s (2016) observations of wild bonobos at Wamba, DRC found no evidence that females employed grooming to develop coalitions. However, more associations resulted in more opportunities to form coalitions. Agonistic support was not reciprocal but unidirectional from older to younger females. Female coalition formation was not always kin related and this is often the case in other primate species (Sterck, Watts and Van Schaik, 1997). In addition to the role of kin selection and reciprocity, Kawazoe (2021) observed in male wild Japanese macaques that the dominance of participants rather than social bond strength determined the occurrence of agonistic support. Furthermore, coalitions are not always formed in lethal aggression cases (e.g., Dias *et al.* 2010; Miller 1998; Wright, 2020; Strum, 2020).

In similarity to grooming, food-sharing in adults may be considered to be reciprocally exchanged for ‘food-for-sex’ or ‘food-for-support’ (Jäggi, 2010). However, while this current study found a positive effect between food sharing and intragroup adulticide, no effect was identified between food-sharing and coalition formation. The purpose of food sharing is likely only leading to coalition formation in a small number of species e.g., where unisex sharing occurs evolving with coalition formation (Jaeggi and Van Schaik, 2011). This current study did not consider the sex dyad which may have impacted on the model’s ability to identify a positive effect of food-sharing on coalition formation, which may then have

favoured the indirect pathway model. Additionally, in the dataset coalition formation amalgamated both intra and intergroup coalitions. Food sharing can make intra-group interactions more socially tolerant (Jäggi, 2010), which may reduce the need for coalition formation especially in species who have limited intergroup interactions or where these interactions are generally peaceful.

While there is likely a role for some prosocial behaviours (e.g., grooming) to drive coalition formation, a factor preventing its evolution in some species may be the role of cognition. Coalitions can be cognitively demanding if prosocial behaviours are used and traded to foster powerful relationships with significant allies or to strategically act to limit other alliances (Silk, 1992; Harcourt and de Waal, 1992; Schülke *et al.*, 2010). However, if these are based on calculated reciprocity, then the benefits of grooming are unlikely to be balanced against occasional coalitionary support, though grooming may provide a psychological willingness to engage (Dunbar, 2010b). Potentially therefore prosocial behaviours may create ‘friendships’ which are formed through prosocial grooming reciprocity and kin selection, but strategic coalitions are built on maximising competitive success and dominance, sometimes but not always via grooming. Therefore, in these species that are more cognitively advanced a more indirect pathway may be favoured. Without this cognitive capacity, the cognitive hypothesis would suggest a limit to the role of coalitions as an approach in aggressive interactions (Harcourt, 1992; Dunbar and Shultz, 2007). Cognition was not included as part of the modelling within this current study but would be a valuable avenue for further research utilising and expanding upon this studies dataset.

#### 5.4.2 Infanticide – the role of food-sharing and coalition formation

The food sharing model offered an improved understanding of the variance in the infanticide data over the allogrooming model (Table 5.6). Again, the results of this study revealed that the two direct effects model (model B(iv)) was the preferred explanatory model and that both coalition formation, and food sharing were identified as being negative predictors of infanticide.

The pathway between coalitions and infanticide may be based on defensive coalitions. Females form defensive coalitions to counter infanticide, for example, Valderrama *et al.*, (1990) described two incidents of mothers receiving support from another female in *Cebus olivaceus*. Likewise, Lowe *et al.* (2019) described in *Pan troglodytes schweinfurthii* an

infanticidal event when a female coalition formed trying to prevent a single intragroup male from attacking a newborn. Males may also form coalitions to protect infants and direct aggression at newcomers (Teichroeb, Sicotte and Wikberg, 2011). Unfortunately, male coalitions within multimale groups are of poor quality and often fail to prevent infanticide and male immigration (Ebensperger, 1998; Teichroeb *et al.*, 2012). It is unclear why the coalitions are poor quality (Teichroeb *et al.*, 2012) though in some species such as *C. vellerosus* male number is not as important as male quality in reducing infanticide risk (Teichroeb, Wikberg and Sicotte, 2009). Furthermore, the degree of reproductive skew, where reproduction favours one or only a few breeders, may limit the extent of coalition formation (Perry, 2012).

Species form coalitions for a range of reasons. For example, they may form proactive coalitions to oust an incumbent male/s and achieve a group take-over (Komorita and Kravitz, 1983; Noë, 1992; Harcourt, 1992; Pope, 2000; Wilson, M. L. *et al.*, 2014), or to diminish the power of neighbouring groups thereby reducing the costs of any future intergroup encounters (Wrangham, 2006). Moreover, coalitions may be defensive to prevent take-over attempts (Treves, 1998; Feh, 1999; Palombit, 2015), or defend a territorial boundary, or as outlined defend against infanticide. Due to the multiplicity of coalitionary behaviour not all species within this studies dataset form coalitions to defend against infanticide. Further analysis should consider categorising the coalition's purpose as it could identify stronger effects of coalitions on infanticide and other violence types.

A direct pathway from the prosocial behaviours of grooming and food sharing to infanticide was also included in the favoured model, and a negative effect was identified between food sharing and infanticide, where higher levels of food sharing results in lower levels of infanticide. Food sharing among adults has evolved in those species that share with infants (Jaeggi and Van Schaik, 2011). Therefore, all species in the dataset that are classified as food sharers do so with both adults and young (chapter 3 section 3.2.1 definition). Food sharing to infants as part of maternal or allomaternal care should inhibit infanticide, and similarly food sharing among adults has the effect of increasing tolerance (Jäggi, 2010). However, the purpose of food sharing among adults may not be the same in each species. Guerreiro Martins *et al.*, (2019) observed that adult to adult food sharing in marmosets predominantly related to female breeders' high energetic needs, while it serves to reinforce cooperative bonds in the more inter-reliant tamarins. This variation in the purpose of food sharing may in part explain why a stronger direct effect was not identified.

The analysis also looked for a direct effect between allogrooming and infanticide however there was not enough evidence to support the effect. Yet there have been examples of grooming leading to infanticide. Grooming offers bonding opportunities between individuals and consequently it enables group members additional close contact to infants. Collins *et al.* (1984), while observing *Papio anubis*, described the infanticidal attack by a single intragroup male on a 7-month-old infant. The attacker had groomed the infant for over 20 minutes prior to the attack, though the attack was primarily directed at the mother. Infants are vulnerable to serious injury when attacked by an adult. Therefore, death can easily occur because of a biproduct of aggression directed towards another individual with whom the infant is in close proximity. Under these circumstances it would be unlikely to lead to a strong selection pressure for the coevolution of grooming and infanticide.

Food sharing and grooming as prosocial behaviours are acting differently on infanticide. Food sharing appears to have the main role in directly reducing infanticide levels, however grooming may be operating via coalition formation to further lower infanticide rates (Figure 5.3). As described earlier in this chapter a potential positive effect of grooming on coalitions was identified. The argument was made that reciprocal grooming can strengthen social bonds and may be exchanged for coalitionary support or allow for more opportunities to form coalitionary relationships. In terms of female coalitions this support may be essential to anti-infanticidal coalitionary defence in some species. Thereby a behaviour may result from a mixture of prosocial components.

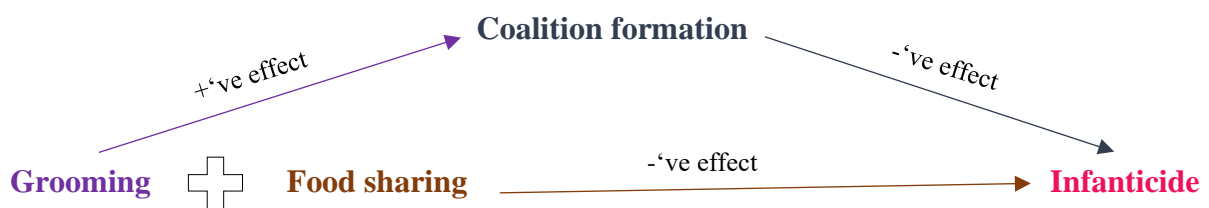


Figure 5.4: The potential utilisation of two prosocial behaviours to lower infanticide risk in some species. Grooming and food sharing operate via separate pathways but produce a combined overall effect of reducing infanticide.

### 5.4.3 Non-lethal aggression – The role of social time

Model comparison identified that the two direct effect models (model B(v) and B(vi)) from grooming/food sharing to non-lethal aggression and coalition formation to non-lethal aggression were preferred. However, the models did not identify any significant effects between the variables. In the previous chapter it was established that coalitions did not have a ‘significant’ effect on non-lethal aggression types (see chapter 3, section 3.3). This chapter confirmed those findings. In some species coalitions or alliances within groups protect members from group-living costs (van Schaik, 1983; Dunbar, and Lehmann, 2013). However, a cost benefit assessment must be made around coalitions to consider whether the local ecology or group sizes make them advantageous for intergroup encounters. In some species a coalition may provide a powerful deterrent reducing intergroup aggression but not for many species.

A direct pathway from the prosocial behaviours to non-lethal aggression was not identified in the analysis when using the separate food sharing and allogrooming datasets. However, when using the ‘Time Social’ dataset social time was identified as a positive predictor of intergroup aggression. ‘Time social’ was a combined measure containing social behaviours such as grooming, food-sharing and coalition data. However, there is a skew to grooming data as this is the most frequent behaviour included in the ‘time-social’ metric, with an estimated 80% of total social time allotted to grooming whereas <1% is due to aggressive or agonistic interactions (Sussman, Garber and Cheverud, 2005).

It has been proposed that groups may be operating in comparison with each other and therefore there may be the evolution of intergroup aggression coevolving with intragroup cooperation, where intragroup cooperative efficiency improves the capacity to cause intergroup damage (De Dreu et al, 2014). Therefore, it was anticipated that there would be an effect identified between prosocial behaviours (or ‘time social’ as a proxy) and intergroup aggression. Further, it has also been suggested that some primates may carryout grooming behaviours to compensate for the psychological stress endured during intergroup aggressive encounters (Terry, 1970; Schino *et al.*, 1988; Radford, Majolo and Aureli, 2016). However, any correlation between intergroup aggression and intragroup prosocial behaviours may depend on the social system of the species. This may affect affiliative intragroup interactions after aggressive intergroup encounters, such as cooperative breeding species which need stronger cohesion between group members when challenged by intergroup conflicts (Yi *et al.*, 2020).



Both food sharing and grooming have the potential to improve tolerance within the group. Though a negative effect was not identified by the model. Tokuyama and Furuichi (2016) identified that female bonobos affiliative interactions may be exchanged for tolerance. Similarly, Kawazoe (2021) found strong bonds predicted wild Japanese macaques to have less frequent aggressive interactions and suggested that tolerance developed during grooming may also result in increased tolerance during food-sharing and general feeding in other species. This may include the within-group scramble and contest food competition that is observed in some species dependent on diet type (see chapters 3 and 4 for discussion). Increased tolerance may therefore be tempered by intragroup feeding competition in some species, limiting the ability of the model to detect an effect of social time on intragroup aggression.

Understanding the factors affecting intragroup and especially intergroup aggression remain challenging as this study's model construction was naïve to the complexity of factors influencing non-lethal aggression. Furthermore, there are a range of functions that prosocial behaviours may have, which vary among different species and their social systems and likely evolve via different mechanisms, including kin selection and reciprocity. However, this chapter has identified some key effects between prosocial behaviours and violence types including an understanding of the independent but complementary roles each affiliative behaviour may have in overall levels of violence.

## 5.5 Conclusion

This chapter aimed to explore the relationship between intragroup prosocial behaviours (grooming, food-sharing, and coalition formation) and the five types of violence identified in Chapter two. It was anticipated that prosocial behaviours, including coalition formation, would lead to increased lethal violence and non-lethal intergroup aggression due to the suggested link between cooperation and intergroup competition (De Dreu, Balliet and Halevy, 2014; De Dreu *et al.*, 2020; De Dreu *et al.*, 2022). Chapter three had already established a positive relationship between coalition formation and adulticide, and this was confirmed by this current chapter's analysis. This chapter then went further by identifying effects between food sharing and infanticide, grooming and coalition formation, coalitions and infanticide, and social time and intergroup aggression.

Given the previously established role of coalitions on lethal aggression, and the literature indicating a reciprocal relationship between prosocial behaviours (e.g., grooming - Watts and Mitani, 2001; Jaeggi and Gurven, 2013) and coalition formation, it was anticipated that there would be an indirect effect of grooming and/or food sharing on violence, indirectly, via their effects on coalition formation. However, model comparison revealed the favoured model for all violence types was that of two independent direct effects e.g., coalition formation to infanticide, plus food sharing to infanticide.

The prosocial behaviours of grooming and food sharing are likely different evolved cooperative behaviours. While having some similar functions in social bonding and the ability to trade for sex or coalitionary support they also have distinct functions (e.g., hygiene hypothesis and nutritional informational hypothesis). While both utilising a combination of evolutionary drivers such as kin selection and reciprocal altruism the balance of these may be different between grooming and food sharing. However, while they are different, these behaviours are not mutually exclusive, and they may interact differently on each type of violence. For example, this chapter proposed that infanticide reduction may utilise grooming and food-sharing behaviours, with grooming operating indirectly via coalition formation and food-sharing operating directly on infanticide. Furthermore, prosocial behaviours of grooming and food-sharing may be distinct from coalition formation in their effects on violence. Negative correlations have been identified previously between prosocial behaviours e.g., sharing and cooperating and violence (e.g., Anderson *et al.*, 2010; McMahon *et al.*,

2013) ,which was also identified within this study, in comparison to the positive correlations between coalition formation and lethal violence types.

This study identified some connections between specific prosocial behaviours and specific violence types. More and stronger effects may be detected in future analysis by controlling for the range of socioecological factors (e.g., diet type – Surbeck (2017), dominance, sex ratio), that act in combination differently on species, population, and individuals.

Furthermore, an important avenue for further study is the role of cognition on cooperative and violent behaviours. Cooperative behaviours in some more cognitively advance species may be able to utilise prosocial behaviours more strategically through remembering these ‘tit for tat’ exchanges where longer term reciprocity will be more important.

## **CHAPTER SIX – THE EVOLUTION OF VIOLENCE IN HUMANS, AND FINAL CONCLUSIONS**

*"Clearly war had to exist. It was a cornerstone of the processes of government. It was the way the Empire got its leaders. The competitive examination system was how it got its bureaucrats and public officials, and warfare was for its leader, perhaps, only a different kind of competitive examination. Admittedly, if you lost you probably weren't allowed to re-sit next year."*

(Interesting Times - Pratchett, 1994, p.97)

### 6.1 Reviewing the aims of this thesis

The aim of this thesis was to investigate primate violence through four research questions. The first question was to determine if violence is one single trait or consists of five distinct types of violence, each with their own evolutionary trajectory. Secondly, to consider the effect of socio-ecological variables on specific violence types. Thirdly, males and females may gain different fitness benefits through engaging in certain violence types and so have different drivers of violence (van Schaik, 1996). Therefore, the study aimed to assess if male and female adulticide data would show the same phylogenetic trends as the combined, non-sex differentiated adulticide data. Lastly, this thesis aimed to consider the potential relationship between intragroup prosocial behaviours including, allogrooming, adult food-sharing and coalitionary support and the five potential violence types. The findings from these research questions have been explored in the preceding chapters largely in relation to non-human primates, therefore what remains is to consider these findings within the context of human violence.

### 6.2 The findings of this thesis in relation to the study of human violence

In chapter two, this study identified that violence can be considered as five distinct types; intra and intergroup adulticide, infanticide and intra and intergroup non-lethal aggression. There were strong/moderate phylogenetic signals associated with the lethal violence types and intragroup aggression. Intergroup aggression however was poorly explained by the phylogenetic model, potentially indicating the importance of socioecological factors. Different species within the dataset demonstrated various combinations of these lethal violence types, from none at all to all three, and also displayed non-lethal aggression to differing extents. Gómez *et al.*, (2016) discovered that a degree of lethal violence in *H. sapiens* arises due to their phylogenetic position within a particularly violent mammalian clade. This thesis added to their findings by identifying that all three lethal violence types were present in several great ape species (*Hominodea*) which includes *H. sapiens*, and in the closely related Old World monkeys (*Cercopithecidae*). Several of the great ape species also appear to be the most violent e.g., chimpanzees (*P. troglodytes*) demonstrate violent attacks that can be extreme and targeted, commonly involving, deep bite wounds, traumatic damage to the throat, genital removal, facial disfigurement, and occasionally broken bones (Muller, 2002; Wrangham, 2006). In similarity *H. sapiens* use a wide range of methods to inflict pain

and suffering, including stretching limbs, dismemberment, specifically design torture devices, burning (Mitchell, 2013) and testicle removal (Loncar, 1998). In contrast to the role of phylogeny on the presence of violence, earlier work suggested that natural aggression is not necessarily part of human evolution but due only to cultural factors. Moore (1990), for example, described the alternating peaceful and warlike tendencies of the Cheyenne hunter-gatherer tribes. Furthermore, decline in lethal violence has been observed in economically affluent societies over the last 600 years (UNODC, 2019), possibly also indicating the role of proximate socioecological factors on human violence.

Genetically humans show little variation (Mace *et al.*, 2016), certainly in comparison to other great apes (Kaessmann *et al.*, 2001), however, there is a great deal of behavioural diversity across populations and between individuals. Higher rates of lethal violence are observed within specific geographic and demographic clusters. For example, declining lethal violence rates have been observed in Europe and Asia, yet other regions experience much higher rates, and the lethal violence rate gap is widening (UNODC, 2019). Between populations, there are differing socioecological conditions, and a great deal of cultural variation (Mace *et al.*, 2016). This cultural and socioecological variation can be observed in human and non-human primates, though in humans' cultural evolution is more extensive and complex.

In chapter three, this study aimed to explore various socioecological variables on levels and types of violence. Several were predictors of specific violence types and included degree of folivory as a negative predictor of intragroup aggression, D-index (as a measure of territoriality) as a positive predictor of intergroup aggression, and coalition formation as a positive predictor of intra and intergroup adulticide. Human aggression research also links violence to certain predictors, including status/power, levels of poverty, and upbringing (Komorita and Kravitz, 1983). Inequality of resources being more strongly linked to violence than other aspects of development (UNODC, 2019). Income inequality for example is positively correlated with increasing levels of violence. For example, when economic resources are evenly distributed then violence is lower in comparison to when they are monopolised (Galtung, 1969). This shows similarity to the contest aggression that is observed in frugivores when attempting to monopolise a resource (e.g., fruit tree), in contrast to scramble competition in folivores, where resources are evenly distributed but finite (Isbell, 1991).

The positive correlation between resource inequality and human lethal violence is not as strong in all countries where a cultural context may again play a role in mediating aggression (UNODC, 2019). Different social influence creates varied behaviour (Bandura, 1977), and societal norms reduce violence levels due, in part, to the rise of the State, the strengthening rule of law, and the increase in literacy and self-discipline (UNODC, 2019). The control of violent behaviour however primarily effects intragroup interactions, as groups are characterised by these shared norms (Mace *et al.*, 2016). Normative values can also be connected to moral systems that reward or punish individuals potentially impacting on reproductive success and trait transmission (Boyd and Richerson, 2009). These moral systems can sit within a religious framework and Whitehouse and Lanman *et al.*, (2014) identified that social cohesion essential for group survival involves sociocultural traditions, such as collective sacred rituals.

Cultural evolution of a group may lead to intergroup conflict as group identity is impacted on by differences in cultural norms, political exclusion, poverty, and cultural status disparities (Langer and Brown, 2008). Intergroup conflict can occur in both human and non-human primates as they seek to secure resources or geographic areas from other groups. When using D-index as a measure of territoriality this study found a positive correlation between territoriality and intergroup aggression. No ecological factors were found to be ‘significantly’ correlated to intergroup aggression, potentially suggesting that social factors are playing a more significant role in intergroup interactions. The role of social behaviours in territoriality has also been observed in previous primate studies (van Schaik, 1996; see: Willems, Hellriegel and van Schaik, 2013; Gómez *et al.*, 2016). In humans powerful state, normative, and moral influences may lead to state sanctioned violence in the form of warfare involving a group willing to fight, potentially at great personal cost for morally significant or sacred values essential to individual and group identity (Atran and Ginges, 2015), and to protect the groups resources.

Warfare, or armed conflict involves violence or military force, threatened, or used for political ends, between two opposing sides (Ministry of Defence, 2015) and is a significant area of research across many disciplines (see: Bribiescas, 2021; Mullon and Lehmann, 2022; Smith, J. E. *et al.*, 2022; De Dreu and Triki, 2022). Warfare requires considerable cooperative within-group effort. Early human and non-human primates demonstrate cooperative behaviour, for example Pliocene human ancestors had social structures that were like those observed in social primates (Foley and Gamble, 2009) but were limited. Modern humans

however have extensive cooperative actions (Melis and Semmann, 2010), indicating a rapid evolution of cooperative behaviour. This is again likely driven by cultural evolution (Boyd and Richerson, 2009) which allows for a quicker adaption to changing environments than natural selection (Boyd and Richerson, 2005; Boyd and Richerson, 2006) both individually and at the group level (Boyd and Richerson, 2009).

An important cooperative behaviour is coalition formation, where two or more individuals or groups agree to cooperate to obtain some mutually wanted result (Komorita and Kravitz, 1983). Coalitions are employed by several competitive primate species (e.g., Macaca, Papio and Pan sp. - Smuts *et al.*, 1987; Kitchen, 2004; Olson, L. E. and Blumstein, 2009) and certainly in human warfare and gang crime. Lethal violence can be adaptive yet can also have deleterious outcomes (de Almeida, Rosa Maria Martins, Cabral and Narvaes, 2015) so by engaging in intra- and intergroup coalitions, the cost to the individual is reduced, shifting the cost benefit ratio in favour of a lethal attack. Coalition formation within this study was found to be a predictor of adulticide. However, Fry and Söderberg, (2013) questioned the importance of coalitions in lethal violence in human evolution, when finding that over 50% of sampled mobile forager bands committed lethal events with only one perpetrator. This view contradicts the findings of other studies which determined that humans have an evolved tendency to form coalitions to undertake lethal violence (see: Wrangham, 1999; Bowles, 2009; Pinker, 2011). Fry and Söderberg, (2013) stated that they considered that lethal violence had been selected against yet gave details of 148 lethal events which included violence over resources and men competing over women, which will have fitness implications for the participants. Furthermore, these mobile forager bands are egalitarian and so lethal violence may be mediated by particular social structures.

Between-group violence may result in some individuals ‘free-riding’, where some members obtain a disproportionate degree of benefits without incurring the costs. In humans, cultural norms and moral systems can result in a strong normative influence which is further strengthened when there is intergroup competition (Deutsch and Gerard, 1955) and has the benefit of limiting the risk of ‘free riding’. Control occurs through coercion, third-party punishment (Riedl *et al.*, 2012), ostracism, rewards or reputation building (Melis and Semmann, 2010). Free-riding behaviour can also be observed in non-human primate species. Furthermore, punishment of free-riders has been observed to occur (e.g. Chimpanzees - Jensen, Call and Tomasello, 2007; though rarely (Rudolf von Rohr, Burkart and Van Schaik, 2011); ‘Policing support hypothesis’ rhesus macaques - Beisner and McCowan, 2013), but not



third-party punishment (Riedl *et al.*, 2012), and not in all species (e.g. *Lemur catta*, Nunn and Deaner, (2004)) despite evolution not favouring cooperation when it is susceptible to exploitation by free riders (Boyd and Richerson, 2009). Larger groups have been linked to increased free riding in both human and non-human primates due to the lower benefits for each group member and the challenges in monitoring free-riding behaviour (Lipford, 1995; Brunner, 1998; Kitchen and Beehner, 2007; Willems, Hellriegel and van Schaik, 2013). Yet, those that do participate continue to contribute at the same level regardless of group size (Lipford, 1995; Brunner, 1998). Humans can form extremely large cooperative groups in comparison to those of non-human primates. Furthermore, in contrast to non-human primates, humans are possibly unique in their ability to understand another's belief and decide when cheaters must be punished, even when not directly affected by the cheater (Hall and Brosnan, 2017). This ability to deliver third-party punishment is aided by the gathering of indirect social information through language use which allows beneficial or detrimental reputations to be built (Melis and Semmann, 2010) and is often termed gossip (Foster, 2004; Dunbar, 2004; Nakamaru and Kawata, 2004).

In chapter five, this study analysed three prosocial behaviours; allogrooming, adult food-sharing, and again coalition formation, to understand their role in the evolution or emergence of violence types. In addition to biochemical mechanisms, primate groups have been considered to bond through reciprocal affiliative behaviours whereby they may subsequently offer coalitionary support (Watts and Mitani, 2001; Jaeggi and Gurven, 2013). An effect was identified between grooming and coalition formation, furthermore effects were identified between food sharing and infanticide, coalitions and infanticide, and social time and intergroup aggression (see Chapter five, section 5.3.2 for details). It was apparent that there were different but possibly complementary effects of each prosocial behaviour on different violence types, for example the effect of grooming on coalition formation, coalition formation on infanticide and food sharing directly on infanticide. Most effects however were not within a 95% CI, but if the analysis had been conducted at genus level, then further or stronger associations may have been established (see: Harvey & Pagel, 1991). Though several studies demonstrate contradictory findings for the role of affiliative behaviours on violence types (e.g., Mitani, Watts and Amstler, 2010; Surbeck, Mundry and Hohmann, 2011) (Vehrencamp, 1983) Nunn and Deaner, 2004).

Food sharing in humans occurs between, young and old (bidirectionally at some points) and between kin and non-kin (Kaplan *et al.*, 2005). Food sharing, particularly of hunted foods

(e.g., meat) is common among hunter-gatherer societies and there are clear protocols with the giving and receiving of food (Barrett, Dunbar and Lycett, 2002). However restricted sharing occurs when the gains from sharing are small or only occur a few times a year (Kaplan *et al.*, 2005). In humans' complex decisions are being made about when and how to cooperate based on the value of the sharable commodity, the current situation and any long-term advantages e.g., mating opportunities. In similarity to the findings in Chapter five where there was no effect of food sharing on coalition formation, human food-sharing does not always conform to patterns of reciprocal altruism (Barrett, Dunbar and Lycett, 2002). Moreover, the identified negative effect of food sharing on infanticide may also be reflected in human studies which have identified a negative correlation between prosocial behaviours e.g., sharing and cooperating, and violence (e.g., Anderson *et al.*, 2010; McMahon *et al.*, 2013). In large scale human societies group interests and social bonding in humans can be facilitated through the use of language. This occurs in part through music (e.g., the positive effect of prosocial songs on prosocial behaviour - Greitemeyer, 2009; Savage *et al.*, 2021), storytelling (Dunbar, 2022), and rituals (Whitehouse and Lanman, 2014) often involving culturally specific stories and songs uniting the group.

Demographic characteristics, such as biological sex are also important both when understanding the motivations of the perpetrator or the conditions that may lead to someone becoming a victim (UNODC, 2019). Large-scale coalitionary intergroup killings e.g., warfare, predominantly involve males as the victim and perpetrator but this is not the main cause of violent deaths in humans. Only 25% of total victims killed are through armed conflict or acts of terrorism, whereas criminal activity and interpersonal violence causes many more deaths (UNODC, 2019) – 2017 data). Lethal interpersonal violence, as a human behaviour, has been observed as far back as the Middle Pleistocene (Sala *et al.*, 2015). Females are mostly victims of interpersonal violence, being killed by intimate partners or other family members (UNODC, 2019). Men are the main perpetrators of lethal violence (Archer, 1988; Jones, 2008; Fry and Söderberg, 2013; UNODC, 2019) and this thesis data also showed that lethal violence was more frequently carried out by males. However, this thesis also identified that male and female committed adulticide was very well explained by phylogeny, indicating the propensity of both sexes to carry out lethal violence.

Male dominated violence is considered to exist because they have stronger intrasexual competition with more benefits and lower costs, such as lower levels of parental investment and higher reproductive rates (Trivers, 1972; Pusey *et al.*, 2008). Similarly, sex plays an

important role in human violence (Archer, 2004; Buss, 1997), with reproductive competition/retention (Buss, 1997), male impulsiveness, sex dimorphism and conception rates indicating that violence is part of a sexually selected adaptive strategy (Archer, 2009). A type of human killing that may appear counter intuitive is intimate partner killing (Table 1.1 - definition). This violence type is largely carried out by males to their female partners (UNODC, 2019). The behaviour has been explained via both evolutionary principles, where there is a conflict of interest between males and females, and social normative gender roles (Archer, 2009). Intimate partner violence appears to be largely stable over time (UNODC, 2019; Office for National Statistics, 2019) with little variation across countries compared to other forms of lethal violence (UNODC, 2019 - but see Archer, 2009).

Female lethal violence is rare but does occur in both human and non-human primates. Parental care makes females risk adverse (Campbell, 1999) and females of many primate species take the primary care role. Death of the mother increases the mortality risk of any dependent children, while the death of a father has less impact (Atrash, 2011). Motivations to engage in lethal violence may be to ensure safety and also to defend resources (Trivers, 1972; Emlen and Oring, 1977; Kappeler and van Schaik, 2002). The results in chapter four identified that there were three positive potentially ‘significant’ socio-ecological predictors of female adulticide including seasonal breeding, group size and coalition formation.

Availability of resources, that are important to reproduction, mediates levels of violence (Archer, 2009) and in seasonally breeding species additional females to the group can limit their reproductive success. Consequently, non-human primates’ female lethal violence may involve killing immigrant females (Pusey *et al.*, 2008), and infants (Bezerra, Souto and Schiel, 2007). Human females are not seasonal breeders and the motivation for attacks is therefore different. Interpersonal violence, for example, has been suggested to be driven by self-protection, where they have often been subject to abuse prior to the crime (Jurik and Winn, 1990; Swan *et al.*, 2008; Linklaters, 2016; Denson *et al.*, 2018).

It has been suggested that there is a reluctance to believe women capable of violence, with discourse often focused on women as the victims of violence (Morrissey, 2003). This may feed into the willingness of men to come forward and report cases of violence committed by females. Though, non-lethal aggression types have been shown to be equally prevalent in males and females when undertaking intimate partner violence (Swan *et al.*, 2008; Denson *et al.*, 2018) and females engaging in more indirect aggression types generally (Table 1.1 definitions) (Denson *et al.*, 2018). Social role theory (Eagly, 1987) considers that the general

predominance of male physical violence over female violence can be attributed to sex-stereotyped roles. In many countries there is the breaking down of these traditional roles which it was suggested may increase female aggression rates (Adler, 1974). However, Jurik and Wimm (1990) found little support for the ‘Liberation’ hypothesis which could expect that a smaller crime gender gap and higher female crime levels will occur in societies with gender equality between men and women (Chu, Heberton and Toh, 2021). Yet, Chu, Heberton and Toh (2021), found their study supported the emancipation/opportunity hypothesis (Simon, 1975) which posits that as women work outside the home their opportunities to commit crime increases, and more generally the liberation hypothesis. Social influence and gender stereotyping cannot be used to explain the differences between sexes in non-human primates, where a similar dichotomy is observed in violence between the sexes. This perhaps indicating the important role in polygynous species of male sexual competition and female risk aversion due to females’ higher levels of parental investment and sexual dimorphism in terms of muscle mass where weight and strength favour males (Archer, 2009) in human and non-human primates.

### 6.3 Concluding remarks and where to go from here

Carrying out comparative research can be challenging, often due to the methodological differences employed by various researchers. These include, focusing on a single species through multiple populations versus a cross-taxa approach, using alternative definitions for specific behaviours, the decision to focus on a particular demographic e.g., female-female interactions, or the method of recording the occurrence rate. If this involves frequency focal sampling, then this varies between individuals so data based on specific individuals may be over or under representative of the species as a whole. Though Sussman and Chapman (2004) found that within their data, social behaviour appeared quite consistent between populations. As generalisation of a theory cannot be made across all primate species based on one species (Crook, 1970) this study successfully created an extensive dataset and explored 104 taxa to understand species and clade specific violent behaviour. In doing so this study has shed further light on the evolved violence traits of non-human and human primates.

This thesis has established that violence can be divided into five phylogenetically distinct violence types and that *H. sapiens*, along with other closely related taxa can show a strong propensity for lethal violence. This adds to existing studies on lethal violence (e.g., Gómez *et*

*al.*, 2016) but then goes further by establishing that lethal violence cannot be considered as one trait, which may influence how future studies wish to categorise their data. A key recommendation therefore from this study is that researchers should conduct research on specific violence types and, unless pertinent to their study, should not amalgamate violence types into a single measure.

Furthermore, this thesis has identified that these specific violence types are likely mediated by the particular socioecological factors that impact on non-human primates including territoriality, resource availability and the formation of coalitions. In several cases these socioecological effects show clear similarities to those identified in the human literature. Likewise, similarities can be drawn between the sex differentiation that can be seen in adulticide in humans and non-human primates where males are the primary aggressors. Through analysing intra and intergroup adulticide separated by the sex of the perpetrator this study determined that the emergence and activation of adulticide is influenced by different socio-ecological factors depending on sex.

Coalition formation was important to both sexes in adulticide. Establishing the relationship between coalitions and the two types of adulticide (intra and intergroup) in this large-scale phylogenetically controlled primate study adds support to the cost-benefit argument around coalition formation in lethal conflict, where operating as a coalition reduces individual risk (Henzi, Weingrill and Barrett, 1999). Coalitions have been considered an interesting area of study because they combine cooperation and conflict, which are often researched individually, so coalition research is important in developing a more complete understanding of social behaviour (Dugatkin, 1998). In attempting to understand the interactions between prosocial behaviours, including coalition formations and violence, this study identified some weak evidence that coalition formation may be affected by allogrooming but identified no effect of food sharing on coalition formation. Food sharing and grooming appear to act differently on individual violence types and coalitions. It was suggested that they may act in combination on some types of violence, and this warrants further research. Furthermore, coalition formation may not be driven through the reciprocal benefits of prosocial behaviours such as grooming, but through punishment. The potentially coercive behaviours leading to coalition formation on the specific violence types, as defined by this study, should be explored.

The analysis conducted in this thesis was carried out on species level data. As there can be variations between populations, analysis on multiple populations within a species and cross-taxa would be the next step. However, data is often not available on multiple populations due to preferences or necessity for a particular site or group. When it does become available then it should be integrated into this large-scale dataset for future analysis. This may also include incorporating additional information on human populations where there can be considerable variation due to extensive and rapid cultural evolution, which may aid in relating the findings of this study to modern humans.

Evolutionary psychology seeks to explore the evolved roots of human behaviour. To strive to develop a complete understanding of human nature it is essential to consider these evolved traits along with culturally evolved traits. This study has addressed the foundation of evolved violence types and the proximate socioecological mechanism that drive and mediate them through an exploration of the primate order. It is a valuable step in understanding the complexities of evolved social behaviour. By incorporating this work, specifically the use of individual violence types, into future studies, including the exploration of cultural evolved traits pertinent to their activation, perhaps further progress can be made in understanding the evolution of violence in all primates.

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## APPENDICES – CHAPTER 1(B)

## Appendix 1(B)A – Survey design

**Primate intra-group/inter-group aggression and conspecific killing**

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**Start of Block: Default Question Block****Study: Evolutionary history of aggression in primates.**

Dear researcher,

My name is Samantha Wakes, and I am a PhD student at the University of Lincoln (UK) - School of Psychology, supervised by Dr Bonaventura Majolo (Lincoln), and Dr Marcello Ruta (Lincoln). My project focuses on the evolutionary history of violence in non-human primates, and aims to analyse:

- i) Whether different types of violence (specifically: inter- and intra-group aggression, inter- and intra-group lethal aggression, and infanticide) show similar/distinct evolutionary trajectories.
- ii) Which social and ecological factors can account for the distribution of these different types of violence across the primate order.

I am currently extracting data from the literature, yet information is often hard to find (particularly on lethal aggression, other than infanticide). I am thus reaching out to the broader community to kindly ask for help in strengthening the database I've been able to compile so far on aggressive and affiliative behaviours. For this purpose, I designed a survey with the specific intention of making it as quick and painless as possible to fill in; the first part should take no more than 3 minutes of your time. The second part might take a little longer. Of course, completing both parts of the survey would be fantastic, but even taking just a few minutes to look at Part 1 would be tremendously helpful!

***Naturally, the nature of the survey means you may be asked to recall details of lethal aggressive acts that you have witnessed or are aware of. Please do not proceed if you feel this would cause you distress.***

Thank you very much for your help.  
Sam

SWake@lincoln.ac.uk

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Page Break



Thank you for agreeing to answer a few questions on violence in your study species. We would like to acknowledge all researchers who complete this survey, and therefore ask for you to fill in your name below. If you prefer your responses to remain anonymous then please leave blank.

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Please enter your email address if you would like to be informed about the results of this project.

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Page Break

### Species Details

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What is the scientific and common name of your study species? Ideally, please use the most recent scientific name. If you have data on multiple populations of the same species, please add the details below. If you have data on more than one species, please fill in the survey separately for each species.

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How long have you studied this species/population(s)? Please either give exact start/end dates or number of years/months.

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What is the location of your study species/population(s)? Please give the name of the country, study site, and/or coordinates.

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## PART 1 - Lethal Aggression



Are you aware of lethal intra-group and/or inter-group lethal aggression in the species you are describing? Based on the definitions given below please select one or more options as appropriate. Please note in this instance lethal aggression does not include infanticide.

**Observed** = The attack and death of the individual was observed (either by yourself or another researcher).

**Inferred** = Not directly witnessed but there was clear evidence of lethal aggression; e.g. severe aggression observed but victim escaped and later disappeared or final attack out of sight, dead body was found with clear canine wounds or other skeletal damage consistent

with a conspecific attack.

- ☐ Observed - Intra-group lethal aggression (1)
- ☐ Inferred - Intra-group lethal aggression (2)
- ☐ Observed - Inter-group lethal aggression (3)
- ☐ Inferred - Inter-group lethal aggression (4)
- ☐ No (5)

*Skip To: Q42 If Are you aware of lethal intra-group and/or inter-group lethal aggression in the species you are d... = No*

Page Break

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*Display This Question:*

*If Are you aware of lethal intra-group and/or inter-group lethal aggression in the species you are d... = Observed - Inter-group lethal aggression*

Using the matrix table below, please select all combinations of **inter-group lethal aggression** you have **observed**. Please use your own definition for the different age classes.

	Adult Female (1)	Adult Male (2)	Sub- adult/Juvenile Female (3)	Sub- adult/Juvenile Male (4)
Adult Female Victim (1)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Adult Male Victim (2)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Sub- adult/Juvenile Female Victim (3)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Sub- adult/Juvenile Male Victim (4)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

*Display This Question:*

*If Are you aware of lethal intra-group and/or inter-group lethal aggression in the species you are d... = Observed - Intra-group lethal aggression*

Using the matrix table below, please select all combinations of **intra-group lethal aggression** you have **observed**. Please use your own definition for the different age classes.

	Adult Female (1)	Adult Male (2)	Sub- adult/Juvenile Female (3)	Sub- adult/Juvenile Male (4)
Adult Female Victim (1)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Adult Male Victim (2)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Sub- adult/Juvenile Female Victim (3)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Sub- adult/Juvenile Male Victim (4)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

Page Break

*Display This Question:*

*If Are you aware of lethal intra-group and/or inter-group lethal aggression in the species you are d... = Inferred - Intra-group lethal aggression*

*Or Are you aware of lethal intra-group and/or inter-group lethal aggression in the species you are d... = Inferred - Inter-group lethal aggression*

Please can you provide further contextual information about the **inferred lethal aggression**, e.g. inferred through bite marks, possible causes, sex of victim and/or aggressor.

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Page Break

For cases where more than one attacker was observed, were the attackers forming a coalitionary attack against the victim? Coalitionary attack here means that attackers appeared to coordinate their attacks to the victim.

- ☐ Yes (1)
- ☐ No (2)
- ☐ Unsure (3)

*Skip To: Q42 If For cases where more than one attacker was observed, were the attackers forming a coalitionary at... = No*

*Skip To: Q34 If For cases where more than one attacker was observed, were the attackers forming a coalitionary at... = Unsure*

*Display This Question:*

*If For cases where more than one attacker was observed, were the attackers forming a coalitionary at... = Yes*

Who was involved in the coalitionary attack? Multiple options can be selected if different lethal events included different coalition demographics.

- ☐ Males only (1)
- ☐ Females only (2)
- ☐ Mixed (3)

Page Break

Thank you for completing Part 1 of the survey. In the second part, I am asking a couple of questions that may take a little longer and that could require some data extraction from long-term records. It would be extremely useful for me if you could also attempt this part, but if

you do not currently have the time please take the opportunity to select 'No' and skip Part 2.  
Thank you very much for your help.

- ☐ Yes - Lets go to Part 2 (1)
- ☐ No - I only wish to complete Part 1 (2)

*Skip To: Q34 If Thank you for completing Part 1 of the survey. In the second part, I am asking a couple of questi... = No - I only wish to complete Part 1*

Page Break

## PART 2a - Aggression



Have you observed intra- or inter-group aggression in your study species? Aggression here means the display of agonistic facial expressions and vocalizations between animals in visual contact (i.e. excluding long-distance aggressive calls advertisement) and/or agonistic physical interactions including chases, pushes, hits, or bites. Please select intra-group, inter-group and non-reproductive unit aggression (solitary out-group individuals, all male bands, immigrating individuals) if you have observed all types.

- ☐ Intra-group (1)
- ☐ Inter-group (2)
- ☐ Non-reproductive unit aggression (4)
- ☐ No aggression observed (3)

*Skip To: Q47 If Have you observed intra- or inter-group aggression in your study species? Aggression here means t... = No aggression observed*

Page Break

*Display This Question:*

*If Have you observed intra- or inter-group aggression in your study species? Aggression here means t... = Intra-group*

For the two questions below, please select the relevant sexes in relation to **intra-group** aggression.

	Male (1)	Female (2)	Both (3)
Which sexes participate in the aggression? (1)	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
Which sex is <u>most</u> actively involved in the aggression? (2)	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>

*Display This Question:*

*If Have you observed intra- or inter-group aggression in your study species? Aggression here means t... = Intra-group*

What is the frequency of this **intra-group** aggression? Please give quantitative data and add details of the unit of measurement (e.g. events/hour/individual); alternatively please give a qualitative description of the aggression observed for each sex combination (e.g. 'rare' or 'high').

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*Display This Question:*

*If Have you observed intra- or inter-group aggression in your study species? Aggression here means t... = Inter-group*



For the two questions below, please select the relevant sexes in relation to **inter-group** aggression.

	Male (1)	Female (2)	Both (3)
Which sexes participate in the aggression? (1)	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
Which sex is most actively involved in the aggression? (2)	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>

*Display This Question:*

*If Have you observed intra- or inter-group aggression in your study species? Aggression here means t... = Inter-group*

What is the frequency of this **inter-group** aggression? Please give quantitative data and add details of the unit of measurement (e.g. events/hour/individual); alternatively please give a qualitative description of the aggression observed for each sex combination (e.g. 'rare' or 'high').

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*Display This Question:*

*If Have you observed intra- or inter-group aggression in your study species? Aggression here means t... = Non-reproductive unit aggression*

For the two questions below, please select the relevant sexes in relation to '**non-reproductive unit**' aggression (solitary out-group individuals, all male bands, immigrating individuals).

	Male (1)	Female (2)	Both (3)
Which sexes participate in the aggression? (1)	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
Which sex is most actively involved in the aggression? (2)	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>

Page Break

## PART 2b - Cooperative/Affiliative Behaviours

Moving on now to cooperative/affiliative behaviours - are the following observed in your species (adults only)? Please select all that apply.

- ☐ Grooming (3)
- ☐ Food Sharing (2)
- ☐ Social play (1)
- ☐ Allo-parental care (4)
- ☐ None (5)

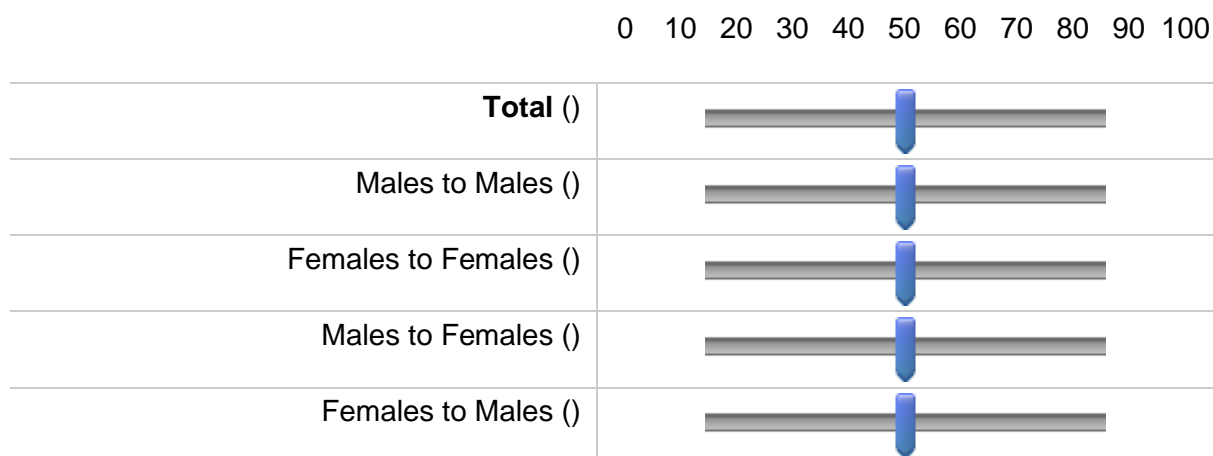
*Skip To: Q34 If Moving on now to cooperative/affiliative behaviours - are the following observed in your species... = None*

*Display This Question:*

*If Moving on now to cooperative/affiliative behaviours - are the following observed in your species... = Grooming*

Using the slider below please select the percentage of the activity budget that is spend grooming. You do not have to move all five sliders; Some researchers focus on a specific sex and others calculate an overall figure. Please do what is appropriate to your research.

Percentage %



*Display This Question:*

*If Moving on now to cooperative/affiliative behaviours - are the following observed in your species... = Food Sharing*

You mentioned your species can be observed food sharing. Please select from the following options to indicate who may engage in this behaviour.

	Same sex - Males (1)	Same sex - Females (2)	Mixed sexes (3)
Adults and offspring (1)	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
Adults only (2)	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
Offspring only (3)	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>
Others (4)	<input type="radio"/>	<input type="radio"/>	<input type="radio"/>

*Display This Question:*

*If Moving on now to cooperative/affiliative behaviours - are the following observed in your species... = Allo-parental care*

You mentioned your species carries out allo-parental care. Please select all who are involved in caring for the infants.

- ☐ Mother (1)
- ☐ Father (2)
- ☐ Other females (3)
- ☐ Other males (4)
- ☐ Female sub-adults (5)
- ☐ Male sub-adults (6)
- ☐ Juveniles (7)

*Display This Question:*

*If You mentioned your species carries out allo-parental care. Please select all who are involved in... = Mother*

*Or You mentioned your species carries out allo-parental care. Please select all who are involved in... = Father*

*Or You mentioned your species carries out allo-parental care. Please select all who are involved in... = Other females*

*Or You mentioned your species carries out allo-parental care. Please select all who are involved in... = Other males*

*Or You mentioned your species carries out allo-parental care. Please select all who are involved in... = Female sub-adults*

*Or You mentioned your species carries out allo-parental care. Please select all who are involved in... = Male sub-adults*

*Or You mentioned your species carries out allo-parental care. Please select all who are involved in... = Juveniles*

Who delivers primary infant care? Please select only one option.

- ☐ Mother (1)
- ☐ Father (2)
- ☐ Other females (3)
- ☐ Other males (4)
- ☐ Female sub-adults (5)
- ☐ Male sub-adults (6)
- ☐ Juveniles (7)

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Page Break

Thank you. Do you have any further comments that you would like to add? Please consider listing below any of your publications that contain useful data and that we could cite.

If you wish to upload copies of your papers or a dataset you will have the opportunity to do so shortly.

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If you wish to upload a file, dataset or papers that further illustrates your comment this would be gratefully received.

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Page Break

Thank you very much for taking the time to complete this survey. Your information will be extremely useful in helping me to complete the database that I need for my PhD project. Thank you again!

If you have any specific questions please feel free to contact either myself;

Samantha Wakes (PhD student)

SWake@lincoln.ac.uk

or

Dr Bonaventura Majolo (Supervisor)

bmajolo@lincoln.ac.uk

End of Block: Default Question Block

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## Appendix 1(B)B – Species lists

Chapter 2 – Violence only	Chapter 3 - Socio-ecological	Chapter 4 – Sex differences	Chapter 5 – Prosocial data			
			Total /combined	Grooming	Food-sharing	Time Social
Alouatta belzebul	Alouatta belzebul	Alouatta belzebul	Alouatta caraya	Alouatta belzebul	Alouatta caraya	Alouatta belzebul
Alouatta caraya	Alouatta caraya	Alouatta caraya	Alouatta palliata	Alouatta caraya	Alouatta palliata	Alouatta caraya
Alouatta guariba	Alouatta guariba	Alouatta guariba	Alouatta pigra	Alouatta guariba	Alouatta pigra	Alouatta guariba
Alouatta palliata	Alouatta palliata	Alouatta palliata	Ateles geoffroyi	Alouatta palliata	Ateles geoffroyi	Alouatta palliata
Alouatta pigra	Alouatta pigra	Alouatta pigra	Brachyteles	Alouatta pigra	Callithrix jacchus	Alouatta pigra
Alouatta	Alouatta	Alouatta	arachnoides	Alouatta	Cebus imitator	Alouatta
seniculus	seniculus	seniculus	Cacajao	seniculus	Cebus olivaceous	seniculus
Aotus azarae	Aotus azarae	Aotus azarae	melanocephalus	Aotus nigriceps	Cercopithecus	Ateles belzebuth
Aotus nancymae	Aotus nigriceps	Aotus nigriceps	Callithrix jacchus	Ateles belzebuth	campbelli	Ateles chamek
Aotus nigriceps	Aotus trivirgatus	Aotus trivirgatus	Cebus imitator	Ateles geoffroyi	Cercopithecus	Ateles geoffroyi
Aotus trivirgatus	Ateles belzebuth	Ateles belzebuth	Cebus olivaceus	Brachyteles	mitis	Ateles hybridus
Ateles belzebuth	Ateles chamek	Ateles chamek	Cercopithecus	arachnoides	Colobus guereza	Ateles paniscus
Ateles chamek	Ateles geoffroyi	Ateles geoffroyi	campbelli	Brachyteles	Erythrocebus	Brachyteles
Ateles geoffroyi	Ateles paniscus	Ateles paniscus	Cercopithecus	hypoxanthus	patas	arachnoides
Ateles hybridus	Brachyteles	Brachyteles	diana	Cacajao calvus	Eulemur fulvus	Brachyteles
Ateles paniscus	arachnoides	arachnoides	Cercopithecus	Cacajao	fulvus	hypoxanthus
Avahi	Brachyteles	Brachyteles	mitis	melanocephalus	Gorilla beringei	Cacajao calvus
meridionalis	hypoxanthus	hypoxanthus			Homo sapiens	

Brachyteles	Cacajao calvus	Cacajao calvus	Chiropotes	Callicebus	Lemur catta	Callicebus
arachnoides	Cacajao	Cacajao	satanas	nigrifrons	Leontocebus	nigrifrons
Brachyteles	melanocephalus	melanocephalus	Colobus guereza	Callicebus	fuscicollis	Callicebus
hypoxanthus	Callicebus	Callicebus	Erythrocebus	torquatus	Lophocebus	torquatus
Cacajao calvus	nigrifrons	nigrifrons	patas	Callithrix jacchus	albigena	Callimico goeldii
Cacajao	Callicebus	Callicebus	Eulemur fulvus	Cebus imitator	Macaca	Callithrix jacchus
melanocephalus	ornatus	ornatus	fulvus	Cebus olivaceus	assamensis	Callithrix kuhlii
Callicebus	Callicebus	Callicebus	Gorilla beringei	Cercopithecus	Macaca fuscata	Callithrix
nigrifrons	personatus	personatus	Gorilla gorilla	ascanius	Macaca mulatta	penicillata
Callicebus	Callicebus	Callicebus	gorilla	Cercopithecus	Macaca radiata	Cebus imitator
ornatus	torquatus	torquatus	Homo sapiens	campbelli	Nasalis larvatus	Cebus olivaceus
Callicebus	Callimico goeldii	Callimico goeldii	Hylobates lar	Cercopithecus	Pan troglodytes	Cercocebus atys
personatus	Callithrix jacchus	Callithrix jacchus	Lemur catta	diana	schweinfurthii	Cercocebus
Callicebus	Callithrix kuhlii	Callithrix kuhlii	Lophocebus	Cercopithecus	Pan troglodytes	galeritus
torquatus	Callithrix	Callithrix	albigena	mitis	verus	Cercocebus
Callimico goeldii	penicillata	penicillata	Macaca arctoides	Chiropotes	Papio anubis	torquatus
Callithrix jacchus	Cebus imitator	Cebus imitator	Macaca	satanas	Papio	Cercopithecus
Callithrix kuhlii	Cebus olivaceus	Cebus olivaceus	fascicularis	Chlorocebus	cynocephalus	ascanius
Callithrix	Cercocebus atys	Cercocebus atys	Macaca fuscata	pygerythrus	Papio ursinus	Cercopithecus
penicillata	Cercocebus	Cercocebus	Macaca mulatta	Colobus guereza	Piliocolobus	campbelli
Cebus imitator	galeritus	galeritus	Nasalis larvatus		kirkii	



Cebus olivaceus	Cercocebus	Cercocebus	Pan paniscus	Colobus	Presbytis thomasi	Cercopithecus
Cercocebus atys	torquatus	torquatus	Pan troglodytes	polykomos	Propithecus	diana
Cercocebus	Cercopithecus	Cercopithecus	schweinfurthii	Colobus	edwardsi	Cercopithecus
galeritus	ascanius	ascanius	Pan troglodytes	vellerosus	Propithecus	mitis
Cercocebus	Cercopithecus	Cercopithecus	verus	Erythrocebus	verreauxi	Chiropotes
torquatus	campbelli	campbelli	Papio anubis	patas	Sapajus nigritus	satanas
Cercopithecus	Cercopithecus	Cercopithecus	Papio	Eulemur fulvus	Semnopithecus	Chlorocebus
ascanius	diana	diana	cynocephalus	fulvus	entellus	pygerythrus
Cercopithecus	Cercopithecus	Cercopithecus	Papio ursinus	Gorilla beringei	Theropithecus	Colobus guereza
campbelli	mitis	mitis	Piliocolobus	Gorilla gorilla	gelada	Colobus
Cercopithecus	Chiropotes	Chiropotes	badius	gorilla	Aotus azarae	polykomos
diana	albinasus	albinasus	temminckii	Homo sapiens	Brachyteles	Colobus
Cercopithecus	Chiropotes	Chiropotes	Piliocolobus	Hylobates lar	arachnoides	vellerosus
mitis	satanas	satanas	kirkii	Hylobates moloch	Cacajao	Eulemur fulvus
Chiropotes	Chlorocebus	Chlorocebus	Pithecia pithecia	Lemur catta	melanocephalus	fulvus
albinasus	pygerythrus	pygerythrus	Presbytis thomasi	Lophocebus	Callimico goeldii	Eulemur
Chiropotes	Chlorocebus	Chlorocebus	Propithecus	albigena	Callithrix kuhlii	rubriventer
satanas	sabaeus	sabaeus	edwardsi	Macaca arctoides	Callithrix	Eulemur rufifrons
Chlorocebus	Chlorocebus	Chlorocebus	Propithecus	Macaca	penicillata	Gorilla gorilla
pygerythrus	tantalus	tantalus	verreauxi	fascicularis	Cercocebus atys	gorilla
	Colobus guereza	Colobus guereza	Saguinus mystax	Macaca fuscata		Hoolock hoolock

Chlorocebus sabaeus	Colobus polykomos	Colobus polykomos	Saimiri sciureus	Macaca mulatta	Cercocebus torquatus	Hylobates albibarbis
Chlorocebus tantalus	Colobus vellerosus	Colobus vellerosus	Sapajus nigritus	Nasalis larvatus	Cercopithecus diana	Hylobates lar
Colobus guereza	Erythrocebus	Erythrocebus	Semnopithecus entellus	Pan paniscus	Chiropotes schweinfurthii	Hylobates moloch
Colobus polykomos	patas	patas	Symphalangus syndactylus	Pan troglodytes	albinasus	Lemur catta
Colobus vellerosus	Eulemur fulvus	Eulemur fulvus	Theropithecus gelada	verus	Chiropotes satanas	Leontocebus fuscicollis
Erythrocebus patas	Eulemur macaco	Eulemur macaco	Varecia variegata	Papio anubis	Gorilla gorilla	Leontopithecus rosalia
Eulemur fulvus fulvus	Eulemur	Eulemur		Papio	gorilla	Lophocebus albigena
Eulemur macaco	rubriventer	rubriventer		cynocephalus	Hylobates albibarbis	Macaca fuscata
Eulemur rubriventer	Eulemur rufifrons	Eulemur rufifrons		Phaner furcifer	Hylobates lar	Macaca nigra
Eulemur rufifrons	Gorilla beringei	Gorilla beringei		Piliocolobus	Leontopithecus rosalia	Nasalis larvatus
Gorilla beringei	Gorilla gorilla	Gorilla gorilla		badius	Pan troglodytes	Pan troglodytes
Gorilla gorilla	gorilla	gorilla		temminckii	schweinfurthii	Pan troglodytes
gorilla	Hapalemur	Hapalemur		Piliocolobus	Macaca arctoides	Pan troglodytes
	griseus	griseus		kirkii	Macaca fascicularis	verus
	Homo sapiens	Homo sapiens		Piliocolobus	Macaca sinica	Papio anubis
	Hoolock hoolock	Hoolock hoolock		tephrosceles	Pan paniscus	Papio
	Hylobates albibarbis	Hylobates albibarbis		Pithecia pithecia		cynocephalus

Hapalemur	Hylobates lar	Hylobates lar		Presbytis	Ptilocolobus	Papio ursinus
griseus	Hylobates moloch	Hylobates moloch		potenziani	badius badius	Ptilocolobus
Homo sapiens	Lemur catta	Lemur catta		Presbytis thomasi	Ptilocolobus	badius badius
Hoolock hoolock	Leontocebus	Leontocebus		Propithecus	badius	Ptilocolobus
Hylobates	fuscicollis	fuscicollis		edwardsi	temminckii	badius
albibarbis	Leontopithecus	Leontopithecus		Propithecus	Pithecia pithecia	temminckii
Hylobates lar	rosalia	rosalia		verreauxi	Saguinus mystax	Ptilocolobus
Hylobates moloch	Lepilemur	Lepilemur		Rhinopithecus	Saimiri sciureus	kirkii
Lemur catta	ruficaudatus	ruficaudatus		bieti	Sapajus apella	Ptilocolobus
Leontocebus	Lophocebus	Lophocebus		Saguinus mystax	Symphalangus	tephrosceles
fuscicollis	albigena	albigena		Saimiri	syndactylus	Presbytis
Leontopithecus	Macaca arctoides	Macaca arctoides		boliviensis	Varecia variegata	potenziani
rosalia	Macaca	Macaca		Saimiri oerstedii		Presbytis thomasi
Lepilemur	assamensis	assamensis		Saimiri sciureus		Propithecus
ruficaudatus	Macaca	Macaca		Sapajus nigritus		diadema
Lophocebus	fascicularis	fascicularis		Semnopithecus		Propithecus
albigena	Macaca fuscata	Macaca fuscata		entellus		edwardsi
Macaca arctoides	Macaca mulatta	Macaca mulatta		Symphalangus		Propithecus
Macaca	Macaca nigra	Macaca nigra		syndactylus		verreauxi
assamensis	Macaca radiata	Macaca radiata		Theropithecus		Rhinopithecus
	Macaca sinica	Macaca sinica		gelada		bieti

Macaca fascicularis	Nasalis larvatus	Nasalis larvatus		Trachypithecus cristatus		Saguinus mystax
Macaca fuscata	Pan paniscus	Pan paniscus		Trachypithecus obscurus		Saimiri boliviensis
Macaca mulatta	Pan troglodytes schweinfurthii	Pan troglodytes schweinfurthii		Varecia variegata		Saimiri oerstedii
Macaca nigra	Pan troglodytes verus	Pan troglodytes verus				Saimiri sciureus
Macaca radiata	Papio anubis	Papio anubis				Sapajus apella
Macaca sinica	Papio	Papio				Sapajus nigratus
Nasalis larvatus	cynocephalus	cynocephalus				Semnopithecus entellus
Pan paniscus	Papio ursinus	Papio ursinus				Symphalangus syndactylus
Pan troglodytes schweinfurthii	Phaner furcifer	Phaner furcifer				Theropithecus gelada
Pan troglodytes verus	Piliocolobus badius badius	Piliocolobus badius badius				Trachypithecus cristatus
Papio anubis	Piliocolobus badius	Piliocolobus badius				Trachypithecus johnii
Papio cynocephalus	temminckii	temminckii				Trachypithecus obscurus
Papio ursinus	Piliocolobus kirkii	Piliocolobus kirkii				Varecia variegata
Phaner furcifer	Piliocolobus tephrosceles	Piliocolobus tephrosceles				
Piliocolobus badius badius	Pithecia pithecia	Pithecia pithecia				

Piliocolobus	Plecturocebus	Plecturocebus				
badius	moloch	moloch				
temminckii	Presbytis	Presbytis				
Piliocolobus	potenziani	potenziani				
kirkii	Presbytis thomasi	Presbytis thomasi				
Piliocolobus	Propithecus	Propithecus				
tephrosceles	diadema	diadema				
Pithecia pithecia	Propithecus	Propithecus				
Plecturocebus	edwardsi	edwardsi				
moloch	Propithecus	Propithecus				
Presbytis	verreauxi	verreauxi				
potenziani	Rhinopithecus	Rhinopithecus				
Presbytis thomasi	bieti	bieti				
Propithecus	Saguinus mystax	Saguinus mystax				
diadema	Saimiri	Saimiri				
Propithecus	boliviensis	boliviensis				
edwardsi	Saimiri oerstedii	Saimiri oerstedii				
Propithecus	Saimiri sciureus	Saimiri sciureus				
verreauxi	Sapajus apella	Sapajus apella				
Rhinopithecus	Sapajus nigritus	Sapajus nigritus				
bieti						

Saguinus mystax	Semnopithecus	Semnopithecus				
Saimiri	entellus	entellus				
boliviensis	Symphalangus	Symphalangus				
Saimiri oerstedii	syndactylus	syndactylus				
Saimiri sciureus	Theropithecus	Theropithecus				
Sapajus apella	gelada	gelada				
Sapajus nigritus	Trachypithecus	Trachypithecus				
Semnopithecus	cristatus	cristatus				
entellus	Trachypithecus	Trachypithecus				
Symphalangus	johnii	johnii				
syndactylus	Trachypithecus	Trachypithecus				
Theropithecus	obscurus	obscurus				
gelada	Varecia variegata	Varecia variegata				
Trachypithecus						
cristatus						
Trachypithecus						
johnii						
Trachypithecus						
obscurus						
Varecia variegata						

## Appendix 1(B)C – Data sources

Species	Sources: <b>Five types of violence</b> (intergroup adulticide; intragroup adulticide; infanticide; intergroup aggression; intragroup aggression), <b>eight key socioecological variables</b> (Substrate; group size; territoriality; number of males; seasonal breeder; diet; dimorphism; coalition) <b>and prosocial variables</b> (time-social, grooming, and food-sharing)
Alouatta belzebul	Galán-Acedo <i>et al.</i> , 2019; Klein, 1974; Majolo <i>et al.</i> , 2020; Myers <i>et al.</i> , 2022; Pinto <i>et al.</i> , 2003; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013.
Alouatta caraya	Bravo and Sallenave, 2003; Chalukian and Rumiz, 1986; Galán-Acedo <i>et al.</i> , 2019; Garber, and Kowalewski, 2011; Grueter <i>et al.</i> , 2013; Heldstab <i>et al.</i> , 2021; Majolo <i>et al.</i> , 2020; Pavé <i>et al.</i> , 2012; Rowe and Myers, 2021; Stavis <i>et al.</i> , 2018; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015; Zunino <i>et al.</i> , 1986.
Alouatta guariba	Chiarello, 1994; Galán-Acedo <i>et al.</i> , 2019; Majolo <i>et al.</i> , 2020; Myers <i>et al.</i> , 2022; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013.
Alouatta palliata	Bezanson <i>et al.</i> , 2008; Clarke, Zucker and Glander, 1994; Dias <i>et al.</i> , 2010; Dixon, 1998; Galán-Acedo <i>et al.</i> , 2019; Givens <i>et al.</i> , 1975; Jaeggi and van Schaik, 2011; Méndez-Carvajal, Santamaría and Moreno, 2005; Powell, Isler, and Barton, 2011; Smuts <i>et al.</i> , 1987; Sussman and Garber, 2004; Rowe and Myers, 2021; Wang and Milton, 2003.
Alouatta pigra	Cunningham, 1982; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Knopff, Knopff and Pavelka, 2004; Pavelka and Knopff, 2004; Myers <i>et al.</i> , 2022; Rowe and Myers, 2021; Smuts <i>et al.</i> , 1987; Van Belle <i>et al.</i> , 2014; Van Belle <i>et al.</i> , 2008; Kitchen, 2004; Van Belle <i>et al.</i> , 2010; Van Belle and Estrada, 2006; Wheeler <i>et al.</i> , 2013
Alouatta seniculus	Agoramoorthy and Rudran, 1995; Crockett and Pope, 1988; Crockett and Sekulic, 1984; Galán-Acedo <i>et al.</i> , 2019; Gómez-Posada & Londono, 2011; Heldstab <i>et al.</i> , 2021; Sussman and Garber, 2004; Majolo <i>et al.</i> , 2020; Pope, 2000; Sekulic, 1983; Willems, Hellriegel and van Schaik, 2013.

Aotus azarae	Campbell <i>et al.</i> , 2011; Dixon, 1998; Fernandez-Duque, 2007; Fernandez-Duque and Huck, 2013; Fernandez-Duque, Rotundo and Sloan, 2001; Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011.
Aotus nancymae	Aquino and Encarnacion, 1986; Campbell <i>et al.</i> , 2011.
Aotus nigriceps	Campbell <i>et al.</i> , 2011; Dunbar, Mac Carron, and Shultz, 2018; Galán-Acedo <i>et al.</i> , 2019; Majolo <i>et al.</i> , 2020; Myers <i>et al.</i> , 2022; Olson and Blumstein, 2009; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013; Wright, 1985; Wright, 1989; Wright, 1994.
Aotus trivirgatus	Campbell <i>et al.</i> , 2011; Fernandes, 1993; Galán-Acedo <i>et al.</i> , 2019; Myers <i>et al.</i> , 2022; Plavcan, van Schaik, and Kappeler, 1995; Wich and Nunn, 2002; Wright, 1978; Wright 1985.
Ateles belzebuth	Bissonnette <i>et al.</i> , 2014; Campbell <i>et al.</i> , 2011; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Heldstab <i>et al.</i> , 2021; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Shimooka, 2005; Shimooka <i>et al.</i> , 2008; Smith and Cheverud, 2002; Willems <i>et al.</i> , 2015; Willems, Hellriegel and van Schaik, 2013.
Ateles chamek	Alvarez <i>et al.</i> , 2015; Galán-Acedo <i>et al.</i> , 2019; Gibson, 2008; Heldstab <i>et al.</i> , 2021; Konstant and Rylands, 2013; Rowe and Myers, 2021; Symington, 1988; van Schaik, 2000; Willems, Hellriegel and van Schaik, 2013.
Ateles geoffroyi	Bissonnette <i>et al.</i> , 2014; Gibson, 2008; Grueter <i>et al.</i> , 2013; Heldstab <i>et al.</i> , 2021; Jaeggi and Van Schaik, 2011; Majolo <i>et al.</i> , 2020; Smith and Cheverud, 2002; Sussman and Garber, 2004; Valero <i>et al.</i> , 2006; Willems, Hellriegel and van Schaik, 2013.
Ateles hybridus	Córdoba, 2014; Link <i>et al.</i> , 2010; Rimbach <i>et al.</i> , 2012; Rimbach <i>et al.</i> , 2015; Rowe and Myers, 2021;
Ateles paniscus	Dixon, 1998; Dunbar, Mac Carron, and Shultz, 2018; Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Plavcan, van Schaik, and Kappeler, 1995; Sussman and Garber, 2004;; Willems, Hellriegel and van Schaik, 2013; van Roosmalen, 1985;;; Smuts <i>et al.</i> , 1987



Avahi meridionalis	Majolo <i>et al.</i> , 2020; Norscia and Borgognini-Tarli, 2008; Willems, Hellriegel and van Schaik, 2013;
Brachyteles arachnoides	Bissonnette <i>et al.</i> , 2014; Campbell <i>et al.</i> , 2011; Dixon, 1998; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Majolo <i>et al.</i> , 2020; Myers <i>et al.</i> , 2022; Strier, 1992; Sussman and Garber, 2004; Talebi, 2020; Talebi, Beltrão-Mendes and Lee, 2009; Willems, Hellriegel and van Schaik, 2013.
Brachyteles hypoxanthus	Campbell <i>et al.</i> , 2011; Dias and Strier, 2003; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Myers <i>et al.</i> , 2022; Powell, Isler and Barton, 2011; Rowe and Myers, 2021.
Cacajao calvus	Barnett <i>et al.</i> , 2005; Bowler <i>et al.</i> , 2013; Bowler and Bodmer, 2009; Campbell <i>et al.</i> , 2011; Galán-Acedo <i>et al.</i> , 2019; Gregory and Bowler, 2015; Grueter <i>et al.</i> , 2013; Rowe and Myers, 2021.
Cacajao melanocephalus	Barnett, 2005; Barnett <i>et al.</i> , 2005; Bezerra <i>et al.</i> , 2011; Boubli, 1997; Galán-Acedo <i>et al.</i> , 2019; Myers <i>et al.</i> , 2022; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013.
Callicebus nigrifrons	Berthet, 2020; Cäsar <i>et al.</i> , 2008; Caselli <i>et al.</i> , 2014; Caselli, 2013; Caselli and Setz, 2011; Ferrari, 2013; Galán-Acedo <i>et al.</i> , 2019; Majolo, 2021; Nagy-Reis and Setz, 2017; Rowe and Myers, 2021.
Callicebus ornatus	Basto González, 2009; Carretero-Pinzón, 2013; Dunbar, Mac Carron, and Shultz, 2018; Fleagle, 2013; Majolo <i>et al.</i> , 2020; Myers <i>et al.</i> , 2022; Veiga, 2013; Willems, Hellriegel and van Schaik, 2013.
Callicebus personatus	Galán-Acedo <i>et al.</i> , 2019; Majolo <i>et al.</i> , 2020; Müller 1996; Müller, 1995; Myers <i>et al.</i> , 2022; Price and Pieade, 2001; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013.
Callicebus torquatus	Campbell <i>et al.</i> , 2011; Cooke, 2012; Holloway, 1974; Majolo <i>et al.</i> , 2020; Myers <i>et al.</i> , 2022; Plavcan, van Schaik, and Kappeler, 1995; Smith and Cheverud, 2002; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.
Callimico goeldii	Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Holloway, 1974; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Porter, 2007; Rehg, 2009; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013.

Callithrix jacchus	Bezerra, Souto, and Schiel, 2007; Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013; Yamamoto <i>et al.</i> , 2014.
Callithrix kuhlii	Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Majolo <i>et al.</i> , 2020; Raboy <i>et al.</i> , 2008; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013;
Callithrix penicillata	Decanini and Macedo, 2008; Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013.
Cebus imitator	Bissonnette <i>et al.</i> , 2014; Galán-Acedo <i>et al.</i> , 2019; Gros-Louis, Perry and Manson, 2003; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Manson, Gros-Louis and Perry, 2004; McKinney, 2010; Myers <i>et al.</i> , 2022; Rowe and Myers, 2021; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.
Cebus olivaceus	Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Miller, 1998; O'Brian, 1991; Robinson, 1986; Robinson, 1988; Rowe and Myers, 2021; Sussman and Garber, 2004; Valderrama, Srikosamatara and Robinson, 1990; Willems, Hellriegel and van Schaik, 2013.
Cercocebus atys	Campbell <i>et al.</i> , 2011; Fruteau <i>et al.</i> , 2010; Fruteau <i>et al.</i> , 2011; Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013.
Cercocebus galeritus	Campbell <i>et al.</i> , 2011; Kinnaird, 1990; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013.
Cercocebus torquatus	Aychet, 2020; Cooke, 2012; Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Mitani, 1991; Plavcan, van Schaik, and Kappeler, 1995; Range and Noe, 2002; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013.
Cercopithecus ascanius	Cords, 1987; Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Smuts <i>et al.</i> , 1987; Struhsaker, 1977; Willems, Hellriegel and van Schaik, 2013.

Cercopithecus campbelli	Buzzard, 2004; Buzzard, 2007; Buzard 2010; Candiotti <i>et al.</i> , 2015; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Hiraiwa-Hasegawa, 1994; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013.
Cercopithecus diana	Buzzard, 2004; Candiotti <i>et al.</i> , 2015; Dunbar, Mac Carron, and Shultz, 2018; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Kane, 2020; McGraw, Plavcan and Adachi-Kanazawa, 2002; Majolo <i>et al.</i> , 2020; Myers <i>et al.</i> , 2022; Willems, Hellriegel and van Schaik, 2013.
Cercopithecus mitis	Butynski, 1982; Butynski, 1990; Cords, 2000; Fairgrieve, 1995; Galán-Acedo <i>et al.</i> , 2019; Glenn and Cords, 2006; Grueter <i>et al.</i> , 2013; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Mitani <i>et al.</i> , 2012; Myers <i>et al.</i> , 2022; Roth and Cords, 2016; Smuts <i>et al.</i> , 1987; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.
Chiropotes albinasus	Ayres (1981) in Smuts <i>et al.</i> , 1987; Boubli, 1997; Chapman, 2007; Galán-Acedo <i>et al.</i> , 2019; Pinto, 2008; Rowe and Myers, 2021; Silvia and Ferrari, 2009.
Chiropotes satanas	Boubli, 1997; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Jaeggi and van Schaik, 2011; Myers <i>et al.</i> , 2022; Rowe and Myers, 2021; Silvia and Ferrari, 2009; Veiga, 2006; Veiga, 2020; Veiga and Farrari, 2006.
Chlorocebus pygerythrus	Bissonnette <i>et al.</i> , 2014; Heldstab <i>et al.</i> , 2021; Majolo <i>et al.</i> , 2020; Menbere and Balakrishnan, 2016; Willems, Hellriegel and van Schaik, 2013.
Chlorocebus sabaeus	Heldstab <i>et al.</i> , 2021; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015.
Chlorocebus tantalus	Cowl, 2019; Galán-Acedo <i>et al.</i> , 2019; Nakagawa, 2008; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015.

Colobus guereza	Eustace <i>et al.</i> , 2015; Flashing, 2001; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Harris and Monfort, 2003; Hiraiwa-Hasegawa, 1994; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Marler, 1972; Onderdonk, 2000; Plavcan, van Schaik, and Kappeler, 1995; Rowe and Myers, 2021; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013;
Colobus polykomos	Campbell <i>et al.</i> , 2011; Dunbar, Mac Carron, and Shultz, 2018; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Heldstab <i>et al.</i> , 2021; Korstjens <i>et al.</i> , 2002; Majolo <i>et al.</i> , 2020; Plavcan, van Schaik, and Kappeler, 1995; Smith and Cheverud, 2002; Wheeler <i>et al.</i> , 2013; Willems, Hellriegel and van Schaik, 2013.
Colobus vellerosus	Badescu <i>et al.</i> , 2016; Bissonnette <i>et al.</i> , 2014; Campbell <i>et al.</i> , 2011; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Sicotte and Macintosh, 2004; Teichroeb, 2020; Teichroeb and Sicotte, 2008; Teichroeb <i>et al.</i> , 2014; Wheeler <i>et al.</i> , 2013; Willems, Hellriegel and van Schaik, 2013.
Erythrocebus patas	Campbell <i>et al.</i> , 2011; Carlson and Isbell, 2001; Enstam, Isbell and De Maar, 2002; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Heldstab <i>et al.</i> , 2021; Isbell <i>et al.</i> , 2009; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Nakagawa, 2008; Pruett and Isbell, 2000; Rowe and Myers, 2021; Smuts <i>et al.</i> , 1987; Willems, Hellriegel and van Schaik, 2013.
Eulemur fulvus fulvus	Cheney, 1987; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Jolly <i>et al.</i> , 2000; Majolo <i>et al.</i> , 2020; Overdorff, 1991; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.
Eulemur macaco	Andrews, 1998; Bayart and Bruno, 2005; Bayart and Simmen, 2005; Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Majolo <i>et al.</i> , 2020; Plavcan, van Schaik, and Kappeler, 1995; Willems, Hellriegel and van Schaik, 2013.
Eulemur rubriventer	Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Kappeler and Fichtel, 2016; Majolo <i>et al.</i> , 2020; Overdorff, 1991; Overdorff, 1993; Overdorff, 1996; Overdorff and Tecot, 2006; Plavcan, van Schaik, and Kappeler, 1995; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.
Eulemur rufifrons	Galán-Acedo <i>et al.</i> , 2019; Kappeler, 2020; Kappeler and Fichtel, 2012; Kappeler and Fichtel, 2016; Overdorff, 1996; Pyritz <i>et al.</i> , 2011; Rowe and Myers, 2021.

Gorilla beringei	Bissonnette <i>et al.</i> , 2014; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Hiraiwa-Hasegawa, 1994; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Mirville <i>et al.</i> , 2018; Robbins, 2008; Rosenbaum, Vecellio and Stoinski, 2016; Rowe and Myers, 2021; Veit, 1998; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015.
Gorilla gorilla gorilla	Bermejo, 2004; Dixon, 1998; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Jaeggi and van Schaik, 2011; Jeffery <i>et al.</i> , 2007; Kappeler, 1995; Majolo <i>et al.</i> , 2020; Plavcan, van Schaik, and Kappeler, 1995; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.
Hapalemur griseus	Galán-Acedo <i>et al.</i> , 2019; Grassi, 2001; Heldstab <i>et al.</i> , 2021; Majolo <i>et al.</i> , 2020; Nievergelt <i>et al.</i> , 1998, Nievergelt <i>et al.</i> , 1999; Plavcan, van Schaik, and Kappeler, 1995; Tan, 1991; Willems, Hellriegel and van Schaik, 2013.
Homo sapiens	Boehm, 2013; Bowles, 2009; Jones, 2007; Kelly, 2013; Khelil <i>et al.</i> , 2019; Majolo <i>et al.</i> , 2020; Roenneberg, 2004; Smith and Cheverud, 2002; UNODC, 2019; Willems, Hellriegel and van Schaik, 2013; Wrangham, 2018.
Hoolock hoolock	Alfred and Sati, 1991; Dixon, 1998; Galán-Acedo <i>et al.</i> , 2019; Islam and Feeroz, 1992; Majolo <i>et al.</i> , 2020; Plavcan, van Schaik, and Kappeler, 1995; Rowe and Myers, 2021; Savini <i>et al.</i> , 2009; Willems, Hellriegel and van Schaik, 2013.
Hylobates albibarbis	Cheyne, 2010; Cheyne, Monks, and Kuswanto, 2010; Cheyne <i>et al.</i> , 2008; Galán-Acedo <i>et al.</i> , 2019; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Vogel <i>et al.</i> , 2009; Wanelik <i>et al.</i> , 2012; Willems, Hellriegel and van Schaik, 2013.
Hylobates lar	Bartlett, 2003; Campbell <i>et al.</i> , 2011; Cheyne, 1987; Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Plavcan, van Schaik, and Kappeler, 1995; Reichard and Sommer, 1997; Smuts <i>et al.</i> , 1987; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.
Hylobates moloch	Galán-Acedo <i>et al.</i> , 2019; Kappeler, 1984; Kim <i>et al.</i> , 2010; Majolo <i>et al.</i> , 2020; Myers <i>et al.</i> , 2022; Willems, Hellriegel and van Schaik, 2013; Yi <i>et al.</i> , 2020.

Lemur catta	Bissonnette <i>et al.</i> , 2014; Dixon, 1998; Grueter <i>et al.</i> , 2013; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Jolly, 1966; Jolly, 1997; Jolly <i>et al.</i> , 2000; Kittler and Dietzel, 2016; Majolo <i>et al.</i> , 2020; Nakamichi, 1997; Pride, 2005; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.
Leontocebus fuscicollis	Garber, 1988; Garber, 1989; Garber, 1997; Herrera, Knogge and Heymann, 2000; Majolo, 2021; Plavcan, van Schaik, and Kappeler, 1995; Sussman and Garber, 2004; Terborgh, 1983; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015.
Leontopithecus rosalia	Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Peres, 1989; Rowe and Myers, 2021; Smith and Cheverud, 2002; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.
Lepilemur ruficaudatus	Galán-Acedo <i>et al.</i> , 2019; Hilgartner, 2006; Hilgartner, 2012; Hilgartner, Zinner, and Kappeler, 2008; Majolo <i>et al.</i> , 2020; Plavcan, van Schaik, and Kappeler, 1995; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013; Zinner <i>et al.</i> , 2003.
Lophocebus albigena	Brown, 2020; Campbell <i>et al.</i> , 2011; Dixon, 1998; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015.
Macaca arctoides	Bissonnette <i>et al.</i> , 2014; Chetry, 2002; Fooden, 1990; Galán-Acedo <i>et al.</i> , 2019; Jaeggi and van Schaik, 2011; Myers <i>et al.</i> , 2022; Richten <i>et al.</i> , 2009; Rowe and Myers, 2021.
Macaca assamensis	Bissonnette <i>et al.</i> , 2014; Borries <i>et al.</i> , 2002; Galán-Acedo <i>et al.</i> , 2019; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Opie <i>et al.</i> , 2013; Ostner <i>et al.</i> , 2013; Schülke and Ostner, 2020; Richter <i>et al.</i> , 2016; Rowe and Myers, 2021; Schülke <i>et al.</i> , 2011; Smith and Cheverud, 2002; Willems, Hellriegel and van Schaik, 2013.
Macaca fascicularis	Bissonnette <i>et al.</i> , 2014; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Heldstab <i>et al.</i> , 2021; Majolo <i>et al.</i> , 2020; Mazumder and Kaburu, 2021; Mishra, 2020; Pal, 2020; Wheeler <i>et al.</i> , 2013; Willems, Hellriegel and van Schaik, 2013.

Macaca fuscata	Bissonnette <i>et al.</i> , 2014; Dixon, 1998; Grueter <i>et al.</i> , 2013; Heldstab <i>et al.</i> , 2021; Hill and Okayasu, 1995; Hiraiwa-Hasegawa, 1994; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Soltis <i>et al.</i> , 2000; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015; Yamada and Nakamichi, 2006.
Macaca mulatta	Bissonnette <i>et al.</i> , 2014; Buhl <i>et al.</i> , 2012; DeClue, 1992; Dixon, 1998; Gill, 2020; Grueter <i>et al.</i> , 2013; Hiraiwa-Hasegawa, 1994; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Wade, 2018; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015.
Macaca nigra	Barrett <i>et al.</i> , 2002; Bissonnette <i>et al.</i> , 2014; Candiotti <i>et al.</i> , 2015; Duboscq <i>et al.</i> , 2013; Galán-Acedo <i>et al.</i> , 2019; Majolo <i>et al.</i> , 2020; Martínez-Íñigo, 2020; O'Brian and Kinnaid, 1997 in Boinski and Garber, 2000; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.
Macaca radiata	Bissonnette <i>et al.</i> , 2014; DeClue, 1992; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Singh <i>et al.</i> , 2006; Smith and Cheverud, 2002; Willems Hellriegel and van Schaik, 2013.
Macaca sinica	DeClue, 1992; Dittus, 1977; Dittus, 1987; Dittus, 1988; Galán-Acedo <i>et al.</i> , 2019; Majolo <i>et al.</i> , 2020; Mittermeier and Wilson, 2013; Plavcan, van Schaik, and Kappeler, 1995; Rowe and Myers, 2021; Smith and Cheverud, 2002; Smuts <i>et al.</i> , 1987; Willems, Hellriegel and van Schaik, 2013.
Nasalis larvatus	Agoramoorthy and Hsu, 2005; Bennett and Sebastian, 1988; Boonratana, 1994; Boonratana, 2000; Dixon, 1998; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Jaeggi and van Schaik, 2011; Matsuda <i>et al.</i> , 2009; Matsuda <i>et al.</i> , 2012; Opie <i>et al.</i> , 2013; Plavcan, van Schaik, and Kappeler, 1995; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013.
Pan paniscus	Bissonnette <i>et al.</i> , 2014; Dixon, 1998; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Hohmann and Fruth, 2002; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Tokuyama, Sakamaki, and Furuichi, 2019; Willems, Hellriegel and van Schaik, 2013.



Pan troglodytes schweinfurthii	Bissonnette <i>et al.</i> , 2014; Dixon, 1998; Goodall, 1977; Goodall, 1986; Grueter <i>et al.</i> , 2013; Hiraiwa-Hasegawa, 1994; Jaeggi and van Schaik, 2011; Kaburu, Inoue and Newton-Fisher, 2013; Lowe <i>et al.</i> , 2019; Lowe <i>et al.</i> , 2020; Majolo <i>et al.</i> , 2020; Mitani, Watts and Amsler, 2010; Muller, 2002 Rowe and Myers, 2021; Sussman and Garber, 2004; Watts, 2004; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015.
Pan troglodytes verus	Bissonnette <i>et al.</i> , 2014; Boesch <i>et al.</i> , 2008; Grueter <i>et al.</i> , 2013; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Nishie and Nakamura, 2018; Pruett, 2006; Pruett <i>et al.</i> , 2017; Rowe and Myers, 2021; Samuni <i>et al.</i> , 2019; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015; Wilson <i>et al.</i> , 2014.
Papio anubis	Bissonnette <i>et al.</i> , 2014; Campbell <i>et al.</i> , 2011; Collins, Busse and Goodall, 1984; Dixon, 1998; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Harding, 1976; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Nakagawa, 2008; Strum, 2020; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.
Papio cynocephalus	Bissonnette <i>et al.</i> , 2014; Campbell <i>et al.</i> , 2011; Galán-Acedo <i>et al.</i> , 2019; Hiraiwa-Hasegawa, 1994; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Markham <i>et al.</i> , 2012; Noe and Sluijter, 1995; Rowe and Myers, 2021; Shopland, 1982; Strum, 1982; Willems, Hellriegel and van Schaik, 2013.
Papio ursinus	Anderson, 1981; Bissonnette <i>et al.</i> , 2014; Brain, 1992; Campbell <i>et al.</i> , 2011; Cheney and Fischer, 2000; Dixon, 1998; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Hall, 1962; Itani, 1982; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Palombit, 2015; Palombit, Rowe and Myers, 2021; Saayman, 1972; Smuts <i>et al.</i> , 1987; van Schaik and Janson, 2000; Willems, Hellriegel and van Schaik, 2013.
Phaner furcifer	Campbell, 2011; Galán-Acedo <i>et al.</i> , 2019; Majolo <i>et al.</i> , 2020; Myers <i>et al.</i> , 2022; Schülke, 2002; Schülke and Kappeler, 2003; Schülke and Kappeler, 2004; Schülke, Kappeler, and Zischler, 2004; Willems, Hellriegel and van Schaik, 2013.
Piliocolobus badius badius	Bissonnette <i>et al.</i> , 2014; Dixon, 1998; Galán-Acedo <i>et al.</i> , 2019; Jaeggi and van Schaik, 2011; Korstjens, Sterck and Noë, 2002; Majolo <i>et al.</i> , 2020; Myers <i>et al.</i> , 2022; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.



Piliocolobus badius temminckii	Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Majolo <i>et al.</i> , 2020; Myers <i>et al.</i> , 2022; Rowe and Myers, 2021; Starin, 1994; Starin, 2006; Starin in Ciochon and Nisbett, 1998; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.
Piliocolobus kirkii	Campbell <i>et al.</i> , 2011; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Majolo <i>et al.</i> , 2020; Nowak, 2007; Rowe and Myers, 2021; Siex, 2003; Willems, Hellriegel and van Schaik, 2013.
Piliocolobus tephrosceles	Campbell <i>et al.</i> , 2011; Galán-Acedo <i>et al.</i> , 2019; Korstjens, 2001; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Struhsaker and Leland, 1985; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015.
Pithecia pithecia	Anzelc, 2009; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Harrison and Norconk, 1999; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Thompson <i>et al.</i> , 2012; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015.
Plecturocebus moloch	Dixon, 1998; Galán-Acedo <i>et al.</i> , 2019; Holloway, 1974; Majolo <i>et al.</i> , 2020; Majolo, 2021; Robinson, 1979; Robinson, 1981; Willems, Hellriegel and van Schaik, 2013; Wright, 1985.
Presbytis potenziani	Dunbar, Mac Carron, and Shultz, 2018; Fuentes, 1996; Fuentes, 2000; Majolo <i>et al.</i> , 2020; Majolo, 2021; Plavcan, van Schaik, and Kappeler, 1995; Sangchantr, 2004; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.
Presbytis thomasi	Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Sterck, 1997; Rowe and Myers, 2021; Steenbeek <i>et al.</i> , 1999; Sterck and Steenbeek, 1997; van Schaik <i>et al.</i> , 1992; Wheeler <i>et al.</i> , 2013; Wich, 2020; Willems, Hellriegel and van Schaik, 2013.
Propithecus diadema	Day <i>et al.</i> , 2009; Galán-Acedo <i>et al.</i> , 2019; Irwin, 2006; Majolo, 2020; Myers <i>et al.</i> , 2022; Plavcan, van Schaik, and Kappeler, 1995; Powzyk, 1997; Rowe and Myers, 2021.

Propithecus edwardsi	Amigo-Nelson, 2006; Erhart and Overdorff, 1998; Galán-Acedo <i>et al.</i> , 2019; Jaeggi and van Schaik, 2011; Morelli <i>et al.</i> , 2009; Myers <i>et al.</i> , 2022; Powell, Isler and Barton, 2011; Randrianirina <i>et al.</i> , 2013; Rowe and Myers, 2021; Wright, 1995; Wright, 2020.
Propithecus verreauxi	Brockman, Cobden and Whitten, 2009; Brockman <i>et al.</i> , 1998; Dixon, 1998; Galán-Acedo <i>et al.</i> , 2019; Garber, 1988; Grueter <i>et al.</i> , 2013; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Lewis <i>et al.</i> , 2003; Littlefield, 2010; Majolo <i>et al.</i> , 2020; Plavcan, van Schaik, and Kappeler, 1995; Sussman and Garber, 2004; Wheeler <i>et al.</i> , 2013; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015.
Rhinopithecus bieti	Campbell <i>et al.</i> , 2011; Grueter <i>et al.</i> , 2013; Huang <i>et al.</i> , 2012; Kirkpatrick <i>et al.</i> , 1998; Rowe and Myers, 2021; Xiang and Grueter, 2007; Zhu <i>et al.</i> , 2016.
Saguinus mystax	Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013.
Saimiri boliviensis	Bissonnette <i>et al.</i> , 2014; Boinski <i>et al.</i> , 2001; Campbell <i>et al.</i> , 2011; Galán-Acedo <i>et al.</i> , 2019; Myers <i>et al.</i> , 2022; Powell, Isler and Barton, 2011; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013.
Saimiri oerstedii	Bissonnette <i>et al.</i> , 2014; Boinski, 1987; Galán-Acedo <i>et al.</i> , 2019; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013; Zimble-DeLorenz and Stone, 2011.
Saimiri sciureus	Bissonnette <i>et al.</i> , 2014; Dixon, 1998; Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Mitchell, 1990; Powell, Isler and Barton, 2011; Rowe and Myers, 2021; Stone, 2014; Terborgh, 1983; Willems, Hellriegel and van Schaik, 2013.
Sapajus apella	Defler, 1982; Galán-Acedo <i>et al.</i> , 2019; Heldstab <i>et al.</i> , 2021; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Plavcan, van Schaik, and Kappeler, 1995; Sussman and Garber, 2004; Willems, Hellriegel and van Schaik, 2013; Wrangham, Gittleman, Chapman, 1993.

Sapajus nigritus	Bissonnette <i>et al.</i> , 2014; Galán-Acedo <i>et al.</i> , 2019; Izar, 2004; Izar <i>et al.</i> , 2012; Majolo <i>et al.</i> , 2020; Myers <i>et al.</i> , 2022; Ramírez-Llorens <i>et al.</i> , 2008; Rowe and Myers, 2021; Scarry & Tujague, 2012 in Willems, Hellriegel and van Schaik, 2013; van Woerden <i>et al.</i> , 2014; Willems, Hellriegel and van Schaik, 2013.
Semnopithecus entellus	Bissonnette <i>et al.</i> , 2014; Cheyne, 1987; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Hiraiwa-Hasegawa, 1988; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Sugiyama, 1965; Sugiyama, 1984; Sussman and Garber, 2004; van Schaik and Janson, 2000; Willems, Hellriegel and van Schaik, 2013; Yoshida, 1967.
Symphalangus syndactylus	Chivers, 1976 in Lappan, 2007; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Myers <i>et al.</i> , 2022; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015.
Theropithecus gelada	Bergman, 2020; Campbell <i>et al.</i> , 2011; Dunbar, Mac Carron, and Shultz, 2018; Galán-Acedo <i>et al.</i> , 2019; Grueter <i>et al.</i> , 2013; Jaeggi and van Schaik, 2011; Majolo <i>et al.</i> , 2020; Mori, Iwamoto, and Bekele, 1997; Plavcan, van Schaik, and Kappeler, 1995; Rowe and Myers, 2021; Smuts <i>et al.</i> , 1987; van Schaik and Janson, 2000; Willems, Hellriegel and van Schaik, 2013; Wilson and Glowacki, 2017.
Trachypithecus cristatus	Bernstein, 1968; Furuya, 1961; Galán-Acedo <i>et al.</i> , 2019; Harding, 2010; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015
Trachypithecus johnii	Campbell <i>et al.</i> , 2011; Majolo <i>et al.</i> , 2020; Myers <i>et al.</i> , 2022; Willems, Hellriegel and van Schaik, 2013; Willems <i>et al.</i> , 2015.
Trachypithecus obscurus	Galán-Acedo <i>et al.</i> , 2019; Leen and Rosely., 2019; Leen <i>et al.</i> , 2019; Majolo <i>et al.</i> , 2020; Rowe and Myers, 2021; Ruslin, Matsuda, and Md-Zain, 2019; Willems, Hellriegel and van Schaik, 2013.
Varecia variegata	Britt and Lambana, 2003; Dunbar, Mac Carron, and Shultz, 2018; Galán-Acedo <i>et al.</i> , 2019; Morland, 1991; Powell, Isler and Barton, 2011; Rowe and Myers, 2021; Sussman and Garber, 2004; Vagell, 2020.

Species which commit at least one form of lethal violence (intragroup lethal violence, intergroup lethal violence, or infanticide)

## Appendix 1(B)D – Tree creation R script

```
#Load full tree
```

```
tree<-read.nexus('mammtree.nex')
```

```
#Load the string of 104 species names.
```

```
tip<-
```

```
("Alouatta_belzebul","Alouatta_caraya","Alouatta_guariba","Alouatta_palliata","Alouatta_pi  
gra","Alouatta_seneculus","Aotus_azarae","Aotus_nancymae","Aotus_nigricaps","Aotus_tri  
virgatus","Aotus_vociferans","Ateles_belzebuth","Ateles_chamek","Ateles_geoffroyi","Ate  
les_hybridus","Ateles_paniscus","Avahi_meridionalis","Brachyteles_arachnoides","Brachytel  
es_hypoxanthus","Cacajao_calvus","Cacajao_melanocephalus","Callicebus_nigrifrons","Call  
icebus_ornatus","Callicebus_personatus","Callicebus_torquatus","Callimico_goeldii","Callit  
hrix_jacchus","Callithrix_kuhlii","Callithrix_penicillata","Cebus_imitator","Cebus_olivaceus  
","Cercocebus_atys","Cercocebus_galeritus","Cercocebus_torquatus","Cercopithecus_ascani  
us","Cercopithecus_campbelli","Cercopithecus_diana","Cercopithecus_mitis","Chiropotes_al  
binasus","Chiropotes_satanas","Chlorocebus_aethiops","Chlorocebus_tantalus","Colobus_gu  
ereza","Colobus_polykomos","Colobus_vellerosus","Erythrocebus_patas","Eulemur_fulvus_  
fulvus","Eulemur_macaco","Eulemur_rubriventer","Gorilla_beringei","Gorilla_gorilla_gorill  
a","Hapalemur_griseus","Homo_sapiens","Hoolock_hoolock","Hylobates_lar","Hylobates_m  
oloch","Lemur_catta","Leontocebus_fuscicollis","Leontopithecus_rosalia","Lepilemur_rufica  
udatus","Lophocebus_albigena","Loris_tardigradus","Macaca_arctoides","Macaca_assamens  
is","Macaca_fascicularis","Macaca_fuscata","Macaca_mulatta","Macaca_nigra","Macaca_ra  
diata","Macaca_sinica","Nasalis_larvatus","Nycticebus_cougang","Pan_paniscus","Pan_trogl  
odytes_schweinfurthii","Pan_troglodytes_verus","Papio_anubis","Papio_cynocephalus","Pap  
io_ursinus","Perodicticus_potto_edwardsi","Phaner_furcifer","Piliocolobus_badius_badius","  
Piliocolobus_badius_temminckii","Piliocolobus_kirkii","Piliocolobus_tephrosceles","Pithec  
a_pithecia","Plecturocebus_moloch","Pongo_pygmaeus","Presbytis_potenziani","Presbytis_t  
homasi","Propithecus_edwardsi","Propithecus_verreauxi","Rhinopithecus_bieti","Saguinus_  
mystax","Saimiri_boliviensis","Saimiri_oerstedii","Saimiri_sciureus","Sapajus_apella","Sapa  
jus_nigritus","Semnopithecus_entellus","Symphalangus_syndactylus","Theropithecus_gelada  
","Trachypithecus_cristatus","Trachypithecus_johnii","Trachypithecus_obscurus","Varecia_v  
ariegata")
```



**APPENDICES – CHAPTER 2**

## Appendix 2A – PCA (all models) Script

## #Prepare

```
library(caper)
```

```
library(phytools)
```

```
library(plotrix)
```

```
setwd("C:\\Users\\swake\\Documents\\PHD - LINCOLN UNI\\R data files\\")
```

## #Load files

```
file.choose()
```

```
aggComp<- read.csv("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 1  
Dataset\\Compare all sets csv.csv", header = TRUE, row.names = 1)
```

```
file.choose ()
```

```
tree<-read.nexus("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 1  
Dataset\\ABSOLUTE MODEL\\104taxa.nex")
```

## #Convert to matrix

```
class(aggComp)
```

```
str(aggComp)
```

```
aggmat<-as.matrix(aggComp)
```

```
class(aggmat)
```

```
str(aggmat)
```

## #PCA

```

pc.phyl<-phyl.pca(tree, aggmatt[,c(1,2,3,4,5)], method="lambda", mode="corr")

summary(pc.phyl); pc.phyl$L; paste("lambda=", pc.phyl$lambda)

round(pc.phyl$L[, c(1:2)]^2 * 100, 2)

plot(pc.phyl)

biplot(pc.phyl)

pc.phyl$Eval

pc.phyl_scores <- as.data.frame(pc.phyl$S)

pc.phyl_scores$names <- row.names(pc.phyl_scores)

plot(pc.phyl_scores$PC1,

pc.phyl_scores$PC2,

main="scatterplot",

xlab="PPC1",

ylab="ppc2", pch=19)

text(pc.phyl_scores$PC1, pc.phyl_scores$PC2+0.01, labels=pc.phyl_scores$names,

col="blue", cex=0.7)

```

## #PCA 2

```

pc.phyl2<-phyl.pca(tree, aggmatt[,c(6,7,8,9,10)], method="lambda", mode="corr")

summary(pc.phyl2); pc.phyl2$L; paste("lambda=", pc.phyl2$lambda)

round(pc.phyl2$L[, c(1:2)]^2 * 100, 2)

plot(pc.phyl2)

biplot(pc.phyl2)

pc.phyl2$Eval

pc.phyl_scores2 <- as.data.frame(pc.phyl2$S)

pc.phyl_scores2$names <- row.names(pc.phyl_scores2)

```

```

plot(pc.phyl_scores2$PC1,
     pc.phyl_scores2$PC2,
     main="scatterplot",
     xlab="PPC1",
     ylab="ppc2", pch=19)

text(pc.phyl_scores2$PC1, pc.phyl_scores2$PC2+0.01, labels=pc.phyl_scores2$names,
     col="blue", cex=0.7)

```

### #PCA 3

```

pc.phyl3<-phyl.pca(tree, aggmatt[,c(11,12,13,14,15)], method="lambda", mode="corr")

summary(pc.phyl3); pc.phyl3$L; paste("lambda=", pc.phyl3$lambda)

round(pc.phyl3$L[, c(1:2)]^2 * 100, 2)

plot(pc.phyl3)

biplot(pc.phyl3)

pc.phyl3$Eval

pc.phyl_scores3 <- as.data.frame(pc.phyl3$S)

pc.phyl_scores3$names <- row.names(pc.phyl_scores3)

plot(pc.phyl_scores3$PC1,
     pc.phyl_scores3$PC2,
     main="scatterplot",
     xlab="PPC1",
     ylab="ppc2", pch=19)

text(pc.phyl_scores3$PC1, pc.phyl_scores3$PC2+0.01, labels=pc.phyl_scores3$names,
     col="blue", cex=0.7)

```



## #PCA 4

```

pc.phyl4<-phyl.pca(tree, aggrmat[,c(16,17,18,19,20)], method="lambda", mode="corr")

summary(pc.phyl4); pc.phyl4$L; paste("lambda=", pc.phyl4$lambda)

round(pc.phyl4$L[, c(1:2)]^2 * 100, 2)

plot(pc.phyl4)

biplot(pc.phyl4)

pc.phyl4$Eval

pc.phyl_scores4 <- as.data.frame(pc.phyl4$S)

pc.phyl_scores4$names <- row.names(pc.phyl_scores4)

plot(pc.phyl_scores4$PC1,

      pc.phyl_scores4$PC2,

      main="scatterplot",

      xlab="PPC1",

      ylab="ppc2", pch=19)

text(pc.phyl_scores4$PC1, pc.phyl_scores4$PC2+0.01, labels=pc.phyl_scores4$names,

     col="blue", cex=0.7)

```

## #PCA 5

```

pc.phyl5<-phyl.pca(tree, aggrmat[,c(21,22,23,24,25)], method="lambda", mode="corr")

summary(pc.phyl5); pc.phyl5$L; paste("lambda=", pc.phyl5$lambda)

round(pc.phyl5$L[, c(1:2)]^2 * 100, 2)

plot(pc.phyl5)

biplot(pc.phyl5)

pc.phyl5$Eval

```

```
pc.phyl_scores5 <- as.data.frame(pc.phyl5$$)

pc.phyl_scores5$names <- row.names(pc.phyl_scores5)

plot(pc.phyl_scores5$PC1,
     pc.phyl_scores5$PC2,
     main="scatterplot",
     xlab="PPC1",
     ylab="ppc2", pch=19)

text(pc.phyl_scores5$PC1, pc.phyl_scores5$PC2+0.01, labels=pc.phyl_scores5$names,
     col="blue", cex=0.7)
```

#Congruence (compare each dataset against baseline and compare ‘lower’ and ‘upper’ datasets as extreme examples of quantitative conversions).

```
factor.congruence(pc.phyl2$L, pc.phyl3$L)
```

## Appendix 2B – PCA and congruence results

## 2B.1 'Baseline' dataset (PCA 1)

```
> summary(pc.phyl); pc.phyl$L; paste("lambda=", pc.phyl$lambda)
```

Importance of components:

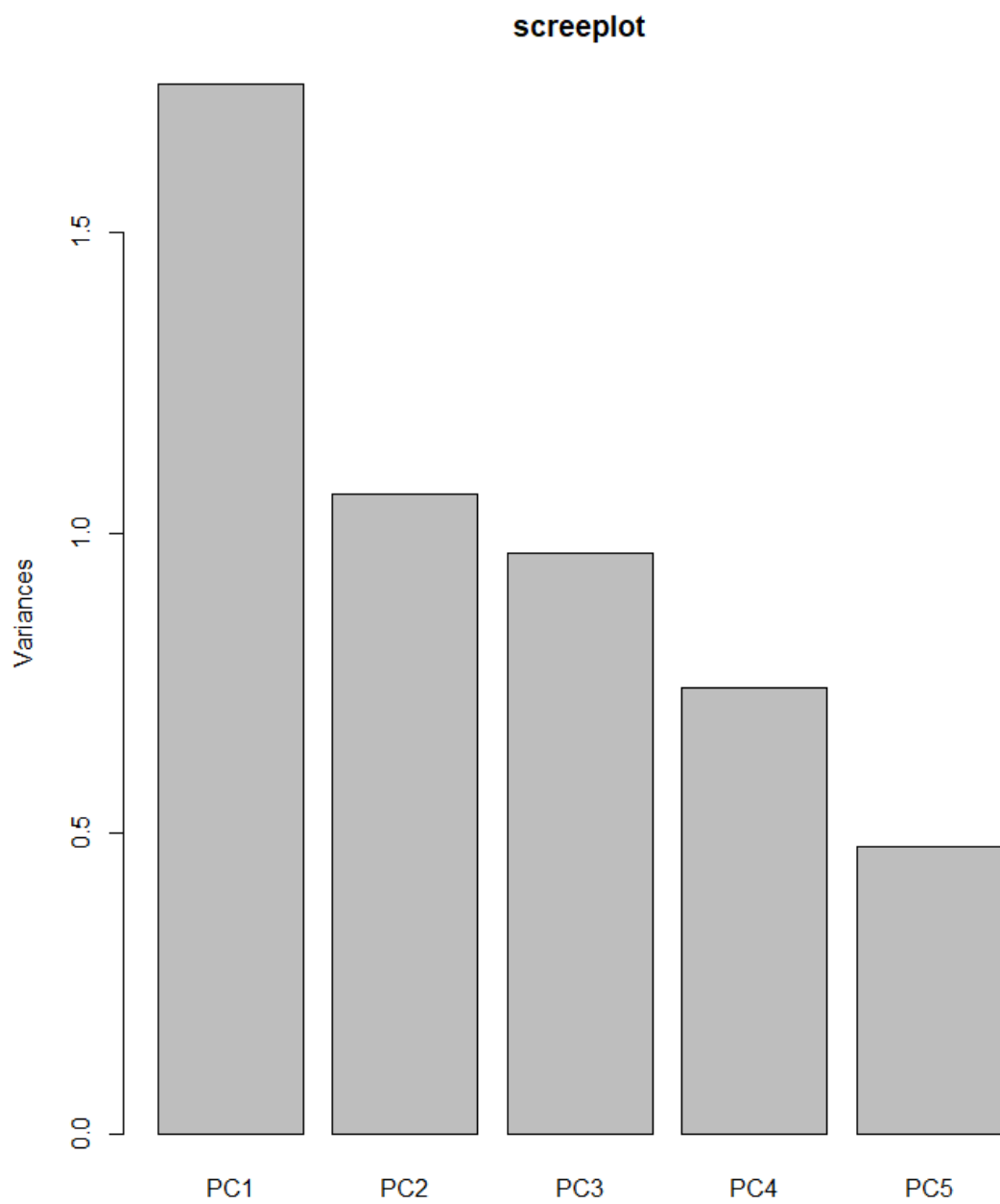
	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.3219702	1.0316573	0.9831205	0.8620211	0.69171644
Proportion of Variance	0.3495211	0.2128633	0.1933052	0.1486161	0.09569433
Cumulative Proportion	0.3495211	0.5623844	0.7556896	0.9043057	1.00000000

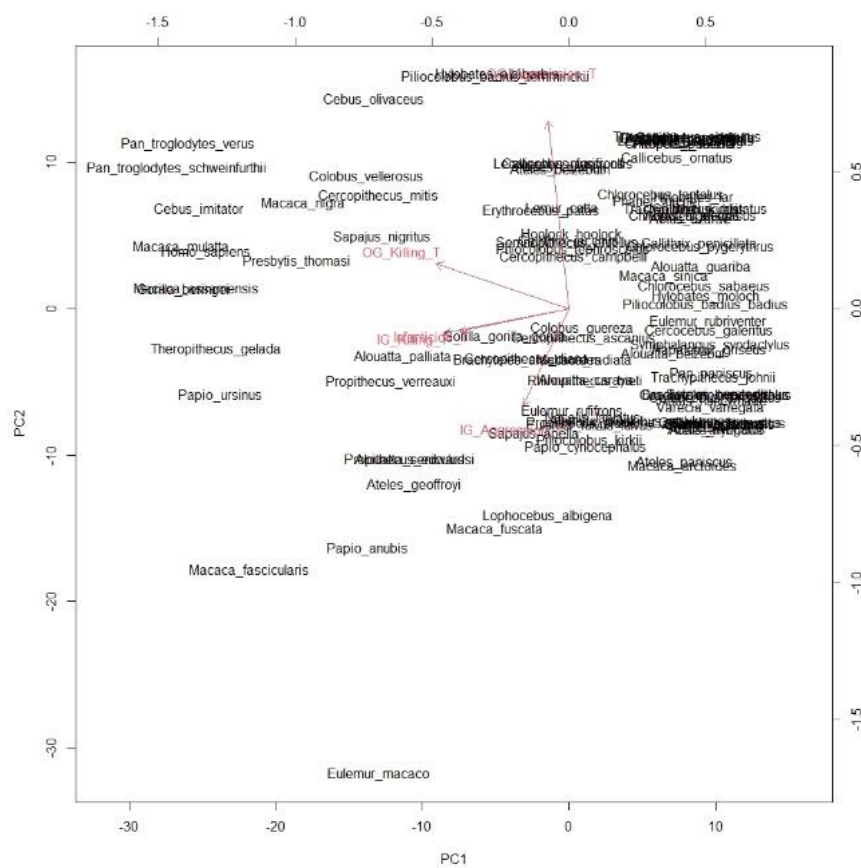
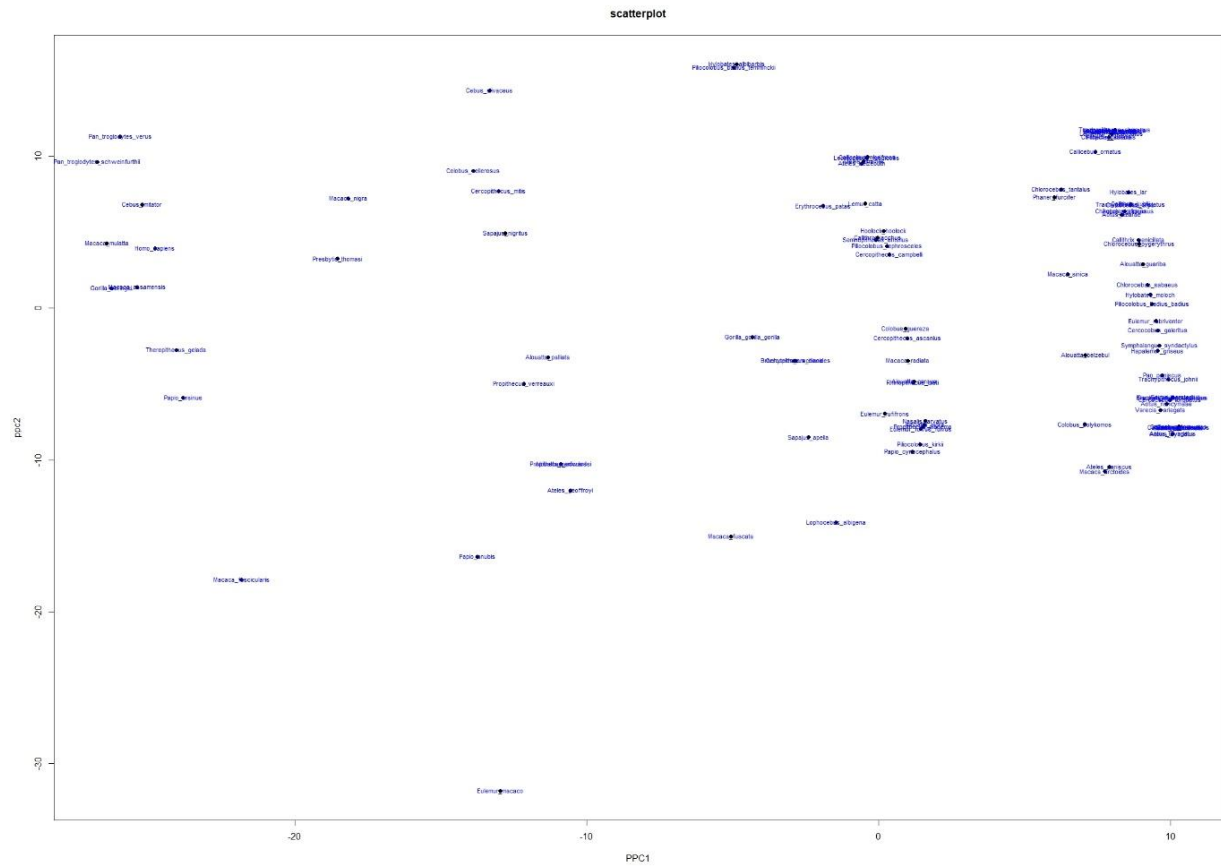
	PC1	PC2	PC3	PC4	PC5
OG_Aggression_T	-0.1279449	0.8857800	0.39241833	0.001031253	-0.21220452
IG_Aggression_T	-0.2764699	-0.4580837	0.81207187	-0.221780278	-0.07124968
OG_Killing_T	-0.8044095	0.2125702	-0.05173333	-0.267024823	0.48348797
IG_Killing_T	-0.7543676	-0.1157488	-0.37942582	-0.281368640	-0.44090751
Infanticide_T	-0.6623101	-0.1062357	0.08020414	0.737171848	-0.01429408

[1] "lambda= 6.61772261257953e-05" / 0.0000662 (very low phylogenetic signal)

	PC1	PC2	PC3	PC4	PC5
PC1	1.747605	0.000000	0.0000000	0.0000000	0.0000000
PC2	0.000000	1.064317	0.0000000	0.0000000	0.0000000
PC3	0.000000	0.000000	0.9665259	0.0000000	0.0000000
PC4	0.000000	0.000000	0.0000000	0.7430805	0.0000000
PC5	0.000000	0.000000	0.0000000	0.0000000	0.4784716

PC1-3 = 75.57%





## 2B.2 'Upper' dataset (PCA 2)

```
> summary(pc.phyl2); pc.phyl2$L; paste("lambda=", pc.phyl2$lambda)
```

Importance of components:

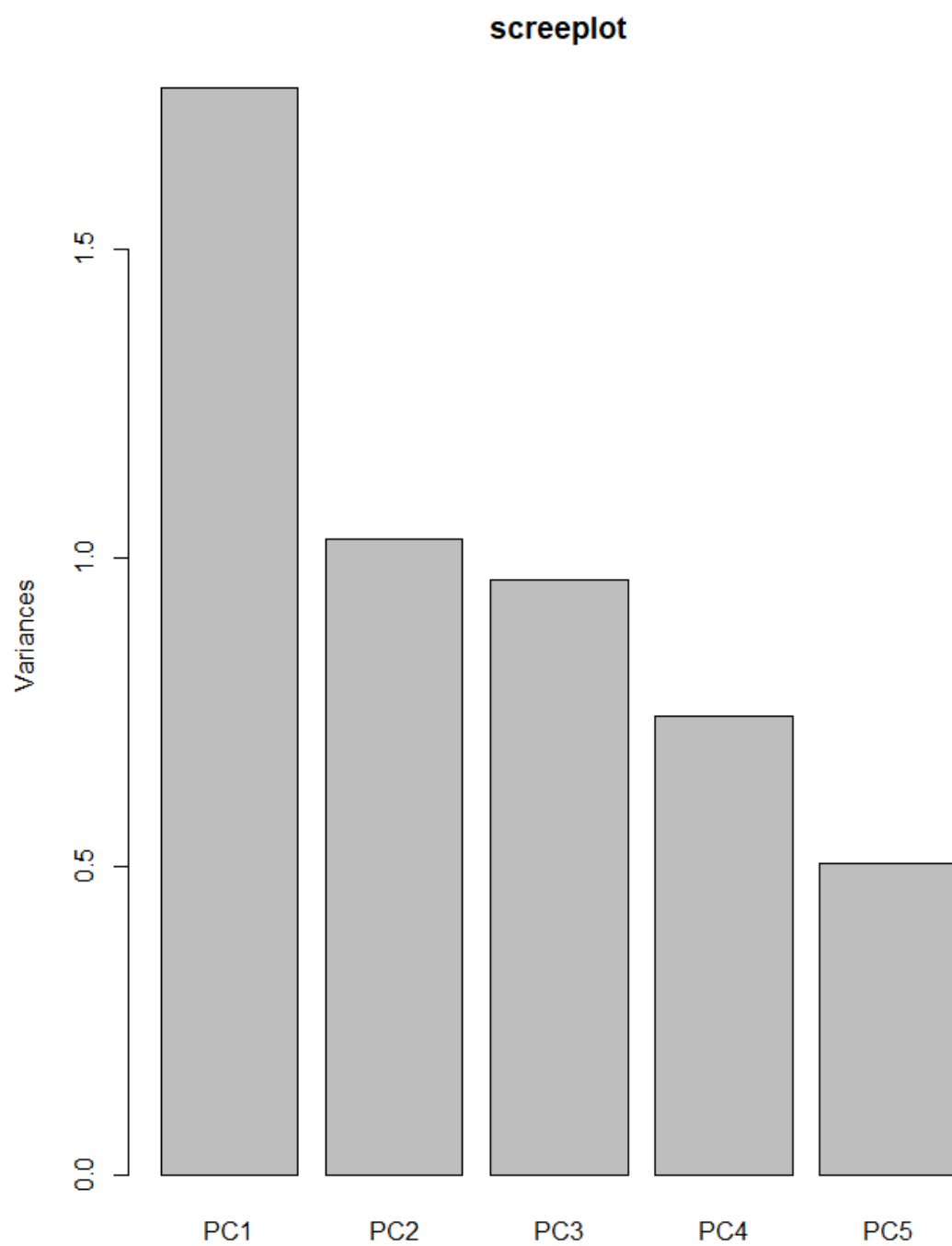
	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.3268224	1.0144163	0.9812108	0.8625427	0.7097517
Proportion of Variance	0.3520915	0.2058081	0.1925549	0.1487960	0.1007495
Cumulative Proportion	0.3520915	0.5578996	0.7504545	0.8992505	1.0000000

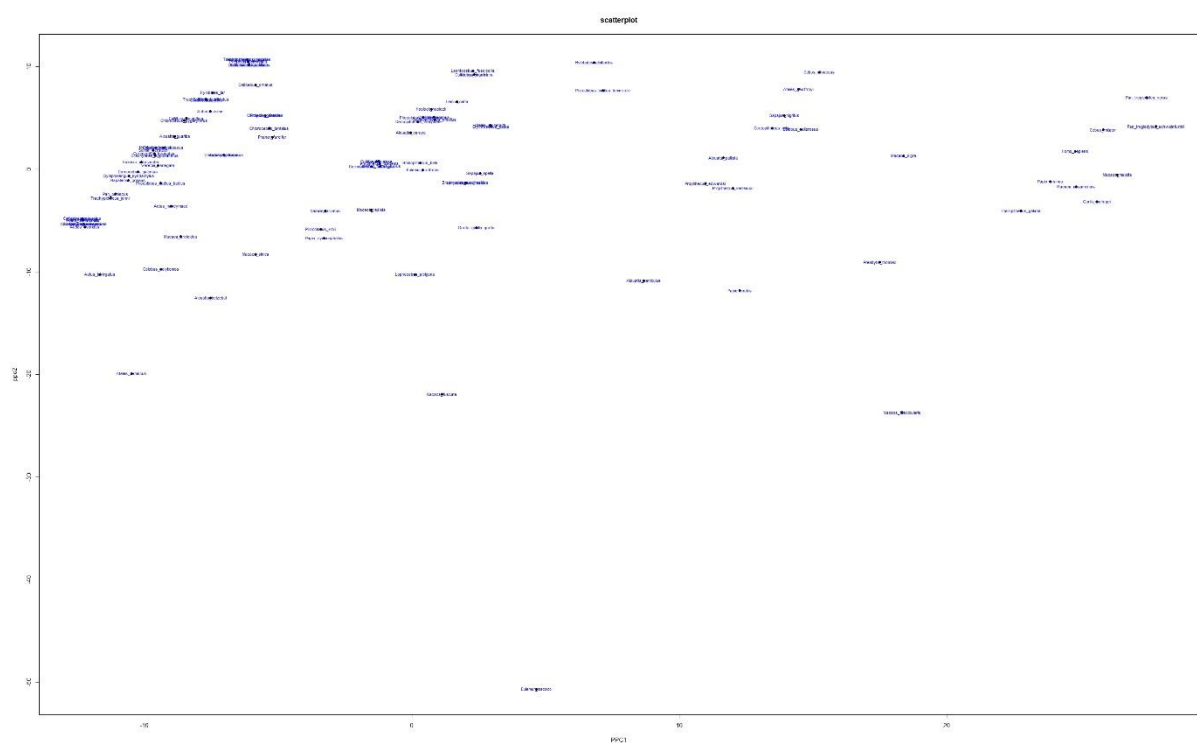
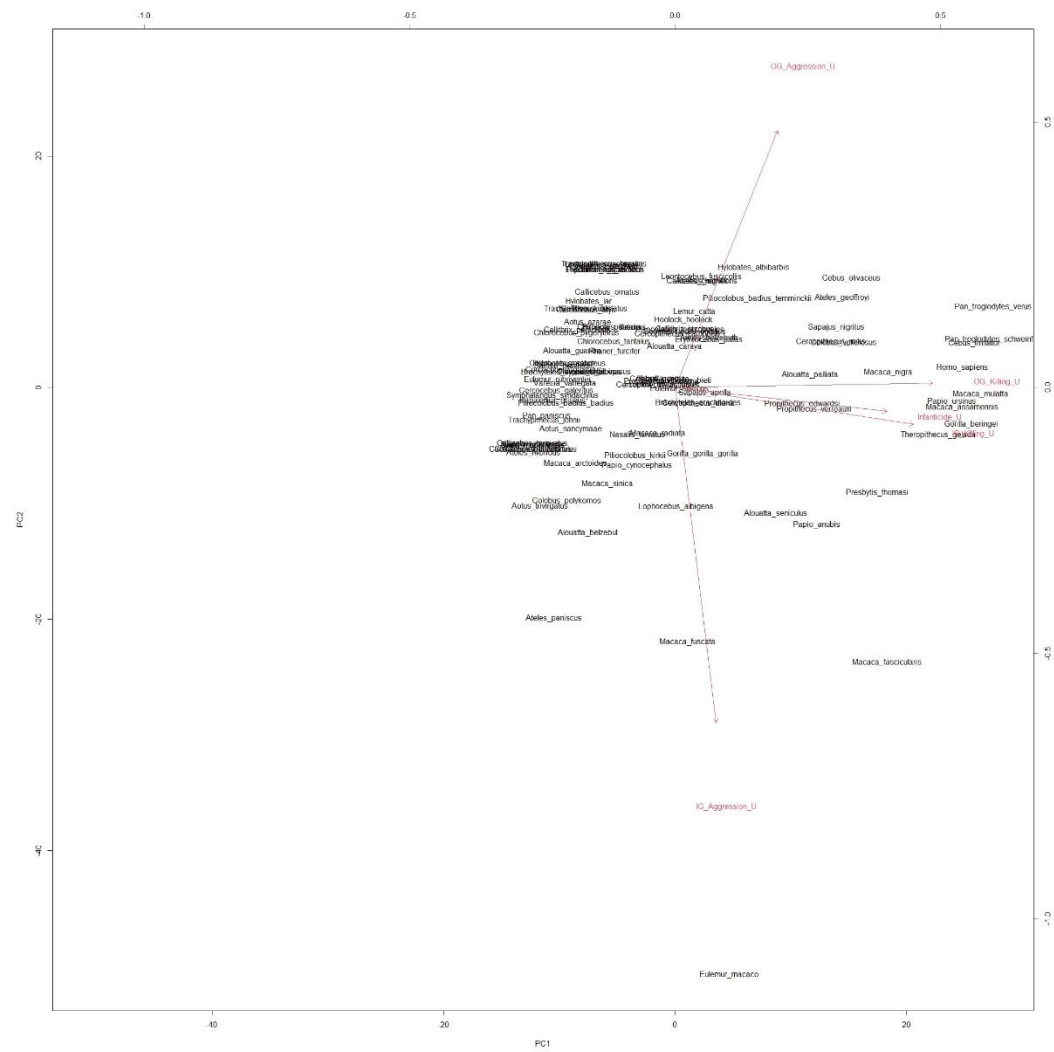
	PC1	PC2	PC3	PC4	PC5
OG_Aggression_U	0.3203251	0.61406228	0.68384184	-0.1530372	-0.17105346
IG_Aggression_U	0.1281637	-0.80054277	0.56131691	-0.1489360	-0.07380207
OG_Killing_U	0.8050322	0.01124739	-0.06697130	-0.3119234	0.50001525
IG_Killing_U	0.7451252	-0.08810242	-0.40692814	-0.2294550	-0.46774595
Infanticide_U	0.6619177	-0.05666301	0.09991319	0.7405618	0.01548891

[1] "lambda= 6.61772261257953e-05"

	PC1	PC2	PC3	PC4	PC5
PC1	1.760458	0.00000	0.0000000	0.0000000	0.0000000
PC2	0.000000	1.02904	0.0000000	0.0000000	0.0000000
PC3	0.000000	0.00000	0.9627747	0.0000000	0.0000000
PC4	0.000000	0.00000	0.0000000	0.7439798	0.0000000
PC5	0.000000	0.00000	0.0000000	0.0000000	0.5037475

PC1-3 = 75.05%







## 2B.3 'Lower' dataset (PCA 3)

```
> summary(pc.phyl3); pc.phyl3$L; paste("lambda=", pc.phyl3$lambda)
```

Importance of components:

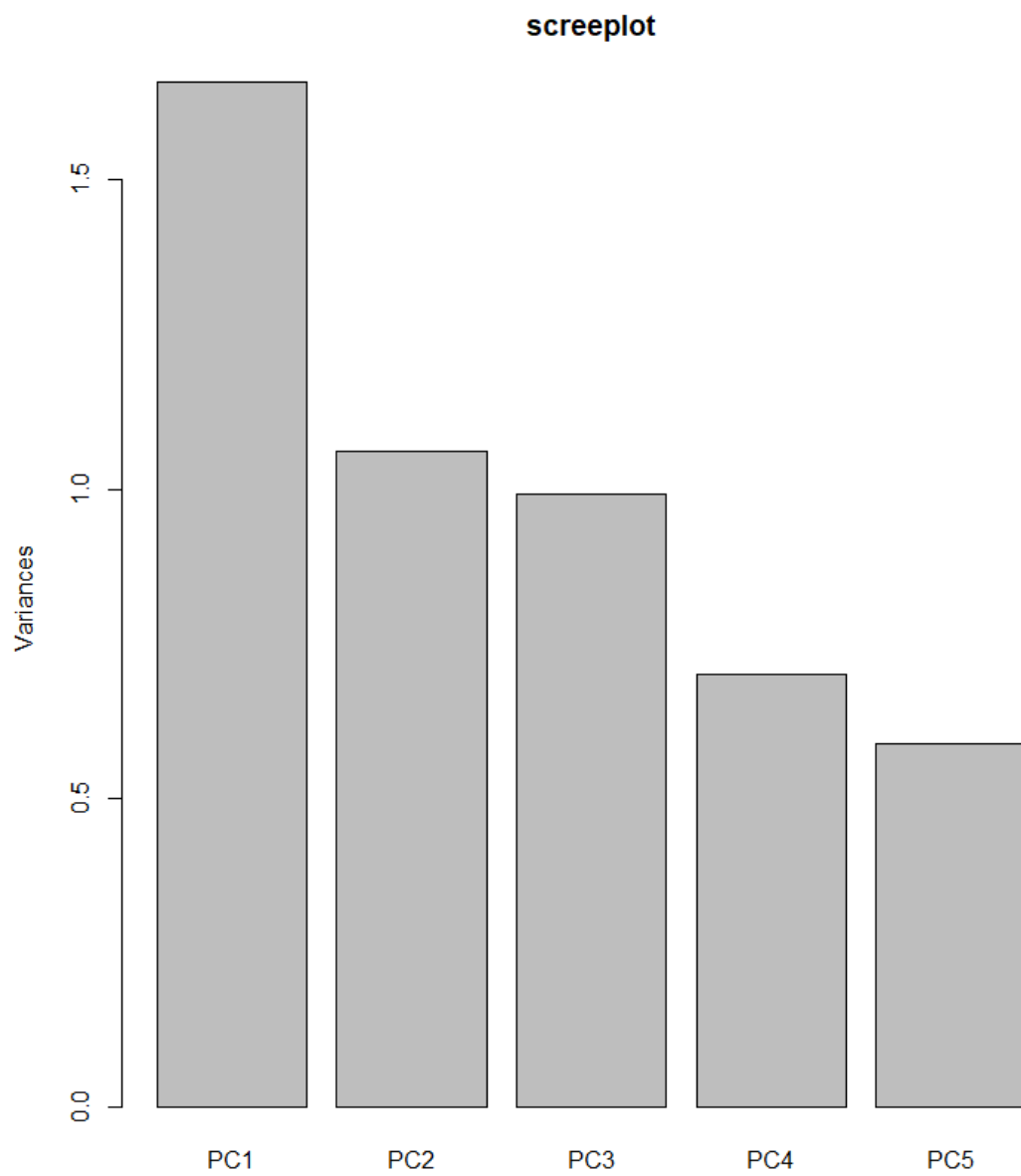
	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.2877906	1.0302404	0.9962642	0.8361120	0.7671862
Proportion of Variance	0.3316809	0.2122790	0.1985085	0.1398167	0.1177149
Cumulative Proportion	0.3316809	0.5439599	0.7424684	0.8822851	1.0000000

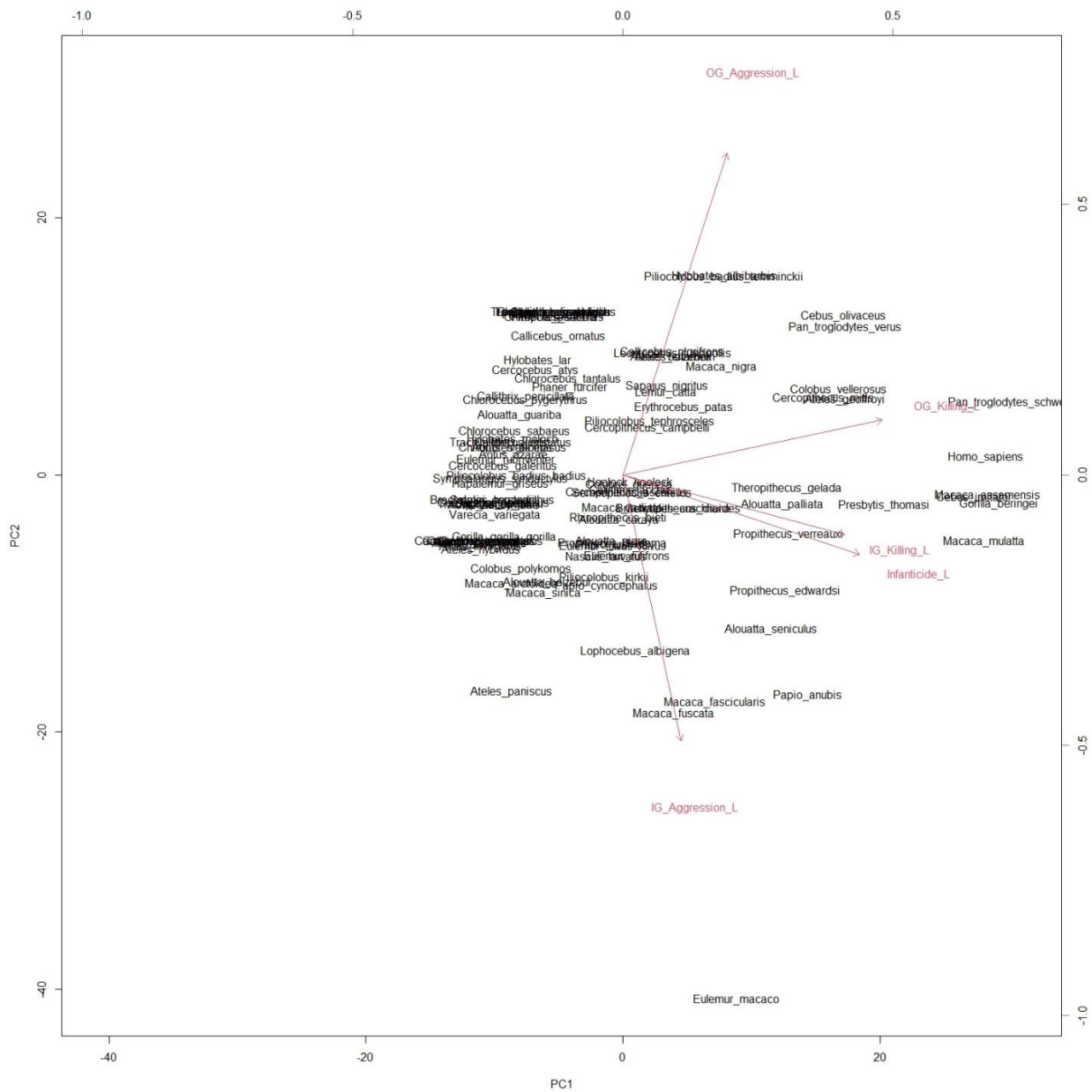
	PC1	PC2	PC3	PC4	PC5
OG_Aggression_L	-0.3097382	0.7657508	0.46579109	0.01117777	-0.3171775
IG_Aggression_L	-0.1726061	-0.6337759	0.71687188	-0.16128527	-0.1691657
OG_Killing_L	-0.7733368	0.1300943	0.12568369	-0.27156040	0.5435846
IG_Killing_L	-0.6608523	-0.1434505	-0.49267262	-0.37083187	-0.4030553
Infanticide_L	-0.7056191	-0.1893314	-0.05615175	0.67947342	-0.0376590

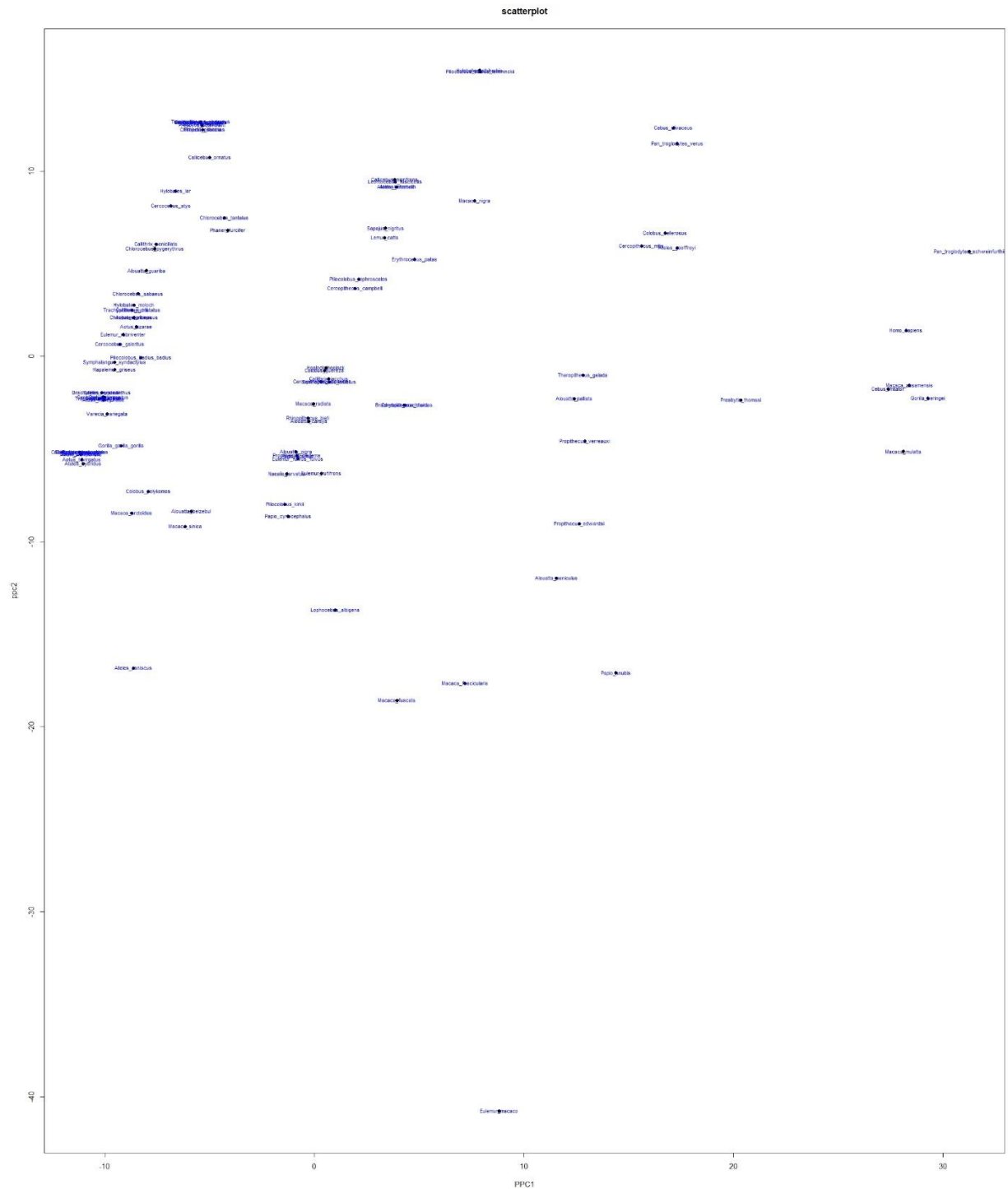
[1] "lambda= 6.61772261257953e-05"

	PC1	PC2	PC3	PC4	PC5
PC1	1.658405	0.000000	0.0000000	0.0000000	0.0000000
PC2	0.000000	1.061395	0.0000000	0.0000000	0.0000000
PC3	0.000000	0.000000	0.9925424	0.0000000	0.0000000
PC4	0.000000	0.000000	0.0000000	0.6990833	0.0000000
PC5	0.000000	0.000000	0.0000000	0.0000000	0.5885746

PC1-3 = 74.25%







## 2B.4 'Absolute' dataset (PCA 4)

```
> summary(pc.phyl4); pc.phyl4$L; paste("lambda=", pc.phyl4$lambda)
```

Importance of components:

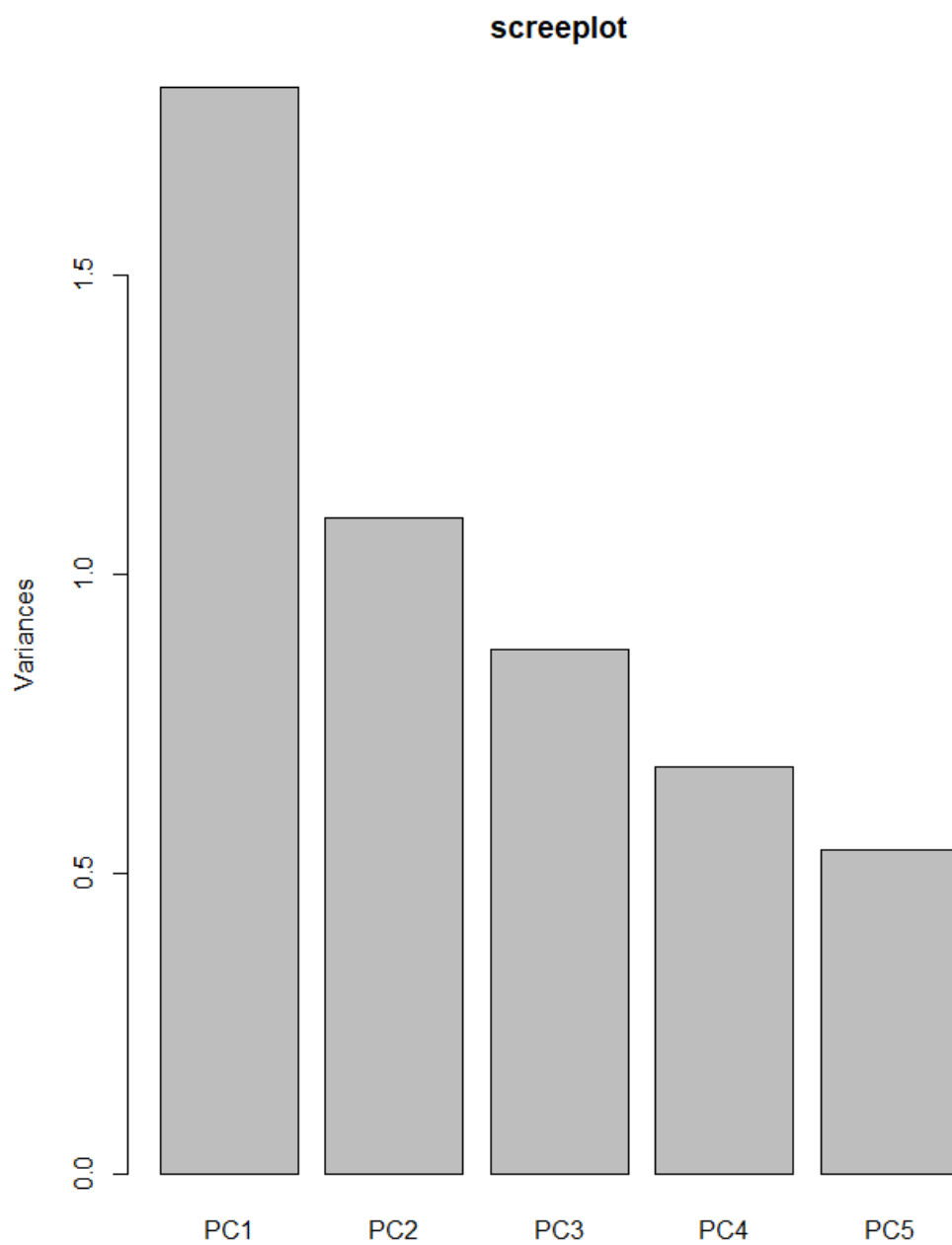
	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.3464013	1.0466057	0.9348203	0.8233561	0.7348575
Proportion of Variance	0.3625593	0.2190767	0.1747778	0.1355831	0.1080031
Cumulative Proportion	0.3625593	0.5816360	0.7564138	0.8919969	1.0000000

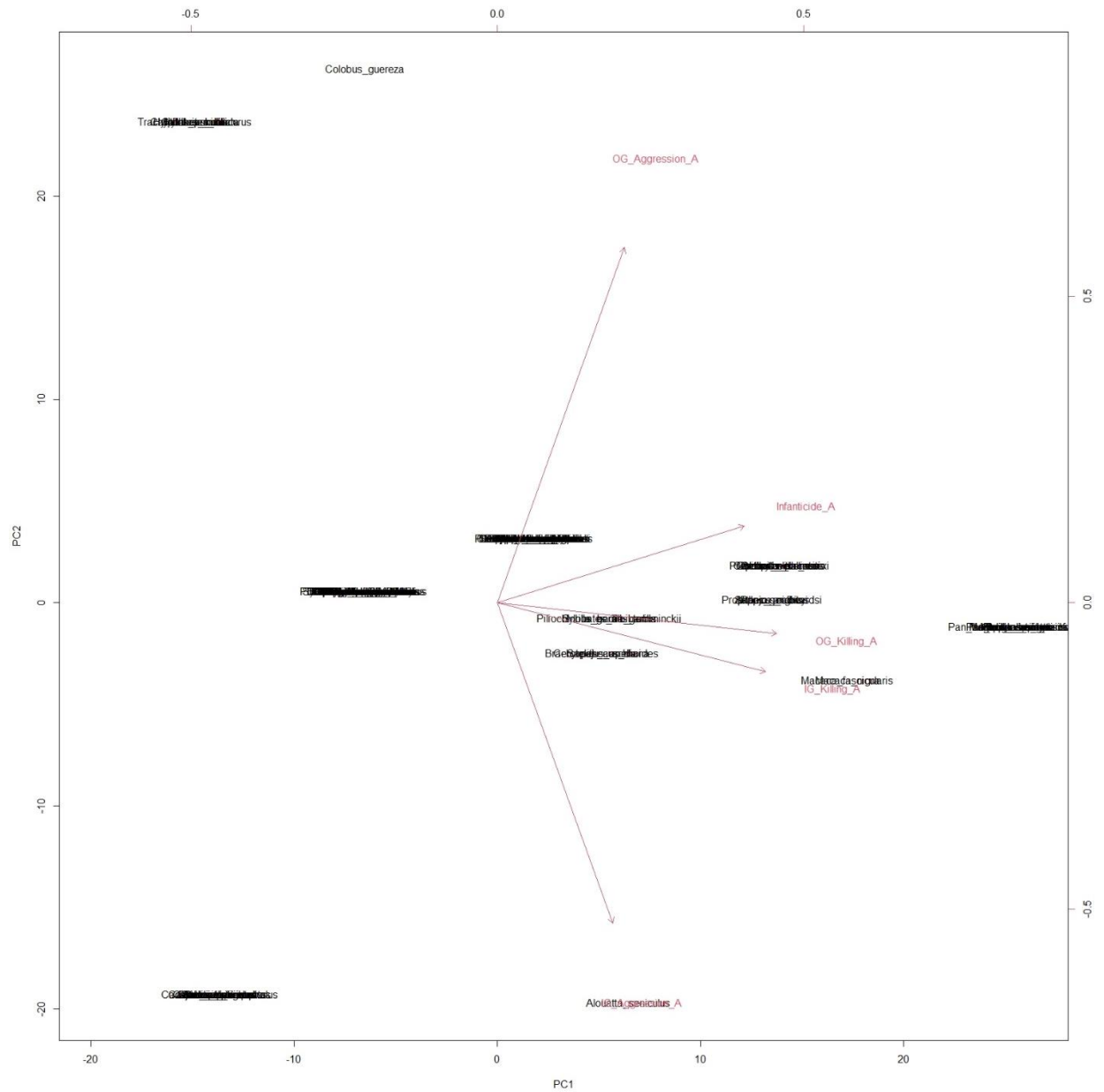
	PC1	PC2	PC3	PC4	PC5
OG_Aggression_A	0.3485482	0.75813871	0.3652403	-0.39852249	0.10732757
IG_Aggression_A	0.3167654	-0.68380429	0.6035983	-0.25540573	0.05008406
OG_Killing_A	0.7673675	-0.06573068	-0.3019416	-0.21637310	-0.51849832
IG_Killing_A	0.7362535	-0.14745621	-0.4206770	-0.06099593	0.50546800
Infanticide_A	0.6782687	0.16418623	0.3286636	0.63507893	-0.04061447

[1] "lambda= 0.0510424025981936"

	PC1	PC2	PC3	PC4	PC5
PC1	1.812797	0.000000	0.000000	0.0000000	0.0000000
PC2	0.000000	1.095384	0.000000	0.0000000	0.0000000
PC3	0.000000	0.000000	0.873889	0.0000000	0.0000000
PC4	0.000000	0.000000	0.000000	0.6779153	0.0000000
PC5	0.000000	0.000000	0.000000	0.0000000	0.5400156

PC1-3 = 75.64%









### 2B.5 'Half-Half' dataset (PCA 5)

```
> summary(pc.phyl5); pc.phyl5$L; paste("lambda=", pc.phyl5$lambda)
```

Importance of components:

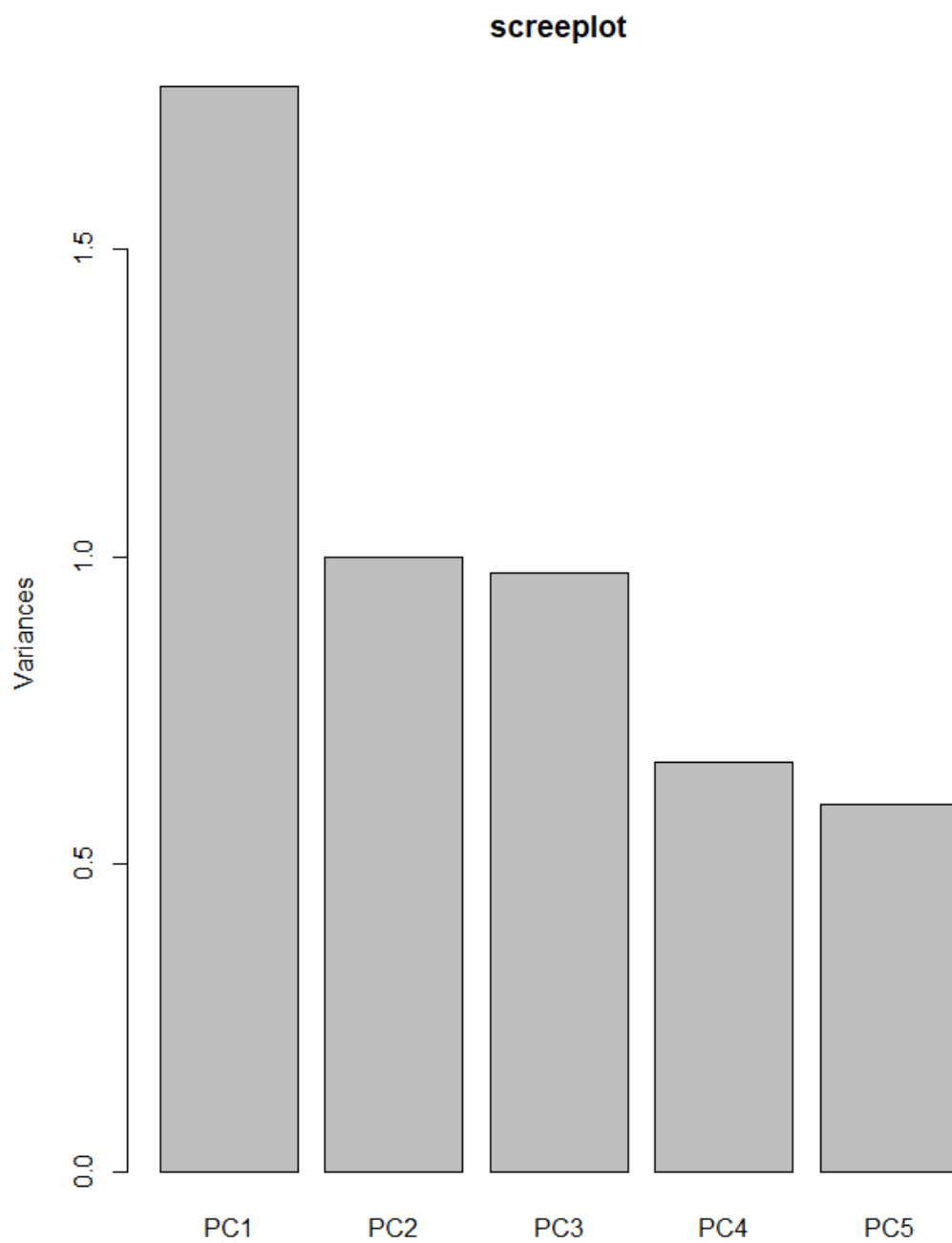
	PC1	PC2	PC3	PC4	PC5
Standard deviation	1.328371	0.9991067	0.9865377	0.8159237	0.7734520
Proportion of Variance	0.352914	0.1996428	0.1946513	0.1331463	0.1196456
Cumulative Proportion	0.352914	0.5525568	0.7472081	0.8803544	1.0000000

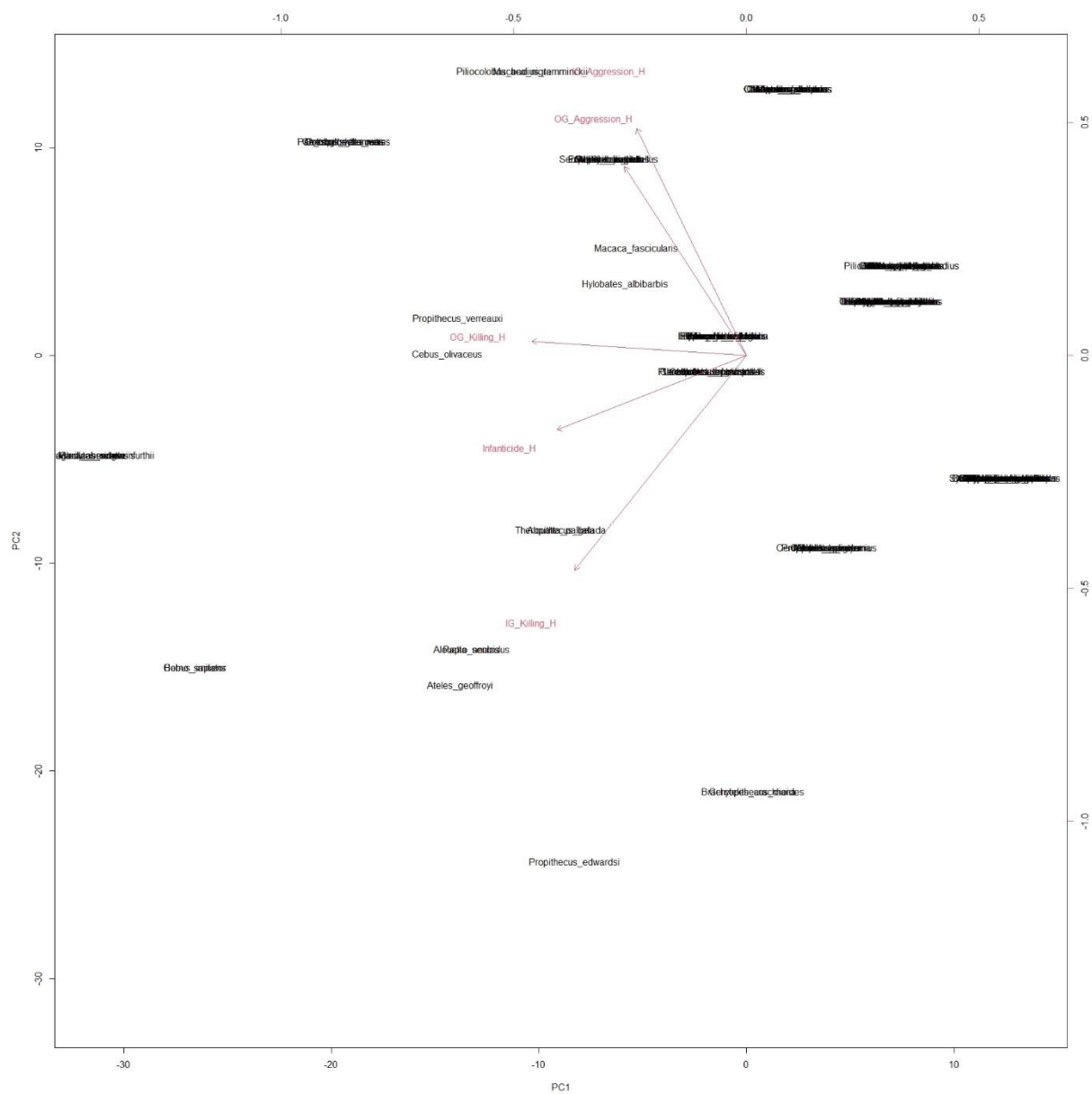
	PC1	PC2	PC3	PC4	PC5
OG_Aggression_H	-0.4354156	0.50619512	0.66859598	0.1229988	0.3033652
IG_Aggression_H	-0.3921988	0.60817177	-0.60931235	-0.2951340	0.1339463
IG_Killing_H	-0.6136562	-0.57504134	0.07546311	-0.4233095	0.3284325
OG_Killing_H	-0.7660964	0.03814155	0.17546547	-0.1172929	-0.6058843
Infanticide_H	-0.6765246	-0.19995122	-0.34422612	0.6087283	0.1152916

[1] "lambda= 6.61772261257953e-05"

	PC1	PC2	PC3	PC4	PC5
PC1	1.76457	0.0000000	0.0000000	0.0000000	0.0000000
PC2	0.000000	0.9982142	0.0000000	0.0000000	0.0000000
PC3	0.000000	0.0000000	0.9732565	0.0000000	0.0000000
PC4	0.000000	0.0000000	0.0000000	0.6657315	0.0000000
PC5	0.000000	0.0000000	0.0000000	0.0000000	0.598228

PC1-3 = 74.72%







## 2B.6 Congruence

### Comparing 'Baseline' and 'Upper'

```
> factor.congruence(pc.phyl$L, pc.phyl2$L)
```

	PC1	PC2	PC3	PC4	PC5
PC1	-0.98	0.18	0.04	-0.01	-0.02
PC2	0.18	0.89	0.37	-0.21	0.06
PC3	-0.03	-0.38	0.92	-0.02	0.04
PC4	0.03	0.18	0.10	0.98	0.04
PC5	-0.03	-0.04	-0.06	-0.03	1.00

### Comparing 'Baseline' and 'Lower'

```
> factor.congruence(pc.phyl$L, pc.phyl3$L)
```

	PC1	PC2	PC3	PC4	PC5
PC1	-0.98	0.15	0.04	0.08	-0.02
PC2	0.16	0.97	0.17	0.00	-0.05
PC3	0.02	-0.18	0.96	0.10	-0.19
PC4	0.08	0.01	-0.11	0.99	-0.03
PC5	-0.01	0.02	0.19	0.05	0.98

### Comparing 'Baseline' and 'Absolute'

```
> factor.congruence(pc.phyl$L, pc.phyl4$L)
```

	PC1	PC2	PC3	PC4	PC5
PC1	-0.99	0.11	0.10	-0.07	0.04
PC2	0.12	0.90	0.00	-0.40	-0.12
PC3	0.10	-0.18	0.91	-0.34	-0.12
PC4	0.02	0.37	0.38	0.84	-0.07
PC5	-0.06	-0.11	-0.13	0.03	-0.98

### Comparing 'Baseline' and 'Half-Half'

```
> factor.congruence(pc.phyl$L, pc.phyl5$L)
```

	PC1	PC2	PC3	PC4	PC5
PC1	0.96	0.25	0.09	0.09	0.04

PC2	-0.13	0.06	0.89	0.12	0.42
PC3	-0.17	0.70	-0.34	-0.09	0.59
PC4	-0.03	-0.16	-0.22	0.94	0.21
PC5	0.19	-0.64	-0.20	-0.30	0.65

Comparing 'Lower' and 'Upper'

```
> factor.congruence(pc.phyl2$L, pc.phyl3$L)
```

	PC1	PC2	PC3	PC4	PC5
PC1	1.00	0.03	-0.05	-0.06	-0.01
PC2	-0.03	0.96	-0.24	0.15	-0.02
PC3	0.05	0.20	0.93	0.19	-0.25
PC4	0.05	-0.19	-0.17	0.96	-0.05
PC5	0.02	0.06	0.23	0.10	0.97

## Appendix 2C – Model brms R script

## ## Prepare session

```
library(caper)
library(ggplot2)
library(ggtree)
library(brms)
```

## ## Import data

## # Phylogeny

```
file.choose()

tree<-read.nexus( "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 1
Dataset\\104taxa.nex")

tree$tip.label<- gsub("_", " ", tree$tip.label)
```

## # Species traits

```
file.choose()

dataA<-read.table("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 1
Dataset\\THEME MODEL\\theme baseline txt.txt", header=T, stringsAsFactors=F)

dataA$SpeciesTree<- gsub("_", " ", dataA$SpeciesTree)
```

## # Check whether species names match, and correct if not

```
dataA$SpeciesTree %in% tree$tip.label
```

## #Run multivariate model

```
priorA <- c(prior(normal(0, 10), class = Intercept, resp = IAggression),
            prior(normal(0, 10), class = Intercept, resp = OGAgression),
            prior(normal(0, 10), class = Intercept, resp = OGKilling),
            prior(normal(0, 10), class = Intercept, resp = IGKilling),
            prior(normal(0, 10), class = Intercept, resp = Infanticide))
```

```

fitAggression<- brm(mvbind(OG_Aggression, IG_Aggression, IG_Killing, OG_Killing,
Infanticide)~ 1 + (1|gr(SpeciesTree, cov= A)),
  family= list(zero_one_inflated_beta(), hurdle_gamma(), bernoulli(), bernoulli(),
bernoulli()),
  data= dataA,
  prior = priorA,
  data2= list(A= vcv.phylo(tree)),
  cores = future::availableCores() -1,
  iter= 4e3,
  control= list(adapt_delta= .99, max_treedepth= 15))

```

### ## Explore outcome and predictions

```
summary(fitAggression, waic= T); bayes_R2(fitAggression)
```

### #Plots

```

pairs(fitAggression)
plot(fitAggression)

```

### #PP Checks

```

pp_check(fitAggression, resp= "OGAggression", nsamples= 1e2)
pp_check(fitAggression, resp= "IGAggression", nsamples= 1e2)
pp_check(fitAggression, resp= "OGKilling", nsamples= 1e2)
pp_check(fitAggression, resp= "IGKilling", nsamples= 1e2)
pp_check(fitAggression, resp= "Infanticide", nsamples= 1e2)

```



## Appendix 2D – ‘Baseline’ results and plots

```
> summary(fitAggression, waic= T); bayes_R2(fitAggression)
```

Family: MV(zero\_one\_inflated\_beta, hurdle\_gamma, bernoulli, bernoulli, bernoulli)

Links: mu = logit; phi = identity; zoi = identity; coi = identity

mu = log; shape = identity; hu = identity

mu = logit

mu = logit

mu = logit

Formula: OG\_Aggression ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

IG\_Aggression ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

IG\_Killing ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

OG\_Killing ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

Infanticide ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

Data: data2a (Number of observations: 104)

Samples: 4 chains, each with iter = 4000; warmup = 2000; thin = 1; total post-warmup samples = 8000

**Group-Level Effects:**

~SpeciesTree (Number of levels: 104)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGAggression_Intercept)	0.06	0.04	0.00	0.16	1.00	2189	3589

sd(IGAggression_Intercept)	0.31	0.10	0.14	0.52	1.00	1495	2741
sd(IGKilling_Intercept)	2.13	2.35	0.42	8.24	1.01	1373	3583
sd(OGKilling_Intercept)	1.23	1.50	0.28	5.37	1.00	1199	2472
sd(Infanticide_Intercept)	0.39	0.26	0.11	1.00	1.00	1748	2155
cor(OGAggression_Intercept,IGAggression_Intercept)	-0.08	0.38	-0.78	0.65	1.00	1099	2818
cor(OGAggression_Intercept,IGKilling_Intercept)	-0.15	0.38	-0.79	0.65	1.01	658	1367
cor(IGAggression_Intercept,IGKilling_Intercept)	0.19	0.28	-0.35	0.72	1.00	1872	3532
cor(OGAggression_Intercept,OGKilling_Intercept)	-0.02	0.38	-0.74	0.71	1.01	783	1676
cor(IGAggression_Intercept,OGKilling_Intercept)	0.33	0.26	-0.23	0.77	1.00	2661	4903
cor(IGKilling_Intercept,OGKilling_Intercept)	0.67	0.18	0.24	0.94	1.00	4232	6637
cor(OGAggression_Intercept,Infanticide_Intercept)	-0.15	0.39	-0.81	0.63	1.01	794	1853
cor(IGAggression_Intercept,Infanticide_Intercept)	0.37	0.29	-0.24	0.85	1.00	2832	5116
cor(IGKilling_Intercept,Infanticide_Intercept)	0.61	0.22	0.08	0.93	1.00	4862	5862
cor(OGKilling_Intercept,Infanticide_Intercept)	0.66	0.21	0.13	0.94	1.00	4797	6388

**Population-Level Effects:**

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGAggression_Intercept	-0.50	0.38	-1.38	0.23	1.00	3921	3484
IGAggression_Intercept	-2.08	1.58	-5.44	1.08	1.00	3519	3763
IGKilling_Intercept	-3.62	6.16	-16.58	9.26	1.00	6017	5265

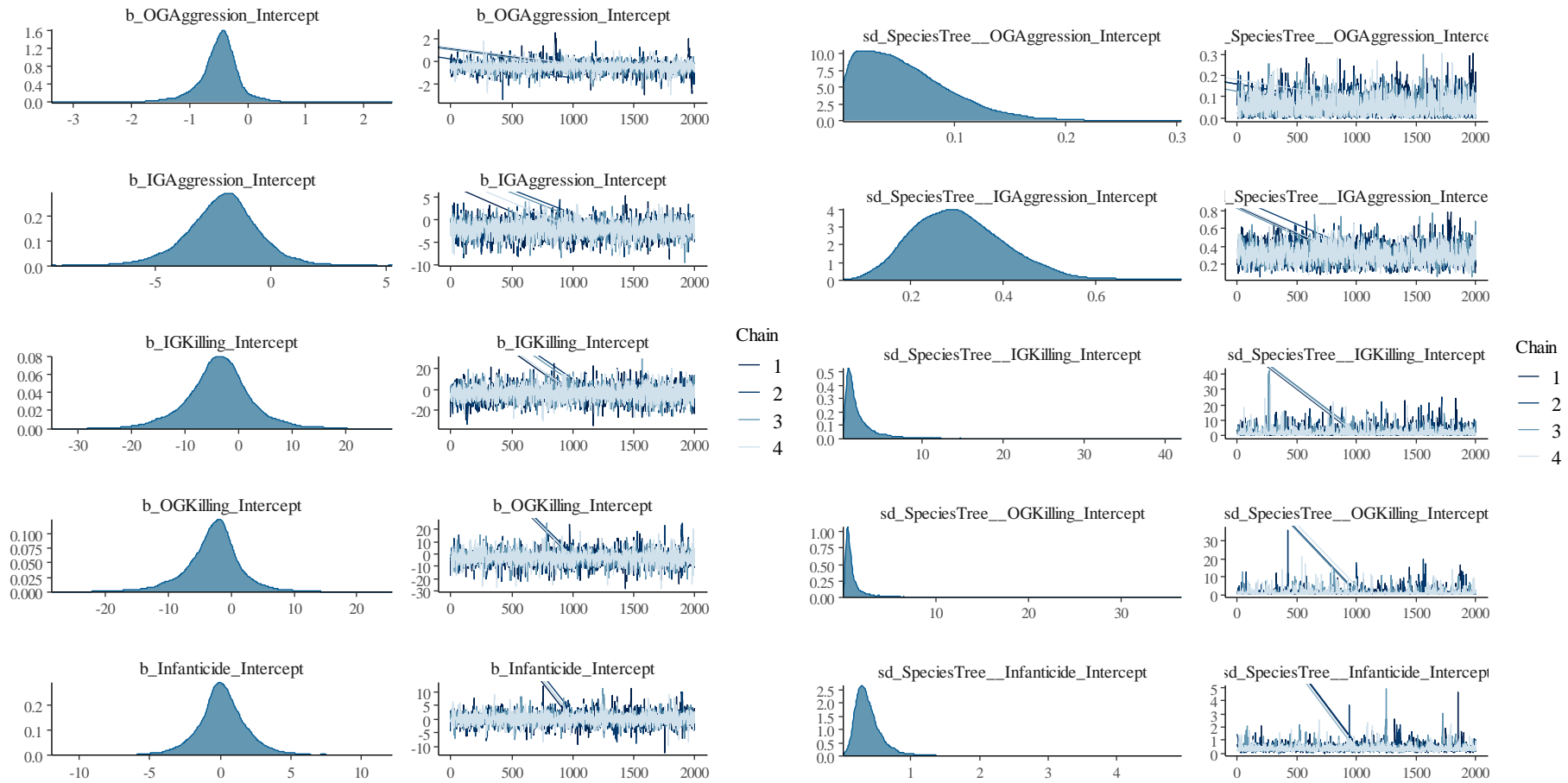
OGKilling_Intercept	-2.82	4.76	-13.43	6.65	1.00	4606	3648
Infanticide_Intercept	0.16	1.89	-3.58	4.12	1.00	3625	3072

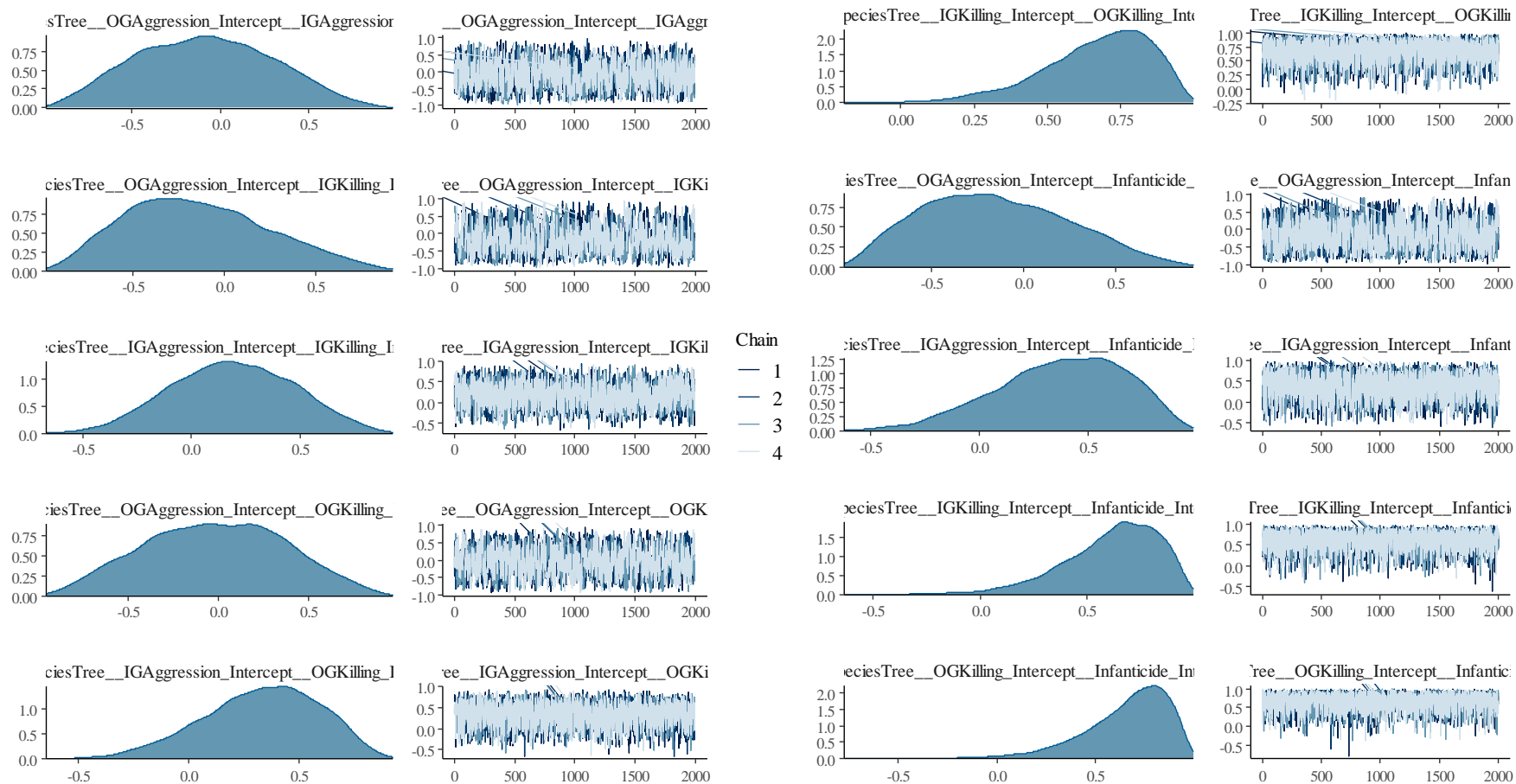
**Family Specific Parameters:**

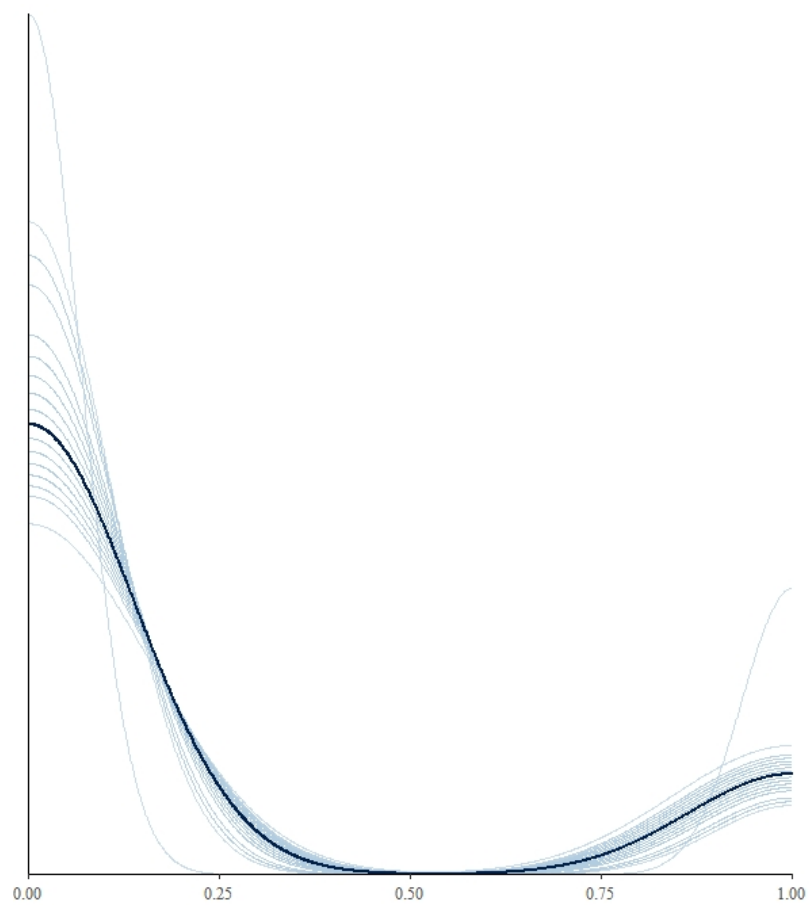
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
phi_OGAggression	2.96	0.48	2.14	4.03	1.00	6874	5339
zoi_OGAggression	0.31	0.04	0.23	0.40	1.00	16648	5654
coi_OGAggression	0.71	0.08	0.54	0.84	1.00	17254	5553
shape_IGAggression	0.50	0.08	0.36	0.69	1.00	2651	3533
hu_IGAggression	0.07	0.02	0.03	0.12	1.00	15387	5675

Samples were drawn using sampling (NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

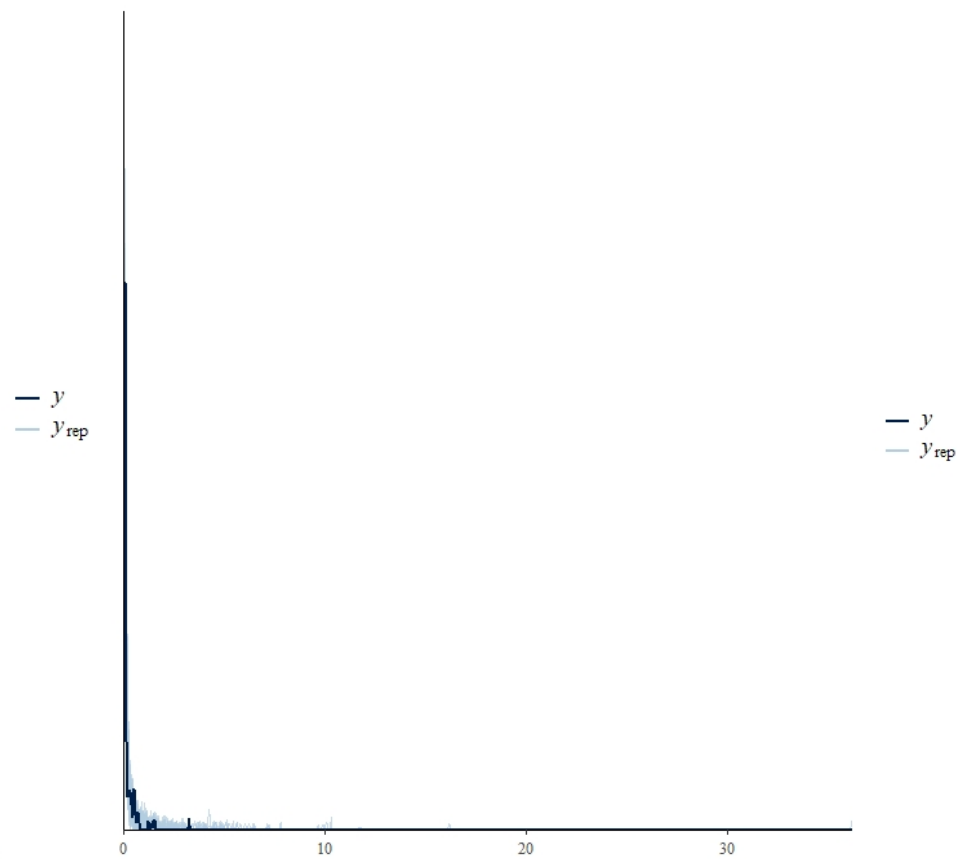
	Estimate	Est.Error	Q2.5	Q97.5	
R2OGAggression	0.01545589	0.01806618	2.538821e-05	0.06335699	(note: 0.00002538821)
R2IGAggression	0.26875427	0.14769870	5.542394e-02	0.59809806	
R2IGKilling	0.60616791	0.18485605	2.582475e-01	0.93956529	
R2OGKilling	0.47705685	0.17279479	1.844691e-01	0.87495816	
R2Infanticide	0.25313583	0.11107664	5.764704e-02	0.50018389	



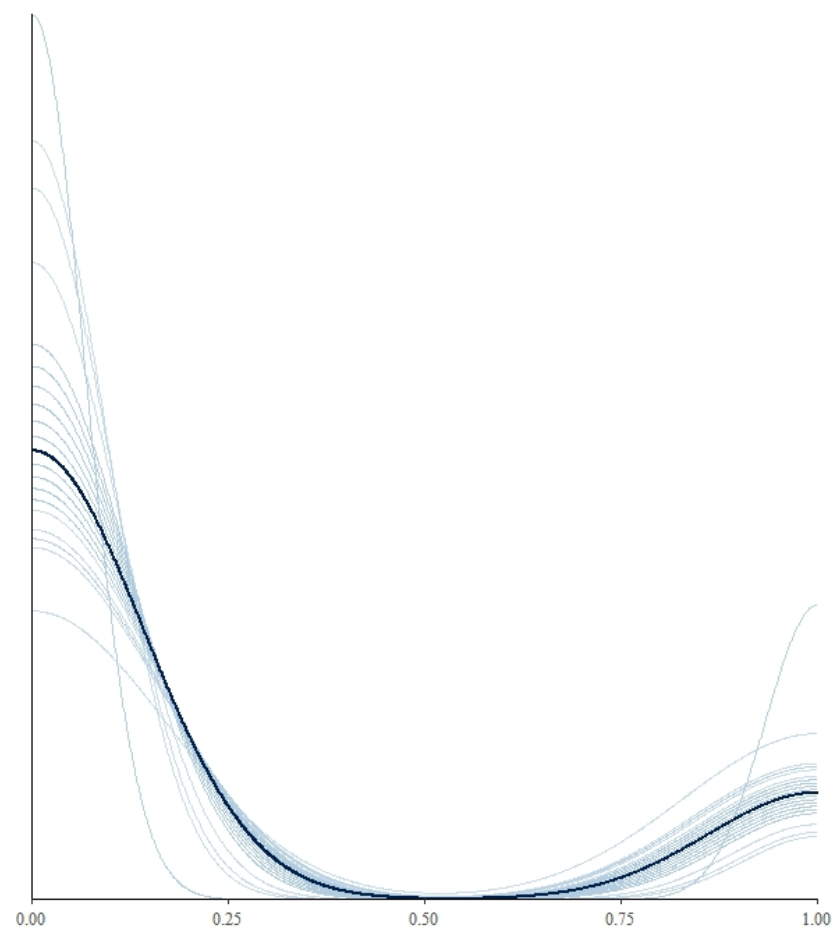




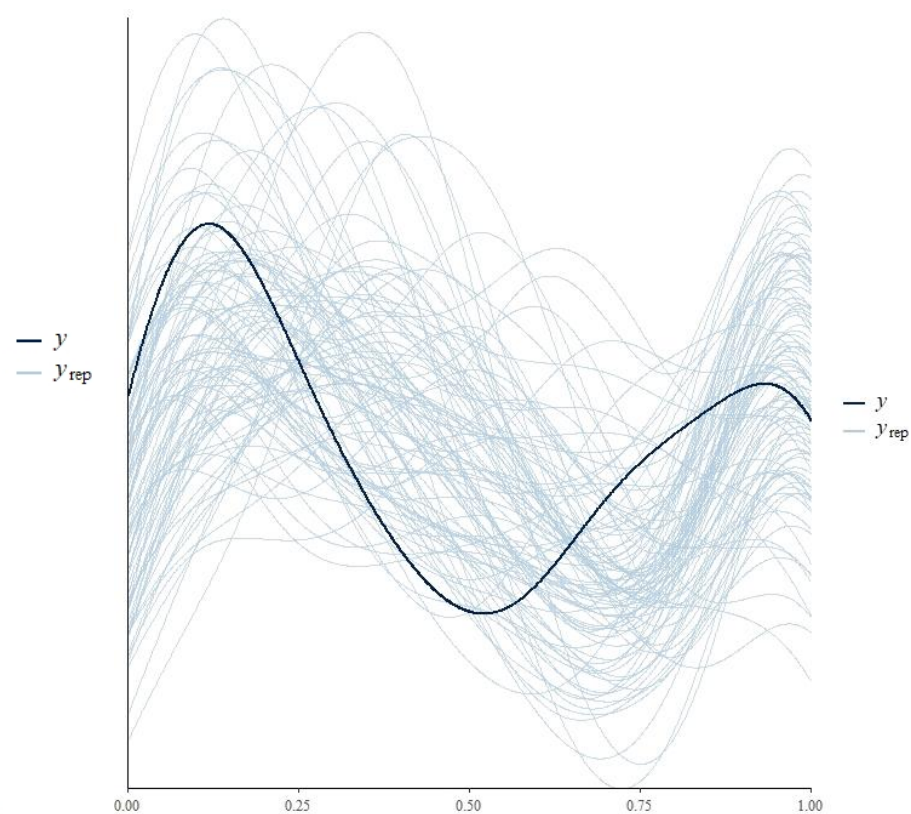
Intragroup Adulticide (IG Killing)



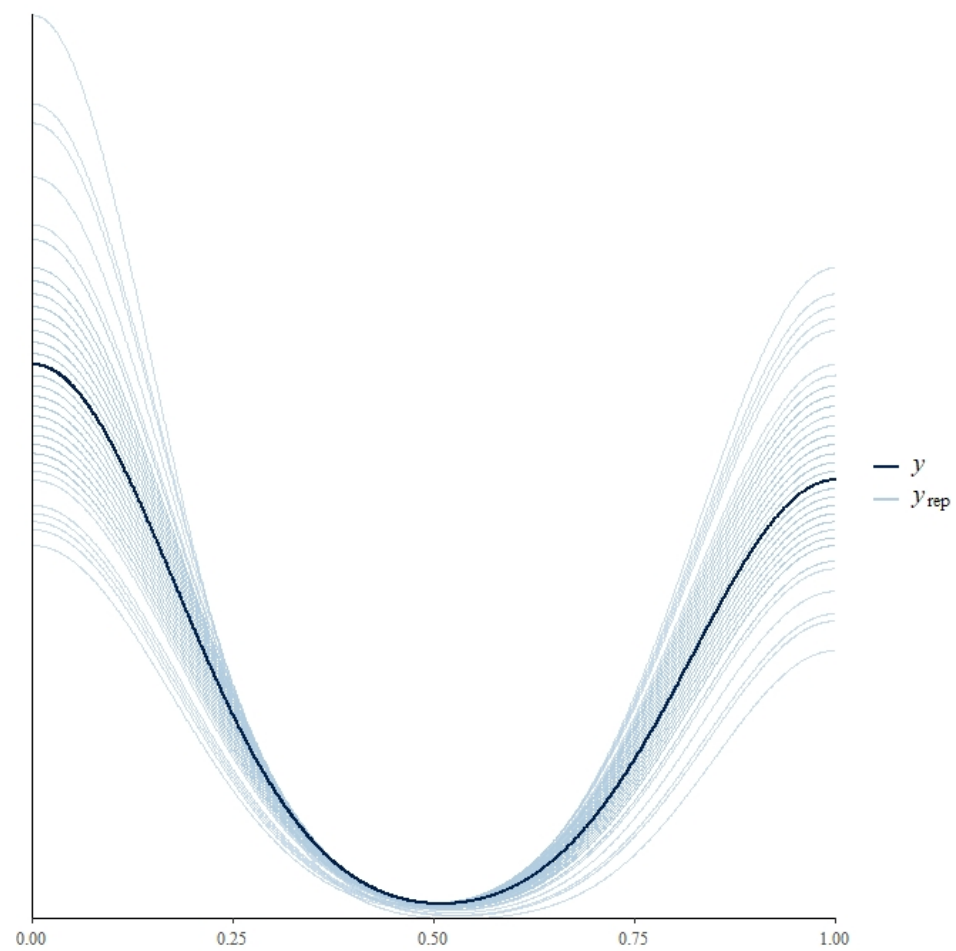
Intragroup aggression



Intergroup adulticide (OG killing)



Intergroup aggression



Infanticide



## Appendix 2E – ‘Absolute’ binary results and plots

```
> summary(fitAbsolute, waic= T); bayes_R2(fitAbsolute)
```

Family: MV(bernoulli, bernoulli, bernoulli, bernoulli, bernoulli)

Links: mu = logit

mu = logit

mu = logit

mu = logit

mu = logit

Formula: OG\_Aggression ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

IG\_Aggression ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

IG\_Killing ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

OG\_Killing ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

Infanticide ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

Data: dataabsolute (Number of observations: 104)

Samples: 4 chains, each with iter = 4000; warmup = 2000; thin = 1;      total post-warmup samples = 8000

Group-Level Effects:

~SpeciesTree (Number of levels: 104)

	Estimate	Est.Error	1-95% CI
sd(OGAggression_Intercept)	2.34	2.85	0.24
sd(IGAggression_Intercept)	1.82	2.21	0.11
sd(IGKilling_Intercept)	1.83	2.26	0.37
sd(OGKilling_Intercept)	1.03	1.18	0.26
sd(Infanticide_Intercept)	0.41	0.26	0.11
cor(OGAggression_Intercept, IGAggression_Intercept)	-0.10	0.34	-0.73
cor(OGAggression_Intercept, IGKilling_Intercept)	0.05	0.30	-0.52
cor(IGAggression_Intercept, IGKilling_Intercept)	0.32	0.31	-0.36
cor(OGAggression_Intercept, OGKilling_Intercept)	0.30	0.29	-0.32
cor(IGAggression_Intercept, OGKilling_Intercept)	0.10	0.31	-0.53
cor(IGKilling_Intercept, OGKilling_Intercept)	0.70	0.17	0.28
cor(OGAggression_Intercept, Infanticide_Intercept)	0.32	0.29	-0.30
cor(IGAggression_Intercept, Infanticide_Intercept)	0.29	0.32	-0.40
cor(IGKilling_Intercept, Infanticide_Intercept)	0.61	0.22	0.09

cor(OGKilling_Intercept,Infanticide_Intercept)	0.66	0.21	0.14
	u-95% CI	Rhat	Bulk_ESS
sd(OGAggression_Intercept)	9.17	1.00	856
sd(IGAggression_Intercept)	7.68	1.00	1384
sd(IGKilling_Intercept)	7.07	1.00	1518
sd(OGKilling_Intercept)	3.99	1.00	1780
sd(Infanticide_Intercept)	1.02	1.00	1905
cor(OGAggression_Intercept,IGAggression_Intercept)	0.54	1.00	2152
cor(OGAggression_Intercept,IGKilling_Intercept)	0.64	1.00	1428
cor(IGAggression_Intercept,IGKilling_Intercept)	0.82	1.00	1073
cor(OGAggression_Intercept,OGKilling_Intercept)	0.79	1.00	1826
cor(IGAggression_Intercept,OGKilling_Intercept)	0.67	1.00	1581
cor(IGKilling_Intercept,OGKilling_Intercept)	0.94	1.00	4646
cor(OGAggression_Intercept,Infanticide_Intercept)	0.80	1.00	2274
cor(IGAggression_Intercept,Infanticide_Intercept)	0.81	1.00	1840
cor(IGKilling_Intercept,Infanticide_Intercept)	0.93	1.00	4437

cor(OGKilling_Intercept,Infanticide_Intercept)	0.94	1.00	4360
Tail_ESS			
sd(OGAggression_Intercept)	2703		
sd(IGAggression_Intercept)	1245		
sd(IGKilling_Intercept)	3291		
sd(OGKilling_Intercept)	2676		
sd(Infanticide_Intercept)	2790		
cor(OGAggression_Intercept,IGAggression_Intercept)	3700		
cor(OGAggression_Intercept,IGKilling_Intercept)	1817		
cor(IGAggression_Intercept,IGKilling_Intercept)	1593		
cor(OGAggression_Intercept,OGKilling_Intercept)	3071		
cor(IGAggression_Intercept,OGKilling_Intercept)	2525		
cor(IGKilling_Intercept,OGKilling_Intercept)	5339		
cor(OGAggression_Intercept,Infanticide_Intercept)	3993		
cor(IGAggression_Intercept,Infanticide_Intercept)	2405		
cor(IGKilling_Intercept,Infanticide_Intercept)	5978		

cor(OGKilling\_Intercept,Infanticide\_Intercept) 5741

Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS
OGAggression_Intercept	2.14	3.51	-4.35	10.07	1.00	3144
IGAggression_Intercept	3.54	4.42	-3.16	13.51	1.00	2901
IGKilling_Intercept	-1.38	2.88	-7.43	3.80	1.00	4738
OGKilling_Intercept	-1.45	2.29	-6.42	2.78	1.00	4857
Infanticide_Intercept	-0.14	1.47	-3.24	2.74	1.00	4160
	Tail_ESS					
OGAggression_Intercept	4116					
IGAggression_Intercept	3263					
IGKilling_Intercept	4213					
OGKilling_Intercept	4573					
Infanticide_Intercept	4417					

Samples were drawn using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
R2OGAggression	0.6087428	0.2349314	0.140479599	0.9749669
R2IGAggression	0.4760679	0.2730574	0.009577519	0.9585573
R2IGKilling	0.5742710	0.1836228	0.230256266	0.9278950
R2OGKilling	0.4495306	0.1625388	0.173338080	0.8308917
R2Infanticide	0.2600228	0.1140144	0.060529864	0.5124472

## Appendix 2F – ‘Half and half’ binary results and plots

```
> summary(fitHalf, waic= T); bayes_R2(fitHalf)
```

Family: MV(bernoulli, bernoulli, bernoulli, bernoulli, bernoulli)

Links: mu = logit

mu = logit

mu = logit

mu = logit

mu = logit

Formula: OG\_Aggression ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

IG\_Aggression ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

IG\_Killing ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

OG\_Killing ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

Infanticide ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

Data: datahalf (Number of observations: 104)

Samples: 4 chains, each with iter = 5000; warmup = 2500; thin = 1;

total post-warmup samples = 10000

Group-Level Effects:

~SpeciesTree (Number of levels: 104)

Estimate

Est.Error

l-95% CI

sd(OGAggression_Intercept)	0.34	0.46	0.02	
sd(IGAggression_Intercept)	0.72	0.78	0.07	
sd(IGKilling_Intercept)	0.52	0.79	0.02	
sd(OGKilling_Intercept)	0.98	1.32	0.18	
sd(Infanticide_Intercept)	0.42	0.39	0.08	
cor(OGAggression_Intercept,IGAggression_Intercept)	0.14	0.34	-0.60	
cor(OGAggression_Intercept,IGKilling_Intercept)	-0.05	0.37	-0.73	
cor(IGAggression_Intercept,IGKilling_Intercept)	0.17	0.34	-0.51	
cor(OGAggression_Intercept,OGKilling_Intercept)	0.17	0.35	-0.58	
cor(IGAggression_Intercept,OGKilling_Intercept)	0.33	0.28	-0.27	
cor(IGKilling_Intercept,OGKilling_Intercept)	0.54	0.30	-0.22	
cor(OGAggression_Intercept,Infanticide_Intercept)	-0.06	0.36	-0.75	
cor(IGAggression_Intercept,Infanticide_Intercept)	0.30	0.30	-0.34	
cor(IGKilling_Intercept,Infanticide_Intercept)	0.51	0.32	-0.29	
cor(OGKilling_Intercept,Infanticide_Intercept)	0.64	0.24	0.02	
	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGAggression_Intercept)	1.36	1.00	848	1014
sd(IGAggression_Intercept)	2.49	1.01	894	1253
sd(IGKilling_Intercept)	2.06	1.00	1197	2124



sd(OGKilling_Intercept)	4.21	1.00	1553	2458
sd(Infanticide_Intercept)	1.21	1.01	1377	1474
cor(OGAggression_Intercept,IGAggression_Intercept)	0.73	1.00	1193	1872
cor(OGAggression_Intercept,IGKilling_Intercept)	0.66	1.00	2476	3708
cor(IGAggression_Intercept,IGKilling_Intercept)	0.77	1.00	4119	3184
cor(OGAggression_Intercept,OGKilling_Intercept)	0.76	1.00	1216	2055
cor(IGAggression_Intercept,OGKilling_Intercept)	0.81	1.00	2696	2756
cor(IGKilling_Intercept,OGKilling_Intercept)	0.93	1.00	1880	1950
cor(OGAggression_Intercept,Infanticide_Intercept)	0.60	1.00	1573	3203
cor(IGAggression_Intercept,Infanticide_Intercept)	0.80	1.00	3373	5092
cor(IGKilling_Intercept,Infanticide_Intercept)	0.93	1.00	1737	2336
cor(OGKilling_Intercept,Infanticide_Intercept)	0.94	1.00	3982	5487

## Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGAggression_Intercept	-0.23	1.30	-2.93	2.46	1.00	3963	3680
IGAggression_Intercept	0.17	2.00	-3.81	4.26	1.00	4500	3654
IGKilling_Intercept	-1.73	1.55	-4.78	1.63	1.00	4620	4230
OGKilling_Intercept	-1.31	2.14	-5.77	2.91	1.00	5172	4821

Infanticide_Intercept	0.39	1.36	-2.25	3.22	1.00	3984	4359
-----------------------	------	------	-------	------	------	------	------

Samples were drawn using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
R2OGAggression	0.1856776	0.1550192	0.001532837	0.5919116
R2IGAggression	0.3712510	0.1829257	0.028219560	0.7601576
R2IGKilling	0.1819913	0.1594823	0.001298786	0.5975589
R2OGKilling	0.3841945	0.1866065	0.084465369	0.8287022
R2Infanticide	0.2496934	0.1301500	0.035977829	0.5533775

## Appendix 2G – ‘Lower-end’ results and plots

```
>summary(fitLower, waic= T); bayes_R2(fitLower)
```

Family: MV(zero\_one\_inflated\_beta, hurdle\_gamma, bernoulli, bernoulli, bernoulli)

Links: mu = identity; sigma = identity

mu = identity; sigma = identity

mu = logit

mu = logit

mu = logit

Formula: OG\_Aggression ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

IG\_Aggression ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

IG\_Killing ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

OG\_Killing ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

Infanticide ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

Data: datalower (Number of observations: 104)

Samples: 4 chains, each with iter = 4000; warmup = 2000; thin = 1;

total post-warmup samples = 8000

Group-Level Effects:

~SpeciesTree (Number of levels: 104)

	Estimate	Est.Error	I-95% CI	
sd(OGAggression_Intercept)	0.03	0.02	0.00	
sd(IGAggression_Intercept)	0.02	0.01	0.00	
sd(IGKilling_Intercept)	0.59	0.89	0.03	
sd(OGKilling_Intercept)	0.97	1.20	0.18	
sd(Infanticide_Intercept)	0.39	0.33	0.08	
cor(OGAggression_Intercept,IGAggression_Intercept)	-0.07	0.39	-0.77	
cor(OGAggression_Intercept,IGKilling_Intercept)	-0.05	0.39	-0.74	
cor(IGAggression_Intercept,IGKilling_Intercept)	0.12	0.37	-0.62	
cor(OGAggression_Intercept,OGKilling_Intercept)	0.13	0.37	-0.62	
cor(IGAggression_Intercept,OGKilling_Intercept)	0.20	0.36	-0.53	
cor(IGKilling_Intercept,OGKilling_Intercept)	0.58	0.27	-0.13	
cor(OGAggression_Intercept,Infanticide_Intercept)	-0.01	0.38	-0.74	
cor(IGAggression_Intercept,Infanticide_Intercept)	0.27	0.35	-0.49	
cor(IGKilling_Intercept,Infanticide_Intercept)	0.54	0.30	-0.20	
cor(OGKilling_Intercept,Infanticide_Intercept)	0.63	0.24	0.02	
	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGAggression_Intercept)	0.08	1.00	692	1273
sd(IGAggression_Intercept)	0.05	1.00	2424	2077
sd(IGKilling_Intercept)	2.62	1.00	1061	1347

sd(OGKilling_Intercept)	4.10	1.00	919	1952
sd(Infanticide_Intercept)	1.12	1.00	1286	1838
cor(OGAggression_Intercept,IGAggression_Intercept)	0.70	1.00	3010	3566
cor(OGAggression_Intercept,IGKilling_Intercept)	0.70	1.00	1330	2600
cor(IGAggression_Intercept,IGKilling_Intercept)	0.77	1.00	1465	2766
cor(OGAggression_Intercept,OGKilling_Intercept)	0.75	1.00	956	1641
cor(IGAggression_Intercept,OGKilling_Intercept)	0.80	1.00	1078	2364
cor(IGKilling_Intercept,OGKilling_Intercept)	0.93	1.00	1691	1726
cor(OGAggression_Intercept,Infanticide_Intercept)	0.68	1.00	1112	2356
cor(IGAggression_Intercept,Infanticide_Intercept)	0.84	1.00	1234	2508
cor(IGKilling_Intercept,Infanticide_Intercept)	0.93	1.00	1720	2232
cor(OGKilling_Intercept,Infanticide_Intercept)	0.94	1.00	2495	4170

## Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGAggression_Intercept	0.47	0.18	0.09	0.87	1.00	2172	2111
IGAggression_Intercept	0.21	0.15	-0.08	0.52	1.00	2633	3703
IGKilling_Intercept	-1.70	1.74	-5.15	1.90	1.00	4100	4588
OGKilling_Intercept	-1.28	2.25	-5.92	3.12	1.00	3904	3832
Infanticide_Intercept	0.41	1.41	-2.25	3.44	1.00	2923	3165

## Family Specific Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma_OGAggression	0.33	0.03	0.26	0.40	1.00	1162	1400
sigma_IGAggression	0.42	0.03	0.36	0.48	1.00	7063	5951

Samples were drawn using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
R2OGAggression	0.12615794	0.13277357	0.0002017285	0.4601386
R2IGAggression	0.08320881	0.06567393	0.0005848708	0.2348778
R2IGKilling	0.20934434	0.17122891	0.0017717310	0.6794021
R2OGKilling	0.38523101	0.18649905	0.0803876690	0.8205892
R2Infanticide	0.24396502	0.12685962	0.0327504664	0.5373638

## Appendix 2H – ‘Upper-end’ results and plots

**>Summary(fitUpper, waic= T); bayes\_R2(fitUpper)**

Family: MV(zero\_one\_inflated\_beta, hurdle\_gamma, bernoulli, bernoulli, bernoulli)

Links: mu = identity; sigma = identity

mu = identity; sigma = identity

mu = logit

mu = logit

mu = logit

Formula: OG\_Aggression ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

IG\_Aggression ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

IG\_Killing ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

OG\_Killing ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

Infanticide ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

Data: dataupper (Number of observations: 104)

Samples: 4 chains, each with iter = 5000; warmup = 2500; thin = 1;

total post-warmup samples = 10000

Group-Level Effects:

~SpeciesTree (Number of levels: 104)

	Estimate	Est.Error	I-95% CI	
sd(OGAggression_Intercept)	0.01	0.01	0.00	
sd(IGAggression_Intercept)	0.02	0.01	0.00	
sd(IGKilling_Intercept)	1.89	2.20	0.37	
sd(OGKilling_Intercept)	1.05	1.19	0.26	
sd(Infanticide_Intercept)	0.37	0.27	0.10	
cor(OGAggression_Intercept,IGAggression_Intercept)	-0.06	0.40	-0.78	
cor(OGAggression_Intercept,IGKilling_Intercept)	-0.07	0.39	-0.76	
cor(IGAggression_Intercept,IGKilling_Intercept)	0.09	0.38	-0.68	
cor(OGAggression_Intercept,OGKilling_Intercept)	0.03	0.39	-0.72	
cor(IGAggression_Intercept,OGKilling_Intercept)	0.11	0.37	-0.65	
cor(IGKilling_Intercept,OGKilling_Intercept)	0.70	0.18	0.27	
cor(OGAggression_Intercept,Infanticide_Intercept)	-0.03	0.40	-0.76	
cor(IGAggression_Intercept,Infanticide_Intercept)	0.17	0.38	-0.63	
cor(IGKilling_Intercept,Infanticide_Intercept)	0.63	0.22	0.11	
cor(OGKilling_Intercept,Infanticide_Intercept)	0.66	0.22	0.12	
	u-95%CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGAggression_Intercept)	0.05	1.00	2340	2097
sd(IGAggression_Intercept)	0.05	1.00	3850	5572
sd(IGKilling_Intercept)	7.46	1.00	2090	5366



sd(OGKilling_Intercept)	4.07	1.00	2369	3455
sd(Infanticide_Intercept)	0.89	1.00	3024	3734
cor(OGAggression_Intercept,IGAggression_Intercept)	0.71	1.00	9957	7495
cor(OGAggression_Intercept,IGKilling_Intercept)	0.69	1.00	1158	2459
cor(IGAggression_Intercept,IGKilling_Intercept)	0.76	1.00	1590	3166
cor(OGAggression_Intercept,OGKilling_Intercept)	0.74	1.00	1331	3192
cor(IGAggression_Intercept,OGKilling_Intercept)	0.76	1.00	1757	3855
cor(IGKilling_Intercept,OGKilling_Intercept)	0.95	1.00	6447	8208
cor(OGAggression_Intercept,Infanticide_Intercept)	0.72	1.00	1561	3747
cor(IGAggression_Intercept,Infanticide_Intercept)	0.81	1.00	2041	3616
cor(IGKilling_Intercept,Infanticide_Intercept)	0.94	1.00	6455	7867
cor(OGKilling_Intercept,Infanticide_Intercept)	0.94	1.00	6274	7630

## Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGAggression_Intercept	0.56	0.10	0.36	0.77	1.00	4095	3277
IGAggression_Intercept	0.23	0.12	-0.01	0.50	1.00	5735	5835
IGKilling_Intercept	-0.97	2.80	-6.92	4.21	1.00	10520	5310
OGKilling_Intercept	-1.07	2.14	-5.51	3.16	1.00	10395	6202
Infanticide_Intercept	0.48	1.25	-2.02	3.07	1.00	7725	6431

## Family Specific Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sigma_OGAggression	0.33	0.03	0.28	0.38	1.00	5420	2879
sigma_IGAggression	0.42	0.03	0.36	0.48	1.00	12542	7953

Samples were drawn using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
R2OGAggression	0.04630437	0.06760690	5.615391e-05	0.2393286
R2IGAggression	0.05487207	0.05540378	1.203331e-04	0.1944805
R2IGKilling	0.57987788	0.18565725	2.300825e-01	0.9286804
R2OGKilling	0.45340270	0.16531093	1.720183e-01	0.8417990
R2Infanticide	0.24111082	0.10892115	5.187487e-02	0.4729458

**APPENDICES – CHAPTER 3**

## Appendix 3A – FAMD results

```

eigenvalue variance.percent cumulative.variance.percent
Dim.1  3.576064    19.867022         19.86702
Dim.2  1.744627     9.692375         29.55940
Dim.3  1.585757     8.809762         38.36916
Dim.4  1.332444     7.402469         45.77163
Dim.5  1.227423     6.819015         52.59064

```

```
> eig.val
```

```

eigenvalue variance.percent cumulative.variance.percent
Dim.1  3.576064    19.867022         19.86702
Dim.2  1.744627     9.692375         29.55940
Dim.3  1.585757     8.809762         38.36916
Dim.4  1.332444     7.402469         45.77163
Dim.5  1.227423     6.819015         52.59064

```

```
> fviz_screplot(data.famd)
```

```
> var <-get_famd_var(data.famd)
```

```
> var
```

FAMD results for variables

```
=====
```

```

Name    Description
1 "$coord"  "Coordinates"
2 "$cos2"   "Cos2, quality of representation"
3 "$contrib" "Contributions"

```

```
> ##Plot of variables
```

```
> fviz_famd_var(data.famd, repel = TRUE)
```

```
> fviz_contrib(data.famd, "var", axes = 3)
```

```
> fviz_contrib(data.famd, "var", axes = 5)
```

```
> #Extract quantitative results
```

```

> quanti.var <- get_famd_var(data.famd, "quanti.var")
> quanti.var

FAMD results for quantitative variables

=====

Name    Description
1 "$coord" "Coordinates"
2 "$cos2"  "Cos2, quality of representation"
3 "$contrib" "Contributions"

> fviz_famd_var(data.famd, "quanti.var", repel = TRUE,
+               col.var = "black")
> # Coordinates of variables
> head(quanti.var$coord)

      Dim.1    Dim.2    Dim.3    Dim.4    Dim.5
Dimorphism  0.71404175 0.0009606302 -0.28474657 -0.11750271 0.31512624
Leaves      0.05280324 -0.5626049696 -0.21195547 0.47960897 -0.34454907
Pop_Density -0.11485534 0.0442918764 -0.06612576 0.69331249 0.25771989
D.Index     -0.38756791 0.5942357202 -0.24043356 0.17777736 -0.04639235
Group_Size  0.71613694 0.1410226502 0.21745369 0.24359787 0.02689285
Rainfall    -0.29458930 -0.3253268291 0.25962099 0.02197722 0.42967630

> # Cos2: quality of representation on the factor map
> head(quanti.var$cos2)

      Dim.1    Dim.2    Dim.3    Dim.4    Dim.5
Dimorphism  0.509855617 9.228103e-07 0.081080608 0.0138068870 0.0993045460
Leaves      0.002788183 3.165244e-01 0.044925121 0.2300247682 0.1187140599
Pop_Density 0.013191749 1.961770e-03 0.004372617 0.4806822108 0.0664195440
D.Index     0.150208888 3.531161e-01 0.057808297 0.0316047890 0.0021522498
Group_Size  0.512852118 1.988739e-02 0.047286108 0.0593399206 0.0007232253
Rainfall    0.086782854 1.058375e-01 0.067403056 0.0004829982 0.1846217257

> # Contributions to the dimensions
> head(quanti.var$contrib)

      Dim.1    Dim.2    Dim.3    Dim.4    Dim.5

```

```

Dimorphism 14.25745238 5.289440e-05 5.1130535 1.03620739 8.09049283
Leaves     0.07796792 1.814280e+01 2.8330393 17.26336748 9.67181554
Pop_Density 0.36889018 1.124464e-01 0.2757432 36.07521793 5.41130156
D.Index    4.20039713 2.024020e+01 3.6454699 2.37194060 0.17534707
Group_Size 14.34124566 1.139922e+00 2.9819263 4.45346327 0.05892227
Rainfall   2.42677019 6.066484e+00 4.2505284 0.03624903 15.04141360

```

```

> fviz_famd_var(data.famd, "quanti.var", col.var = "contrib",
+   gradient.cols = c("#00AFBB", "#E7B800", "#FC4E07"),
+   repel = TRUE)
> fviz_famd_var(data.famd, "quanti.var", col.var = "cos2",
+   gradient.cols = c("#00AFBB", "#E7B800", "#FC4E07"),
+   repel = TRUE)

```

```
> ##Qualitative variables
```

```
> quali.var <- get_famd_var(data.famd, "quali.var")
```

```
> quali.var
```

FAMD results for qualitative variable categories

```
=====
```

Name	Description
1 "\$coord"	"Coordinates"
2 "\$cos2"	"Cos2, quality of representation"
3 "\$contrib"	"Contributions"

```
> fviz_famd_var(data.famd, "quali.var", col.var = "contrib",
```

```
+   gradient.cols = c("#00AFBB", "#E7B800", "#FC4E07"))
```

```
Error in `rowNamesDF`-(x, value = value) :
```

```
duplicate 'row.names' are not allowed
```

In addition: Warning message:

```
non-unique values when setting 'row.names': 'Arboreal', 'No', 'Terrestrial', 'Yes'
```

```
> ##Ind doesn't work!
```

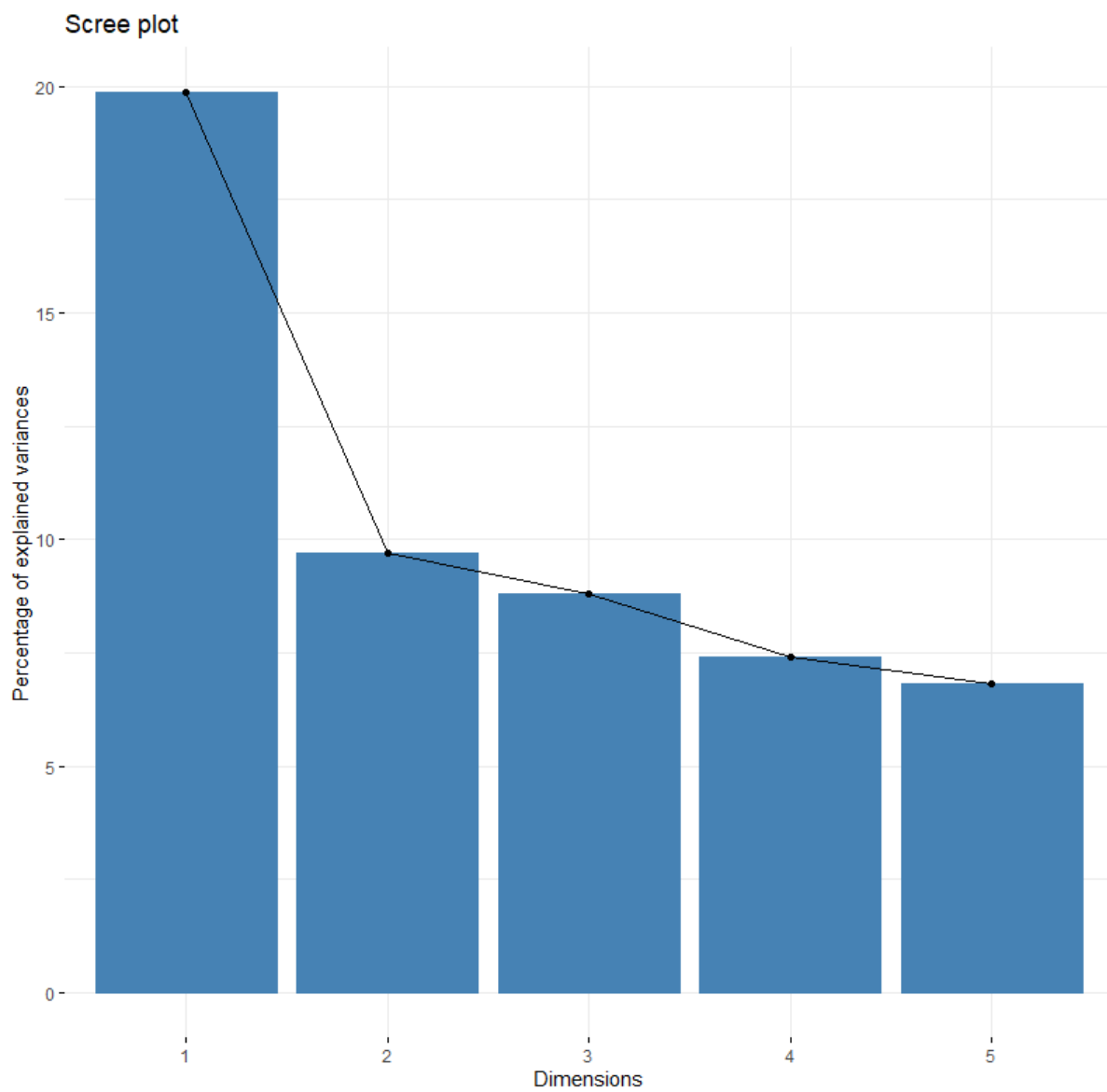
```
> ind <- get_famd_ind(data.famd)
```

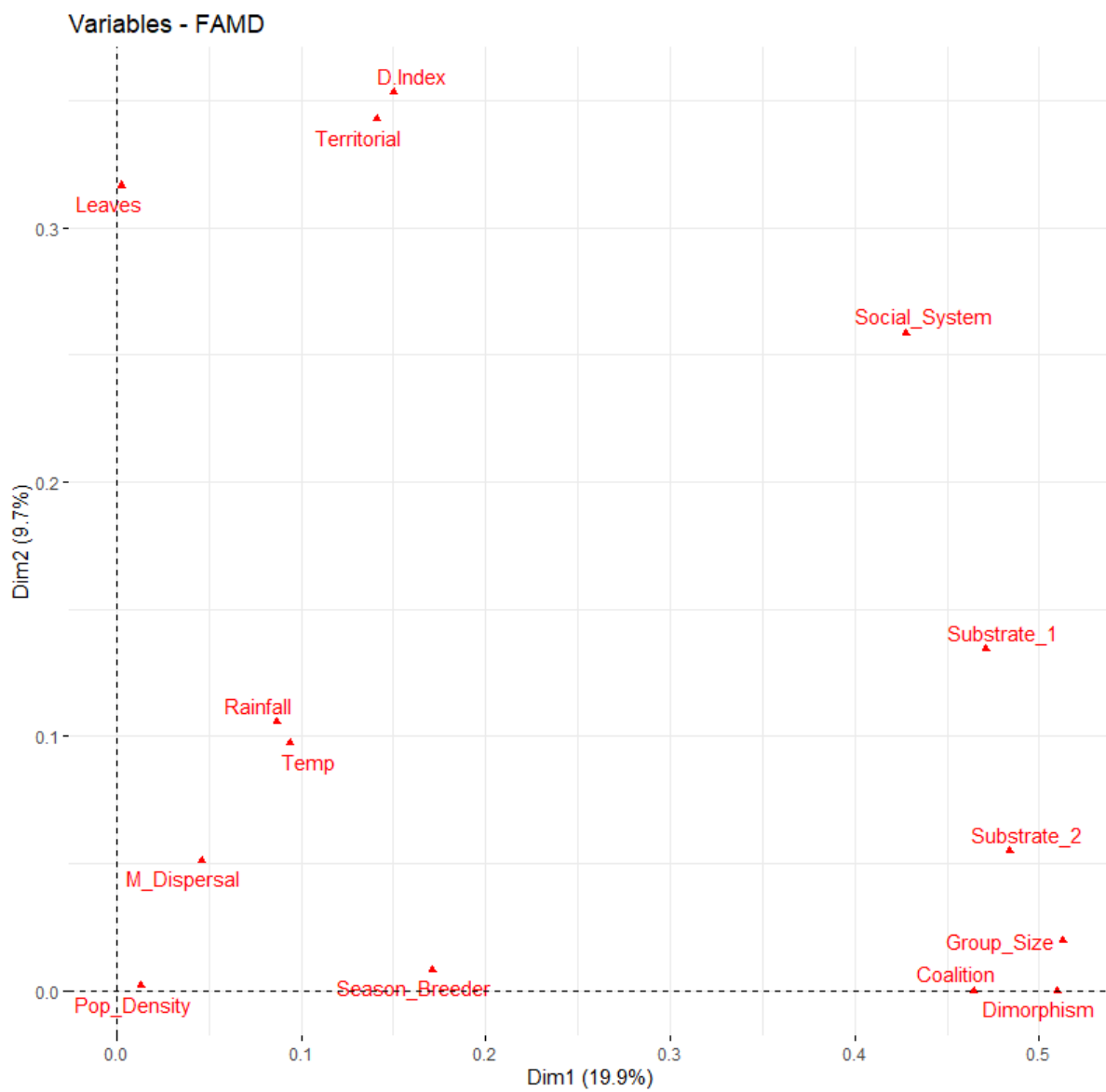
```
> ind
```

FAMD results for individuals

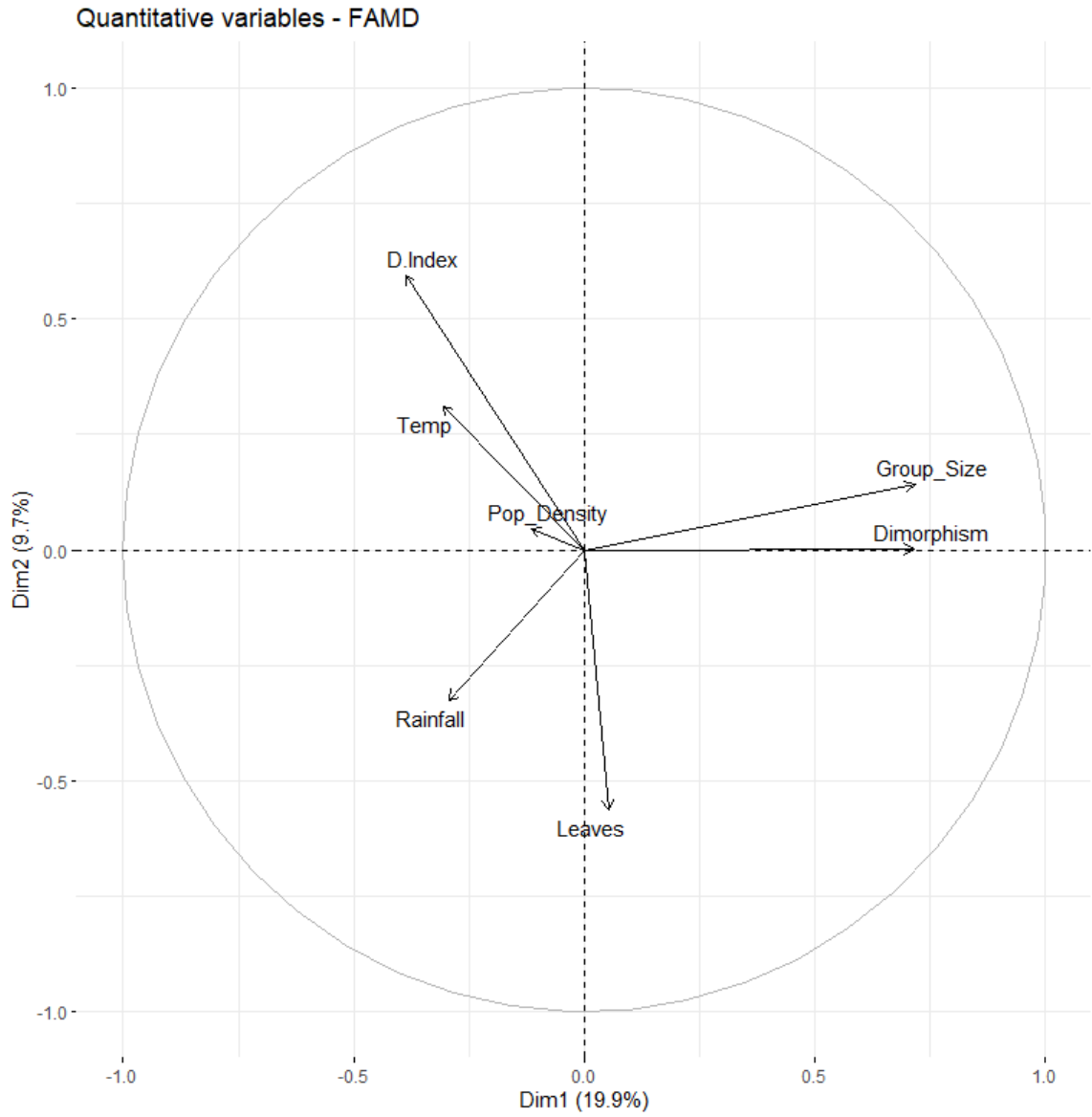
```
=====

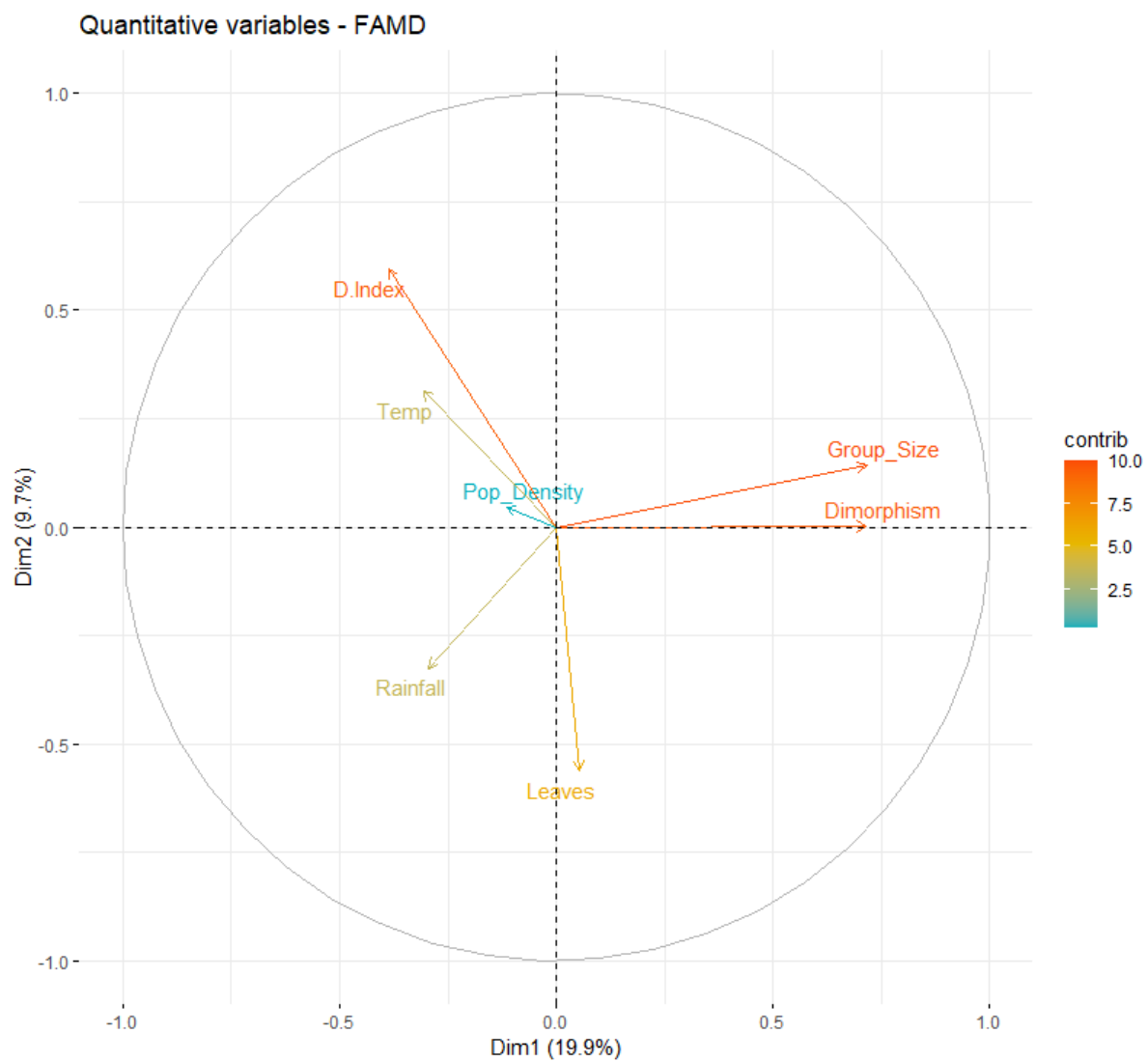
Name    Description
1 "$coord" "Coordinates"
2 "$cos2"  "Cos2, quality of representation"
3 "$contrib" "Contributions"
> fviz_famd_ind(data.famd, col.ind = "cos2",
+               gradient.cols = c("#00AFBB", "#E7B800", "#FC4E07"),
+               repel = TRUE)
Error in `.rowNamesDF<` (x, value = value) :
  duplicate 'row.names' are not allowed
In addition: Warning message:
non-unique values when setting 'row.names': 'Arboreal', 'No', 'Terrestrial', 'Yes'
```

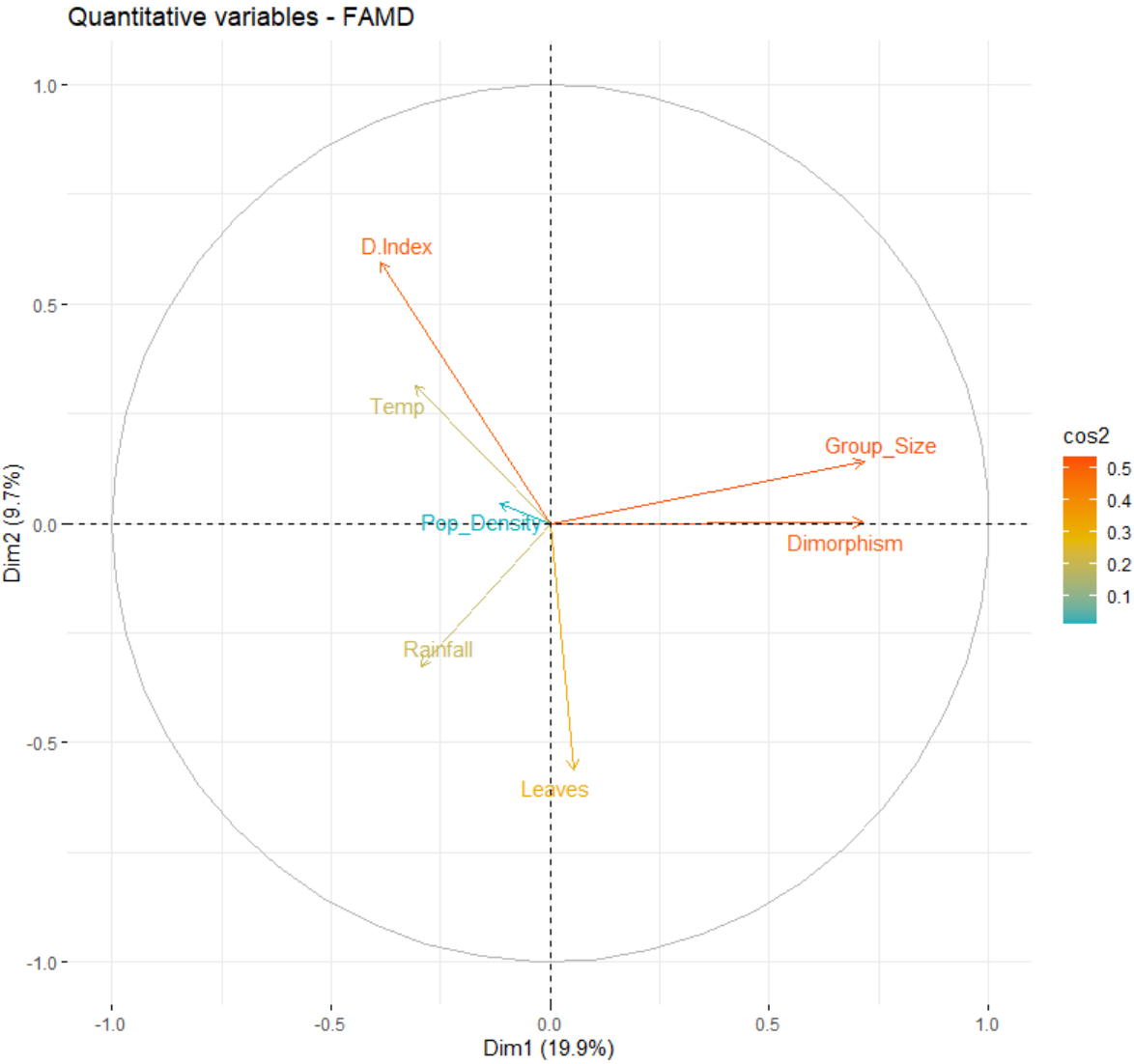












## Appendix 3B – Tree pruning, R code

```
Tip<-c("Aotus_nancymaae", "Ateles_hybridus", "Avahi_meridionalis")  
101tree<-drop.tip(phy, tip, trim.internal=TRUE, rooted=is.rooted(phy))  
write.nexus (pruned, file="pruned.nex")
```

## Appendix 3C – Model scripts (3 models)

## ## Prepare session

```
library(caper)
```

```
library(ggplot2)
```

```
library(ggtree)
```

```
library(brms)
```

## ## Import data

## # Phylogeny

```
file.choose()
```

```
tree<-read.nexus("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 2  
Dataset\\Q2taxa.nex")
```

```
tree$tip.label<- gsub("_", " ", tree$tip.label)
```

## # Species traits

```
file.choose()
```

```
dataB<-read.table("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 2  
Dataset\\Final Q2 data txt.txt", header=T, stringsAsFactors=F)
```

```
dataB$SpeciesTree<- gsub("_", " ", dataB$SpeciesTree)
```

## # Check whether species names match, and correct if not

```
dataB$SpeciesTree %in% tree$tip.label
```

## #Run multivariate model

```
priorB <- c(prior(normal(0, 10), class = Intercept, resp = IGAggression),
  prior(normal(0, 10), class = Intercept, resp = OGAggression),
  prior(normal(0, 10), class = Intercept, resp = OGKilling),
  prior(normal(0, 10), class = Intercept, resp = IGKilling),
  prior(normal(0, 10), class = Intercept, resp = Infanticide))
```

```
fitAggressionB<- brm(mvbind(OG_Aggression, IG_Aggression, IG_Killing, OG_Killing,
  Infanticide)~ 1 + (1|p|gr(SpeciesTree, cov= A)),
  family= list(zero_one_inflated_beta(), hurdle_gamma(), bernoulli(), bernoulli(),
  bernoulli()),
  data= dataB,
  prior = priorB,
  data2= list(A= vcv.phylo(tree)),
  cores = future::availableCores() -1,
  iter= 4e3,
  control= list(adapt_delta= .99, max_treedepth= 15))
```

```
## Explore outcome and predictions
```

```
summary(fitAggressionB, waic= T); bayes_R2(fitAggressionB)
```

```
#Plots
```

```
pairs(fitAggressionB)
```

```
plot(fitAggressionB)
```

### #PP Checks

```
pp_check(fitAggressionB, resp= "OGAggression", nsamples= 1e2)
pp_check(fitAggressionB, resp= "IGAggression", nsamples= 1e2)
pp_check(fitAggressionB, resp= "OGKilling", nsamples= 1e2)
pp_check(fitAggressionB, resp= "IGKilling", nsamples= 1e2)
pp_check(fitAggressionB, resp= "Infanticide", nsamples= 1e2)
```

### #save model

```
saveRDS(fitAggressionB, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 2
Dataset\\Q2 RESULTS\\Aggressionbasic")
```

### #Run second multivariate model

```
priorC <- c(prior(normal(0, 10), class = Intercept, resp = IGAggression),
            prior(normal(0, 5), class = b, resp = IGAggression),
            prior(normal(0, 10), class = Intercept, resp = OGAggression),
            prior(normal(0, 5), class = b, resp = OGAggression),
            prior(normal(0, 10), class = Intercept, resp = OGKilling),
            prior(normal(0, 5), class = b, resp = OGKilling),
            prior(normal(0, 10), class = Intercept, resp = IGKilling),
            prior(normal(0, 5), class = b, resp = IGKilling),
            prior(normal(0, 10), class = Intercept, resp = Infanticide),
            prior(normal(0, 5), class = b, resp = Infanticide))
```

```

fitAggressionC<- brm(mvbind(OG_Aggression, IG_Aggression, IG_Killing, OG_Killing,
Infanticide)~ No_Males + Leaves + Season_Breeder + D_Index + Group_Size + Substrate_1
+ Dimorphism + Coalition + (1|gr(SpeciesTree, cov= A)),

      family= list(zero_one_inflated_beta(), hurdle_gamma(), bernoulli(), bernoulli(),
bernoulli()),

      data= dataB,

      prior = priorC,

      data2= list(A= vcv.phylo(tree)),

      cores = future::availableCores() -1,

      iter= 4e3,

      control= list(adapt_delta= .99, max_treedepth= 15))

```

### ## Explore outcome and predictions

```
summary(fitAggressionC, waic= T); bayes_R2(fitAggressionC)
```

### #Plots

```

pairs(fitAggressionC)

plot(fitAggressionC)

```

### #PP Checks

```

pp_check(fitAggressionC, resp= "OGAggression", nsamples= 1e2)

pp_check(fitAggressionC, resp= "IGAggression", nsamples= 1e2)

pp_check(fitAggressionC, resp= "OGKilling", nsamples= 1e2)

pp_check(fitAggressionC, resp= "IGKilling", nsamples= 1e2)

pp_check(fitAggressionC, resp= "Infanticide", nsamples= 1e2)

```



```
#save model
```

```
saveRDS(fitAggressionC, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 2
Dataset\\Q2 RESULTS\\AggressionAllVariables")
```

```
#Run third multivariate model
```

```
bf_OG_Agg <- bf(OG_Aggression ~ D.Index + No_Males + Group_Size + Coalition +
Substrate_1 + (1|gr(species, cor=A)) + zero_one_inflated_beta())
```

```
bf_IG_Agg <- bf(IG_Aggression ~ D.Index + Dimorphism + Leaves +Substrate_1 +
Group_size + (1|gr(species, cor=A)) + hurdle_gamma())
```

```
bf_OG_Kill <- bf(OG_Killing ~ D.Index + Season_Breeder + Coalition + No_Males +
Substrate_1 + (1|gr(species, cor=A)) + bernoulli())
```

```
bf_IG_Kill <- bf(IG_Killing ~ Coalitions + No_Males + Season_Breeder +Substrate_1 +
Leaves + (1|gr(species, cor=A)) + bernoulli())
```

```
bf_Infanticide <- bf(Infanticide ~ D.Index + Season_Breeder + Coalition + No_Males +
Substrate_1 + (1|gr(species, cor=A)) + bernoulli())
```

```
FitAggressionD <- brm(
```

```
  bf_OG_Agg + bf_IG_Agg + bf_OG_Kill + bf_IG_Kill + bf_Infanticide +
  set_rescor(FALSE),
```

```
  data = dataB,
```

```
  prior = priorC,
```

```
  data2= list(A= vcv.phylo(tree)),
```

```
  cores = future::availableCores() -1,
```

```
  iter= 4e3,
```

```
  control= list(adapt_delta= .99, max_treedepth= 15))
```

### ## Explore outcome and predictions

```
summary(fitAggressionD, waic= T); bayes_R2(fitAggressionD)
```

### #Plots

```
pairs(fitAggressionD)
```

```
plot(fitAggressionD)
```

### #PP Checks

```
pp_check(fitAggressionD, resp= "OGAggression", nsamples= 1e2)
```

```
pp_check(fitAggressionD, resp= "IGAggression", nsamples= 1e2)
```

```
pp_check(fitAggressionD, resp= "OGKilling", nsamples= 1e2)
```

```
pp_check(fitAggressionD, resp= "IGKilling", nsamples= 1e2)
```

```
pp_check(fitAggressionD, resp= "Infanticide", nsamples= 1e2)
```

### #save model

```
saveRDS(fitAggressionD, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 2  
Dataset\\Q2 RESULTS\\Aggressionsspecificvariables")
```

## Appendix 3D – Basic model results (no additional predictor variables)

```
> summary(fitAggressionB, waic= T); bayes_R2(fitAggressionB)
```

Family: MV(zero\_one\_inflated\_beta, hurdle\_gamma, bernoulli, bernoulli, bernoulli)

Links: mu = logit; phi = identity; zoi = identity; coi = identity

mu = log; shape = identity; hu = identity

mu = logit

mu = logit

mu = logit

Formula: OG\_Aggression ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

IG\_Aggression ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

IG\_Killing ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

OG\_Killing ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

Infanticide ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

Data: dataB (Number of observations: 101)

Samples: 4 chains, each with iter = 4000; warmup = 2000; thin = 1; total post-warmup samples = 8000

**Group-Level Effects:**

~SpeciesTree (Number of levels: 101)

Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
----------	-----------	----------	----------	------	----------	----------

sd(OGAggression_Intercept)	0.07	0.05	0.00	0.18	1.00	1769	2897
sd(IGAggression_Intercept)	0.24	0.09	0.10	0.45	1.00	1526	2890
sd(IGKilling_Intercept)	2.00	2.24	0.38	7.82	1.00	1511	4528
sd(OGKilling_Intercept)	1.19	1.46	0.28	5.20	1.00	1144	1779
sd(Infanticide_Intercept)	0.39	0.26	0.11	1.00	1.00	1653	2363
cor(OGAggression_Intercept,IGAggression_Intercept)	-0.09	0.38	-0.77	0.66	1.01	1310	2451
cor(OGAggression_Intercept,IGKilling_Intercept)	-0.18	0.36	-0.79	0.58	1.00	707	1179
cor(IGAggression_Intercept,IGKilling_Intercept)	0.26	0.28	-0.30	0.77	1.00	1624	4051
cor(OGAggression_Intercept,OGKilling_Intercept)	-0.04	0.37	-0.72	0.66	1.01	698	1594
cor(IGAggression_Intercept,OGKilling_Intercept)	0.38	0.27	-0.18	0.84	1.00	2273	4389
cor(IGKilling_Intercept,OGKilling_Intercept)	0.66	0.19	0.24	0.93	1.00	4370	6051
cor(OGAggression_Intercept,Infanticide_Intercept)	-0.23	0.38	-0.84	0.57	1.00	893	1305
cor(IGAggression_Intercept,Infanticide_Intercept)	0.32	0.31	-0.33	0.84	1.00	2516	4515
cor(IGKilling_Intercept,Infanticide_Intercept)	0.60	0.22	0.07	0.92	1.00	4539	5663
cor(OGKilling_Intercept,Infanticide_Intercept)	0.62	0.22	0.11	0.93	1.00	4365	6440

**Population-Level Effects:**

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGAggression_Intercept	-0.49	0.43	-1.47	0.37	1.00	3800	4029
IGAggression_Intercept	-2.23	1.22	-4.79	0.13	1.00	3858	3946

IGKilling_Intercept	-3.58	6.11	-16.60	9.29	1.00	4802	4609
OGKilling_Intercept	-2.78	4.51	-12.44	6.11	1.00	4147	4009
Infanticide_Intercept	0.28	2.02	-3.67	4.33	1.00	3327	3118

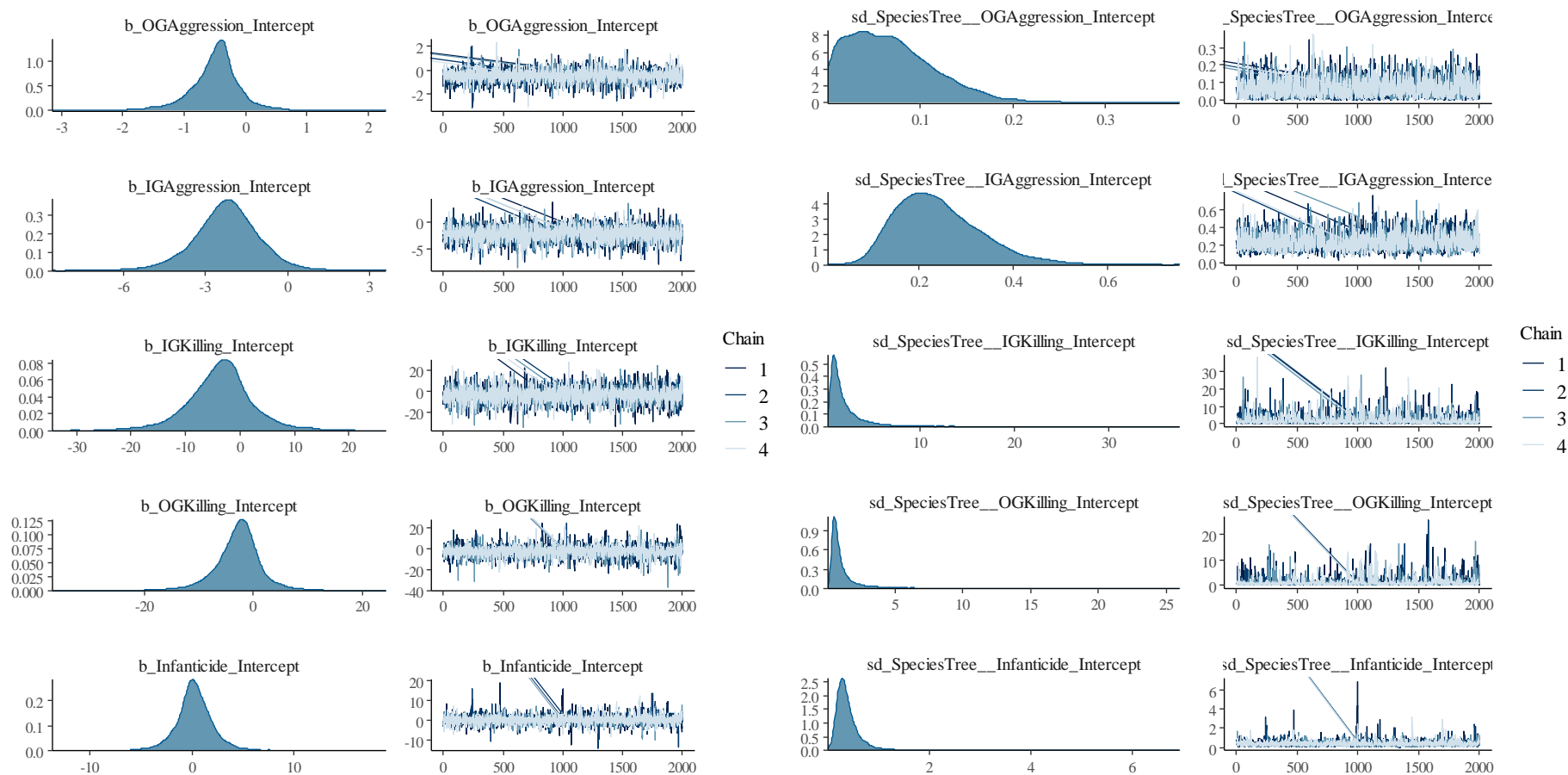
**Family Specific Parameters:**

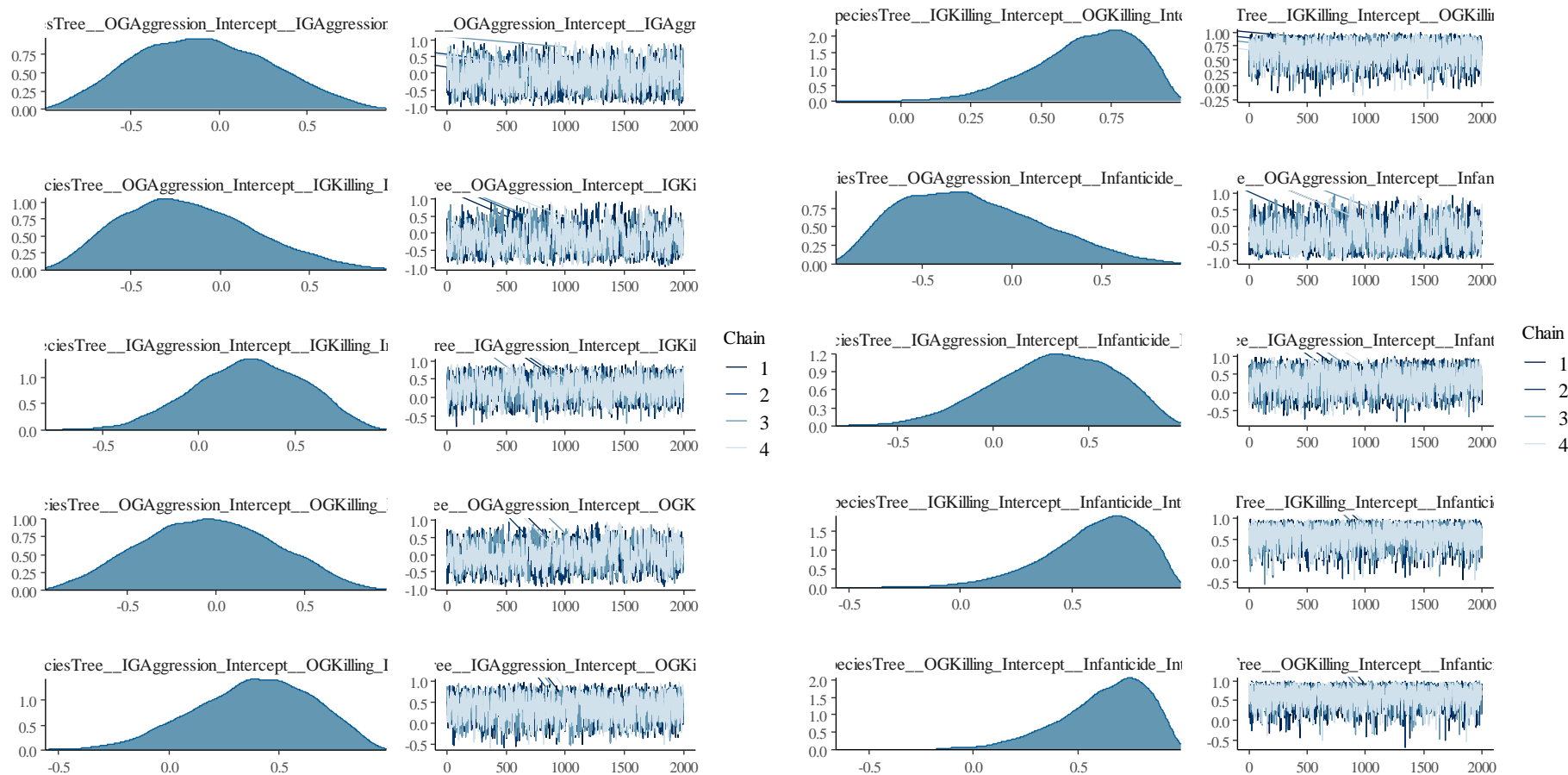
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
phi_OGAggression	3.06	0.55	2.16	4.30	1.00	4792	5422
zoi_OGAggression	0.30	0.04	0.22	0.39	1.00	13998	5493
coi_OGAggression	0.75	0.07	0.59	0.88	1.00	15513	5788
shape_IGAggression	0.47	0.07	0.35	0.64	1.00	3140	4062
hu_IGAggression	0.07	0.03	0.03	0.12	1.00	12518	4856

Samples were drawn using sampling (NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

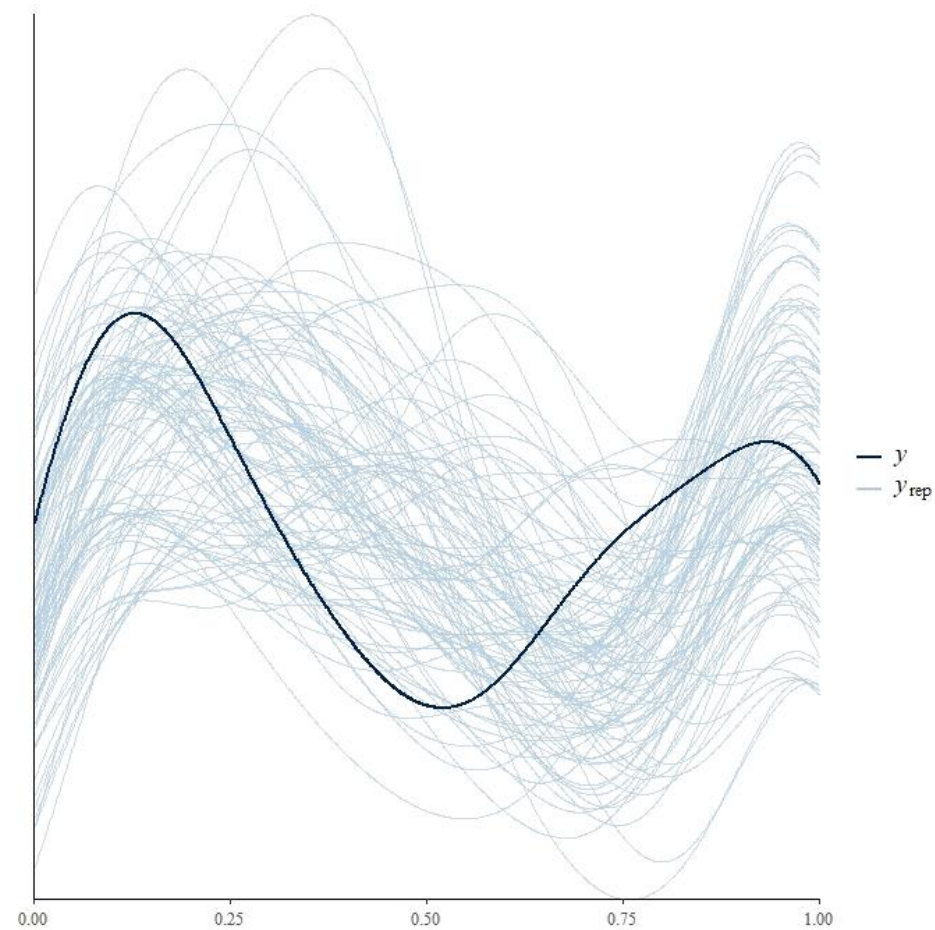
	Estimate	Est.Error	Q2.5	Q97.5
R2OGAggression	0.02243032	0.02328496	4.751492e-05	0.08355896
R2IGAggression	0.25489679	0.13750838	5.366182e-02	0.54731577
R2IGKilling	0.59194664	0.18741270	2.303343e-01	0.93588000
R2OGKilling	0.47214139	0.17251275	1.877576e-01	0.87410143
R2Infanticide	0.25700462	0.11341448	5.794433e-02	0.50585869

## Plots - MCMC chains, posterior distributions, and pp checks

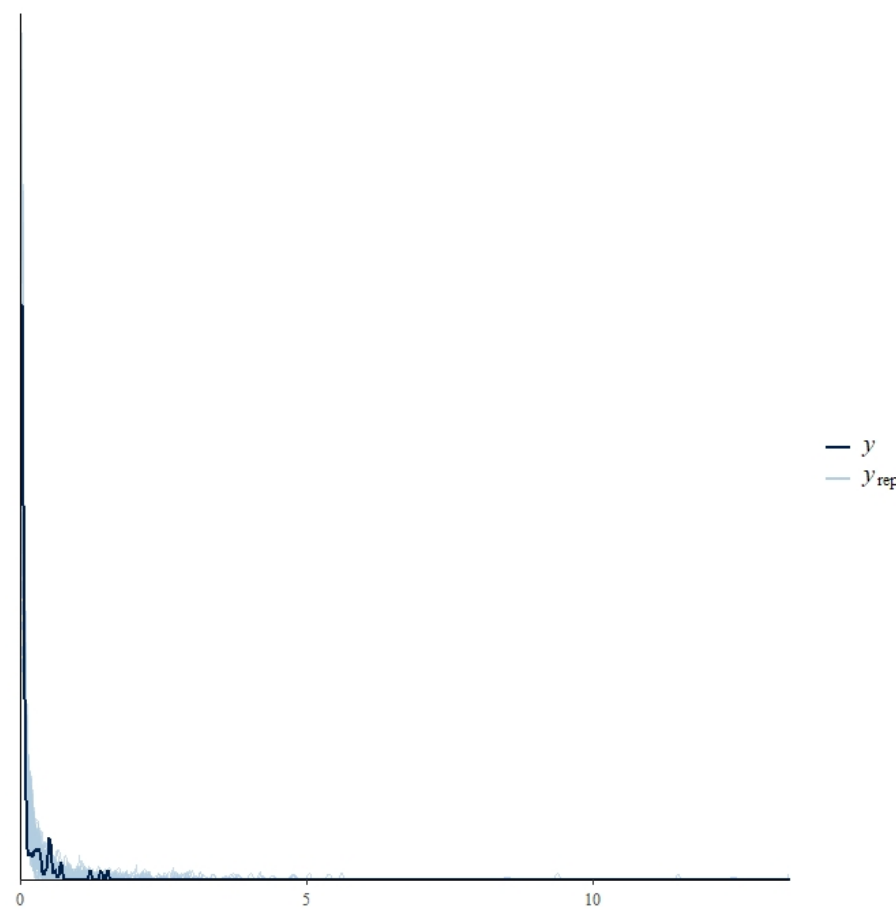




PP Check – OG Aggression

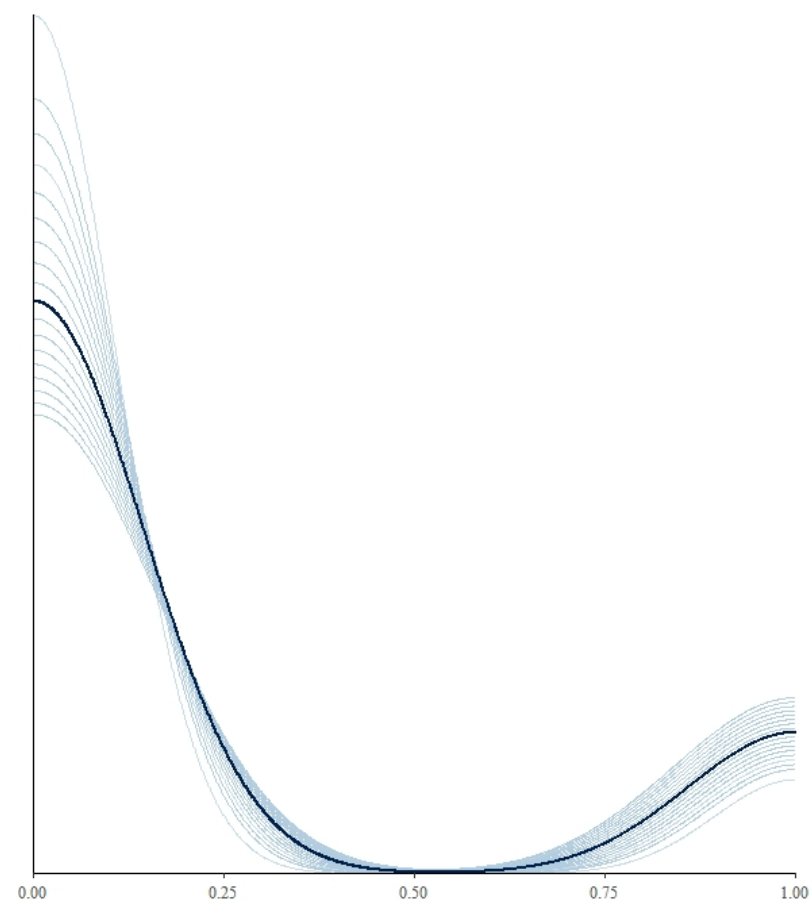


PP Check – IG Aggression

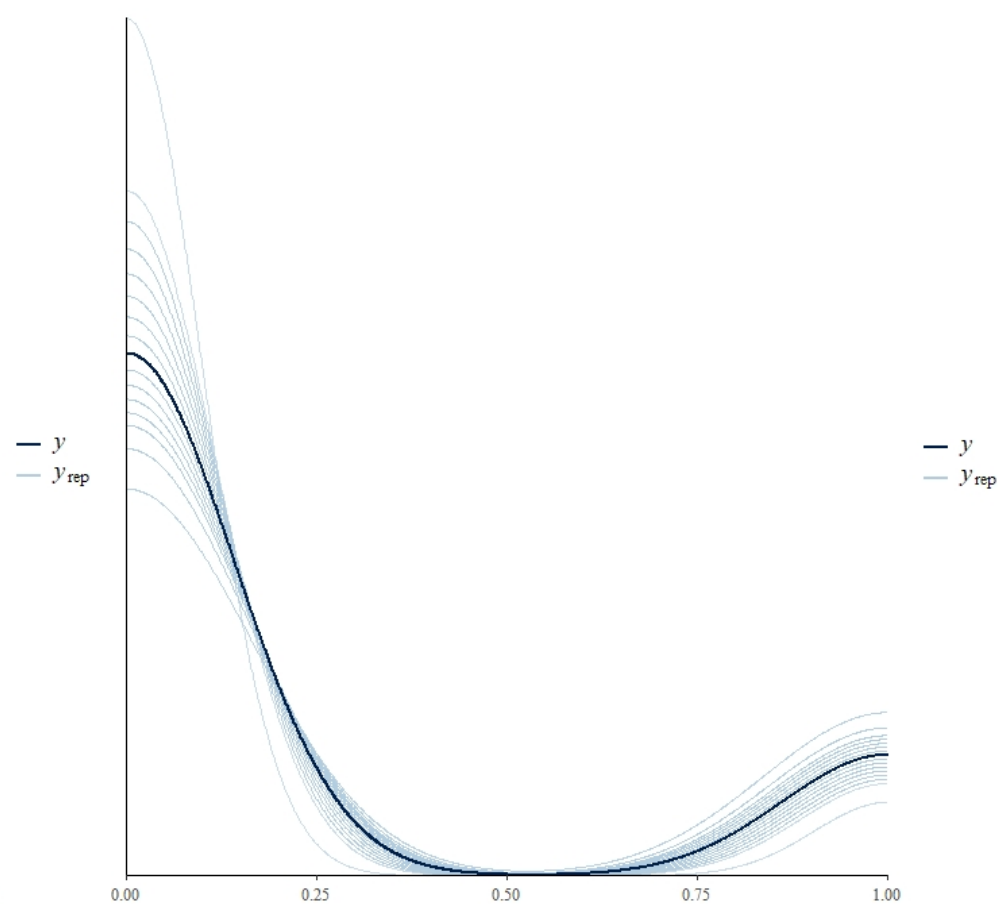




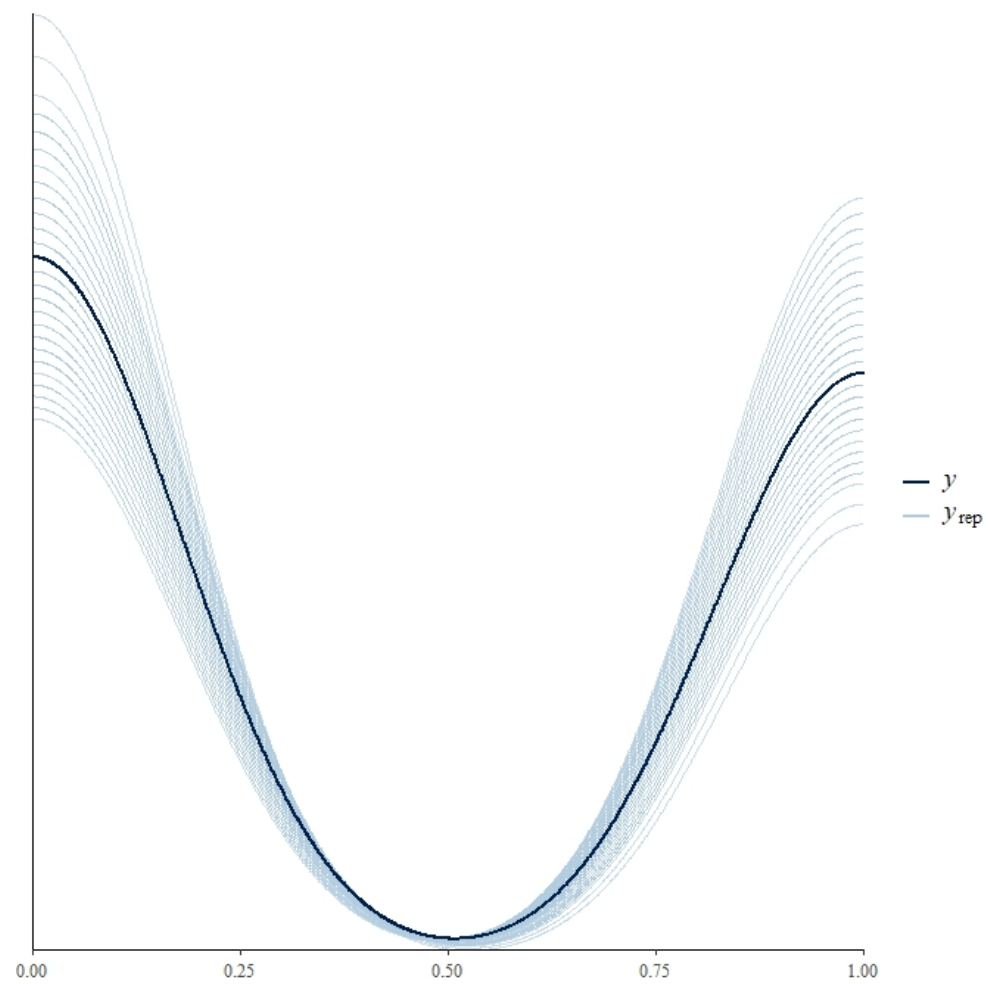
PP Check – OG Killing



PP Check – IG Killing



## PP Check - Infanticide



## Appendix 3E – Model with all socioecological variables

**summary(fitAggressionC, waic= T); bayes\_R2(fitAggressionC)**

Family: MV(zero\_one\_inflated\_beta, hurdle\_gamma, bernoulli, bernoulli, bernoulli)

Links: mu = logit; phi = identity; zoi = identity; coi = identity

mu = log; shape = identity; hu = identity

mu = logit

mu = logit

mu = logit

Formula: OG\_Aggression ~ No\_Males + Leaves + Season\_Breeder + D.Index + Group\_Size + Substrate\_1 + Dimorphism + Coalition + (1 | gr(SpeciesTree, cov = A))

IG\_Aggression ~ No\_Males + Leaves + Season\_Breeder + D.Index + Group\_Size + Substrate\_1 + Dimorphism + Coalition + (1 | gr(SpeciesTree, cov = A))

IG\_Killing ~ No\_Males + Leaves + Season\_Breeder + D.Index + Group\_Size + Substrate\_1 + Dimorphism + Coalition + (1 | gr(SpeciesTree, cov = A))

OG\_Killing ~ No\_Males + Leaves + Season\_Breeder + D.Index + Group\_Size + Substrate\_1 + Dimorphism + Coalition + (1 | gr(SpeciesTree, cov = A))

Infanticide ~ No\_Males + Leaves + Season\_Breeder + D.Index + Group\_Size + Substrate\_1 + Dimorphism + Coalition + (1 | gr(SpeciesTree, cov = A))

Data: dataB (Number of observations: 101)

Samples: 4 chains, each with iter = 4000; warmup = 2000; thin = 1; total post-warmup samples = 8000

**Group-Level Effects:**

~SpeciesTree (Number of levels: 101)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGAggression_Intercept)	0.07	0.05	0.01	0.18	1.00	2168	3065
sd(IGAggression_Intercept)	0.32	0.10	0.15	0.55	1.00	1098	2358
sd(IGKilling_Intercept)	5.38	5.87	0.99	19.16	1.00	1476	2474
sd(OGKilling_Intercept)	5.84	7.93	1.11	21.91	1.00	996	568
sd(Infanticide_Intercept)	5.93	4.74	1.93	17.01	1.00	2198	2435

**Population-Level Effects:**

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGAggression_Intercept	-0.87	0.95	-2.74	1.00	1.00	7534	6340
IGAggression_Intercept	-1.30	2.06	-5.28	2.87	1.00	4655	5411
IGKilling_Intercept	-6.56	12.37	-30.31	19.08	1.00	4515	4788
OGKilling_Intercept	-6.21	12.90	-31.40	18.77	1.00	1431	715
Infanticide_Intercept	1.79	11.77	-20.86	25.67	1.00	4954	5772
OGAggression_No_MaleM	0.36	0.34	-0.30	1.04	1.00	8284	5761
OGAggression_Leaves	0.03	0.59	-1.11	1.19	1.00	9977	6019
OGAggression_Season_BreederYes	0.08	0.32	-0.54	0.72	1.00	6084	6582
OGAggression_D.Index	0.39	0.15	0.10	0.69	1.00	8544	6414
OGAggression_Group_Size	-0.00	0.01	-0.02	0.02	1.00	8386	6604
OGAggression_Substrate_1Terrestrial	0.39	0.36	-0.32	1.10	1.00	9760	6383

OGAggression_Dimorphism	-0.41	0.53	-1.45	0.63	1.00	9192	6076
OGAggression_CoalitionYes	0.09	0.35	-0.57	0.78	1.00	9750	5940
IGAggression_No_MalesM	-0.13	0.52	-1.14	0.92	1.00	6446	6157
IGAggression_Leaves	-2.15	1.07	-4.19	-0.01	1.00	6977	5620
IGAggression_Season_BreederYes	-0.68	0.49	-1.64	0.26	1.00	7498	7148
IGAggression_D.Index	0.18	0.14	-0.08	0.48	1.00	4899	4867
IGAggression_Group_Size	-0.03	0.02	-0.07	0.00	1.00	6006	5617
IGAggression_Substrate_1Terrestrial	0.44	0.64	-0.80	1.67	1.00	6441	6490
IGAggression_Dimorphism	-0.32	0.93	-2.14	1.47	1.00	4938	5708
IGAggression_CoalitionYes	0.62	0.61	-0.55	1.82	1.00	6666	6551
IGKilling_No_MalesM	-1.16	3.56	-8.42	5.81	1.00	6333	5764
IGKilling_Leaves	4.00	4.44	-4.93	12.51	1.00	6940	5756
IGKilling_Season_BreederYes	-0.14	3.41	-6.99	6.81	1.00	6236	5111
IGKilling_D.Index	-1.78	2.44	-7.52	2.19	1.00	4238	4158
IGKilling_Group_Size	0.15	0.25	-0.14	0.77	1.00	3410	2236
IGKilling_Substrate_1Terrestrial	-1.96	3.71	-9.31	5.48	1.00	7098	5589
IGKilling_Dimorphism	-0.11	4.05	-8.26	7.74	1.00	6469	5011
IGKilling_CoalitionYes	6.07	4.07	-2.31	13.96	1.00	5093	4983
OGKilling_No_MalesM	-1.95	3.59	-9.26	5.32	1.00	5910	3764
OGKilling_Leaves	3.46	4.32	-5.38	11.91	1.00	7132	5956

OGKilling_Season_BreederYes	0.12	3.32	-6.16	7.26	1.00	5857	5326
OGKilling_D.Index	-1.07	2.34	-6.49	3.00	1.00	4063	2917
OGKilling_Group_Size	0.14	0.33	-0.17	0.77	1.00	1180	556
OGKilling_Substrate_1Terrestrial	-3.17	3.58	-10.26	4.36	1.00	6309	4324
OGKilling_Dimorphism	-0.39	4.09	-8.84	7.42	1.00	6395	5139
OGKilling_CoalitionYes	5.80	3.69	-1.63	13.07	1.00	5045	3448
Infanticide_No_MalesM	-5.73	3.46	-12.73	0.95	1.00	6280	5836
Infanticide_Leaves	2.58	4.28	-5.92	11.20	1.00	9354	6792
Infanticide_Season_BreederYes	4.10	3.22	-2.07	10.81	1.00	6391	5142
Infanticide_D.Index	-0.46	1.81	-4.43	2.90	1.00	4083	3928
Infanticide_Group_Size	0.00	0.19	-0.36	0.34	1.00	3459	3333
Infanticide_Substrate_1Terrestrial	-0.71	3.29	-7.43	5.57	1.00	4802	5345
Infanticide_Dimorphism	-2.72	3.71	-10.32	4.25	1.00	6475	6206
Infanticide_CoalitionYes	2.98	3.51	-3.76	10.36	1.00	6167	5999

**Family Specific Parameters:**

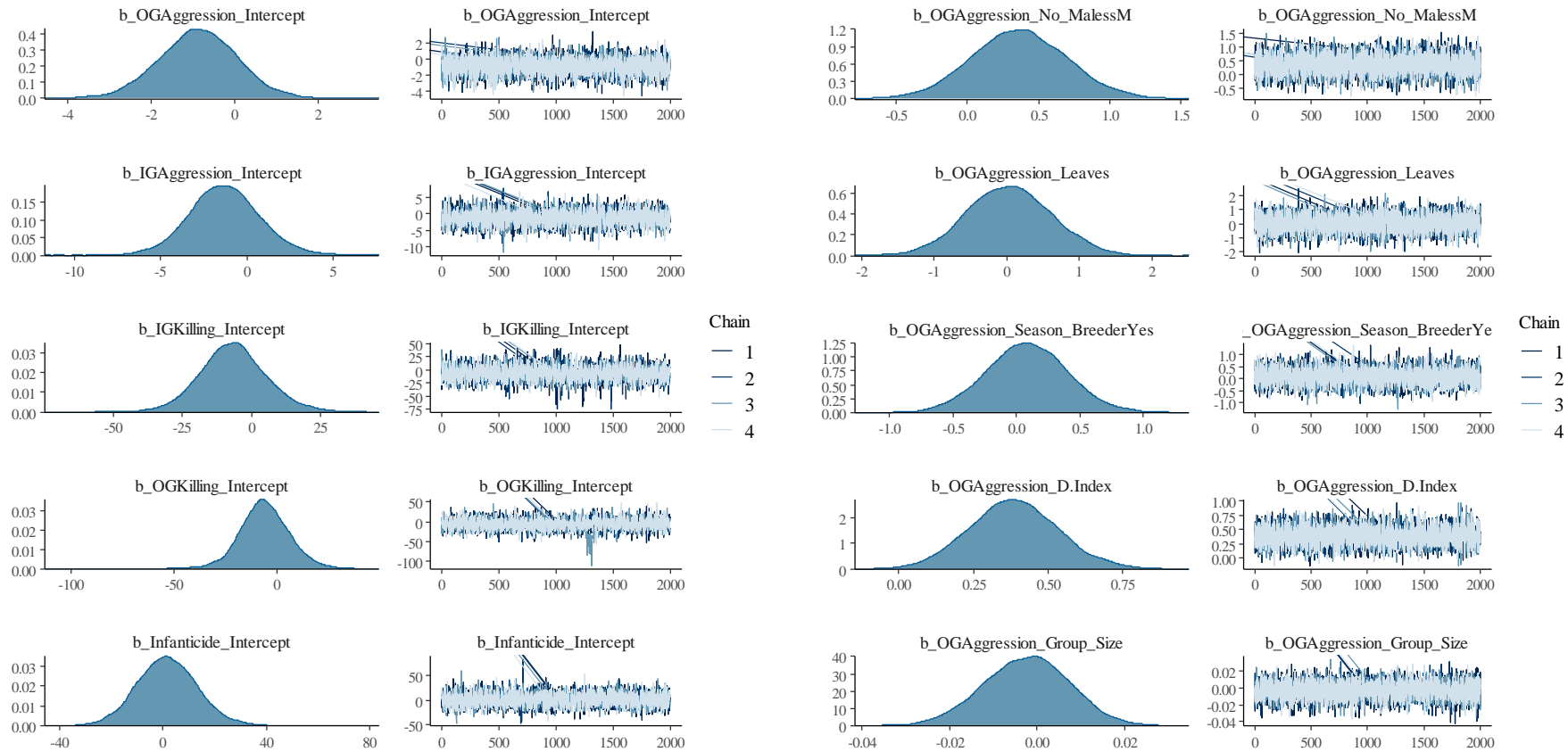
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
phi_OGAggression	3.44	0.61	2.39	4.80	1.00	5299	5221
zoi_OGAggression	0.30	0.05	0.22	0.39	1.00	10088	4863
coi_OGAggression	0.75	0.07	0.59	0.88	1.00	12425	5333

shape_IGAggression	0.55	0.10	0.39	0.78	1.00	1769	3257
hu_IGAggression	0.07	0.02	0.03	0.12	1.00	10733	5254

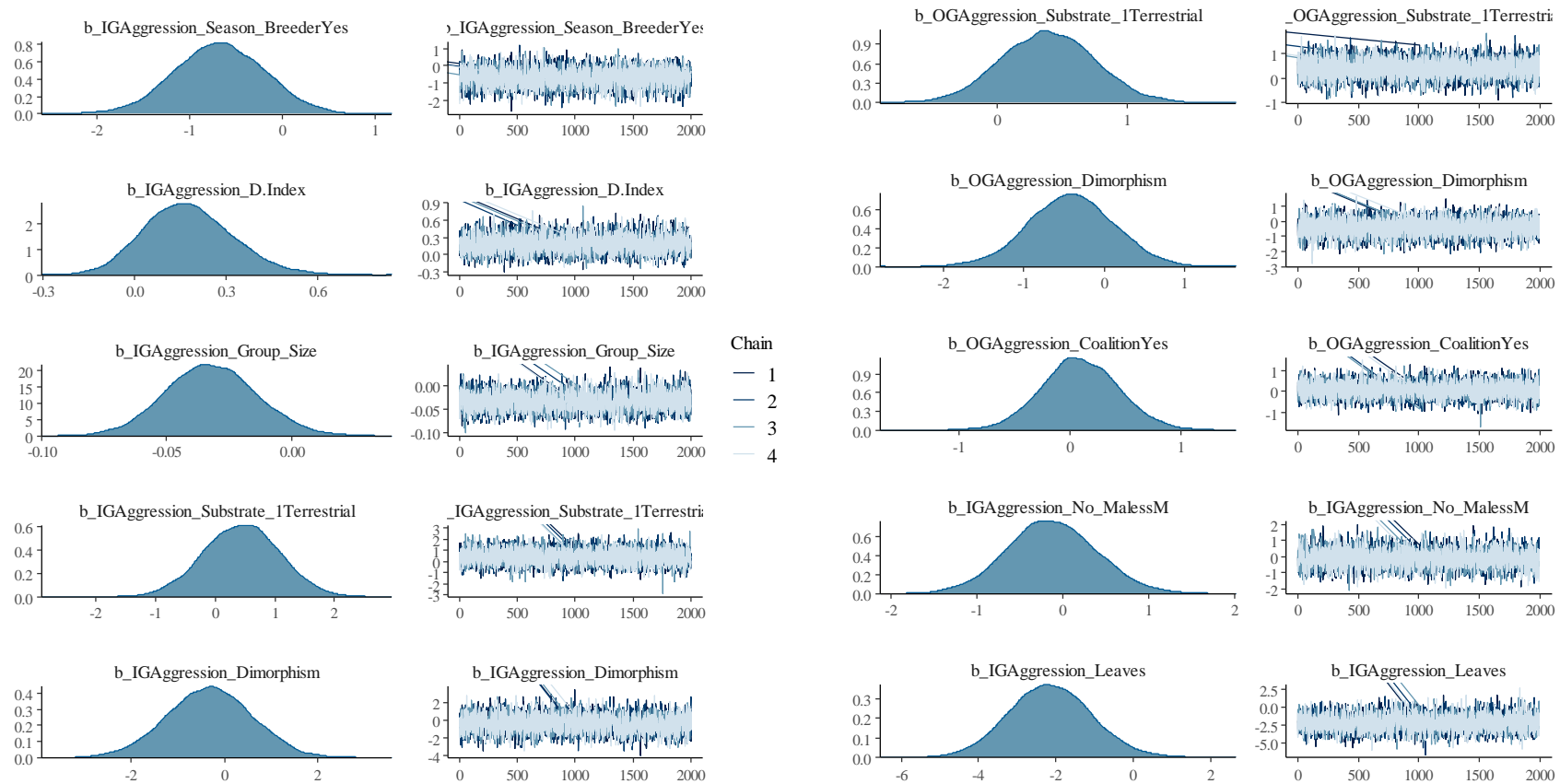
Samples were drawn using sampling (NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

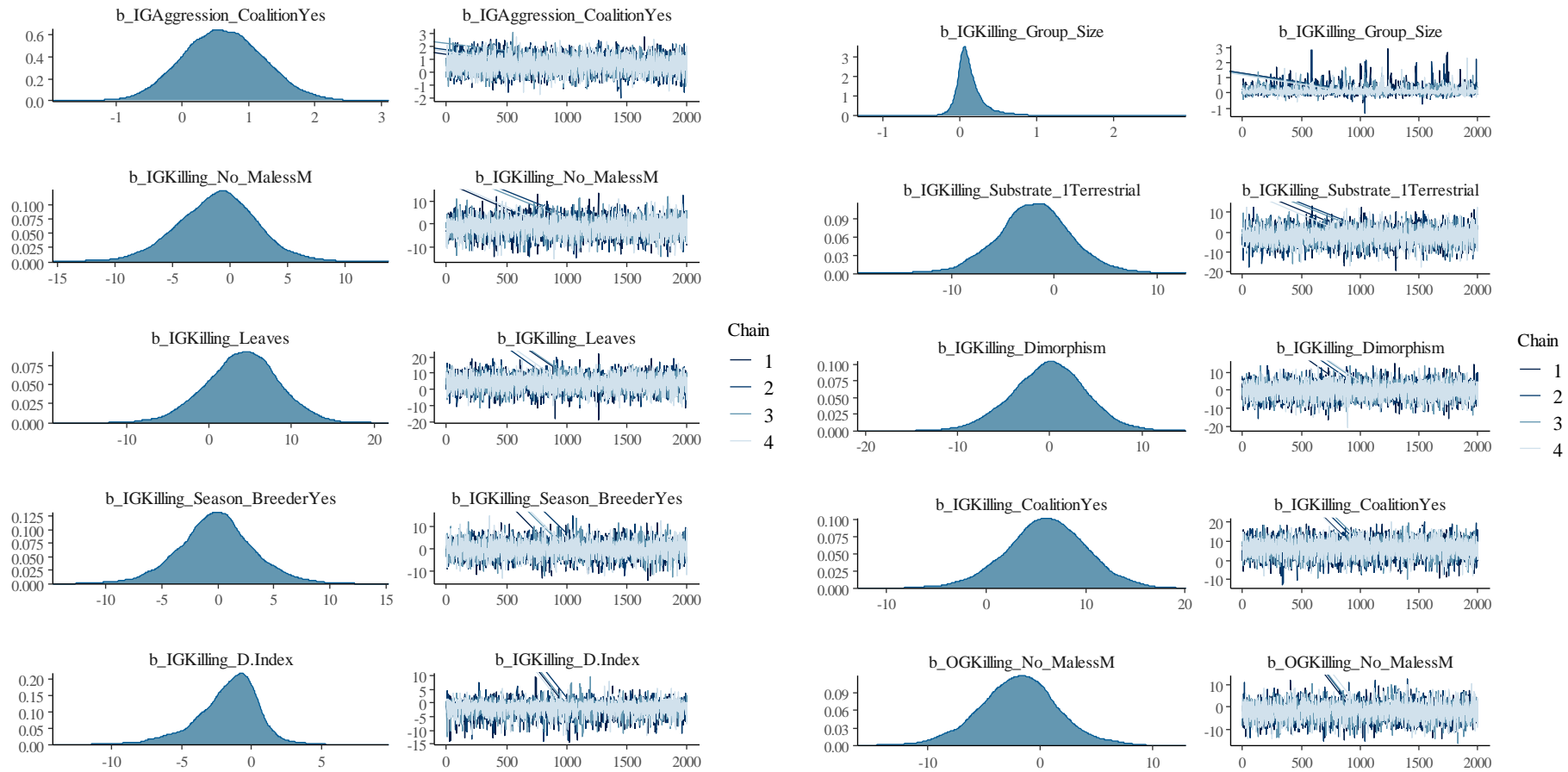
	Estimate	Est.Error	Q2.5	Q97.5
R2OGAggression	0.09554213	0.03029239	0.04235654	0.1606888
R2IGAggression	0.47256874	0.08445909	0.25544894	0.6118958
R2IGKilling	0.81148647	0.11848369	0.53939562	0.9877830
R2OGKilling	0.81413774	0.11472320	0.55074301	0.9887384
R2Infanticide	0.85444095	0.07779959	0.67905029	0.9770612

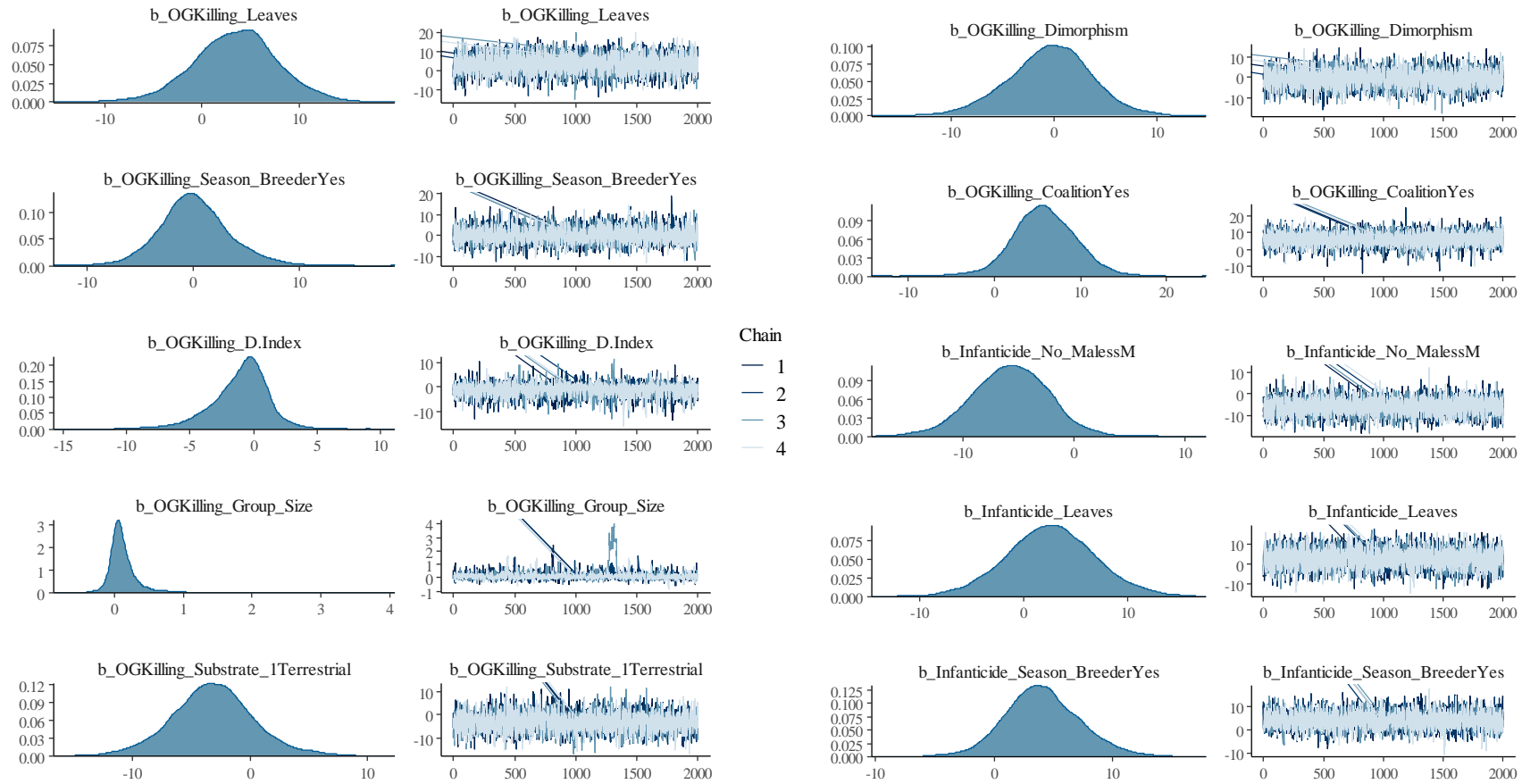
## Plots - MCMC chains, posterior distributions, and pp checks

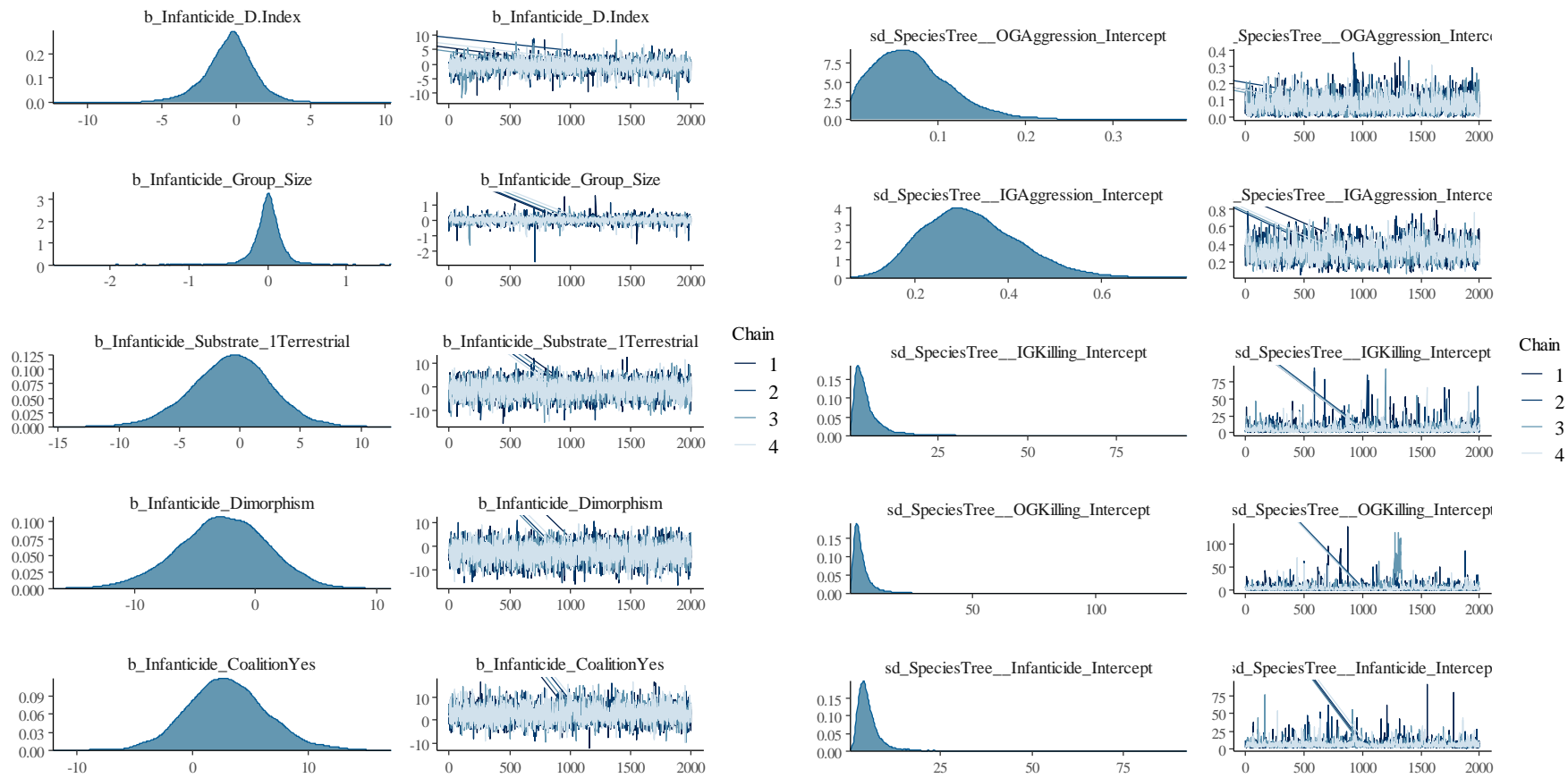




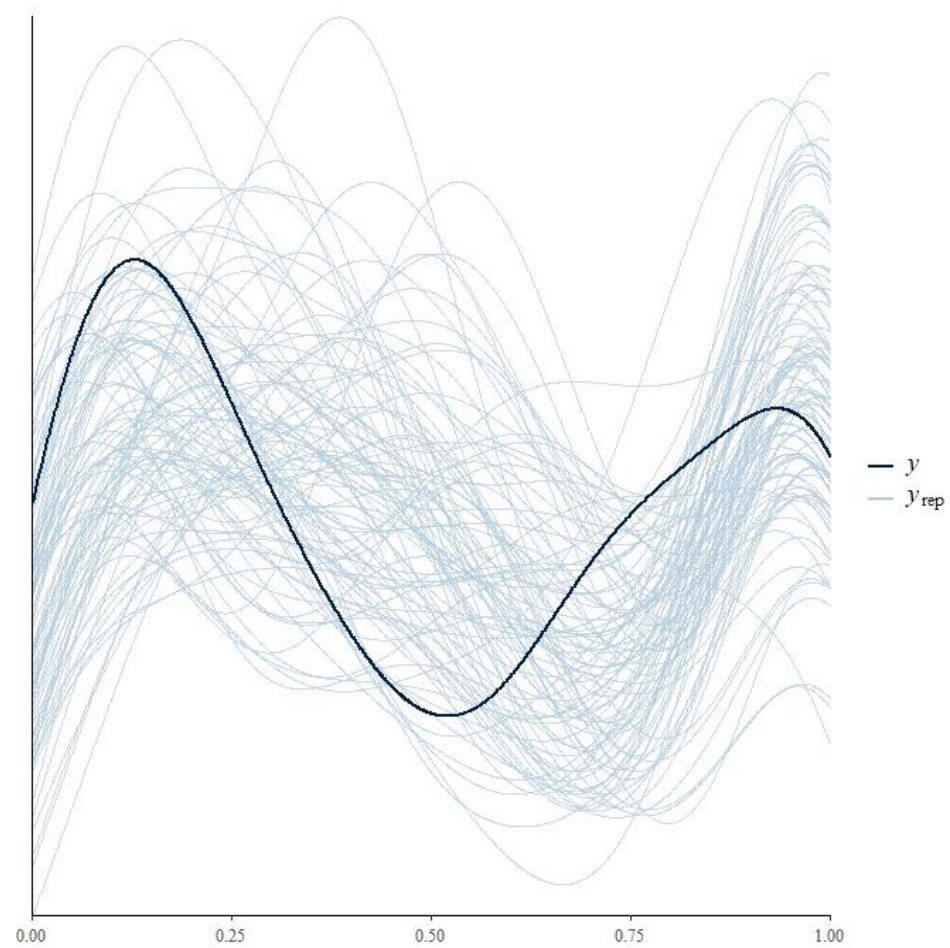




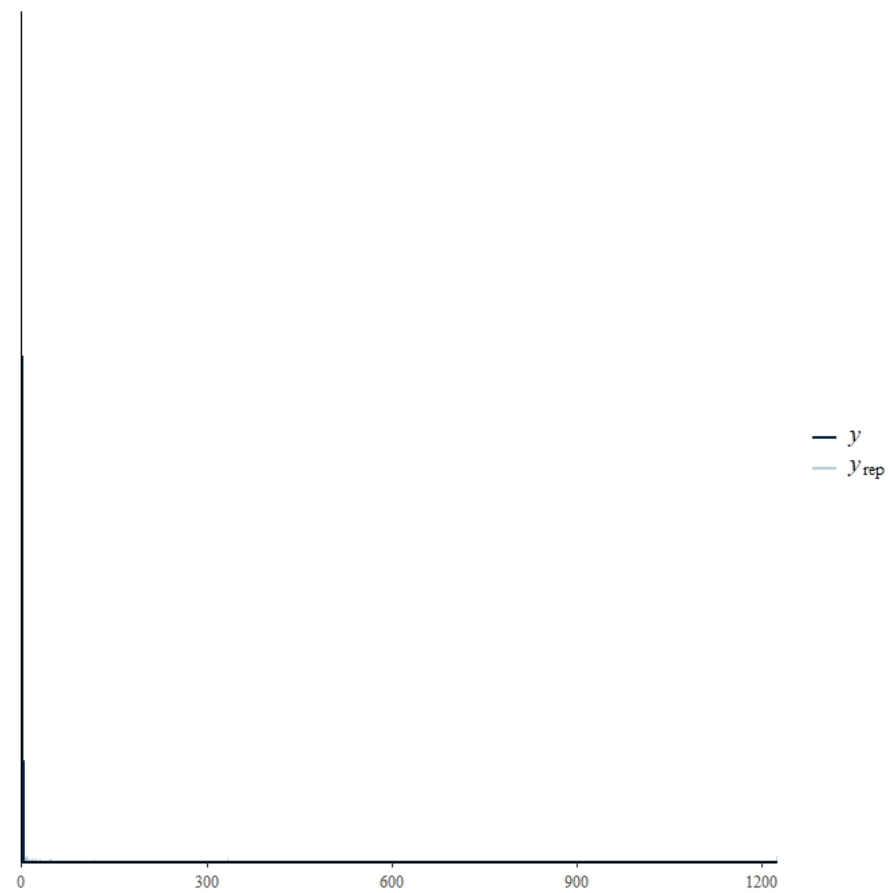




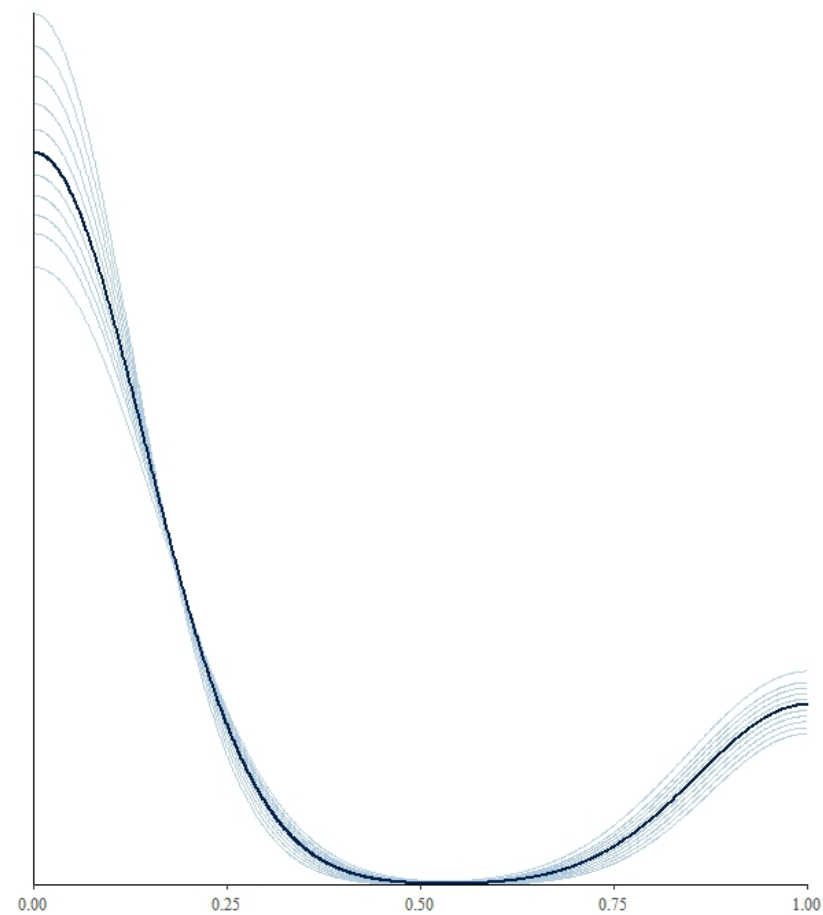
PP Plot – OG Aggression



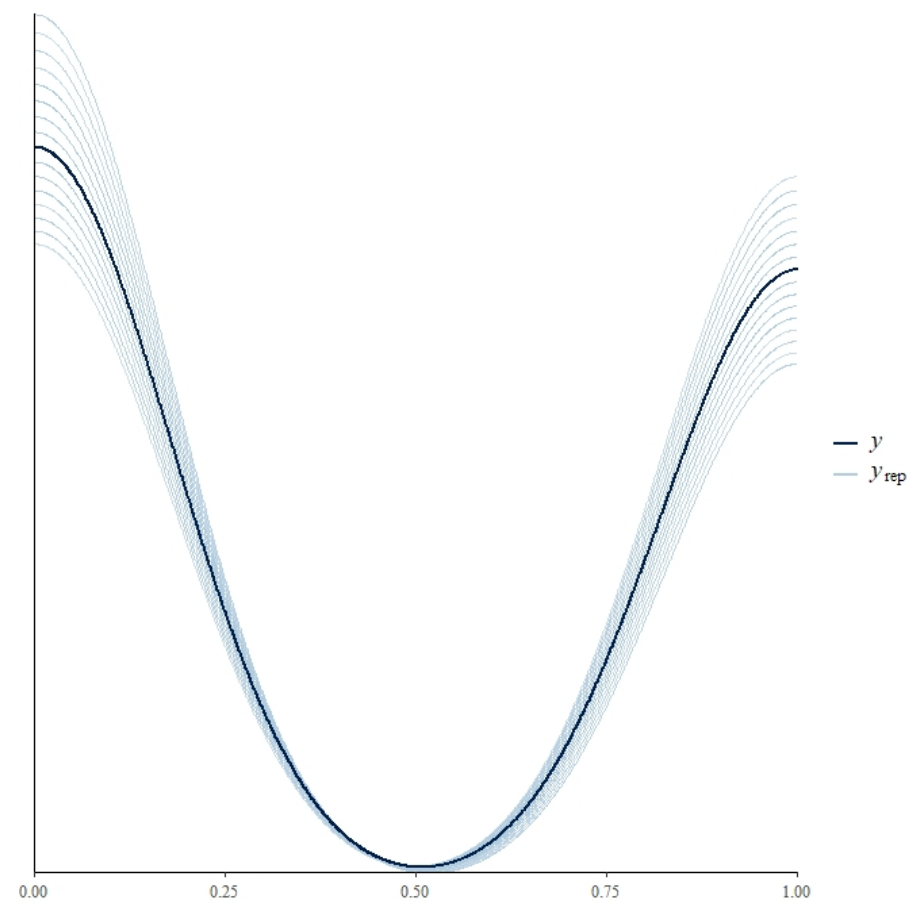
PP Plot – IG Aggression



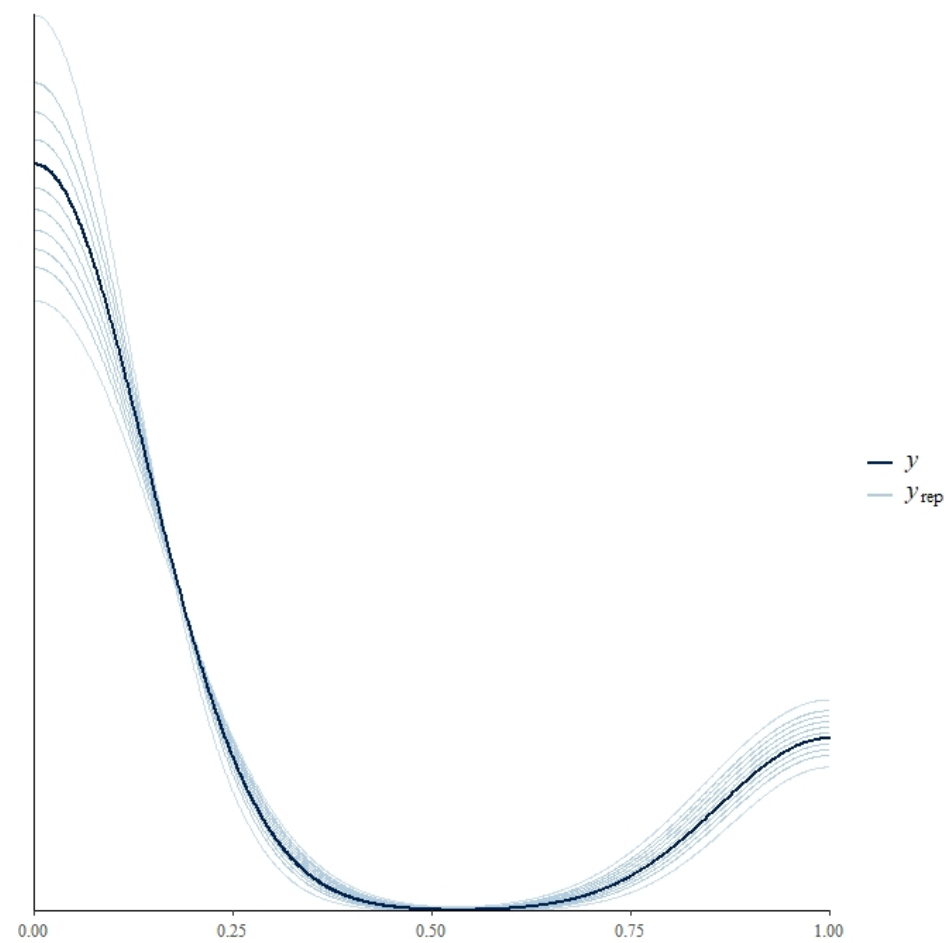
PP Plot – OG Killing



PP Plot - Infanticide



PP Plot – IG Killing



## Appendix 3F – Model with aggression specific socioecological variables

```
> summary(FitAggressionD, waic= T); bayes_R2(FitAggressionD)
```

Family: MV(zero\_one\_inflated\_beta, hurdle\_gamma, bernoulli, bernoulli, bernoulli)

Links: mu = logit; phi = identity; zoi = identity; coi = identity

mu = log; shape = identity; hu = identity

mu = logit

mu = logit

mu = logit

Formula: OG\_Aggression ~ D.Index + No\_Males + Group\_Size + Coalition + Substrate\_1 + (1 | gr(SpeciesTree, cov = A))

IG\_Aggression ~ Coalition + Dimorphism + Leaves + Substrate\_1 + Group\_Size + (1 | gr(SpeciesTree, cov = A))

OG\_Killing ~ D.Index + Season\_Breeder + Coalition + No\_Males + Substrate\_1 + (1 | gr(SpeciesTree, cov = A))

IG\_Killing ~ Coalition + No\_Males + Season\_Breeder + Substrate\_1 + Dimorphism + (1 | gr(SpeciesTree, cov = A))

Infanticide ~ D.Index + Season\_Breeder + Coalition + No\_Males + Group\_Size + (1 | gr(SpeciesTree, cov = A))

Data: dataB (Number of observations: 101)

Samples: 4 chains, each with iter = 7000; warmup = 3500; thin = 1;

total post-warmup samples = 14000

**Group-Level Effects:**

~SpeciesTree (Number of levels: 101)



	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGAggression_Intercept)	0.06	0.04	0.00	0.17	1.00	3407	5666
sd(IGAggression_Intercept)	0.28	0.09	0.13	0.49	1.00	2167	3579
sd(OGKilling_Intercept)	2.98	2.50	0.40	8.75	1.00	1776	1774
sd(IGKilling_Intercept)	2.47	2.25	0.29	7.50	1.00	1785	1999
sd(Infanticide_Intercept)	4.25	3.29	0.52	12.11	1.00	1219	577

**Population-Level Effects:**

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGAggression_Intercept	-1.28	0.57	-2.42	-0.16	1.00	9895	7954
IGAggression_Intercept	-1.07	1.80	-4.51	2.55	1.00	9153	8610
OGKilling_Intercept	-3.21	8.52	-19.94	14.92	1.00	9732	8404
IGKilling_Intercept	-7.06	8.55	-24.67	10.49	1.00	10824	10231
Infanticide_Intercept	-0.48	9.41	-19.61	18.43	1.00	8909	9681
OGAggression_D.Index	0.40	0.14	0.13	0.69	1.00	17997	11086
OGAggression_No_MalessM	0.35	0.31	-0.27	0.97	1.00	16763	10990
OGAggression_Group_Size	-0.00	0.01	-0.02	0.02	1.00	18358	11466
OGAggression_CoalitionYes	0.07	0.33	-0.56	0.72	1.00	17171	10983
OGAggression_Substrate_1Terrestrial	0.25	0.32	-0.38	0.87	1.00	19024	10180

IGAggression_CoalitionYes	0.50	0.55	-0.59	1.60	1.00	11883	9712
IGAggression_Dimorphism	-0.42	0.85	-2.10	1.24	1.00	12677	10395
IGAggression_Leaves	-2.32	1.03	-4.34	-0.30	1.00	10744	10325
IGAggression_Substrate_1Terrestrial	0.70	0.60	-0.50	1.87	1.00	12008	11010
IGAggression_Group_Size	-0.04	0.02	-0.07	-0.00	1.00	10843	10423
OGKilling_D.Index	-0.95	1.68	-5.09	1.62	1.00	7546	6554
OGKilling_Season_BreederYes	-0.93	2.34	-5.57	4.10	1.00	12256	7912
OGKilling_CoalitionYes	5.80	3.16	0.64	12.78	1.00	5183	9490
OGKilling_No_MalelessM	-1.86	2.87	-8.13	3.41	1.00	10352	9395
OGKilling_Substrate_1Terrestrial	-2.77	2.85	-8.85	2.47	1.00	8787	9070
IGKilling_CoalitionYes	6.87	3.39	1.06	14.26	1.00	8657	9591
IGKilling_No_MalelessM	-0.98	2.73	-7.17	4.06	1.00	10333	8532
IGKilling_Season_BreederYes	-0.56	2.42	-5.75	4.26	1.00	10155	8619
IGKilling_Substrate_1Terrestrial	-1.06	2.74	-7.07	4.03	1.00	8605	8671
IGKilling_Dimorphism	0.35	3.24	-6.30	6.99	1.00	13919	9450
Infanticide_D.Index	-0.44	1.42	-3.71	2.22	1.00	7350	6573
Infanticide_Season_BreederYes	3.59	2.90	-1.34	9.82	1.00	3736	8273
Infanticide_CoalitionYes	2.70	3.10	-3.02	9.42	1.00	7986	9359
Infanticide_No_MalelessM	-5.35	3.22	-12.32	0.08	1.00	3334	6609
Infanticide_Group_Size	-0.02	0.12	-0.28	0.21	1.00	6367	5981

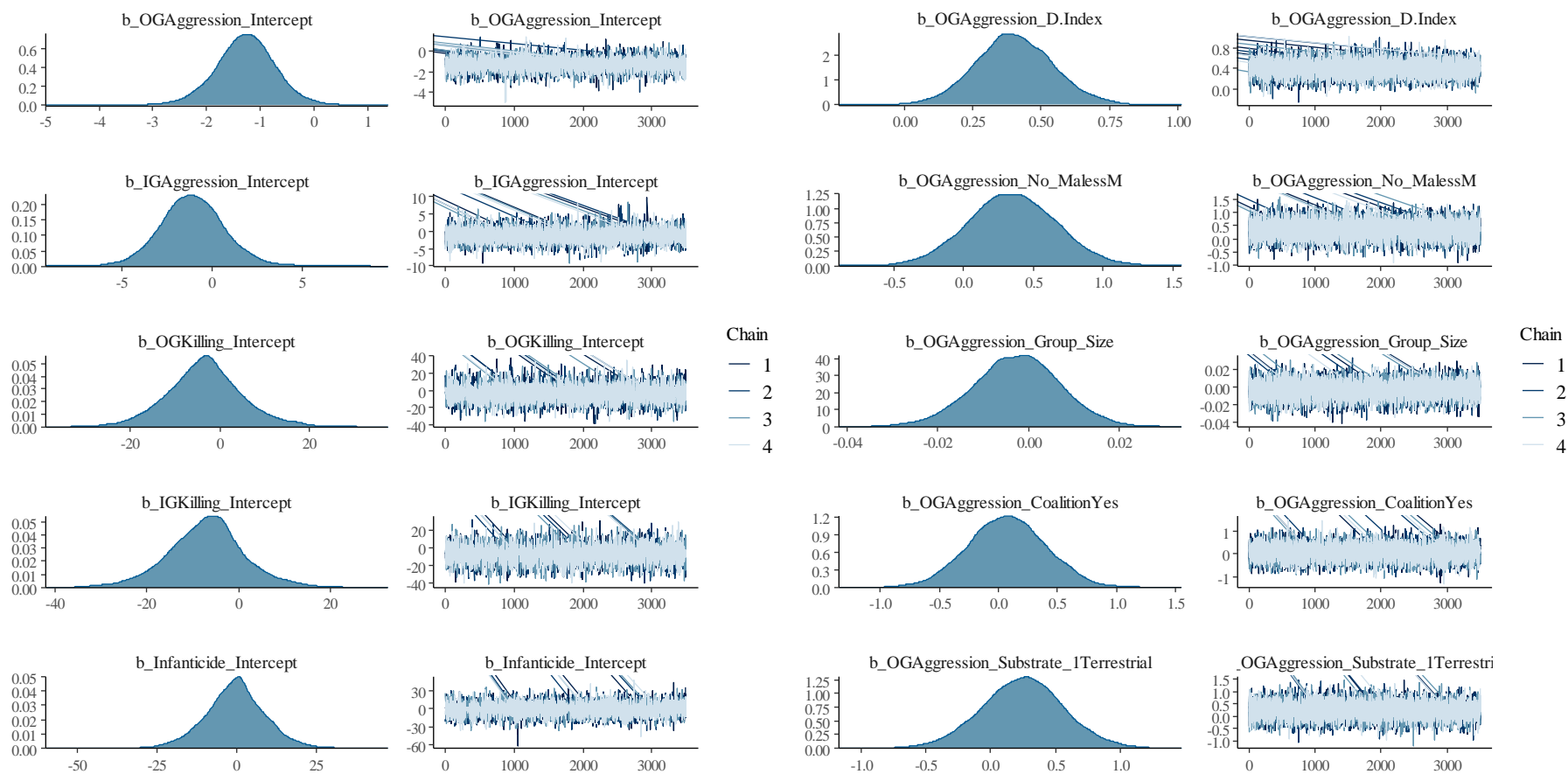
**Family Specific Parameters:**

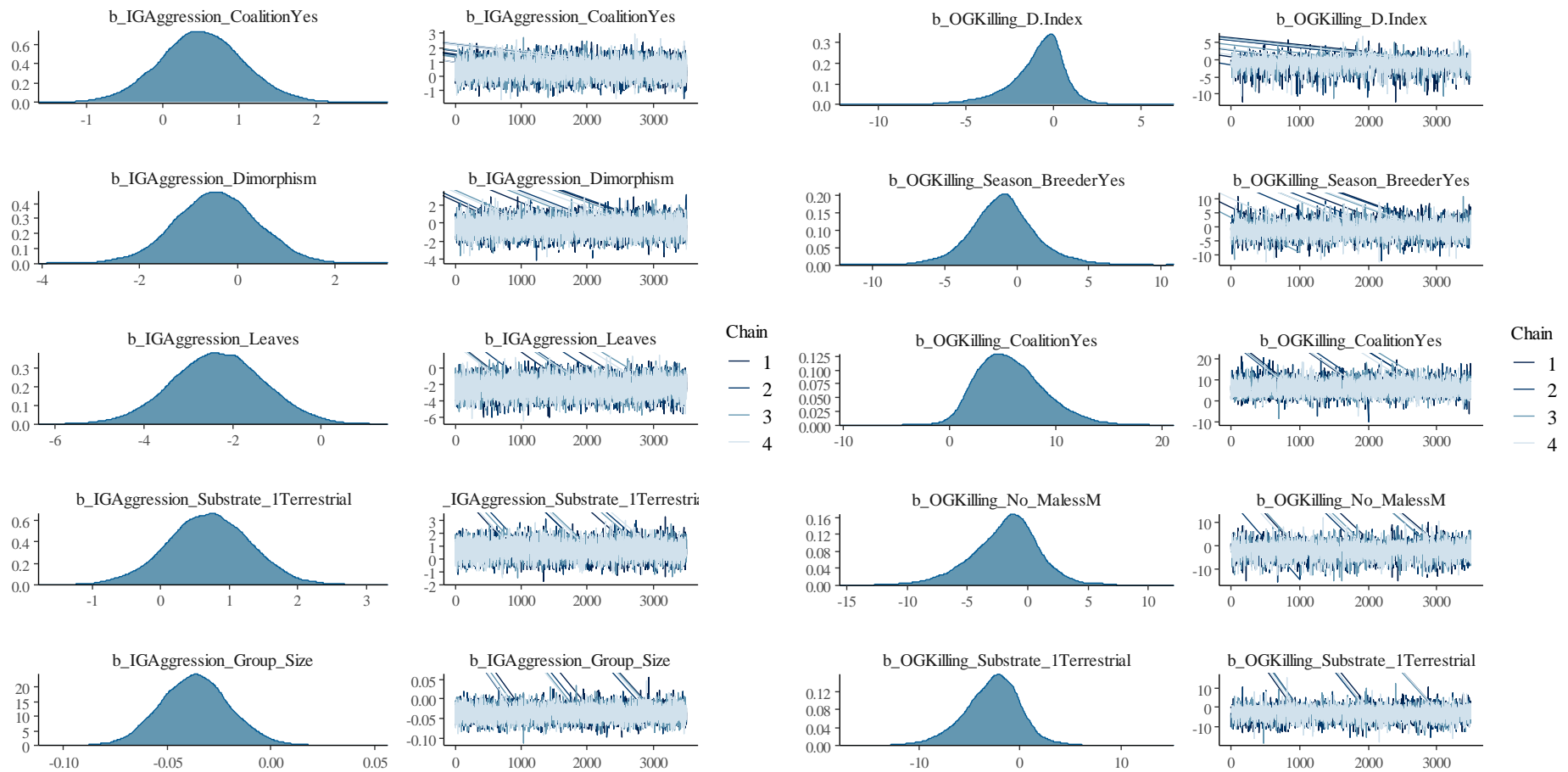
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
phi_OGAggression	3.42	0.58	2.44	4.72	1.00	10510	9780
zoi_OGAggression	0.30	0.04	0.22	0.39	1.00	23994	9813
coi_OGAggression	0.75	0.07	0.59	0.88	1.00	27570	9677
shape_IGAggression	0.52	0.09	0.38	0.72	1.00	4028	5515
hu_IGAggression	0.07	0.02	0.03	0.12	1.00	26188	8716

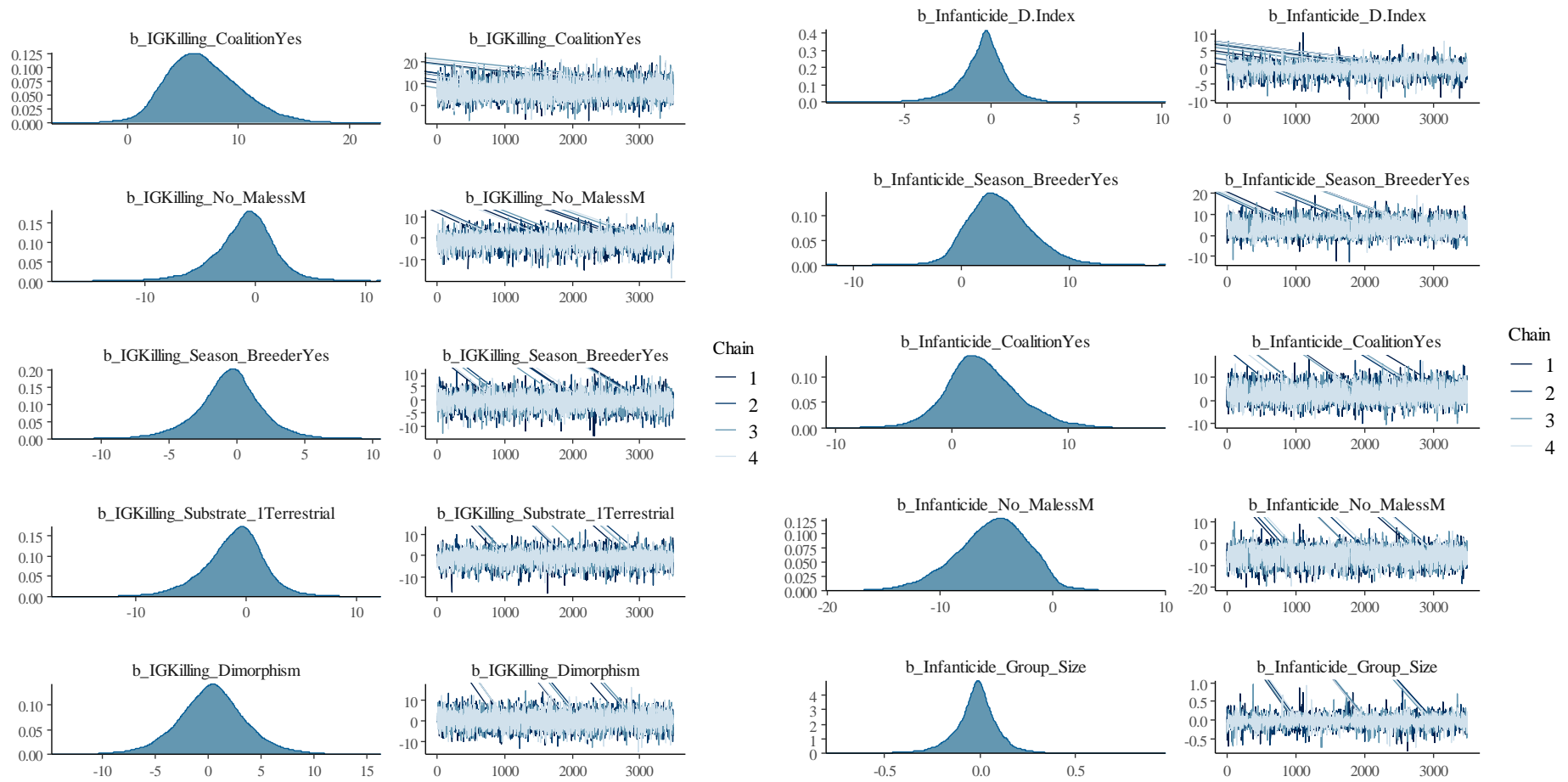
Samples were drawn using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

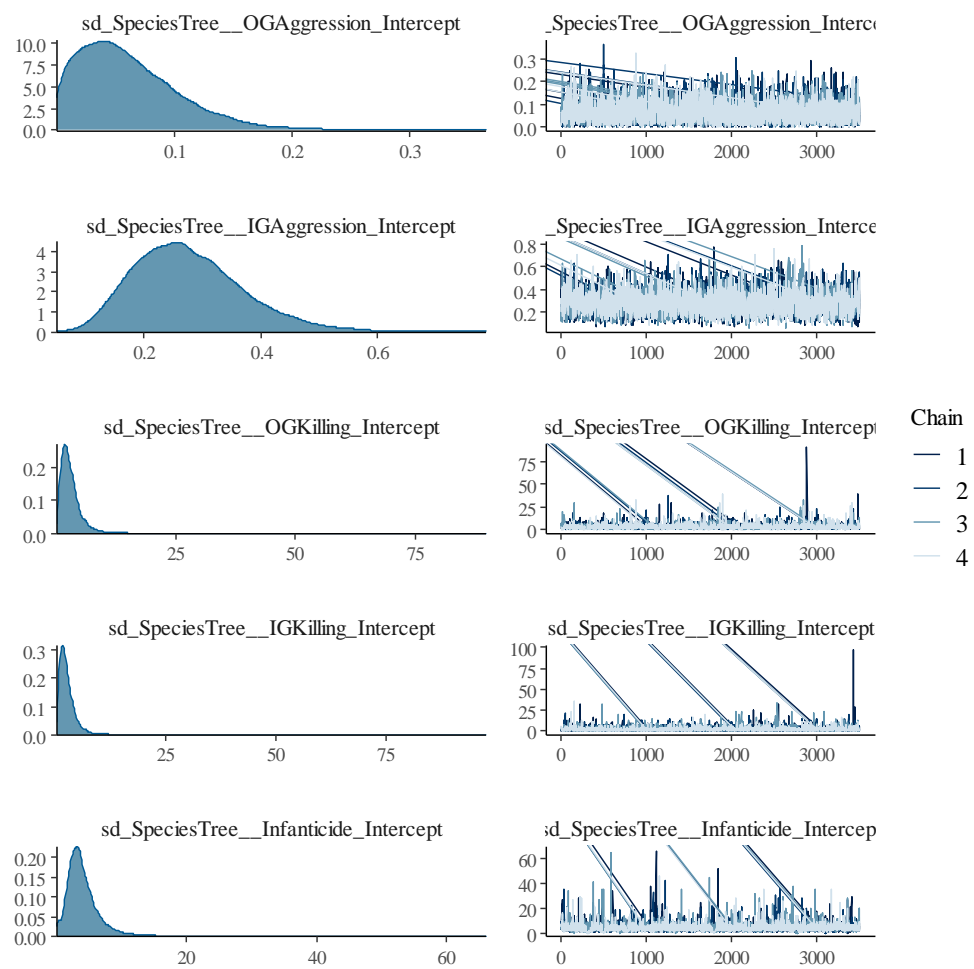
	Estimate	Est.Error	Q2.5	Q97.5
R2OGAggression	0.08319774	0.02851794	0.03434042	0.1468809
R2IGAggression	0.41858869	0.10774373	0.17905246	0.5981241
R2OGKilling	0.71246673	0.15700787	0.34009013	0.9489953
R2IGKilling	0.67925736	0.16574456	0.29778258	0.9390232
R2Infanticide	0.78653639	0.13729915	0.36408703	0.9558268

## Plots - MCMC chains, posterior distributions, and pp checks

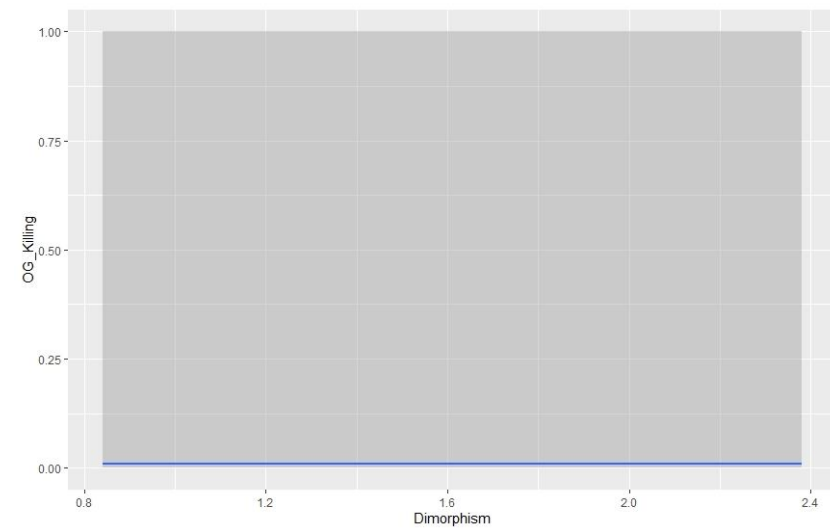
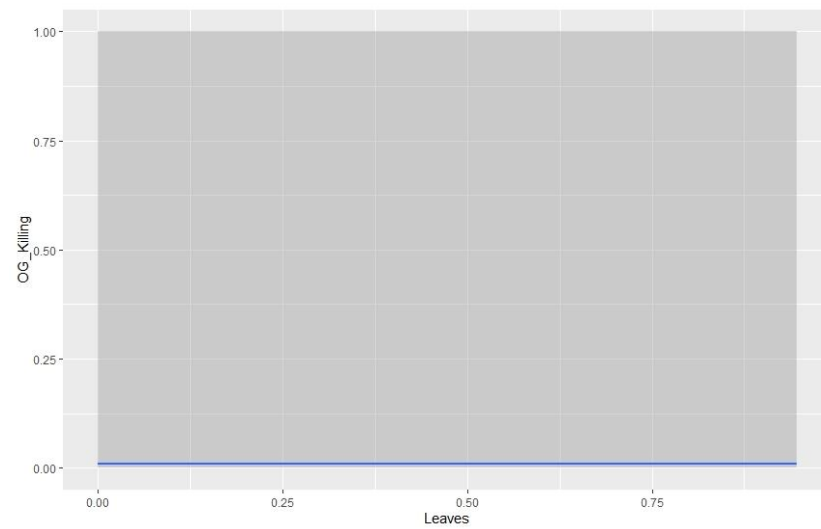
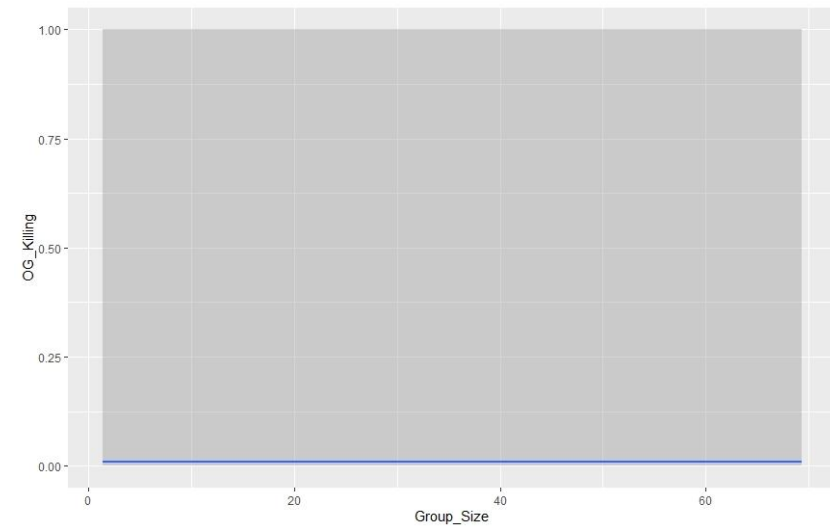
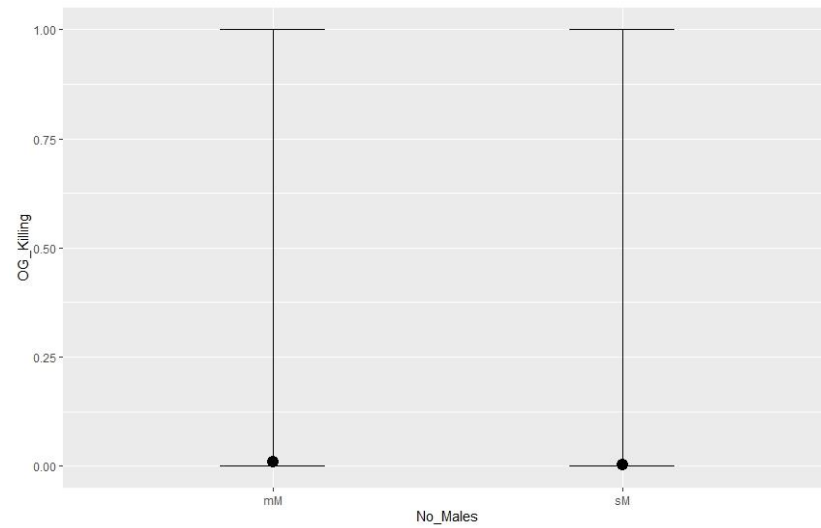




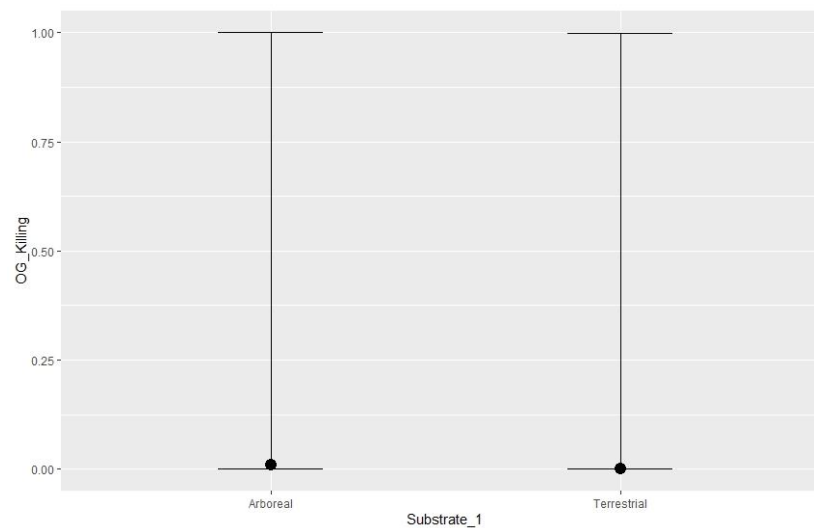
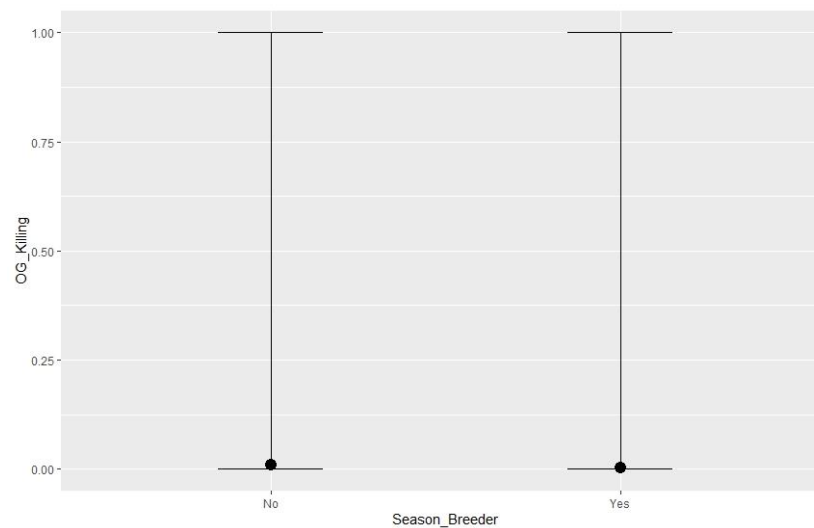
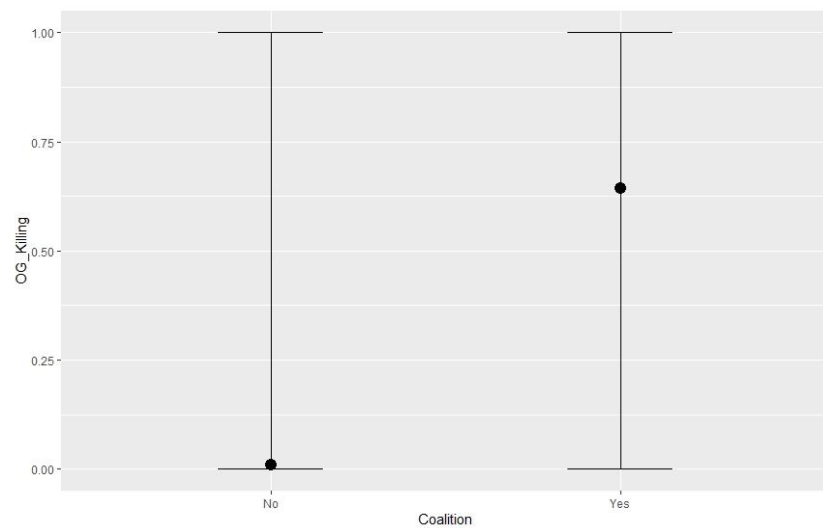
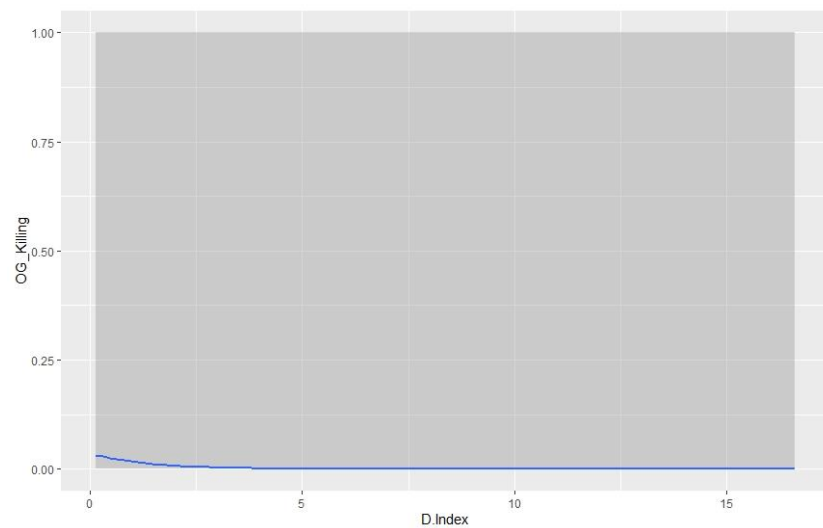


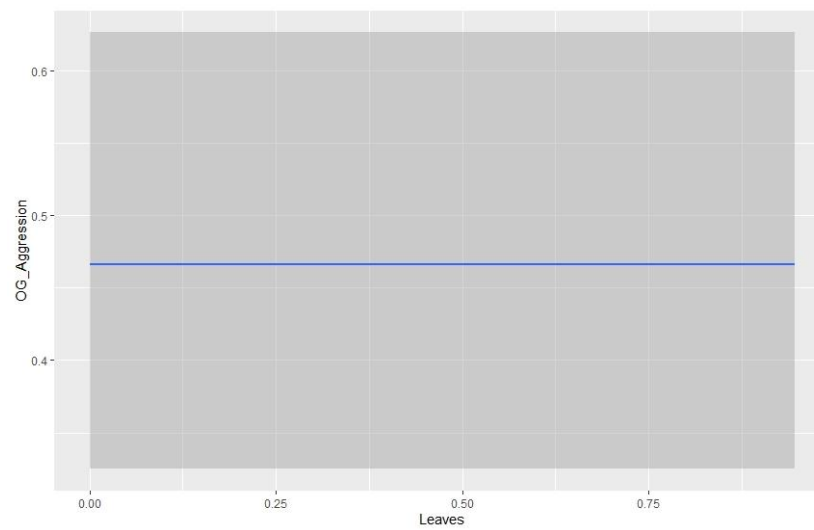
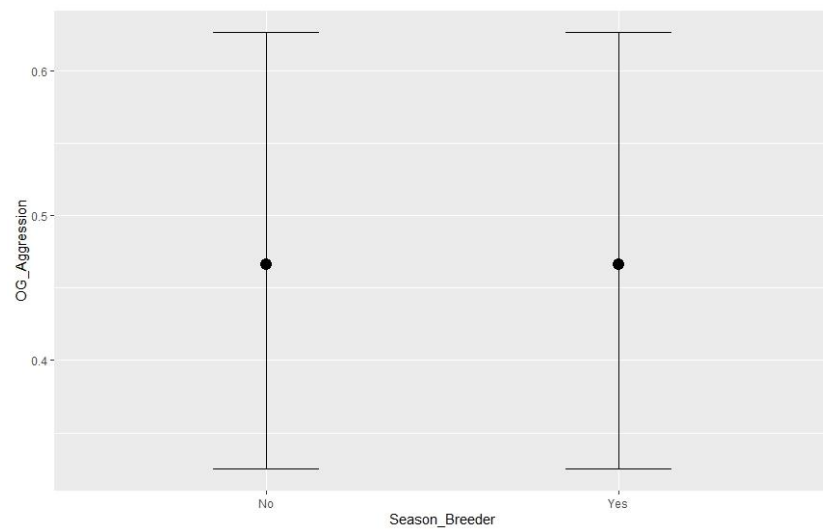
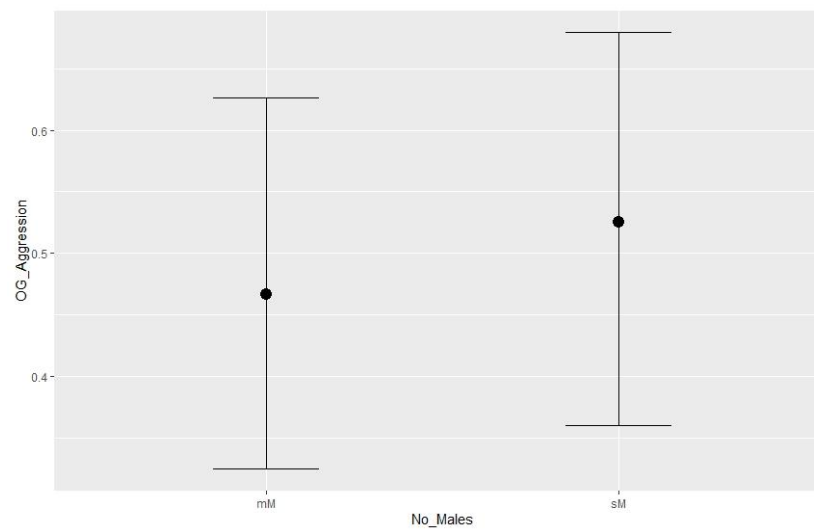
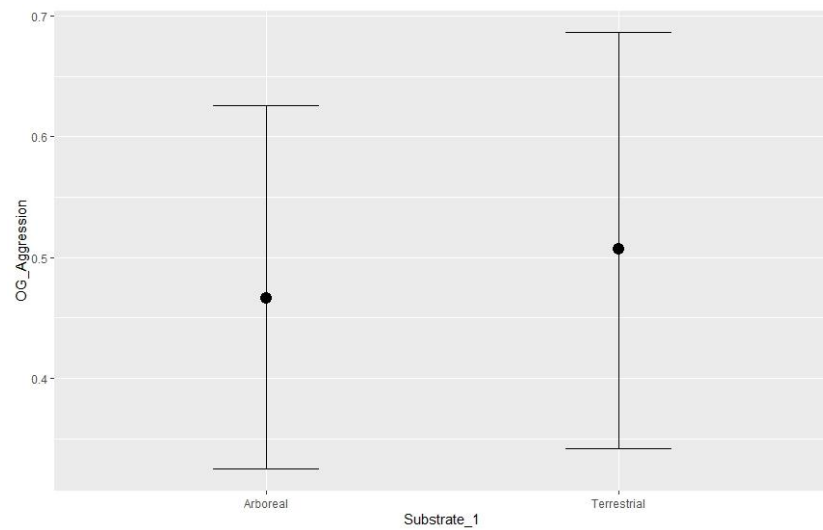


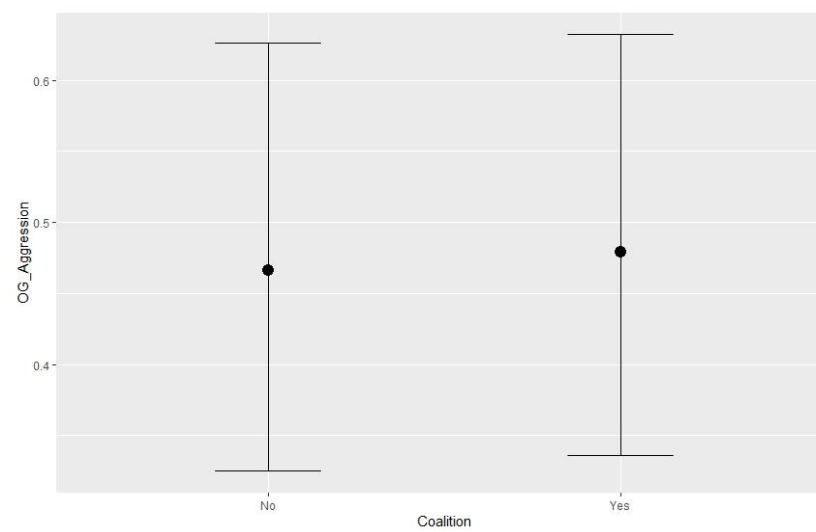
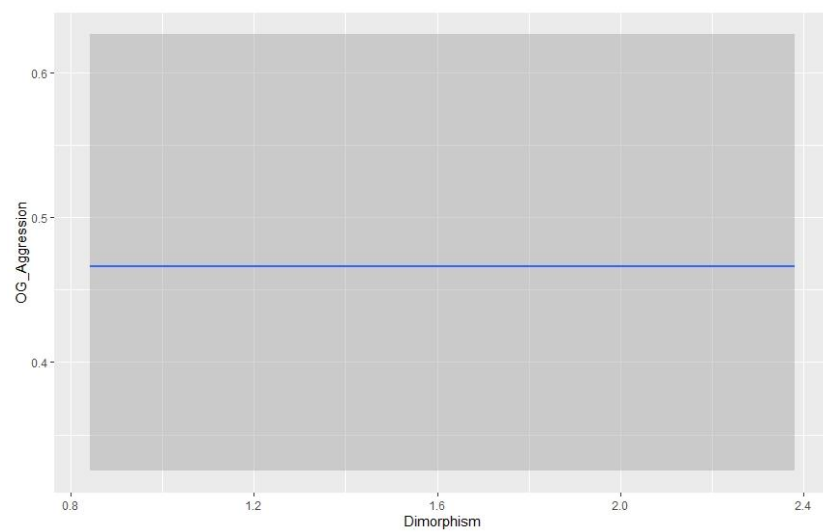
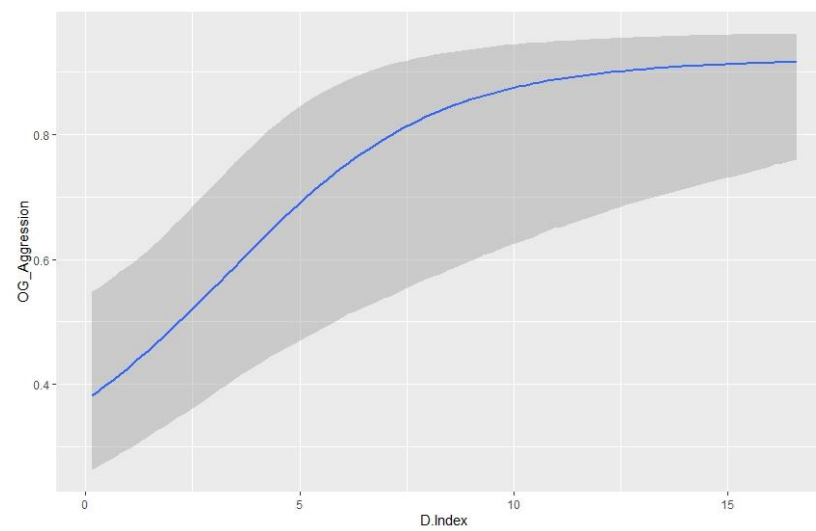
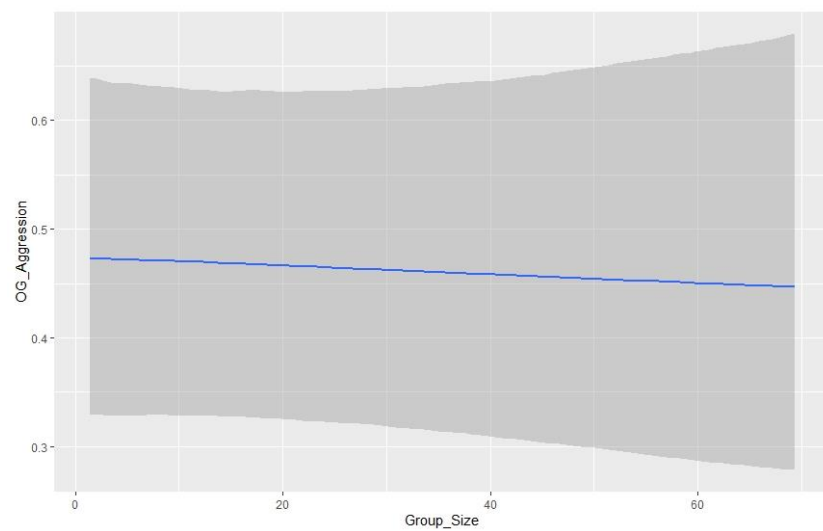
## Appendix 3G – Conditional effects ('Specific' model)

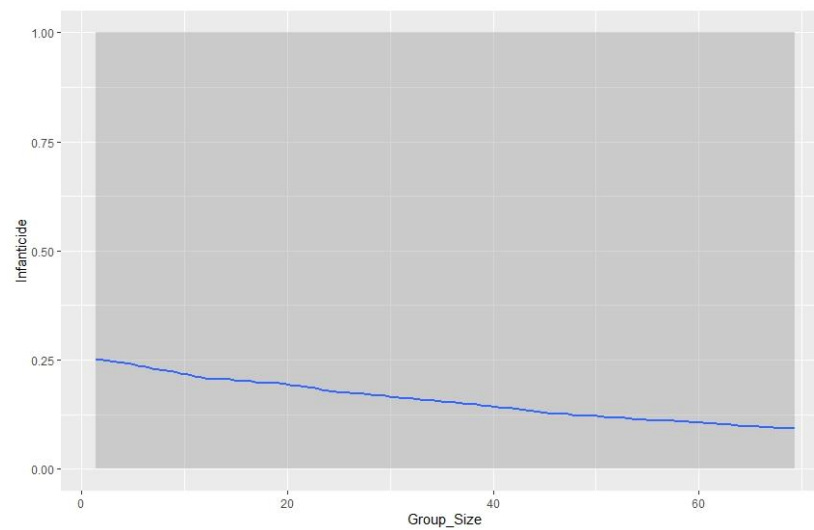
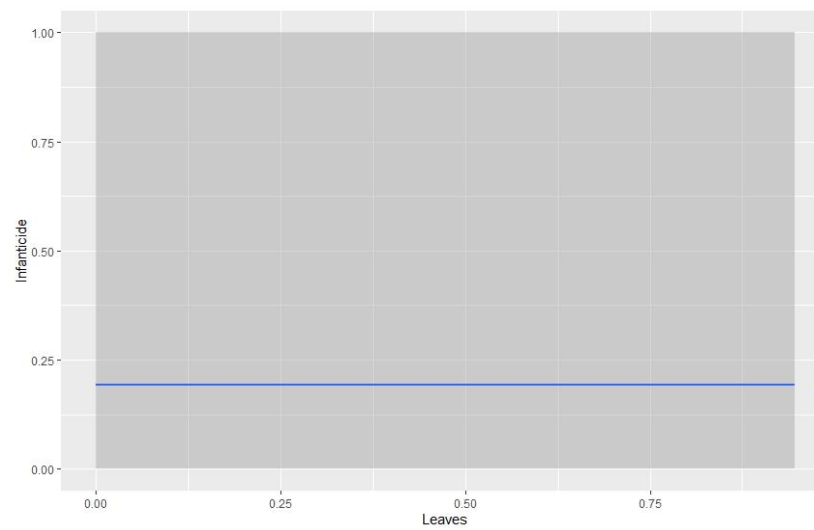
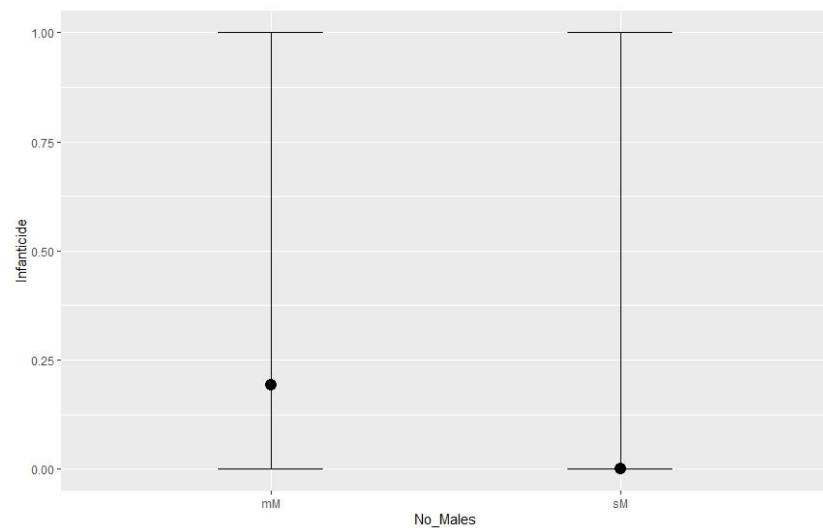
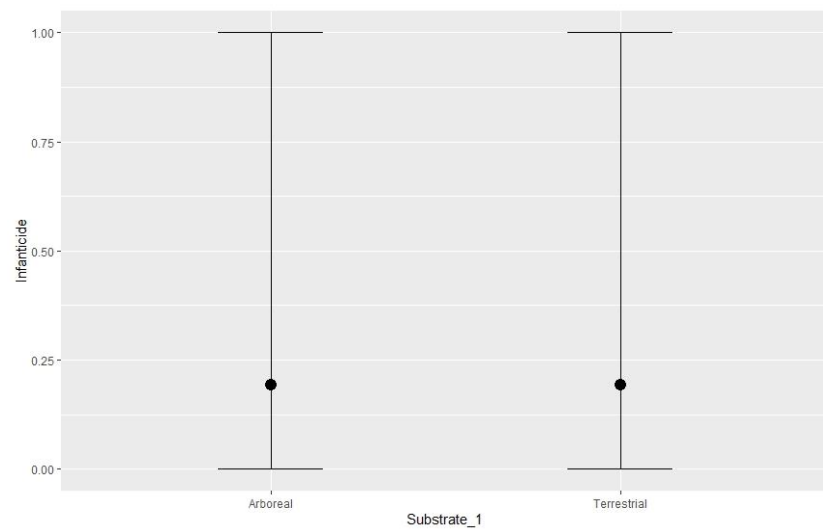


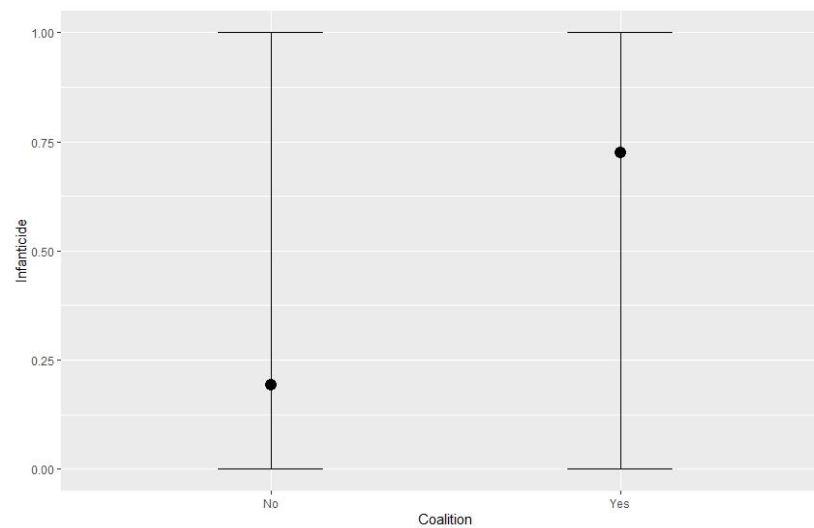
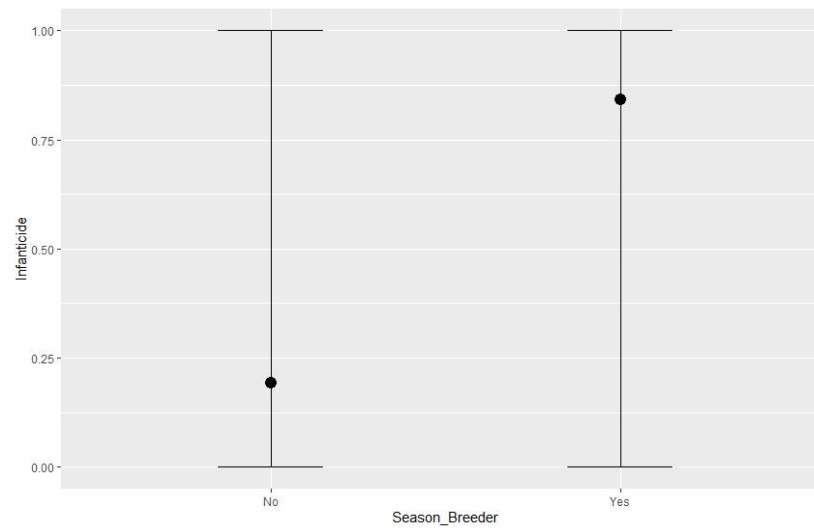
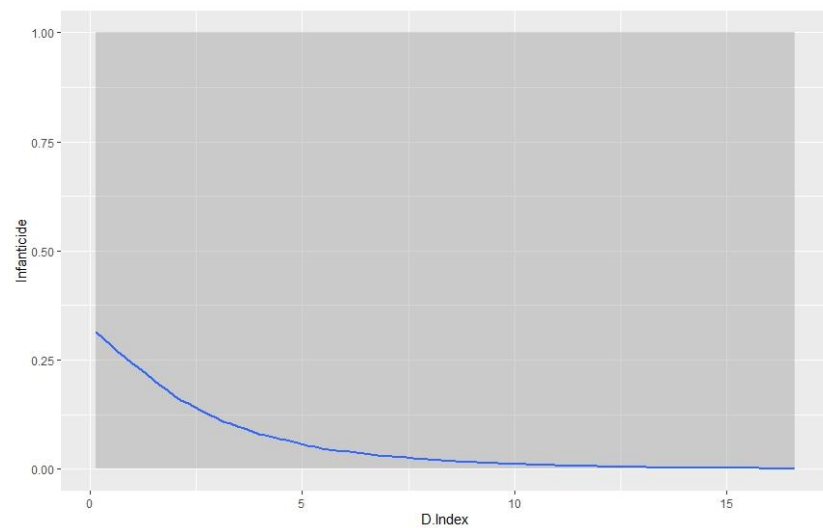
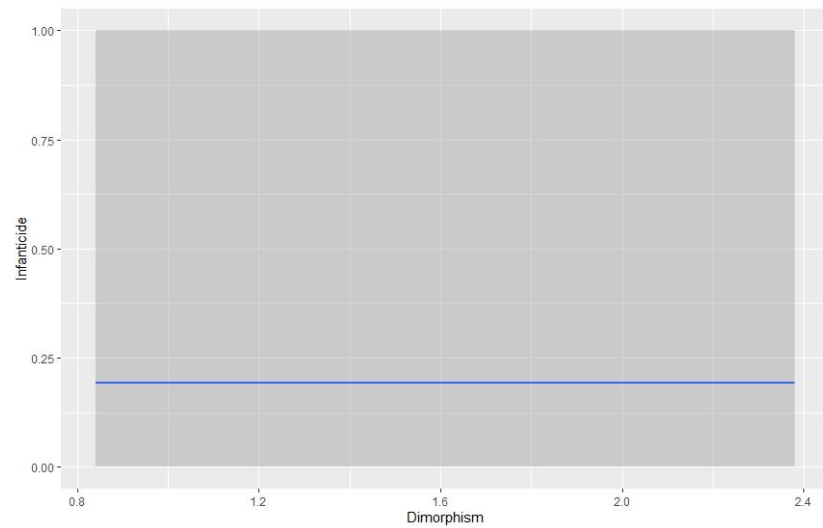


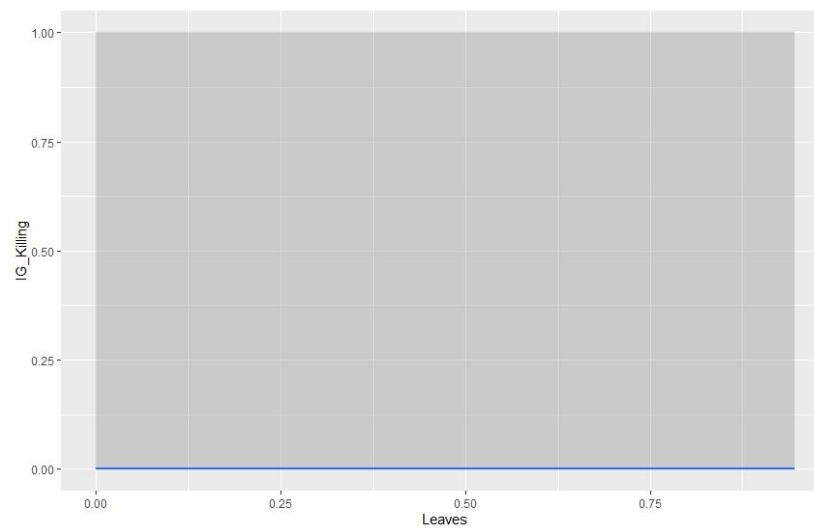
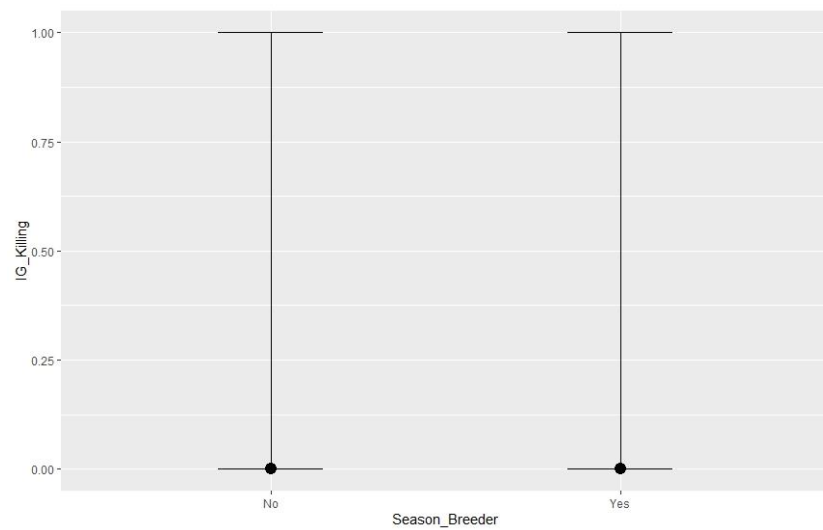
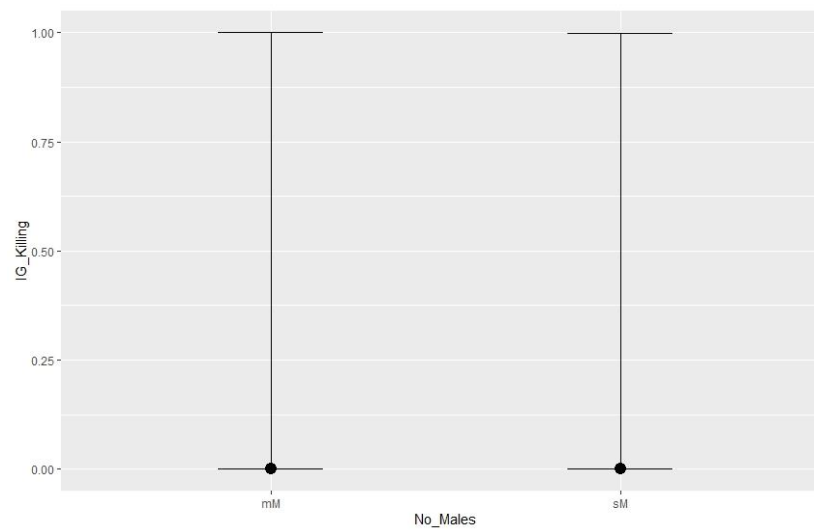
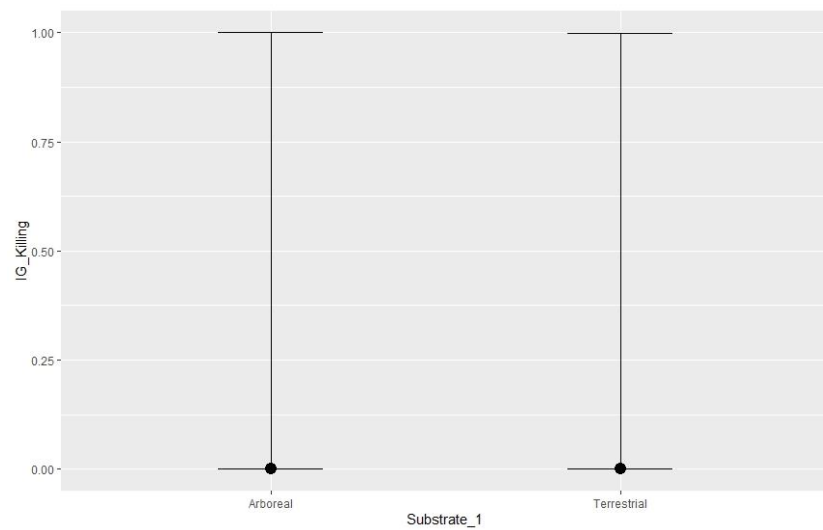


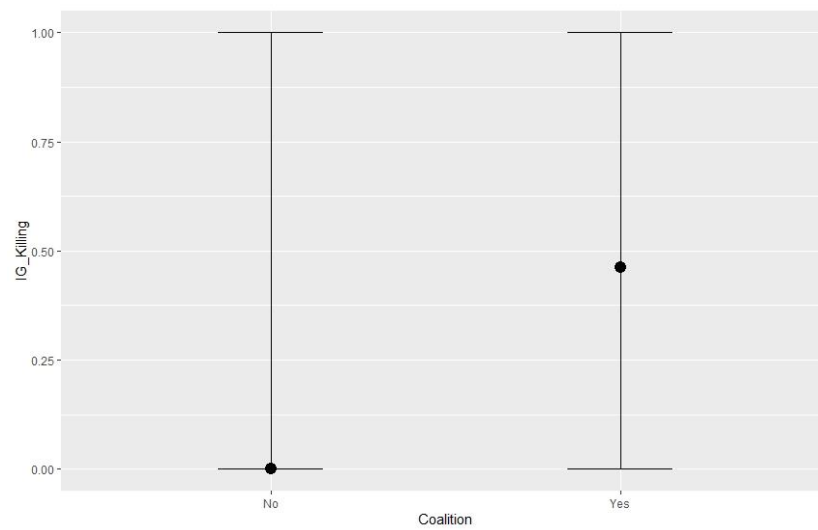
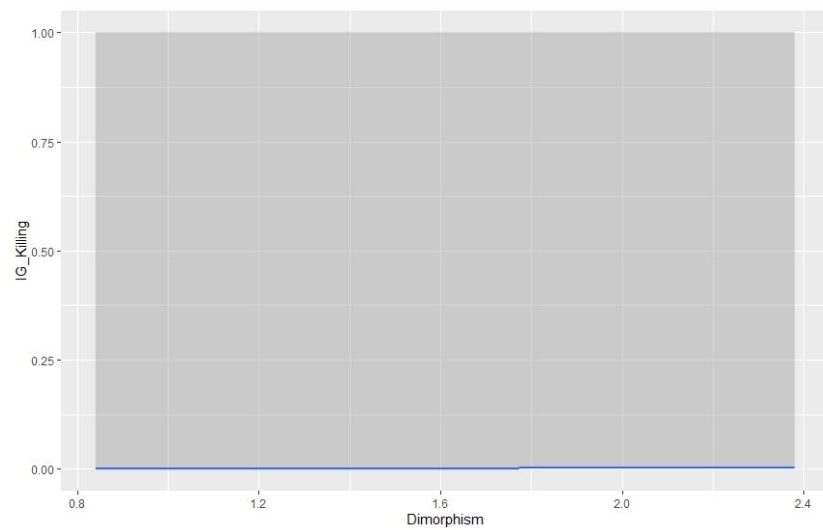
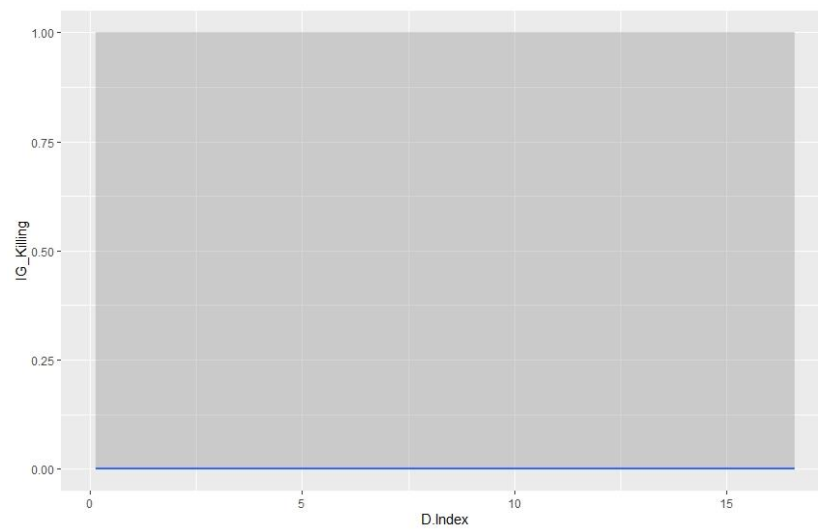
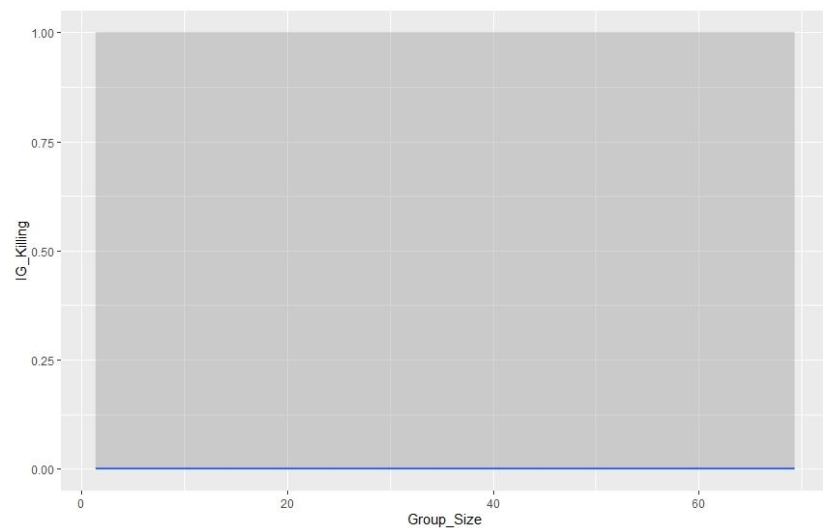


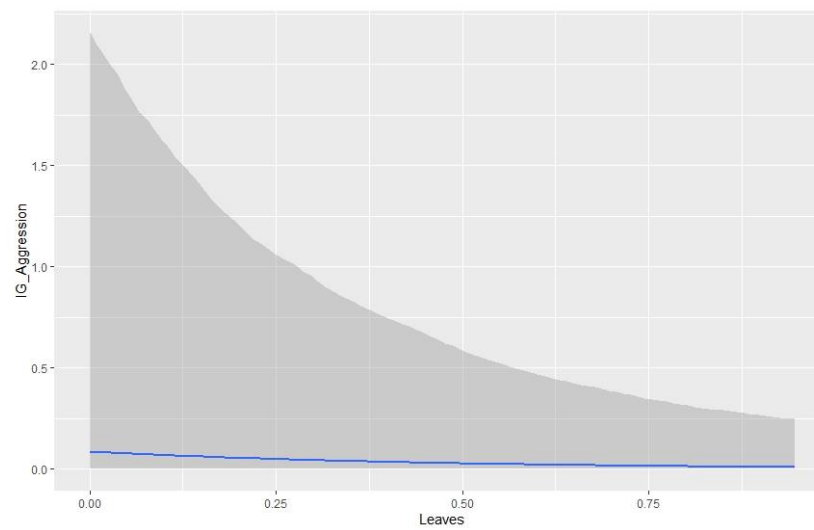
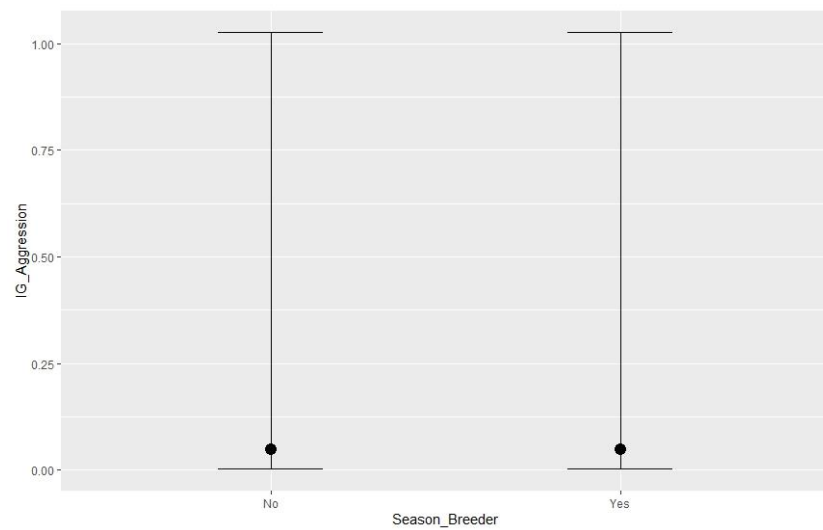
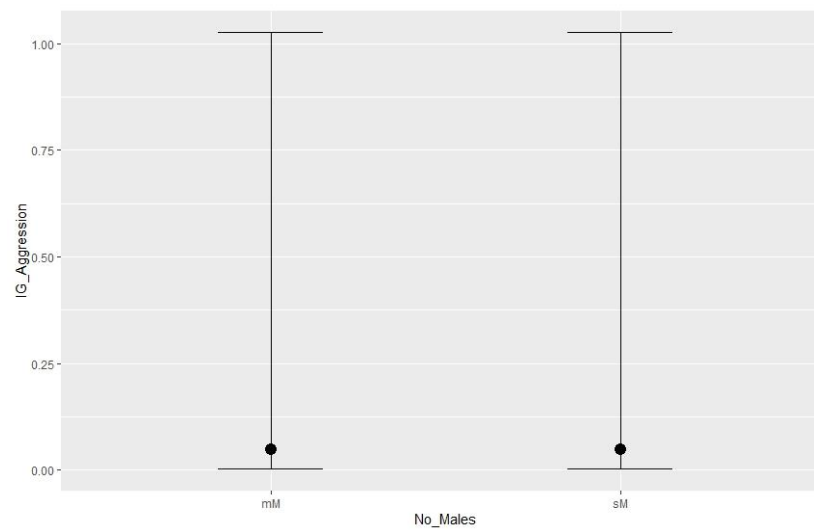
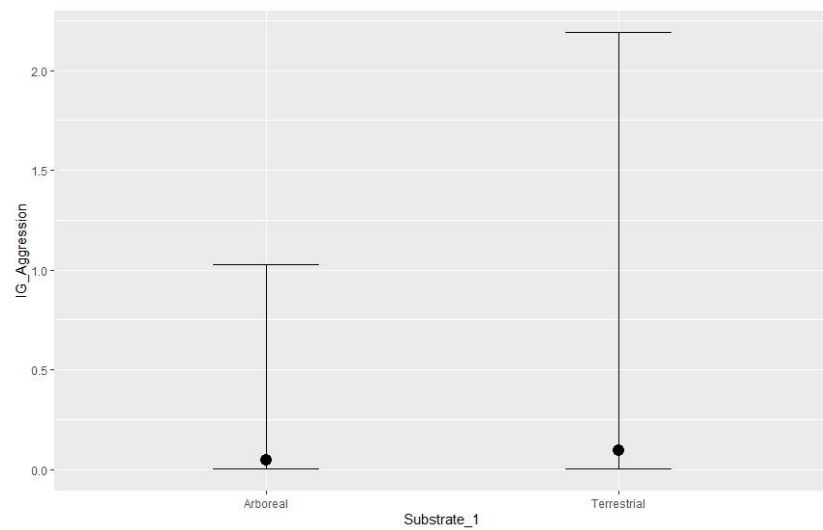




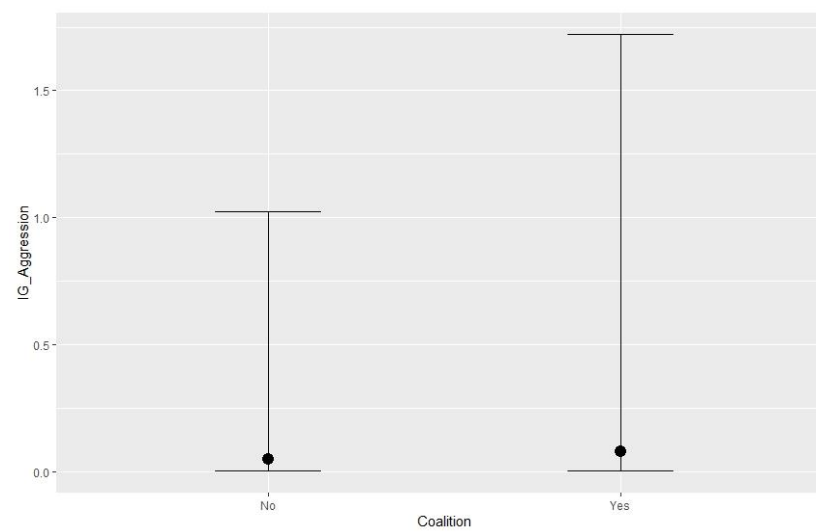
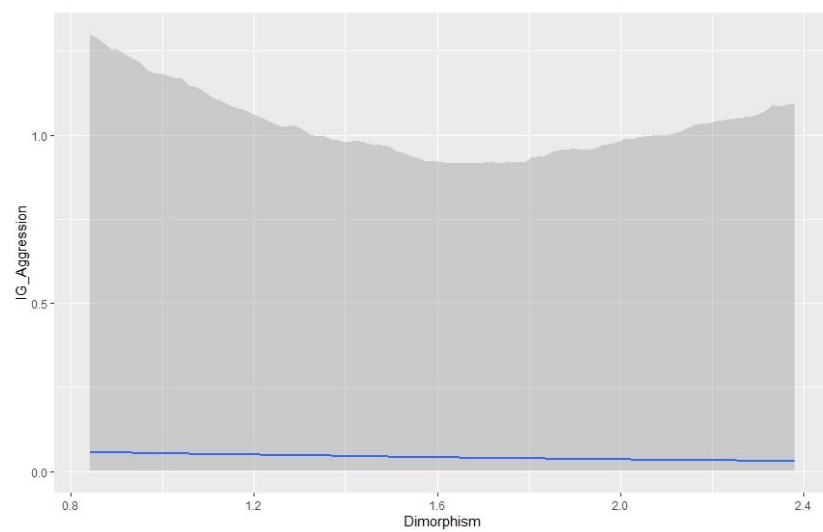
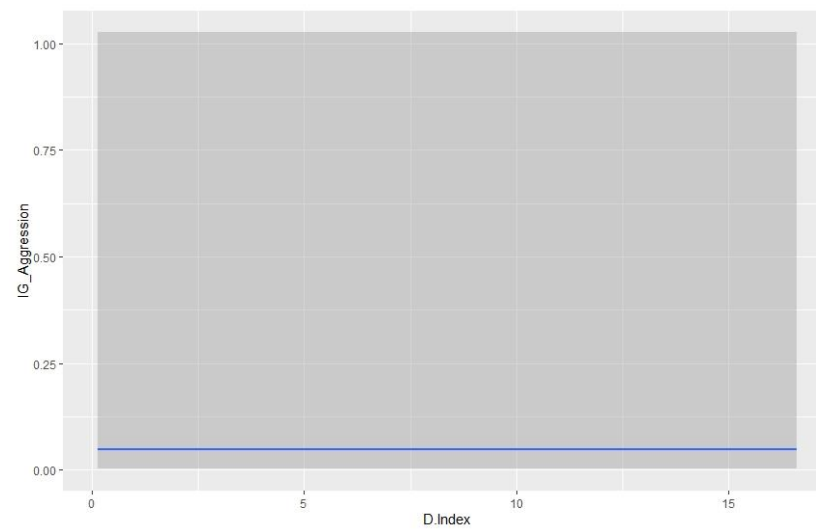
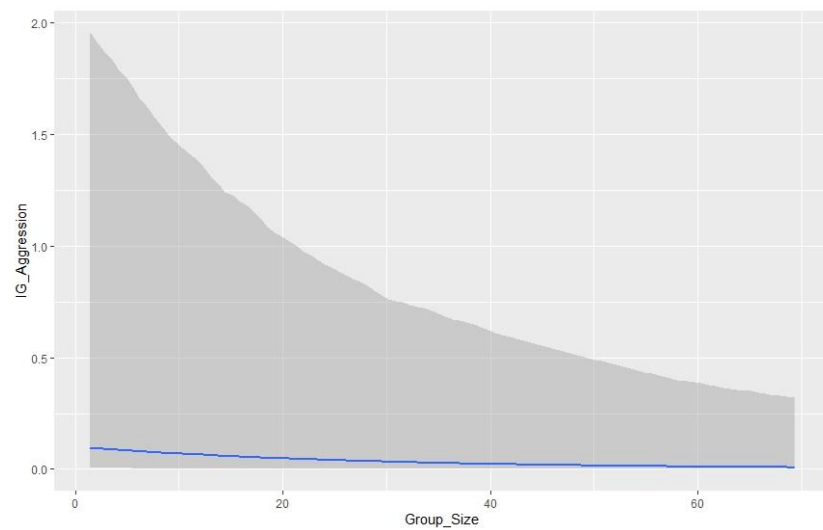












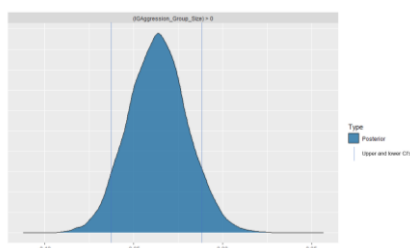
Appendix 3H – Hypothesis testing (class *b*)

```
> hypothesis(ASV, "IGAggression_Leaves < 0", class = "b")
```

	Hypothesis	Estimate	Est.Error	CI.Lower	CI.Upper	Evid.Ratio	Post.Prob	Star
1	(IGAggression_Lea... < 0	-2.32	1.03	-4.03	-0.62	84.37	0.99	*

```
> hypothesis(ASV, "IGAggression_Group_Size < 0", class = "b")
```

	Hypothesis	Estimate	Est.Error	CI.Lower	CI.Upper	Evid.Ratio	Post.Prob	Star
1	(IGAggression_Gro... < 0	-0.04	0.02	-0.06	-0.01	58.57	0.98	*



```
> hypothesis(ASV, "OGAggression_D.Index > 0", class = "b")
```

	Hypothesis	Estimate	Est.Error	CI.Lower	CI.Upper	Evid.Ratio	Post.Prob	Star
1	(OGAggression_D.I... > 0	0.4	0.14	0.17	0.64	410.76	1	*

```
> hypothesis(ASV, "OGKilling_CoalitionYes > 0", class = "b")
```

	Hypothesis	Estimate	Est.Error	CI.Lower	CI.Upper	Evid.Ratio	Post.Prob	Star
1	(OGKilling_Coalit... > 0	5.8	3.16	1.34	11.5	73.47	0.99	*

```
> hypothesis(ASV, "IGKilling_CoalitionYes > 0", class = "b")
```

	Hypothesis	Estimate	Est.Error	CI.Lower	CI.Upper	Evid.Ratio	Post.Prob	Star
1	(IGKilling_Coalit... > 0	6.87	3.39	2	12.83	73.87	0.99	*

- 'CI': 90%-CI for one-sided and 95%-CI for two-sided hypotheses.
- '\*': For one-sided hypotheses, the posterior probability exceeds 95%
- for two-sided hypotheses, the value tested against lies outside the 95%-CI.
- Posterior probabilities of point hypotheses assume equal prior probabilities.
- Evidence ratio can be from 0 to inf.

Appendix 3I – Presence/absence chart

Species	Intergroup adulticide	Intragroup adulticide	Infanticide	No. Males	Season Breeder	Dispersal	Coalition	Substrate	Territorial
Alouatta belzebul	0	0	0	0	0	0			
Alouatta caraya	0	0			0	0			
Alouatta guariba	0	0	0	0	0	0			0
Alouatta palliata		0			0	0			0
Alouatta pigra	0	0			0	0			0
Alouatta seniculus	0				0	0			
Aotus azarae	0	0	0	0		0	0		0
Aotus nigriceps	0	0	0	0		0	0		
Aotus trivirgatus	0	0	0	0		0	0		
Ateles belzebuth	0	0			0				
Ateles chamek	0	0			0				
Ateles geoffroyi	0				0				0
Ateles paniscus	0	0	0		0				
Brachyteles arachoides	0		0						0
Brachyteles hypoxanthus	0	0	0						0
Cacajao calvus	0	0	0						
Cacajao melaocephalus	0	0	0						0
Callicebus nigrifrons	0	0		0		0	0		
Callicebus ornatus	0	0	0	0	0	0	0		
Callicebus personatus	0	0	0	0		0	0		
Callicebus torquatus	0	0	0	0		0	0		
Callimico goeldii	0	0	0			0	0		0
Callithrix jacchus	0	0			0	0	0		
Callithrix kuhlii	0	0	0		0	0	0		
Callithrix penicillata	0	0	0			0			
Cebus imitator					0	0			
Cebus olivaceus		0			0	0			
Cercocebus atys	0	0	0		0	0		0	0
Cercocebus galeritus	0	0	0		0	0	0	0	
Cercocebus torquatus	0	0	0		0	0		0	0

Species	Intergroup adulticide	Intragroup adulticide	Infanticide	No. Males	Season Breeder	Dispersal	Coalition	Substrate	Territorial
Cercopithecus ascanius	0	0		0		0			
Cercopithecus campbelli	0	0		0		0	0		
Cercopithecus diana	0		0	0		0			
Cercopithecus mitis		0		0	0	0			
Chiropotes albinasus	0	0	0				0		
Chiropotes satanas	0	0	0				0		
Chlorocebus pygerythrus	0	0	0		0	0		0	
Chlorocebus sabaues	0	0	0		0	0		0	
Chlorocebus tantalus	0	0	0		0	0	0	0	
Colobus guereza	0	0			0	0	0		0
Colobus polykomos	0	0	0		0	0	0		0
Colobus vellerosus		0			0	0			0
Erythrocebus patas	0	0		0		0		0	
Eulemur fulvus fulvus	0	0				0	0		
Eulemur macaco	0	0				0	0		
Eulemur rubriventer	0	0	0	0		0	0		
Eulemur rufifrons	0	0				0	0		0
Gorilla beringei					0	0		0	0
Gorilla gorilla gorilla		0	0	0	0	0	0	0	0
Hapalemur griseus	0	0	0	0		0	0	1	
Homo sapiens					0	0		0	0
Hoolock hoolock	0	0		0		0	0		
Hylobates albibarbis		0	0	0	0	0			
Hylobates lar	0	0	0	0	0	0	0		
Hylobates moloch	0	0	0	0	0	0	0		
Lemur catta	0	0				0	0	0	
Leontocebus fuscicollis	0	0				0	0		
Leontopithecus rosalia	0	0	0		0	0	0		
Lepilemur ruficaudatus	0	0	0	0		0	0		
Lophocebus albigena	0	0			0	0			0
Macaca arctoides	0	0	0		0	0		0	
Macaca assamensis						0			0

Species	Intergroup adulticide	Intragroup adulticide	Infanticide	No. Males	Season Breeder	Dispersal	Coalition	Substrate	Territorial
Macaca fascicularis			0			0			
Macaca fuscata	0	0				0		0	
Macaca mulatta						0		0	0
Macaca nigra			0		0	0		0	
Macaca radiata	0	0				0		0	
Macaca sinica	0	0	0			0			
Nasalis larvatus	0	0		0	0	0	0		0
Pan paniscus	0	0	0		0			0	0
Pan troglodytes schweinfurthii					0			0	0
Pan troglodytes verus					0			0	0
Papio anubis	0				0	0		0	
Papio cyocephalus	0	0			0	0		0	
Papio ursinus					0	0		0	0
Phaner furcifer	0	0	0	0		0	0	0	
Piliocolobus badius badius	0	0	0		0				
Piliocolobus badius temminckii		0	0			0			
Piliocolobus kirkii	0	0			0	0			0
Piliocolobus tephrosceles	0	0			0	0			0
Pithecia pithecia	0	0	0	0	0	0	0		
Plecturocebus moloch	0	0	0	0		0	0		
Presbytis potenziani	0	0	0	0		0	0		0
Presbytis thomasi		0		0	0	0	0		
Propithecus diadema	0	0		0		0	0		
Propithecus edwardsi	0			0		0	0		0
Propithecus verreauxi		0				0	0		
Rhipithecus bieti	0	0		0	0	0	0	0	0
Saguinus mystax	0	0	0		0	0	0		
Saimiri boliviensis	0	0	0			0			
Saimiri oerstedii	0	0	0				0		
Saimiri sciureus	0	0	0			0			0
Sapajus apella	0		0	0	0	0			
Sapajus nigritus	0				0	0			

Species	Intergroup adulticide	Intragroup adulticide	Infanticide	No. Males	Season Breeder	Dispersal	Coalition	Substrate	Territorial
<i>Semopithecus entellus</i>	0	0		0		0		0	0
<i>Symphalangus syndactylus</i>	0	0	0	0	0	0	0		
<i>Theropithecus gelada</i>					0	0		0	
<i>Trachypithecus cristatus</i>	0	0	0	0	0	0	0		0
<i>Trachypithecus johnii</i>	0	0	0	0	0	0	0		0
<i>Trachypithecus obscurus</i>	0	0	0		0	0	0		0
<i>Varecia variegata</i>	0	0	0			0			0

## APPENDICES – CHAPTER 4

## Appendix 4A – Model scripts

```

library(caper)
library(ggplot2)
library(ggtree)
library(brms)

## Import data
# Phylogeny
file.choose()
tree<-read.nexus("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 4
Dataset\\Q4taxa.nex")
tree$tip.label<- gsub("_", " ", tree$tip.label)

# Species traits
file.choose()
data2b<-read.table("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 4
Dataset\\Q4 data1.txt", header=T, stringsAsFactors=F)
data4$SpeciesTree<- gsub("_", " ", data4$SpeciesTree)

# Check whether species names match, and correct if not
Data4$SpeciesTree %in% tree$tip.label

#Run multivariate model
priorOG <- c(prior(normal(0, 10), class = Intercept, resp = OGGKillingM),
             prior(normal(0, 5), class = b, resp = OGGKillingM),
             prior(normal(0, 10), class = Intercept, resp = OGGKillingF),
             prior(normal(0, 5), class = b, resp = OGGKillingF))

priorIG <- c(prior(normal(0, 10), class = Intercept, resp = IGGKillingM),
             prior(normal(0, 5), class = b, resp = IGGKillingM),
             prior(normal(0, 10), class = Intercept, resp = IGGKillingF),

```

```
prior(normal(0, 5), class = b, resp = IGKillingF))
```

```
priorOG2 <- c(prior(normal(0, 10), class = Intercept, resp = OGKillingM),
  prior(normal(0, 5), class = b, resp = OGKillingM),
  prior(normal(0, 10), class = Intercept, resp = OGKillingF),
  prior(normal(0, 5), class = b, resp = OGKillingF))
```

```
priorIG2 <- c(prior(normal(0, 10), class = Intercept, resp = IGKillingM),
  prior(normal(0, 5), class = b, resp = IGKillingM),
  prior(normal(0, 10), class = Intercept, resp = IGKillingF),
  prior(normal(0, 5), class = b, resp = IGKillingF))
```

```
priorsex <- c(prior(normal(0, 10), class = Intercept, resp = FemaleKilling),
  prior(normal(0, 5), class = b, resp = FemaleKilling),
  prior(normal(0, 10), class = Intercept, resp = MaleKilling),
  prior(normal(0, 5), class = b, resp = MaleKilling))
```

#### *4A.1 Aggression types separated by sex and by sex and type in a phylogenetic only model*

```
fitAgg2bphylo<- brm(mvbind(Male_Killing, Female_Killing, IG_Killing_M, IG_Killing_F,
  OG_Killing_M, OG_Killing_F) ~ 1 + (1|p|gr(SpeciesTree, cov= A)),
  family= list(bernoulli(), bernoulli(), bernoulli(), bernoulli(), bernoulli()),
  bernoulli()),
  prior = priorphylo,
  data= data2b,
  data2= list(A= vcv.phylo(tree)),
  cores = future::availableCores() -1,
  iter= 4e3,
  control= list(adapt_delta= .99, max_treedepth= 15),
  save_pars = save_pars(all = TRUE))
```



*4A.2 Aggression separated only by sex – ‘All’ variables model*

```
fitAgg2bsex<- brm(mvbind(Male_Killing, Female_Killing) ~ No_Males + Leaves +
Season_Breeder + D.Index + Group_Size + Substrate_1 + Dimorphism + Coalition +
(1|p|gr(SpeciesTree, cov= A)),
```

```
family= list(bernoulli(), bernoulli()),

prior = priorsex,

data= data2b,

data2= list(A= vcv.phylo(tree)),

cores = future::availableCores() -1,

iter= 4e3,

control= list(adapt_delta= .99, max_treedepth= 15),

save_pars = save_pars(all = TRUE))
```

*4A.3 Aggression separated by type (intra and inter) and sex (male / female) – ‘All’ variables model*

```
fitAgg2bIG<- brm(mvbind(IG_Killing_M, IG_Killing_F) ~ No_Males + Leaves +
Season_Breeder + D.Index + Group_Size + Substrate_1 + Dimorphism + Coalition +
(1|p|gr(SpeciesTree, cov= A)),
```

```
family= list(bernoulli(), bernoulli()),

prior = priorIG,

data= data2b,

data2= list(A= vcv.phylo(tree)),

cores = future::availableCores() -1,

iter= 4e3,

control= list(adapt_delta= .99, max_treedepth= 15),

save_pars = save_pars(all = TRUE))
```

```
fitAgg2bOG<- brm(mvbind(OG_Killing_M, OG_Killing_F) ~ No_Males + Leaves +
Season_Breeder + D.Index + Group_Size + Substrate_1 + Dimorphism + Coalition +
(1|p|gr(SpeciesTree, cov= A)),
```

```
family= list(bernoulli(), bernoulli()),

prior = priorOG,

data= data2b,

data2= list(A= vcv.phylo(tree)),

cores = future::availableCores() -1,

iter= 4e3,

control= list(adapt_delta= .99, max_treedepth= 15),

save_pars = save_pars(all = TRUE))
```

#### *4A.4 Aggression separated only by sex – ‘Specific’ variables model*

```
fitAgg2bIGx<- brm(mvbind(IG_Killing_M, IG_Killing_F) ~ t2(Leaves, D.Index,
Group_Size, Dimorphism) + (1|p|gr(SpeciesTree, cov= A)),
```

```
family= list(bernoulli(), bernoulli()),

prior = priorIG,

data= data2b,

data2= list(A= vcv.phylo(tree)),

cores = future::availableCores() -1,

iter= 4e3,

control= list(adapt_delta= .99, max_treedepth= 15),

save_pars = save_pars(all = TRUE))
```

*4A.5 Aggression separated by type (intra and inter) and sex (male / female) – ‘Specific’ variables model*

```
bf_OG_Kill_M <- bf(OG_Killing_M ~ D.Index + Season_Breeder + Coalition + No_Males
+ Substrate_1 + (1|p|gr(SpeciesTree, cov= A)), family = bernoulli())
```

```
bf_OG_Kill_F <- bf(OG_Killing_F ~ D.Index + Season_Breeder + Coalition + No_Males +
Substrate_1 + (1|p|gr(SpeciesTree, cov= A)), family = bernoulli())
```

```
bf_IG_Kill_F <- bf(IG_Killing_F ~ Coalition + No_Males + Season_Breeder + Substrate_1
+ Dimorphism + (1|p|gr(SpeciesTree, cov= A)), family = bernoulli())
```

```
bf_IG_Kill_M <- bf(IG_Killing_M ~ Coalition + No_Males + Season_Breeder + Substrate_1
+ Dimorphism + (1|p|gr(SpeciesTree, cov= A)), family = bernoulli())
```

```
fitAgg2bspecOG <- brm(
  bf_OG_Kill_M + bf_OG_Kill_F + set_rescor(FALSE),
  data = data2b,
  prior = priorOG2,
  data2= list(A= vcv.phylo(tree)),
  cores = future::availableCores() -1,
  iter= 4e3,
  control= list(adapt_delta= .99, max_treedepth= 15),
  save_pars = save_pars(all = TRUE))
```

```
fitAgg2bspecIG <- brm(
  bf_IG_Kill_M + bf_IG_Kill_F + set_rescor(FALSE),
  data = data2b,
  prior = priorIG2,
```

```
data2= list(A= vcv.phylo(tree)),  
cores = future::availableCores() -1,  
iter= 6e3,  
control= list(adapt_delta= .99, max_treedepth= 15),  
save_pars = save_pars(all = TRUE))
```

Appendix 4B – Aggression phylogenetic influence (divided by sex only / divided by sex and lethal type)

**> summary(fitAgg2bphylo, waic= T); bayes\_R2(fitAgg2bphylo)**

Family: MV(bernoulli, bernoulli, bernoulli, bernoulli, bernoulli, bernoulli)

Links: mu = logit

mu = logit

mu = logit

mu = logit

mu = logit

mu = logit

Formula: Male\_Killing ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

Female\_Killing ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

IG\_Killing\_M ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

IG\_Killing\_F ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

OG\_Killing\_M ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

OG\_Killing\_F ~ 1 + (1 | p | gr(SpeciesTree, cov = A))

Data: data4 (Number of observations: 101) Samples: 4 chains, each with iter = 4000; warmup = 2000; thin = 1; total post-warmup samples = 8000

Group-Level Effects:

~SpeciesTree (Number of levels: 101)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(MaleKilling_Intercept)	6.96	6.48	2.13	20.20	1.00	5702	4408
sd(FemaleKilling_Intercept)	5.71	5.33	1.46	17.12	1.00	7152	5637
sd(IGKillingM_Intercept)	5.25	4.69	1.30	15.91	1.00	4432	4508
sd(IGKillingF_Intercept)	4.12	3.87	0.83	12.87	1.00	5820	5111
sd(OGKillingM_Intercept)	6.29	5.27	1.79	18.82	1.00	5759	4865
sd(OGKillingF_Intercept)	4.83	4.39	1.16	14.52	1.00	6550	6331
cor(MaleKilling_Intercept,FemaleKilling_Intercept)	0.65	0.14	0.33	0.88	1.00	2827	4231
cor(MaleKilling_Intercept,IGKillingM_Intercept)	0.81	0.09	0.59	0.95	1.00	3271	4974
cor(FemaleKilling_Intercept,IGKillingM_Intercept)	0.54	0.16	0.19	0.81	1.00	3554	4668
cor(MaleKilling_Intercept,IGKillingF_Intercept)	0.47	0.20	0.05	0.80	1.00	3551	4562

cor(FemaleKilling_Intercept,IGKillingF_Intercept)	0.77	0.13	0.46	0.95	1.00	5080	6078
cor(IGKillingM_Intercept,IGKillingF_Intercept)	0.56	0.19	0.13	0.86	1.00	4784	5996
cor(MaleKilling_Intercept,OGKillingM_Intercept)	0.92	0.05	0.80	0.98	1.00	4131	5212
cor(FemaleKilling_Intercept,OGKillingM_Intercept)	0.66	0.14	0.32	0.89	1.00	3328	5151
cor(IGKillingM_Intercept,OGKillingM_Intercept)	0.65	0.13	0.36	0.86	1.00	4591	5055
cor(IGKillingF_Intercept,OGKillingM_Intercept)	0.41	0.20	-0.02	0.76	1.00	4258	5717
cor(MaleKilling_Intercept,OGKillingF_Intercept)	0.71	0.14	0.37	0.92	1.00	3454	4898
cor(FemaleKilling_Intercept,OGKillingF_Intercept)	0.85	0.09	0.62	0.97	1.00	5301	6231
cor(IGKillingM_Intercept,OGKillingF_Intercept)	0.51	0.18	0.13	0.80	1.00	5481	6380
cor(IGKillingF_Intercept,OGKillingF_Intercept)	0.59	0.17	0.20	0.87	1.00	6696	6120
cor(OGKillingM_Intercept,OGKillingF_Intercept)	0.76	0.13	0.43	0.95	1.00	4927	6216

## Population-Level Effects:

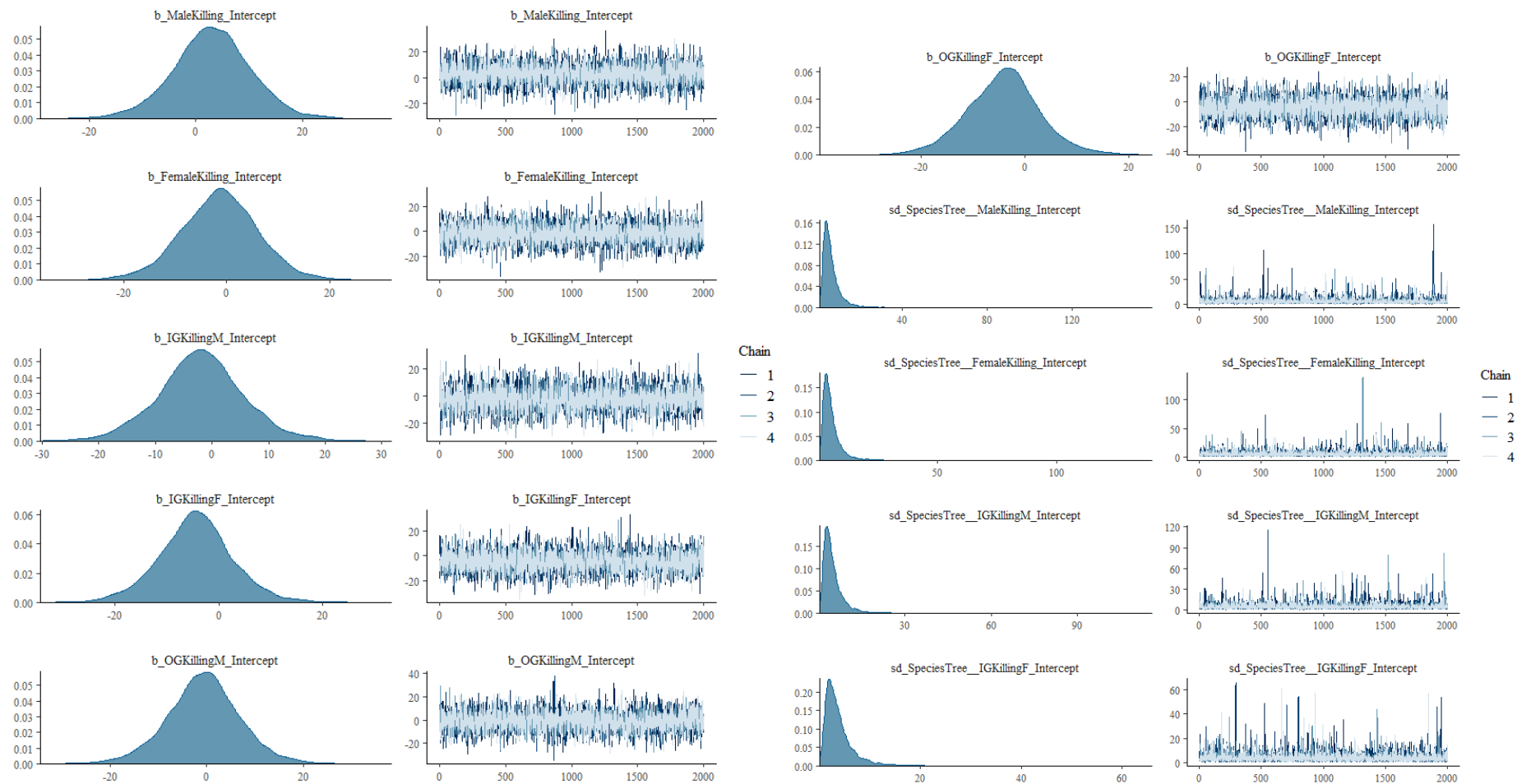
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
MaleKilling_Intercept	2.98	7.38	-12.08	17.37	1.00	4672	5571
FemaleKilling_Intercept	-1.41	7.49	-16.62	13.18	1.00	5893	6145

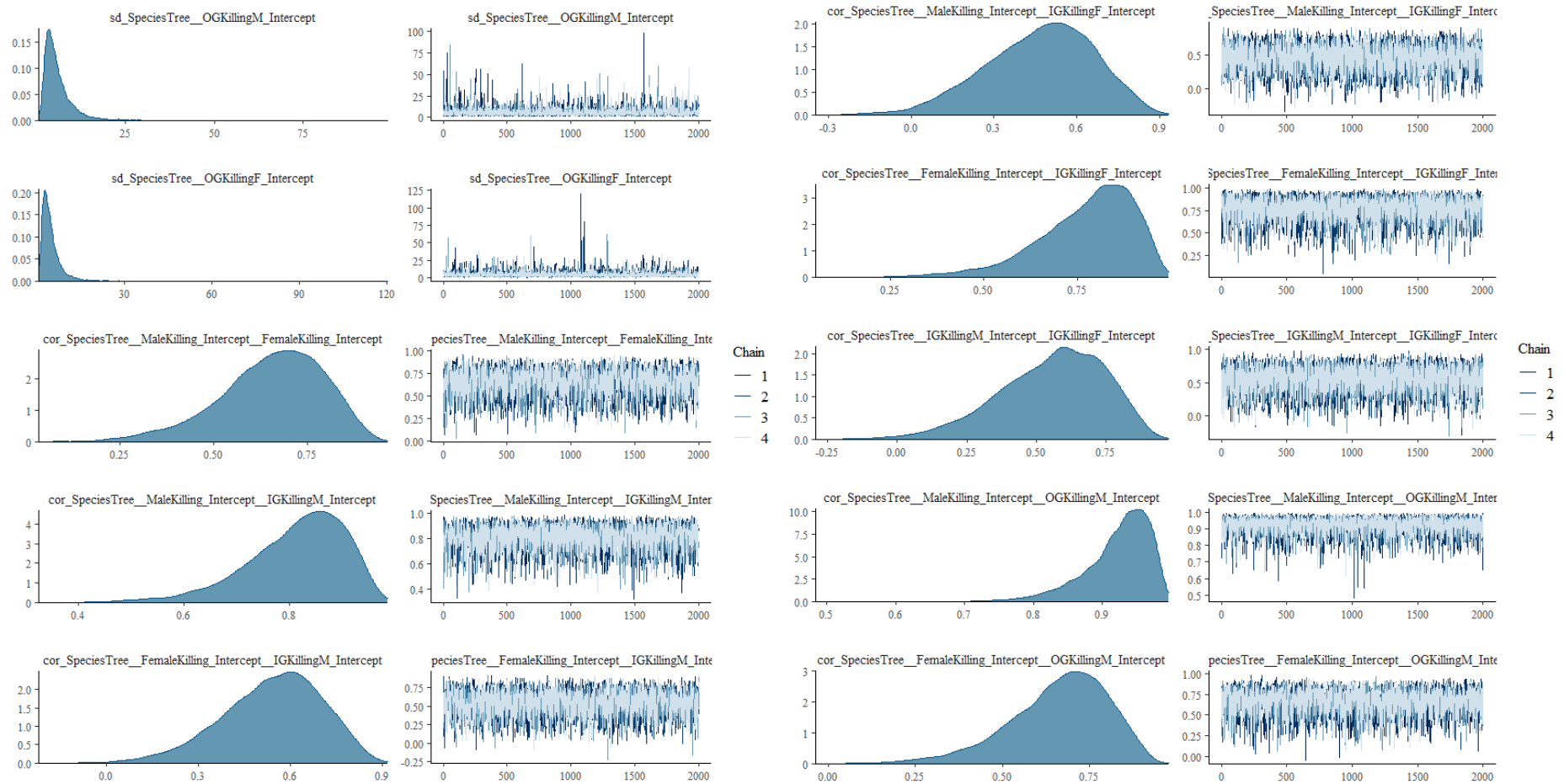
IGKillingM_Intercept	-1.94	7.68	-17.06	14.04	1.00	5268	5699
IGKillingF_Intercept	-4.38	7.26	-19.12	10.35	1.00	5582	5670
OGKillingM_Intercept	-0.63	7.55	-15.90	14.50	1.00	5750	5838
OGKillingF_Intercept	-4.12	7.12	-18.49	10.40	1.00	5878	5306

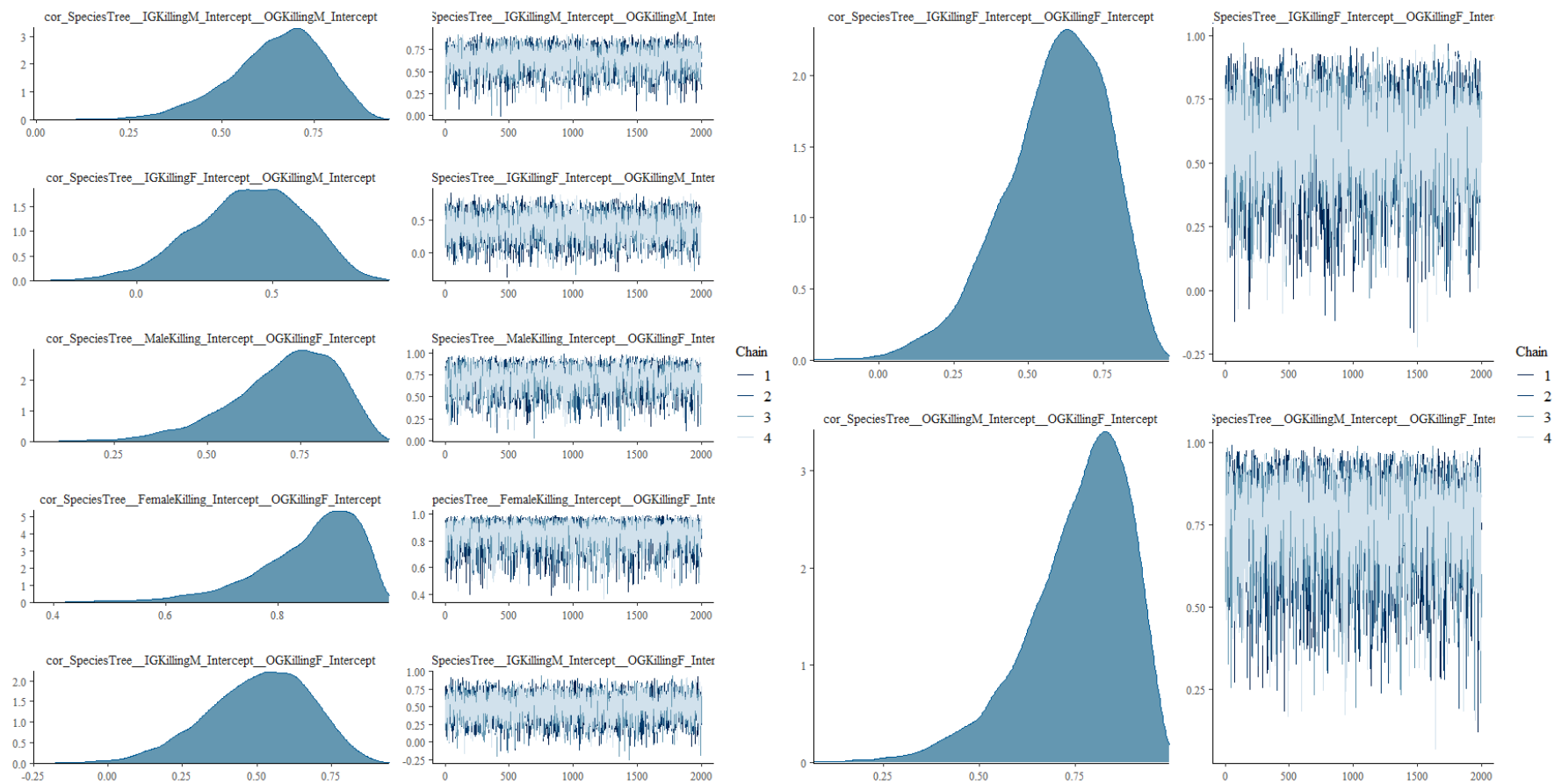
Samples were drawn using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
R2MaleKilling	0.9248736	0.05162856	0.8016845	0.9976209
R2FemaleKilling	0.8619079	0.10447345	0.6130206	0.9981697
R2IGKillingM	0.8501980	0.10206971	0.6034916	0.9923606
R2IGKillingF	0.7313508	0.19549862	0.2423661	0.9969589
R2OGKillingM	0.8880961	0.07454821	0.7140847	0.9955686
R2OGKillingF	0.7990046	0.14601301	0.4403832	0.9967403









## Appendix 4C - Intergroup Lethal Violence Model – separated by sex

```
> summary(fitAggression2b, waic= T); bayes_R2(fitAggression2b)
```

Family: MV(bernoulli, bernoulli)

Links: mu = logit

mu = logit

Formula: OG\_Killing\_F ~ No\_Males + Leaves + Season\_Breeder + D.Index + Group\_Size + Substrate\_1 + Dimorphism + Coalition + (1 | p |  
gr(SpeciesTree, cov = A))

OG\_Killing\_M ~ No\_Males + Leaves + Season\_Breeder + D.Index + Group\_Size + Substrate\_1 + Dimorphism + Coalition + (1 | p |  
gr(SpeciesTree, cov = A))

Data: data4 (Number of observations: 101)

Samples: 4 chains, each with iter = 4000; warmup = 2000; thin = 1; total post-warmup samples = 8000

Group-Level Effects:

~SpeciesTree (Number of levels: 101)

Estimate Est.Error l-95% CI u-95% CI Rhat Bulk\_ESS Tail\_ESS

sd(OGKillingF_Intercept)	8.50	8.51	1.98	29.89	1.00	2971	3106
sd(OGKillingM_Intercept)	8.59	9.30	2.22	31.08	1.00	1537	860
cor(OGKillingF_Intercept,OGKillingM_Intercept)	0.93	0.08	0.72	1.00	1.00	1626	2653

## Population-Level Effects:

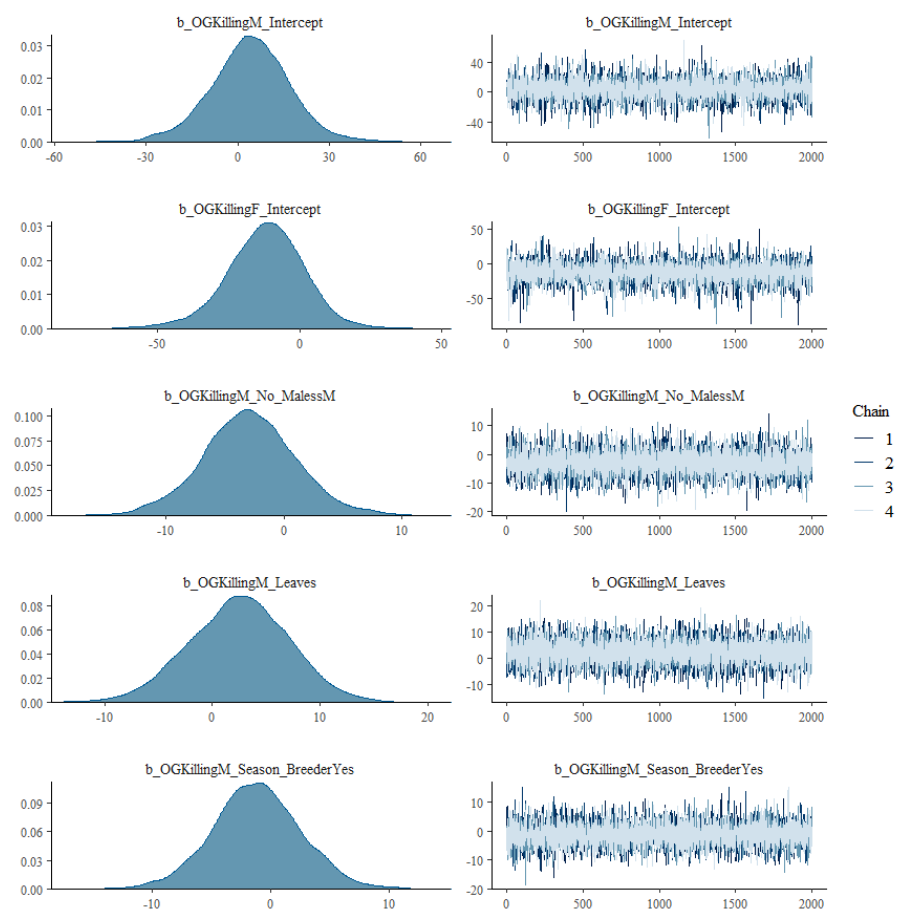
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGKillingF_Intercept	-11.89	13.96	-40.35	15.07	1.00	5191	4483
OGKillingM_Intercept	3.64	14.03	-24.37	30.40	1.00	2293	1379
OGKillingF_No_MalessM	-1.32	4.24	-9.84	6.72	1.00	8451	6417
OGKillingF_Leaves	-0.00	4.54	-8.84	8.72	1.00	11164	5920
OGKillingF_Season_BreederYes	2.31	3.93	-5.74	10.06	1.00	7036	5654
OGKillingF_D.Index	-0.14	2.94	-6.37	5.90	1.00	5113	4903
OGKillingF_Group_Size	0.31	0.36	-0.14	1.22	1.00	2902	2863
OGKillingF_Substrate_1Terrestrial	0.04	4.11	-8.11	8.25	1.00	6849	5448
OGKillingF_Dimorphism	-2.46	4.46	-11.28	6.43	1.00	8268	6103
OGKillingF_CoalitionYes	4.22	4.57	-4.95	13.08	1.00	7656	4820

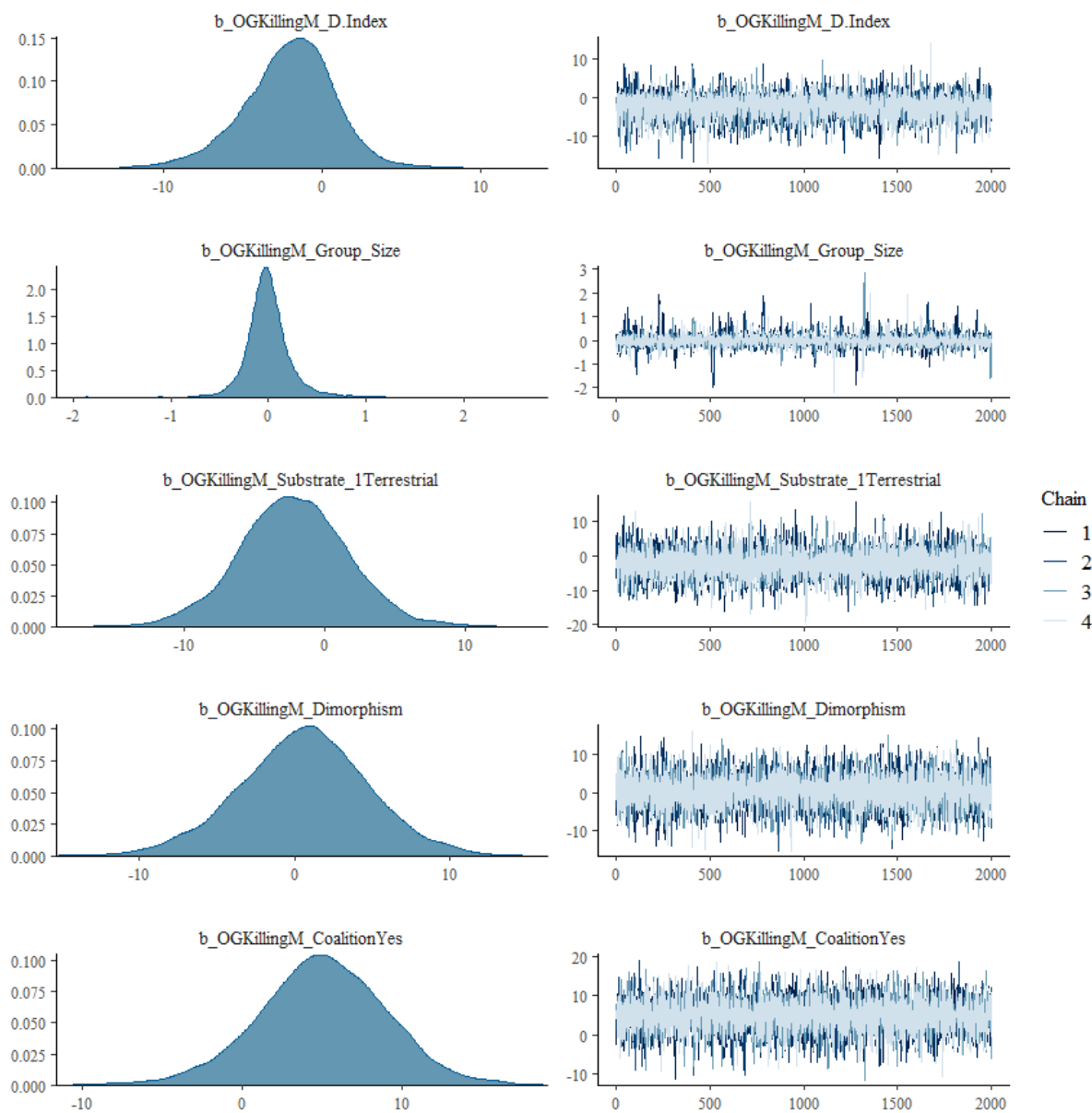
OGKillingM_No_MalessM	-2.93	3.95	-10.80	4.99	1.00	6083	5069
OGKillingM_Leaves	2.54	4.62	-6.90	11.54	1.00	8665	5566
OGKillingM_Season_BreederYes	-1.10	3.76	-8.43	6.63	1.00	6384	5076
OGKillingM_D.Index	-2.07	2.98	-8.56	3.40	1.00	5519	4538
OGKillingM_Group_Size	0.02	0.34	-0.44	0.70	1.01	1639	888
OGKillingM_Substrate_1Terrestrial	-2.19	3.86	-9.87	5.67	1.00	6365	5512
OGKillingM_Dimorphism	0.63	4.16	-7.65	8.60	1.00	9186	6978
OGKillingM_CoalitionYes	5.07	4.02	-3.17	12.84	1.00	5646	4643

Samples were drawn using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
R2OGKillingF	0.832841	0.12521013	0.5432076	0.9993459
R2OGKillingM	0.884720	0.07717845	0.7081095	0.9965471

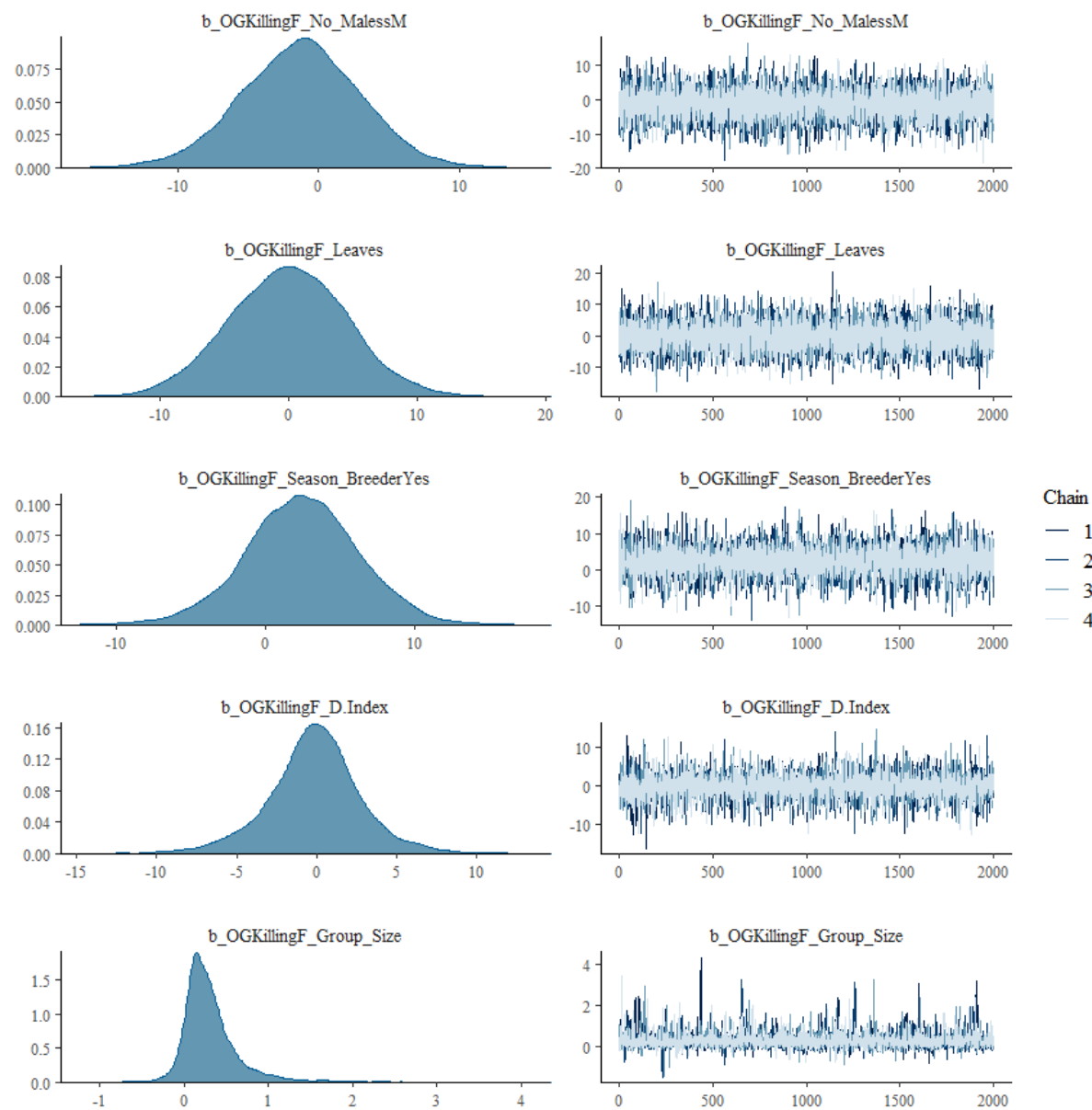
## Intergroup lethal aggression 'all' plots



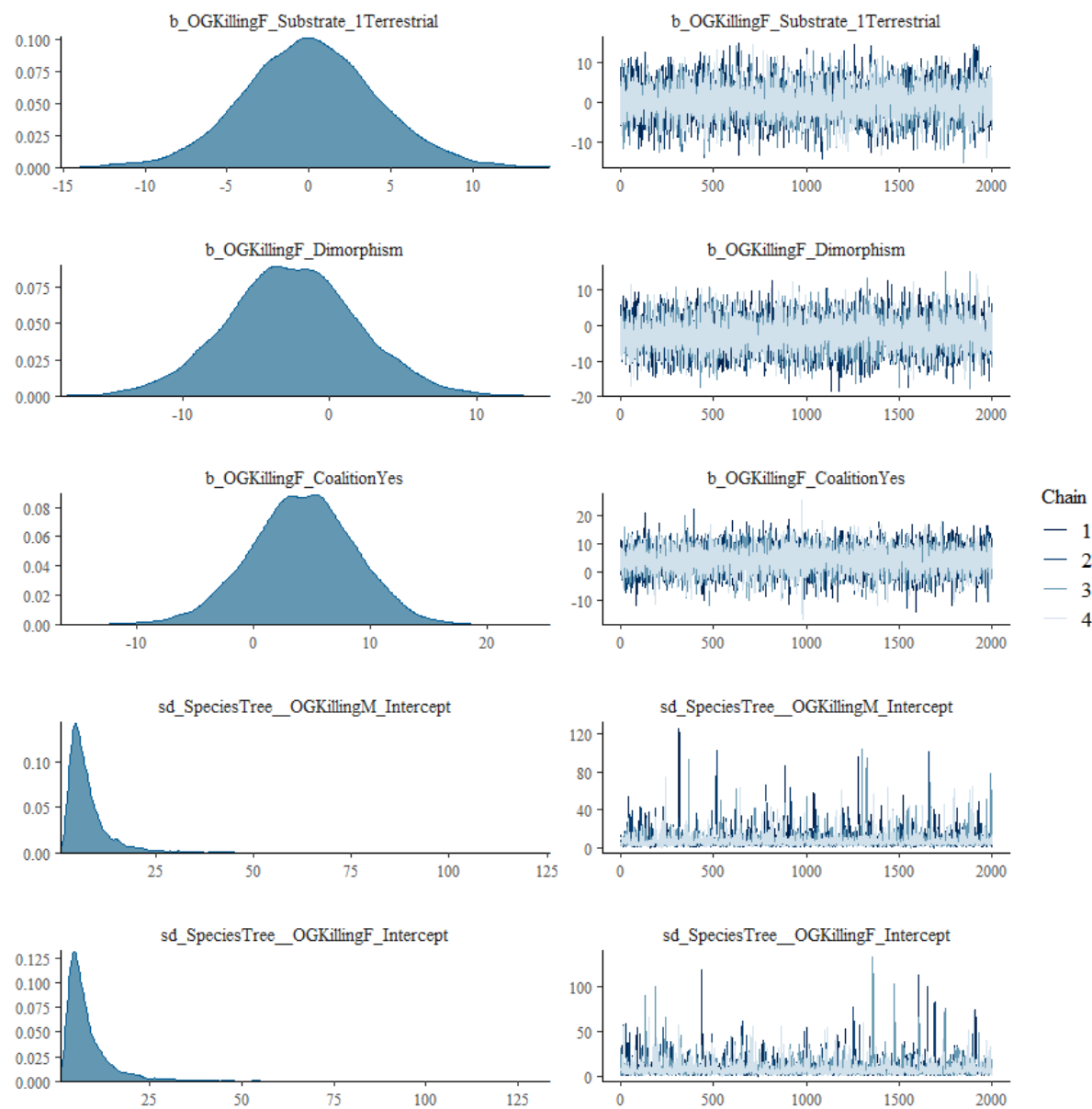




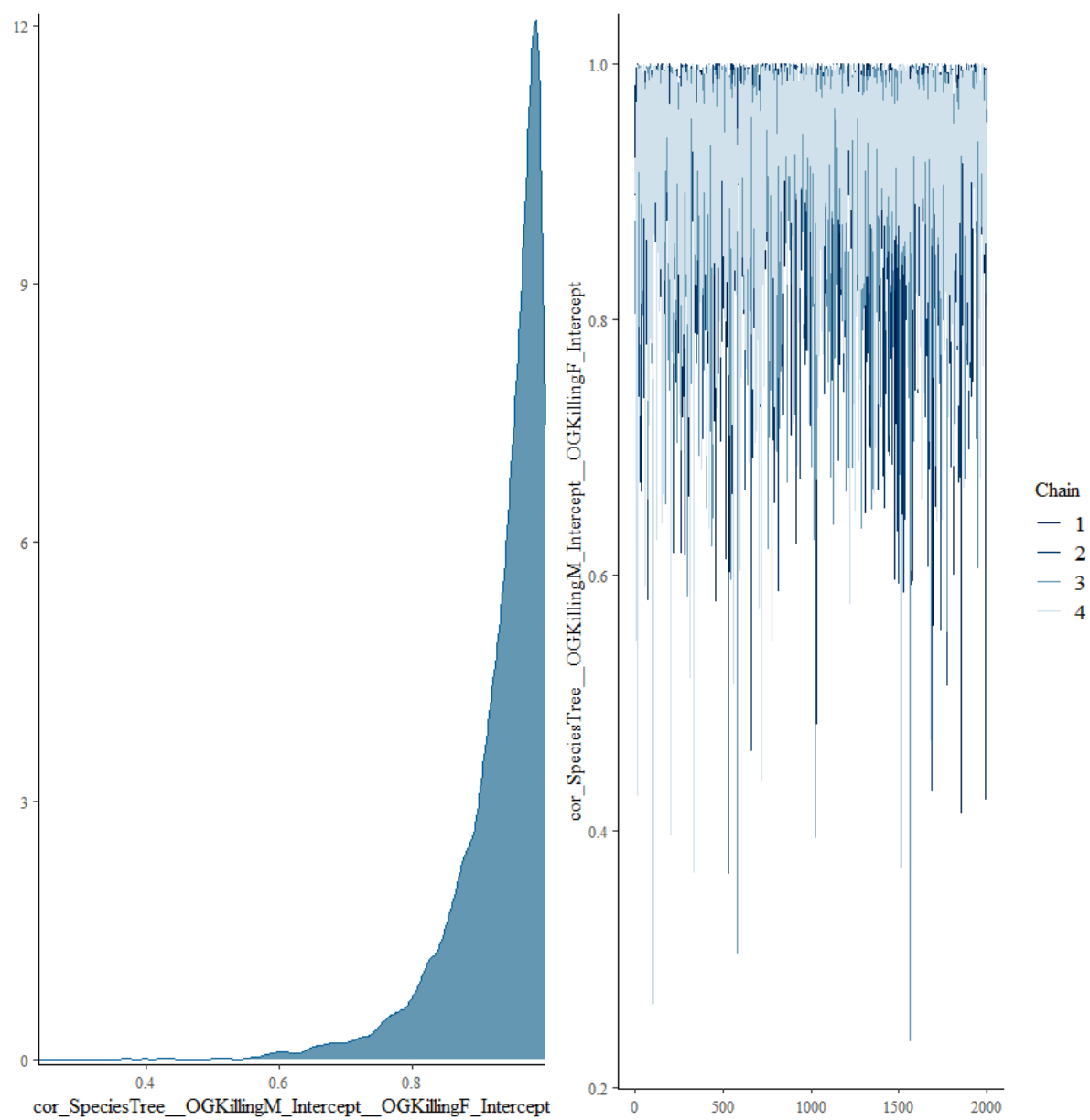




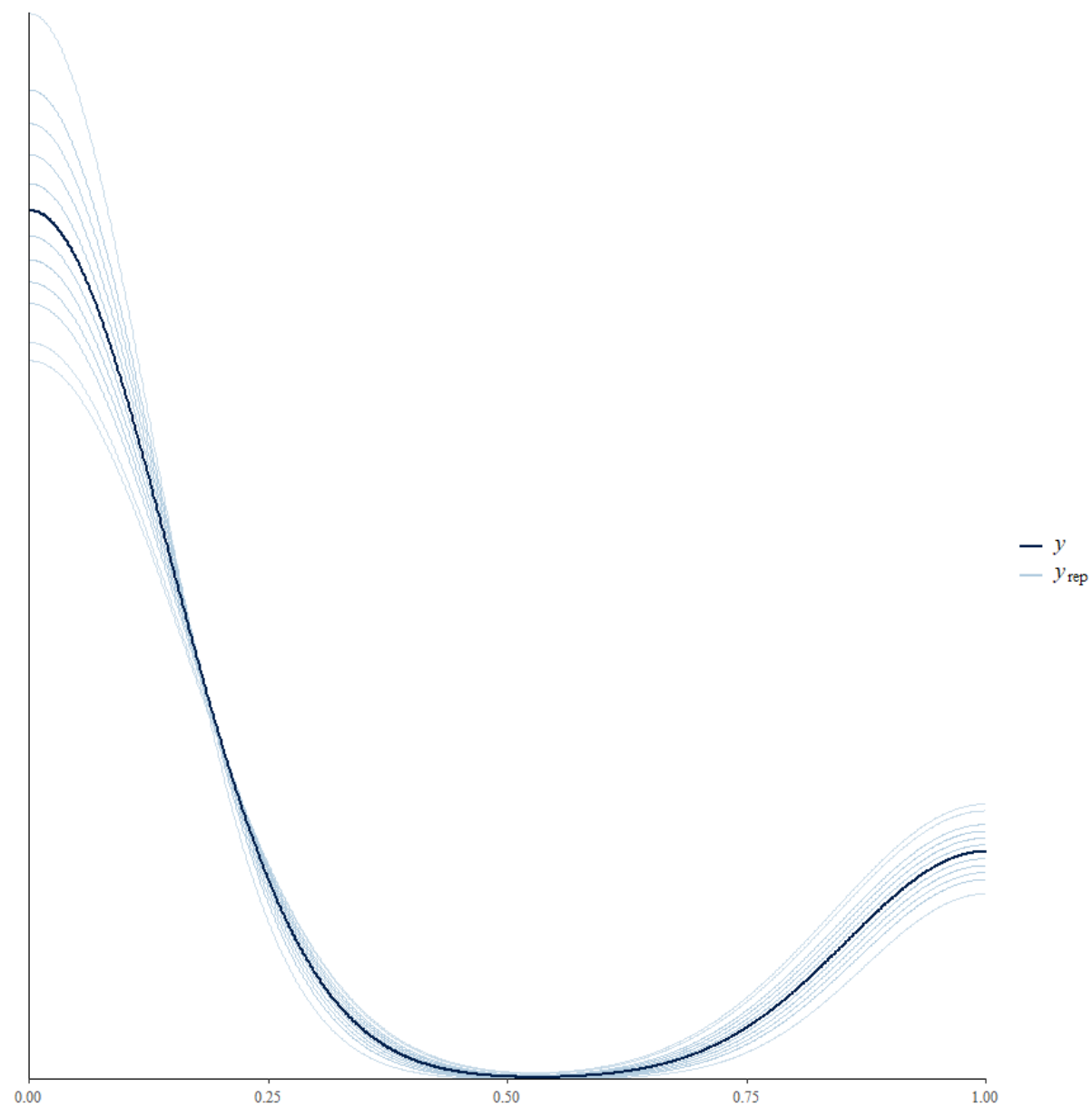






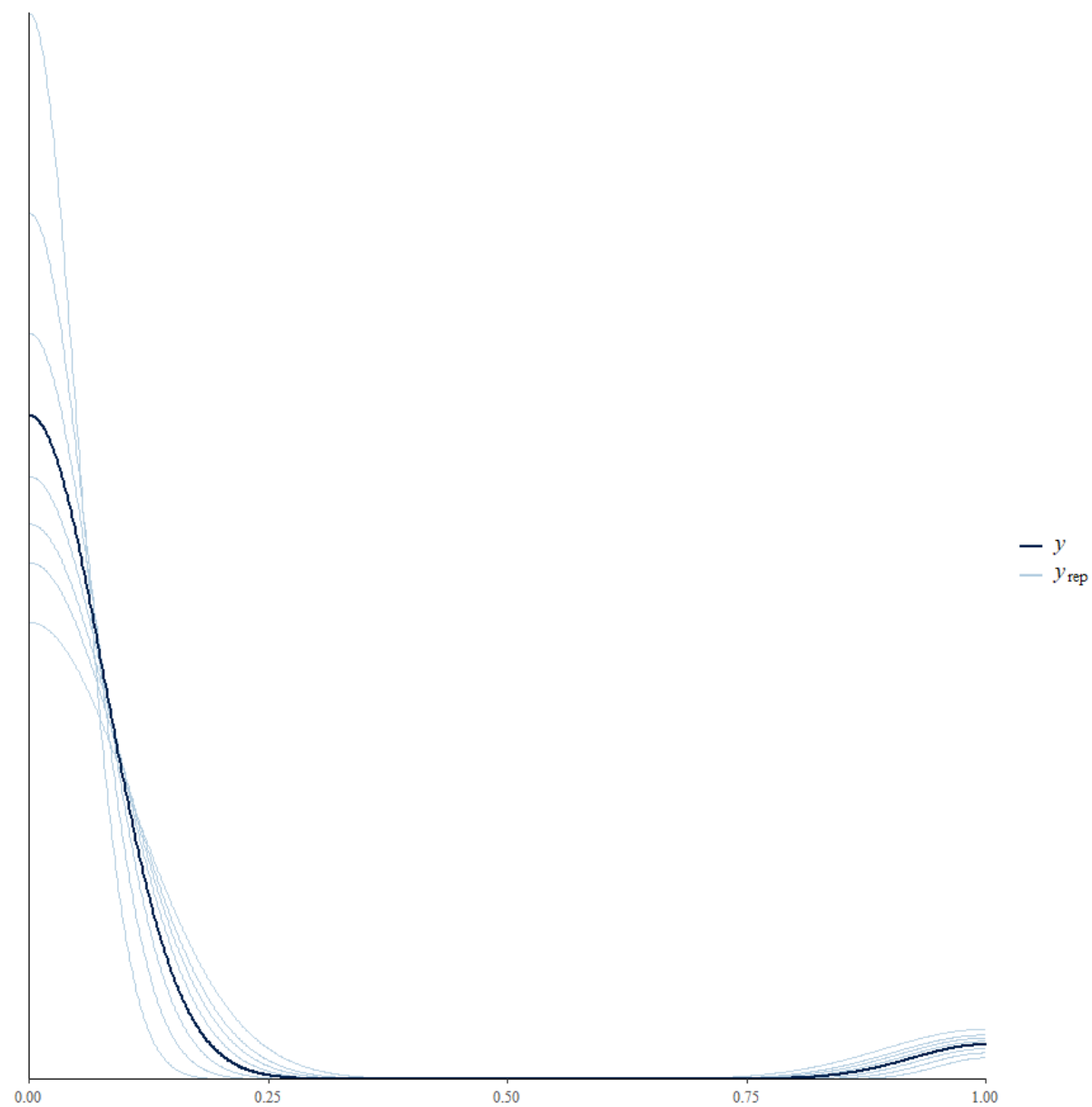








PP check Intergroup Lethal Aggression (Males)



PP check Intragroup Lethal Aggression (Females)

## Appendix 4D - Intragroup Lethal Violence Model – separated by sex

```
> summary(fitAgg2bIG, waic= T); bayes_R2(fitAgg2bIG)
```

Family: MV(bernoulli, bernoulli)

Links: mu = logit

mu = logit

Formula: IG\_Killing\_M ~ No\_Males + Leaves + Season\_Breeder + D.Index + Group\_Size + Substrate\_1 + Dimorphism + Coalition + (1 | p |  
gr(SpeciesTree, cov = A))

IG\_Killing\_F ~ No\_Males + Leaves + Season\_Breeder + D.Index + Group\_Size + Substrate\_1 + Dimorphism + Coalition + (1 | p |  
gr(SpeciesTree, cov = A))

Data: data2b (Number of observations: 101)

Samples: 4 chains, each with iter = 4000; warmup = 2000; thin = 1;

total post-warmup samples = 8000

Group-Level Effects:

~SpeciesTree (Number of levels: 101)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(IGKillingM_Intercept)	9.38	9.36	1.77	34.52	1.00	2195	2353
sd(IGKillingF_Intercept)	2.19	1.55	0.53	5.92	1.00	2866	3604
cor(IGKillingM_Intercept,IGKillingF_Intercept)	0.80	0.19	0.30	0.99	1.00	3777	4513

## Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
IGKillingM_Intercept	-5.70	15.51	-39.12	23.10	1.00	4226	3216
IGKillingF_Intercept	-3.86	9.50	-22.13	16.46	1.00	5628	4584
IGKillingM_No_MalessM	-1.70	4.26	-10.18	6.78	1.00	7374	6051
IGKillingM_Leaves	3.18	4.84	-6.51	12.42	1.00	6642	5972
IGKillingM_Season_BreederYes	-1.33	4.22	-9.73	7.25	1.00	5783	5259
IGKillingM_D.Index	-1.52	3.01	-8.38	4.14	1.00	4657	4263
IGKillingM_Group_Size	0.32	0.45	-0.16	1.52	1.00	2871	2004
IGKillingM_Substrate_1Terrestrial	-1.40	4.21	-9.53	7.06	1.00	7736	6415
IGKillingM_Dimorphism	0.30	4.50	-8.65	9.15	1.00	9157	6043

IGKillingM_CoalitionYes	3.07	4.48	-6.14	11.67	1.00	7026	5280
IGKillingF_No_MaleSSM	2.08	3.34	-4.77	8.51	1.00	6361	5683
IGKillingF_Leaves	1.03	4.18	-7.30	9.06	1.00	9138	6610
IGKillingF_Season_BreederYes	5.67	3.07	-0.05	12.16	1.00	7331	5460
IGKillingF_D.Index	-6.28	2.80	-12.22	-1.30	1.00	7150	5889
IGKillingF_Group_Size	0.04	0.12	-0.20	0.28	1.00	5049	3820
IGKillingF_Substrate_1Terrestrial	-1.74	3.05	-8.05	4.01	1.00	7407	5933
IGKillingF_Dimorphism	-1.99	3.83	-9.58	5.40	1.00	9286	6221
IGKillingF_CoalitionYes	4.95	3.92	-2.95	12.65	1.00	6265	5371

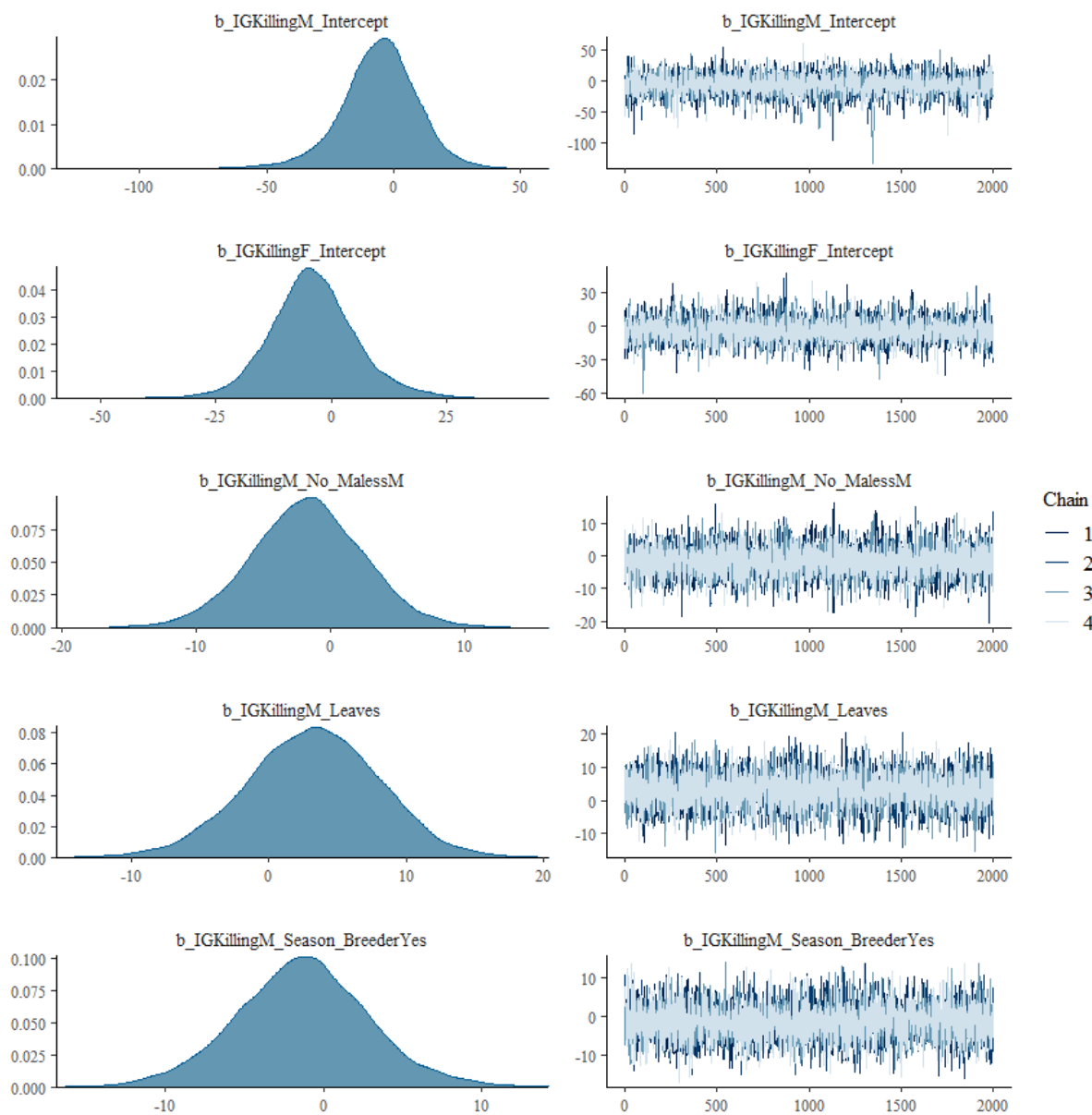
Samples were drawn using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

Estimate	Est.Error	Q2.5	Q97.5
----------	-----------	------	-------

R2IGKillingM	0.8807062	0.09392666	0.6515167	0.9992906
--------------	-----------	------------	-----------	-----------

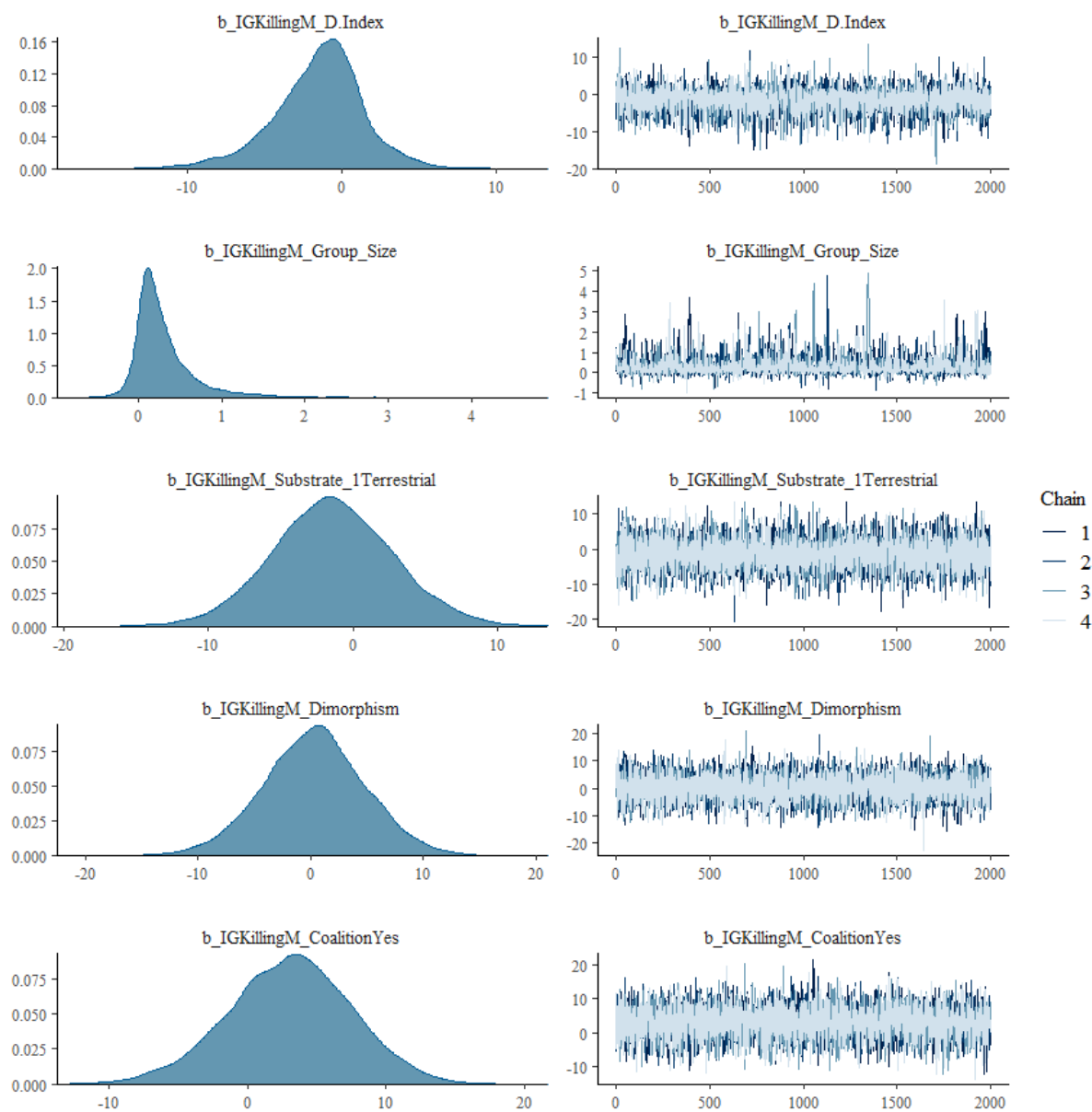
R2IGKillingF	0.7213257	0.15220523	0.3931986	0.9733230
--------------	-----------	------------	-----------	-----------

Intragroup lethal aggression 'all' plots

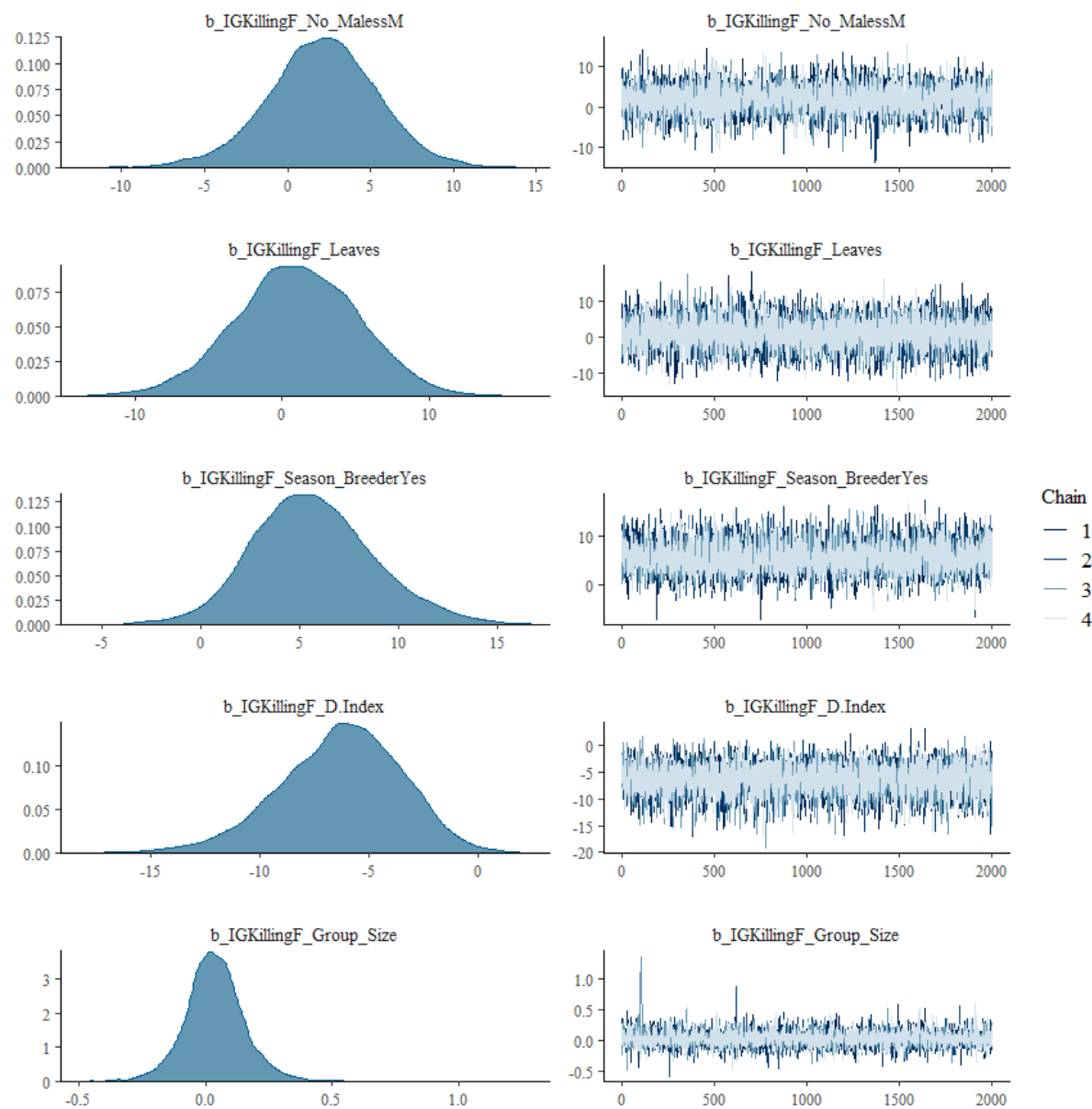




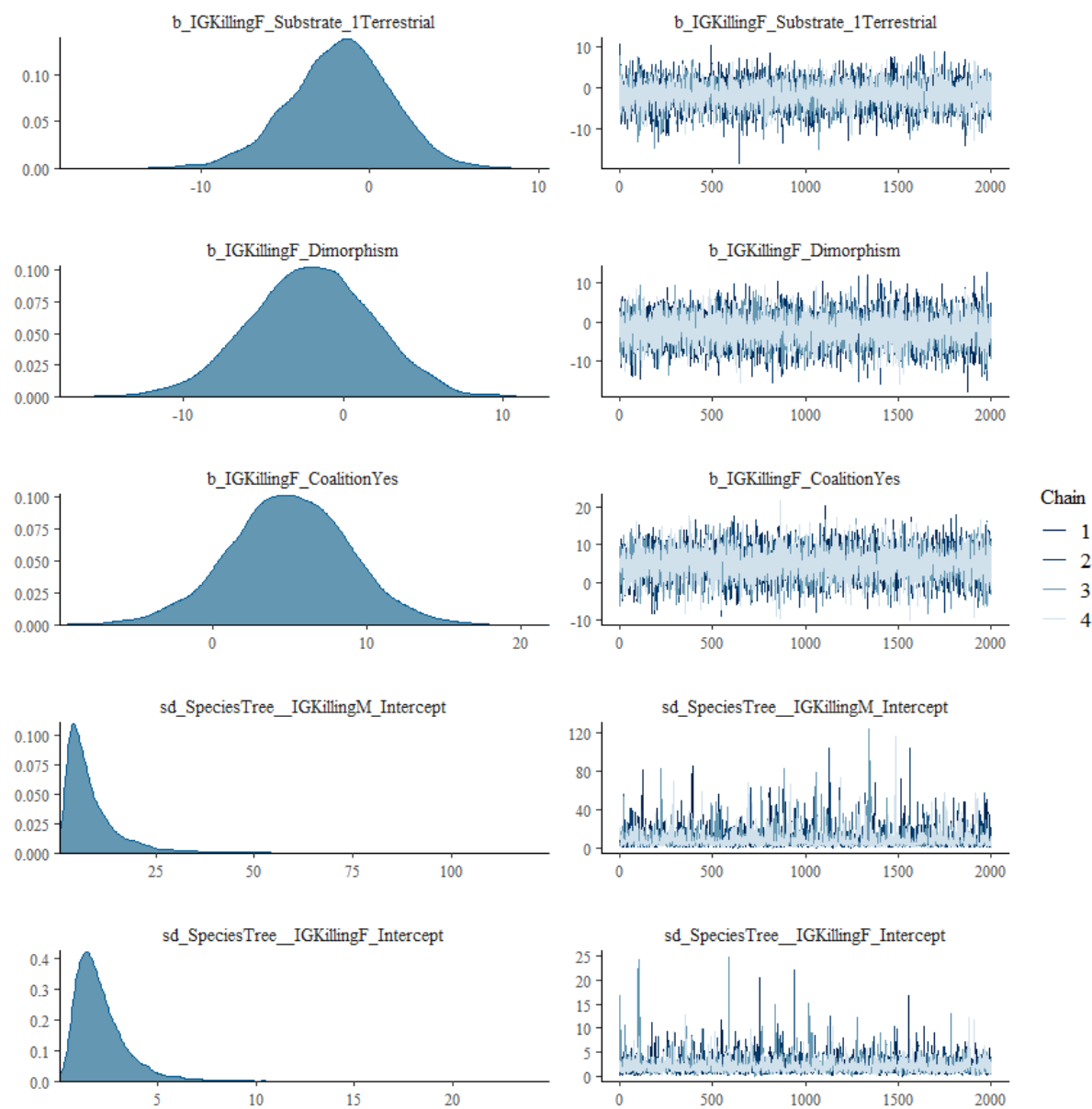




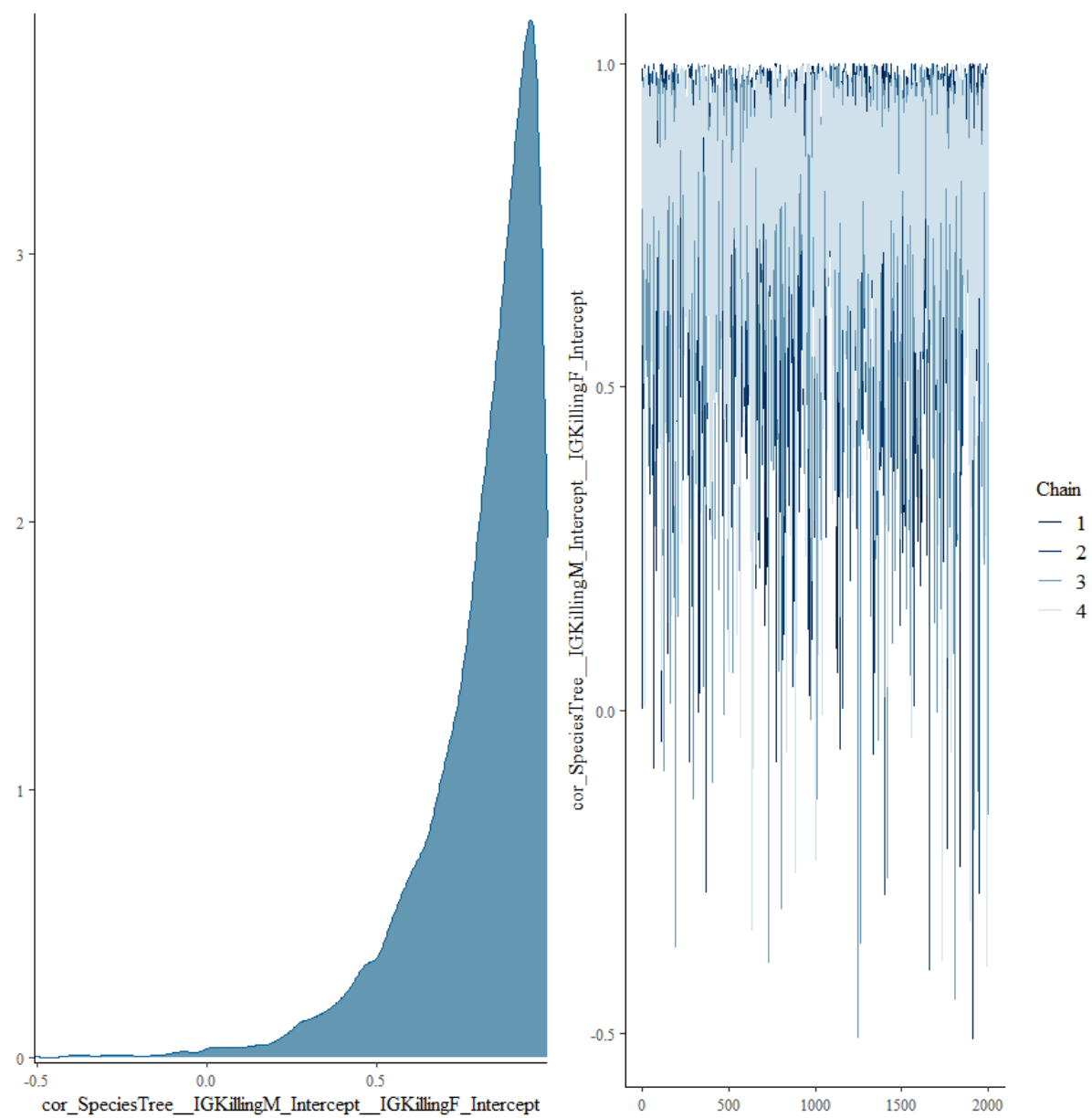




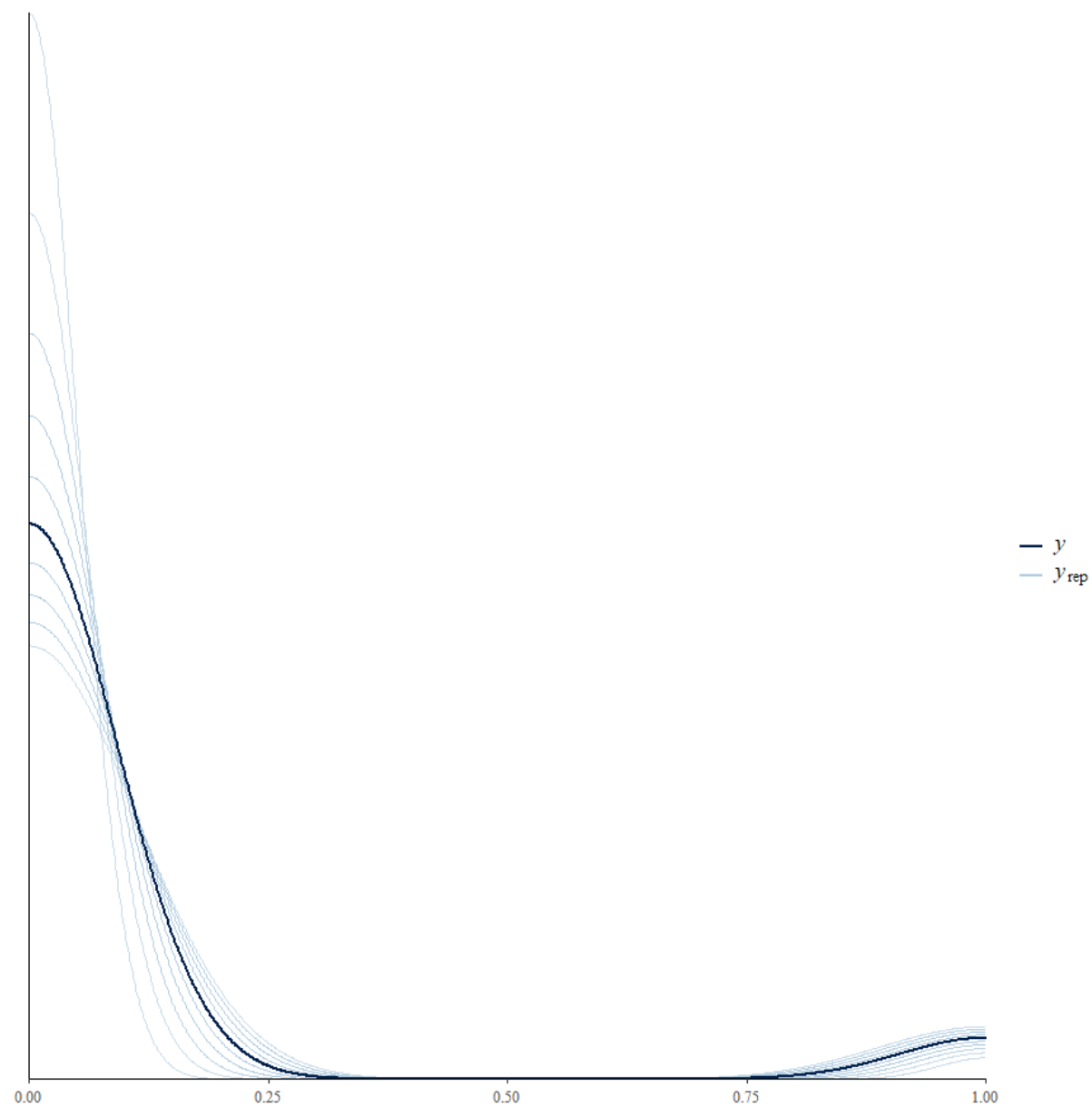




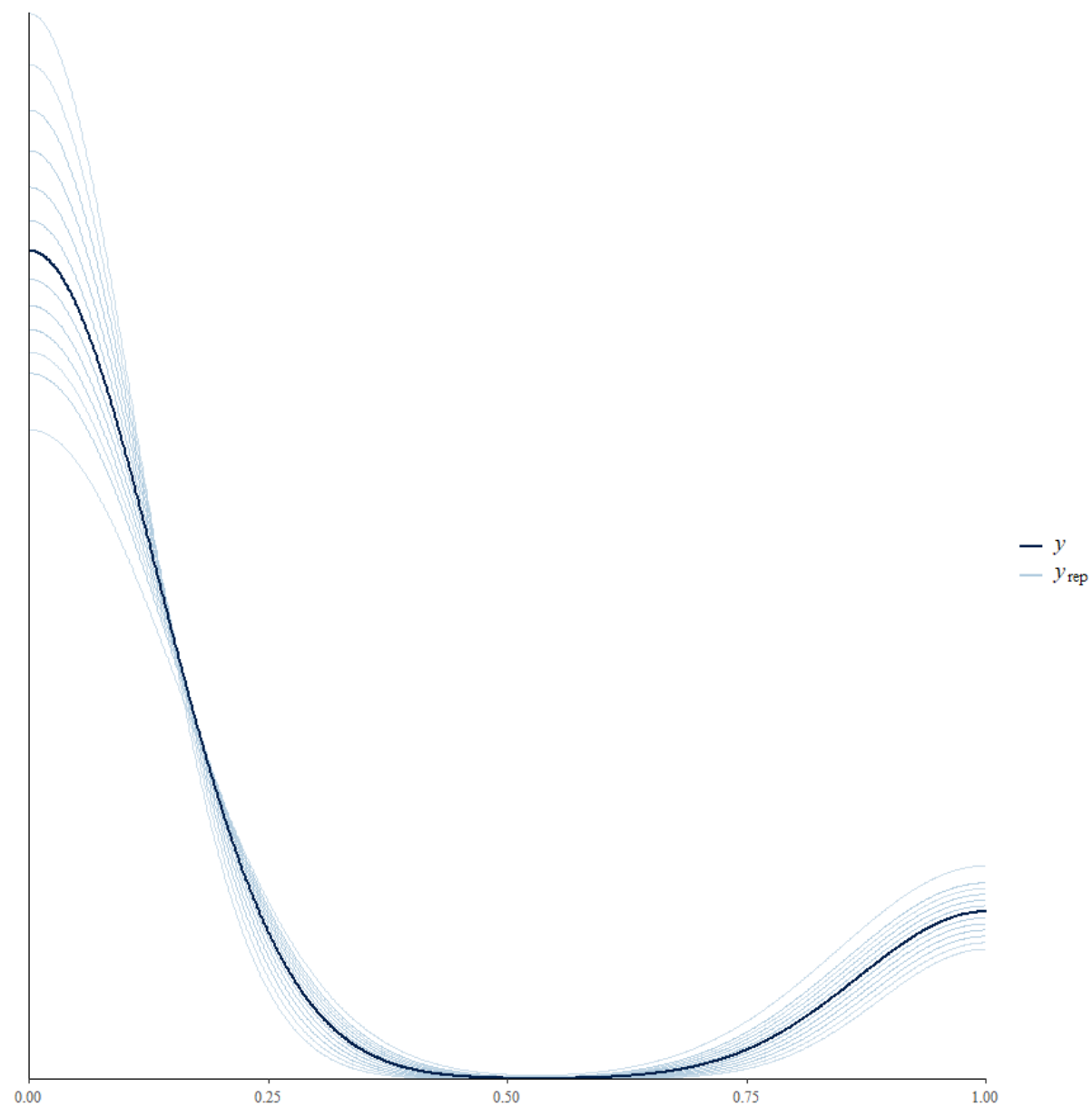








PP check Intragroup Lethal Aggression (Females)



PP check Intragroup Lethal Aggression (Males)

## Appendix 4E – Intergroup Lethal Violence ‘Specific’ model

```
> summary(fitAgg2bspecOG, waic= T); bayes_R2(fitAgg2bspecOG)
```

Family: MV(bernoulli, bernoulli)

Links: mu = logit

mu = logit

Formula: OG\_Killing\_M ~ D.Index + Season\_Breeder + Coalition + No\_Males + Substrate\_1 + (1 | p | gr(SpeciesTree, cov = A))

OG\_Killing\_F ~ D.Index + Season\_Breeder + Coalition + No\_Males + Substrate\_1 + (1 | p | gr(SpeciesTree, cov = A))

Data: data2b (Number of observations: 101)

Samples: 4 chains, each with iter = 4000; warmup = 2000; thin = 1;

total post-warmup samples = 8000

Group-Level Effects:

~SpeciesTree (Number of levels: 101)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGKillingM_Intercept)	5.17	3.59	1.49	13.90	1.00	2099	3381
sd(OGKillingF_Intercept)	4.65	4.04	1.10	14.23	1.00	2462	4324
cor(OGKillingM_Intercept,OGKillingF_Intercept)	0.91	0.09	0.67	1.00	1.00	2006	3077

## Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGKillingM_Intercept	3.56	9.17	-14.62	22.13	1.00	3592	4658
OGKillingF_Intercept	-8.56	8.92	-25.33	10.62	1.00	3882	4617
OGKillingM_D.Index	-1.76	2.28	-6.96	2.23	1.00	4427	4922
OGKillingM_Season_BreederYes	-1.09	3.05	-7.04	5.15	1.00	4860	4911
OGKillingM_CoalitionYes	5.03	3.47	-1.68	12.19	1.00	5148	5169
OGKillingM_No_MalessM	-2.63	3.52	-9.92	4.28	1.00	5044	5092
OGKillingM_Substrate_1Terrestrial	-2.84	3.38	-9.60	3.78	1.00	5257	5529
OGKillingF_D.Index	-0.55	2.16	-5.37	3.33	1.00	4451	4303
OGKillingF_Season_BreederYes	0.89	3.06	-5.14	7.20	1.00	5217	4987
OGKillingF_CoalitionYes	5.96	3.95	-1.78	13.92	1.00	5926	5407
OGKillingF_No_MalessM	-1.84	3.71	-9.67	5.16	1.00	6432	5452
OGKillingF_Substrate_1Terrestrial	0.65	3.38	-6.01	7.64	1.00	4813	4849

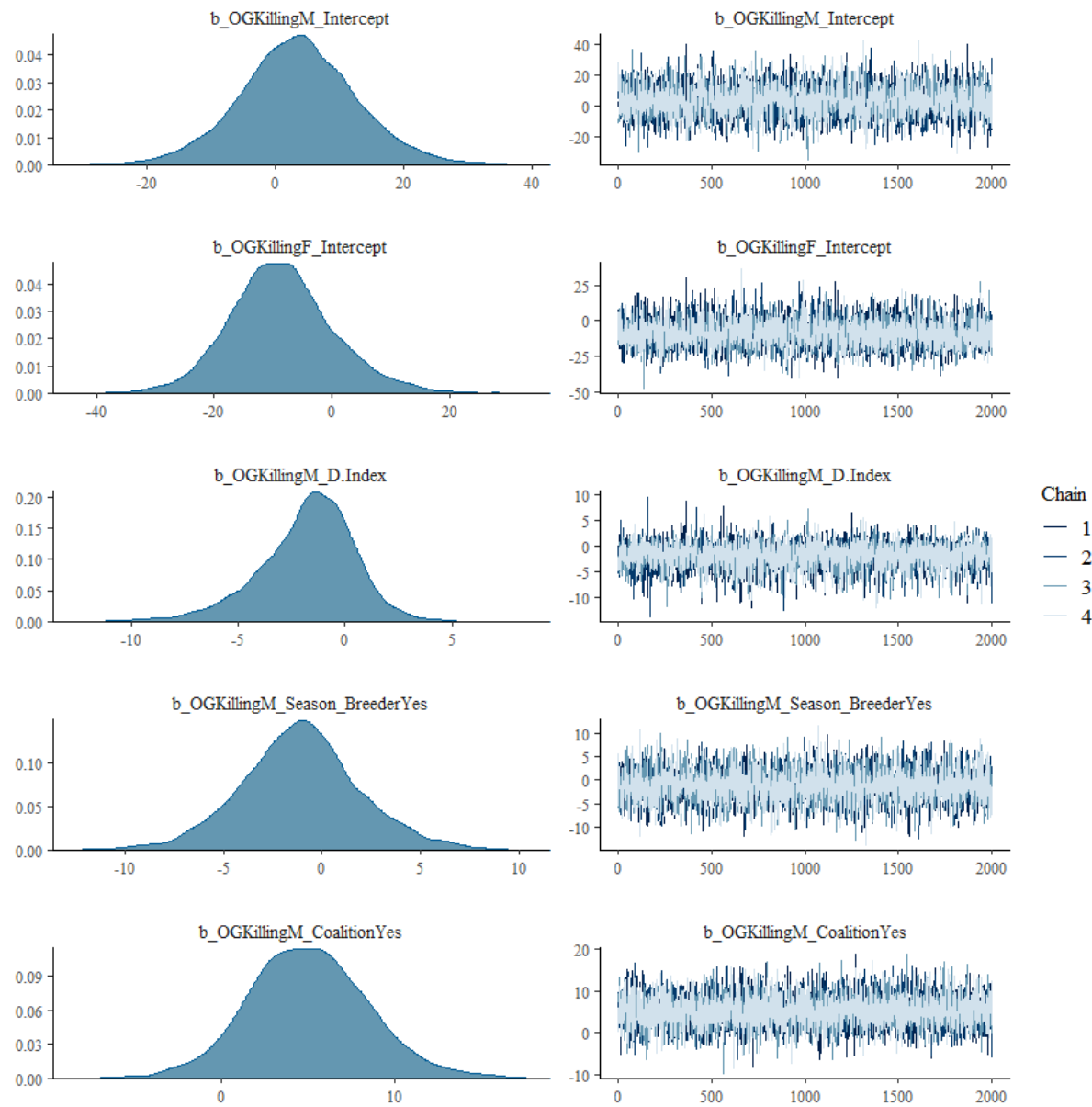
Samples were drawn using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
R2OGKillingM	0.8396208	0.09286705	0.6268877	0.9827409

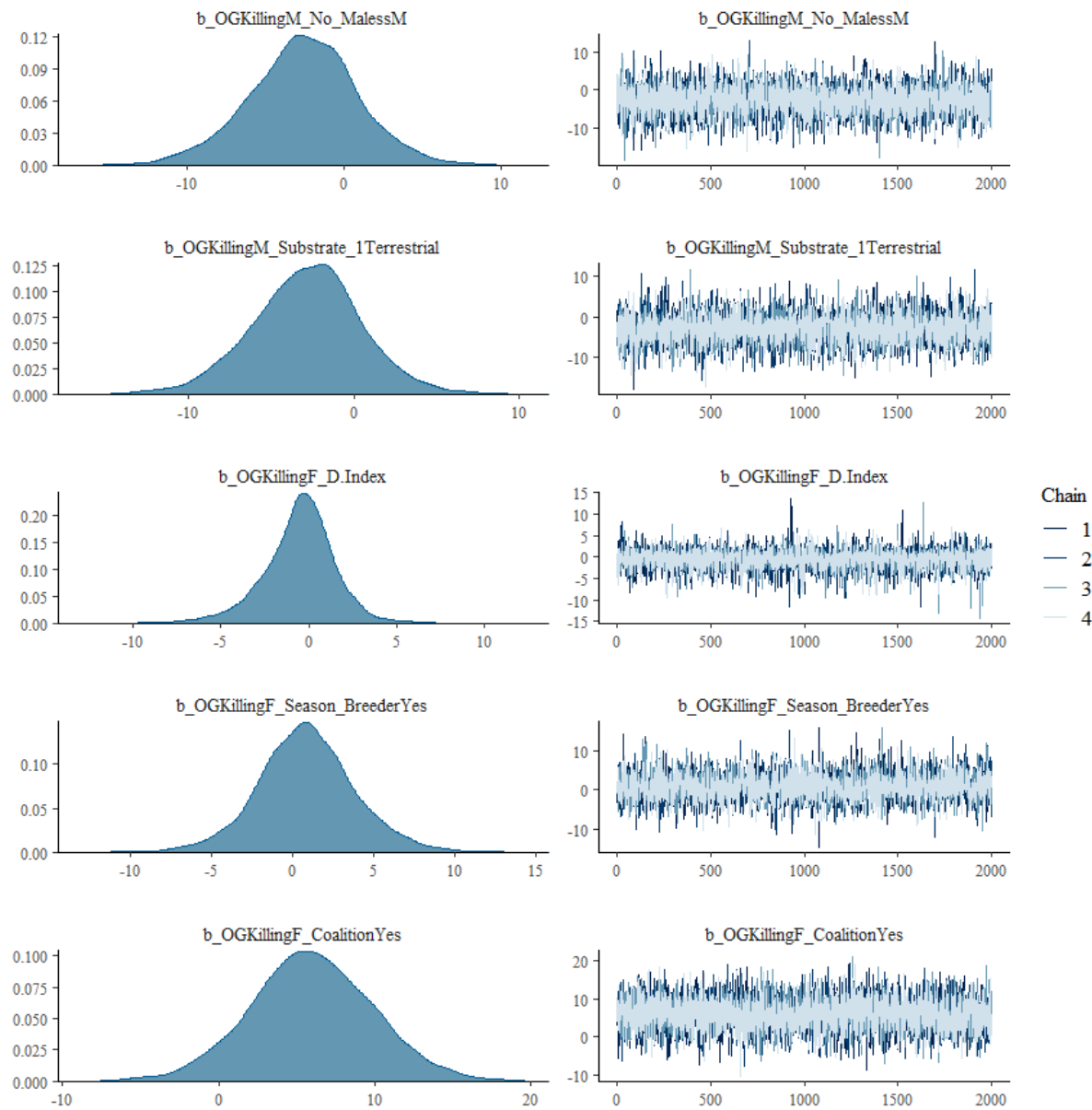
R2OGKillingF 0.7378285 0.15872886 0.3834938 0.9914282

Intergroup specific lethal aggression plots

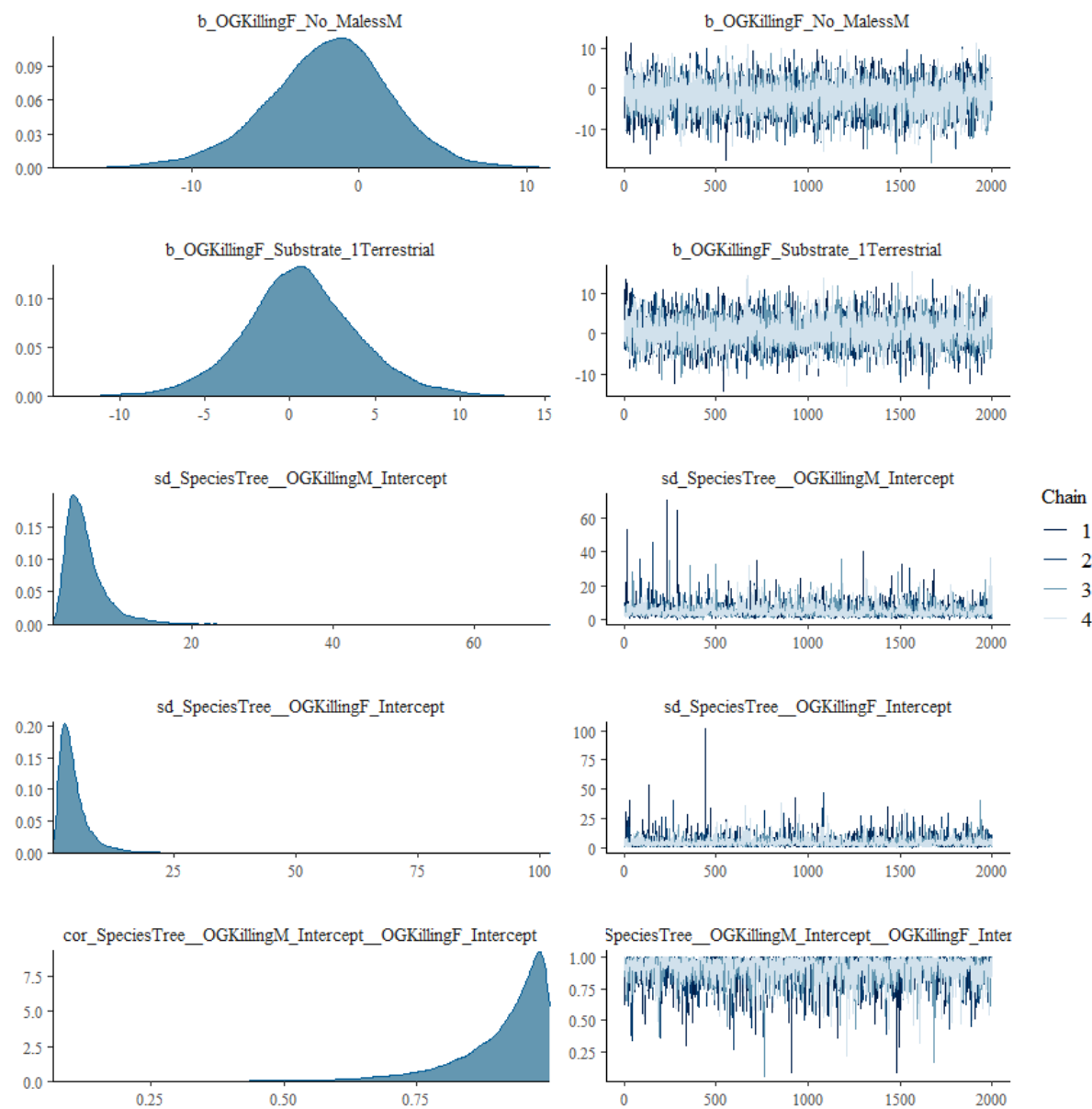














## Appendix 4F – Intragroup Lethal Violence ‘Specific’ Model

```
> summary(fitAgg2bspecIG, waic= T); bayes_R2(fitAgg2bspecIG)
```

Family: MV(bernoulli, bernoulli)

Links: mu = logit

mu = logit

Formula: IG\_Killing\_M ~ Coalition + No\_Males + Season\_Breeder + Substrate\_1 + Dimorphism + (1 | p | gr(SpeciesTree, cov = A))

IG\_Killing\_F ~ Coalition + No\_Males + Season\_Breeder + Substrate\_1 + Dimorphism + (1 | p | gr(SpeciesTree, cov = A))

Data: data2b (Number of observations: 101)

Samples: 4 chains, each with iter = 6000; warmup = 3000; thin = 1;

total post-warmup samples = 12000

Group-Level Effects:

~SpeciesTree (Number of levels: 101)

	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(IGKillingM_Intercept)	4.75	3.83	1.06	14.26	1.00	2791	3328

sd(IGKillingF_Intercept)	2.85	2.39	0.50	8.89	1.00	3591	4653
cor(IGKillingM_Intercept,IGKillingF_Intercept)	0.84	0.17	0.38	1.00	1.00	3643	5083

## Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
IGKillingM_Intercept	-1.85	10.10	-21.81	18.31	1.00	7162	7701
IGKillingF_Intercept	-9.58	9.03	-27.28	8.73	1.00	8034	6829
IGKillingM_CoalitionYes	4.55	3.84	-3.14	12.08	1.00	8118	8583
IGKillingM_No_MalessM	-1.99	3.51	-9.17	5.00	1.00	8716	7963
IGKillingM_Season_BreederYes	-2.43	3.38	-9.34	4.42	1.00	6342	7004
IGKillingM_Substrate_1Terrestrial	-1.16	3.49	-8.08	6.03	1.00	7254	7835
IGKillingM_Dimorphism	0.85	3.96	-7.05	8.58	1.00	10927	8937
IGKillingF_CoalitionYes	4.82	4.04	-3.28	12.89	1.00	8820	8325
IGKillingF_No_MalessM	0.83	3.32	-6.00	7.38	1.00	8232	7664
IGKillingF_Season_BreederYes	5.15	3.18	-0.72	11.93	1.00	7327	7547
IGKillingF_Substrate_1Terrestrial	-0.43	2.92	-6.72	5.13	1.00	7116	6971



IGKillingF_Dimorphism	-1.86	4.00	-9.78	6.11	1.00	11156	8782
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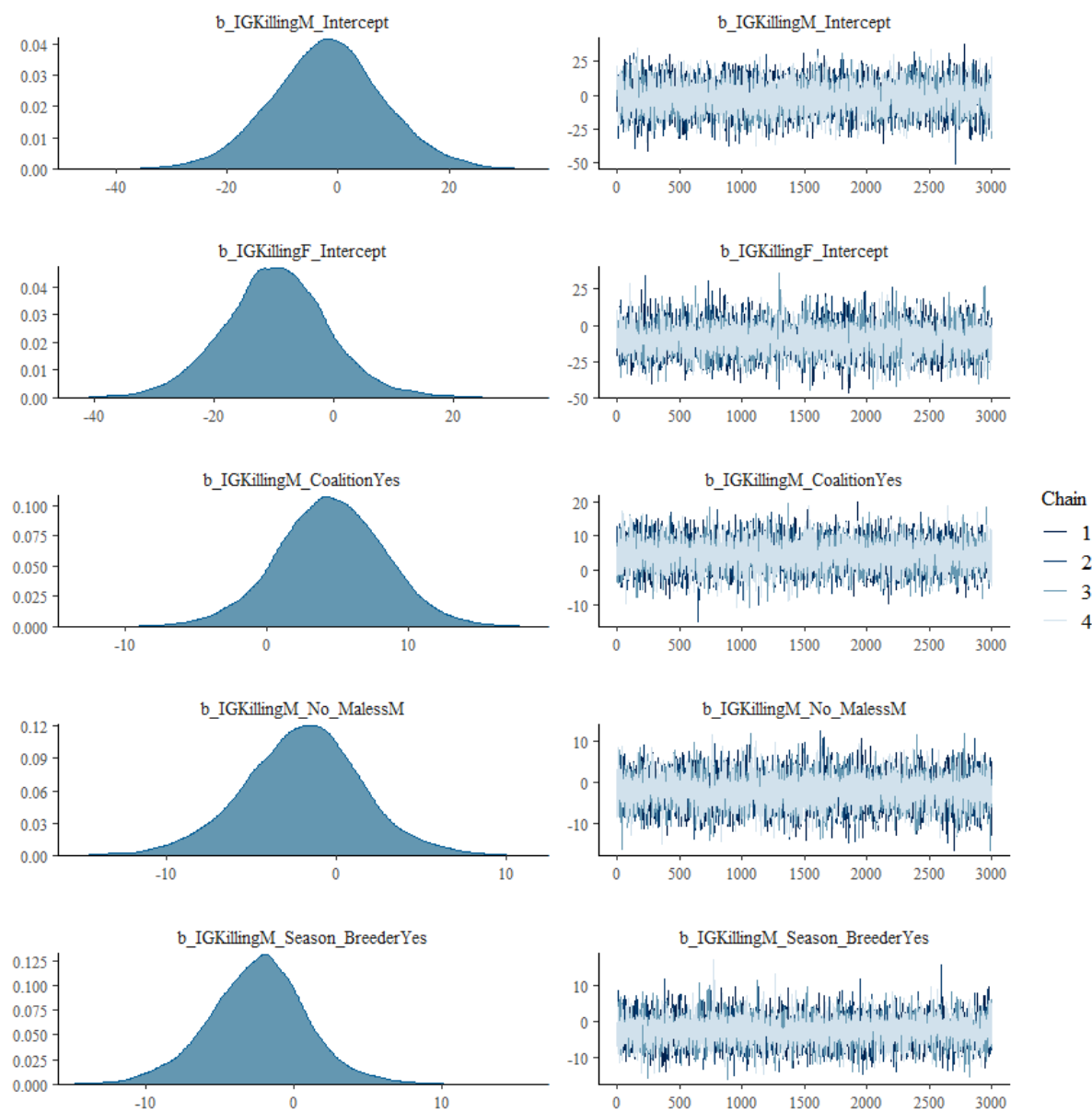
Samples were drawn using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

Estimate	Est.Error	Q2.5	Q97.5
----------	-----------	------	-------

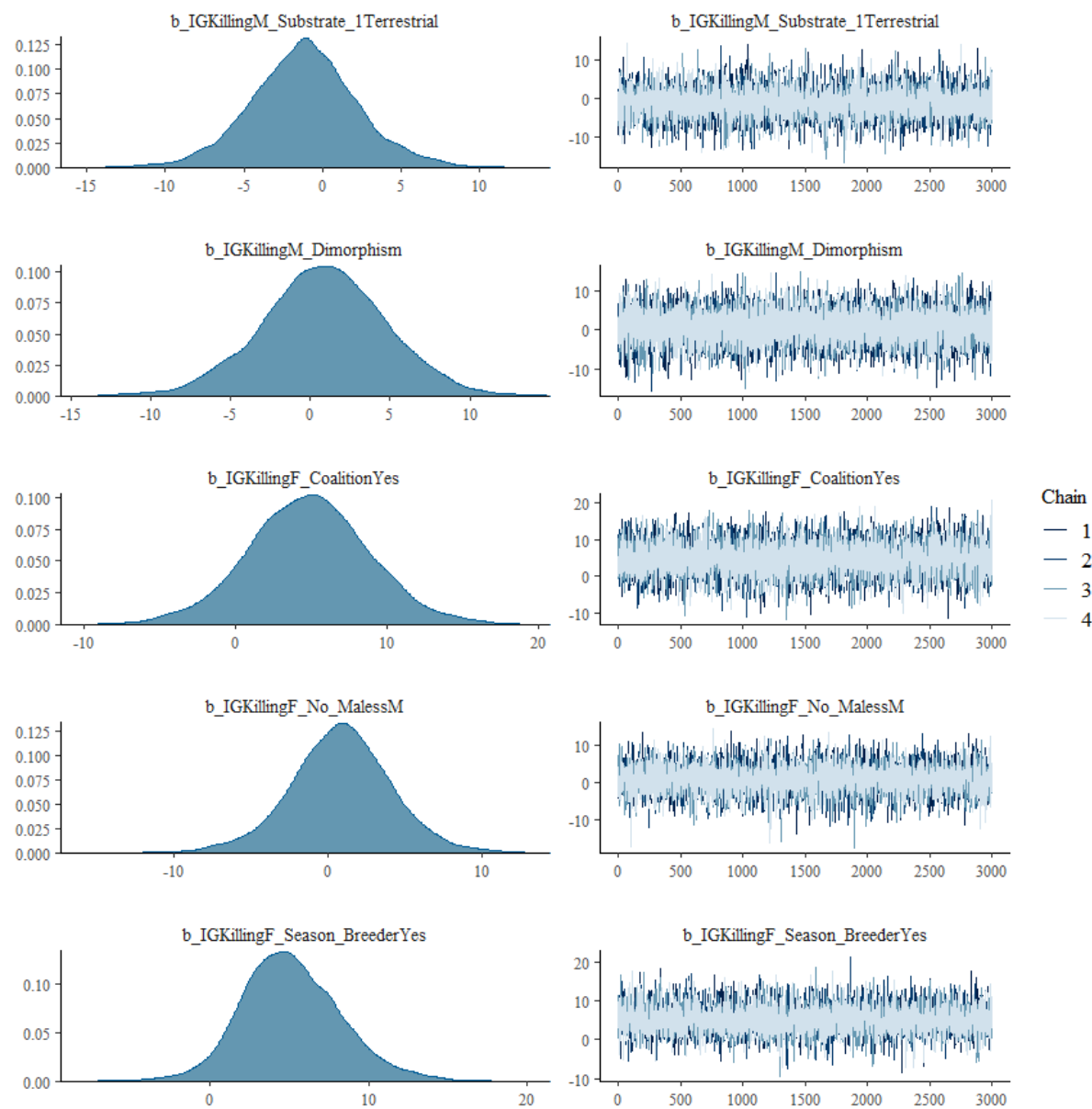
R2IGKillingM	0.8094973	0.1184469	0.5344305	0.9871526
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R2IGKillingF	0.6390199	0.2006878	0.2044167	0.9766261
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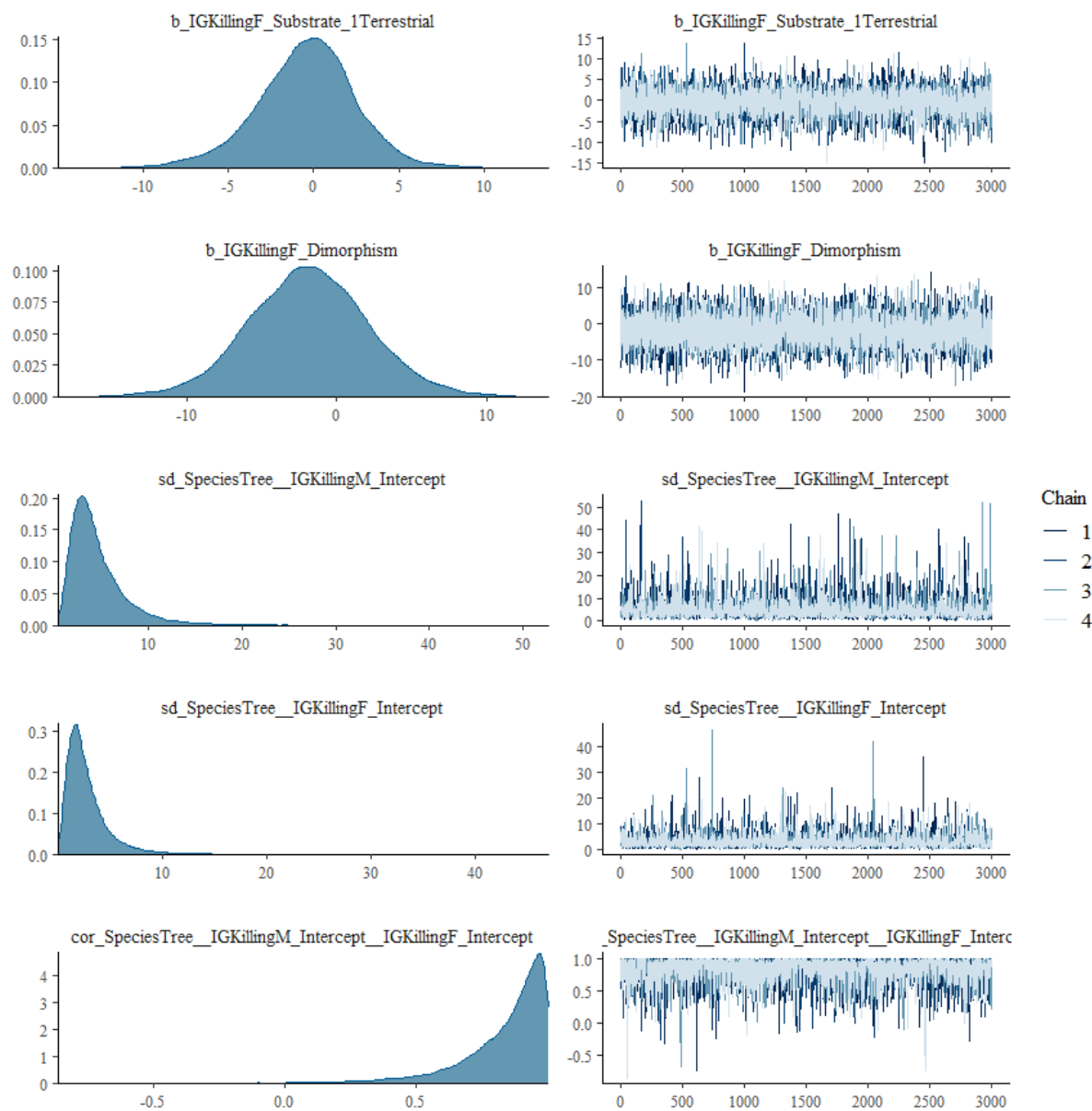
Intragroup 'specific' killing pairs plots















## Appendix 4G – All lethal violence split by sex

```
> summary(fitAgg2bsex, waic= T); bayes_R2(fitAgg2bsex)
```

Family: MV(bernoulli, bernoulli)

Links: mu = logit

mu = logit

Formula: Male\_Killing ~ No\_Males + Leaves + Season\_Breeder + D.Index + Group\_Size + Substrate\_1 + Dimorphism + Coalition + (1 | p |  
gr(SpeciesTree, cov = A))

Female\_Killing ~ No\_Males + Leaves + Season\_Breeder + D.Index + Group\_Size + Substrate\_1 + Dimorphism + Coalition + (1 | p |  
gr(SpeciesTree, cov = A))

Data: data2b (Number of observations: 101)

Samples: 4 chains, each with iter = 4000; warmup = 2000; thin = 1;

total post-warmup samples = 8000

Group-Level Effects:

~SpeciesTree (Number of levels: 101)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(MaleKilling_Intercept)	5.62	4.44	1.74	16.41	1.00	2310	2587
sd(FemaleKilling_Intercept)	4.25	3.90	1.15	12.91	1.00	2447	2814
cor(MaleKilling_Intercept,FemaleKilling_Intercept)	0.92	0.09	0.68	1.00	1.00	2592	4656

## Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
MaleKilling_Intercept	4.05	11.82	-18.98	26.96	1.00	5158	5071
FemaleKilling_Intercept	-10.01	10.50	-30.91	11.05	1.00	6180	5216
MaleKilling_No_MalessM	-3.15	3.53	-10.22	3.74	1.00	6848	5625
MaleKilling_Leaves	3.85	4.31	-4.96	12.18	1.00	7473	5749
MaleKilling_Season_BreederYes	-2.50	3.33	-9.01	4.44	1.00	5432	5181
MaleKilling_D.Index	-1.86	2.39	-7.25	2.30	1.00	4498	4562
MaleKilling_Group_Size	-0.03	0.17	-0.34	0.33	1.00	3408	2633
MaleKilling_Substrate_1Terrestrial	-2.21	3.57	-9.29	5.14	1.00	5409	5094
MaleKilling_Dimorphism	-0.10	3.89	-7.80	7.50	1.00	7536	6233

MaleKilling_CoalitionYes	6.28	3.65	-0.75	13.51	1.00	6293	5653
FemaleKilling_No_MalessM	0.59	3.38	-6.63	6.96	1.00	6656	5959
FemaleKilling_Leaves	0.44	4.22	-7.74	8.60	1.00	10532	5948
FemaleKilling_Season_BreederYes	4.77	3.18	-1.37	11.32	1.00	6206	5218
FemaleKilling_D.Index	-2.00	2.28	-7.05	2.10	1.00	5274	4569
FemaleKilling_Group_Size	0.17	0.16	-0.06	0.54	1.00	3875	2980
FemaleKilling_Substrate_1Terrestrial	-2.26	3.31	-9.05	4.28	1.00	6699	4795
FemaleKilling_Dimorphism	-1.97	3.86	-9.87	5.52	1.00	7923	5535
FemaleKilling_CoalitionYes	6.24	4.00	-1.79	14.00	1.00	7137	5087

Samples were drawn using sampling(NUTS). For each parameter, Bulk\_ESS

and Tail\_ESS are effective sample size measures, and Rhat is the potential

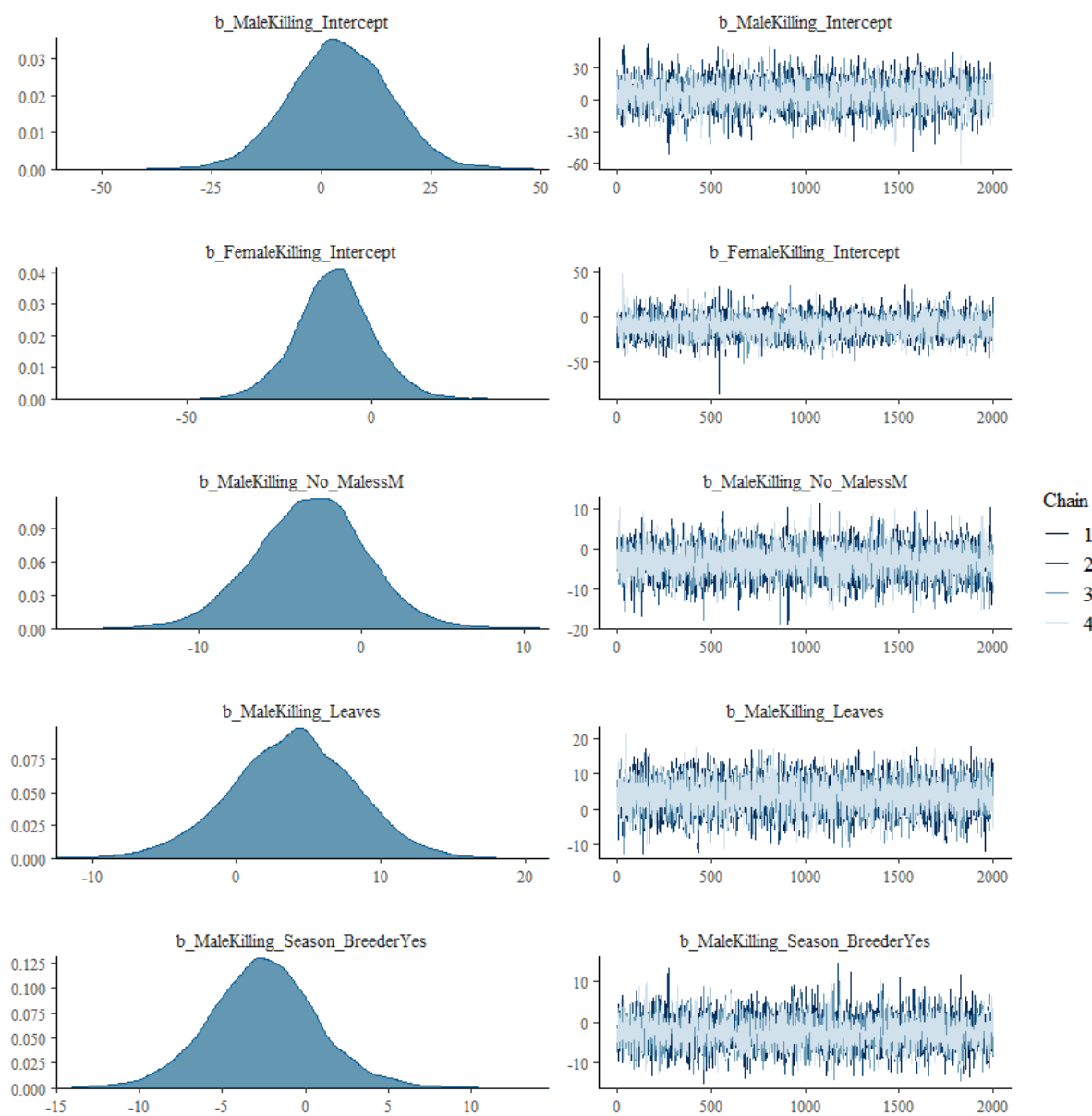
scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
--	----------	-----------	------	-------

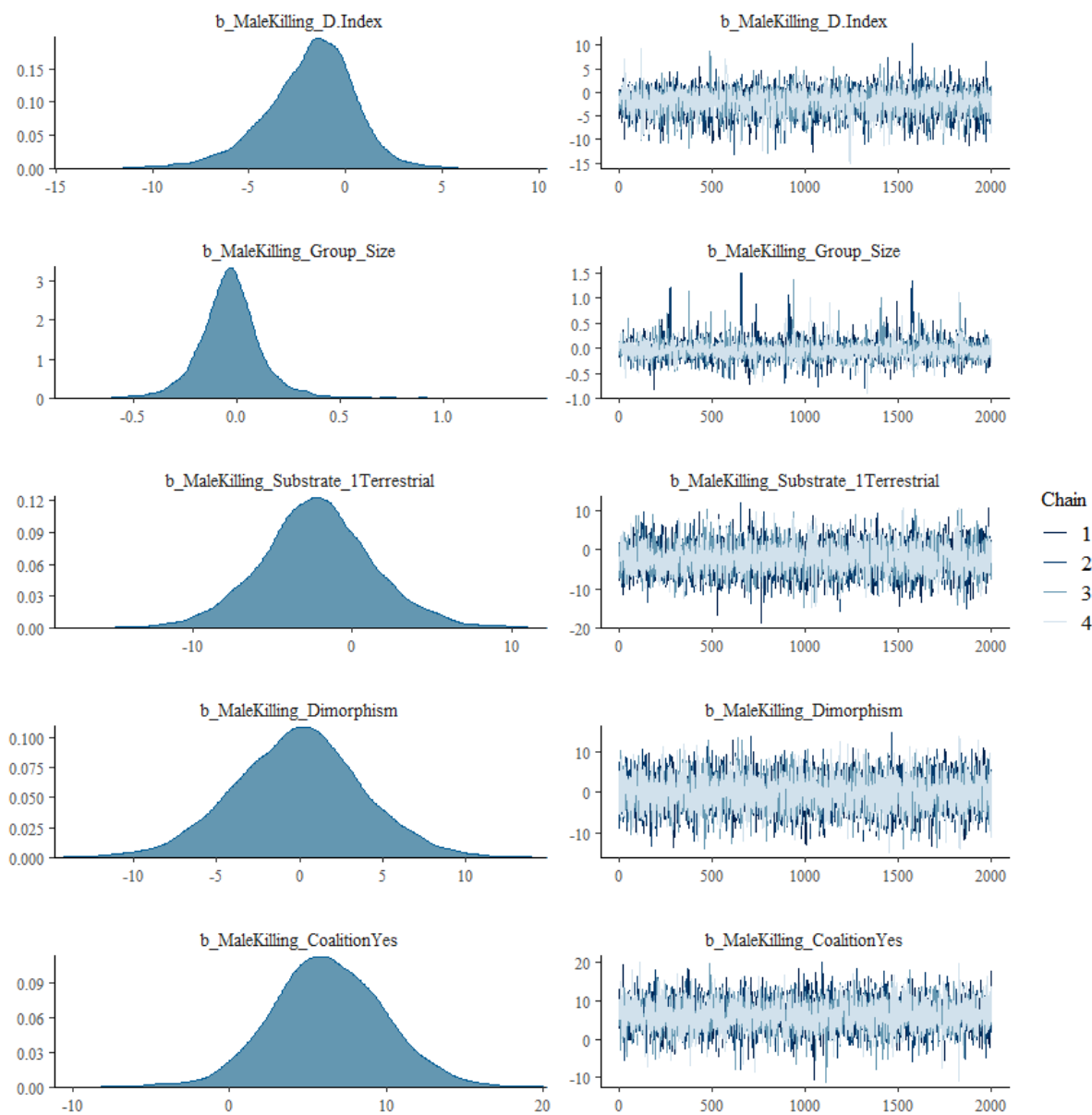
R2MaleKilling	0.8564213	0.07807915	0.6833558	0.9827121
---------------	-----------	------------	-----------	-----------

R2FemaleKilling	0.7527404	0.13067041	0.4750063	0.9765135
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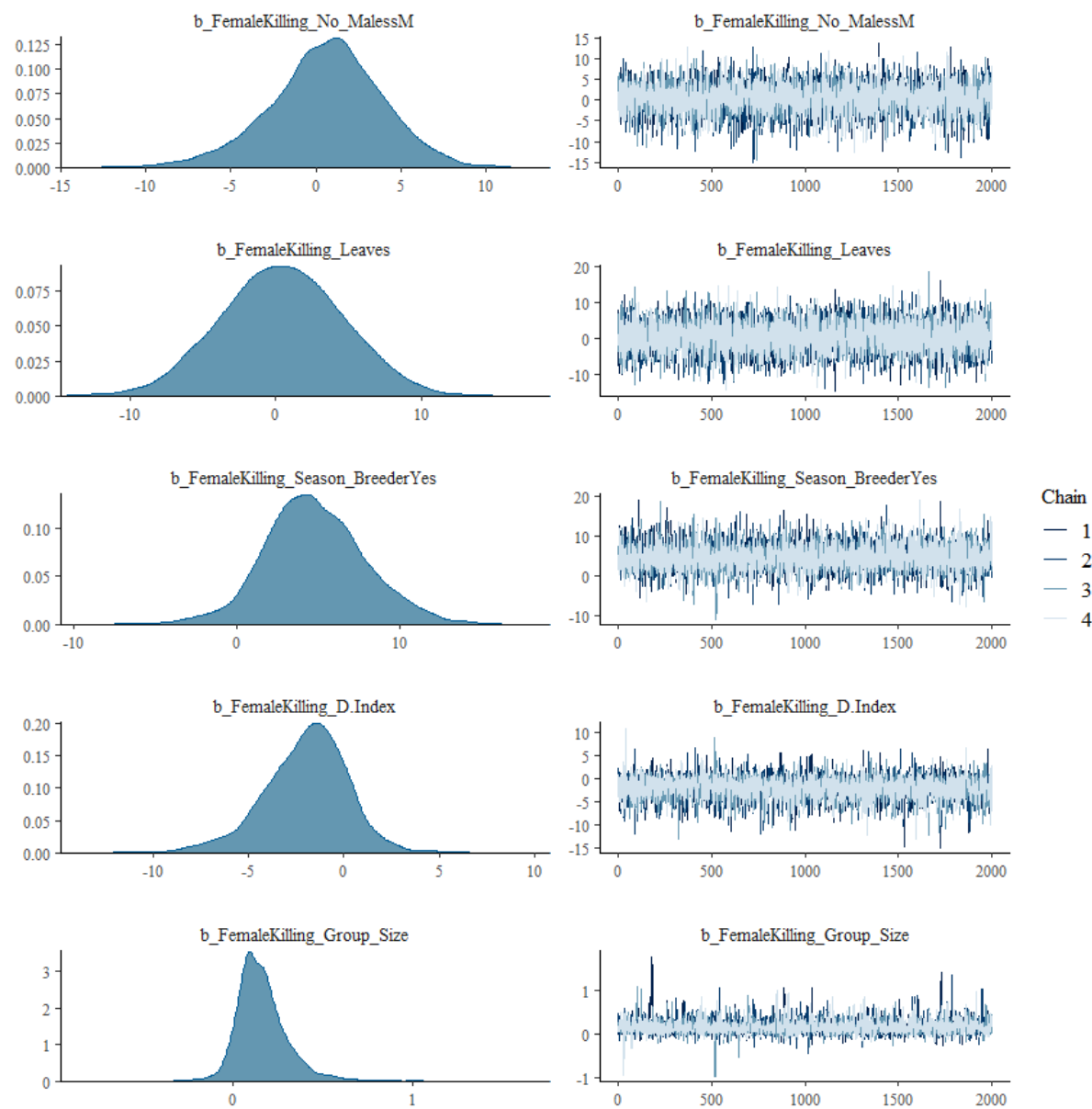




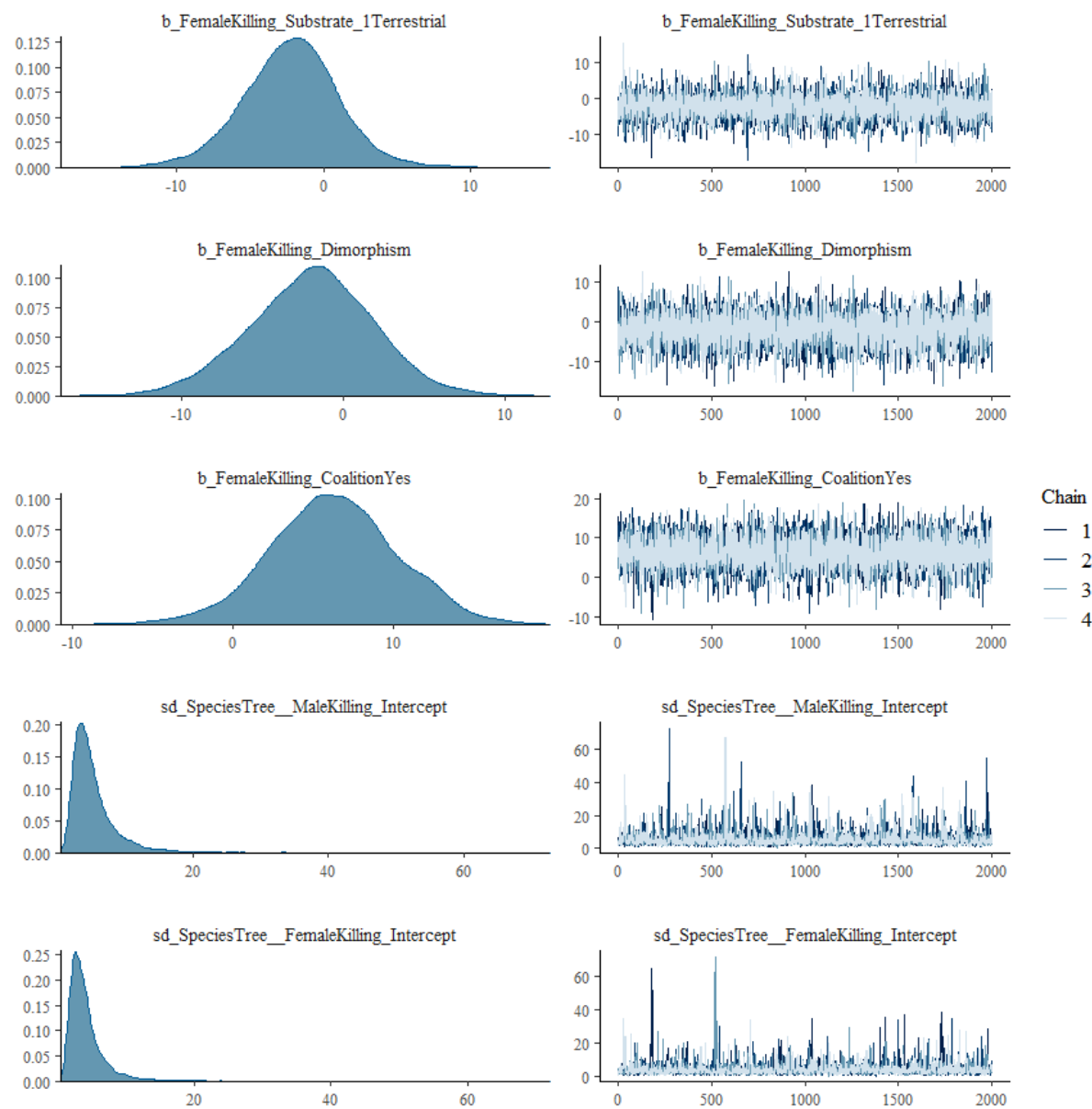




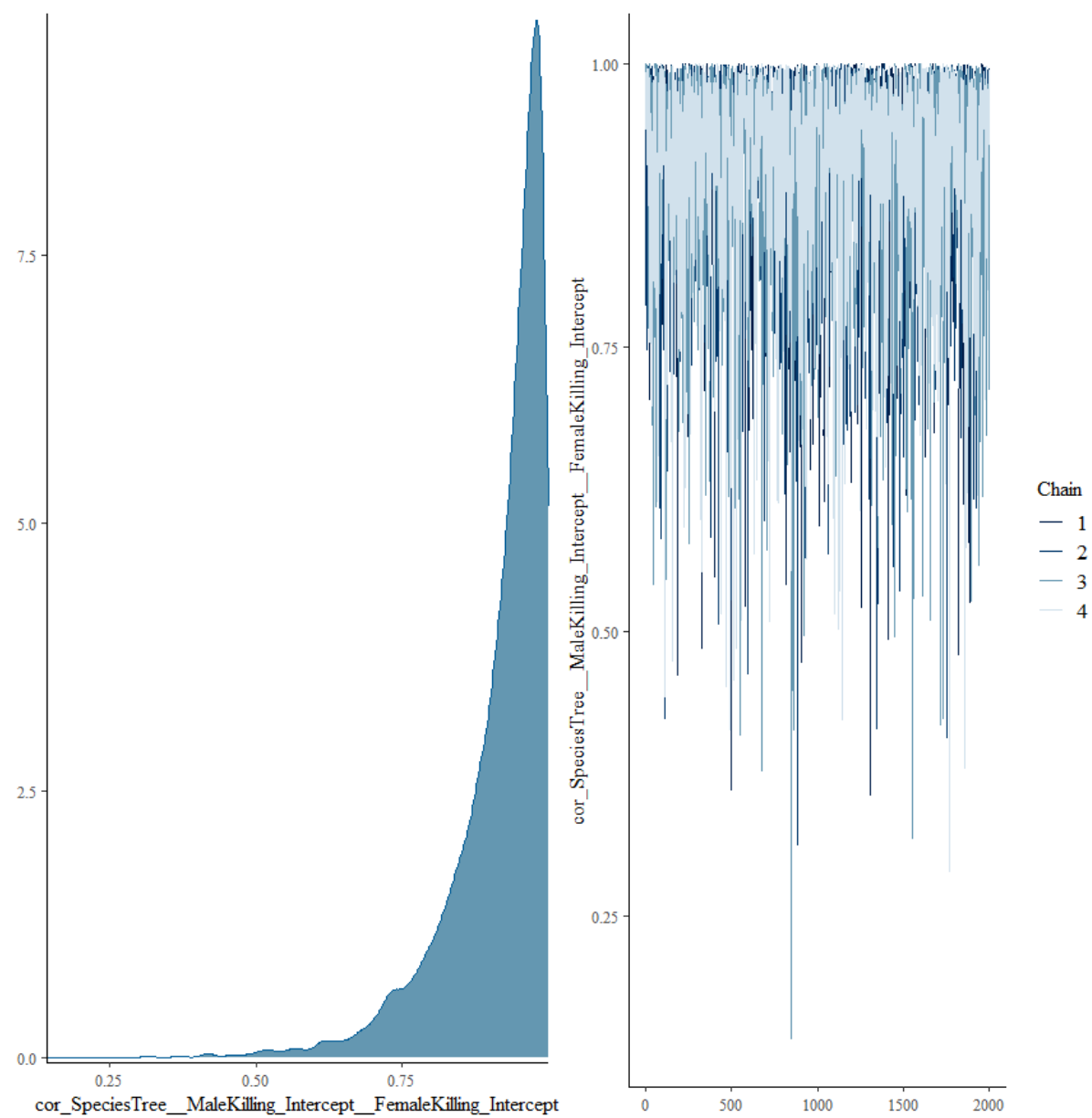




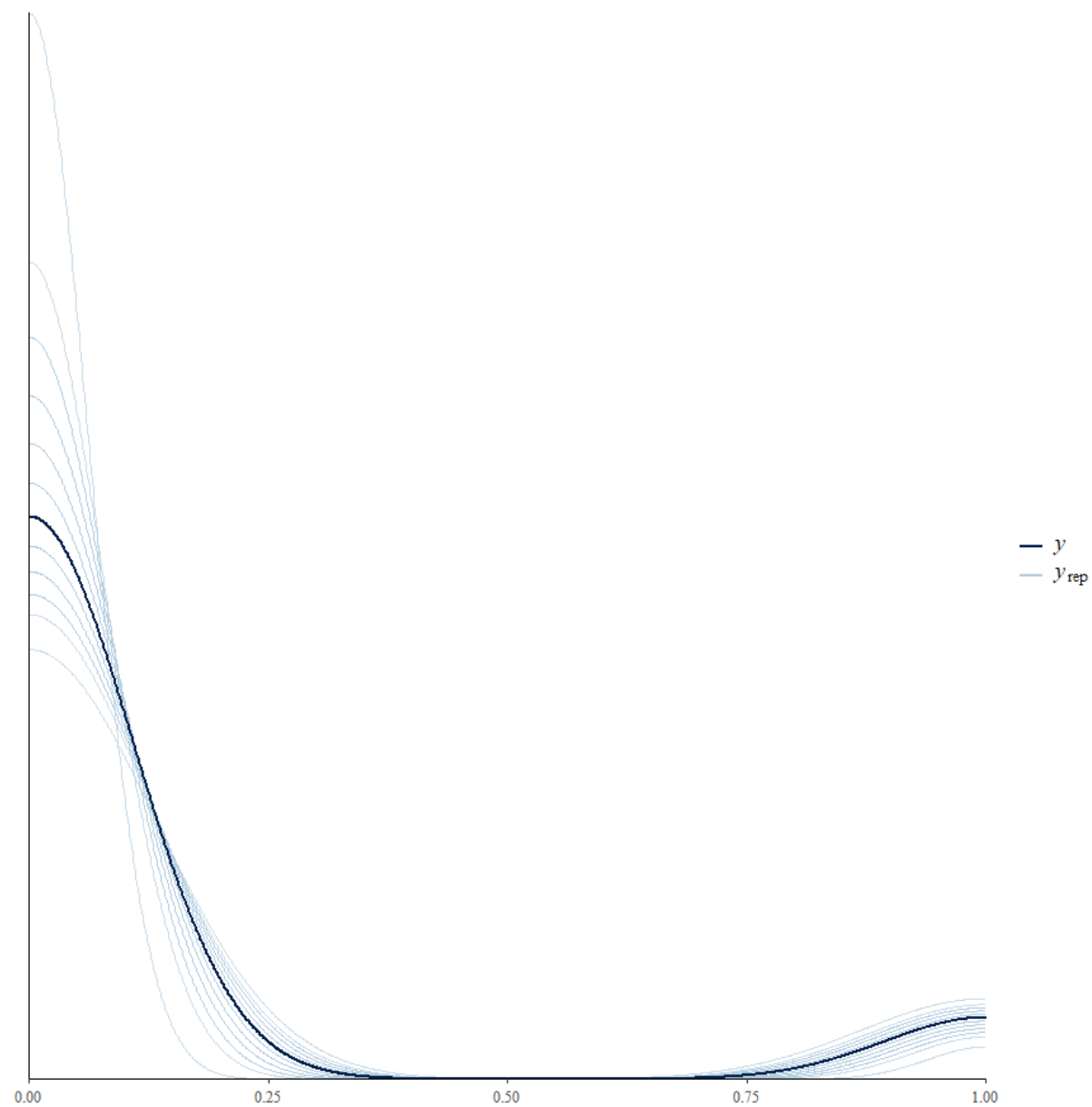






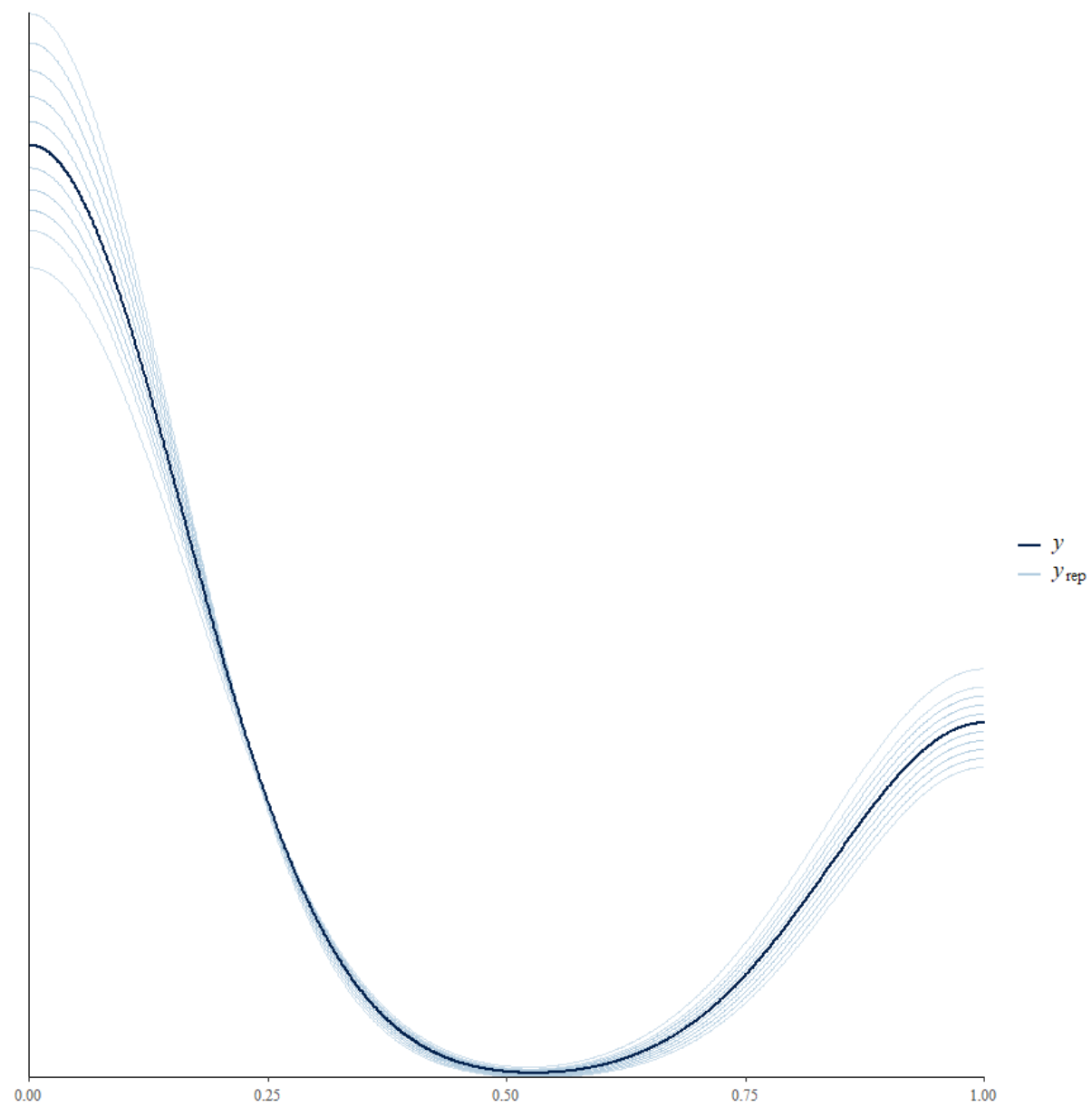






PP Check Female Killing – All types



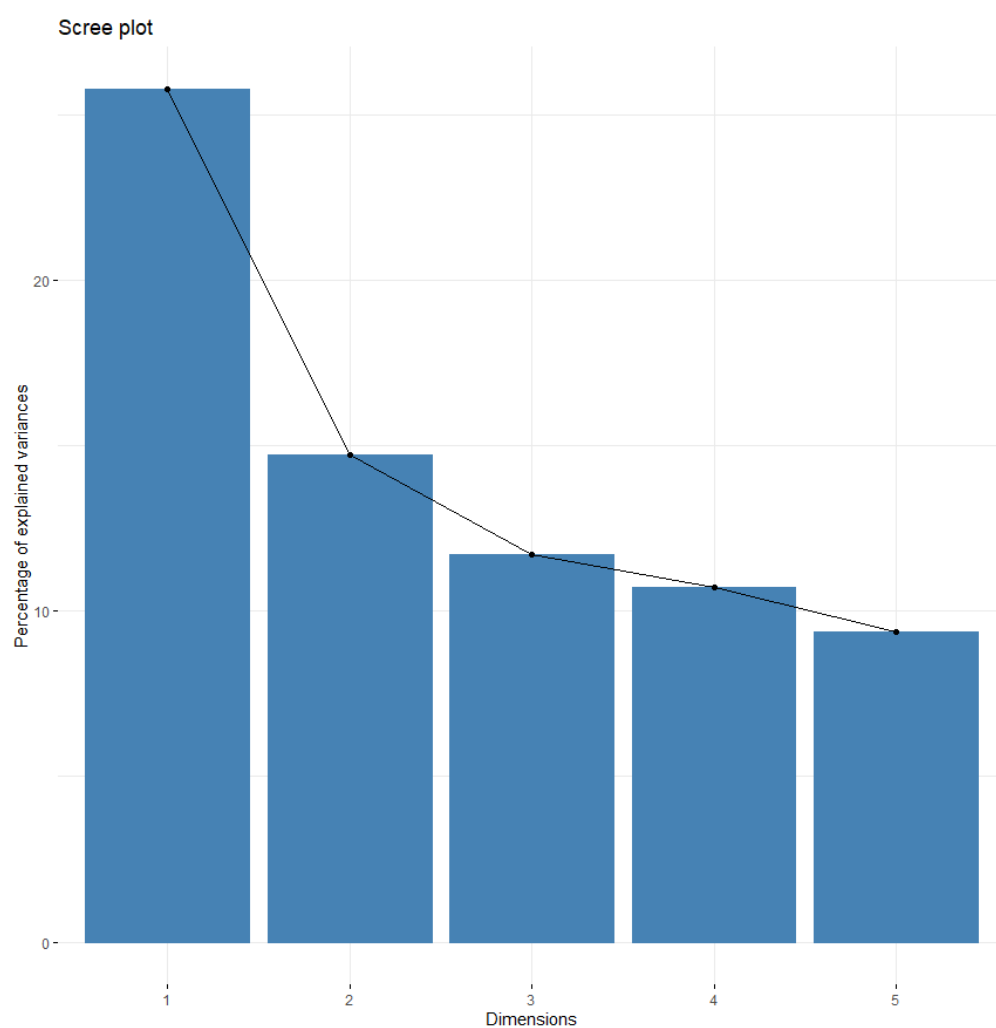


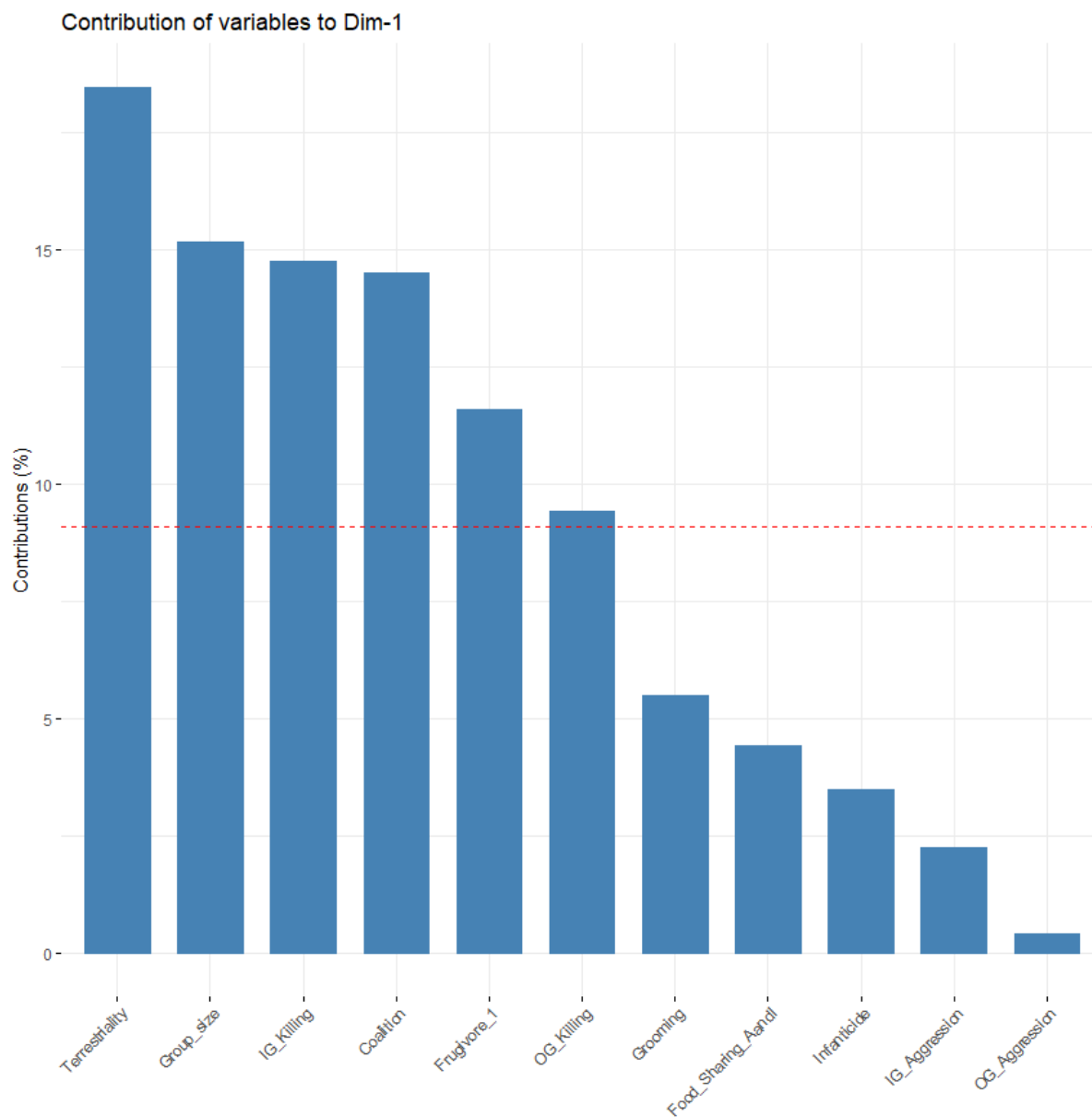
PP Checks Male Killing (all types)

## APPENDICES – CHAPTER 5

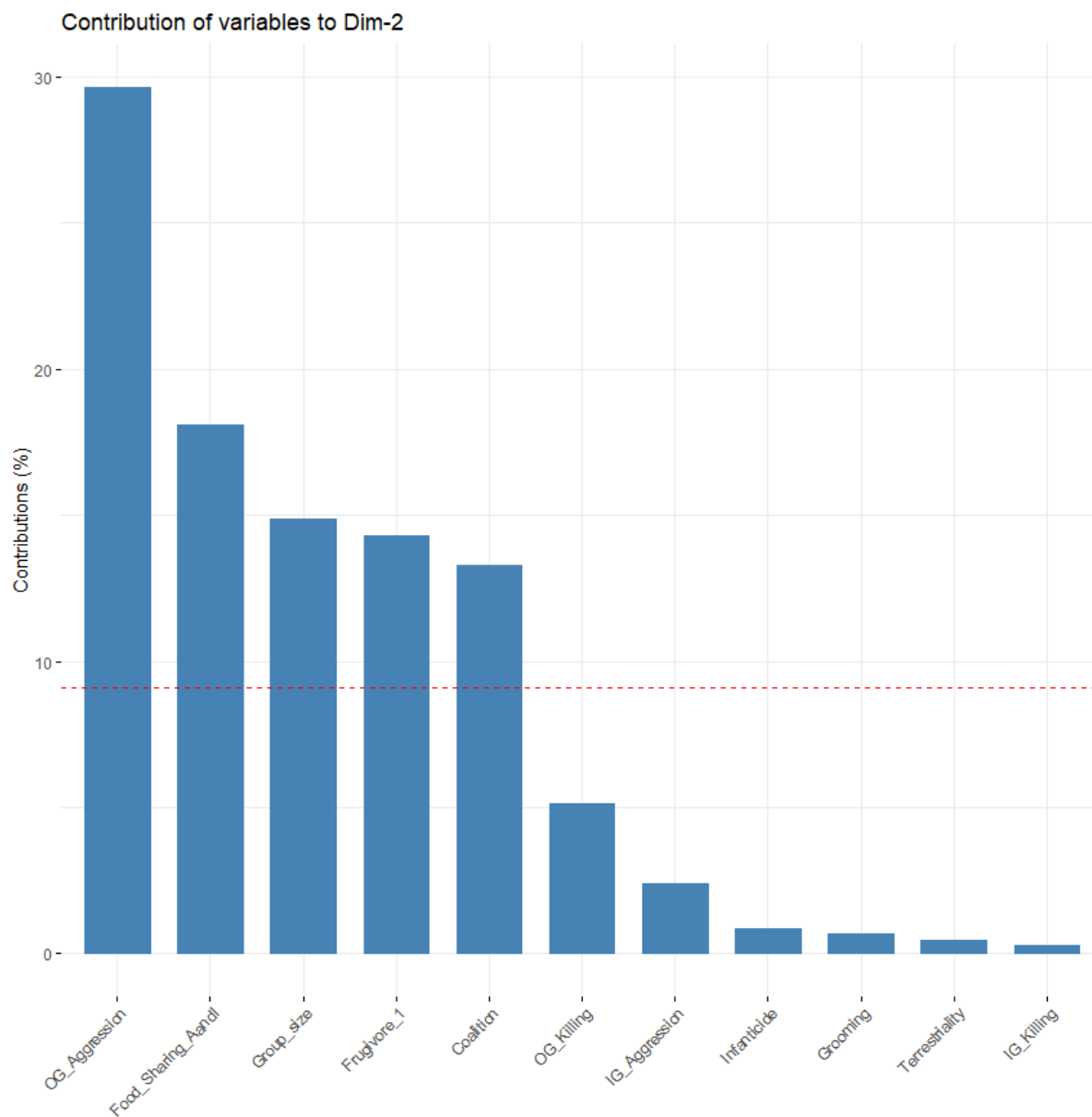
## Appendix 5A – FAMD

	eigenvalue	variance.percent	cumulative.variance.percent
Dim.1	2.833161	25.756010	25.75601
Dim.2	1.618997	14.718159	40.47417
Dim.3	1.288893	11.717208	52.19138
Dim.4	1.179747	10.724970	62.91635
Dim.5	1.031323	9.375659	72.29201

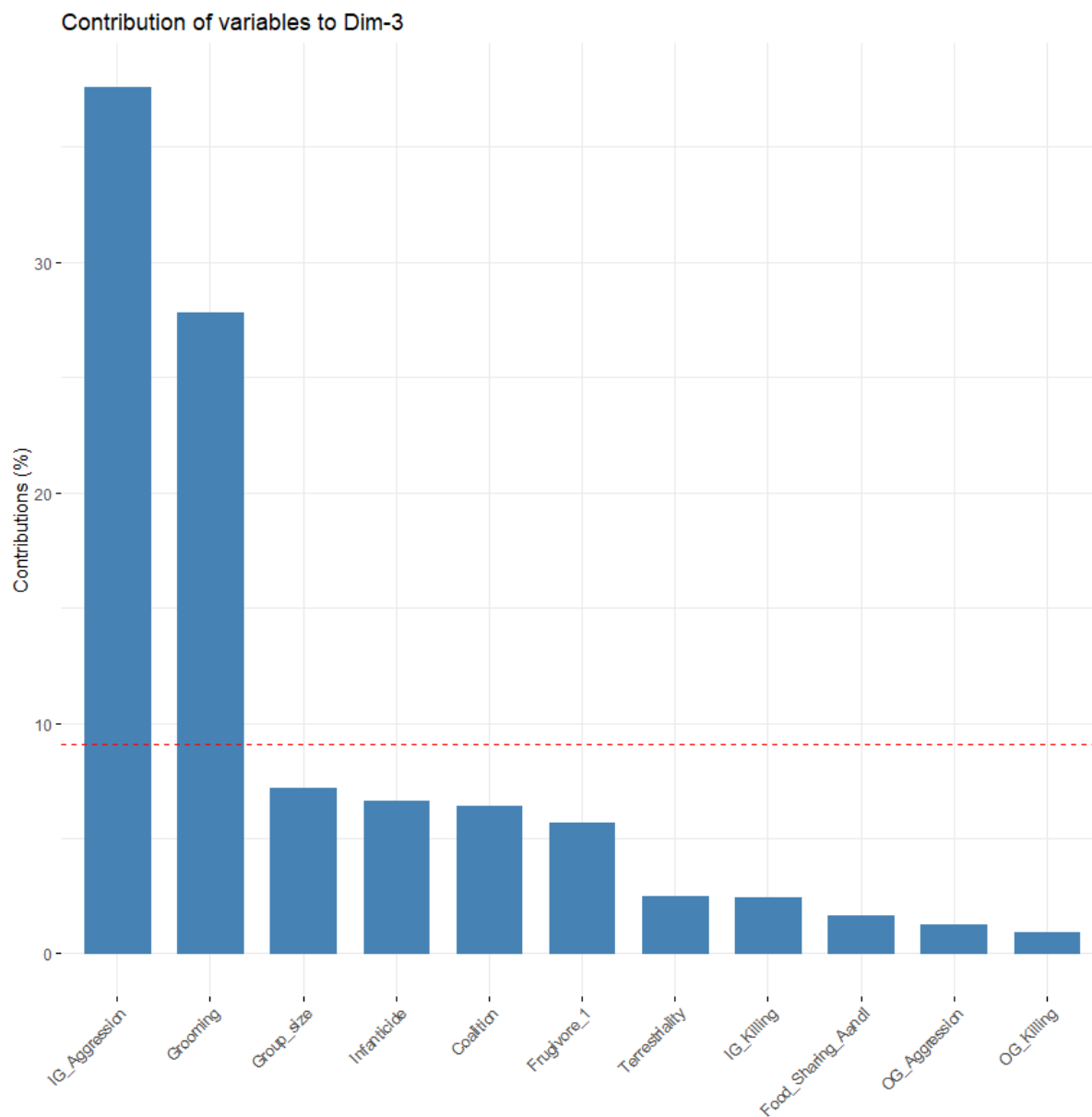




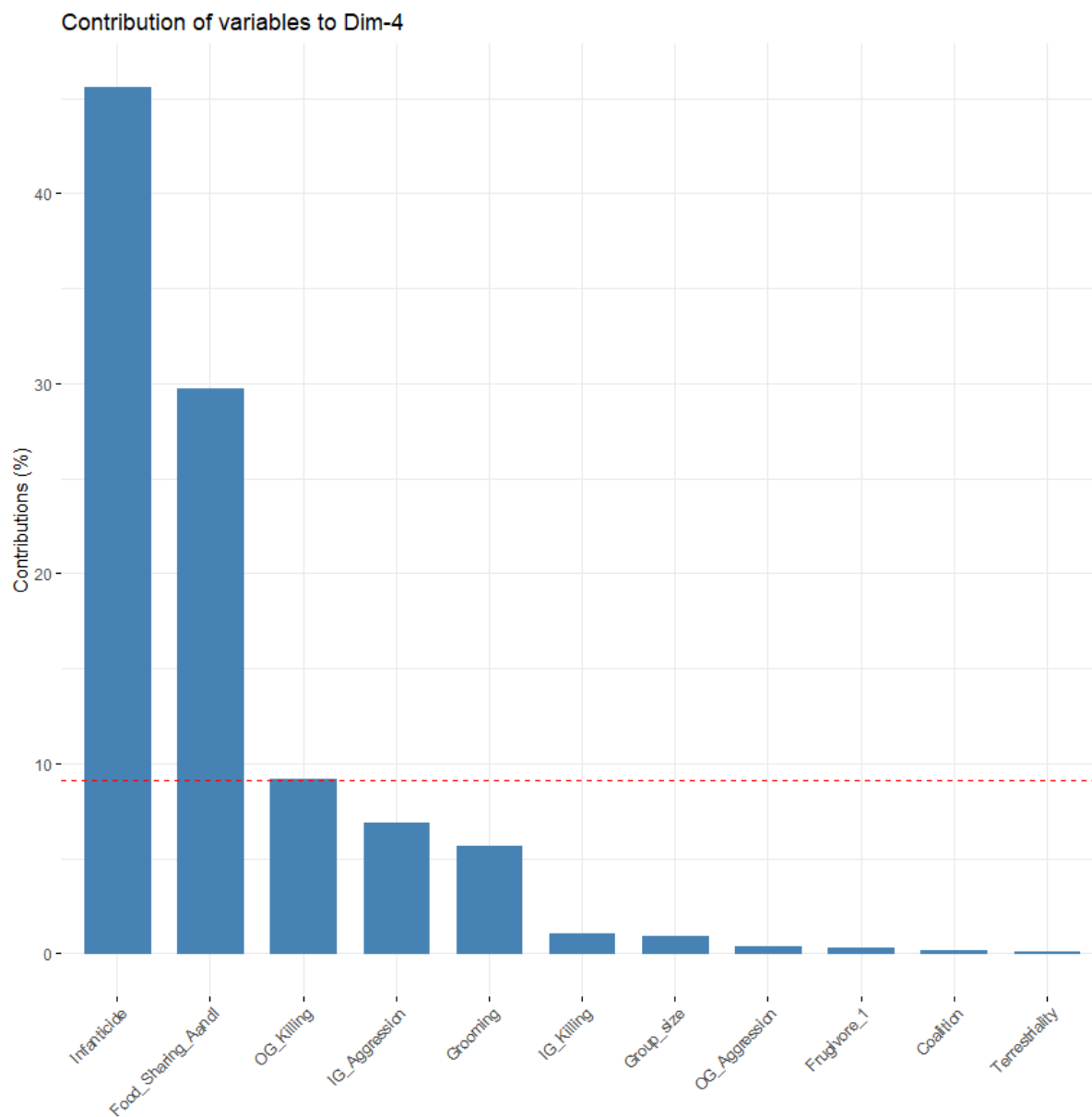
Visualisation of the contribution of variables to the principal dim-1. The red dashed line on the graph above indicates the expected average value, If the contributions were uniform



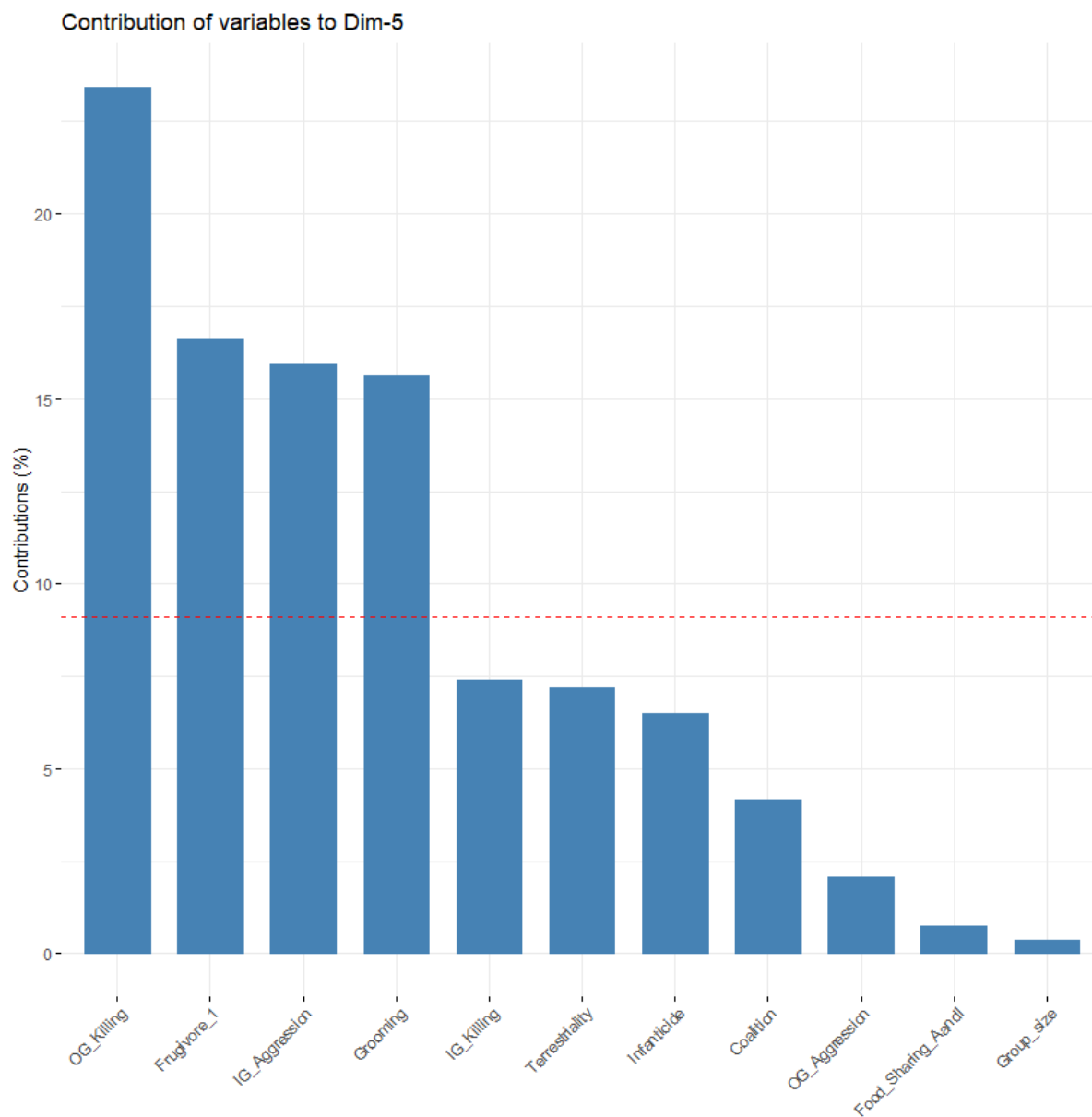
Visualisation of the contribution of variables to the principal dim-2. The red dashed line on the graph above indicates the expected average value, If the contributions were uniform



Visualisation of the contribution of variables to the principal dim-3. The red dashed line on the graph above indicates the expected average value, If the contributions were uniform

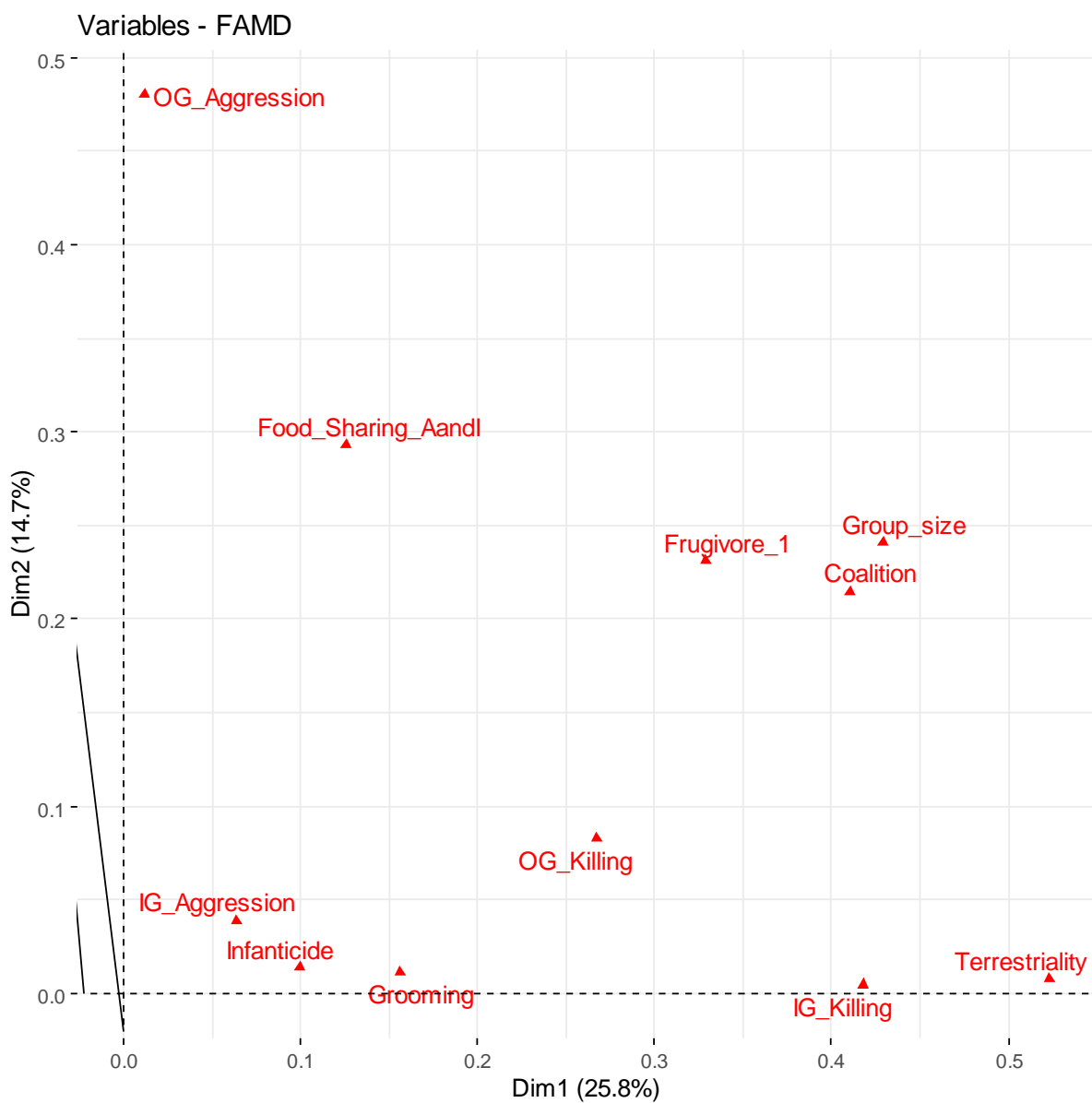


Visualisation of the contribution of variables to the principal dim-4. The red dashed line on the graph above indicates the expected average value, If the contributions were uniform

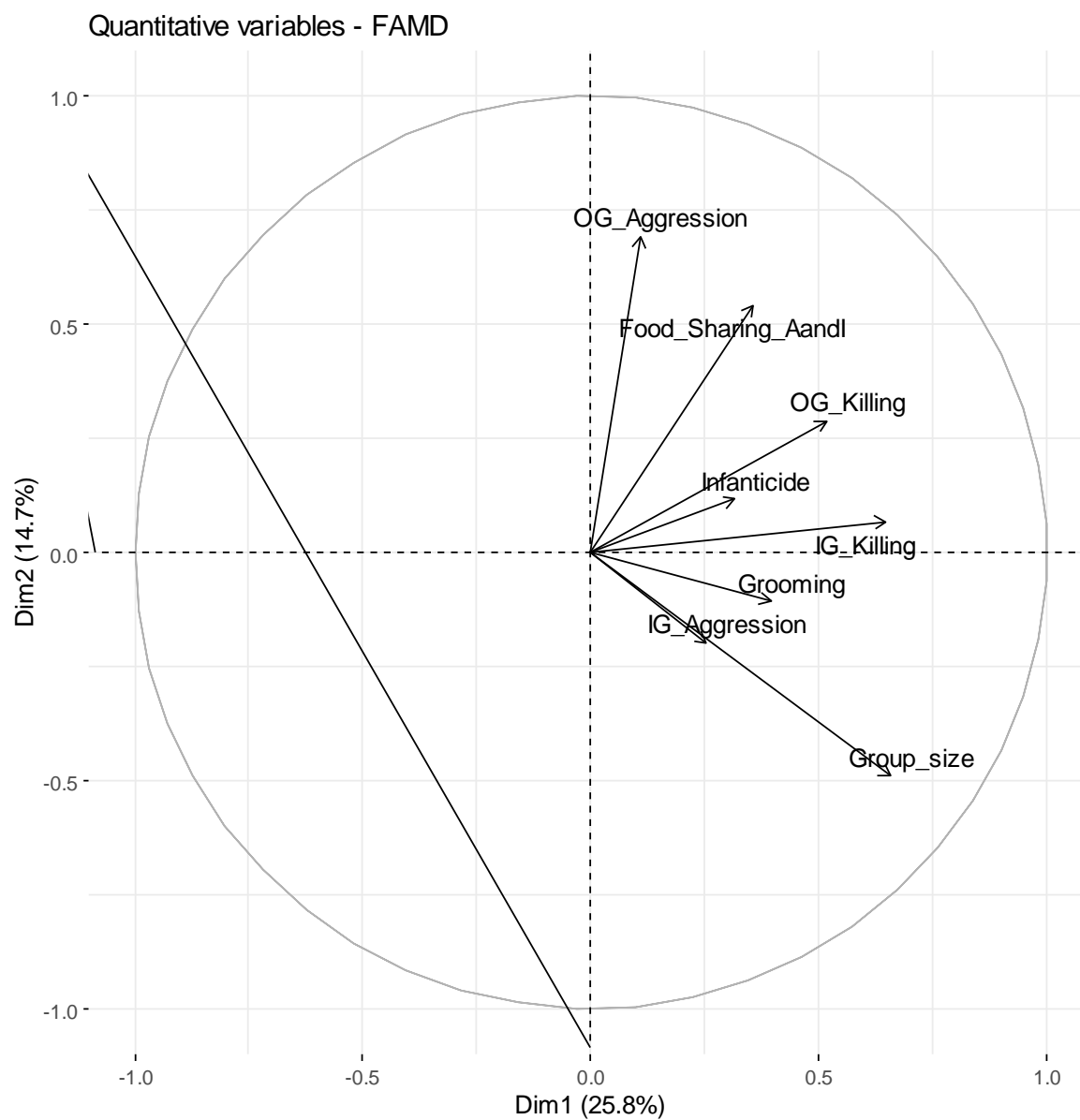


Visualisation of the contribution of variables to the principal dim-5. The red dashed line on the graph above indicates the expected average value, If the contributions were uniform

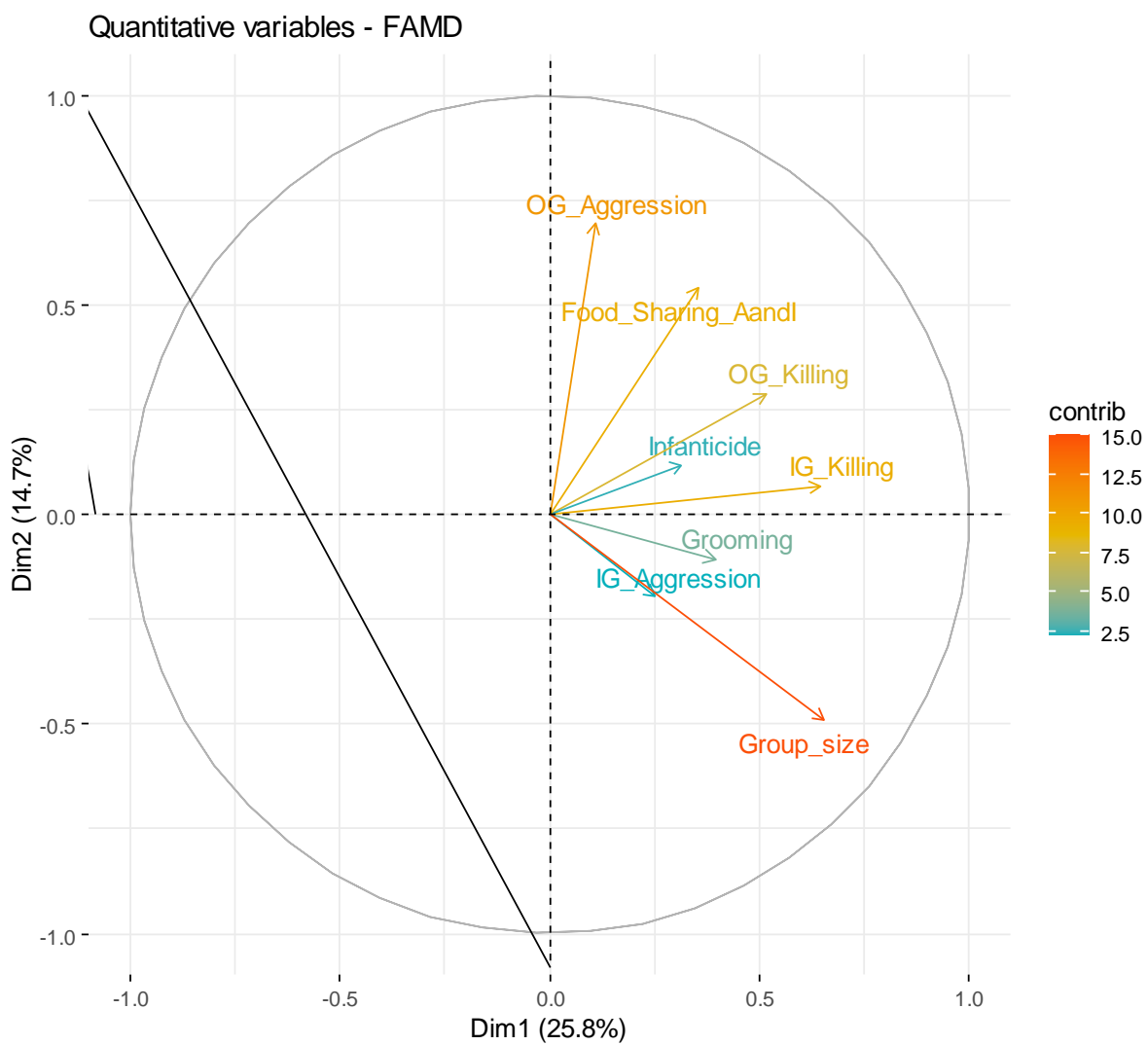




The correlation between qualitative and quantitative variables and the principal dimensions



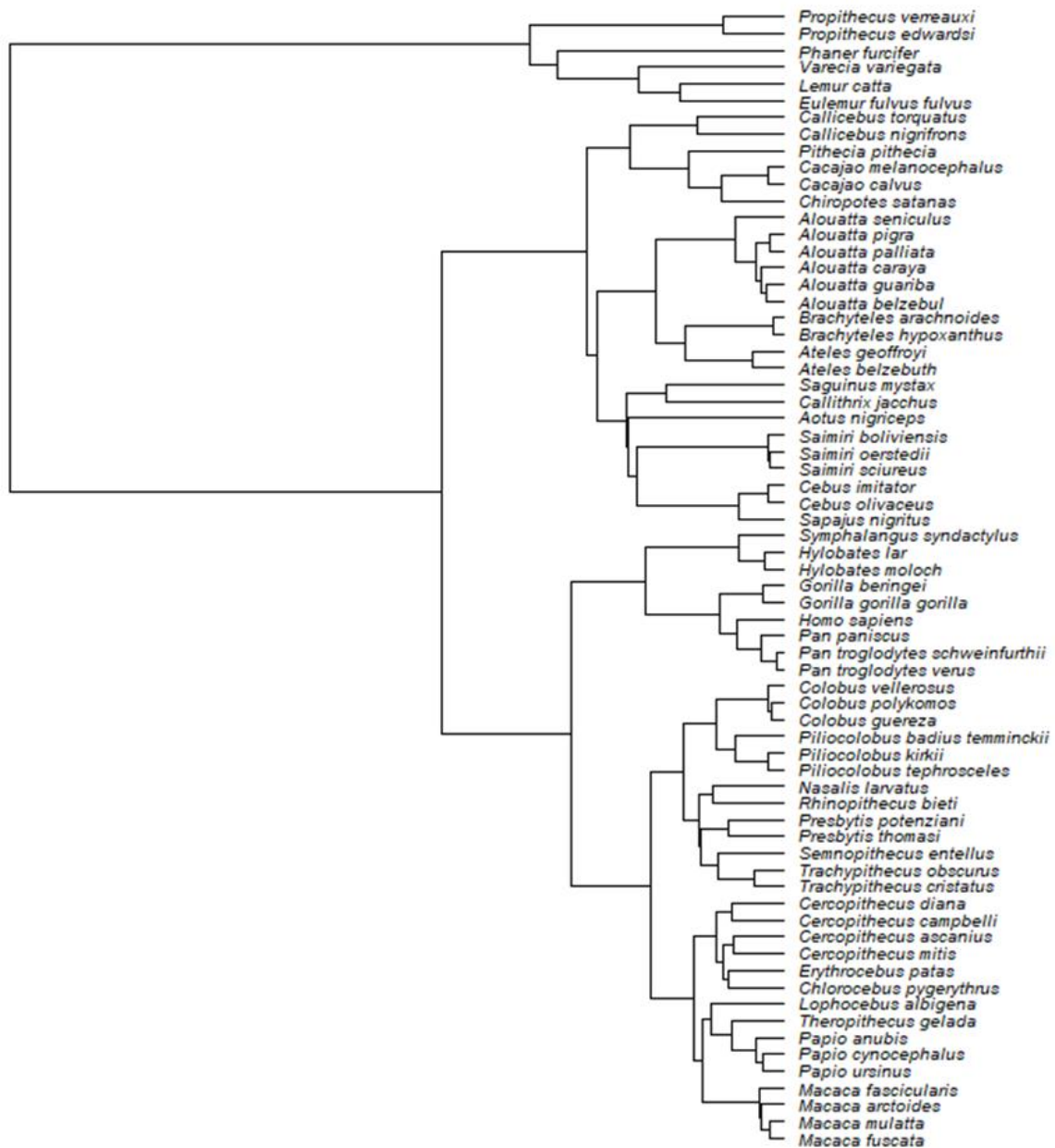
Quantitative/binary variables plotted against the principal dimensions



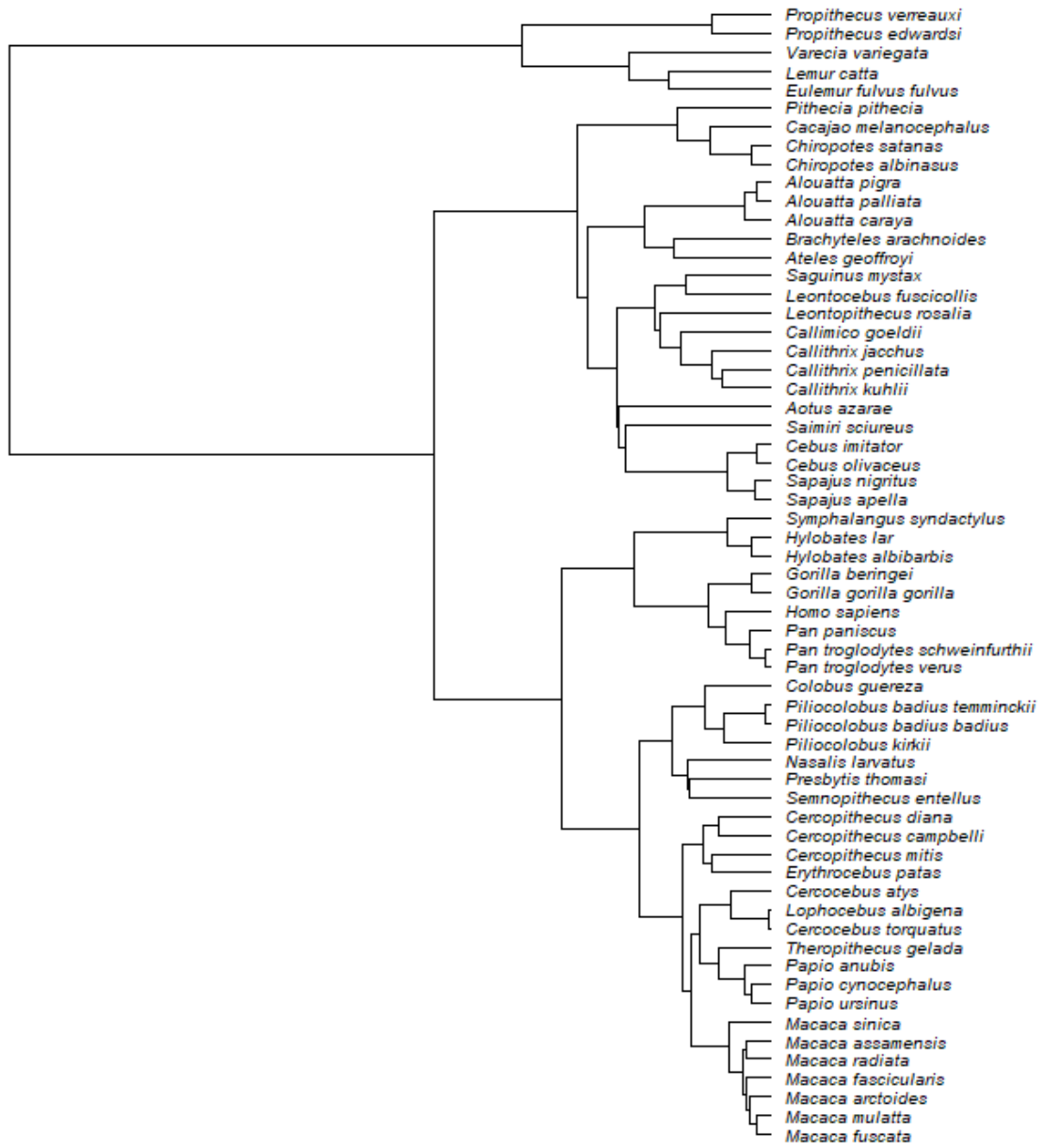
Quantitative by contribution to the principle dimensions

## Appendix 5B – Phylogenetic trees used in the analysis

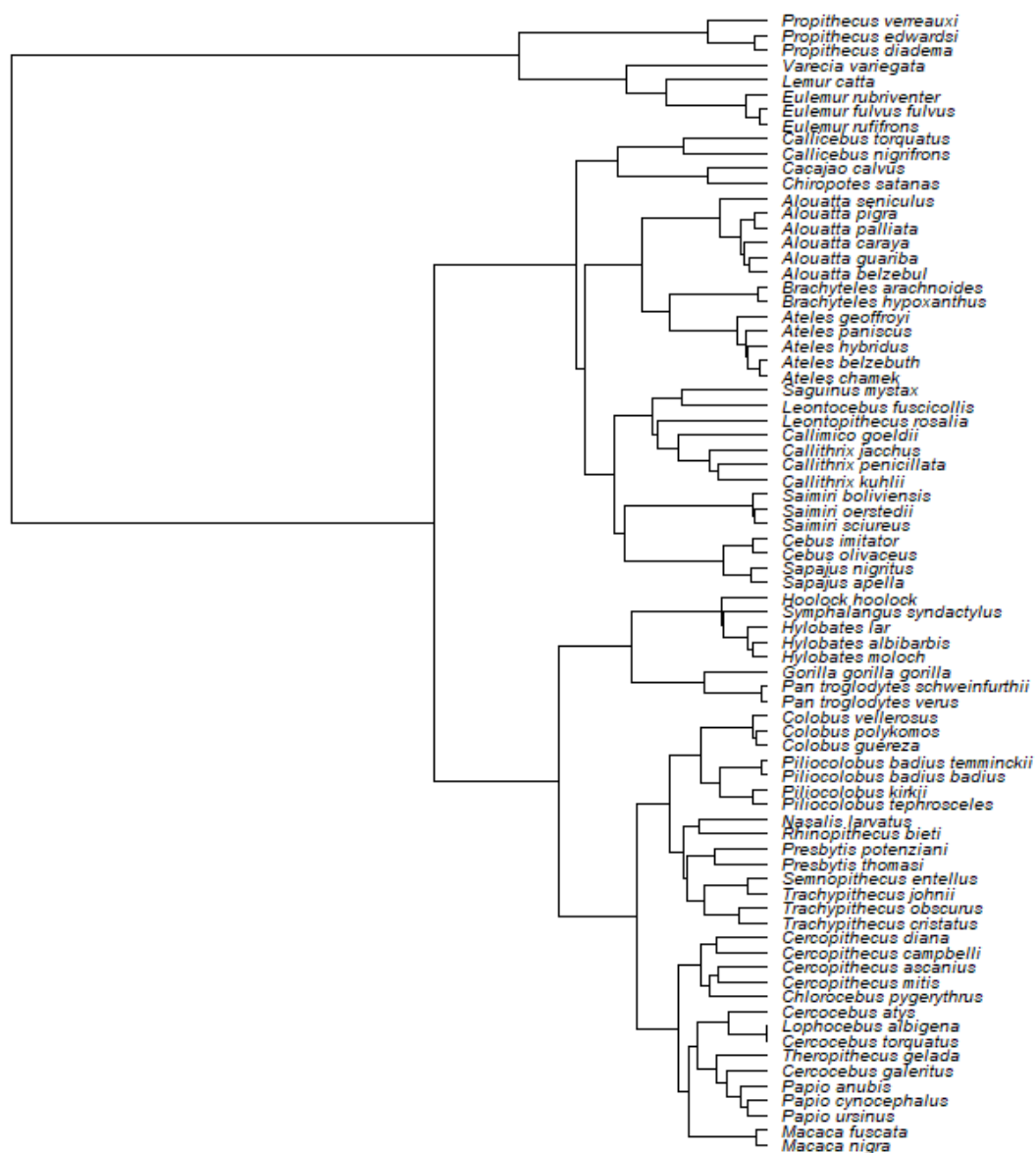
## 5B.1 Grooming data tree (68 species)



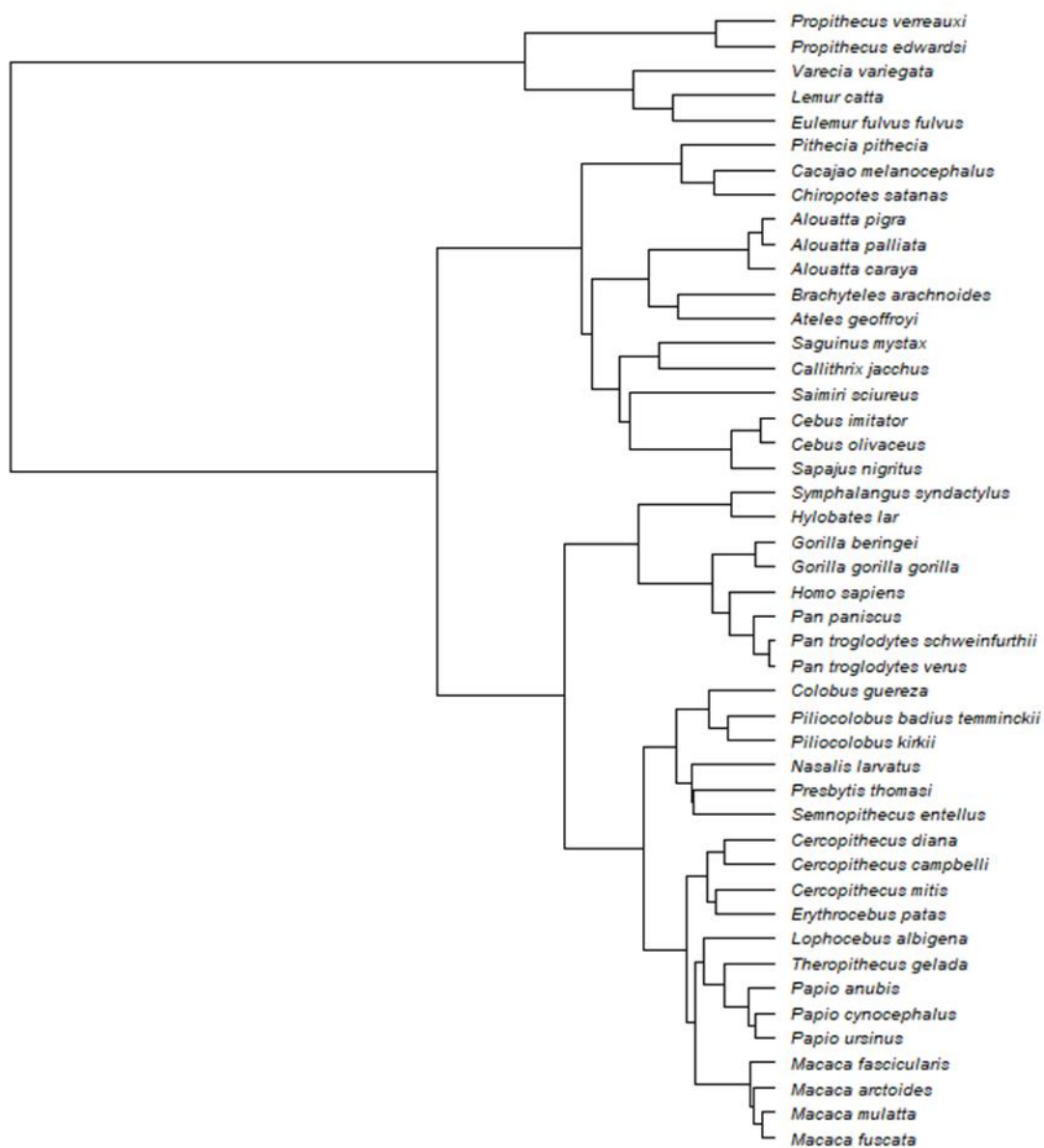
## 5B.2 Food-sharing data tree (61 species)



## 5B.3 Time-social data tree (77 species)



## 5B.4 Mixed model data tree (46 species)



## Appendix 5C – R Script

## #Load packages

```
library(caper)
```

```
library(ggplot2)
```

```
library(ggtree)
```

```
library(brms)
```

## ## Import data

## # Phylogeny (food, grooming, social, all)

```
phylo1 <- ape::read.nexus("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3  
Dataset\\61taxafood.nex")
```

```
phylo1$tip.label<- gsub("_", " ", phylo1$tip.label)
```

```
phylo2 <- ape::read.nexus("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3  
Dataset\\77treesocial.nex")
```

```
phylo2$tip.label<- gsub("_", " ", phylo2$tip.label)
```

```
phylo3 <- ape::read.nexus("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3  
Dataset\\68treegrooming.nex")
```

```
phylo3$tip.label<- gsub("_", " ", phylo3$tip.label)
```

```
phylo4 <- ape::read.nexus("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3  
Dataset\\46treeall.nex")
```

```
phylo4$tip.label<- gsub("_", " ", phylo4$tip.label)
```



## # Species traits (food sharing)

```
file.choose()
```

```
data1<-read.table("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3  
Dataset\\Q3 Food txt.txt", header=T, stringsAsFactors=F)
```

```
data1$SpeciesTree<- gsub("_", " ", data1$SpeciesTree)
```

## #Species traits (social time)

```
file.choose()
```

```
dataF<-read.table("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3  
Dataset\\Q3 Social time.txt", header=T, stringsAsFactors=F)
```

```
dataF$SpeciesTree<- gsub("_", " ", dataF$SpeciesTree)
```

## # Species traits (grooming)

```
file.choose()
```

```
dataG<-read.table("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3  
Dataset\\Q3 grooming txt.txt", header=T, stringsAsFactors=F)
```

```
dataG$SpeciesTree<- gsub("_", " ", dataG$SpeciesTree)
```

## #Species traits (all)

```
file.choose()
```

```
dataA<-read.table("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3  
Dataset\\Mixed data txt.txt", header=T, stringsAsFactors=F)
```

```
dataA$SpeciesTree<- gsub("_", " ", dataA$SpeciesTree)
```

## # Check whether species names match, and correct if not

```
data1$SpeciesTree %in% phylo1$tip.label
```

```
dataF$SpeciesTree %in% phylo2$tip.label
```

```
dataG$SpeciesTree %in% phylo3$tip.label
```

```
dataA$SpeciesTree %in% phylo4$tip.label
```

```
#matrix (alter phylo as appropriate)
```

```
A <- ape::vcv.phylo(phylo4, corr = FALSE)
```

```
#Priors
```

```
priorA <- c(prior(normal(0, 10), class = Intercept, resp = OGGKilling),
            prior(normal(0, 5), class = b, resp = OGGKilling),
            prior(normal(0, 10), class = Intercept, resp = IGGKilling),
            prior(normal(0, 5), class = b, resp = IGGKilling))
```

```
priorB <- c(prior(normal(0, 10), class = Intercept, resp = OGGKilling),
            prior(normal(0, 5), class = b, resp = OGGKilling),
            prior(normal(0, 10), class = Intercept, resp = IGGKilling),
            prior(normal(0, 5), class = b, resp = IGGKilling),
            prior(normal(0, 10), class = Intercept, resp = Coalition),
            prior(normal(0, 5), class = b, resp = Coalition))
```

```
priorC <- c(prior(normal(0, 10), class = Intercept, resp = Infanticide),
            prior(normal(0, 5), class = b, resp = Infanticide))
```

```
priorD <- c(prior(normal(0, 10), class = Intercept, resp = OGGKilling),
            prior(normal(0, 5), class = b, resp = OGGKilling),
            prior(normal(0, 10), class = Intercept, resp = IGGKilling),
            prior(normal(0, 5), class = b, resp = IGGKilling))
```

```
priorE <- c(prior(normal(0, 10), class = Intercept, resp = IGAggression),
  prior(normal(0, 5), class = b, resp = IGAggression),
  prior(normal(0, 10), class = Intercept, resp = OGAggression),
  prior(normal(0, 5), class = b, resp = OGAggression))
```

### ##Run models

# Model A - Both a direct and indirect (through its influence on Coalitions) effect of grooming on OGAggression:

```
bfkillG <- bf(mvbind(OG_Killing, IG_Killing) ~ Grooming + Coalition + (1|gr(SpeciesTree,
cov= A)))
```

```
bfCoal <- bf(Coalition ~ Grooming + (1|gr(SpeciesTree, cov= A)))
```

```
Coalitionkill1<- brm(bfkillG + bfCoal + set_rescor(FALSE),
  family = list(bernoulli(), bernoulli(), bernoulli()),
  data= dataG,
  prior = priorB,
  data2= list(A = A),
  cores = future::availableCores() -1,
  iter= 9e3,
  control= list(adapt_delta= .99, max_treedepth= 15),
  save_pars = save_pars(all = TRUE))
```

```
saveRDS(Coalitionkill1, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\Coalitionkill1.rds")
```

```
summary(Coalitionkill1, waic= T); bayes_R2(Coalitionkill1)
```

```
bfkillIF <- bf(mvbind(OG_Killing, IG_Killing) ~ Food_Sharing_AandI + Coalition +
(1|gr(SpeciesTree, cov= A)))
```

```
bfCoalF <- bf(Coalition ~ Food_Sharing_AandI + (1|gr(SpeciesTree, cov= A)))
```

```
Coalitionkill1F<- brm(bfkillF + bfCoalF + set_rescor(FALSE),
  family = list(bernoulli(), bernoulli(), bernoulli()),
  data= data1,
  prior = priorB,
  data2= list(A = A),
  cores = future::availableCores() -1,
  iter= 9e3,
  control= list(adapt_delta= .99, max_treedepth= 15),
  save_pars = save_pars(all = TRUE))
```

```
saveRDS(Coalitionkill1F, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\Coalitionkill1F.rds")
```

```
summary(Coalitionkill1F, waic= T); bayes_R2(Coalitionkill1F)
```

```
bfinfG <- bf(Infanticide ~ Grooming + Coalition + (1|gr(SpeciesTree, cov= A)))
```

```
bfCoal <- bf(Coalition ~ Grooming + (1|gr(SpeciesTree, cov= A)))
```

```
CoalitionInf1<- brm(bfinfG + bfCoal + set_rescor(FALSE),
  family = list(bernoulli(), bernoulli()),
  data= dataG,
  prior = priorC,
  data2= list(A = A),
  cores = future::availableCores() -1,
  iter= 9e3,
  control= list(adapt_delta= .99, max_treedepth= 15),
  save_pars = save_pars(all = TRUE))
```

```
saveRDS(CoalitionInf1, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\CoalitionInf1.rds")
```

```
summary(CoalitionInf1, waic= T); bayes_R2(CoalitionInf1)
```

```
bfinfF <- bf(Infanticide ~ Food_Sharing_AandI + Coalition + (1|gr(SpeciesTree, cov= A)))
```

```
bfCoalF <- bf(Coalition ~ Food_Sharing_AandI + (1|gr(SpeciesTree, cov= A)))
```

```
CoalitionInf1F<- brm(bfinfF + bfCoalF + set_rescor(FALSE),
  family = list(bernoulli(), bernoulli()),
  data= data1,
  prior = priorC,
  data2= list(A = A),
  cores = future::availableCores() -1,
  iter= 9e3,
  control= list(adapt_delta= .99, max_treedepth= 15),
  save_pars = save_pars(all = TRUE))
```

```
saveRDS(CoalitionInf1F, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\CoalitionInf1F.rds")
```

```
summary(CoalitionInf1F, waic= T); bayes_R2(CoalitionInf1F)
```

```
bfaggG <- bf(mvbind(OG_Aggression, IG_Aggression) ~ Food_Sharing_AandI + Coalition
+ (1|gr(SpeciesTree, cov= A)))
```

```
bfCoalaggF <- bf(Coalition ~ Food_Sharing_AandI + (1|gr(SpeciesTree, cov= A)))
```

```
Coalitionagg1<- brm(bfaggG + bfCoalaggF + set_rescor(FALSE),
  family = list(zero_one_inflated_beta(), hurdle_gamma(), bernoulli()),
  data= data1,
```

```
prior = priorE,
data2= list(A = A),
cores = future::availableCores() -1,
iter= 8e3,
control= list(adapt_delta= .999, max_treedepth= 19),
save_pars = save_pars(all = TRUE))
```

```
saveRDS(Coalitionagg1, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\Coalitionagg1.rds")
```

```
summary(Coalitionagg1, waic= T); bayes_R2(Coalitionagg1)
```

### #Model B - two independent direct effects:

```
Coalitionkill2<- brm(mvbind(OG_Killing, IG_Killing) ~ Grooming + Coalition +
(1|p|gr(SpeciesTree, cov = A)),
```

```
family = list(bernoulli(), bernoulli()),
data= dataG,
prior = priorA,
data2= list(A = A),
cores = future::availableCores() -1,
iter= 8e3,
control= list(adapt_delta= .99, max_treedepth= 15),
save_pars = save_pars(all = TRUE))
```

```
saveRDS(Coalitionkill2, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\Coalitionkill2.rds")
```

```
summary(Coalitionkill2, waic= T); bayes_R2(Coalitionkill2)
```

```
Coalitionkill2F<- brm(mvbind(OG_Killing, IG_Killing) ~ Food_Sharing_AandI + Coalition
+ (1|p|gr(SpeciesTree, cov = A)),
```

```

family = list(bernoulli(), bernoulli()),
data= data1,
prior = priorA,
data2= list(A = A),
cores = future::availableCores() -1,
iter= 8e3,
control= list(adapt_delta= .99, max_treedepth= 15),
save_pars = save_pars(all = TRUE))

```

```

saveRDS(Coalitionkill2F, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\Coalitionkill2F.rds")

```

```

summary(Coalitionkill2F, waic= T); bayes_R2(Coalitionkill2F)

```

```

Coalitioninf2<- brm(Infanticide ~ Grooming + Coalition + (1|p|gr(SpeciesTree, cov = A)),
  family = bernoulli(),
  data= dataG,
  data2= list(A = A),
  cores = future::availableCores() -1,
  iter= 5e3,
  control= list(adapt_delta= .999, max_treedepth= 20),
  save_pars = save_pars(all = TRUE))

```

```

saveRDS(Coalitioninf2, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\Coalitioninf2.rds")

```

```

summary(Coalitioninf2, waic= T); bayes_R2(Coalitioninf2)

```

```

Coalitioninf2F<- brm(Infanticide ~ Food_Sharing_AandI + Coalition + (1|p|gr(SpeciesTree,
cov = A)),
  family = bernoulli(),
  data= data1,

```

```

data2= list(A = A),
cores = future::availableCores() -1,
iter= 5e3,
control= list(adapt_delta= .999, max_treedepth= 20),
save_pars = save_pars(all = TRUE))

```

```

saveRDS(Coalitioninf2F, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\Coalitioninf2F.rds")

```

```

summary(Coalitioninf2F, waic= T); bayes_R2(Coalitioninf2F)

```

```

Coalitionagg2F<- brm(mvbind(OG_Aggression, IG_Aggression) ~ Food_Sharing_AandI +
Coalition + (1|gr(SpeciesTree, cov = A)),

```

```

family = list(zero_one_inflated_beta(), hurdle_gamma()),
data= data1,
prior = priorE,
data2= list(A = A),
cores = future::availableCores() -1,
iter= 9e3,
control= list(adapt_delta= .99, max_treedepth= 15),
save_pars = save_pars(all = TRUE))

```

```

saveRDS(Coalitionagg2F, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\Coalitionagg2F.rds")

```

```

summary(Coalitionagg2F, waic= T); bayes_R2(Coalitionagg2F)

```

**#Model C - only an indirect effect of grooming through Coalitions:**

```

bfkill3G <- bf(mvbind(OG_Killing, IG_Killing) ~ Coalition + (1|gr(SpeciesTree, cov= A)))

```

```

bfCoal3 <- bf(Coalition ~ Grooming + (1|gr(SpeciesTree, cov= A)))

```



```

Coalitionkill3G<- brm(bfkill3G + bfCoal3 + set_rescor(FALSE),
  family = list(bernoulli(), bernoulli(), bernoulli()),
  data= dataG,
  prior = priorB,
  data2= list(A = A),
  cores = future::availableCores() -1,
  iter= 9e3,
  control= list(adapt_delta= .99, max_treedepth= 15),
  save_pars = save_pars(all = TRUE))

saveRDS(Coalitionkill3G, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\Coalitionkill3G.rds")

summary(Coalitionkill3G, waic= T); bayes_R2(Coalitionkill3G)

bfkill3F <- bf(mvbind(OG_Killing, IG_Killing) ~ Coalition + (1|gr(SpeciesTree, cov= A)))
bfCoal3F <- bf(Coalition ~ Food_Sharing_AandI + (1|gr(SpeciesTree, cov= A)))

Coalitionkill3F<- brm(bfkill3F + bfCoal3F + set_rescor(FALSE),
  family = list(bernoulli(), bernoulli(), bernoulli()),
  data= data1,
  prior = priorB,
  data2= list(A = A),
  cores = future::availableCores() -1,
  iter= 9e3,
  control= list(adapt_delta= .99, max_treedepth= 15),
  save_pars = save_pars(all = TRUE))

```

```
saveRDS(Coalitionkill3F, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\Coalitionkill3F.rds")
```

```
summary(Coalitionkill3F, waic= T); bayes_R2(Coalitionkill3F)
```

```
bfinf3G <- bf(Infanticide ~ Coalition + (1|gr(SpeciesTree, cov= A)))
```

```
bfCoal3 <- bf(Coalition ~ Grooming + (1|gr(SpeciesTree, cov= A)))
```

```
Coalitioninf3G<- brm(bfinf3G + bfCoal3 + set_rescor(FALSE),
  family = list(bernoulli(), bernoulli()),
  data= dataG,
  prior = priorC,
  data2= list(A = A),
  cores = future::availableCores() -1,
  iter= 9e3,
  control= list(adapt_delta= .99, max_treedepth= 15),
  save_pars = save_pars(all = TRUE))
```

```
saveRDS(Coalitioninf3G, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\Coalitioninf3G.rds")
```

```
summary(Coalitioninf3G, waic= T); bayes_R2(Coalitioninf3G)
```

```
bfinf3F <- bf(Infanticide ~ Coalition + (1|gr(SpeciesTree, cov= A)))
```

```
bfCoal3F <- bf(Coalition ~ Food_Sharing_AandI + (1|gr(SpeciesTree, cov= A)))
```

```
Coalitioninf3F<- brm(bfinf3F + bfCoal3F + set_rescor(FALSE),
  family = list(bernoulli(), bernoulli()),
  data= data1,
  prior = priorC,
```

```

data2= list(A = A),
cores = future::availableCores() -1,
iter= 9e3,
control= list(adapt_delta= .99, max_treedepth= 15),
save_pars = save_pars(all = TRUE))

```

```

saveRDS(Coalitioninf3F, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\Coalitioninf3F.rds")

```

```

summary(Coalitioninf3F, waic= T); bayes_R2(Coalitioninf3F)

```

```

bfagg3F <- bf(mvbind(OG_Aggression, IG_Aggression) ~ Coalition + (1|gr(SpeciesTree,
cov= A)))

```

```

bfCoal3F <- bf(Coalition ~ Food_Sharing_AandI + (1|gr(SpeciesTree, cov= A)))

```

```

Coalitionagg3F<- brm(bfagg3F + bfCoal3F + set_rescor(FALSE),
  family = list(zero_one_inflated_beta(), hurdle_gamma() , bernoulli()),
  data= data1,
  prior = priorE,
  data2= list(A = A),
  cores = future::availableCores() -1,
  iter= 9e3,
  control= list(adapt_delta= .99, max_treedepth= 15),
  save_pars = save_pars(all = TRUE))

```

```

saveRDS(Coalitionagg3F, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3
Dataset\\Coalitionagg3F.rds")

```

```

summary(Coalitionagg3F, waic= T); bayes_R2(Coalitionagg3F)

```

```
#Checks and plots (model name altered as appropriate)
```

```
#Plots
```

```
pairs(Coalitioninf3G)
```

```
plot(Coalitioninf3G)
```

```
plot(conditional_effects(Coalitioninf3G), points = TRUE)
```

```
#Additional info regarding percentage distribution above or below zero.
```

```
post <- posterior_samples(Coalitioninf3G)
```

```
Meanfood <-
```

```
mean(post$cor_SpeciesTree__IGKilling_Food_Sharing_AandI__Coalition_Intercept > 0)
```

```
plot(Meanfood)
```

```
#PP Checks (adjust outcome variable and model as necessary)
```

```
pp_check(Coalitioninf3G, resp= "Grooming", nsamples= 1e2)
```

```
pp_check(Coalitioninf3G, resp= "IGAggression", ndraws = 1e2)
```

```
pp_check(Coalitioninf3G, resp= "Coalition", ndraws = 1e2)
```

```
pp_check(Coalitioninf3G, resp= "IGKilling", ndraws = 1e2)
```

```
pp_check(Coalitioninf3G, resp= "Infanticide", ndraws= 1e2)
```

```
#load files/models (load models that were created as part of a different session)
```

```
file.choose()
```

```
Coalitioninf3G<- readRDS("C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3  
Dataset\\Coalitioninf3G.rds")
```

```
##loo compare and k-fold (model name altered as appropriate)
```

```
#Grooming adult lethal
```

```
loo3LG<- add_criterion(Coalitionionkill1, "kfold")
```

```
loo2LG<- add_criterion(Coalitionkill2, "kfold")
```

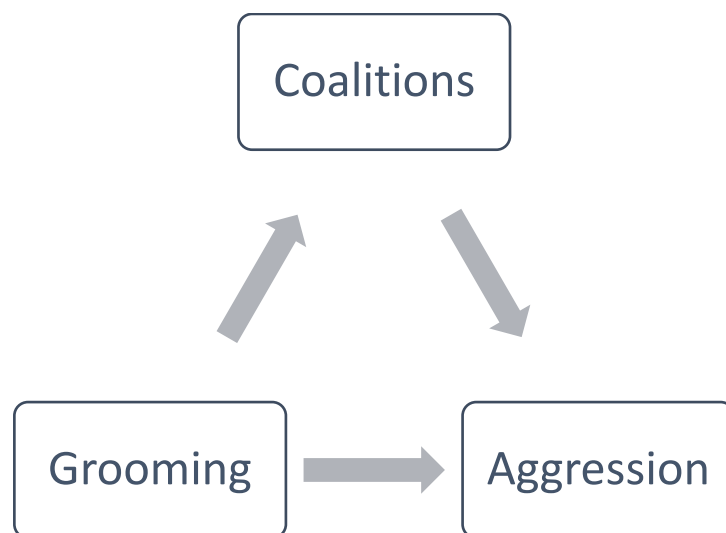
```
loo1LG<- add_criterion(Coalitionkill3G, "kfold")
```

```
saveRDS(loo3LG, "C:\\Users\\swake\\OneDrive - University of Lincoln\\Question 3  
Dataset\\loo3LG.rds")
```

```
loo_compare(loo1LG, loo2LG, loo3LG, criterion = "kfold")
```

```
# Repeat for food-sharing and infanticide
```

## Appendix 5D – Model A - Both a direct and indirect effect

*5D.1 Model A(i) Adulthood and grooming*

```

> summary(Coalitionkill11, waic= T); bayes_R2(Coalitionkill11)
Family: MV(bernoulli, bernoulli, bernoulli)
Links: mu = logit
       mu = logit
       mu = logit
Formula: OG_Killing ~ Grooming + Coalition + (1 | gr(SpeciesTree, cov = A))

```

```
IG_Killing ~ Grooming + Coalition + (1 | gr(SpeciesTree, cov = A))
```

```
Coalition ~ Grooming + (1 | gr(SpeciesTree, cov = A))
```

```
Data: dataG (Number of observations: 68)
```

```
Draws: 4 chains, each with iter = 9000; warmup = 4500; thin = 1;
```

```
total post-warmup draws = 18000
```

#### Group-Level Effects:

```
~SpeciesTree (Number of levels: 68)
```

	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGKilling_Intercept)	1.08	1.52	0.05	4.96	1.00	1239	4488
sd(IGKilling_Intercept)	0.59	0.68	0.02	2.24	1.00	1774	3998
sd(Coalition_Intercept)	3.81	3.69	0.76	12.16	1.00	6127	6573

#### Population-Level Effects:

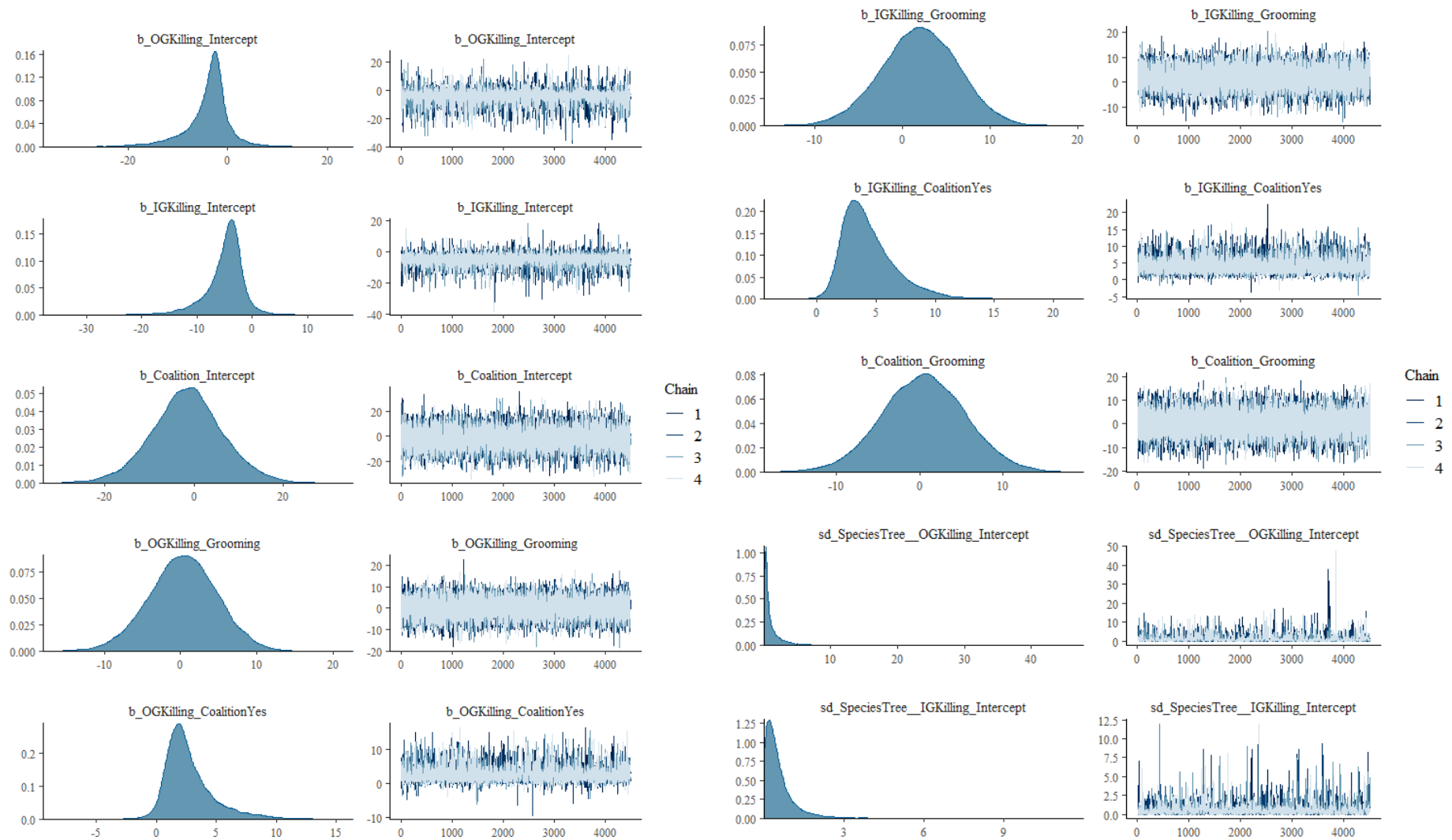
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGKilling_Intercept	-3.97	4.85	-16.44	4.46	1.00	7683	5917
IGKilling_Intercept	-5.00	3.71	-14.19	0.93	1.00	6774	4680
Coalition_Intercept	-1.49	8.04	-17.70	14.70	1.00	12229	12951
OGKilling_Grooming	0.31	4.45	-8.64	8.85	1.00	20406	13832
OGKilling_CoalitionYes	2.73	2.11	-0.11	8.38	1.00	4459	5731
IGKilling_Grooming	1.93	4.36	-6.88	10.30	1.00	16501	11570

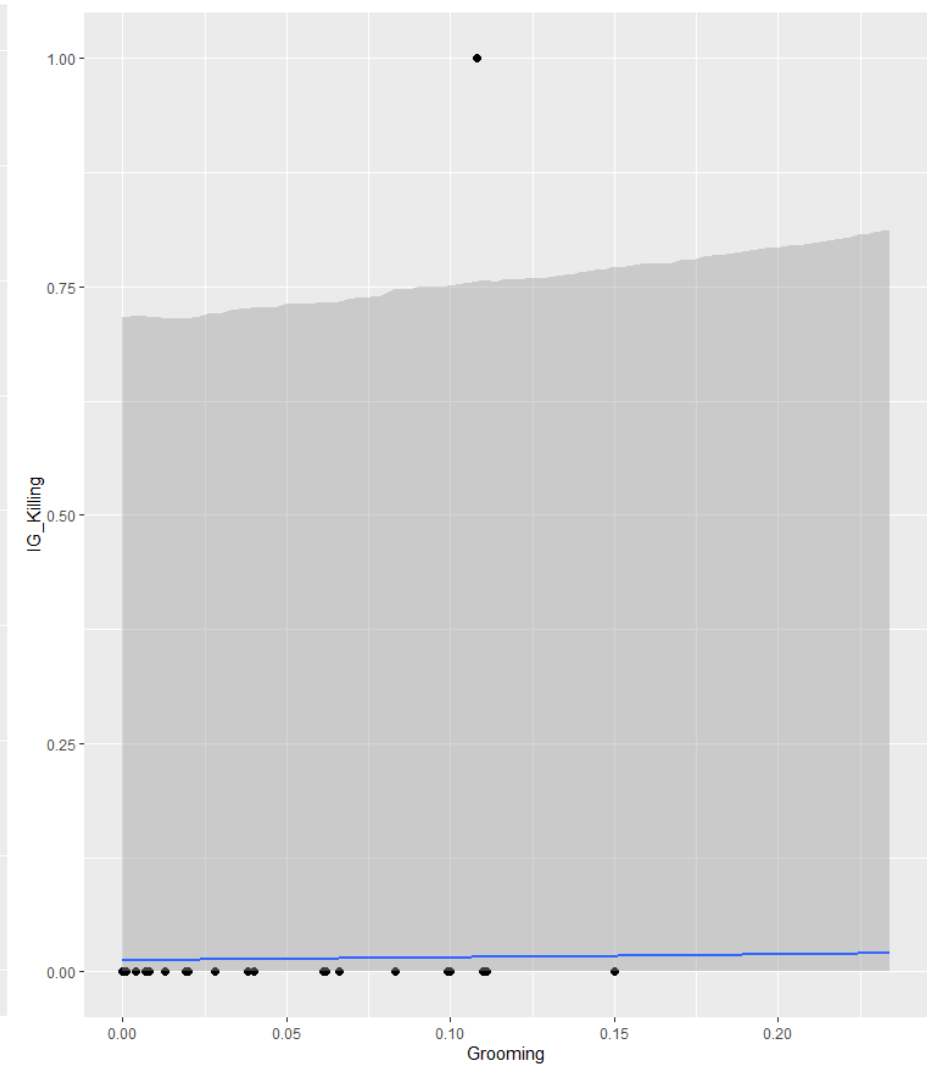
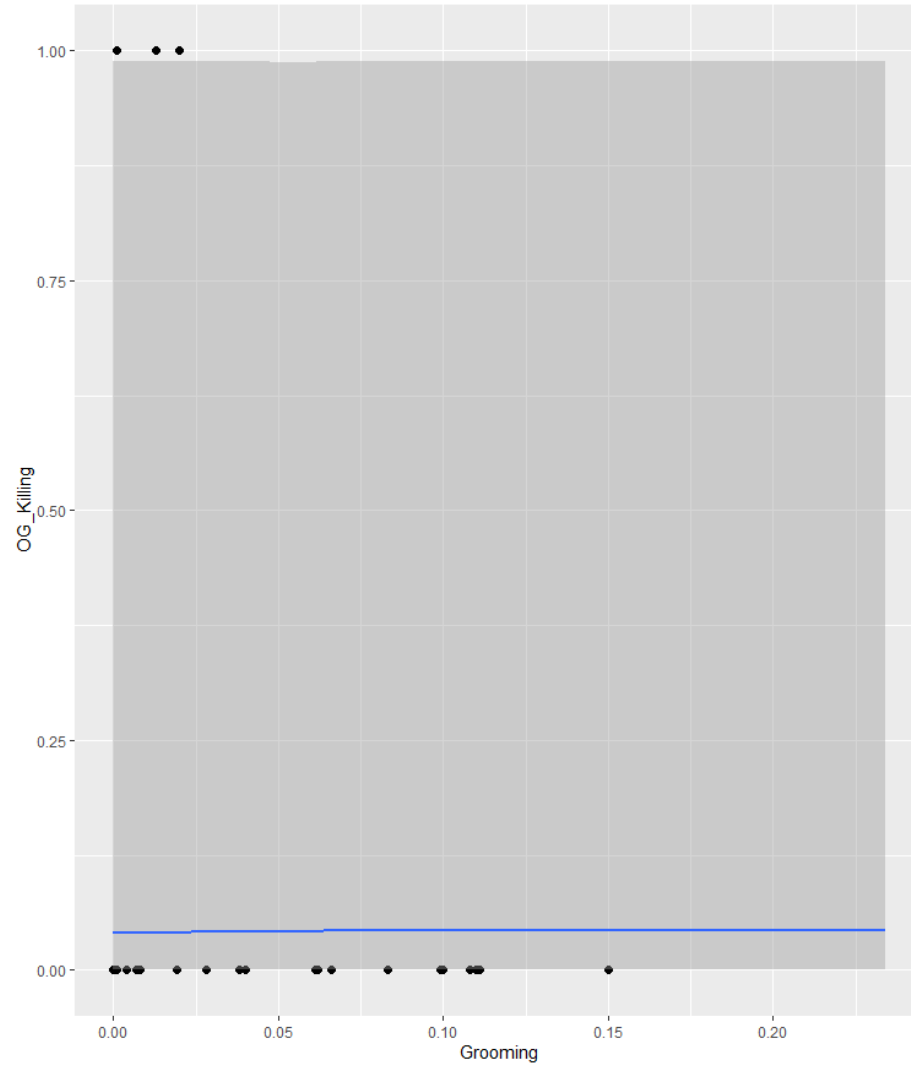
IGKilling_CoalitionYes	4.38	2.23	1.26	9.87	1.00	5960	6732
Coalition_Grooming	0.48	5.00	-9.37	10.30	1.00	29078	13339

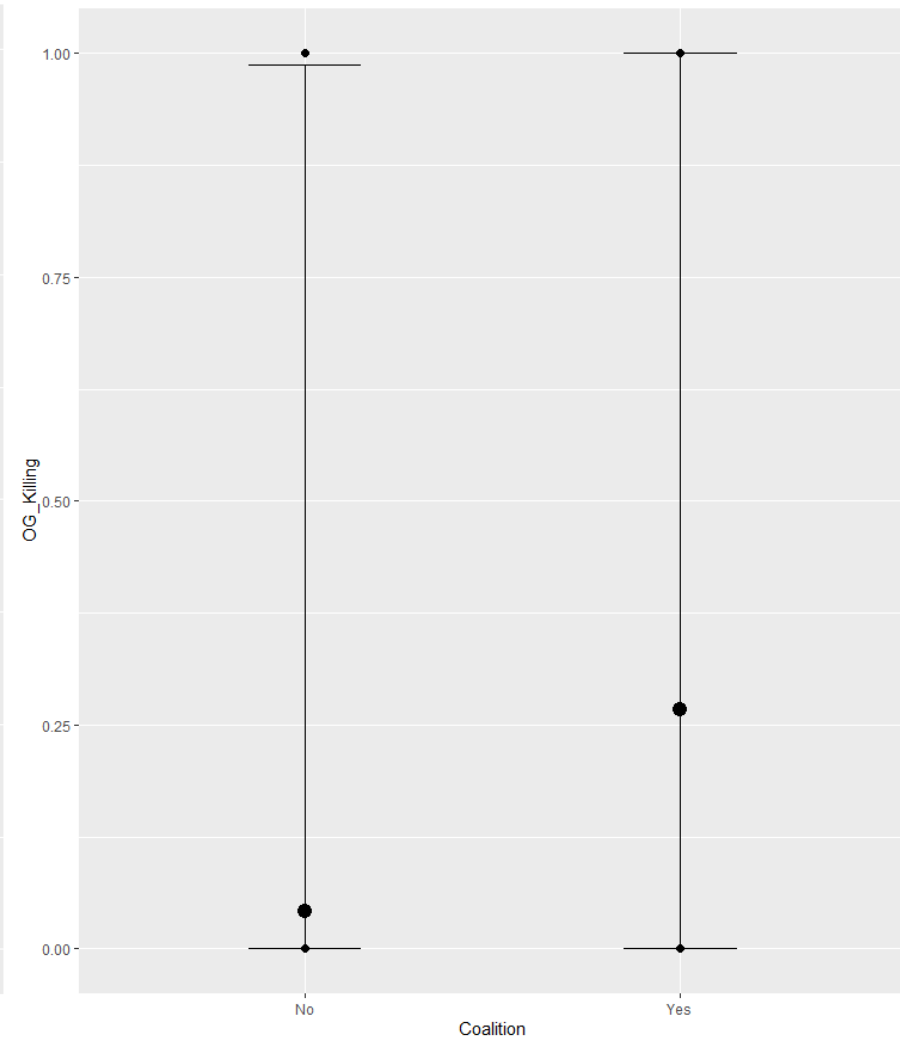
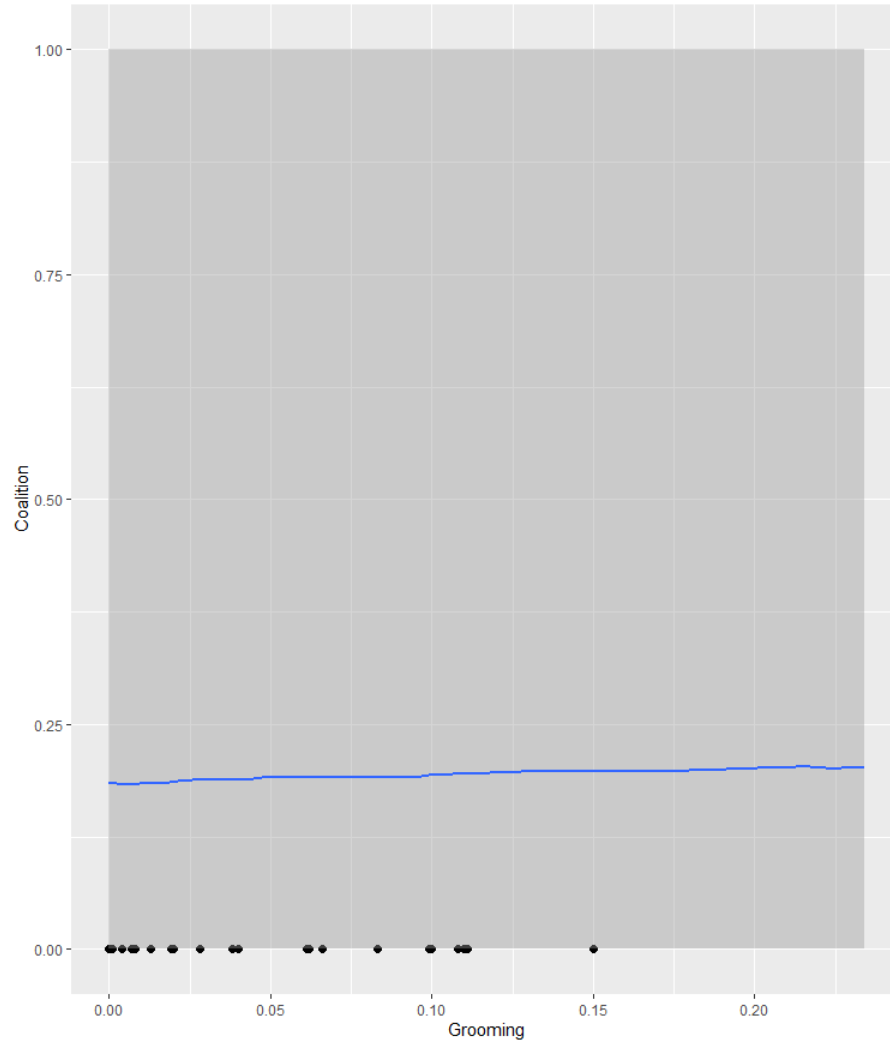
Draws were sampled using `sampling(NUTS)`. For each parameter, `Bulk_ESS` and `Tail_ESS` are effective sample size measures, and `Rhat` is the potential scale reduction factor on split chains (at convergence, `Rhat` = 1).

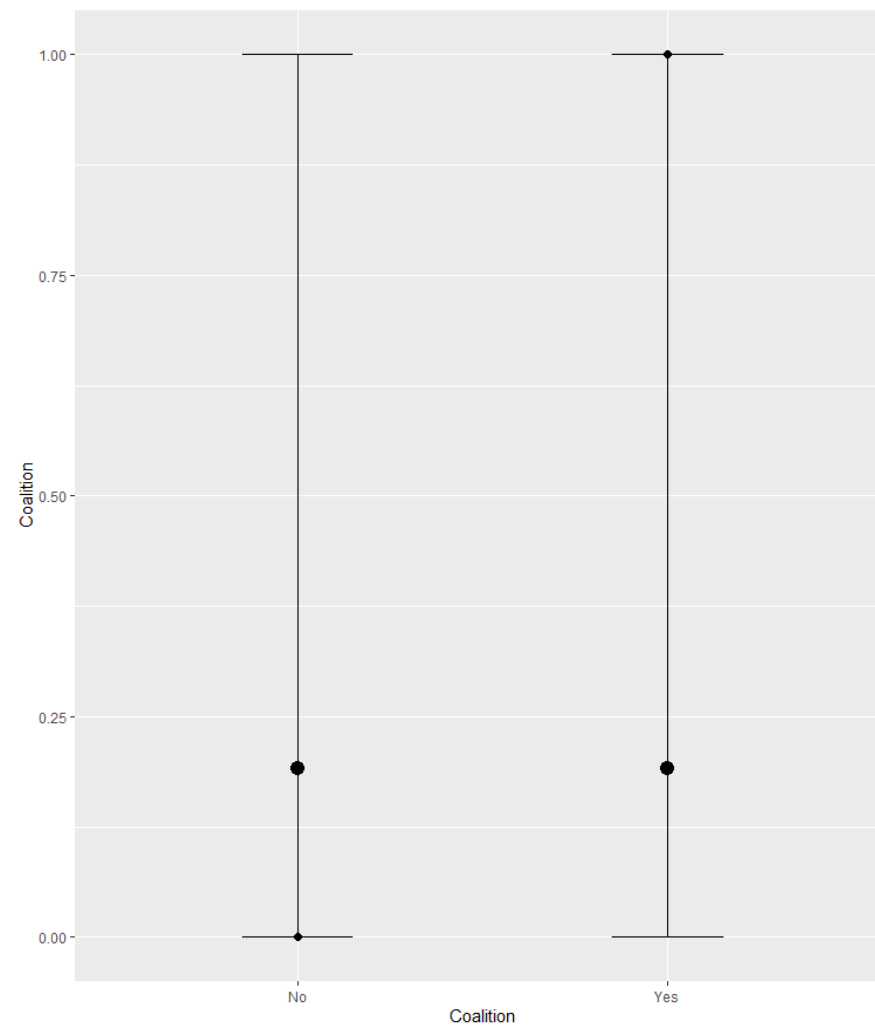
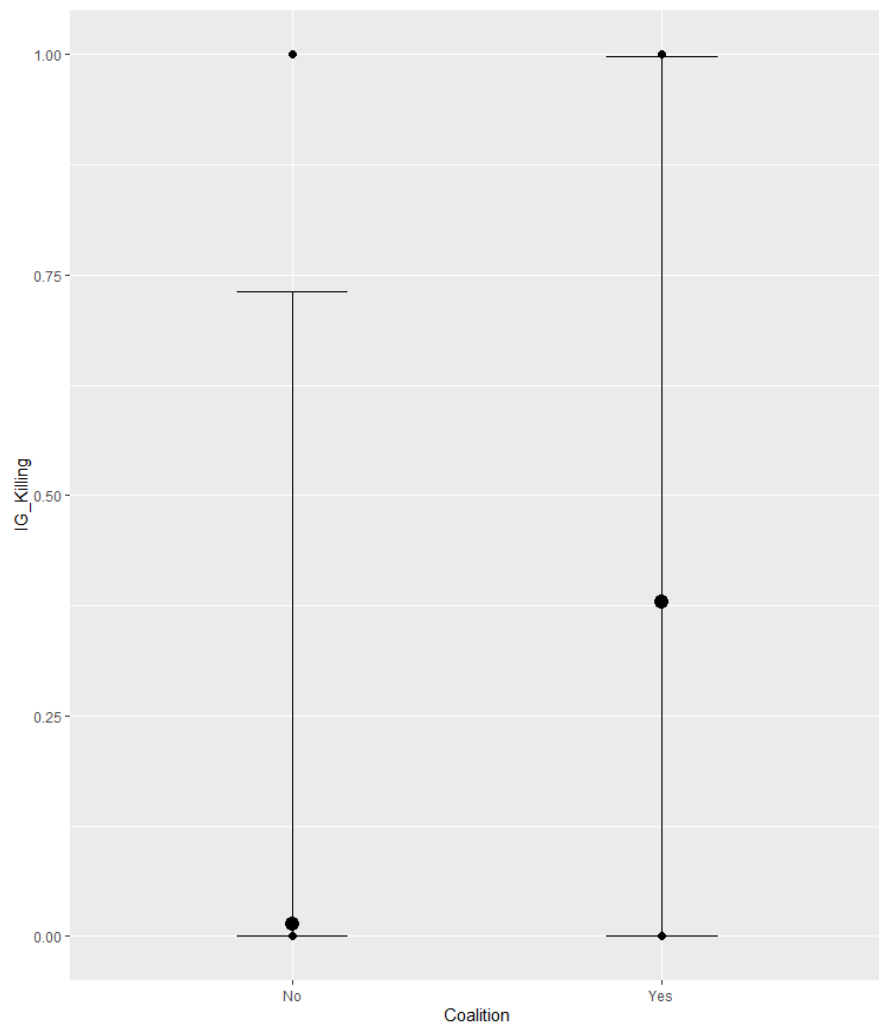
	Estimate	Est.Error	Q2.5	Q97.5
R2OGKilling	0.4263116	0.2292653	0.07024735	0.8949251
R2IGKilling	0.3689595	0.1758231	0.09644996	0.7572975
R2Coalition	0.8445293	0.1071329	0.58319171	0.9925771

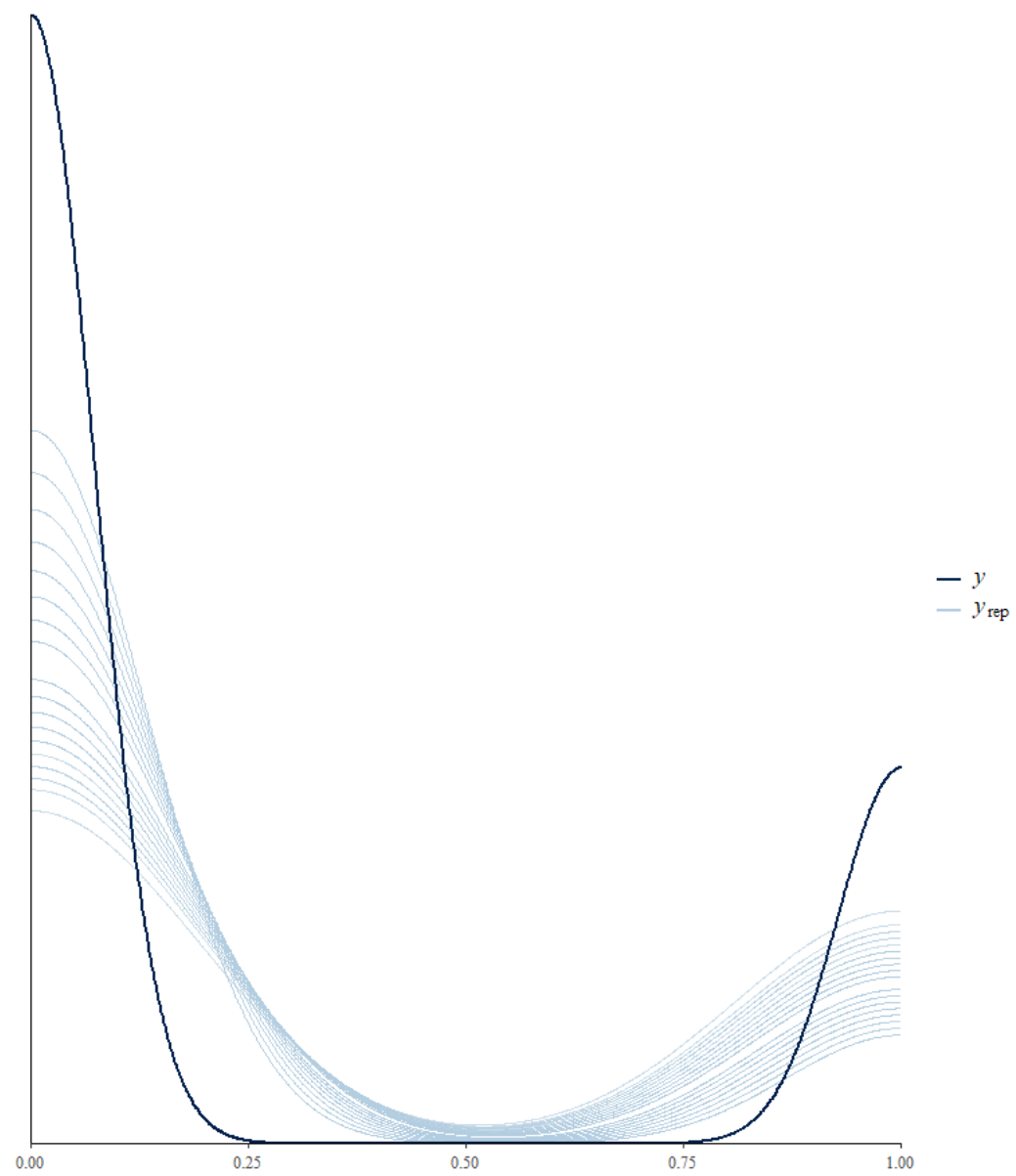


*Plot, Conditional effects, PP checks*



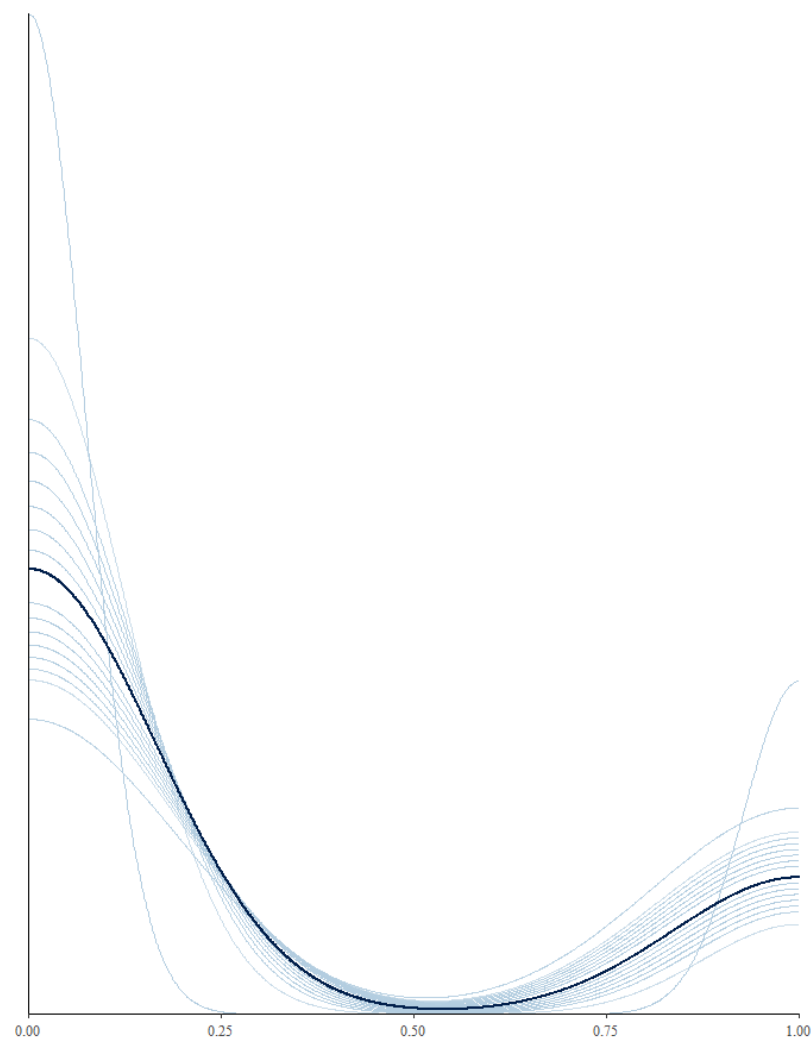




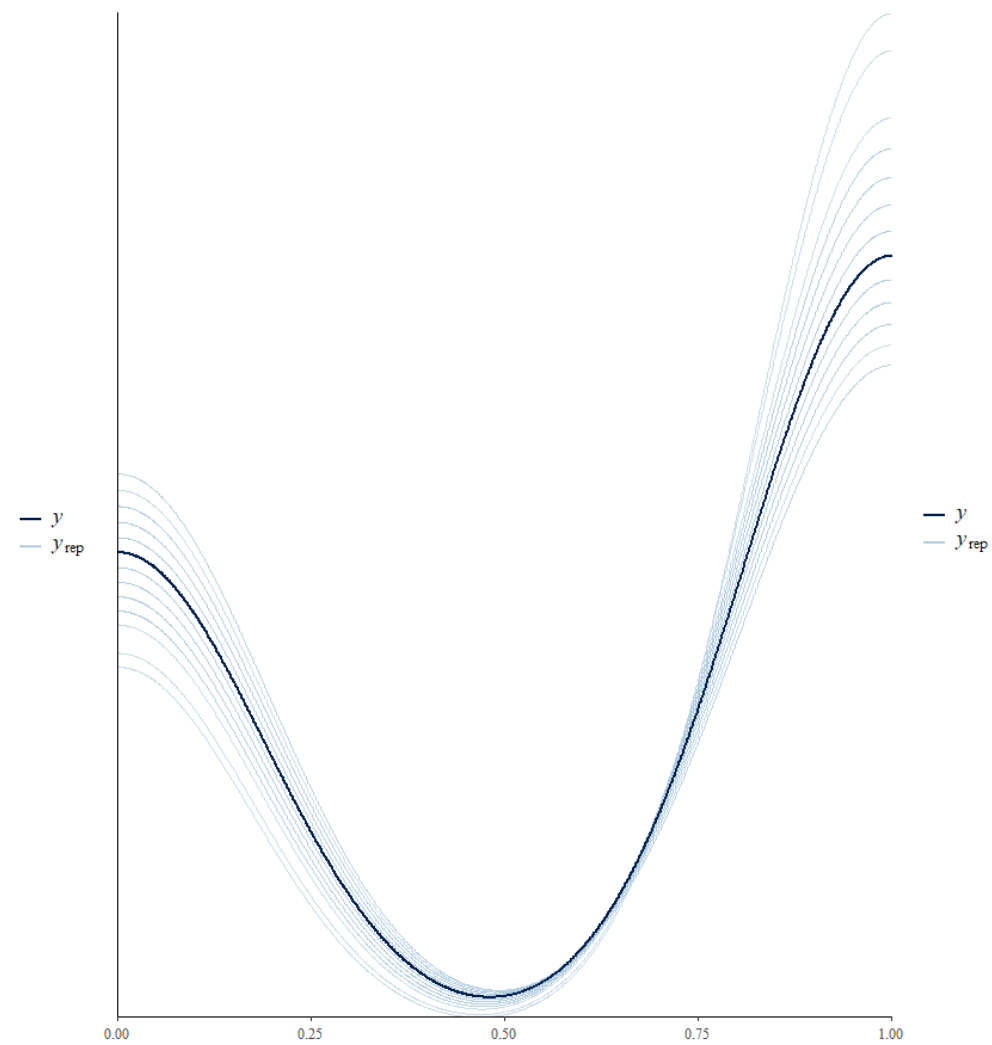


Intergroup adulticide (OG Killing)

Intragroup adulticide (IG Killing)



Coalition



### 5D.2 Model A(ii) Adulticide and food-sharing

```
> summary(Coalitionkill1F, waic= T); bayes_R2(Coalitionkill1F)
Family: MV(bernoulli, bernoulli, bernoulli)
Links: mu = logit
      mu = logit
      mu = logit
Formula: OG_Killing ~ Food_Sharing_AandI + Coalition + (1 | gr(SpeciesTree, cov = A))
        IG_Killing ~ Food_Sharing_AandI + Coalition + (1 | gr(SpeciesTree, cov = A))
        Coalition ~ Food_Sharing_AandI + (1 | gr(SpeciesTree, cov = A))
Data: data1 (Number of observations: 61)
Draws: 4 chains, each with iter = 9000; warmup = 4500; thin = 1;
      total post-warmup draws = 18000
```

Group-Level Effects:

~SpeciesTree (Number of levels: 61)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGKilling_Intercept)	1.01	1.74	0.03	5.61	1.00	1056	2982
sd(IGKilling_Intercept)	1.45	1.40	0.04	4.82	1.00	1737	3136
sd(Coalition_Intercept)	4.44	4.35	0.79	14.35	1.00	5624	5272

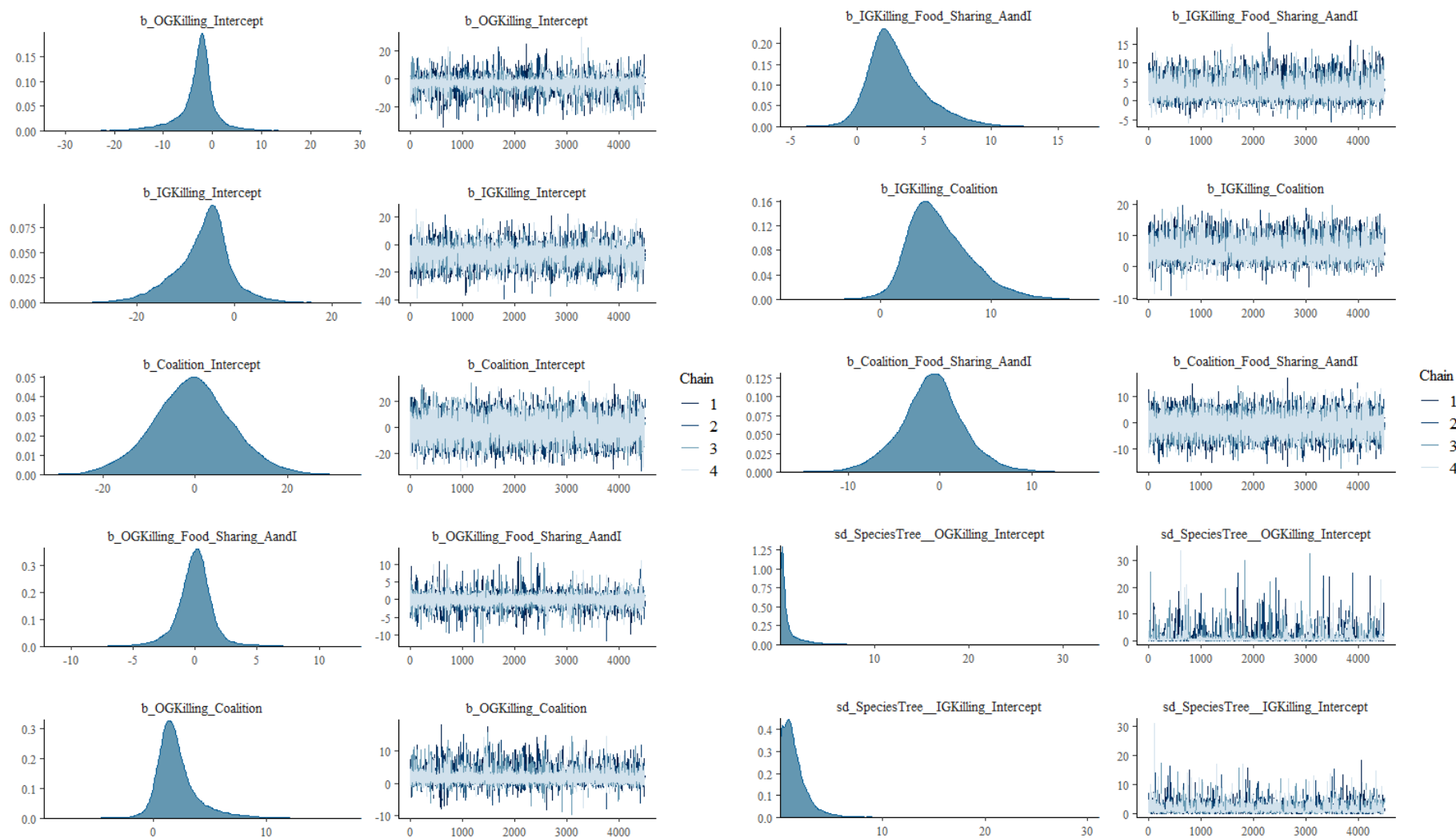
## Population-Level Effects:

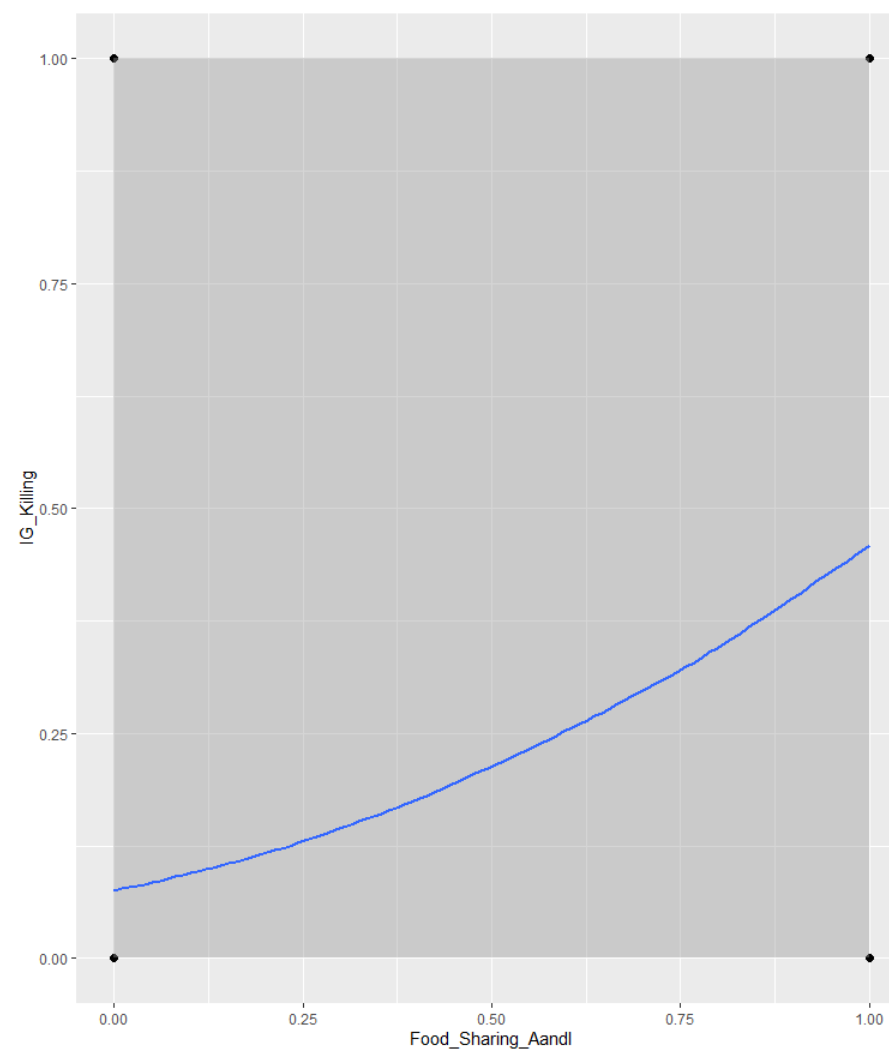
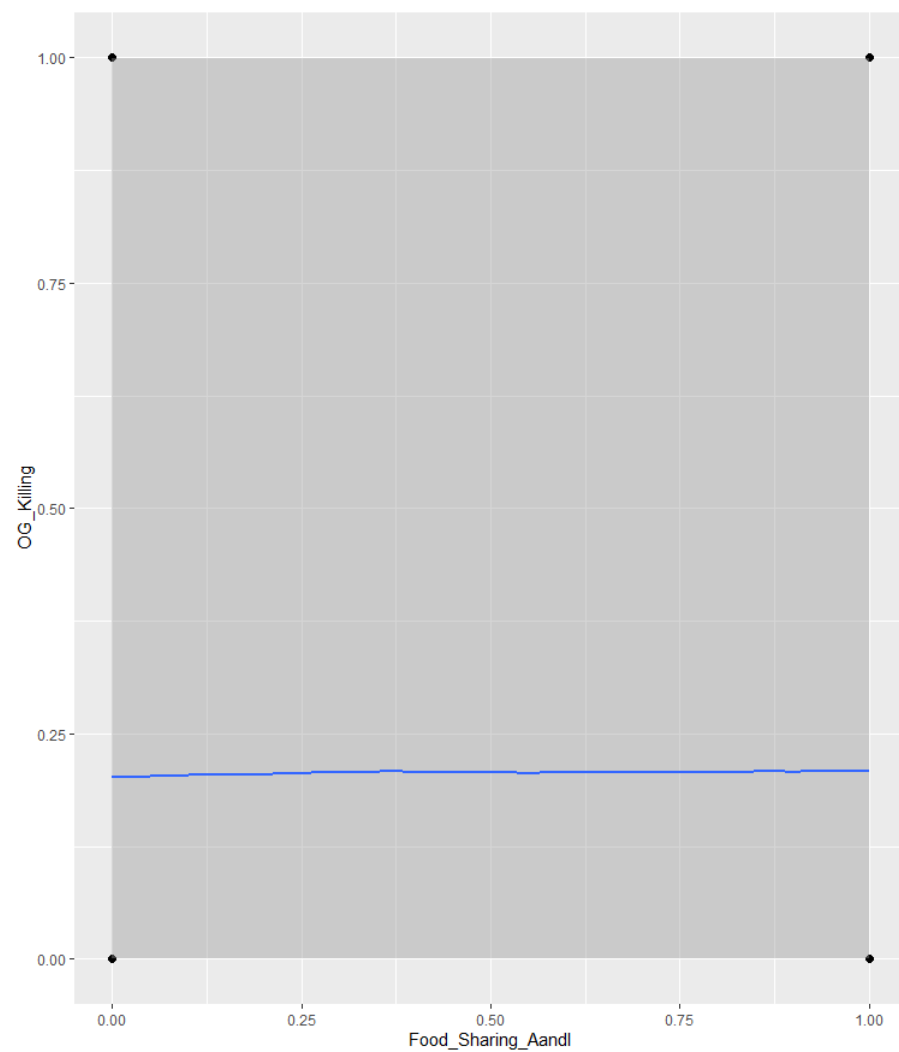
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGKilling_Intercept	-3.05	4.37	-14.02	5.33	1.00	9817	4893
IGKilling_Intercept	-6.55	5.91	-19.86	4.65	1.00	10032	9551
Coalition_Intercept	-0.58	8.49	-17.61	16.47	1.00	14283	13291
OGKilling_Food_Sharing_AandI	-0.03	1.61	-3.48	3.08	1.00	11724	5068
OGKilling_Coalition	2.10	1.98	-0.69	7.34	1.00	6643	4586
IGKilling_Food_Sharing_AandI	3.01	2.24	-0.45	8.40	1.00	8343	10525
IGKilling_Coalition	5.41	2.90	0.82	12.10	1.00	7771	12090
Coalition_Food_Sharing_AandI	-0.86	3.52	-8.00	6.28	1.00	15174	12984

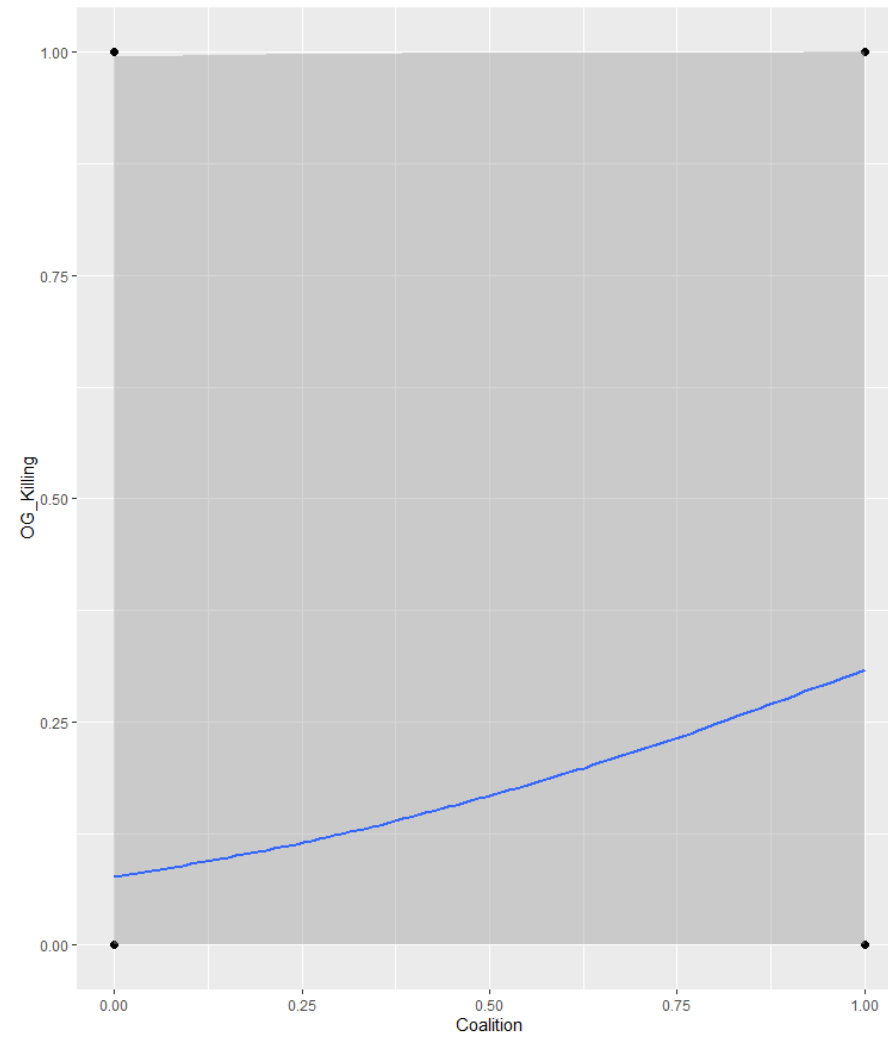
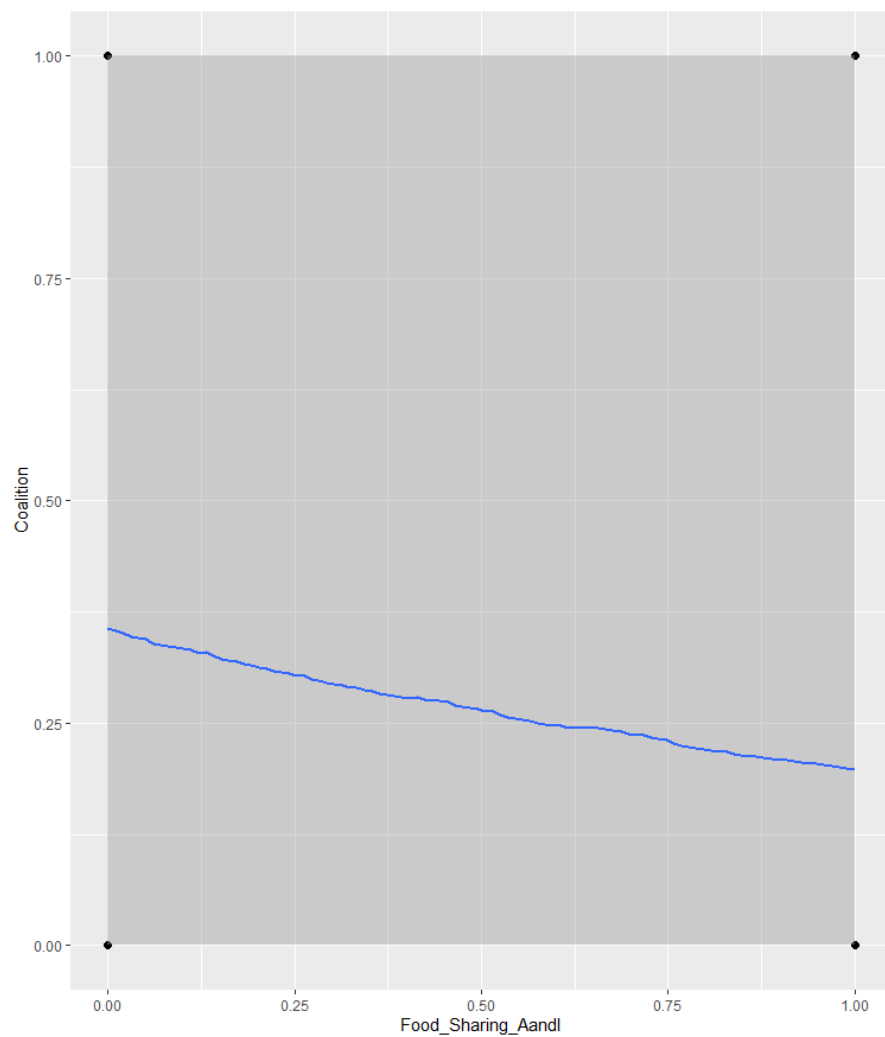
Draws were sampled using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

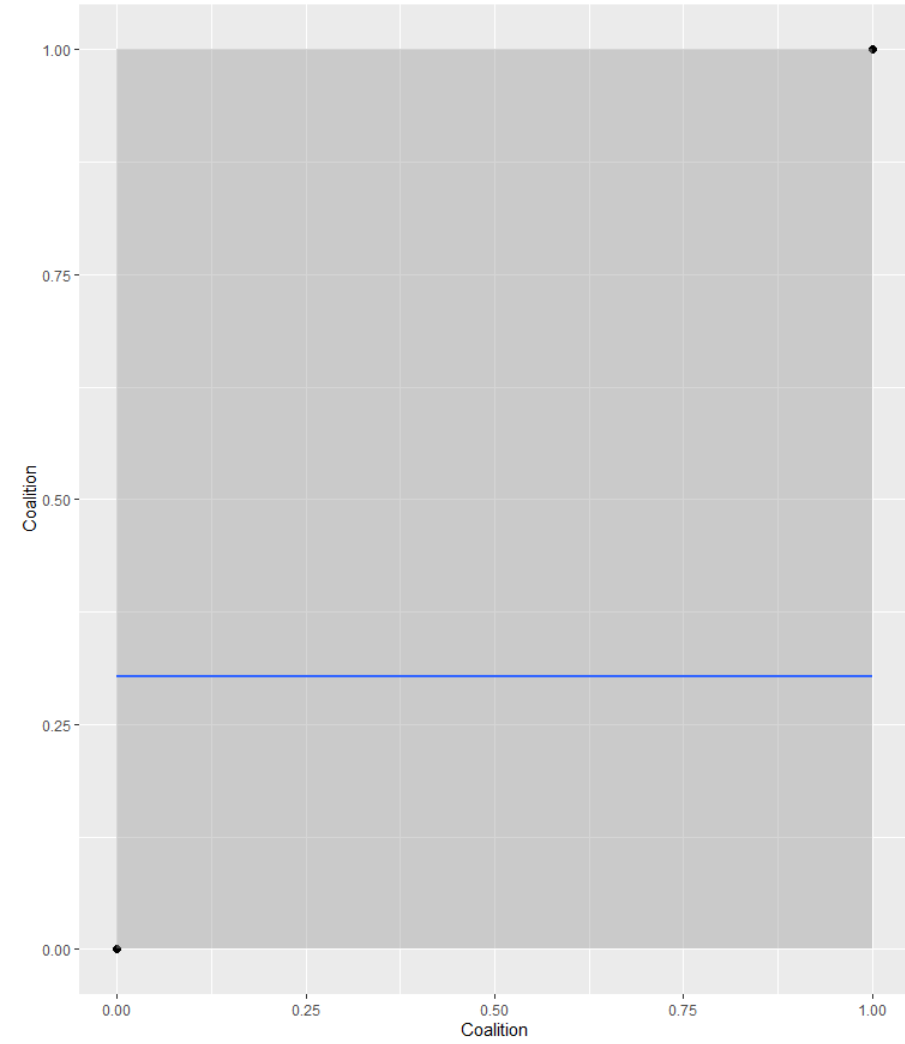
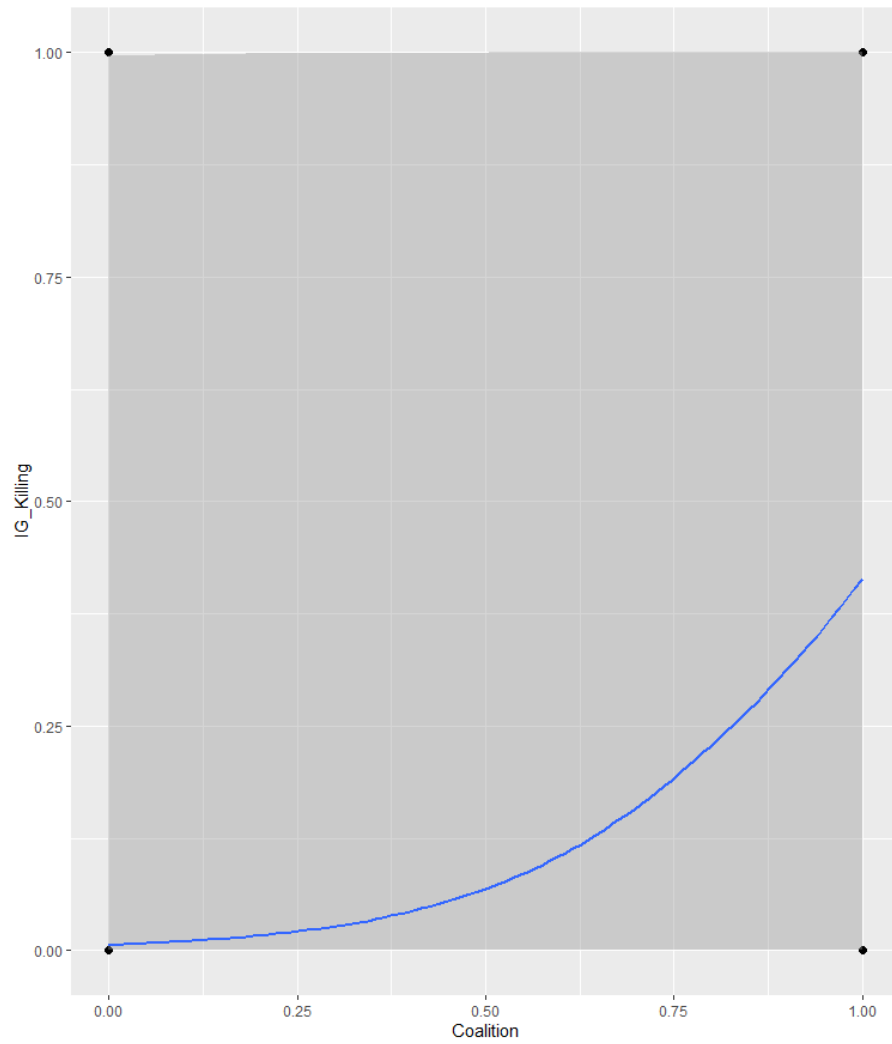
	Estimate	Est.Error	Q2.5	Q97.5
R2OGKilling	0.3708007	0.2270229	0.0575721	0.8853659
R2IGKilling	0.6001564	0.1997238	0.1969153	0.9243453
R2Coalition	0.8587662	0.1103377	0.5768926	0.9969039



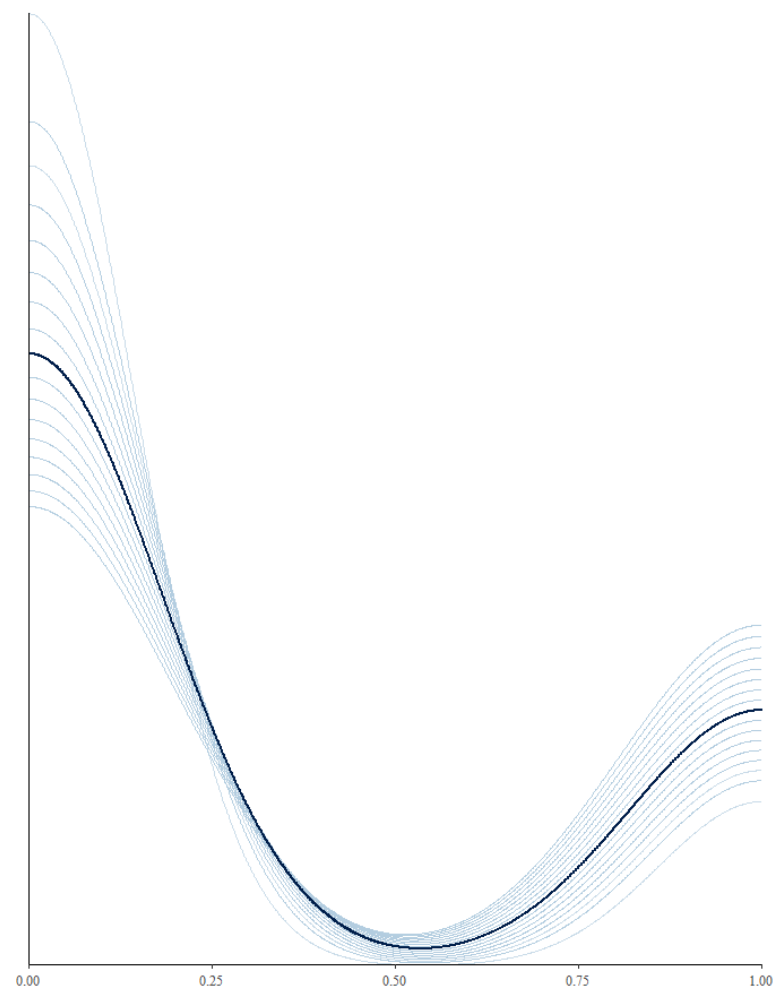
*Plot, Conditional effects, PP checks*



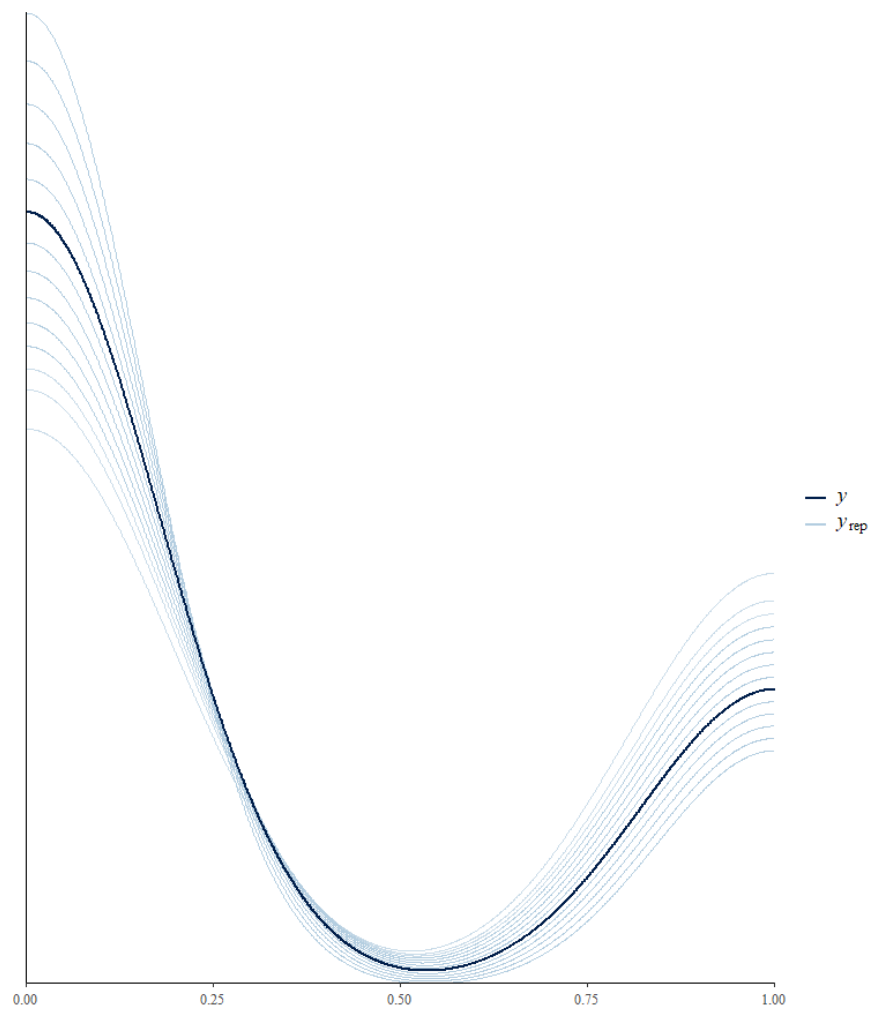




Intergroup adulticide (OG Killing)



Intragroup adulticide (IG Killing)



*5D.3 Model A(iii) Infanticide and grooming*

```

> summary(CoalitionInfl, waic= T); bayes_R2(CoalitionInfl)
Family: MV(bernoulli, bernoulli)
Links: mu = logit
       mu = logit
Formula: Infanticide ~ Grooming + Coalition + (1 | gr(SpeciesTree, cov = A))
       Coalition ~ Grooming + (1 | gr(SpeciesTree, cov = A))
Data: dataG (Number of observations: 68)
Draws: 4 chains, each with iter = 9000; warmup = 4500; thin = 1;
       total post-warmup draws = 18000

Group-Level Effects:
~SpeciesTree (Number of levels: 68)

```

	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Infanticide_Intercept)	2.95	3.07	0.07	10.72	1.00	999	1294
sd(Coalition_Intercept)	6.30	7.64	0.96	23.90	1.00	5394	5916

```

Population-Level Effects:

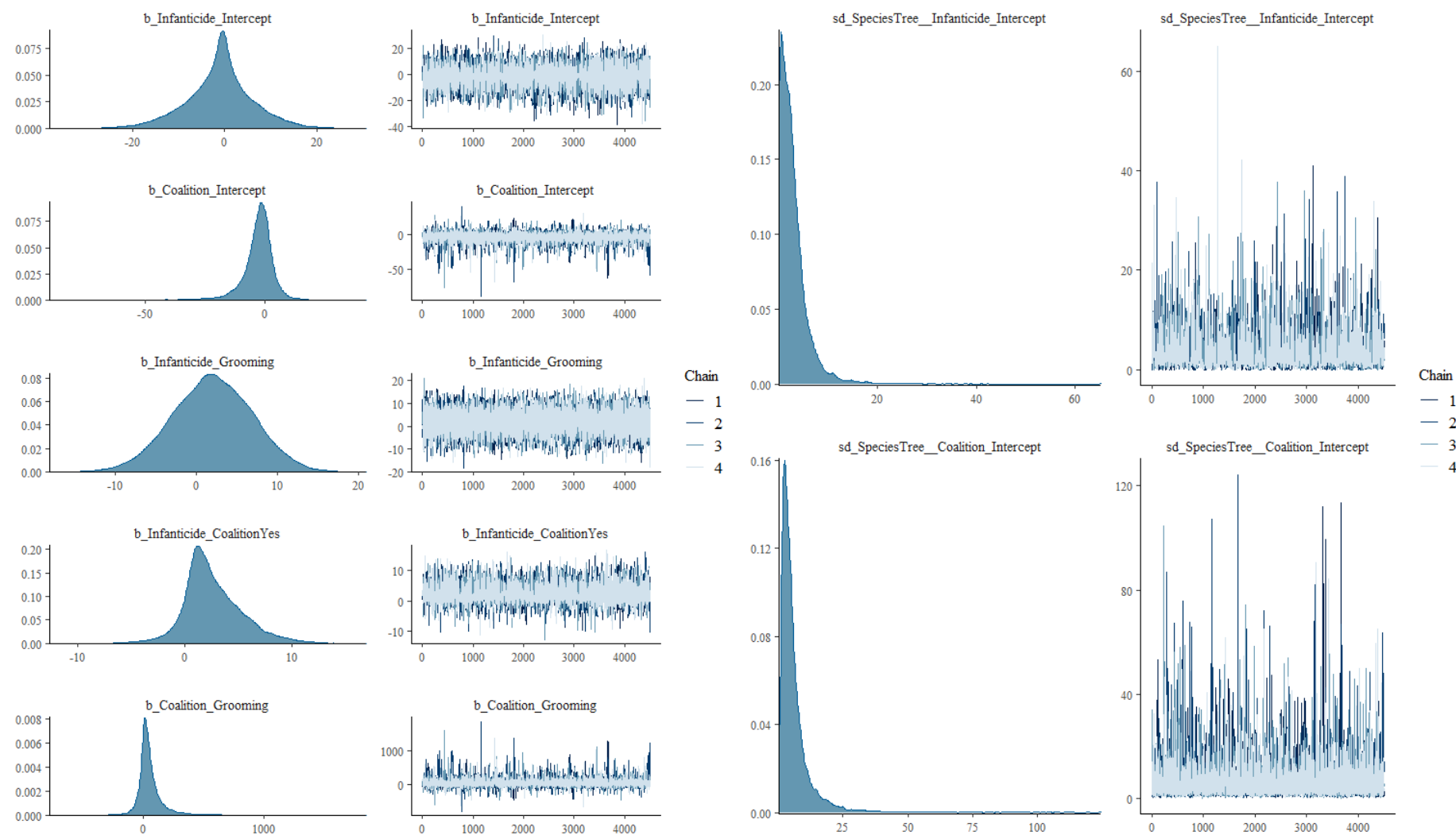
```

	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Infanticide_Intercept	-1.09	7.30	-16.79	13.77	1.00	11490	10936

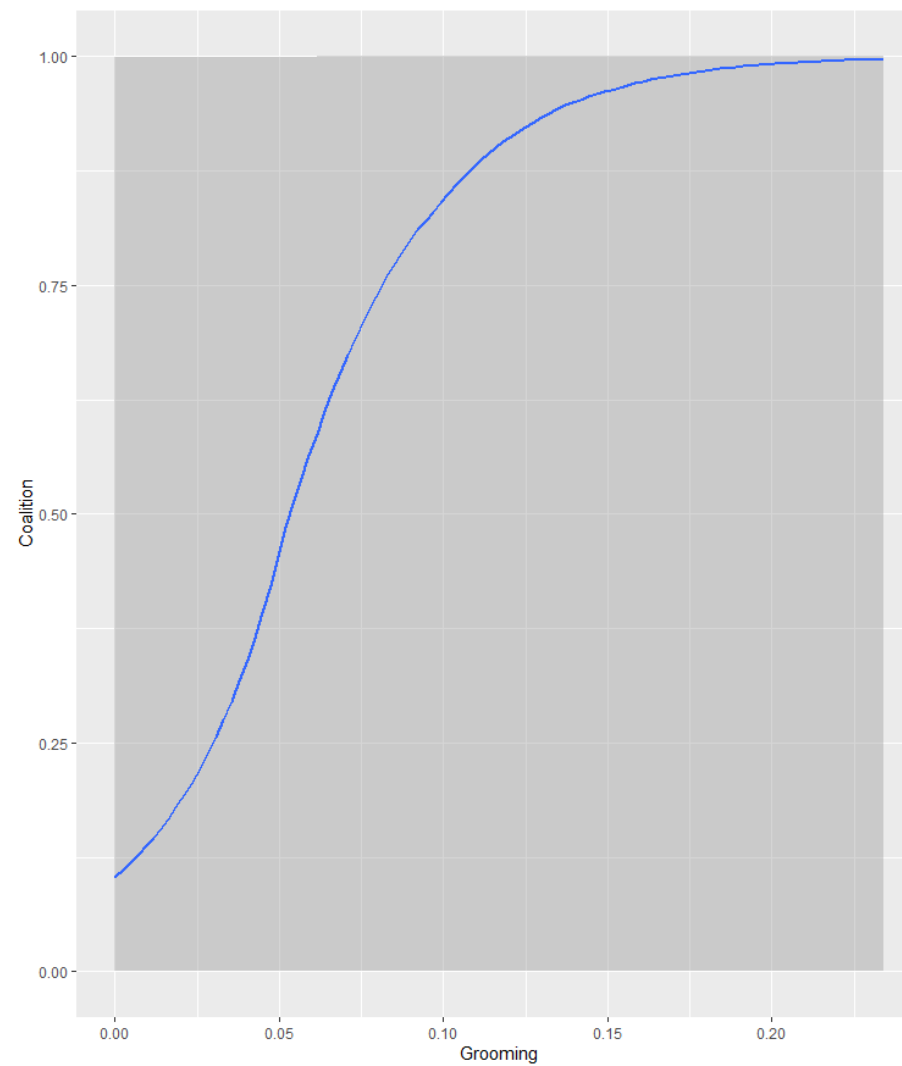
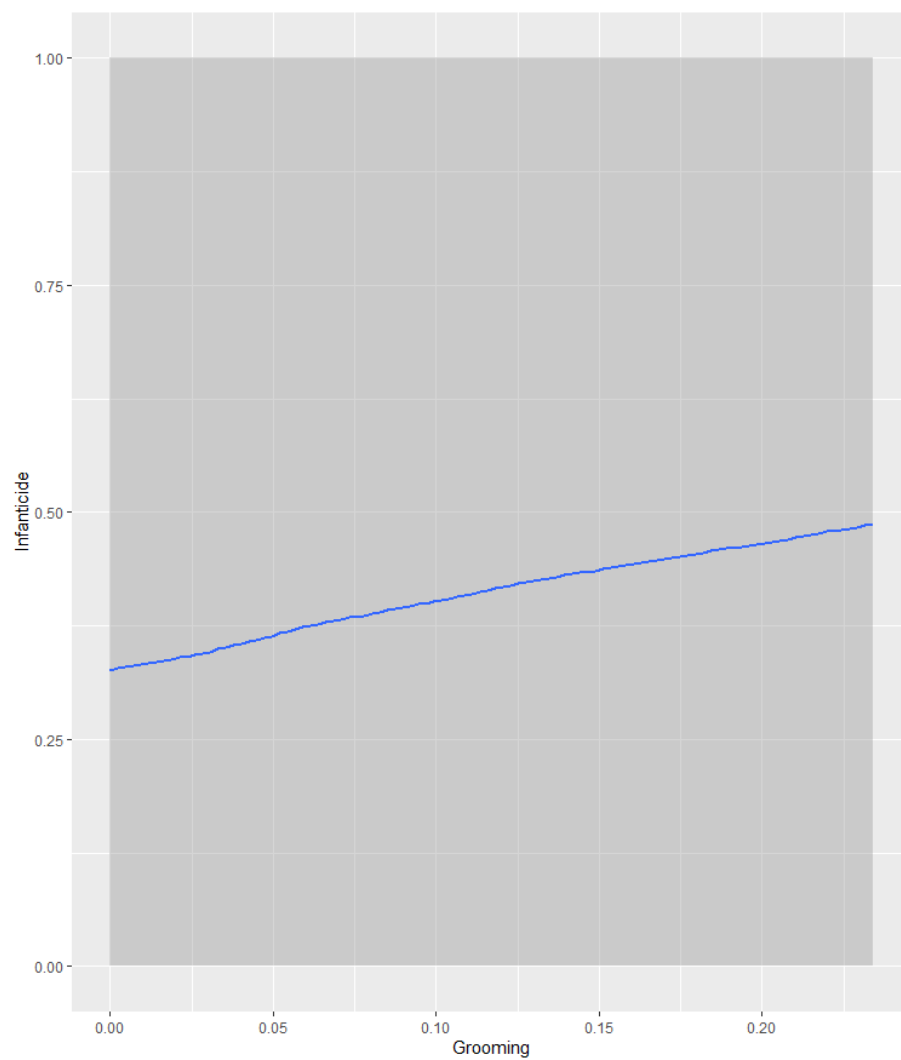
Coalition_Intercept	-3.09	7.28	-19.62	7.87	1.00	6128	3547
Infanticide_Grooming	2.01	4.87	-7.65	11.37	1.00	8820	13270
Infanticide_CoalitionYes	2.61	2.78	-2.29	9.09	1.00	5991	9805
Coalition_Grooming	56.70	129.92	-103.11	366.15	1.00	5543	3348

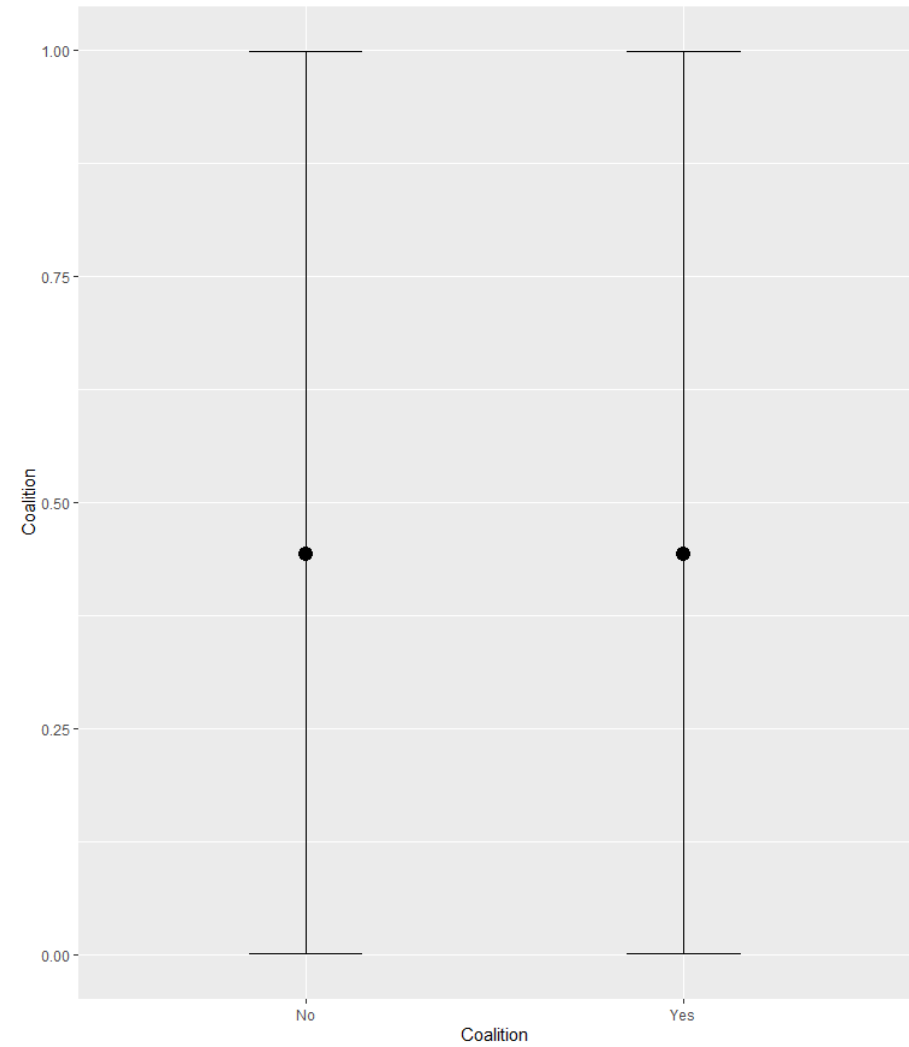
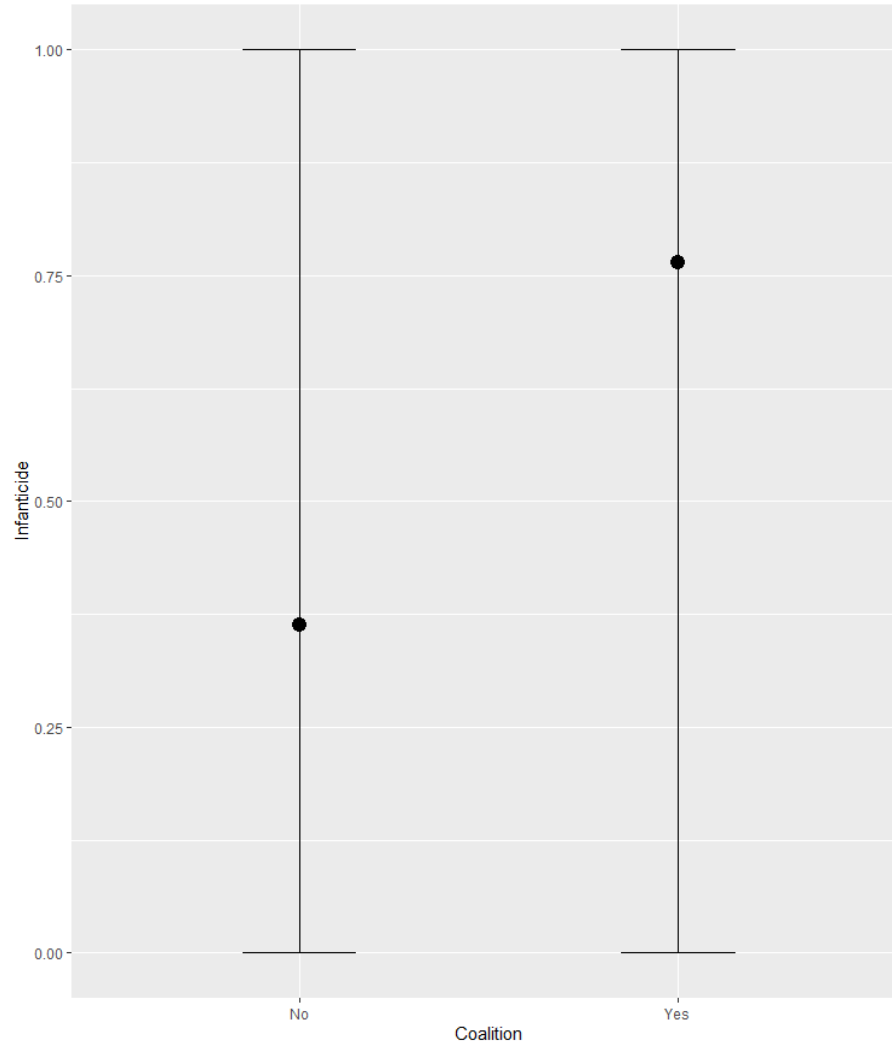
Draws were sampled using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
R2Infanticide	0.6837611	0.23946727	0.1052273	0.9745268
R2Coalition	0.8843026	0.09519232	0.6421981	0.9991090

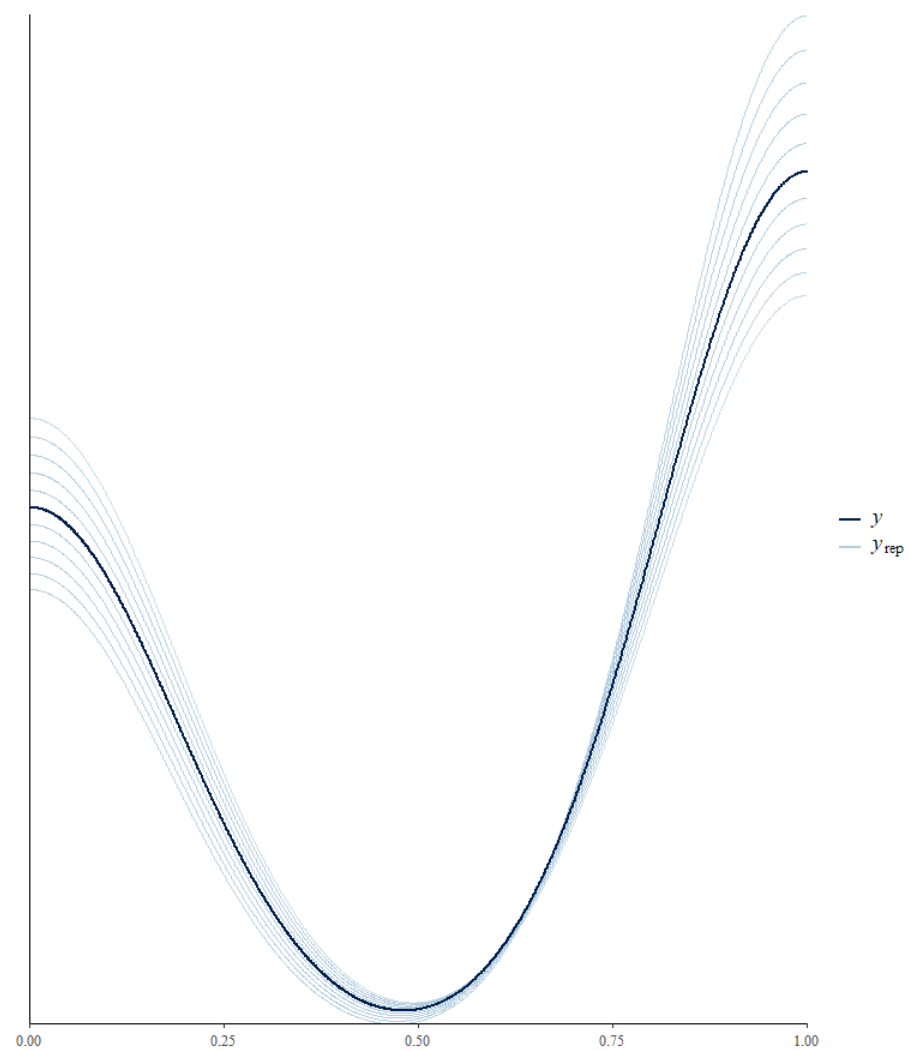
*Plot, Conditional effects, PP checks*



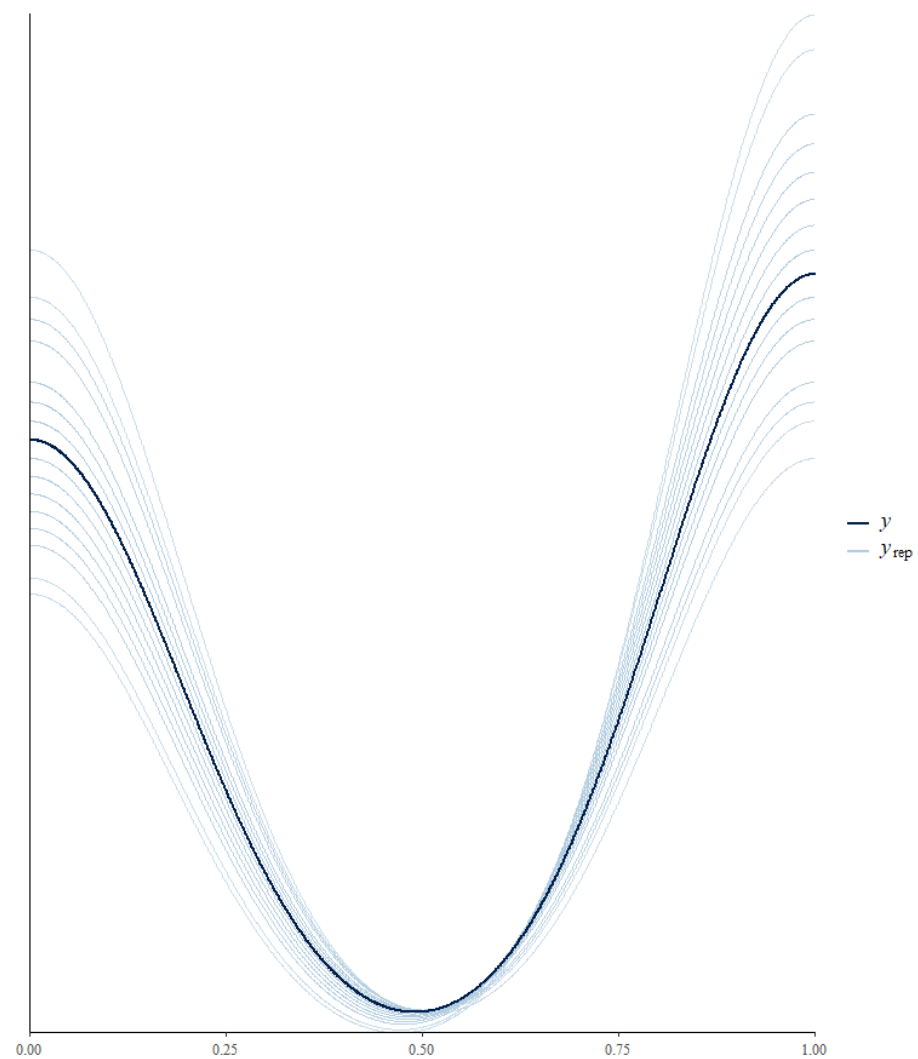




Coalition



Infanticide



*5D.4 Model A(iv) Infanticide and food-sharing*

```
> summary(CoalitionInflF, waic= T); bayes_R2(CoalitionInflF)
Family: MV(bernoulli, bernoulli)
Links: mu = logit
       mu = logit
Formula: Infanticide ~ Food_Sharing_AandI + Coalition + (1 | gr(SpeciesTree, cov = A))
       Coalition ~ Food_Sharing_AandI + (1 | gr(SpeciesTree, cov = A))
Data: data1 (Number of observations: 61)
Draws: 4 chains, each with iter = 9000; warmup = 4500; thin = 1;
       total post-warmup draws = 18000
```

## Group-Level Effects:

```
~SpeciesTree (Number of levels: 61)
```

	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Infanticide_Intercept)	3.52	3.39	0.31	11.70	1.00	1861	1372
sd(Coalition_Intercept)	6.49	9.33	0.72	26.28	1.00	3366	4064

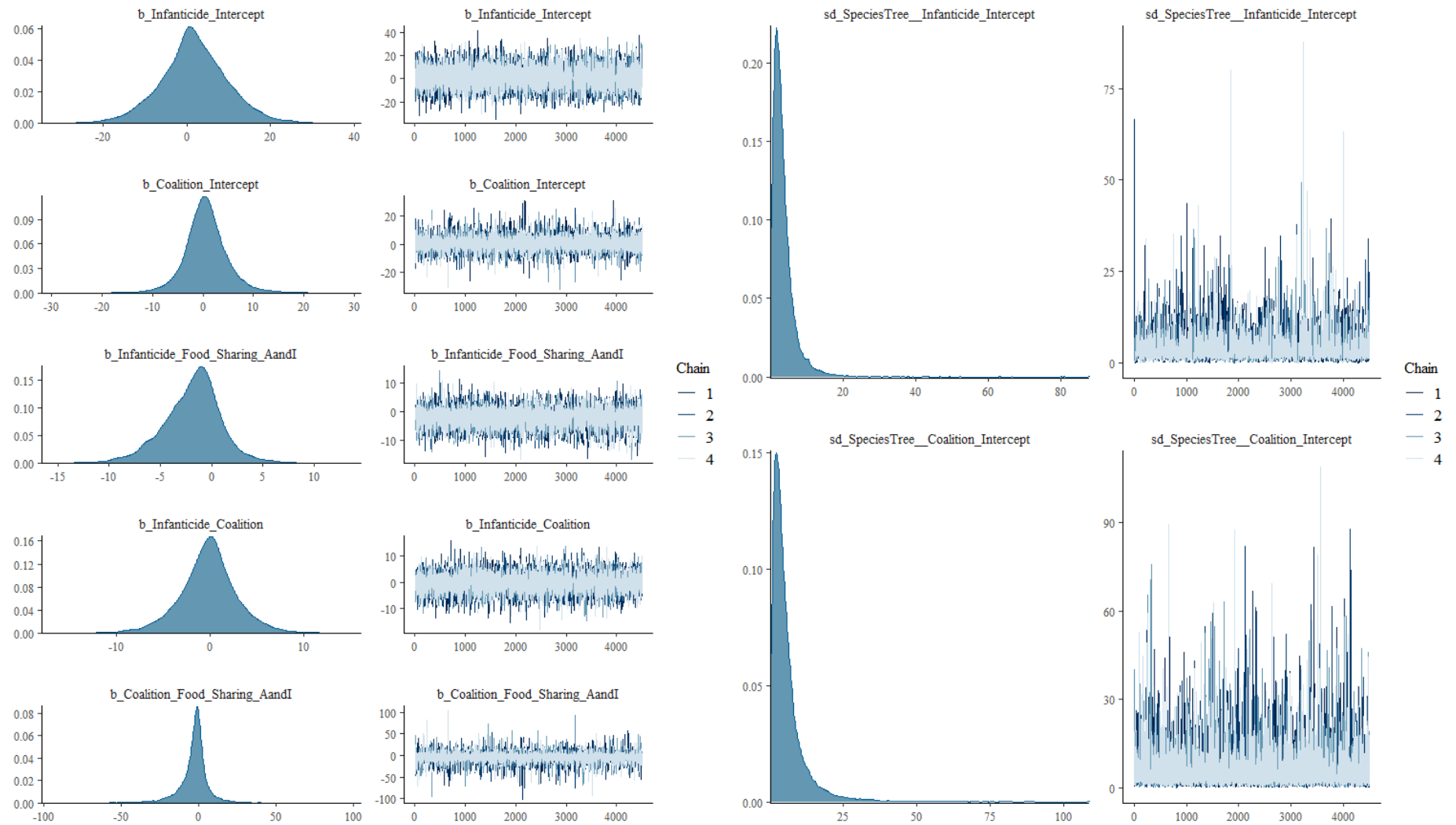
## Population-Level Effects:

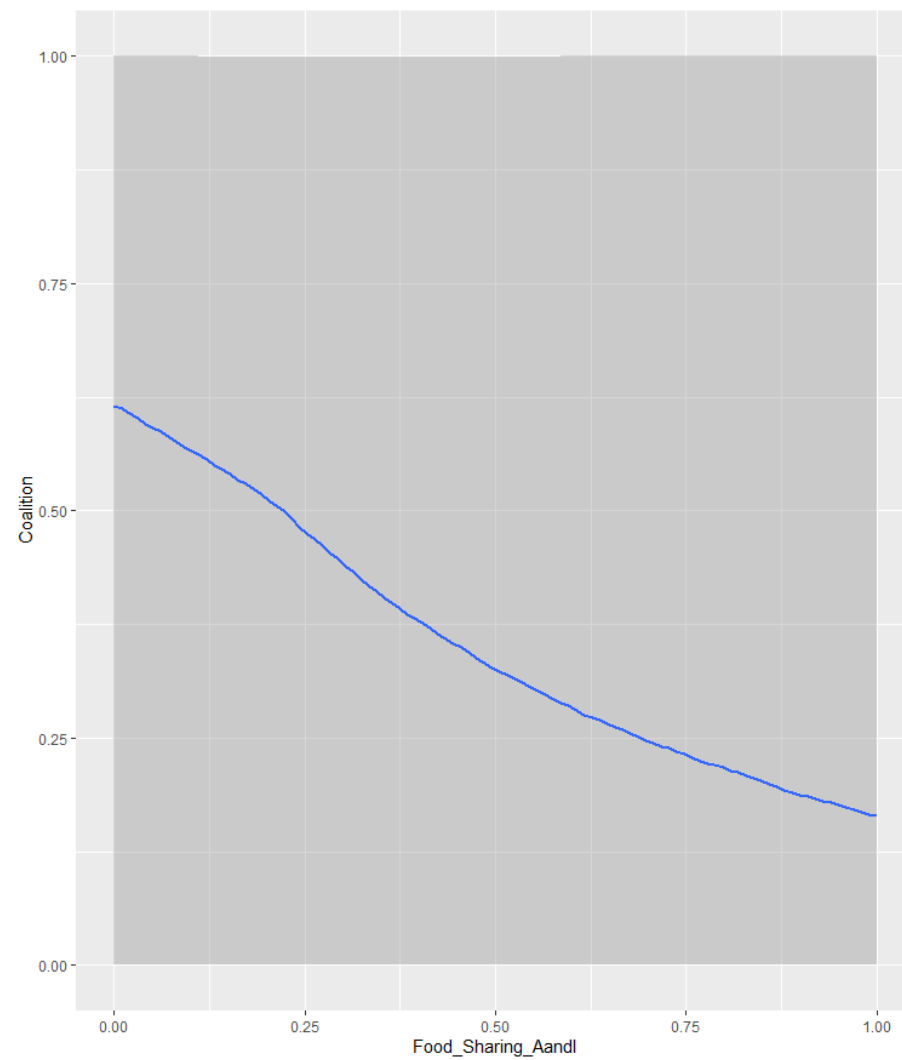
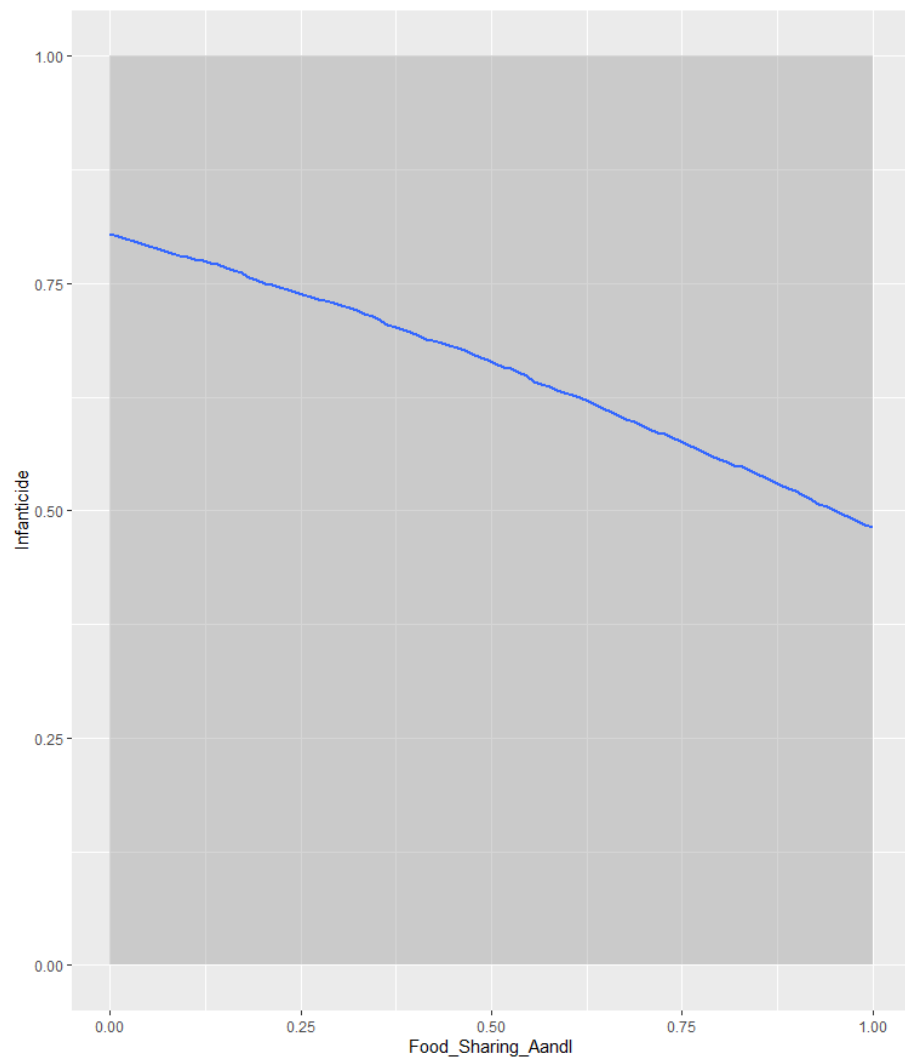
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Infanticide_Intercept	1.58	8.08	-15.01	18.07	1.00	10282	12007

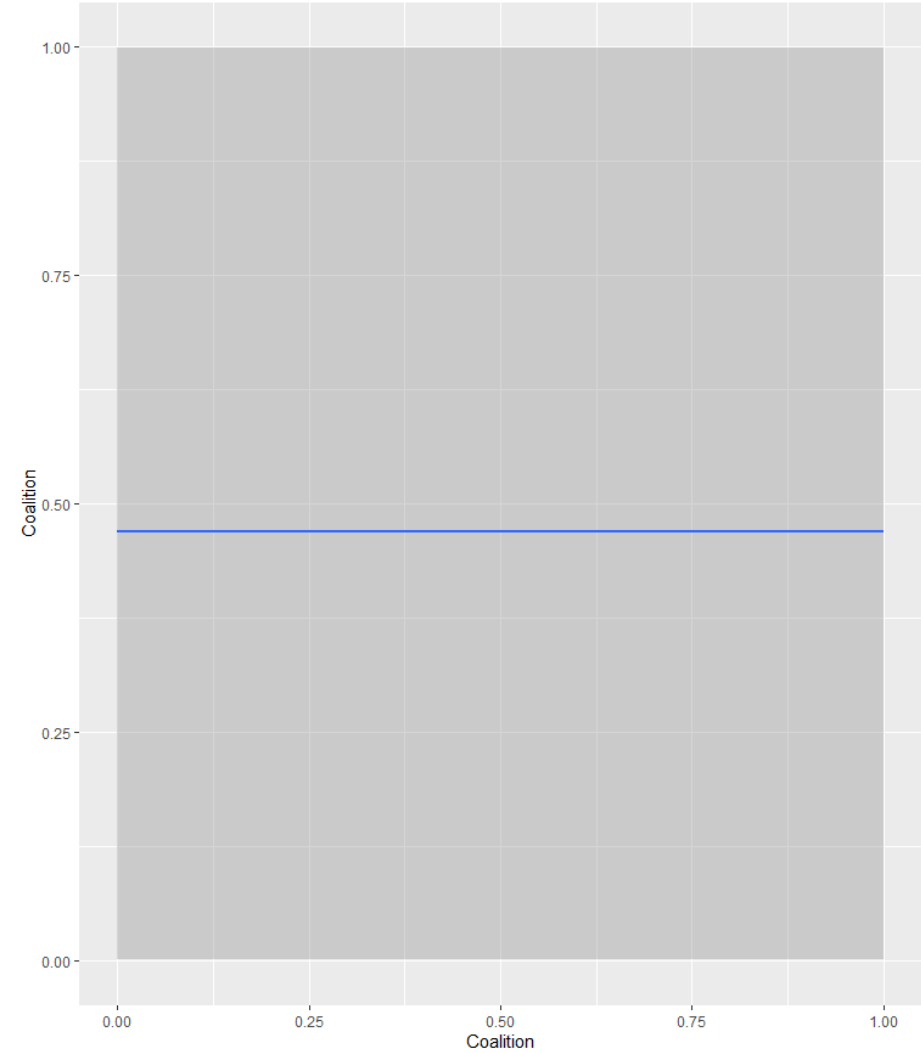
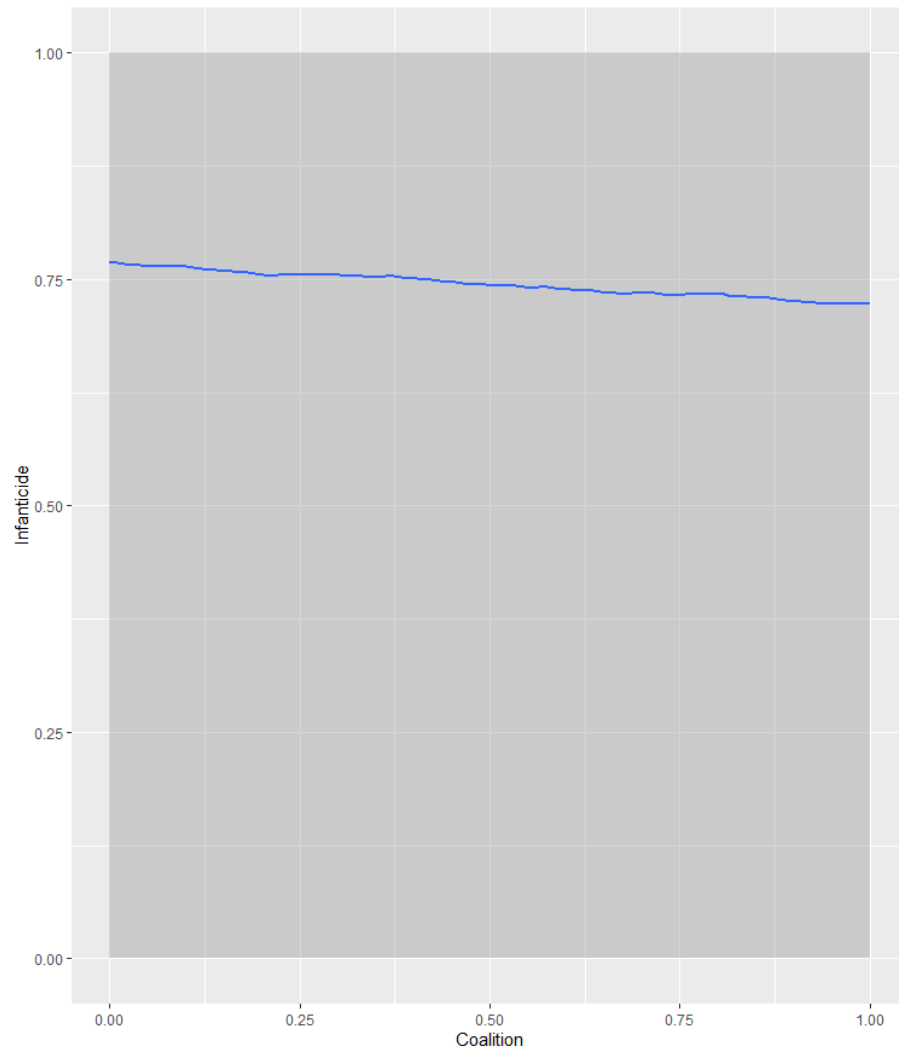
Coalition_Intercept	0.80	5.10	-8.24	11.73	1.00	6131	4037
Infanticide_Food_Sharing_AandI	-1.92	2.92	-8.29	3.57	1.00	9438	10172
Infanticide_Coalition	-0.20	3.06	-6.54	6.19	1.00	10223	10693
Coalition_Food_Sharing_AandI	-3.58	13.94	-34.73	16.77	1.00	5096	4062

Draws were sampled using `sampling(NUTS)`. For each parameter, `Bulk_ESS` and `Tail_ESS` are effective sample size measures, and `Rhat` is the potential scale reduction factor on split chains (at convergence, `Rhat = 1`).

	Estimate	Est.Error	Q2.5	Q97.5
R2Infanticide	0.7349391	0.1781983	0.2503977	0.9672677
R2Coalition	0.8728457	0.1164216	0.5599724	0.9996901

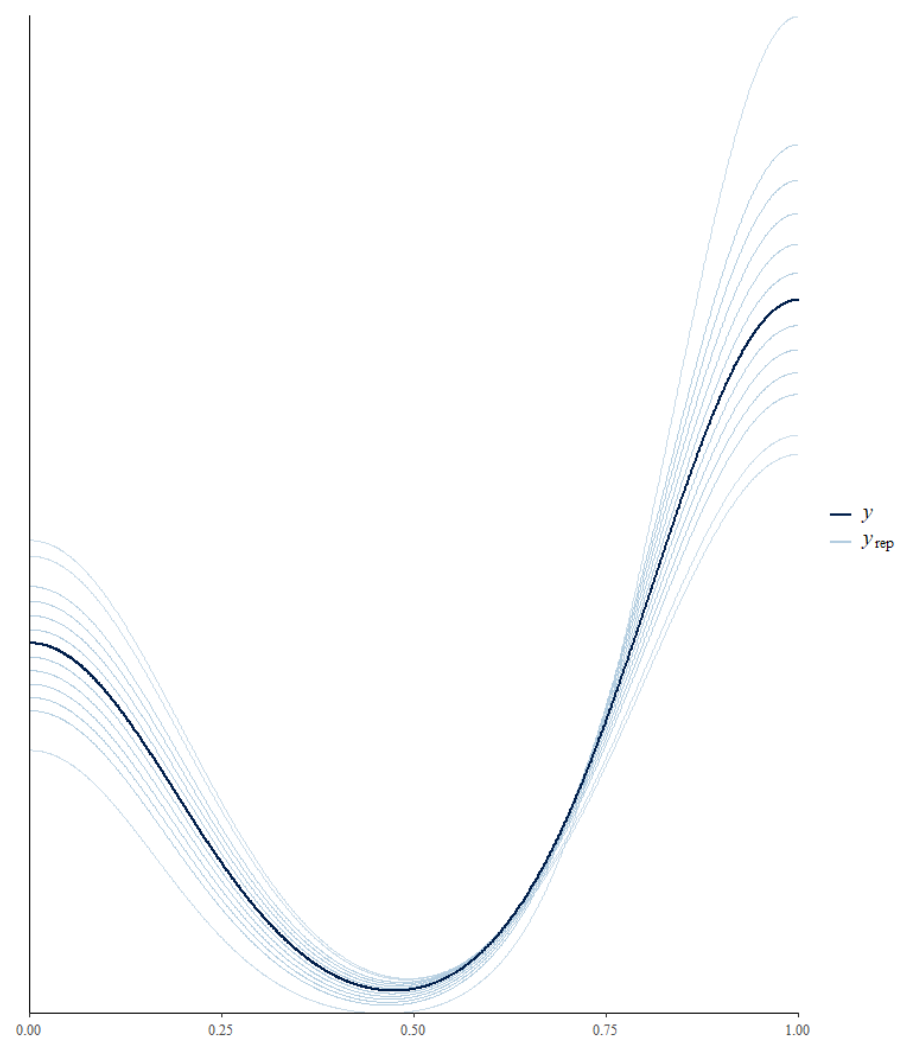
*Plot, Conditional effects, PP checks*



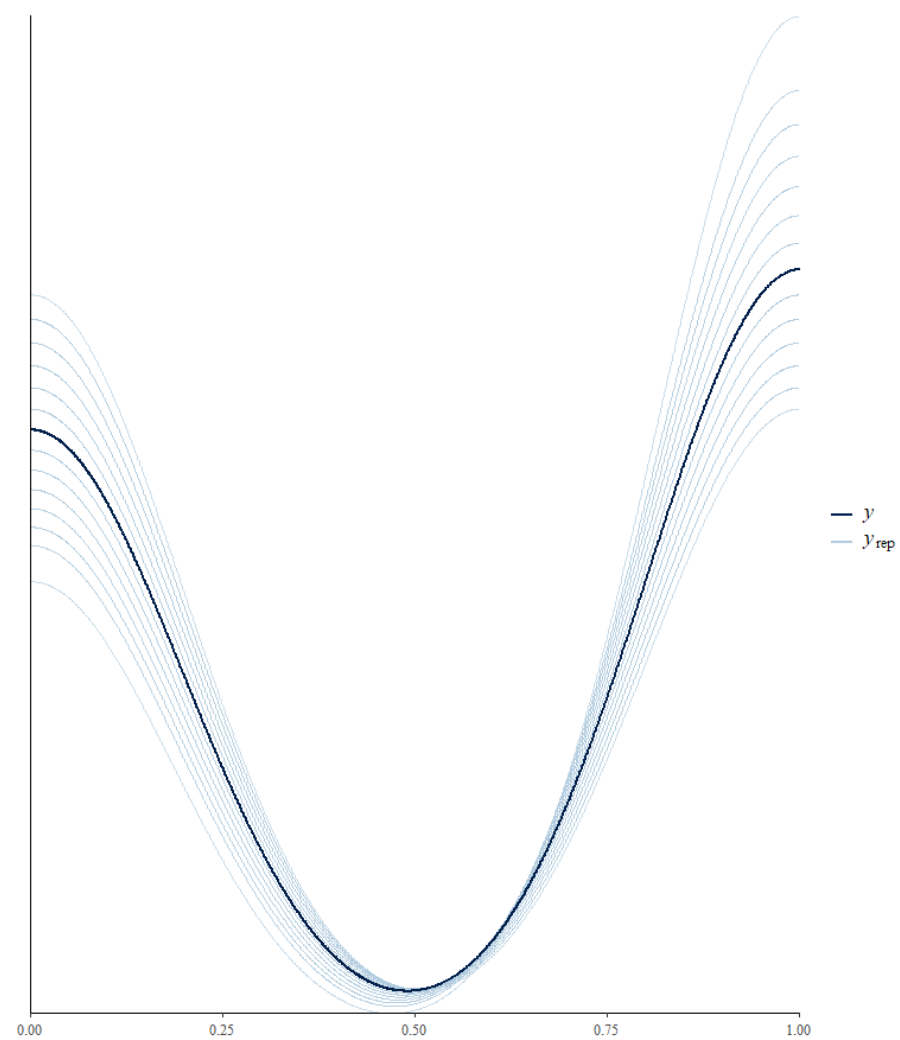




Coalition



Infanticide



*5D.5 Model A(v) Non-lethal aggression and grooming*

```

> summary(Coalitionagg1G, waic= T); bayes_R2(Coalitionagg1G)

Family: MV(zero_one_inflated_beta, hurdle_gamma, bernoulli)

Links: mu = logit; phi = identity; zoi = identity; coi = identity
       mu = log; shape = identity; hu = identity
       mu = logit

Formula: OG_Aggression ~ Grooming + Coalition + (1 | gr(SpeciesTree, cov = A))
        IG_Aggression ~ Grooming + Coalition + (1 | gr(SpeciesTree, cov = A))
        Coalition ~ Grooming + (1 | gr(SpeciesTree, cov = A))

Data: dataG (Number of observations: 68)

Draws: 4 chains, each with iter = 6000; warmup = 3000; thin = 1;
       total post-warmup draws = 12000

Group-Level Effects:

~SpeciesTree (Number of levels: 68)

      Estimate Est.Error 1-95% CI u-95% CI Rhat Bulk_ESS Tail_ESS

```

sd(OGAggression_Intercept)	0.09	0.09	0.00	0.35	1.01	723	321
sd(IGAggression_Intercept)	0.27	0.11	0.10	0.52	1.00	1697	3499
sd(Coalition_Intercept)	6.45	7.57	0.92	25.65	1.00	3076	3462

## Population-Level Effects:

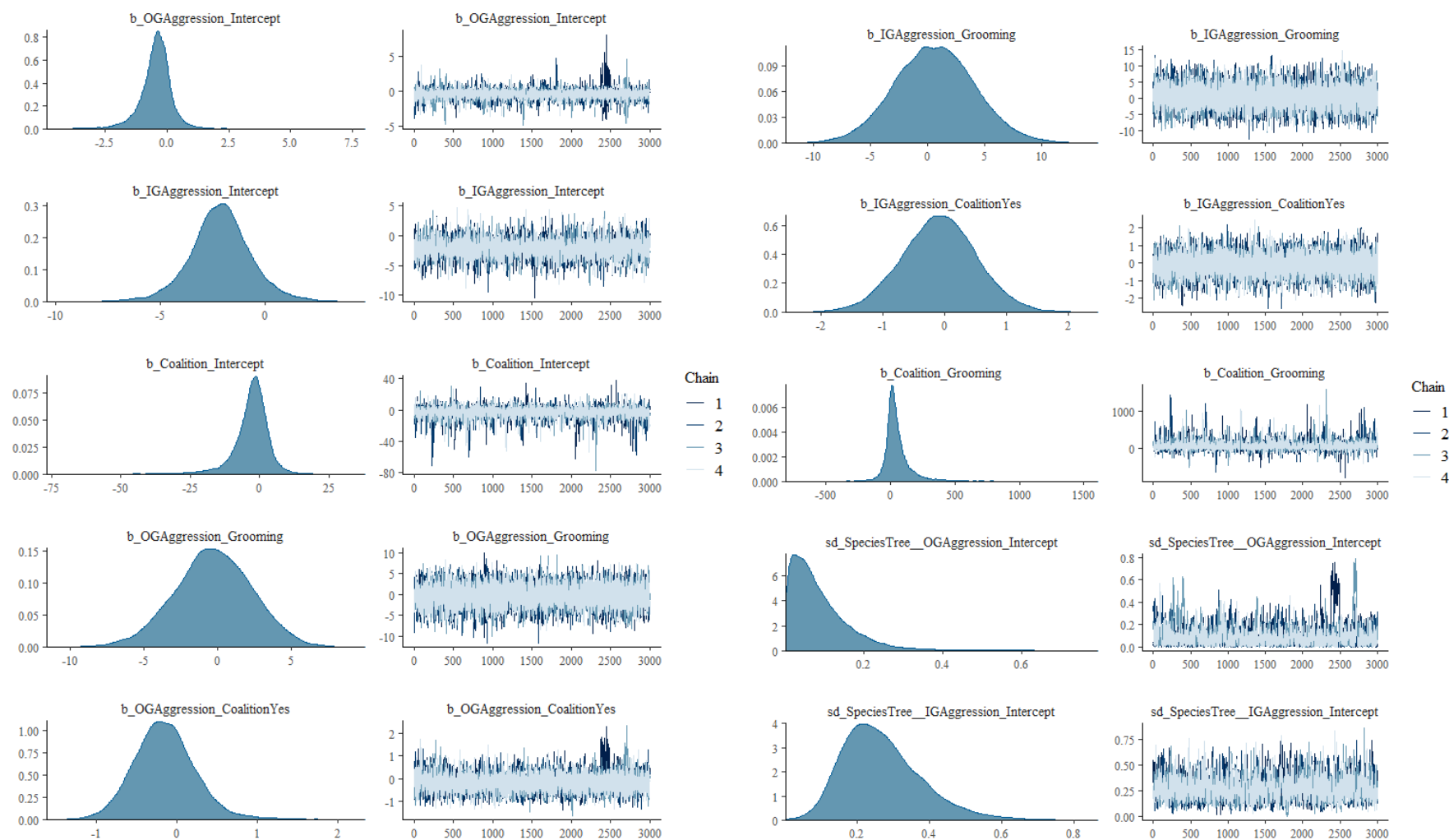
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGAggression_Intercept	-0.45	0.72	-2.03	0.82	1.00	4802	2366
IGAggression_Intercept	-2.11	1.50	-5.14	0.99	1.00	5319	5864
Coalition_Intercept	-3.23	7.55	-21.89	7.91	1.00	3733	2053
OGAggression_Grooming	-0.28	2.62	-5.46	4.74	1.00	14550	7525
OGAggression_CoalitionYes	-0.15	0.39	-0.85	0.67	1.00	2231	1244
IGAggression_Grooming	0.63	3.49	-6.15	7.63	1.00	11005	9574
IGAggression_CoalitionYes	-0.09	0.61	-1.30	1.11	1.00	9301	8790
Coalition_Grooming	61.12	136.95	-105.27	415.06	1.00	3536	1950

## Family Specific Parameters:

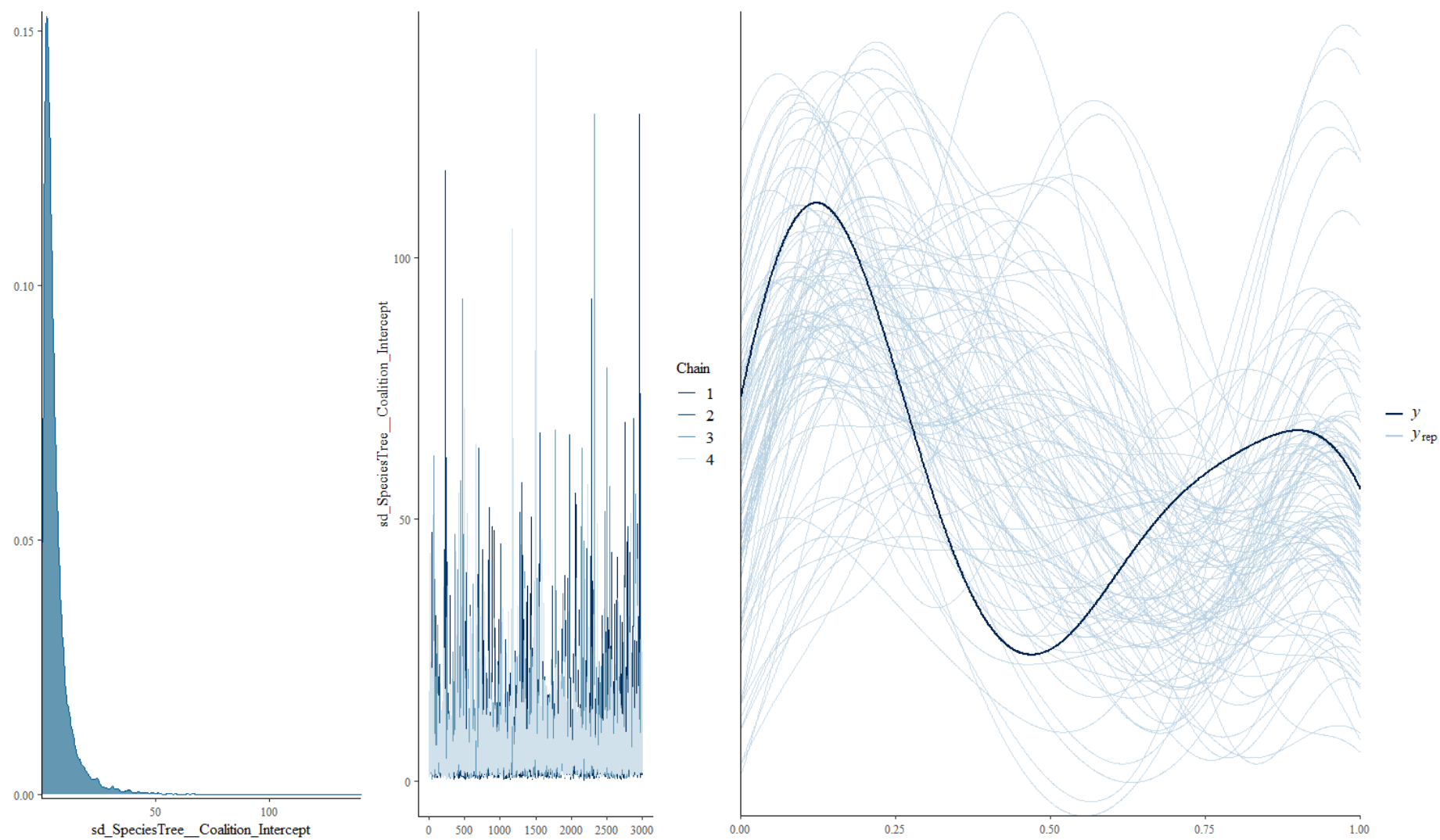
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
phi_OGAggression	3.41	4.70	1.90	6.91	1.01	854	336
zoi_OGAggression	0.29	0.05	0.19	0.40	1.00	18683	8425
coi_OGAggression	0.71	0.10	0.50	0.88	1.00	17956	7906
shape_IGAggression	0.47	0.10	0.32	0.70	1.00	3152	4509
hu_IGAggression	0.07	0.03	0.02	0.14	1.00	17128	8037

Draws were sampled using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

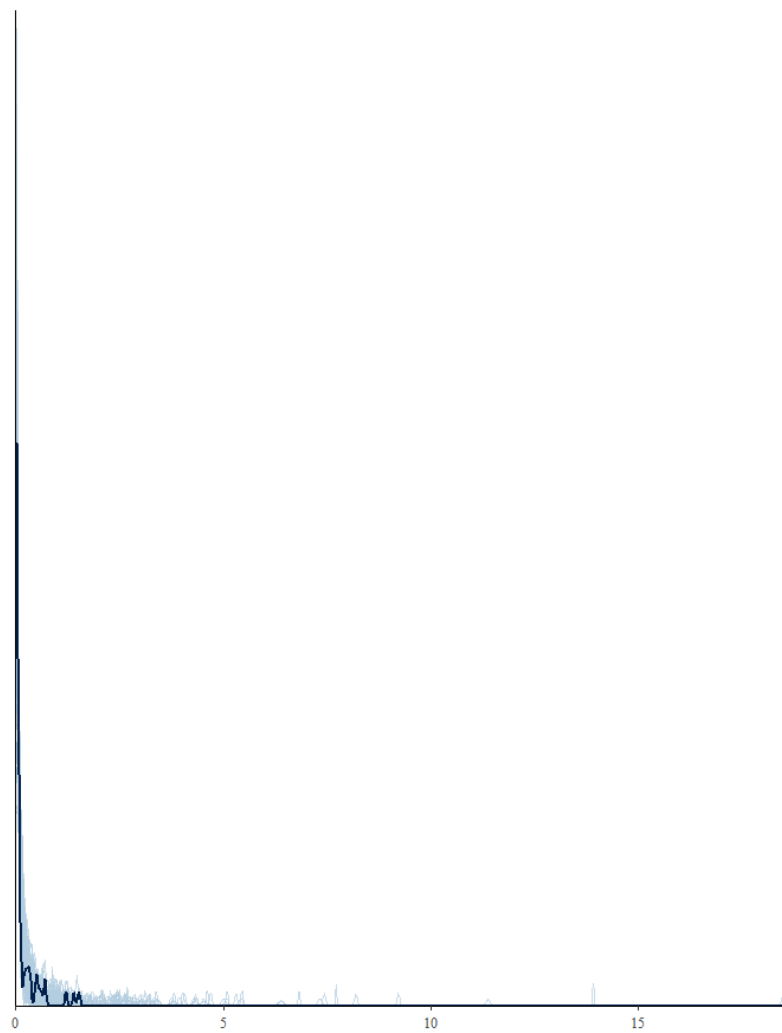
	Estimate	Est.Error	Q2.5	Q97.5
R2OGAggression	0.04555851	0.05035735	0.002154242	0.1943622
R2IGAggression	0.35779585	0.15195208	0.079966347	0.6267412
R2Coalition	0.88431711	0.09760589	0.635991467	0.9993350

*Plot, Conditional effects, PP checks*

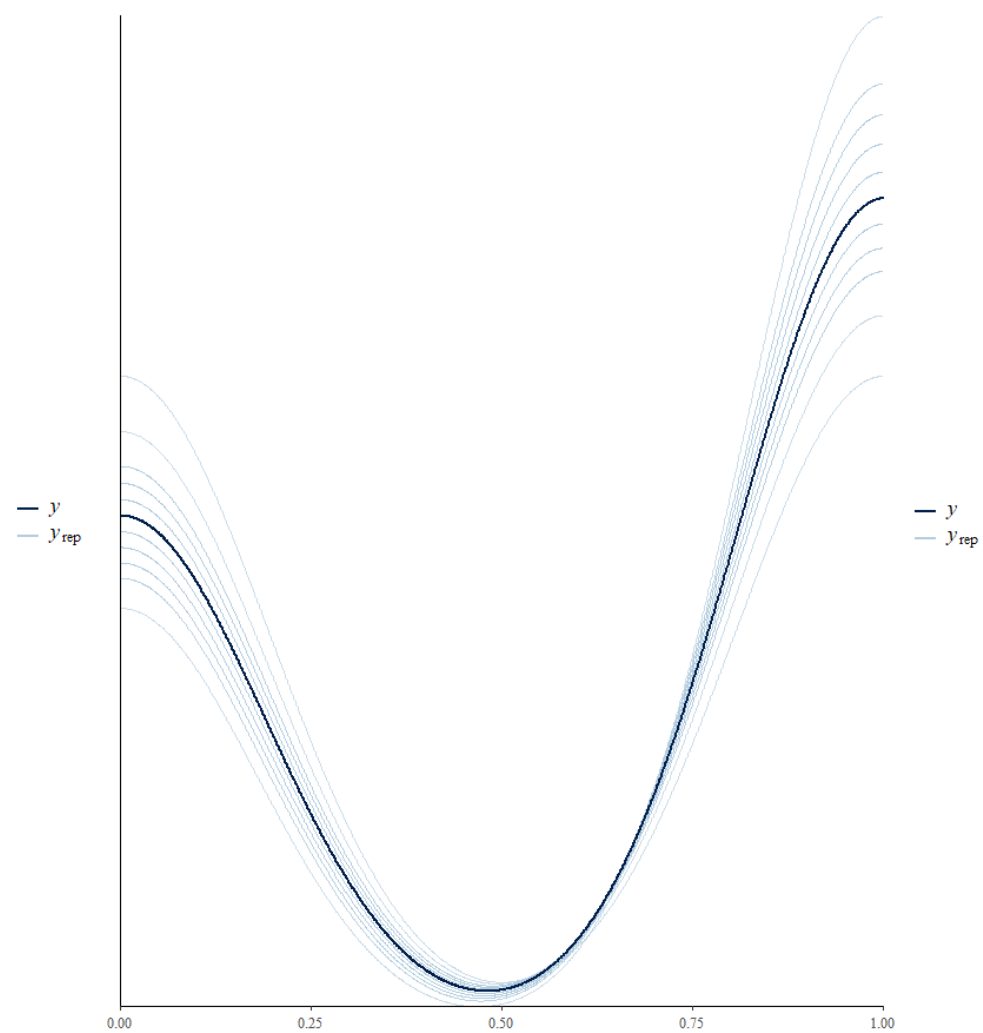
## Intergroup aggression (OG Aggression)



Intragroup aggression (IG Aggression)



Coalition



*5D.6 Model A(vi) Non-lethal aggression and food-sharing*

```
> summary(Coalitionagg1, waic= T); bayes_R2(Coalitionagg1)
Family: MV(zero_one_inflated_beta, hurdle_gamma, bernoulli)
Links: mu = logit; phi = identity; zoi = identity; coi = identity
       mu = log; shape = identity; hu = identity
       mu = logit
Formula: OG_Aggression ~ Food_Sharing_AandI + Coalition + (1 | gr(SpeciesTree, cov = A))
        IG_Aggression ~ Food_Sharing_AandI + Coalition + (1 | gr(SpeciesTree, cov = A))
        Coalition ~ Food_Sharing_AandI + (1 | gr(SpeciesTree, cov = A))
Data: data1 (Number of observations: 61)
Draws: 4 chains, each with iter = 8000; warmup = 4000; thin = 1;
       total post-warmup draws = 16000
```

## Group-Level Effects:

```
~SpeciesTree (Number of levels: 61)
```

	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGAggression_Intercept)	0.09	0.07	0.00	0.26	1.00	2754	2940
sd(IGAggression_Intercept)	0.27	0.08	0.14	0.46	1.00	3961	6213
sd(Coalition_Intercept)	6.34	8.21	0.74	26.46	1.00	3869	3673



## Population-Level Effects:

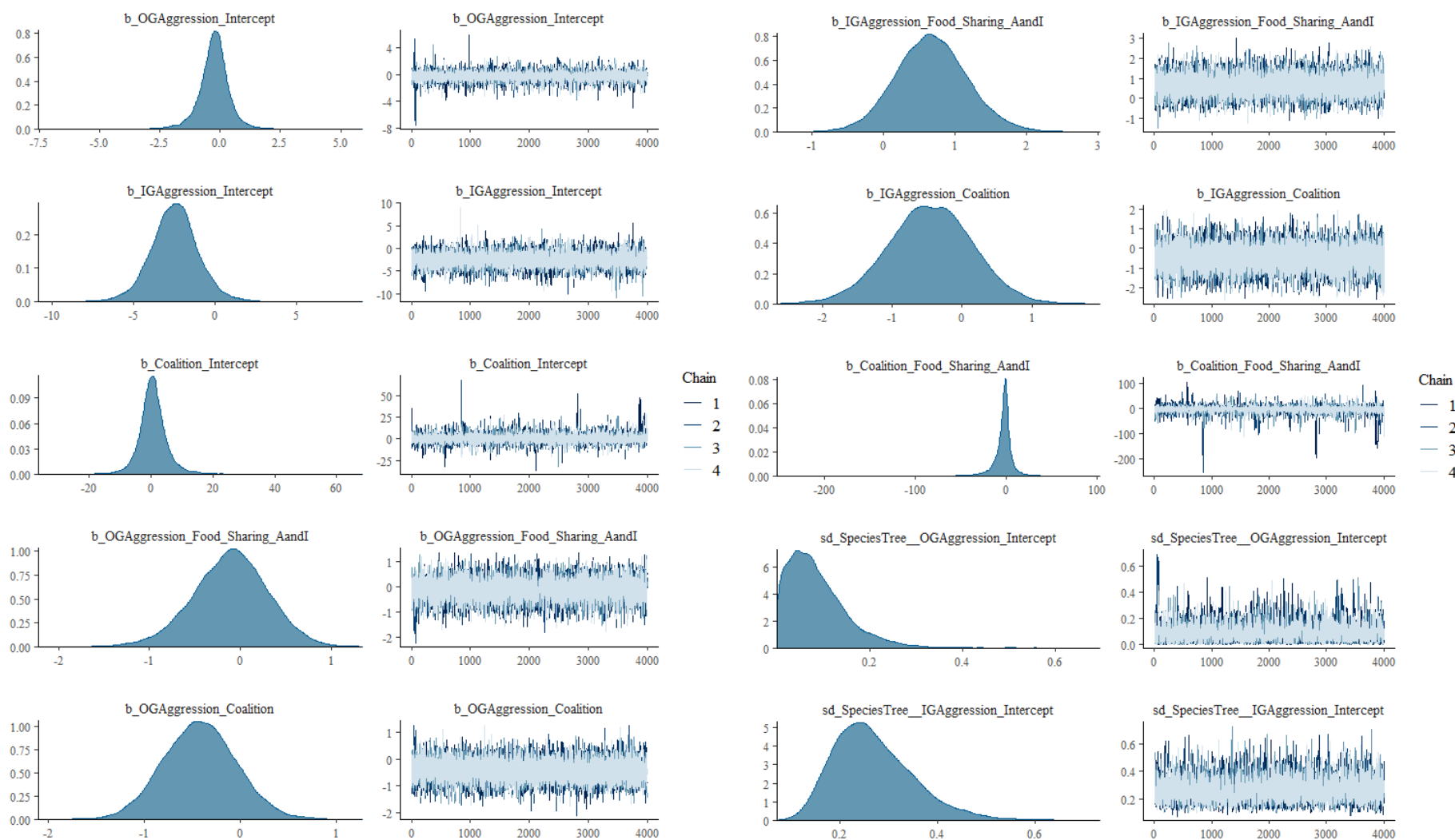
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGAggression_Intercept	-0.25	0.65	-1.61	1.00	1.00	9795	6252
IGAggression_Intercept	-2.49	1.47	-5.46	0.45	1.00	8721	8849
Coalition_Intercept	0.83	5.27	-8.28	11.63	1.00	5569	3329
OGAggression_Food_Sharing_AandI	-0.11	0.41	-0.96	0.68	1.00	10168	7817
OGAggression_Coalition	-0.42	0.38	-1.15	0.32	1.00	21495	12079
IGAggression_Food_Sharing_AandI	0.68	0.50	-0.28	1.69	1.00	16316	12473
IGAggression_Coalition	-0.46	0.61	-1.68	0.74	1.00	14266	13090
Coalition_Food_Sharing_AandI	-3.84	14.67	-33.79	16.34	1.00	5206	2692

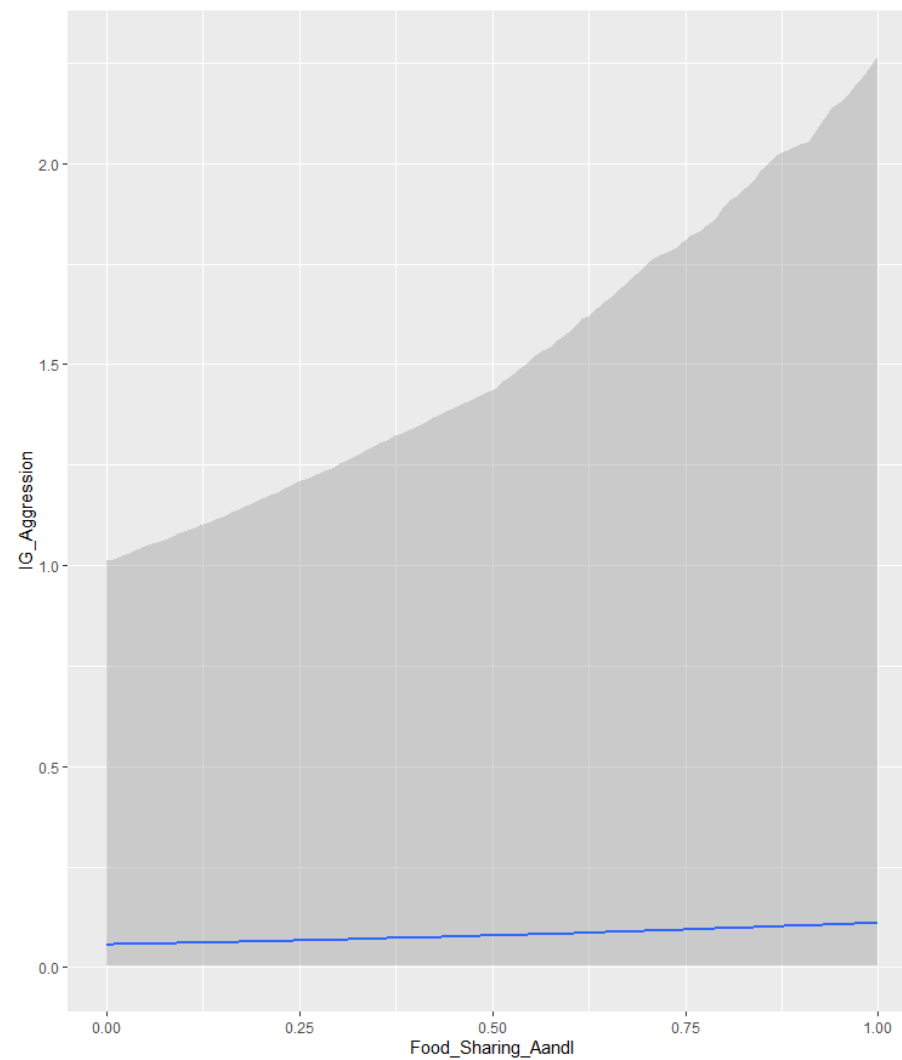
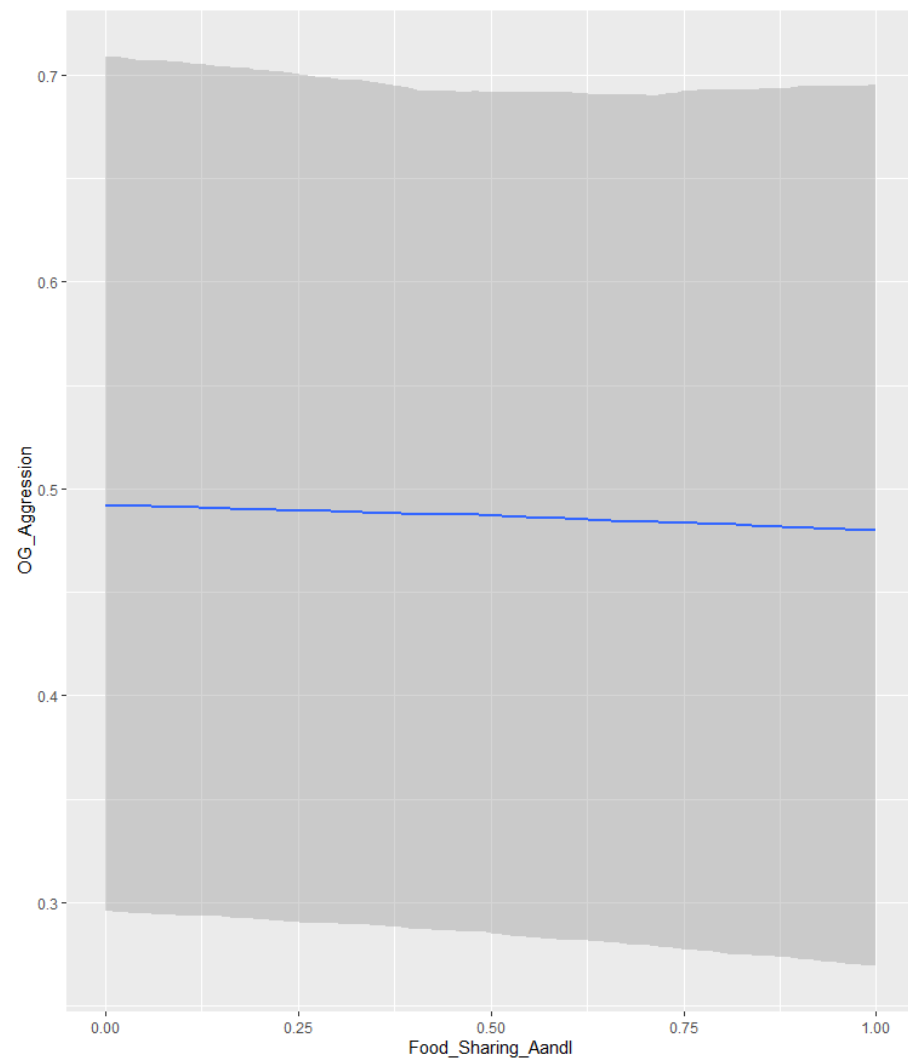
## Family Specific Parameters:

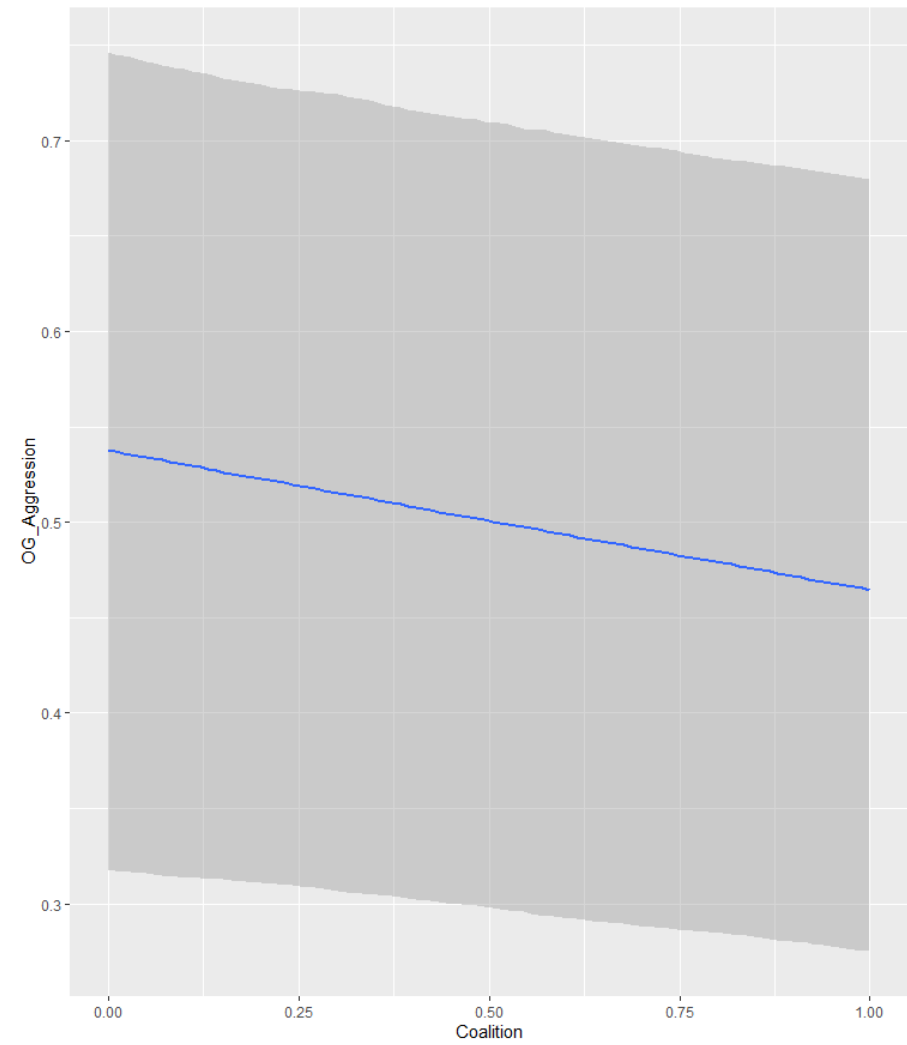
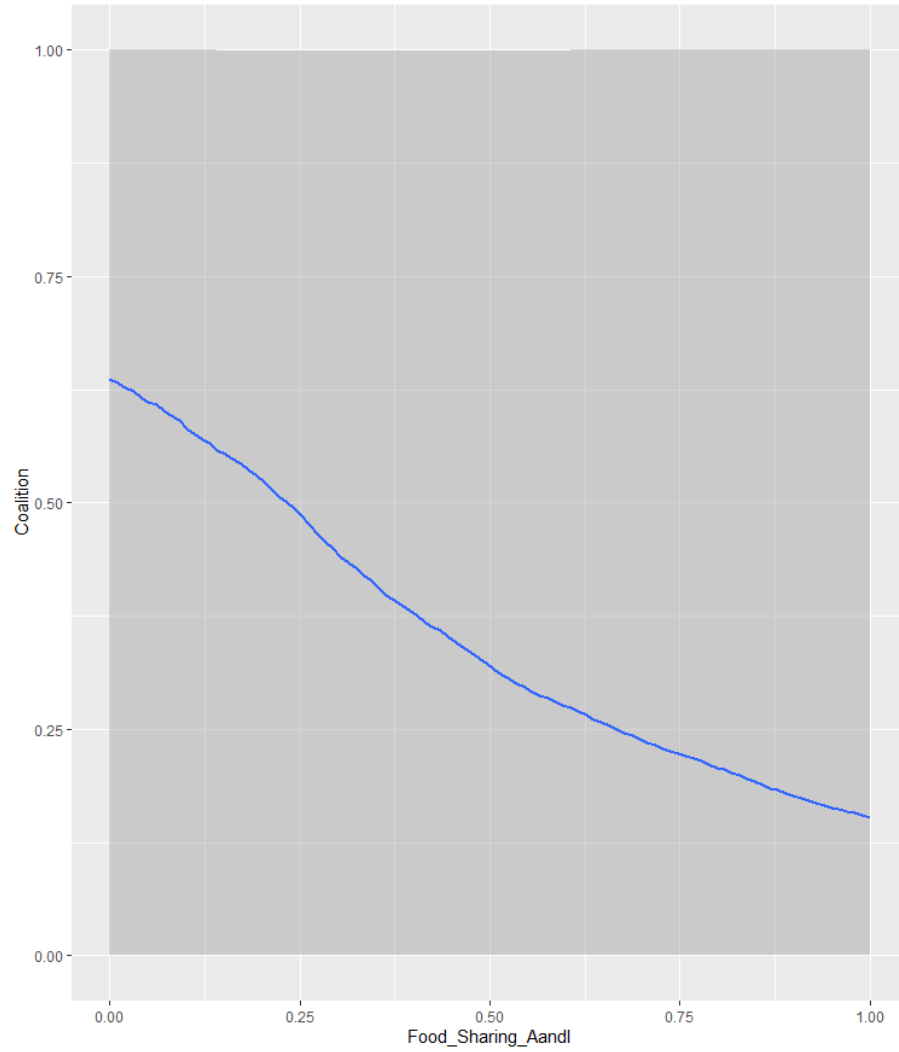
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
phi_OGAggression	3.11	1.59	1.92	5.00	1.00	4642	3375
zoi_OGAggression	0.25	0.05	0.16	0.37	1.00	31206	10843
coi_OGAggression	0.82	0.09	0.62	0.96	1.00	28450	10446
shape_IGAggression	0.64	0.14	0.42	0.96	1.00	6668	7583
hu_IGAggression	0.08	0.03	0.03	0.16	1.00	28905	11423

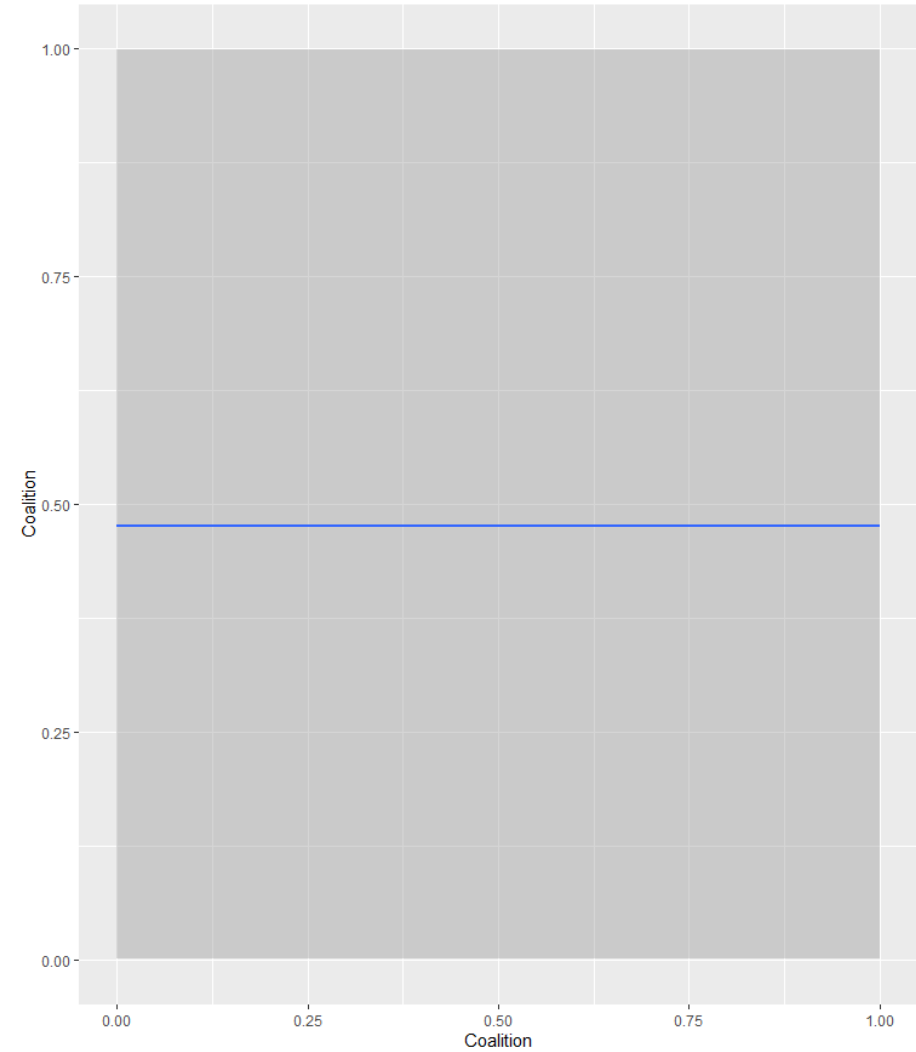
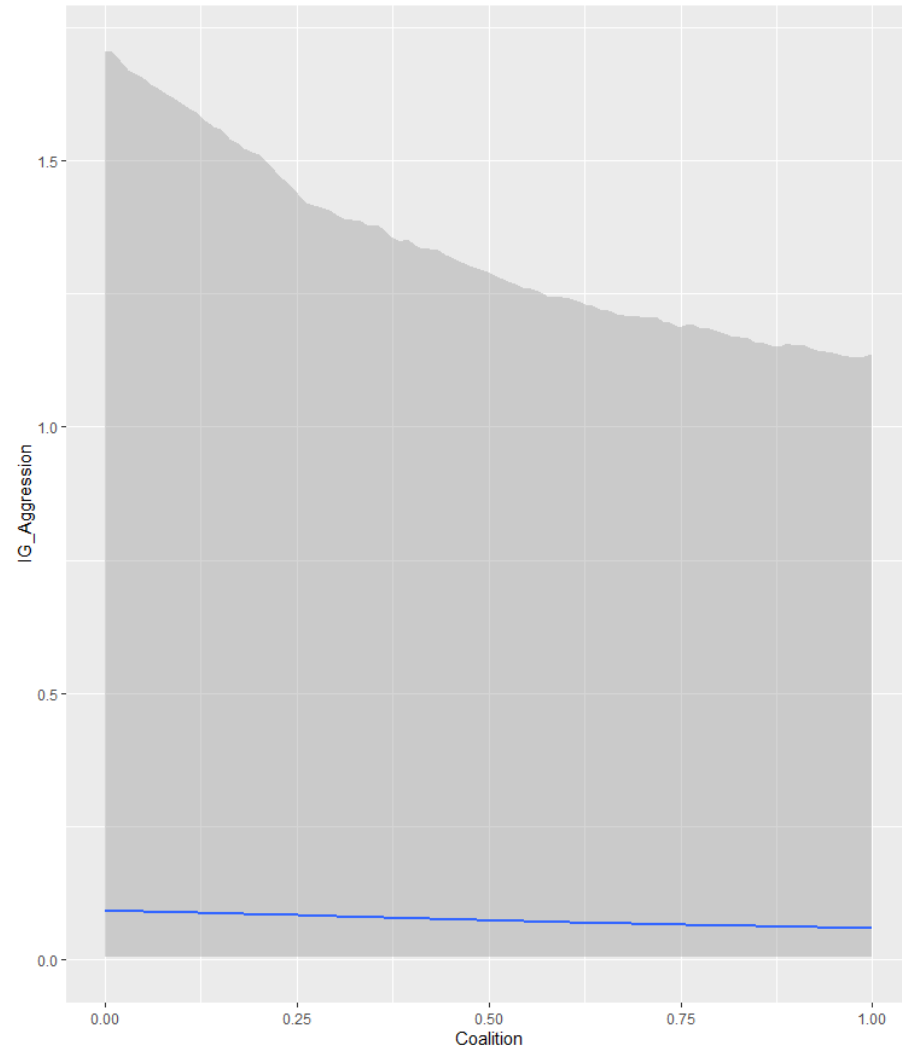
Draws were sampled using `sampling(NUTS)`. For each parameter, `Bulk_ESS` and `Tail_ESS` are effective sample size measures, and `Rhat` is the potential scale reduction factor on split chains (at convergence, `Rhat = 1`).

	Estimate	Est.Error	Q2.5	Q97.5
R2OAggression	0.0640938	0.05100717	0.004594351	0.1912257
R2IAGgression	0.3846009	0.15742696	0.109657332	0.6791960
R2Coalition	0.8720321	0.11694393	0.566677265	0.9996903

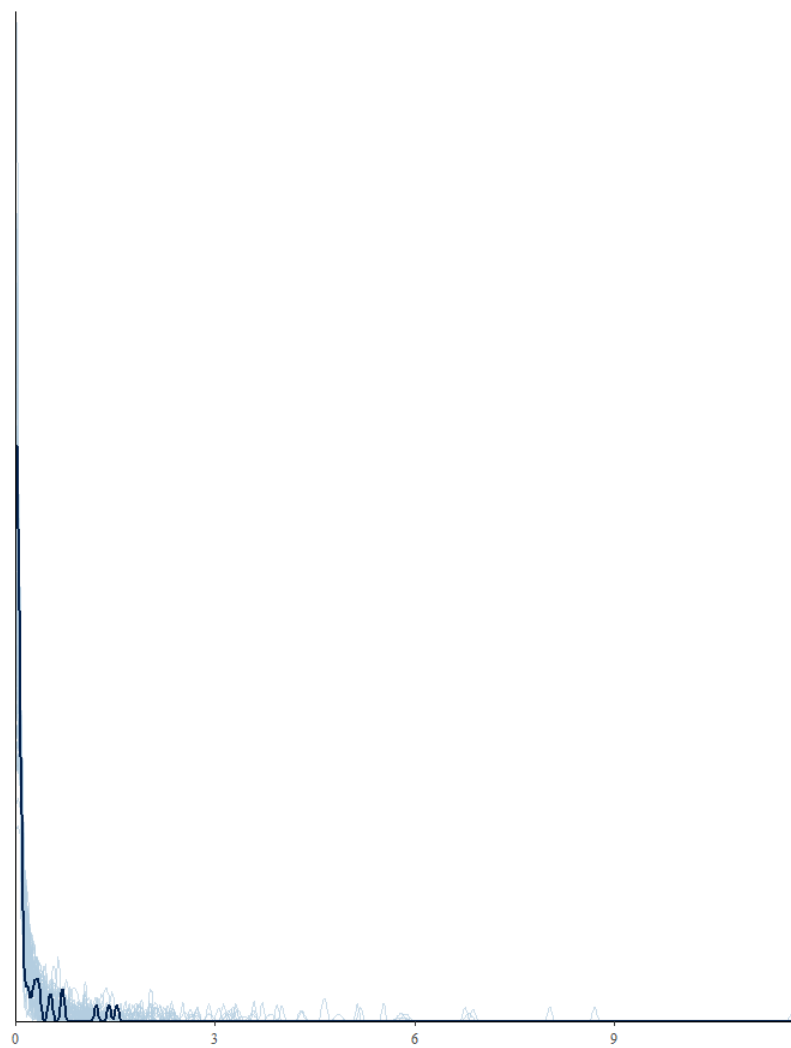
*Plot, Conditional effects, PP plot*



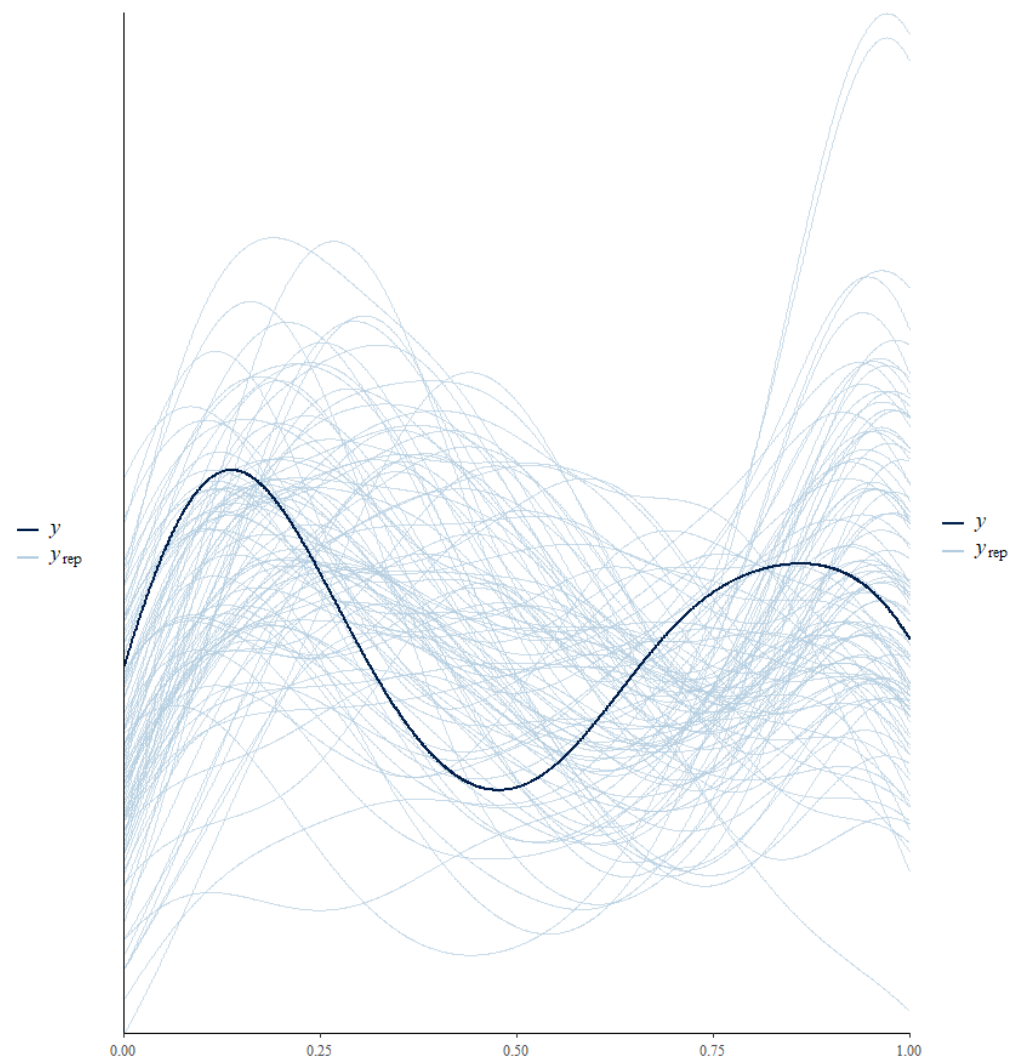




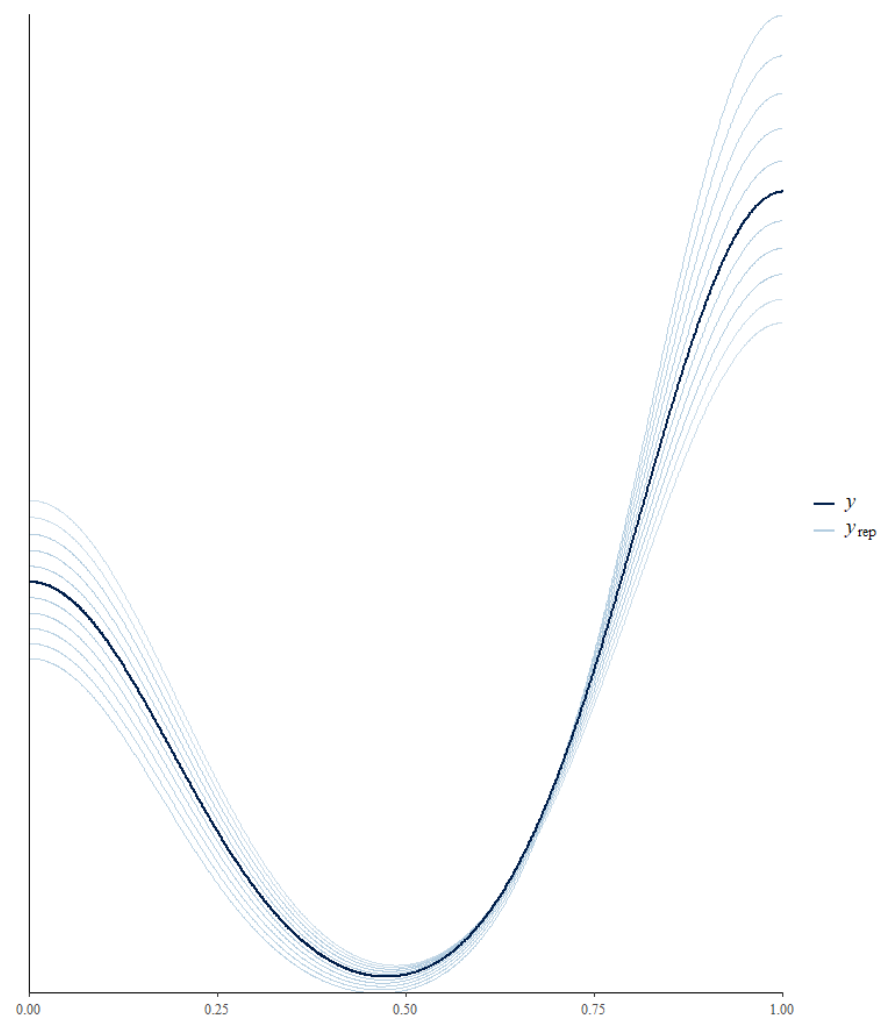
Intragroup aggression (IG Aggression)



Intergroup aggression (OG Aggression)

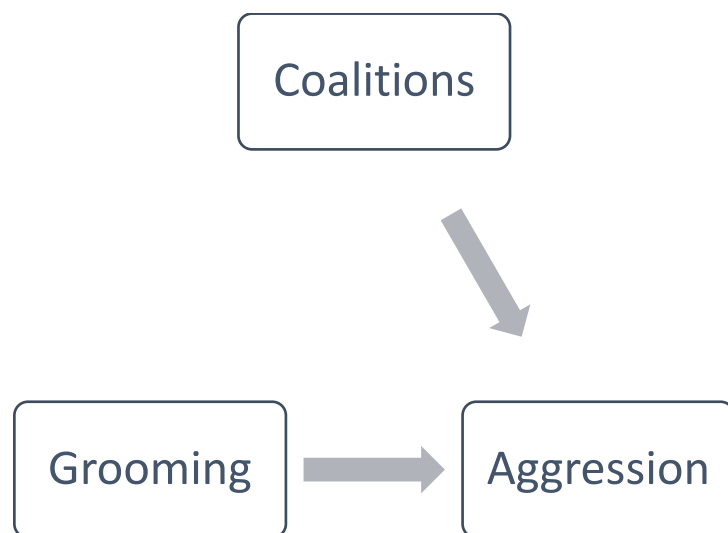


Coalition





Appendix 5E – Model B - Two independent direct effects:



### 5E.1 Model B(i) Adulticide and grooming

```

> summary(Coalitionkill2, waic= T); bayes_R2(Coalitionkill2)
Family: MV(bernoulli, bernoulli)
Links: mu = logit
       mu = logit
Formula: OG_Killing ~ Grooming + Coalition + (1 | p | gr(SpeciesTree, cov = A))
         IG_Killing ~ Grooming + Coalition + (1 | p | gr(SpeciesTree, cov = A))
  
```

Data: dataG (Number of observations: 68)

Draws: 4 chains, each with iter = 8000; warmup = 4000; thin = 1;

total post-warmup draws = 16000

Group-Level Effects:

~SpeciesTree (Number of levels: 68)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGKilling_Intercept)	1.11	1.43	0.13	4.92	1.00	1685	4665
sd(IGKilling_Intercept)	0.69	0.66	0.06	2.35	1.00	2511	3373
cor(OGKilling_Intercept,IGKilling_Intercept)	0.68	0.31	-0.17	0.99	1.00	5193	6497

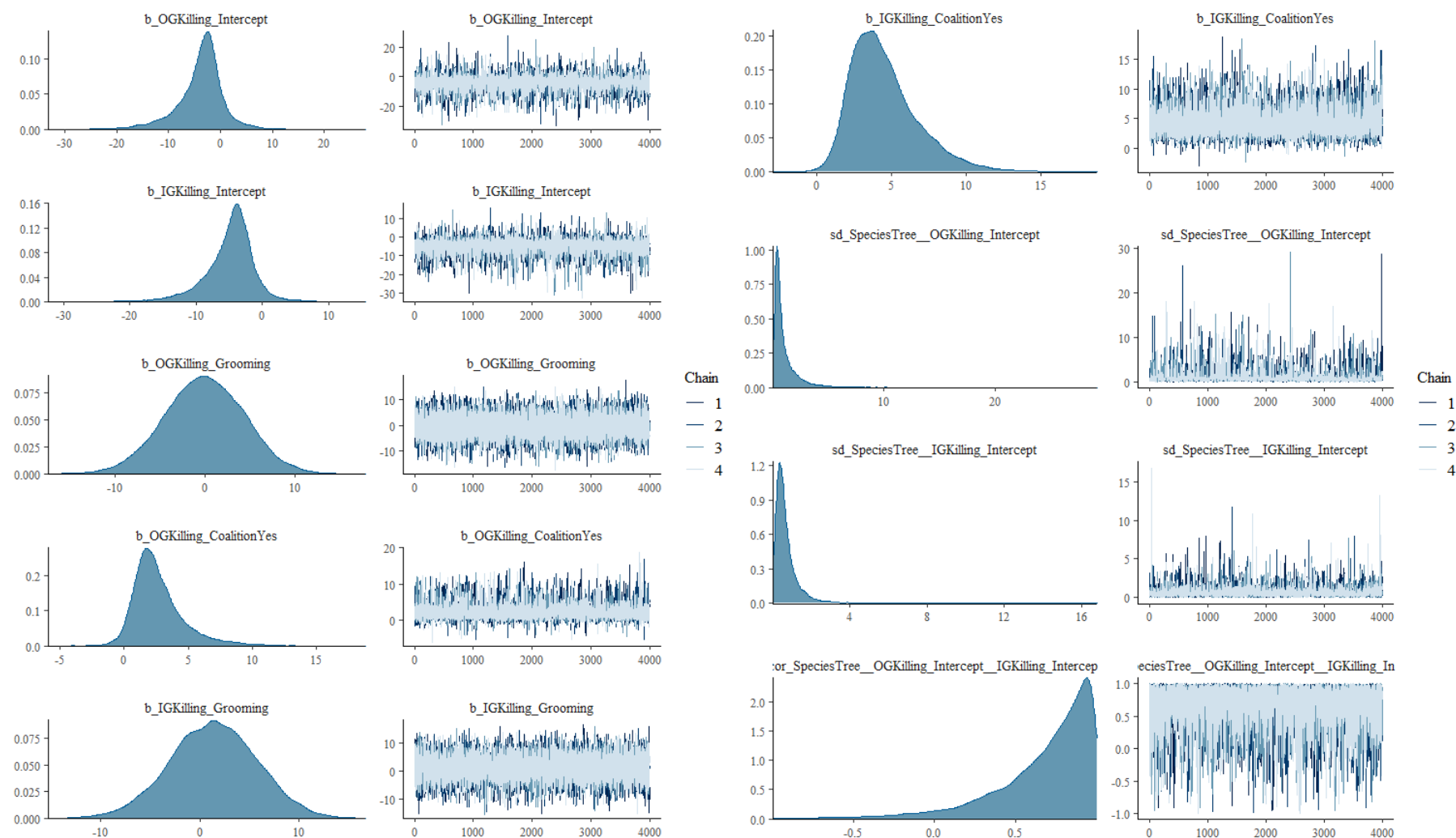
Population-Level Effects:

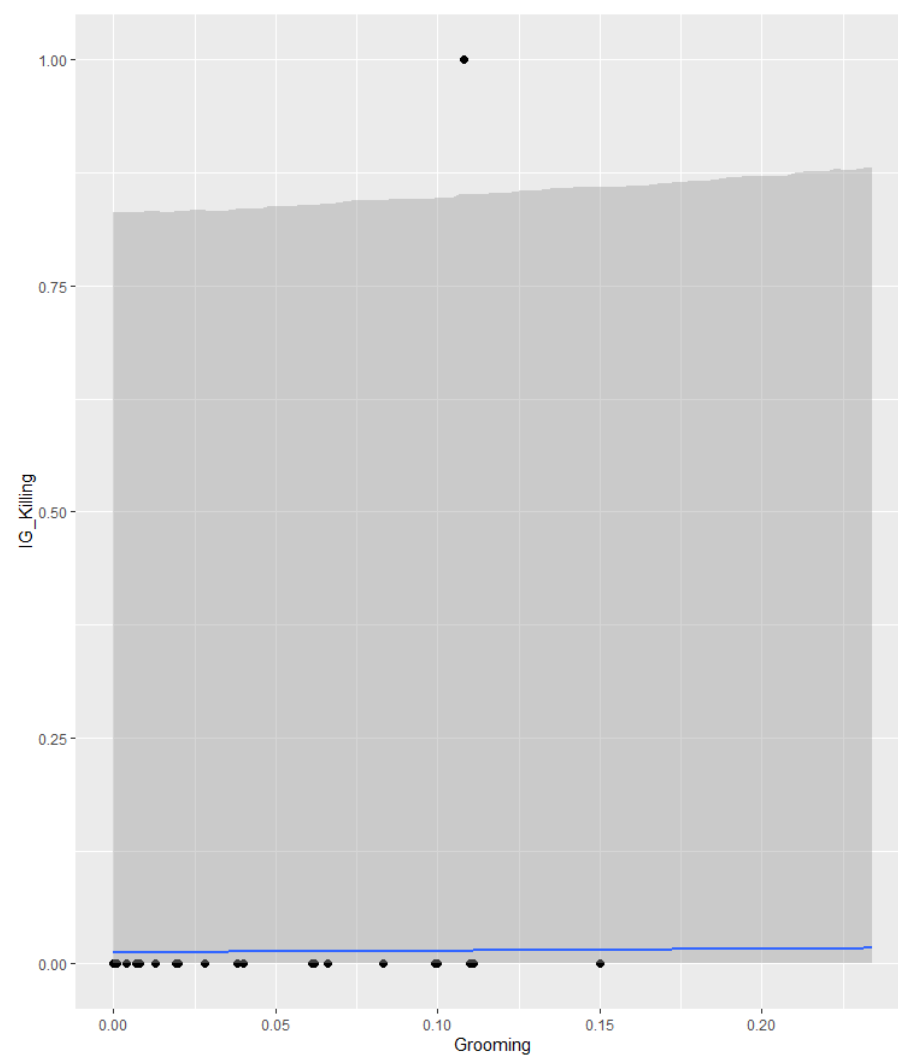
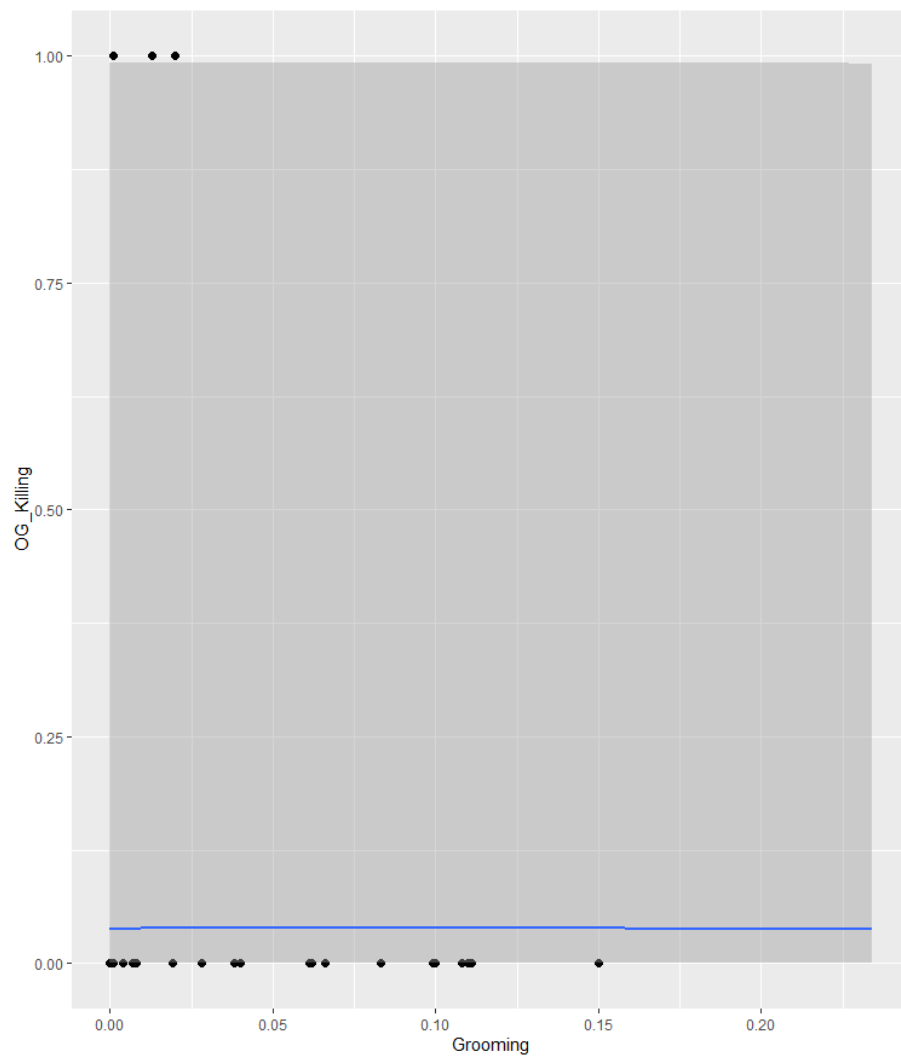
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGKilling_Intercept	-3.85	4.80	-15.52	4.96	1.00	6714	6684
IGKilling_Intercept	-4.94	3.85	-14.17	1.59	1.00	6904	6429
OGKilling_Grooming	-0.12	4.41	-8.84	8.48	1.00	23048	12662
OGKilling_CoalitionYes	2.68	2.10	-0.25	8.24	1.00	5510	5317
IGKilling_Grooming	1.35	4.37	-7.30	9.86	1.00	21082	11813
IGKilling_CoalitionYes	4.53	2.29	1.23	10.06	1.00	6495	7630

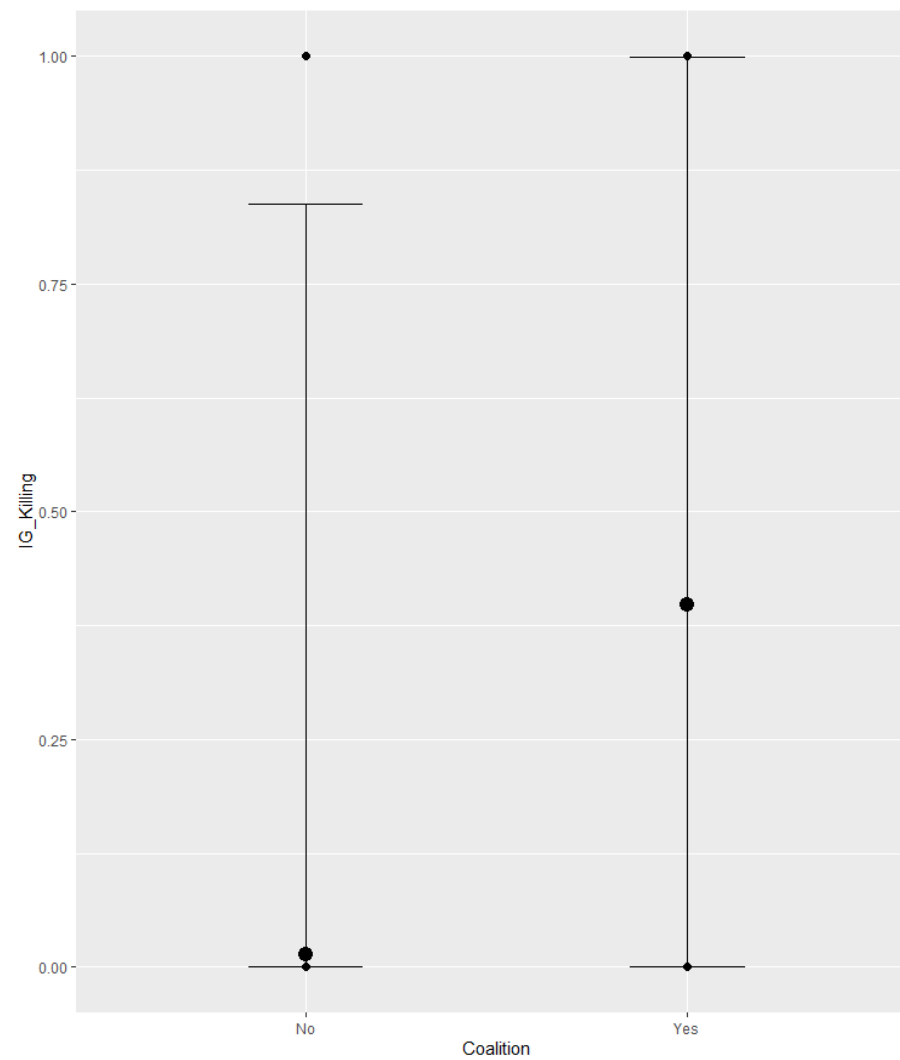
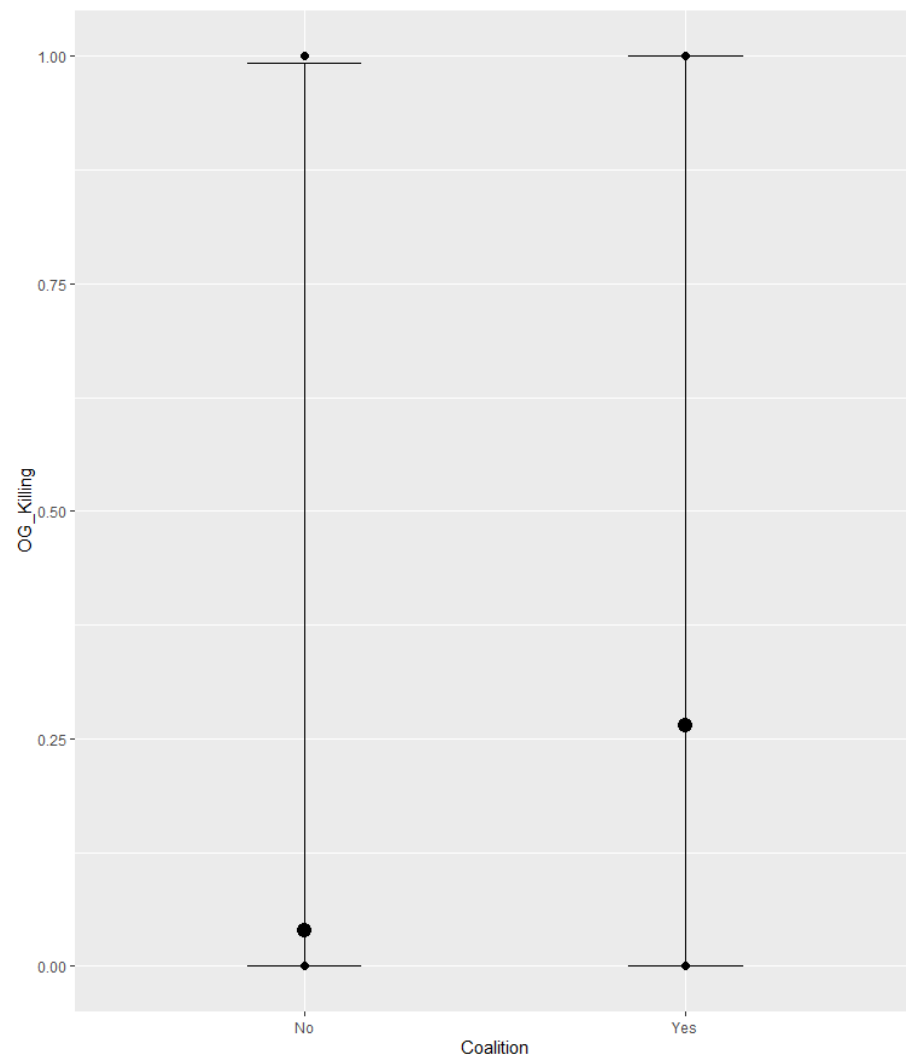
Draws were sampled using sampling(NUTS). For each parameter, Bulk\_ESS

and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

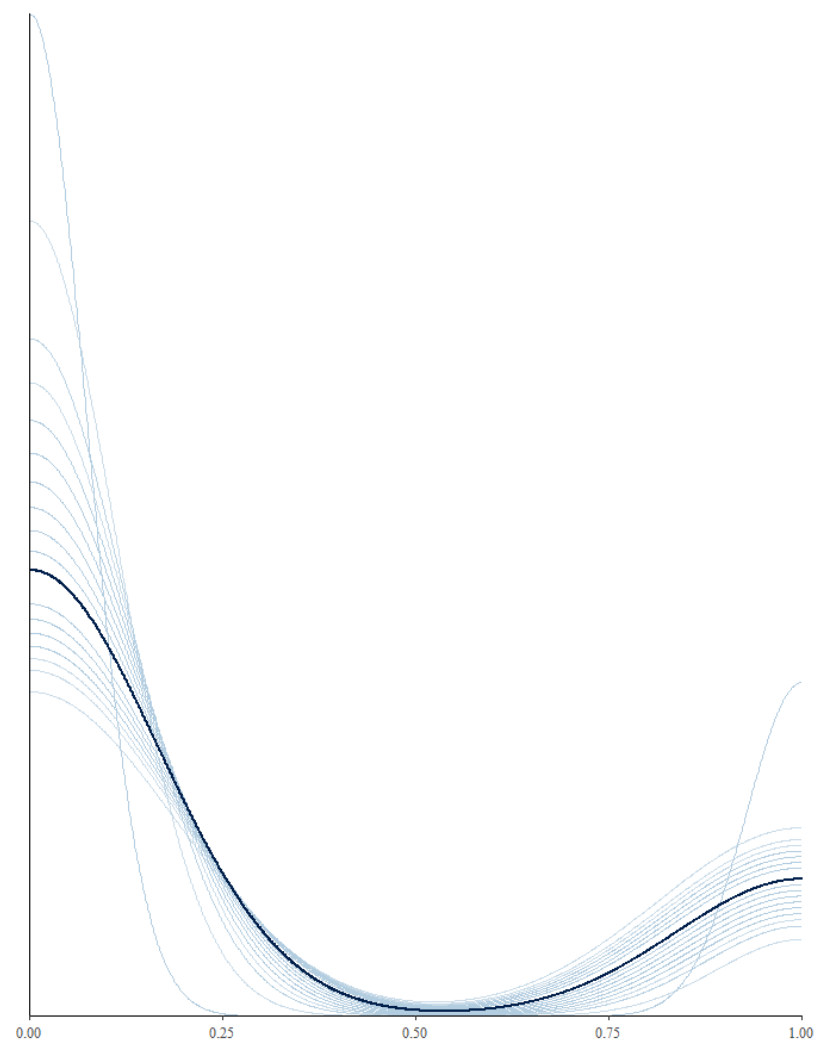
	Estimate	Est.Error	Q2.5	Q97.5
R2OGKilling	0.4536270	0.2036489	0.115817	0.8835766
R2IGKilling	0.4113712	0.1628566	0.128224	0.7644312

*Plot, Conditional effects, PP checks*

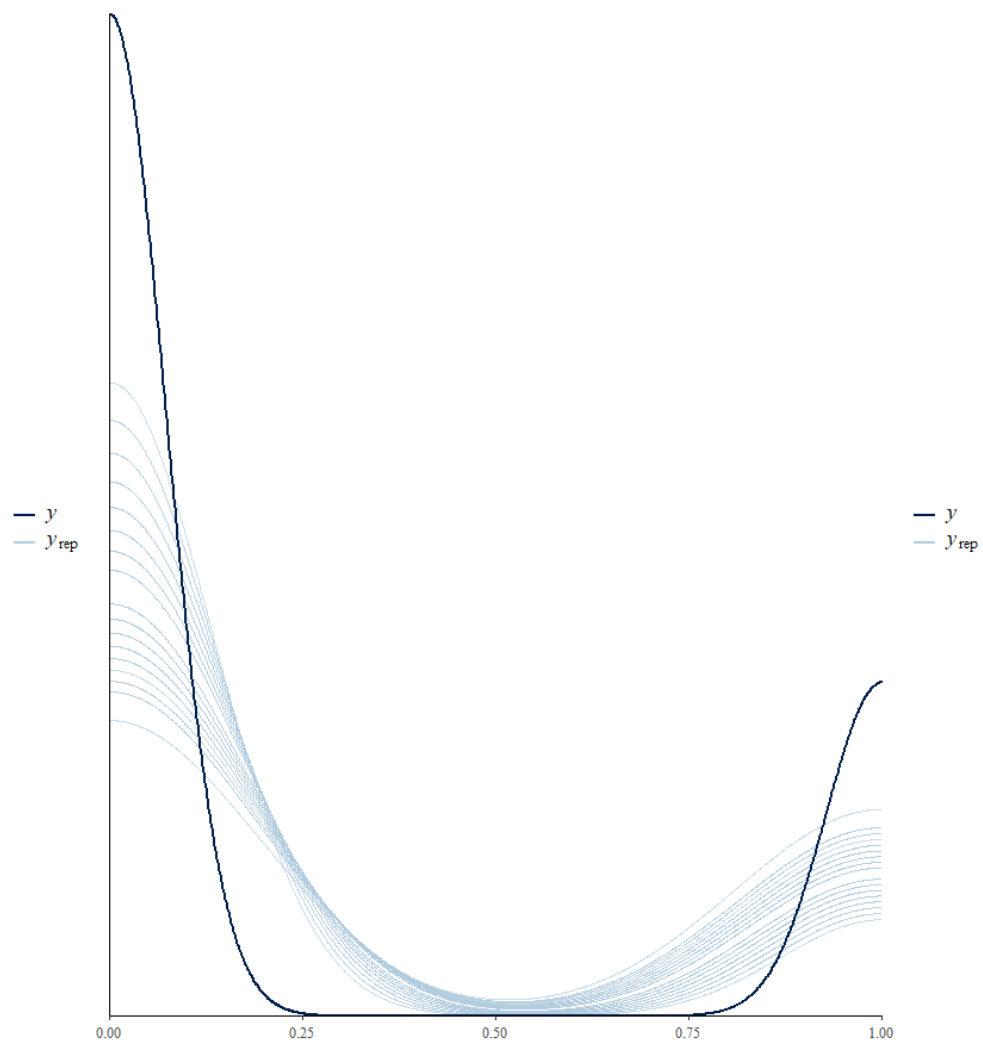




Intragroup aduldicide (IG Killing)



Intergroup aduldicide (OG Killing)



*5E.2 Model B(ii) Adulthood and food-sharing*

```
> summary(Coalitionkill2F, waic= T); bayes_R2(Coalitionkill2F)
```

```
Family: MV(bernoulli, bernoulli)
```

```
Links: mu = logit
```

```
mu = logit
```

```
Formula: OG_Killing ~ Food_Sharing_AandI + Coalition + (1 | p | gr(SpeciesTree, cov = A))
```

```
IG_Killing ~ Food_Sharing_AandI + Coalition + (1 | p | gr(SpeciesTree, cov = A))
```

```
Data: data1 (Number of observations: 61)
```

```
Draws: 4 chains, each with iter = 8000; warmup = 4000; thin = 1;
```

```
total post-warmup draws = 16000
```

Group-Level Effects:

~SpeciesTree (Number of levels: 61)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGKilling_Intercept)	1.57	2.56	0.11	7.62	1.00	1155	3312
sd(IGKilling_Intercept)	1.61	1.45	0.11	5.02	1.00	2114	2498
cor(OGKilling_Intercept,IGKilling_Intercept)	0.64	0.30	-0.14	0.98	1.00	2959	3737

Population-Level Effects:

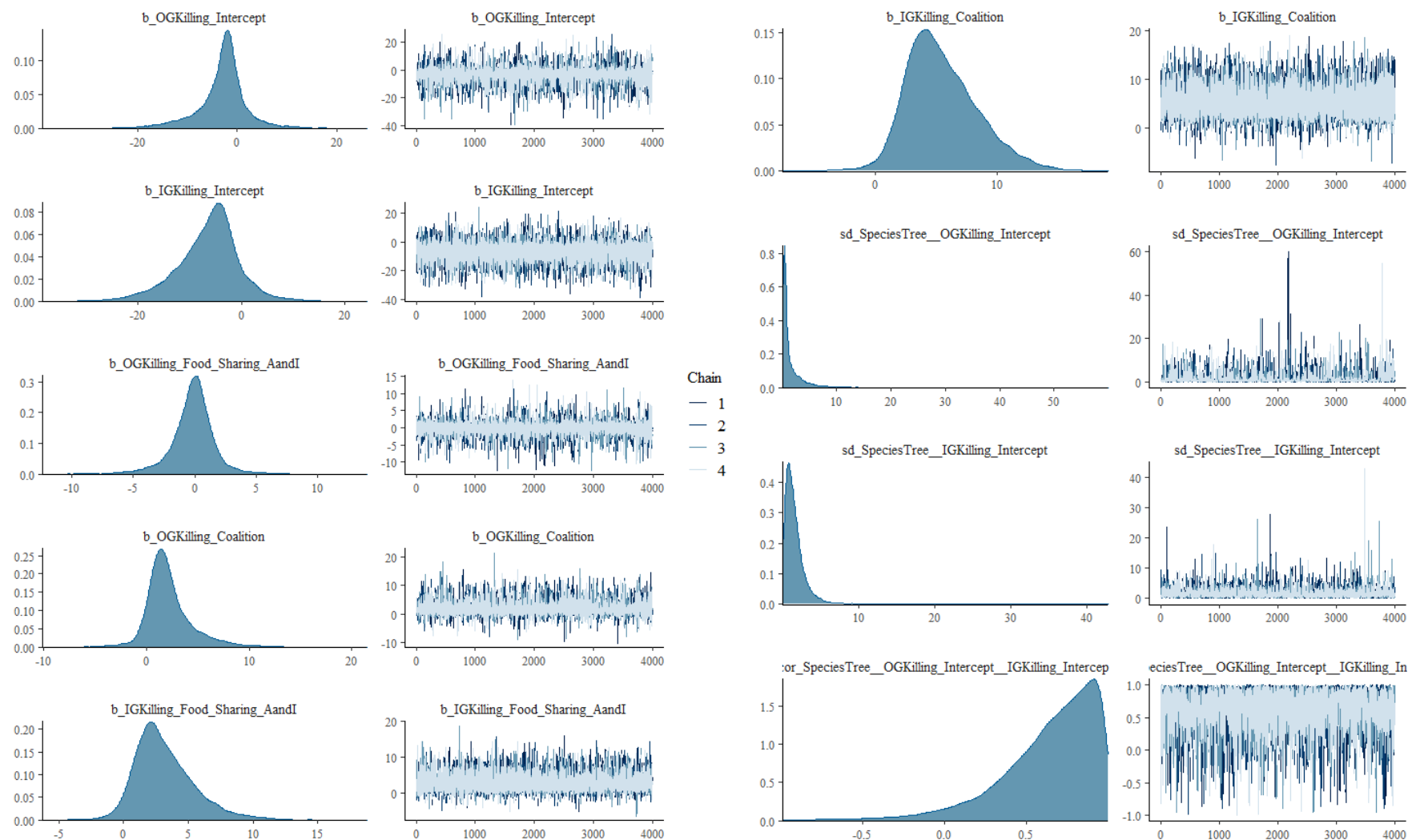
Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
----------	-----------	----------	----------	------	----------	----------

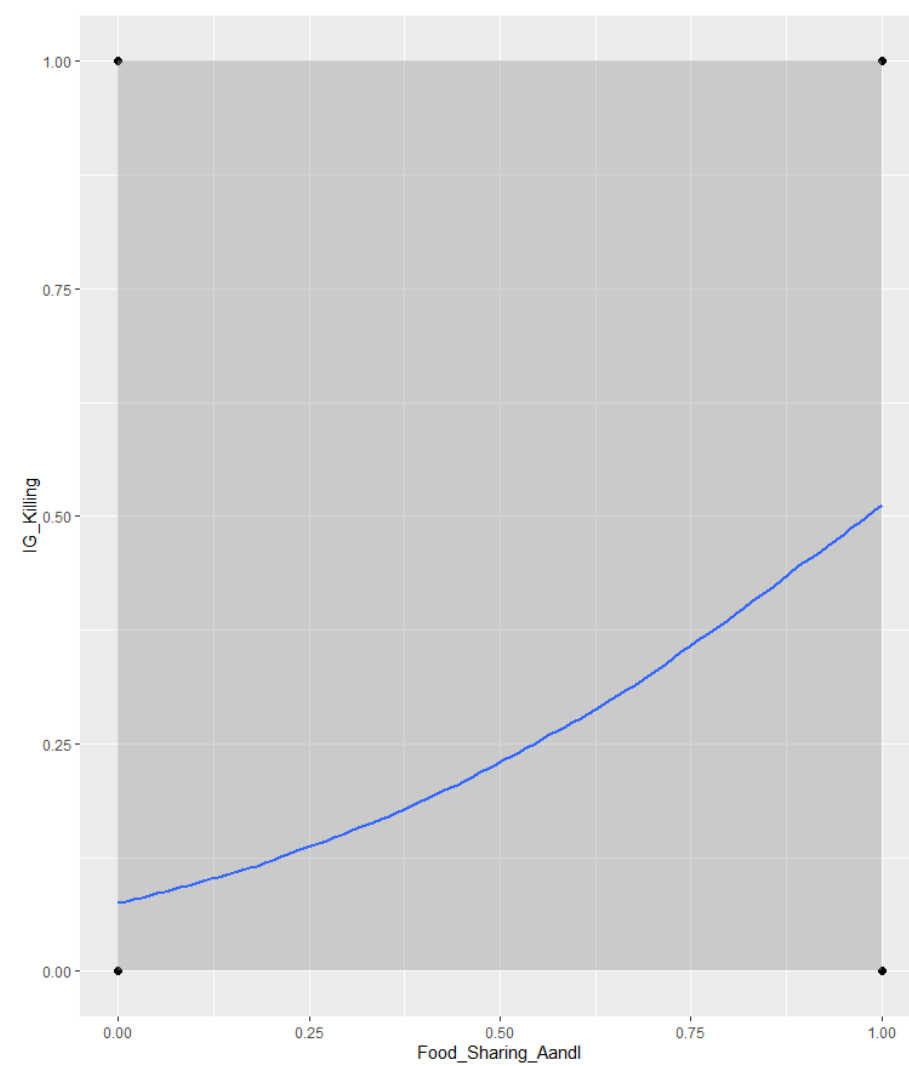
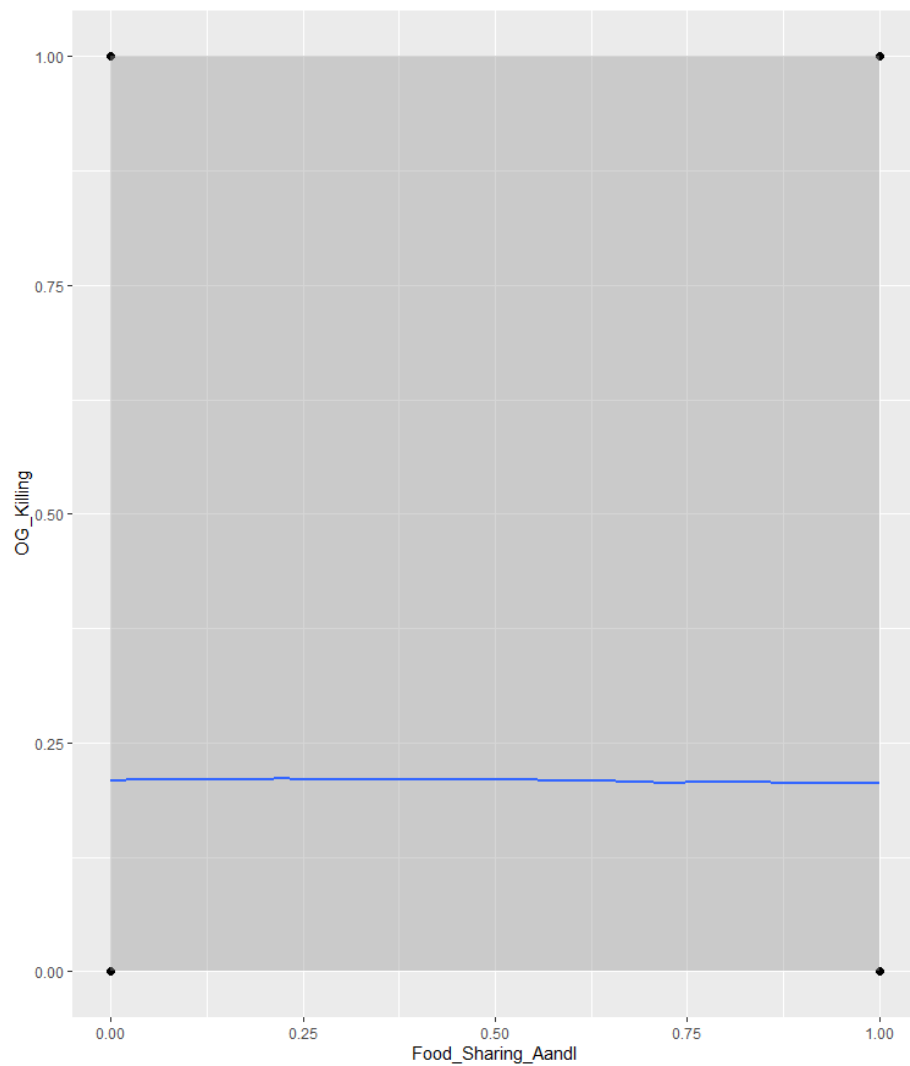


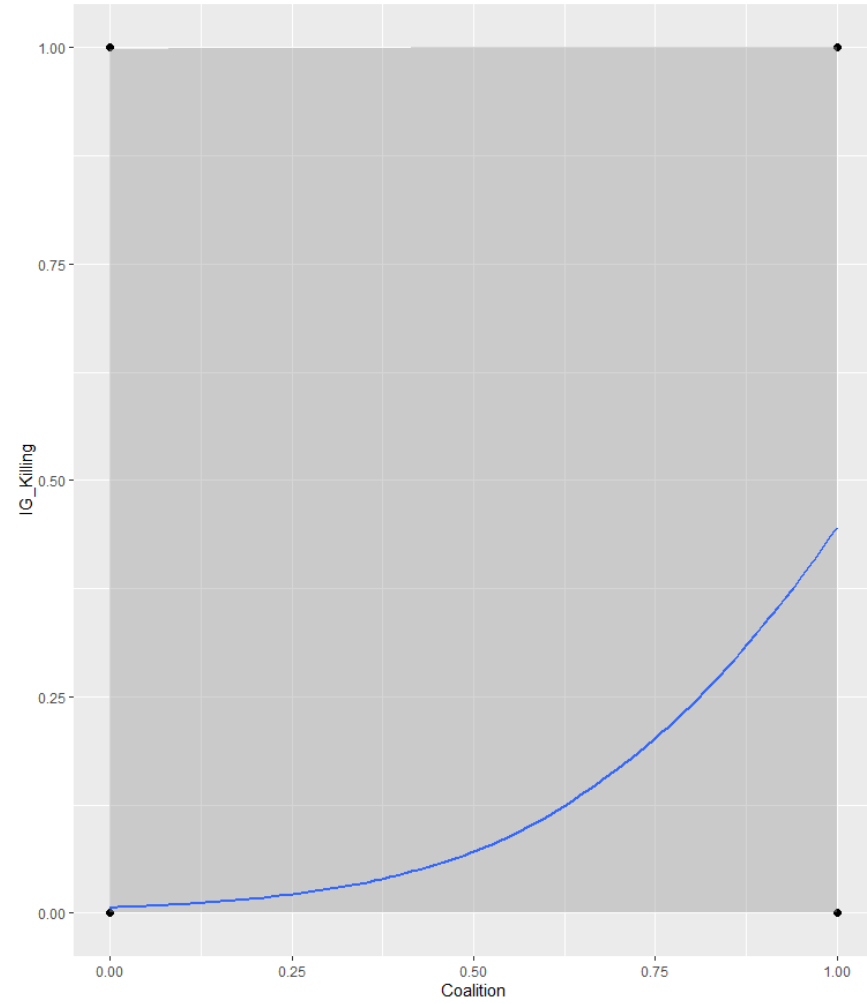
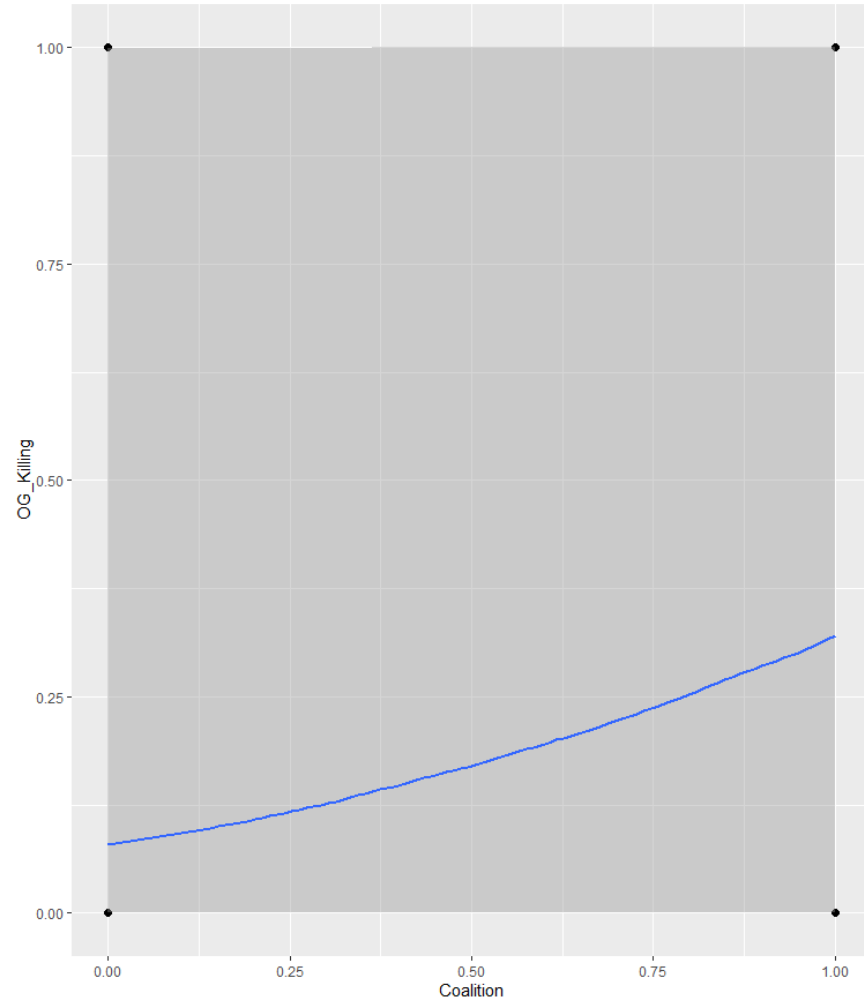
OGKilling_Intercept	-3.08	5.40	-16.18	7.48	1.00	6110	5373
IGKilling_Intercept	-6.50	6.17	-20.48	5.10	1.00	8764	8637
OGKilling_Food_Sharing_AandI	-0.18	1.98	-4.67	3.65	1.00	6890	3572
OGKilling_Coalition	2.20	2.34	-1.41	8.19	1.00	5281	5174
IGKilling_Food_Sharing_AandI	3.18	2.34	-0.43	8.87	1.00	6343	7148
IGKilling_Coalition	5.48	2.96	0.73	12.16	1.00	8288	9992

Draws were sampled using `sampling(NUTS)`. For each parameter, `Bulk_ESS` and `Tail_ESS` are effective sample size measures, and `Rhat` is the potential scale reduction factor on split chains (at convergence, `Rhat` = 1).

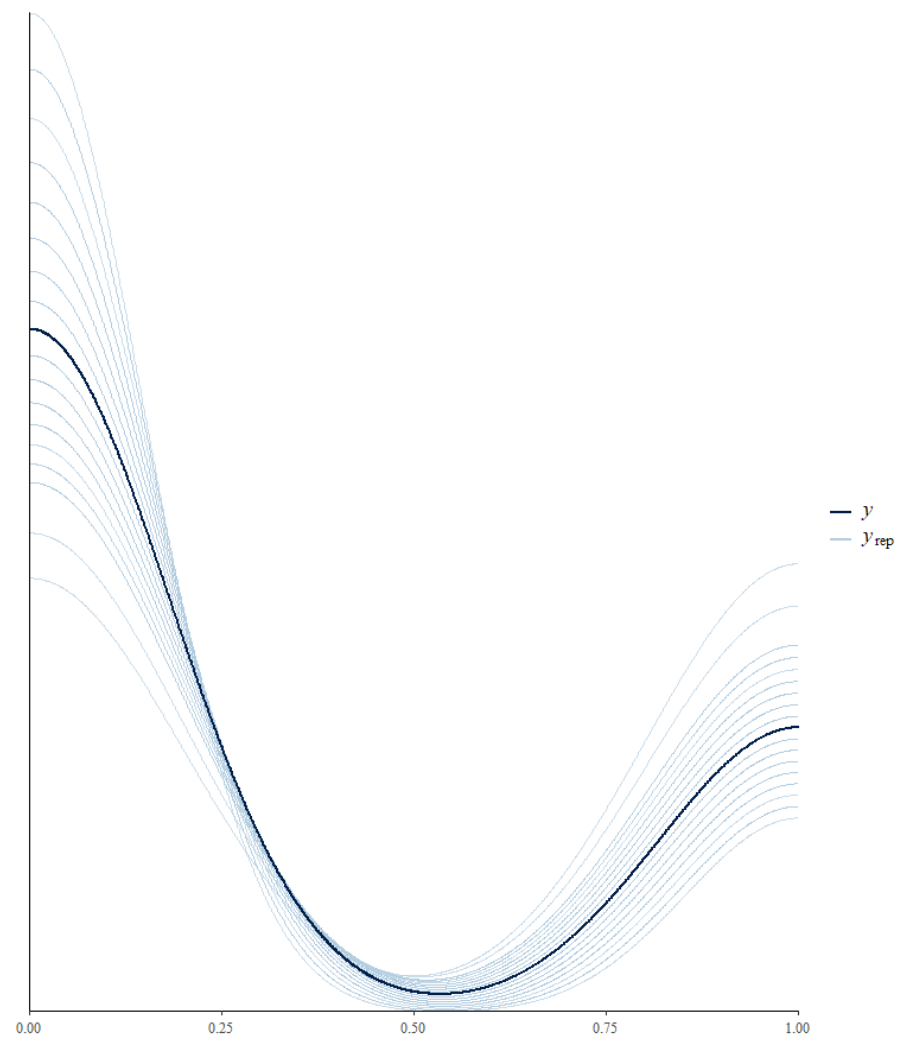
	Estimate	Est.Error	Q2.5	Q97.5
R2OGKilling	0.4602026	0.2358619	0.1003909	0.9278047
R2IGKilling	0.6332144	0.1799169	0.2526501	0.9301207

*Plot, Conditional effects, PP checks*

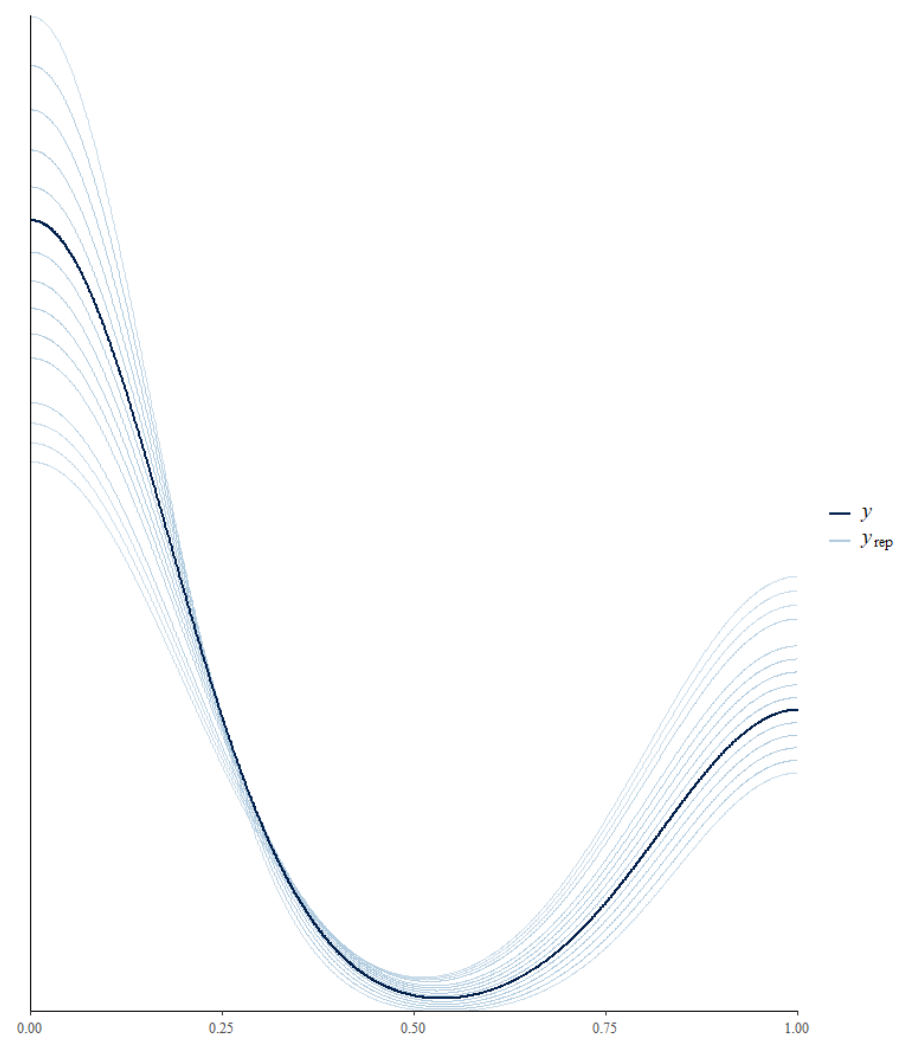




Intergroup aduldicide (OG Killing)



Intragroup aduldicide (IG Killing)



### 5E.3 Model B(iii) Infanticide and grooming

```
> summary(Coalitioninf2, waic= T); bayes_R2(Coalitioninf2)
Family: bernoulli
Links: mu = logit
Formula: Infanticide ~ Grooming + Coalition + (1 | p | gr(SpeciesTree, cov = A))
Data: dataG (Number of observations: 68)
Draws: 4 chains, each with iter = 8000; warmup = 4000; thin = 1;
       total post-warmup draws = 16000
```

#### Group-Level Effects:

```
~SpeciesTree (Number of levels: 68)
```

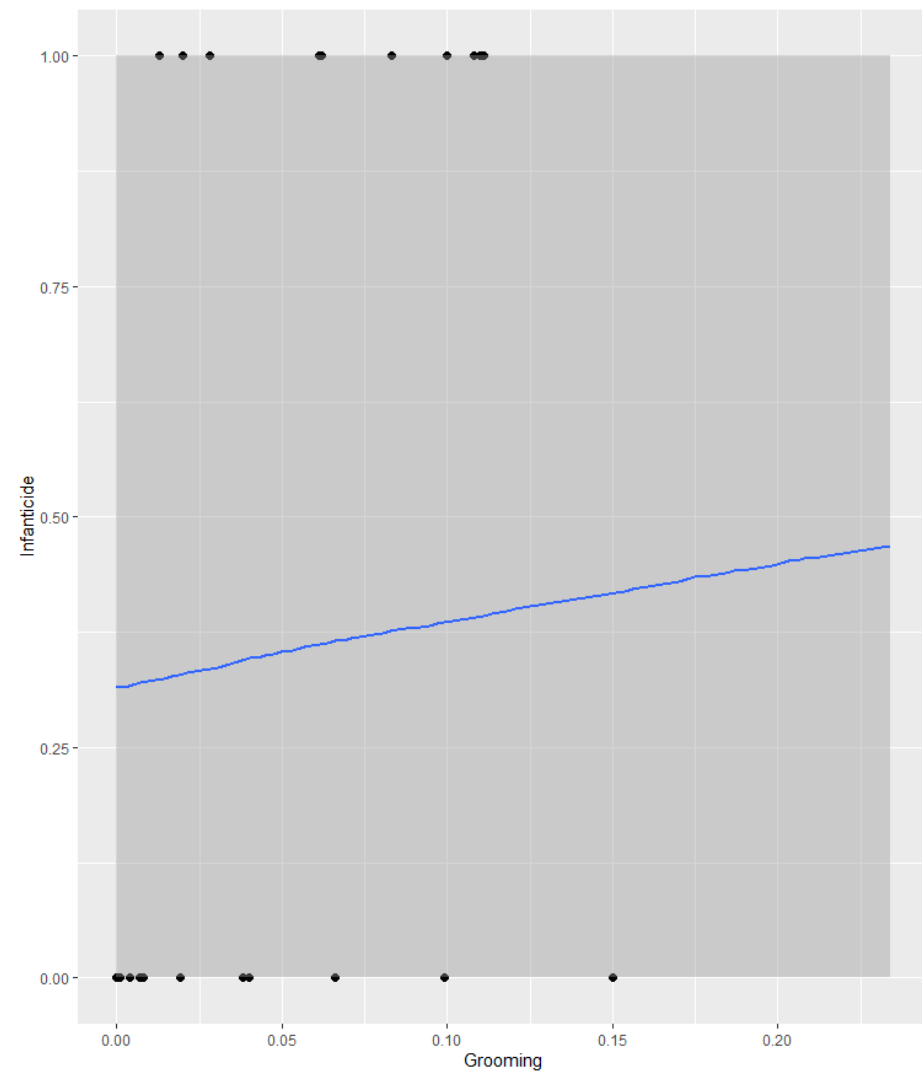
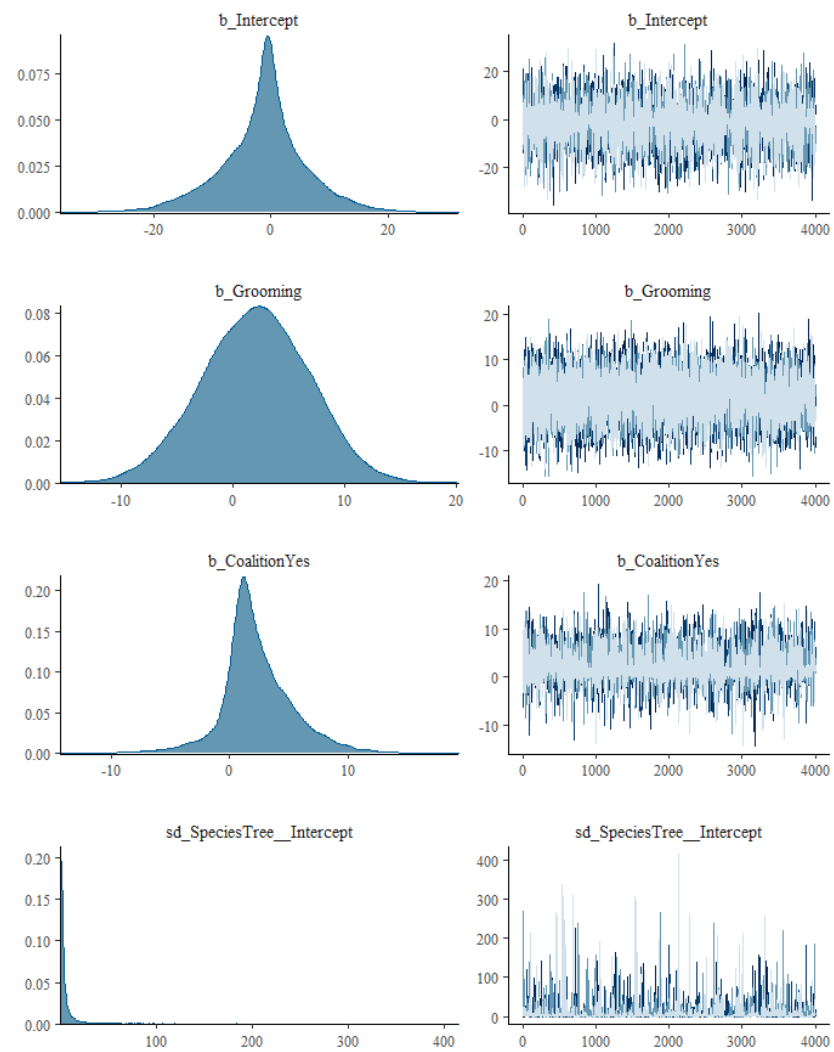
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	6.13	17.22	0.08	38.20	1.00	798	1297

#### Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-1.12	7.57	-17.39	14.66	1.00	6710	7534
Grooming	1.88	4.98	-8.15	11.28	1.00	5566	9501
CoalitionYes	2.46	3.01	-3.38	9.30	1.00	4468	5046

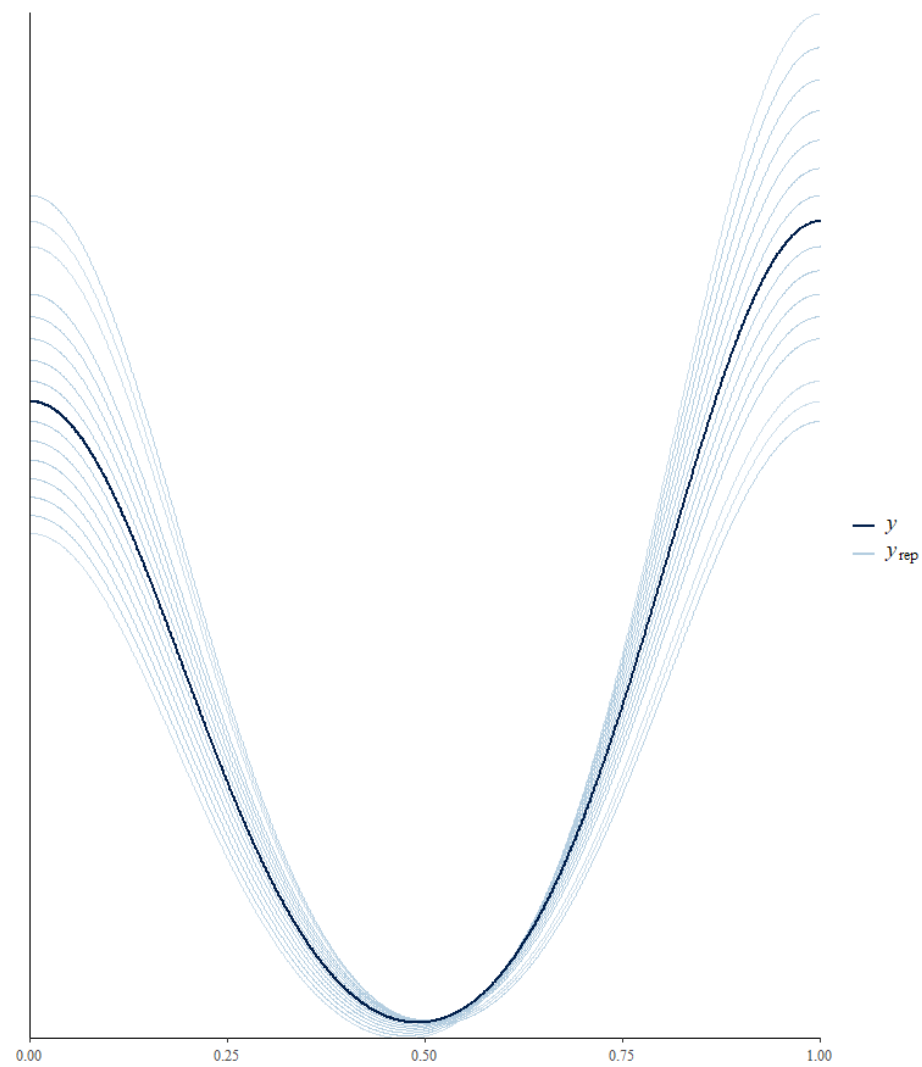
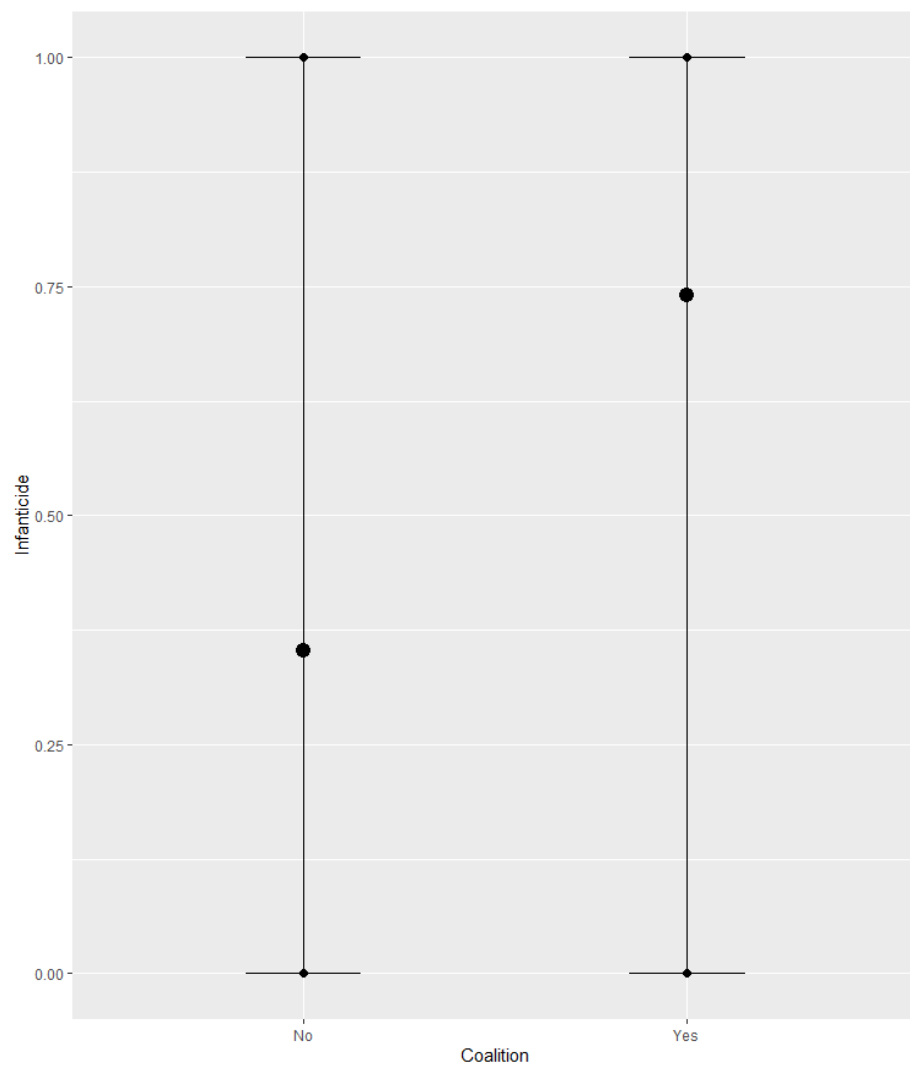
Draws were sampled using `sampling(NUTS)`. For each parameter, `Bulk_ESS` and `Tail_ESS` are effective sample size measures, and `Rhat` is the potential scale reduction factor on split chains (at convergence, `Rhat = 1`).

	Estimate	Est.Error	Q2.5	Q97.5
R2	0.6934499	0.2500493	0.1114007	0.9983354

*Plot, Conditional effects, PP checks*



Infanticide



*5E.4 Model B(iv) Infanticide and food-sharing*

```
> summary(Coalitioninf2F, waic= T); bayes_R2(Coalitioninf2F)
Family: bernoulli
Links: mu = logit
Formula: Infanticide ~ Food_Sharing_AandI + Coalition + (1 | p | gr(SpeciesTree, cov = A))
Data: data1 (Number of observations: 61)
Draws: 4 chains, each with iter = 5000; warmup = 2500; thin = 1;
       total post-warmup draws = 10000
```

## Group-Level Effects:

```
~SpeciesTree (Number of levels: 61)
```

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	10.96	18.83	0.31	63.24	1.00	748	616

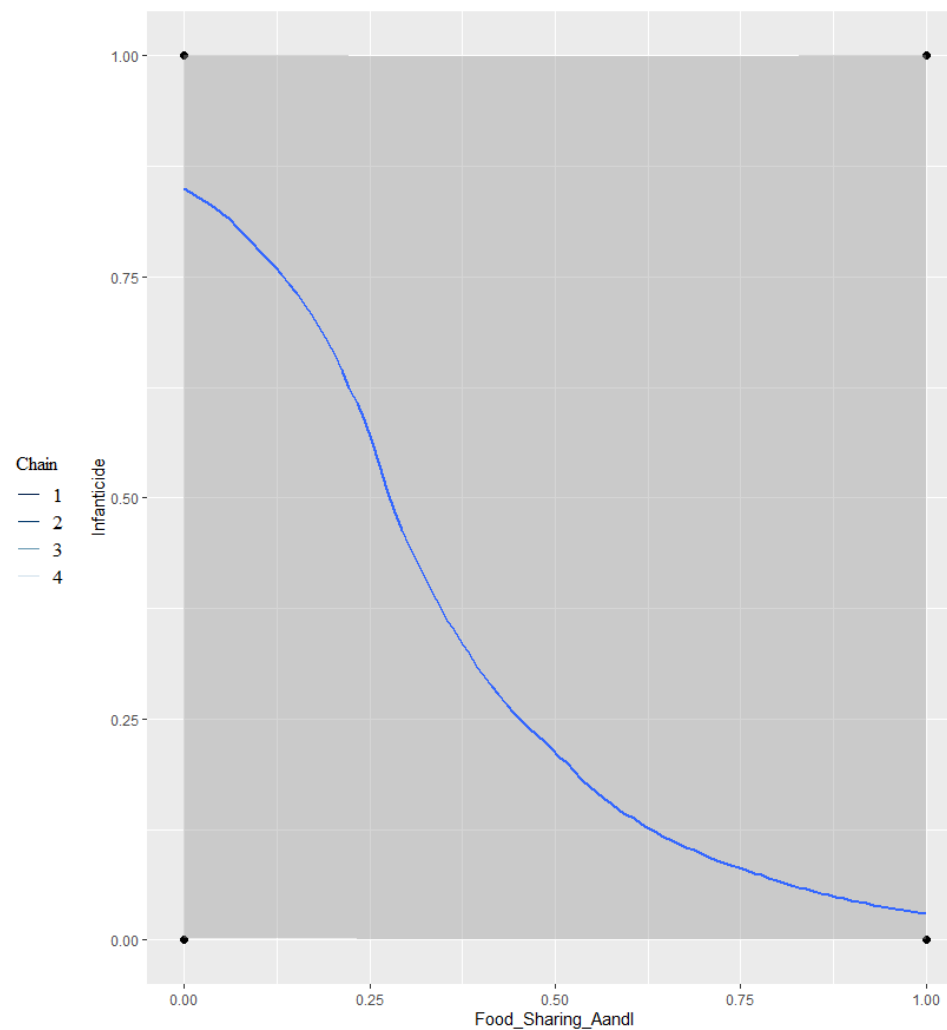
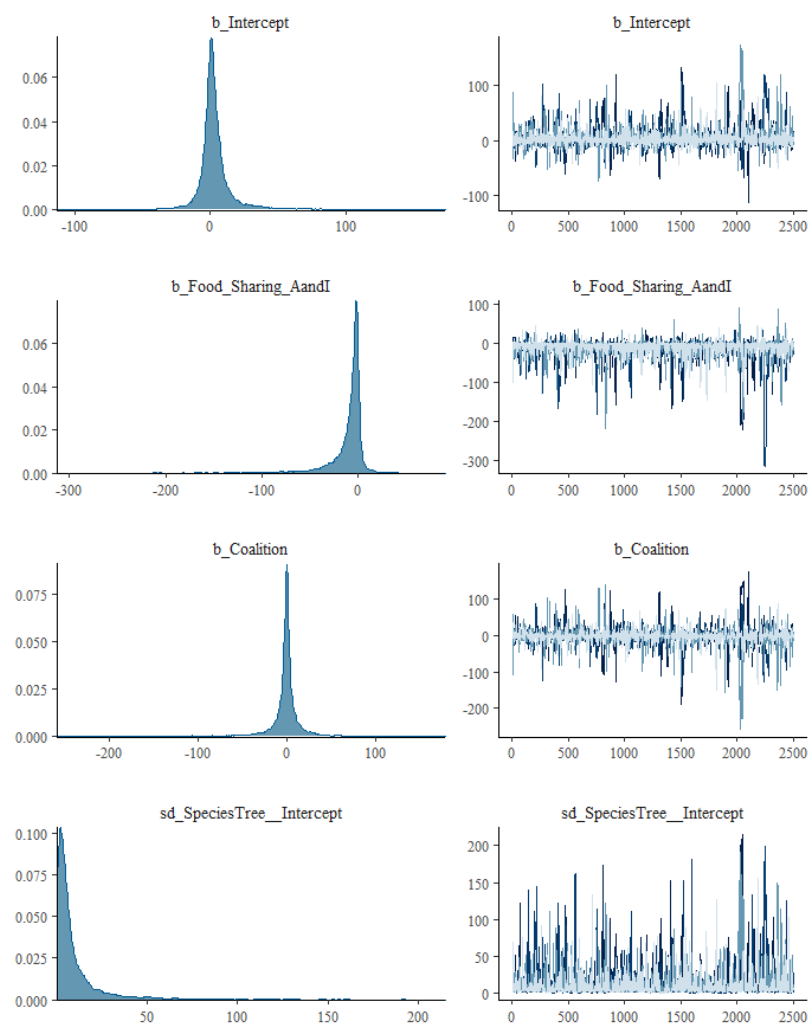
## Population-Level Effects:

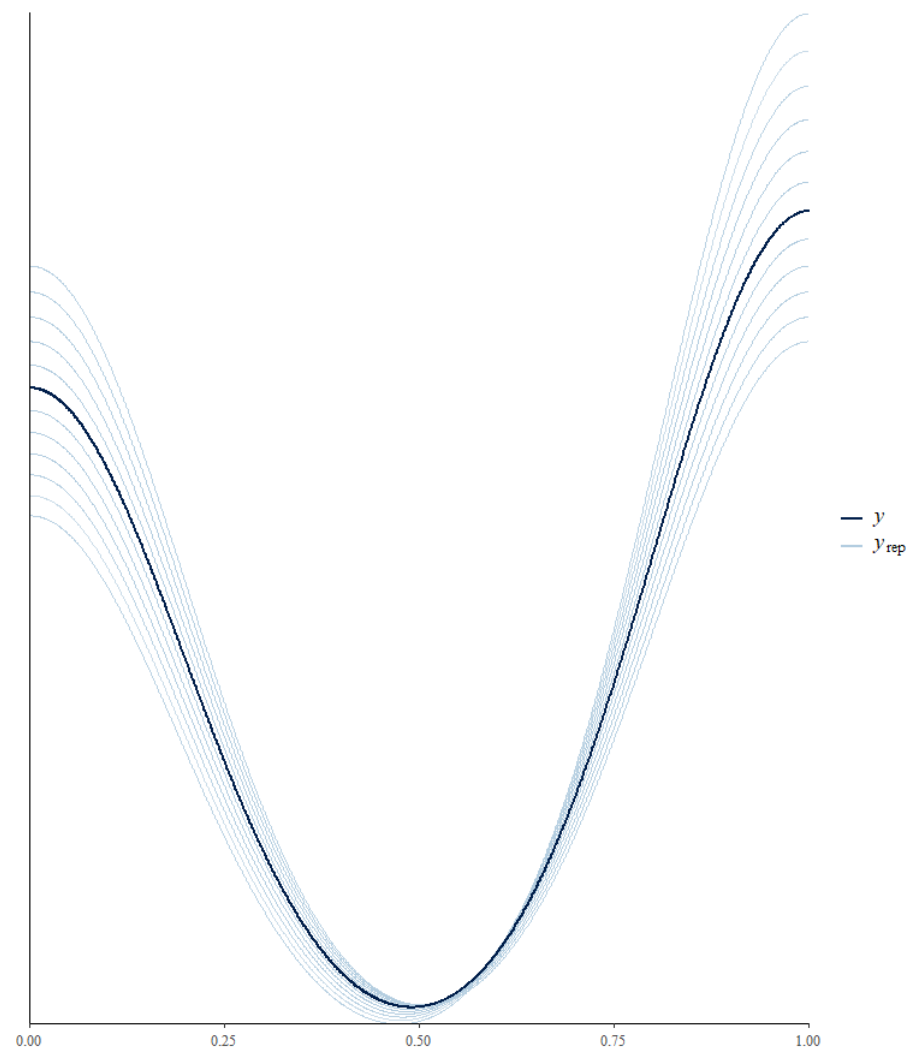
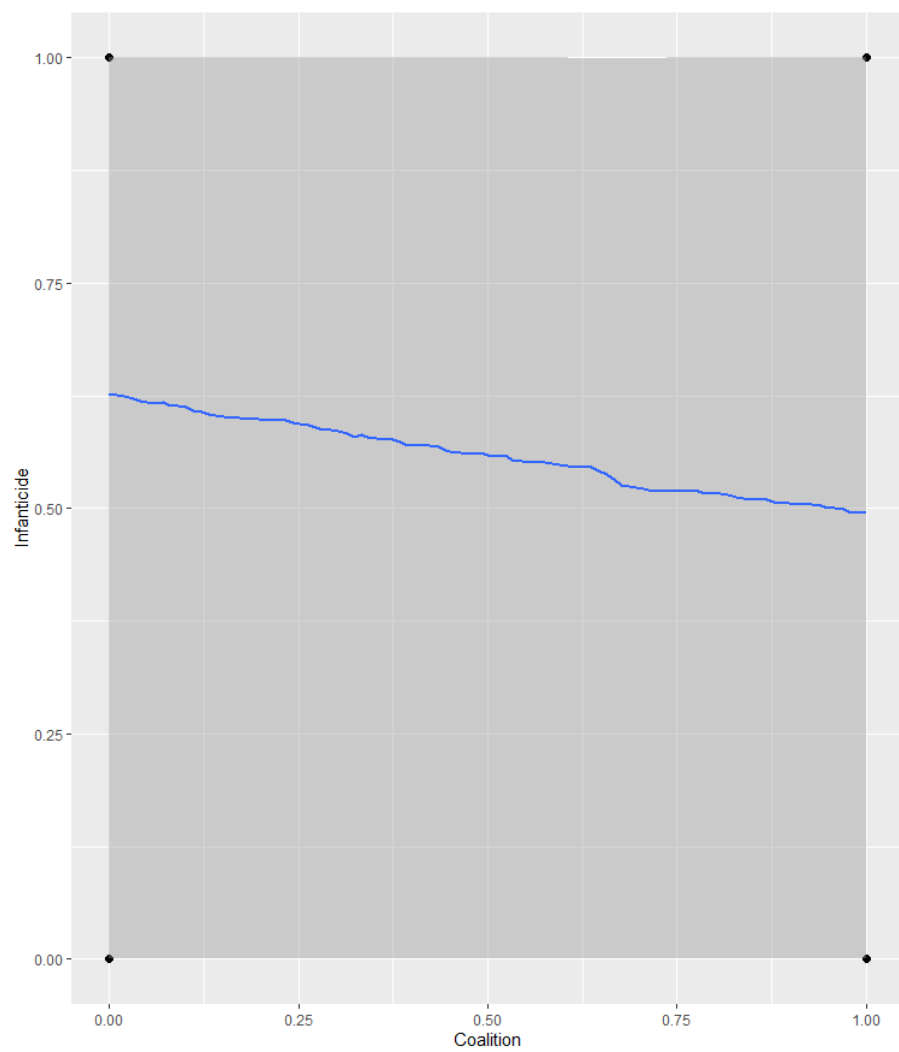
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	4.30	16.84	-19.18	49.76	1.00	1626	768
Food_Sharing_AandI	-11.53	26.36	-82.15	8.73	1.00	1519	791
Coalition	-1.64	23.03	-52.01	36.09	1.00	1800	947

Draws were sampled using `sampling(NUTS)`. For each parameter, `Bulk_ESS` and `Tail_ESS` are effective sample size measures, and `Rhat` is the potential scale reduction factor on split chains (at convergence, `Rhat = 1`).

	Estimate	Est.Error	Q2.5	Q97.5
R2	0.8063817	0.1937525	0.2489391	0.9998631

*Plot, Conditional effects, PP checks*





### 5E.5 Model B(v) Non-lethal aggression and grooming

```
> summary(Coalitionagg2G, waic= T); bayes_R2(Coalitionagg2G)
Family: MV(zero_one_inflated_beta, hurdle_gamma)
Links: mu = logit; phi = identity; zoi = identity; coi = identity
       mu = log; shape = identity; hu = identity
Formula: OG_Aggression ~ Grooming + Coalition + (1 | p | gr(SpeciesTree, cov = A))
         IG_Aggression ~ Grooming + Coalition + (1 | p | gr(SpeciesTree, cov = A))
Data: dataG (Number of observations: 68)
Draws: 4 chains, each with iter = 8000; warmup = 4000; thin = 1;
       total post-warmup draws = 16000
```

#### Group-Level Effects:

```
~SpeciesTree (Number of levels: 68)
```

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGAggression_Intercept)	0.08	0.08	0.00	0.31	1.00	2072	1362
sd(IGAggression_Intercept)	0.28	0.11	0.10	0.53	1.00	3133	5533
cor(OGAggression_Intercept,IGAggression_Intercept)	-0.01	0.54	-0.94	0.92	1.00	2157	4870

#### Population-Level Effects:

Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
----------	-----------	----------	----------	------	----------	----------

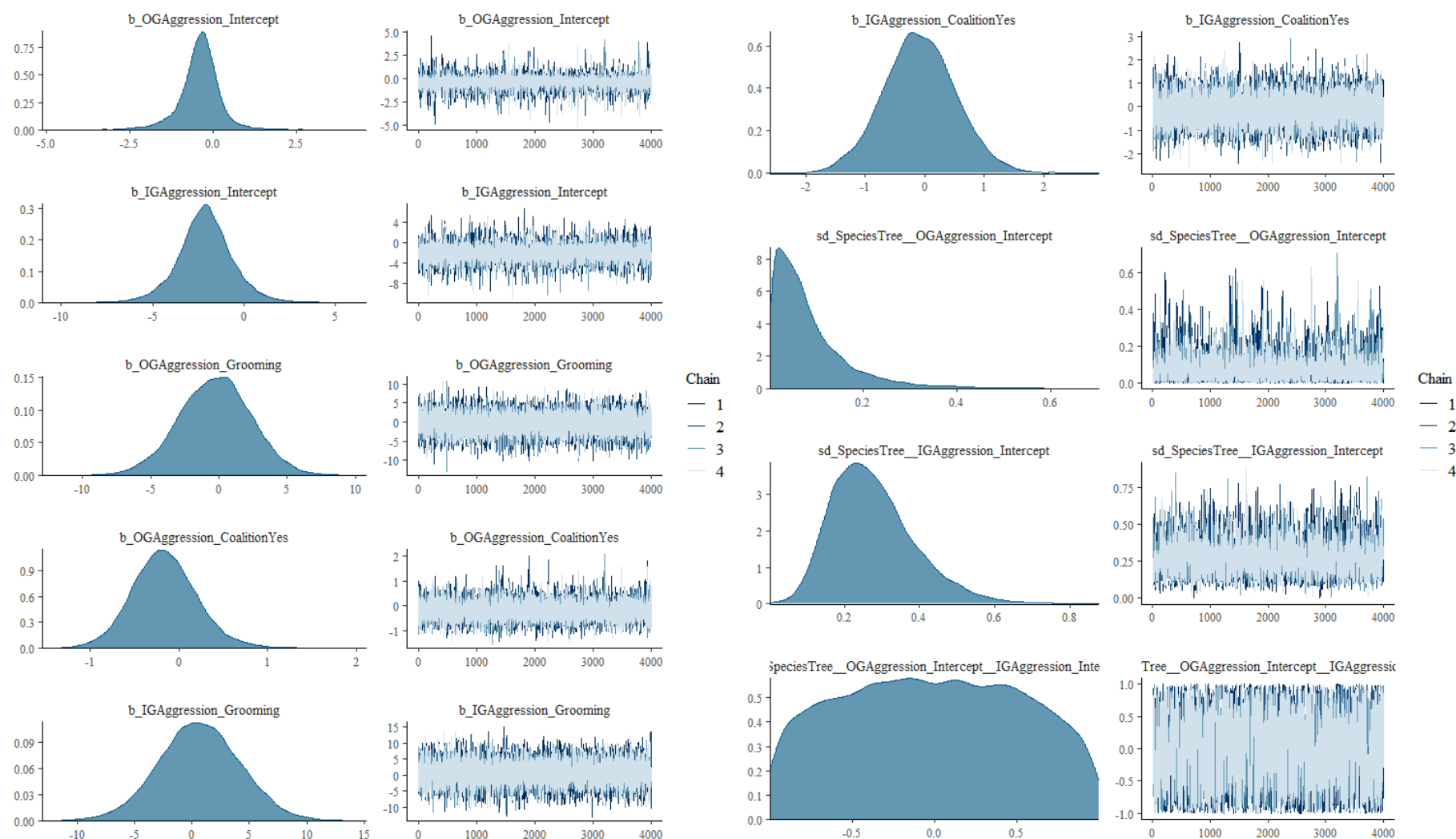
OGAggression_Intercept	-0.40	0.66	-1.85	0.88	1.00	6307	4270
IGAggression_Intercept	-2.12	1.55	-5.24	1.03	1.00	9953	9220
OGAggression_Grooming	-0.28	2.64	-5.56	4.86	1.00	14754	12058
OGAggression_CoalitionYes	-0.16	0.37	-0.86	0.62	1.00	8890	5745
IGAggression_Grooming	0.65	3.53	-6.28	7.60	1.00	17215	10886
IGAggression_CoalitionYes	-0.09	0.61	-1.29	1.14	1.00	15584	11074

## Family Specific Parameters:

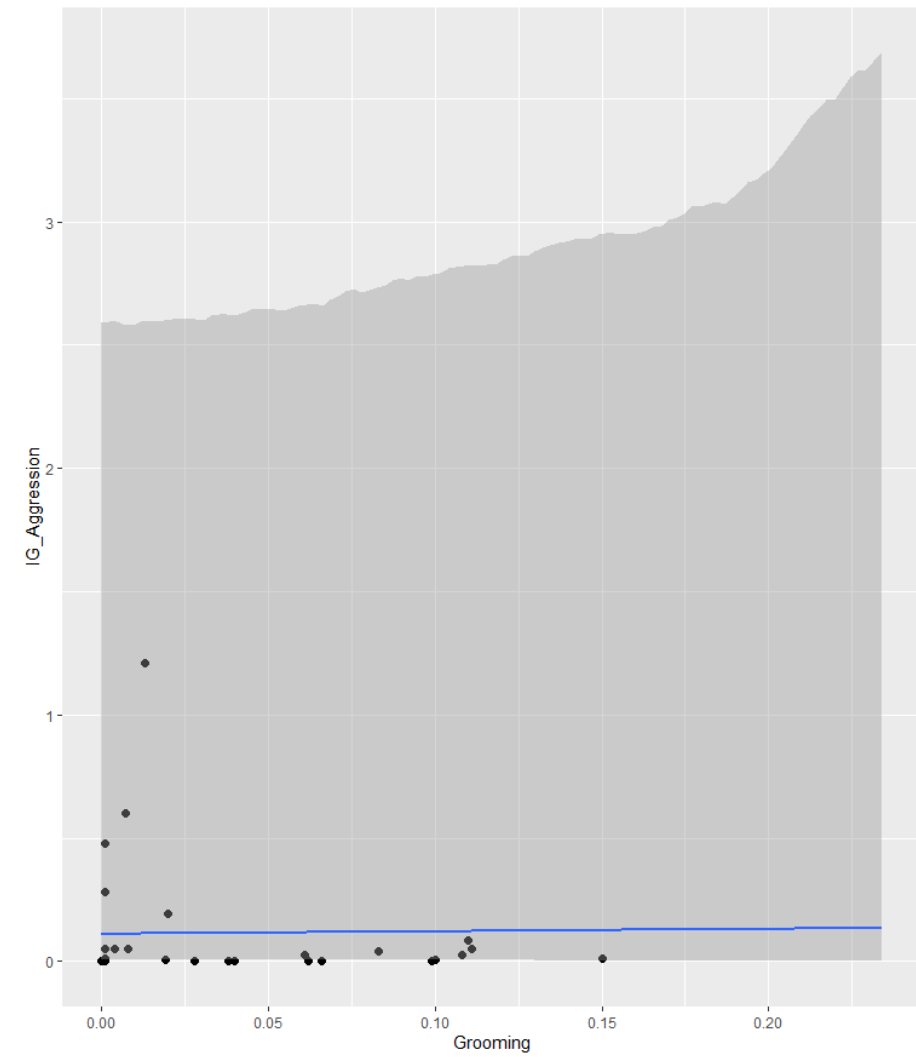
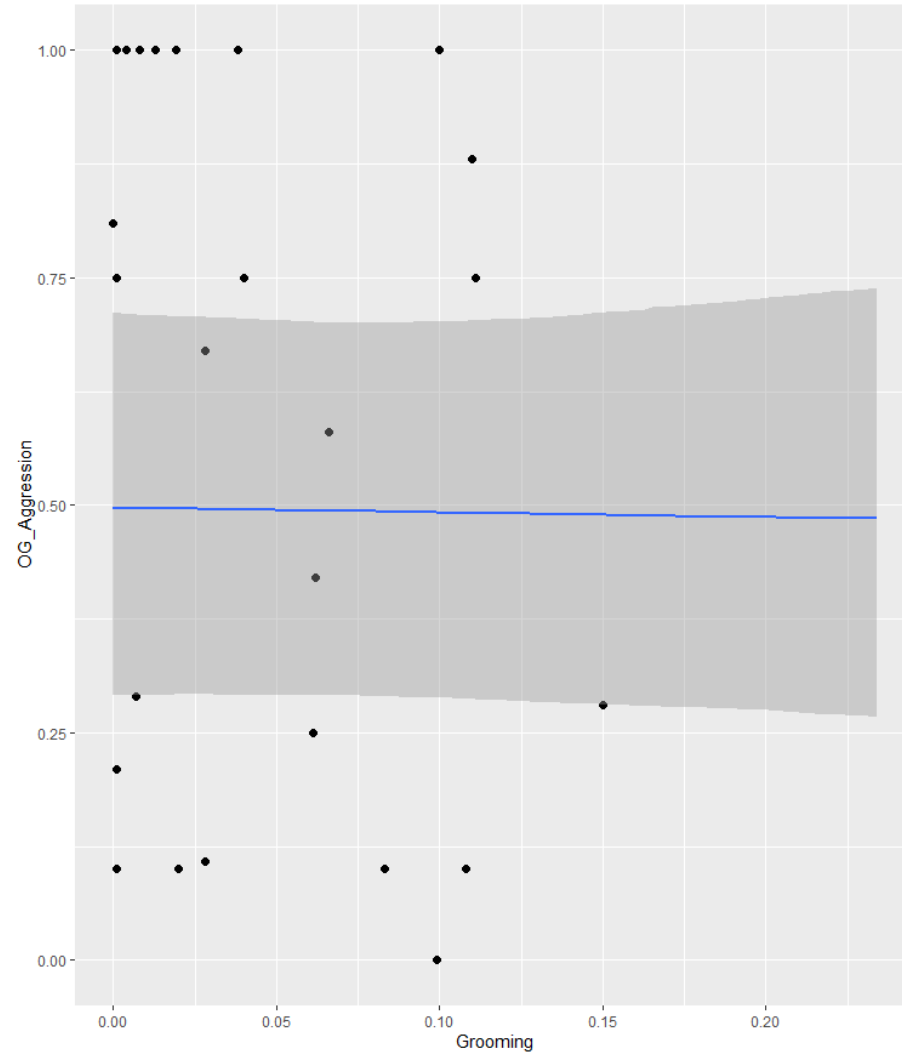
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
phi_OGAggression	3.04	1.48	1.86	5.84	1.00	2981	1530
zoi_OGAggression	0.29	0.05	0.19	0.40	1.00	31180	10982
coi_OGAggression	0.71	0.10	0.51	0.88	1.00	31662	10791
shape_IGAggression	0.48	0.10	0.32	0.70	1.00	5390	7782
hu_IGAggression	0.07	0.03	0.02	0.14	1.00	28072	10614

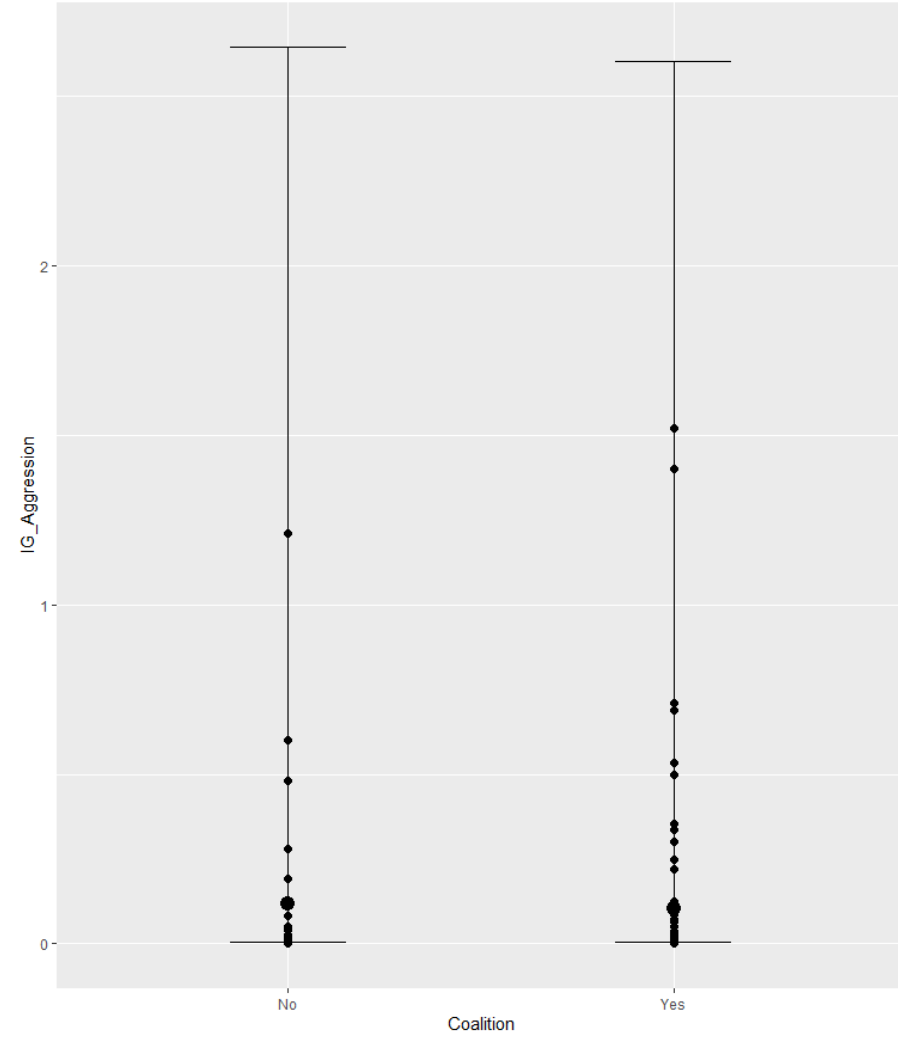
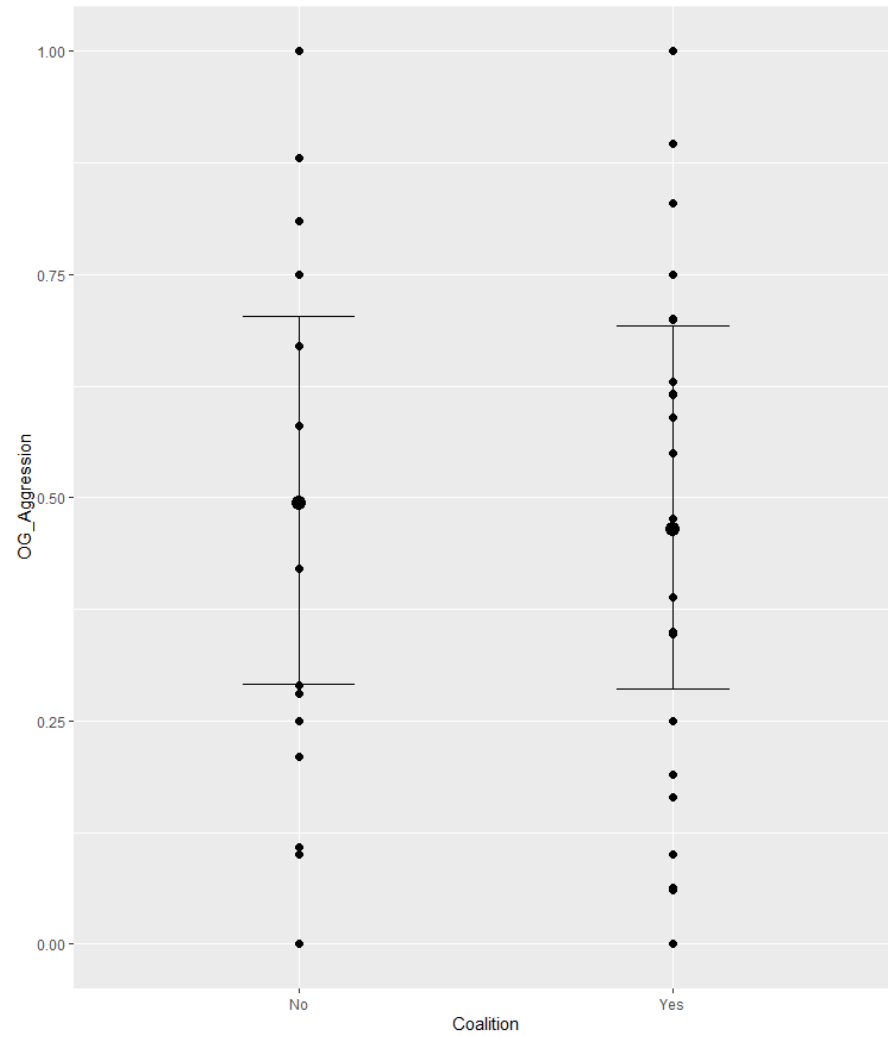
Draws were sampled using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
R2OGAggression	0.04048204	0.0445867	0.002042723	0.1700917
R2IGAggression	0.35956388	0.1517305	0.080342542	0.6313227

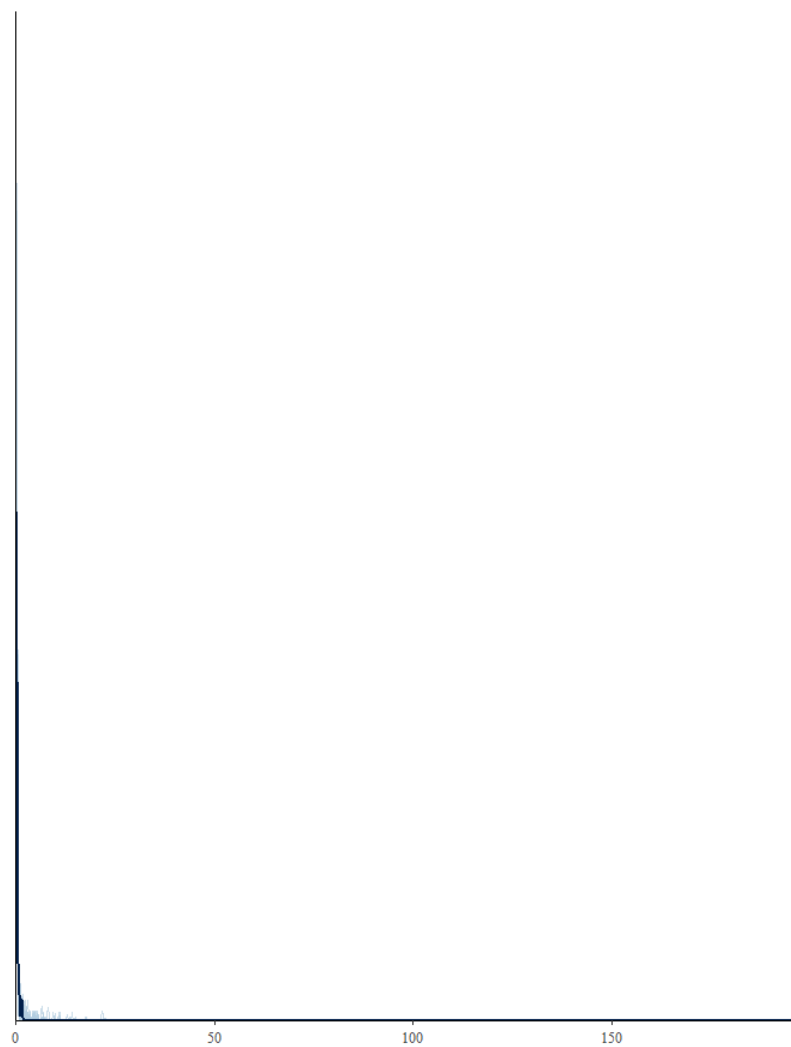
*Plot, Conditional effects, PP checks*



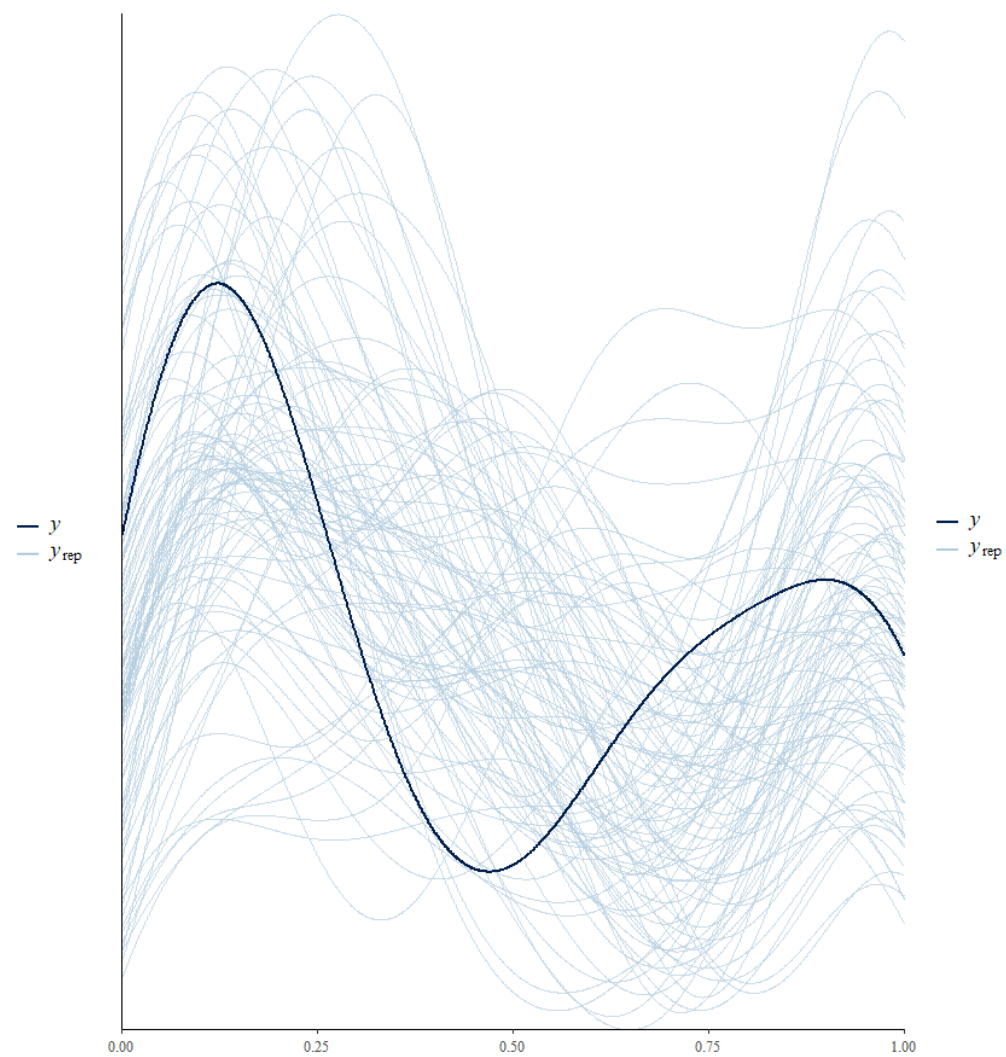




IG Aggression



OG Aggression



*5E.6 Model B(vi) Non-lethal aggression and food-sharing*

```

> summary(Coalitionagg2F, waic= T); bayes_R2(Coalitionagg2F)
Family: MV(zero_one_inflated_beta, hurdle_gamma)
Links: mu = logit; phi = identity; zoi = identity; coi = identity
       mu = log; shape = identity; hu = identity
Formula: OG_Aggression ~ Food_Sharing_AandI + Coalition + (1 | p | gr(SpeciesTree, cov = A))
         IG_Aggression ~ Food_Sharing_AandI + Coalition + (1 | p | gr(SpeciesTree, cov = A))
Data: data1 (Number of observations: 61)
Draws: 4 chains, each with iter = 9000; warmup = 4500; thin = 1;
       total post-warmup draws = 18000

Group-Level Effects:
~SpeciesTree (Number of levels: 61)


```

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS
Tail_ESS						
sd(OGAggression_Intercept)	0.08	0.06	0.00	0.23	1.00	2999
3375						
sd(IGAggression_Intercept)	0.27	0.08	0.14	0.46	1.00	5812
9662						
cor(OGAggression_Intercept, IGAggression_Intercept)	-0.13	0.50	-0.94	0.85	1.00	2085
3327						

## Population-Level Effects:

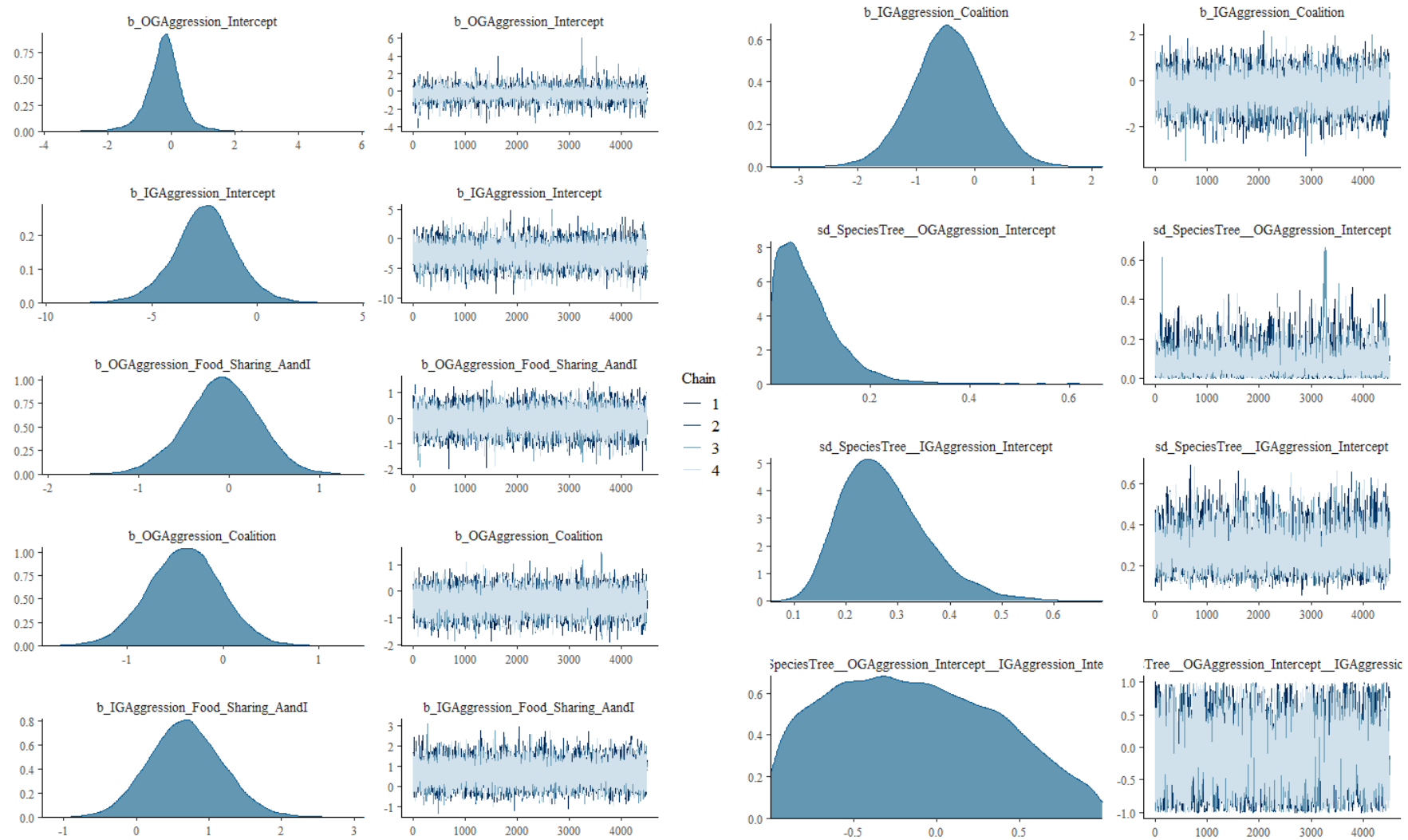
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGAggression_Intercept	-0.22	0.57	-1.43	0.90	1.00	9668	7963
IGAggression_Intercept	-2.49	1.49	-5.50	0.47	1.00	10976	10893
OGAggression_Food_Sharing_AandI	-0.08	0.40	-0.89	0.68	1.00	15386	8799
OGAggression_Coalition	-0.40	0.38	-1.14	0.34	1.00	18915	13255
IGAggression_Food_Sharing_AandI	0.68	0.50	-0.26	1.70	1.00	17645	14110
IGAggression_Coalition	-0.44	0.62	-1.66	0.76	1.00	16711	14429

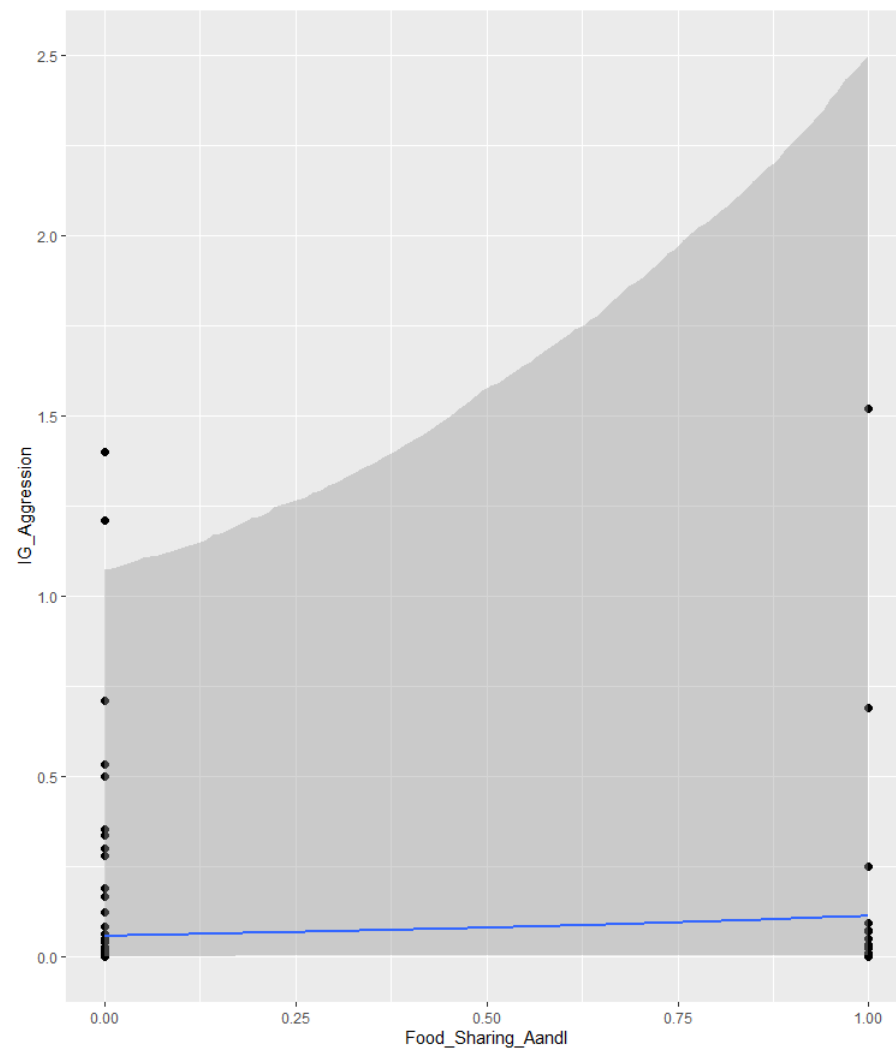
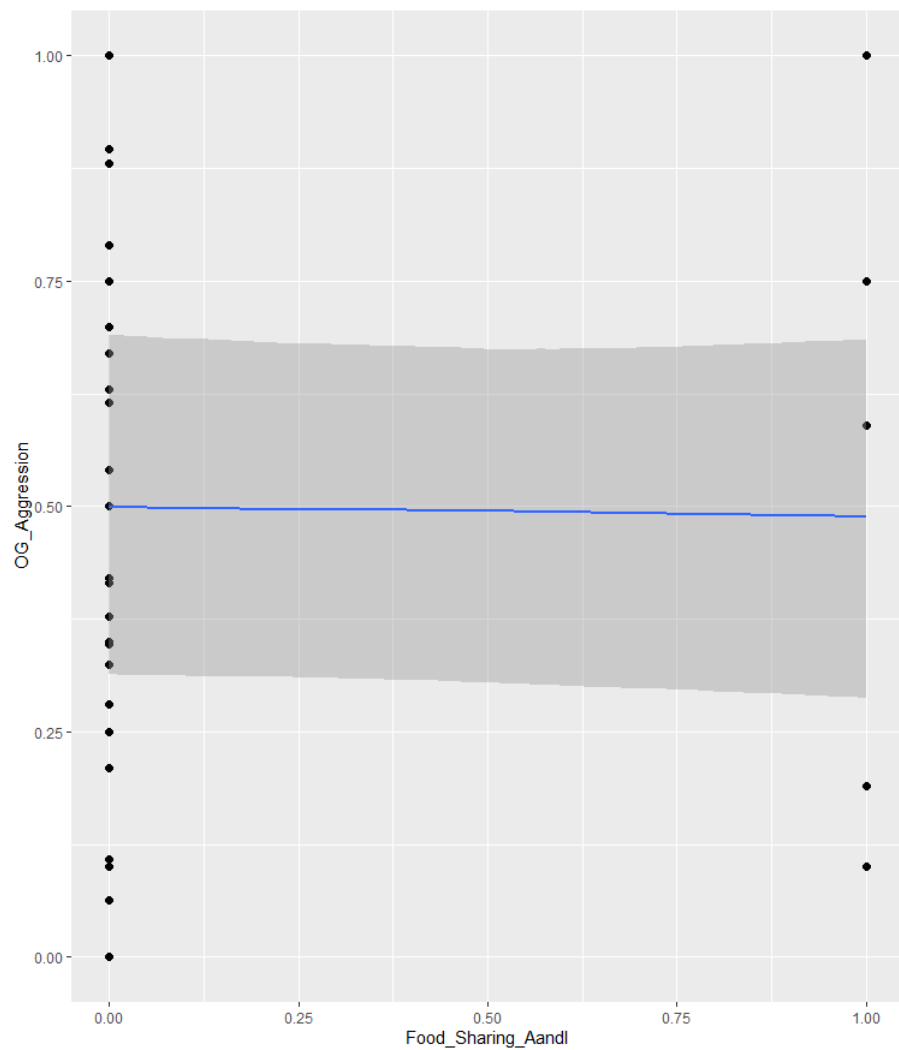
## Family Specific Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
phi_OGAggression	2.97	1.26	1.88	4.64	1.00	5944	4148
zoi_OGAggression	0.25	0.05	0.16	0.37	1.00	33184	12466
coi_OGAggression	0.82	0.09	0.62	0.96	1.00	30124	10719
shape_IGAggression	0.64	0.13	0.43	0.95	1.00	9836	11943
hu_IGAggression	0.08	0.03	0.03	0.16	1.00	30886	11933

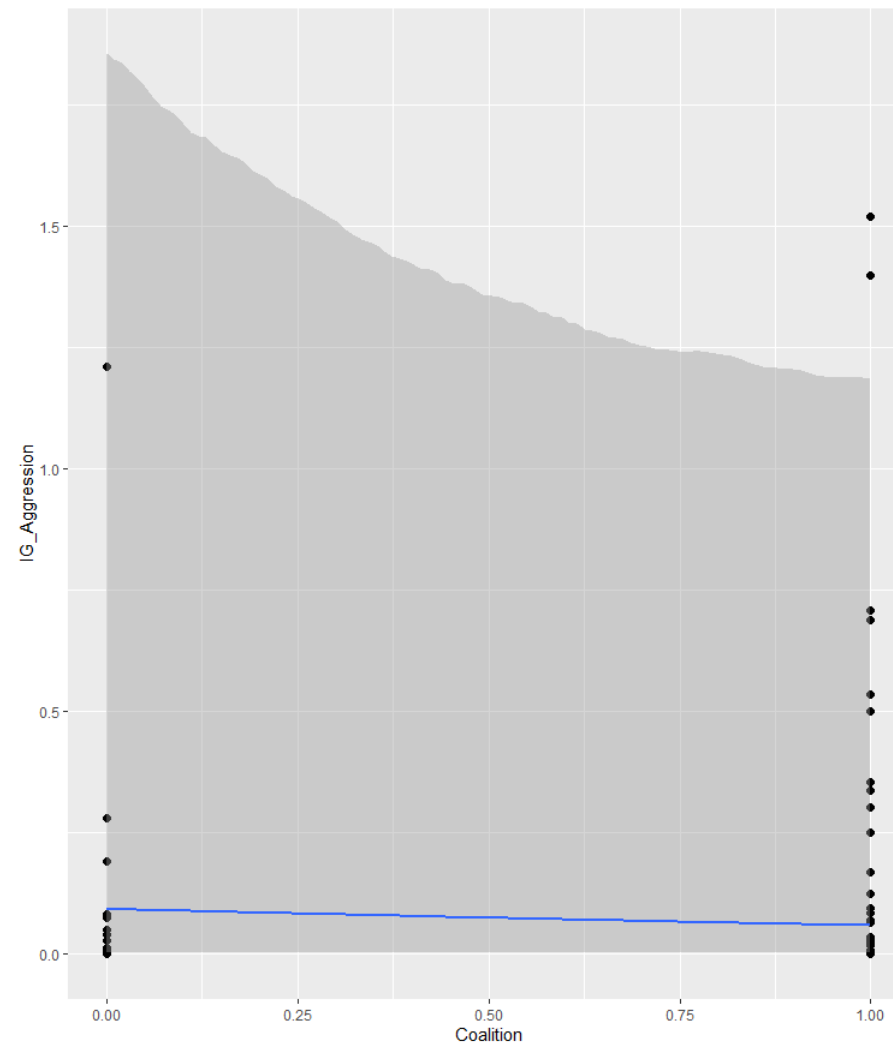
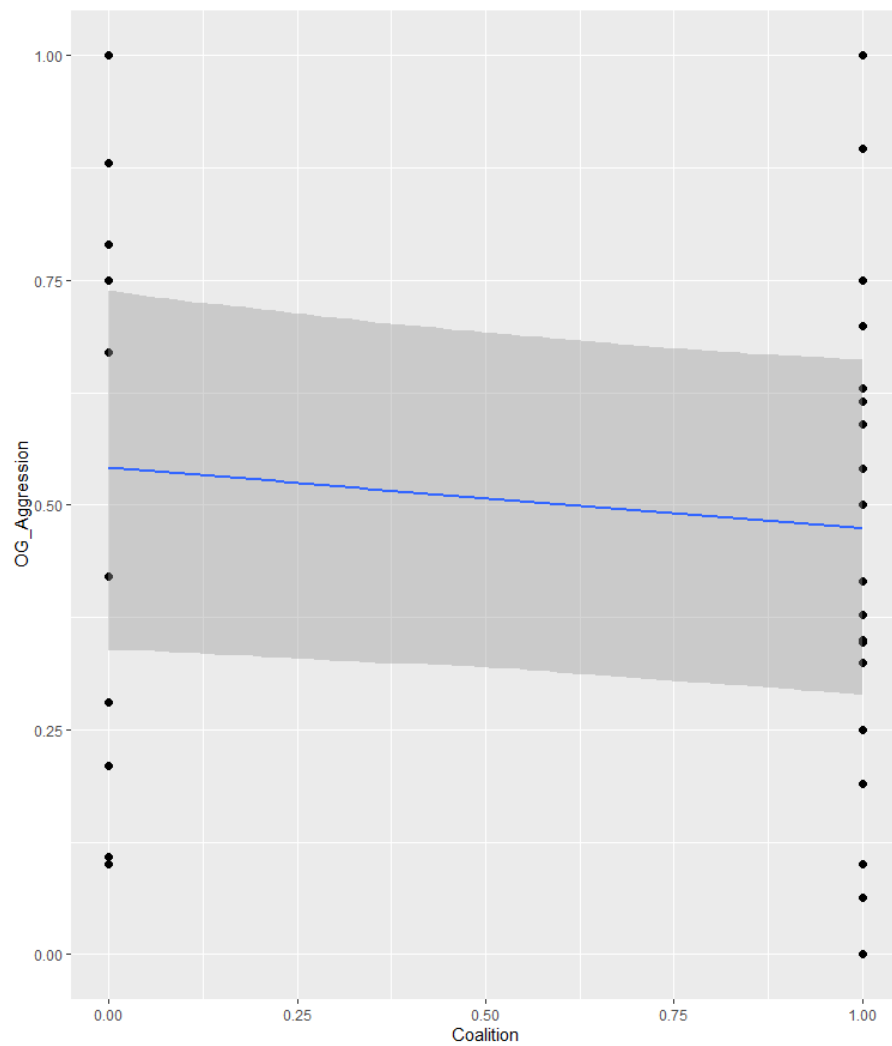
Draws were sampled using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
R2OGAggression	0.05618272	0.04633189	0.00399199	0.1711498
R2IGAggression	0.38468934	0.15718292	0.11246267	0.6755929

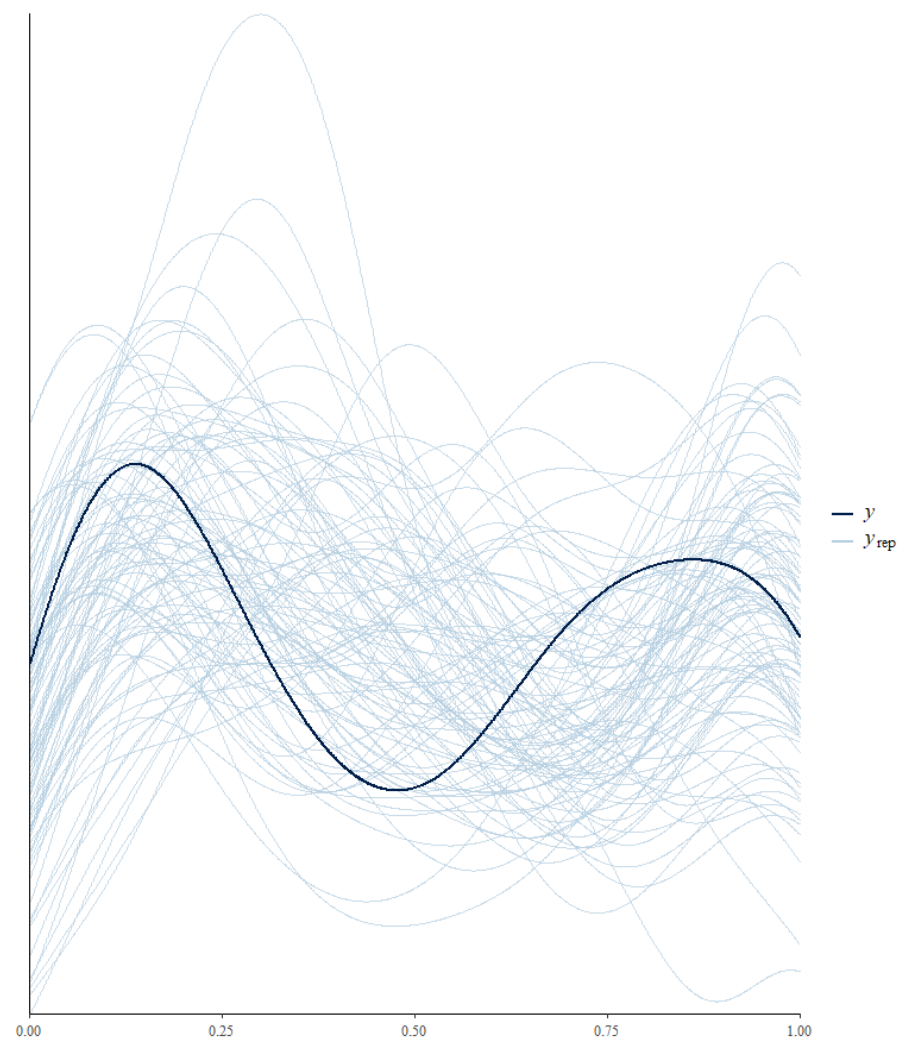
*Plot, Conditional effects, PP checks*



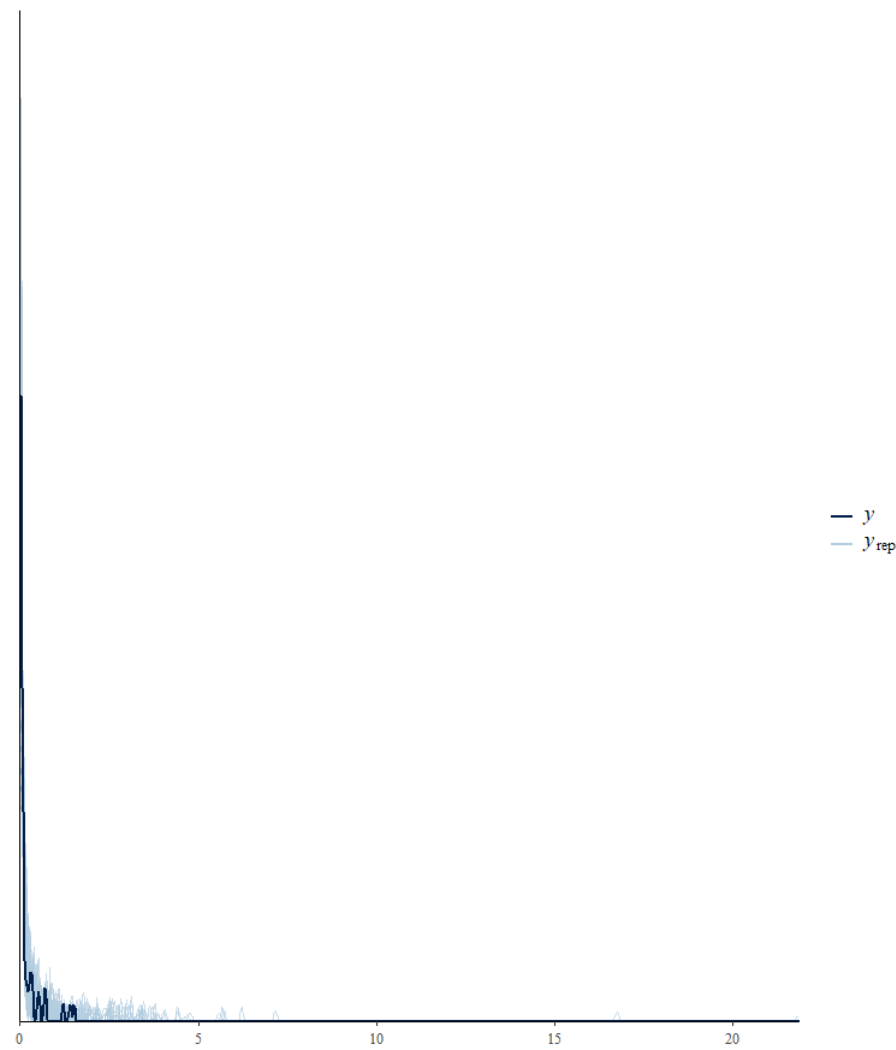




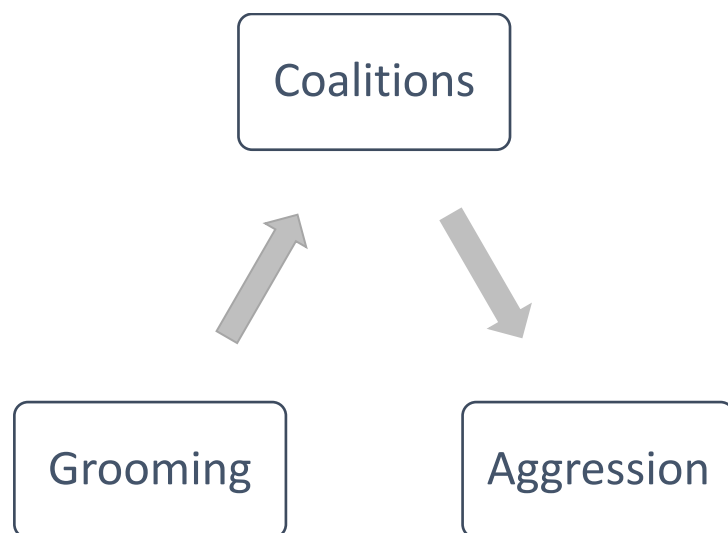
OG Aggression



IG Aggression



## Appendix 5F – Model C - Only an indirect effect of grooming through coalitions

*5F.1 Model C(i) Adulticide and grooming*

```

> summary(Coalitionkill13G, waic= T); bayes_R2(Coalitionkill13G)
Family: MV(bernoulli, bernoulli, bernoulli)
Links: mu = logit
       mu = logit
       mu = logit
Formula: OG_Killing ~ Coalition + (1 | gr(SpeciesTree, cov = A))
  
```

```
IG_Killing ~ Coalition + (1 | gr(SpeciesTree, cov = A))
```

```
Coalition ~ Grooming + (1 | gr(SpeciesTree, cov = A))
```

```
Data: dataG (Number of observations: 68)
```

```
Draws: 4 chains, each with iter = 9000; warmup = 4500; thin = 1;
```

```
total post-warmup draws = 18000
```

#### Group-Level Effects:

```
~SpeciesTree (Number of levels: 68)
```

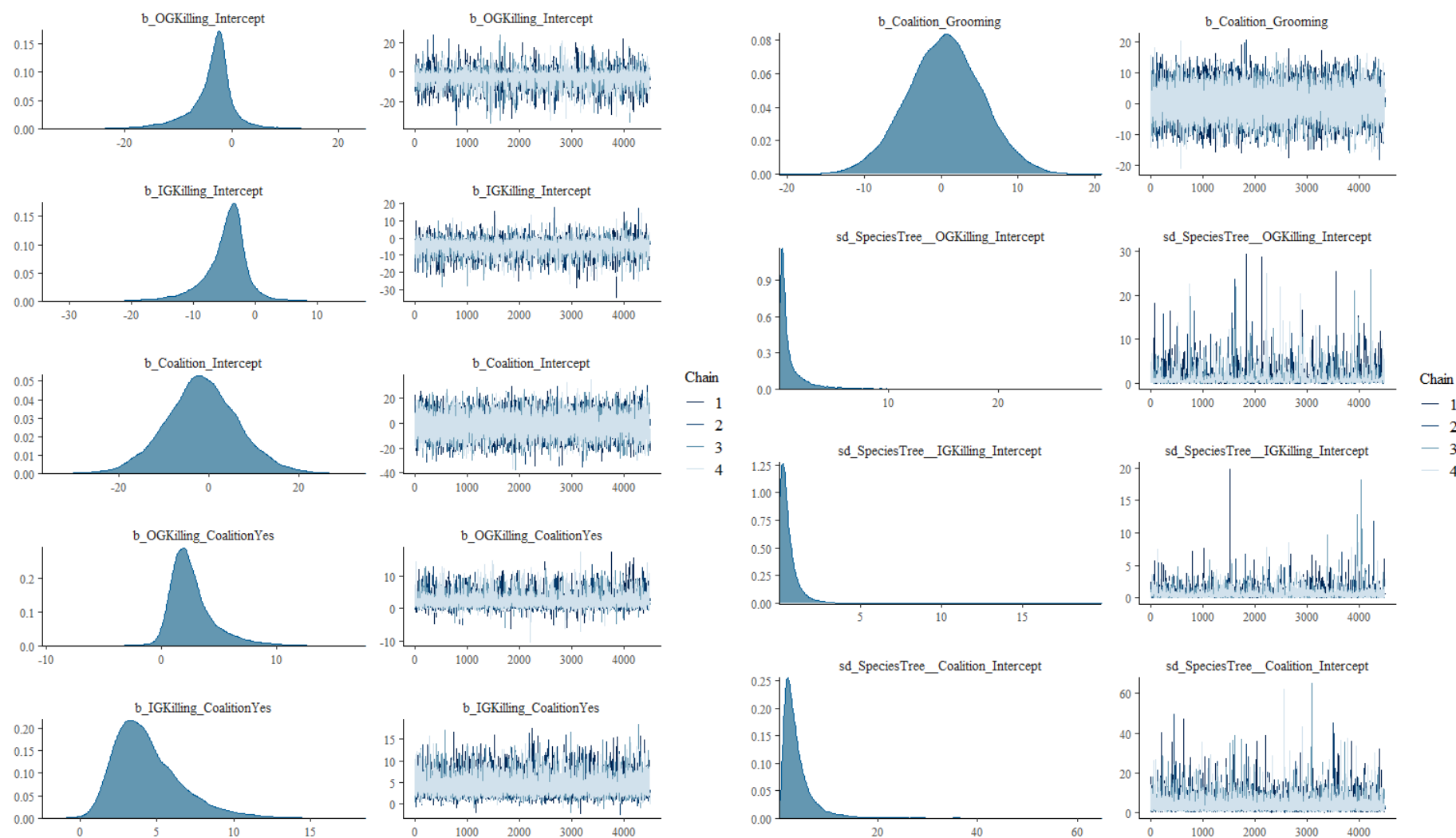
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGKilling_Intercept)	1.02	1.52	0.06	4.91	1.00	1385	4226
sd(IGKilling_Intercept)	0.60	0.70	0.02	2.35	1.00	2048	4888
sd(Coalition_Intercept)	3.82	3.36	0.80	12.39	1.00	6555	7359

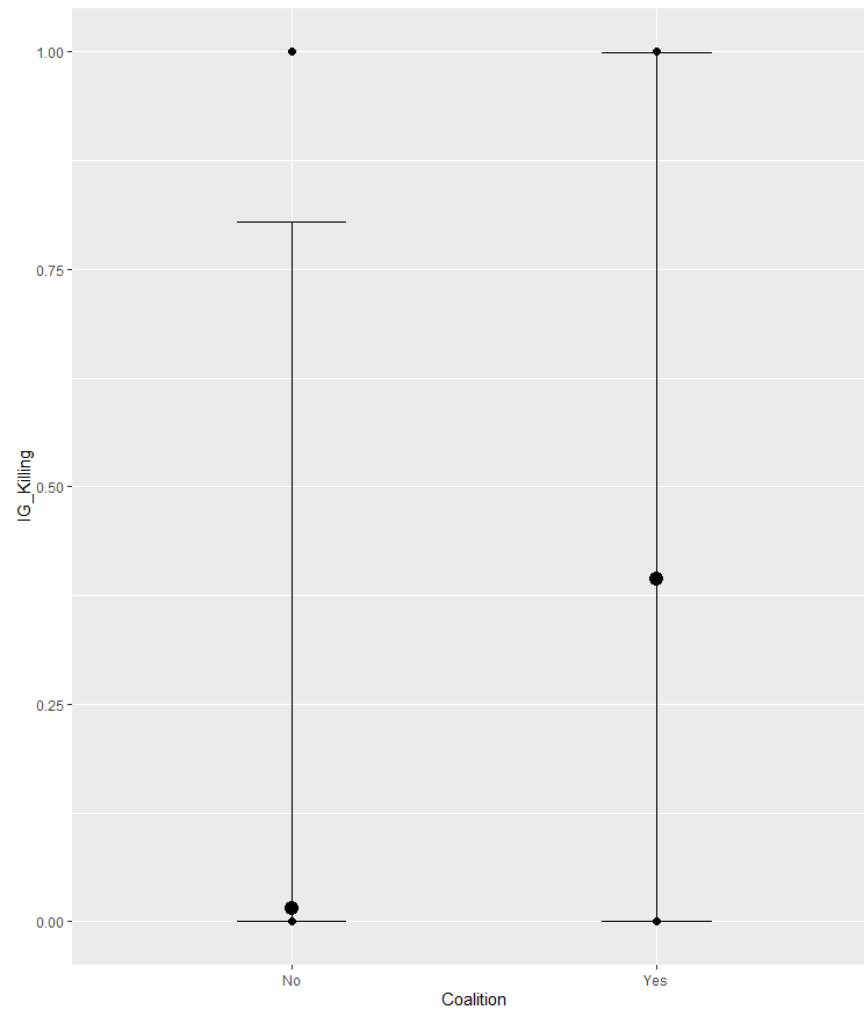
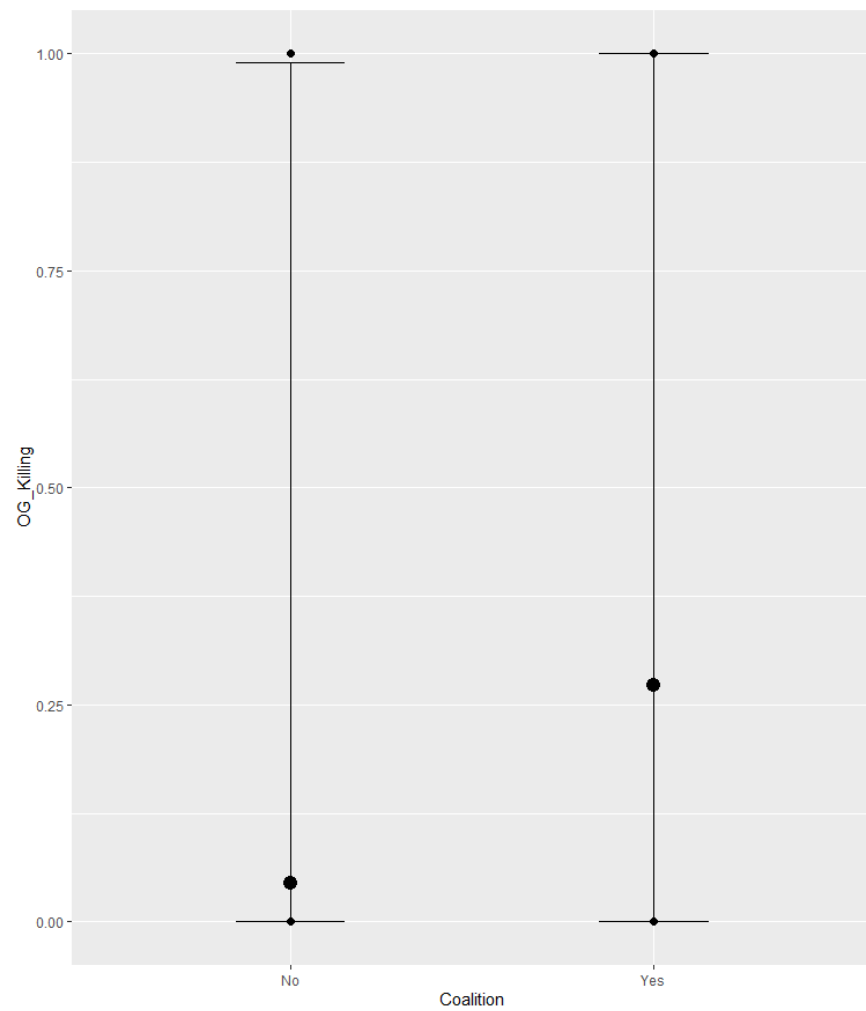
#### Population-Level Effects:

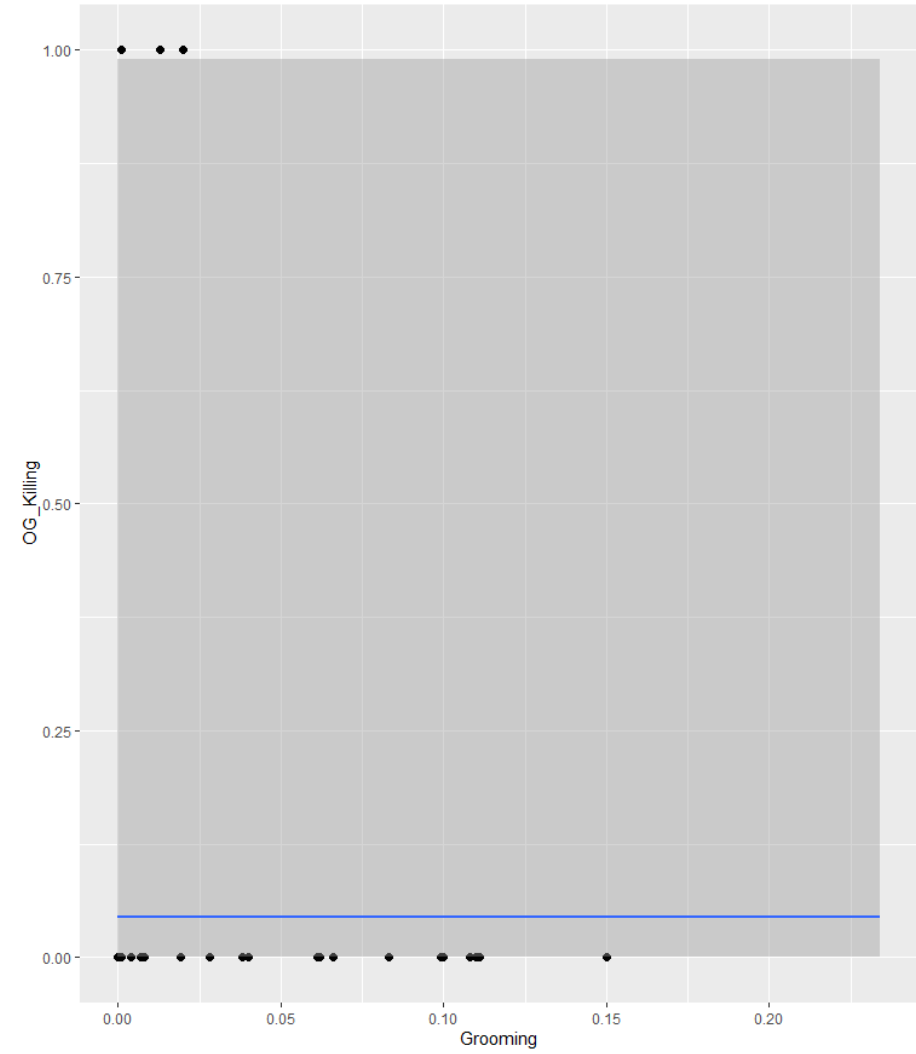
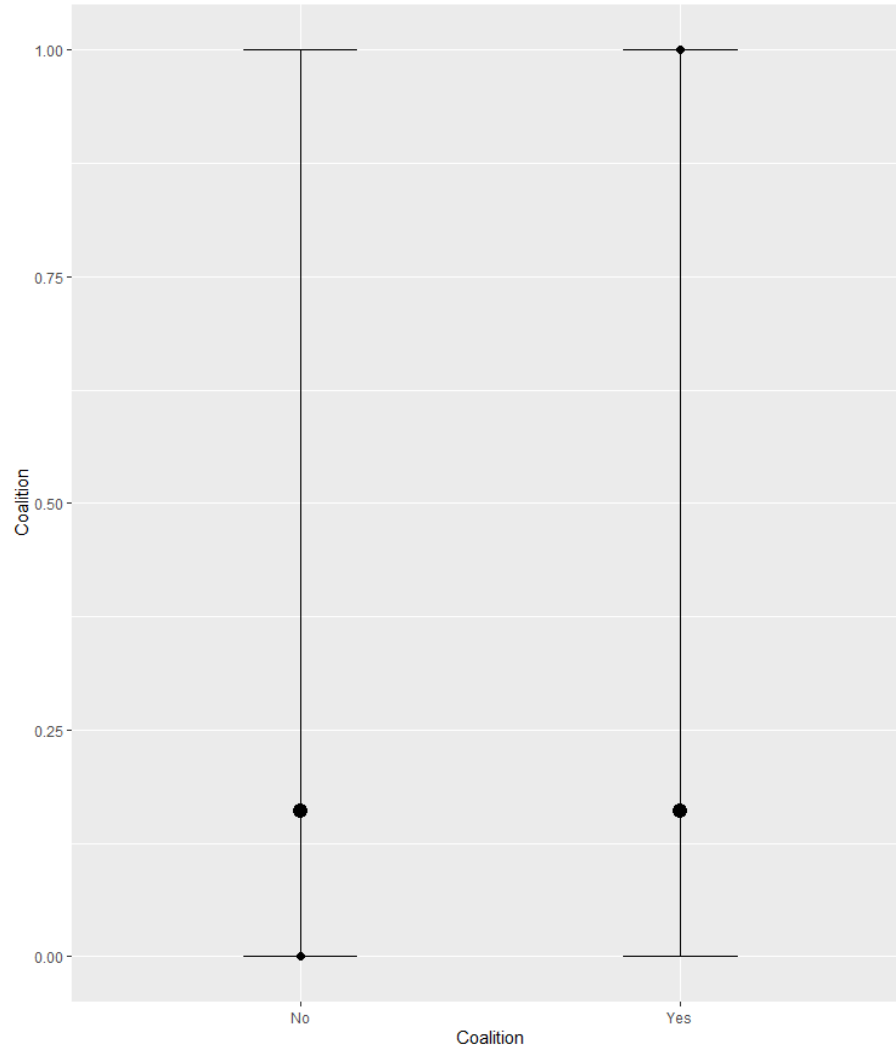
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGKilling_Intercept	-3.80	4.67	-15.49	4.57	1.00	7668	5709
IGKilling_Intercept	-4.77	3.69	-14.00	1.42	1.00	8797	6943
Coalition_Intercept	-1.59	8.12	-17.59	14.71	1.00	14891	14050
OGKilling_CoalitionYes	2.65	2.04	-0.07	8.03	1.00	4335	4800
IGKilling_CoalitionYes	4.40	2.24	1.21	9.92	1.00	6699	7438
Coalition_Grooming	0.44	4.92	-9.32	10.17	1.00	30565	13077

Draws were sampled using `sampling(NUTS)`. For each parameter, `Bulk_ESS` and `Tail_ESS` are effective sample size measures, and `Rhat` is the potential scale reduction factor on split chains (at convergence, `Rhat = 1`).

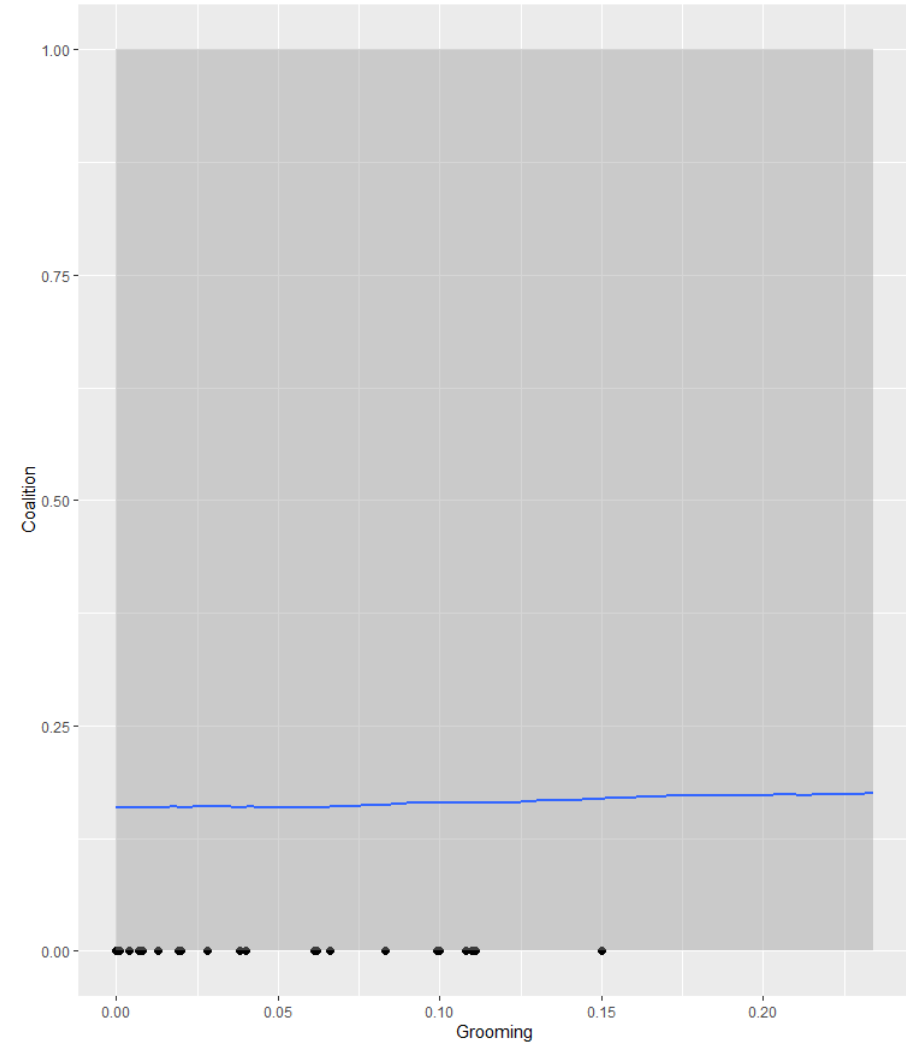
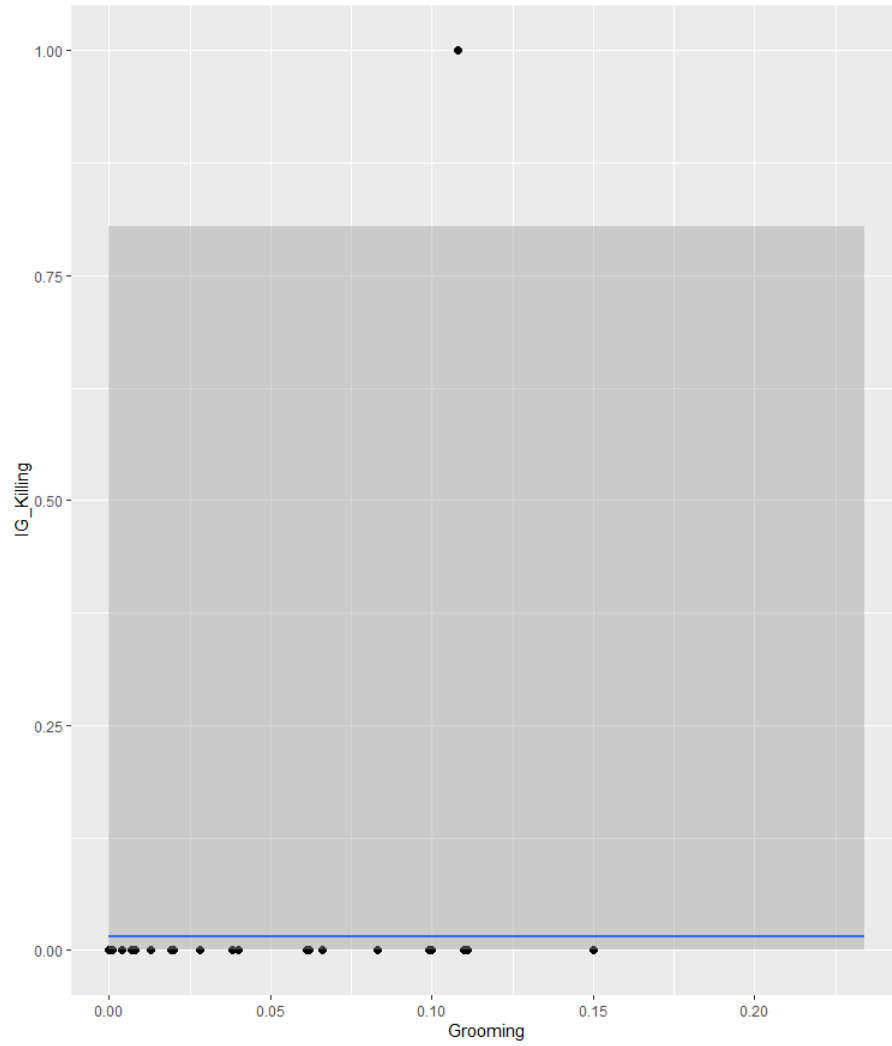
	Estimate	Est.Error	Q2.5	Q97.5
R2OGKilling	0.4091077	0.2264633	0.06365575	0.8866954
R2IGKilling	0.3711629	0.1783577	0.08827413	0.7596403
R2Coalition	0.8465649	0.1044146	0.59887014	0.9928936

*Plot, Conditional effects, PP checks*

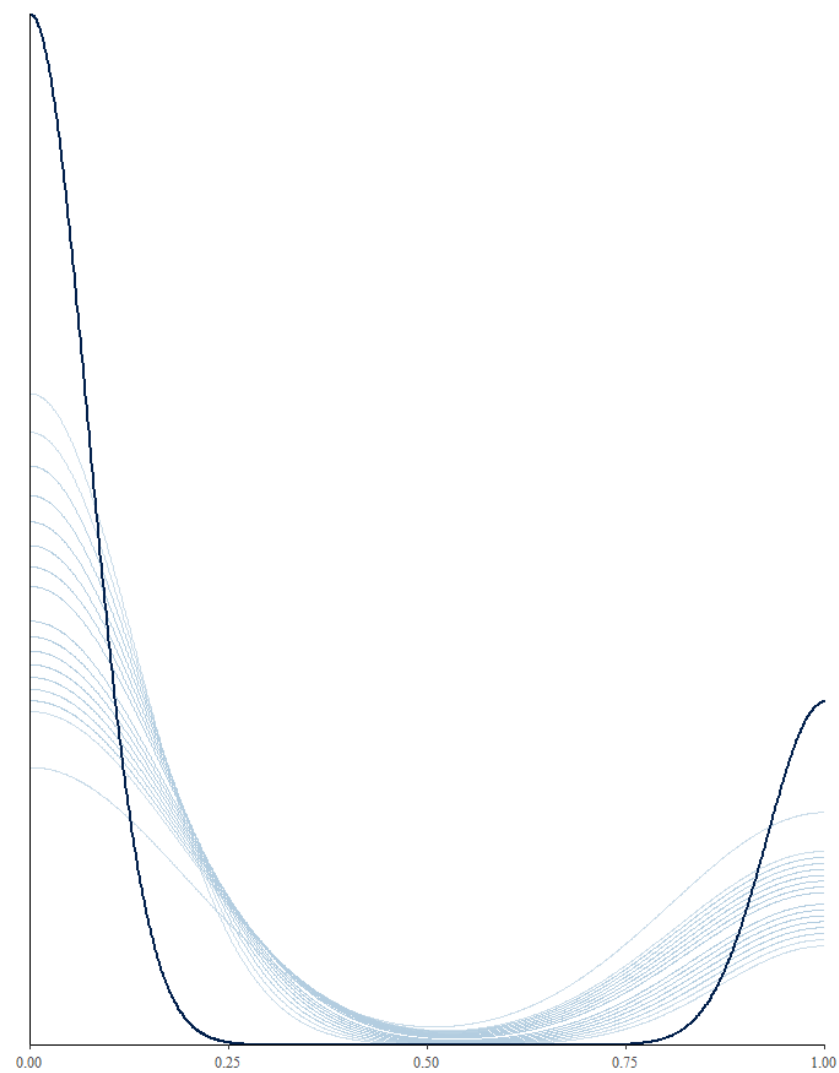




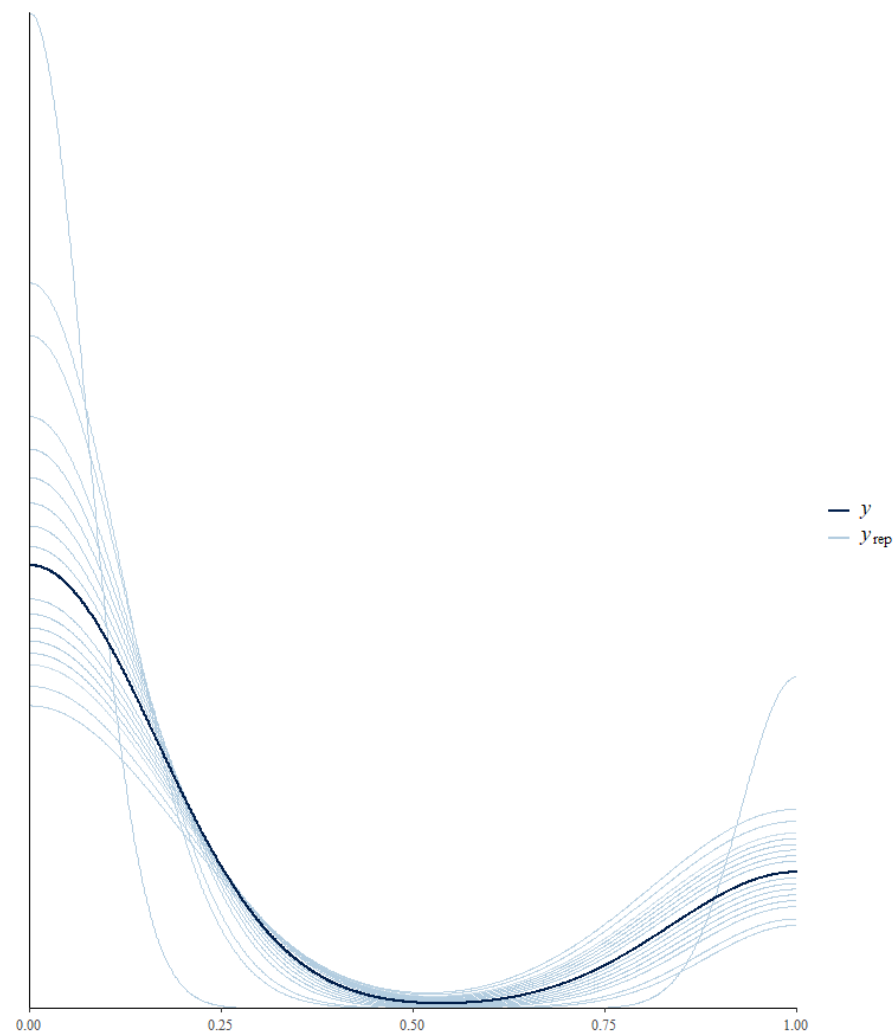




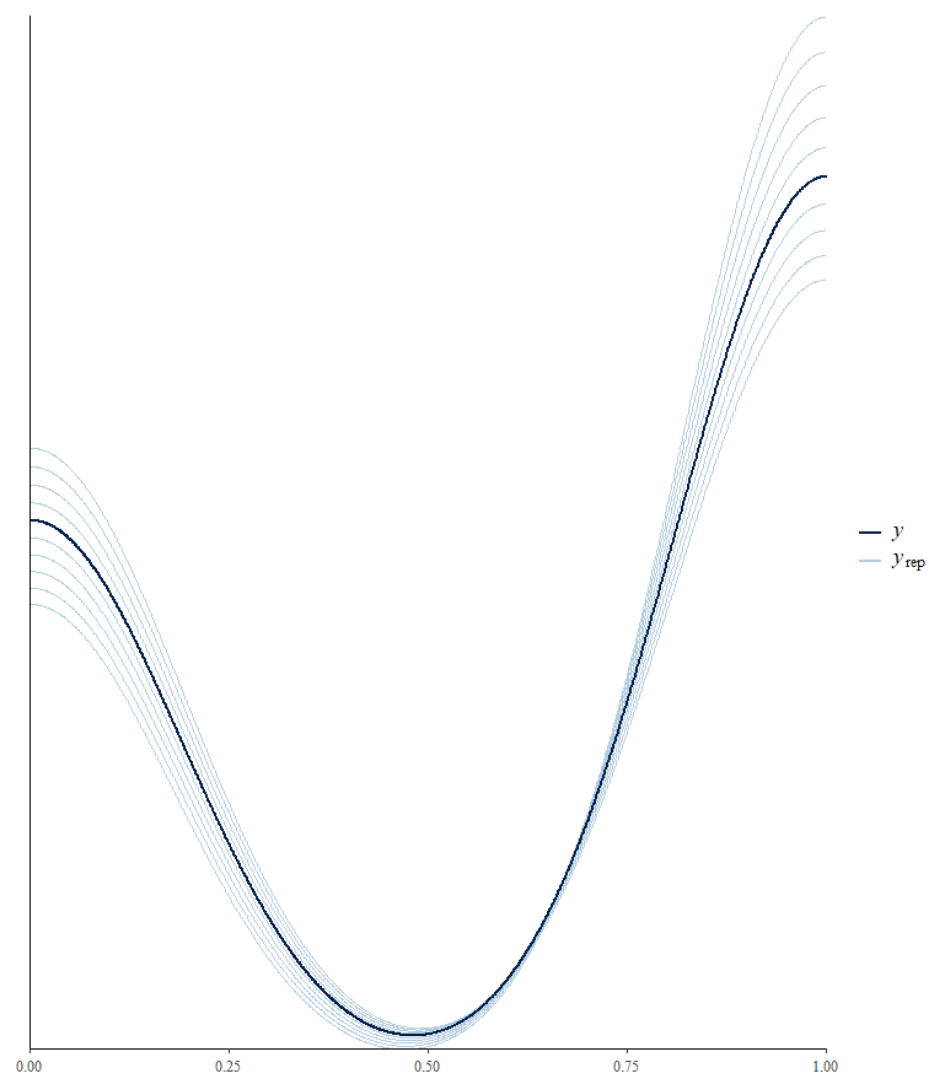
OG Killing



IG Killing



Coalition



*5F.2 Model C(ii) Adulticide and food-sharing*

```

> summary(Coalitionkill13F, waic= T); bayes_R2(Coalitionkill13F)
Family: MV(bernoulli, bernoulli, bernoulli)
Links: mu = logit
      mu = logit
      mu = logit
Formula: OG_Killing ~ Coalition + (1 | gr(SpeciesTree, cov = A))
        IG_Killing ~ Coalition + (1 | gr(SpeciesTree, cov = A))
        Coalition ~ Food_Sharing_AandI + (1 | gr(SpeciesTree, cov = A))
Data: data1 (Number of observations: 61)
Draws: 4 chains, each with iter = 9000; warmup = 4500; thin = 1;
      total post-warmup draws = 18000

Group-Level Effects:
~SpeciesTree (Number of levels: 61)

```

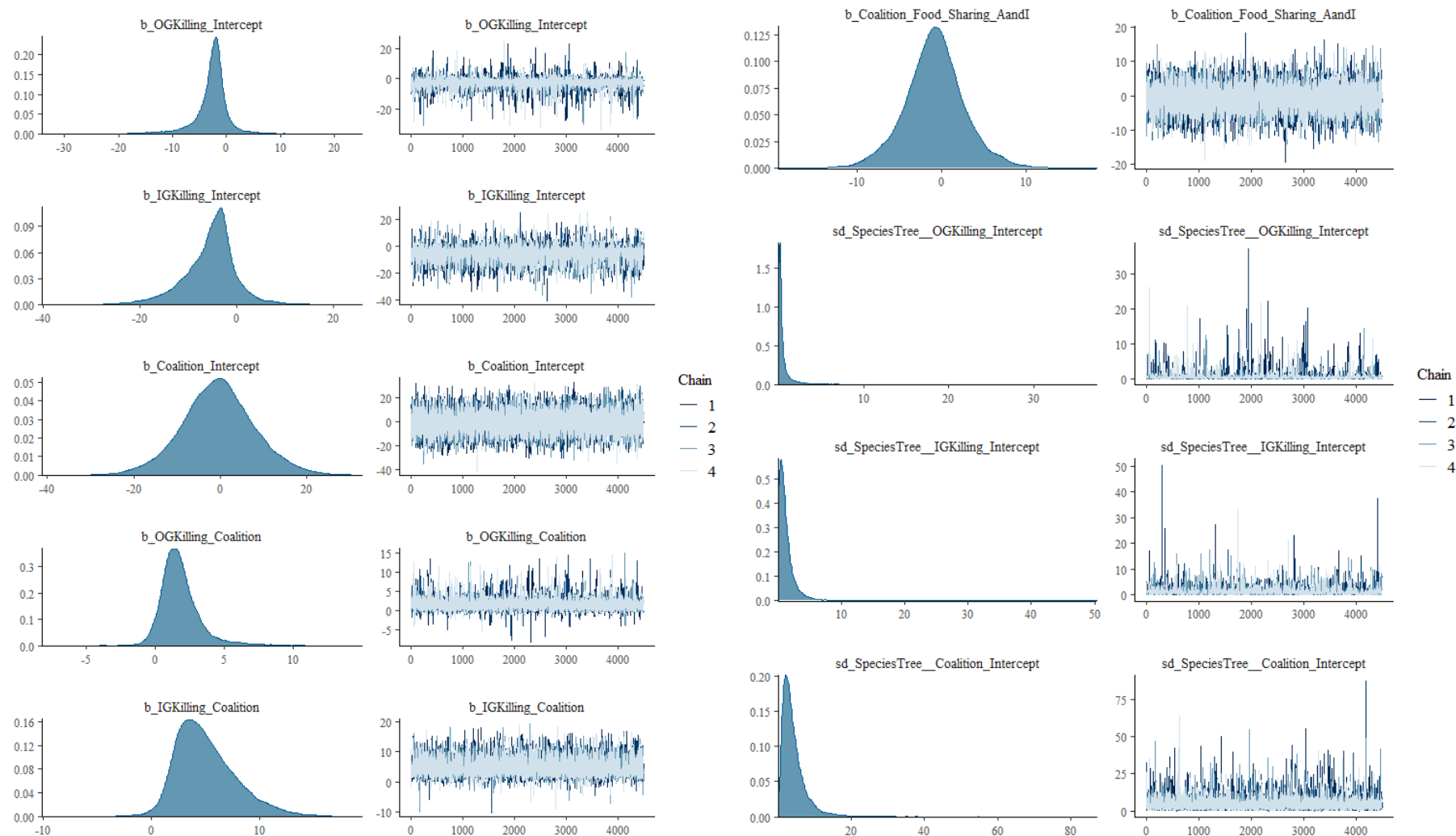
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGKilling_Intercept)	0.64	1.20	0.02	3.53	1.00	1046	1356
sd(IGKilling_Intercept)	1.28	1.48	0.04	4.77	1.00	1654	2769
sd(Coalition_Intercept)	4.44	3.90	0.77	14.19	1.00	5584	5840

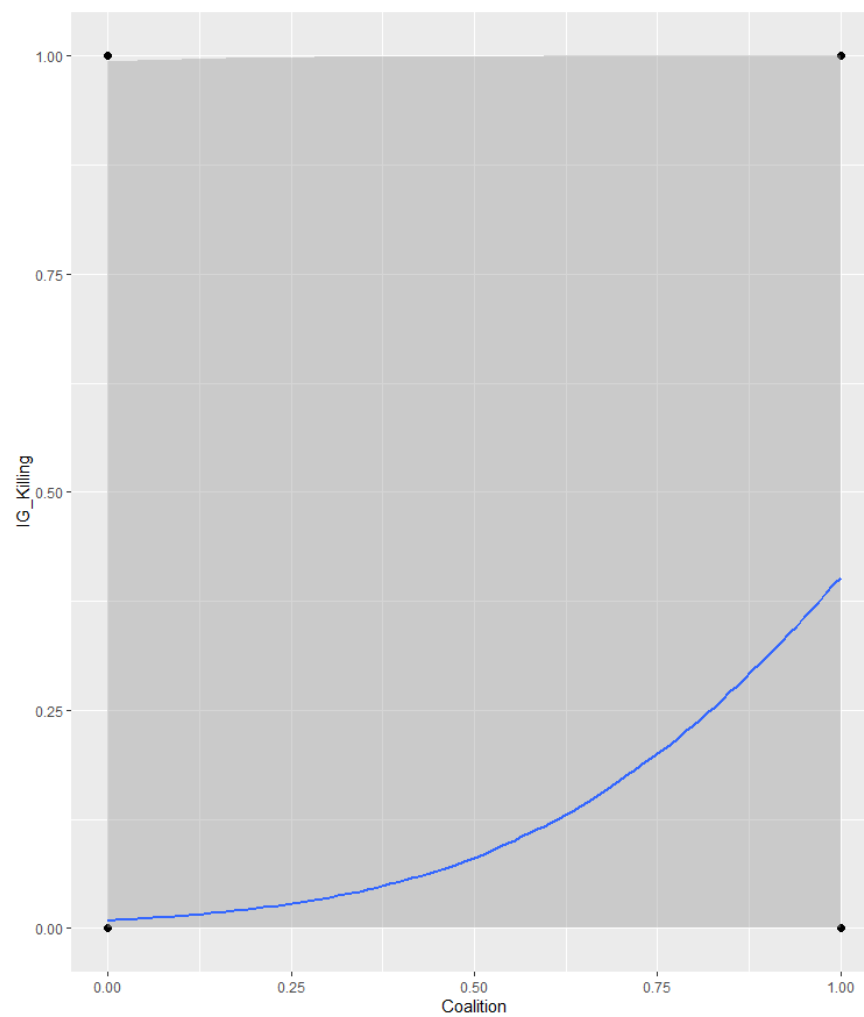
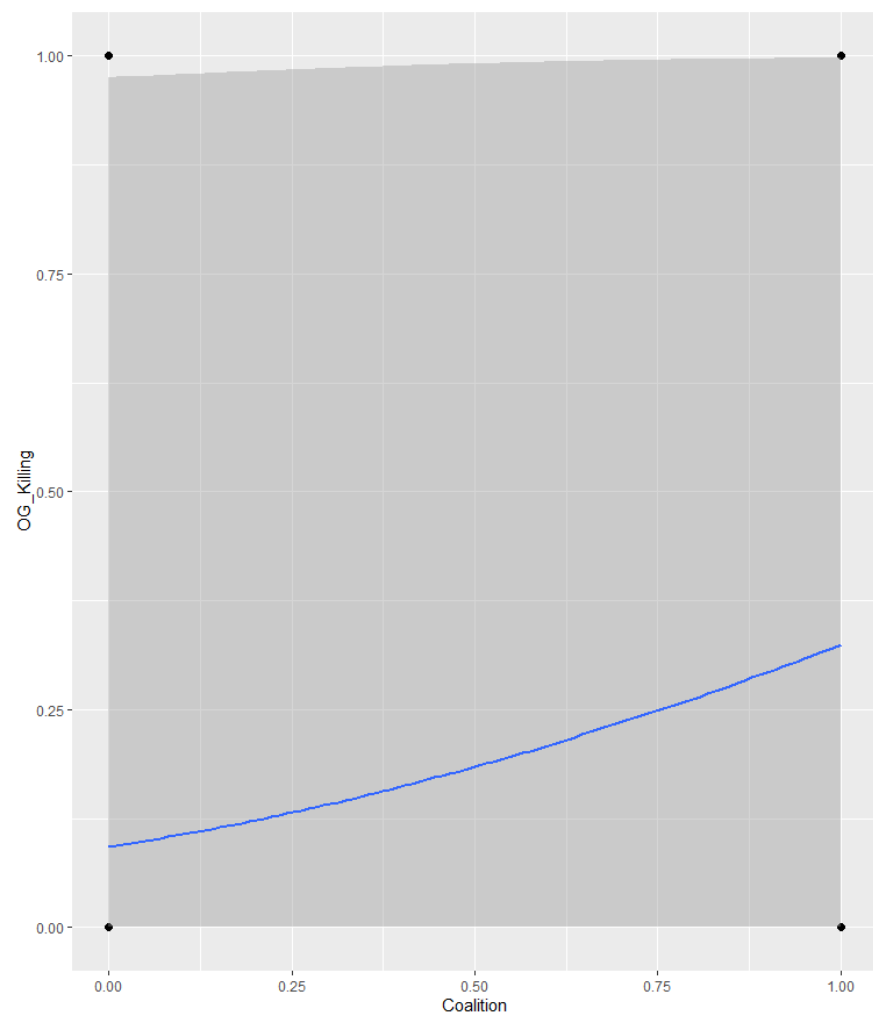
## Population-Level Effects:

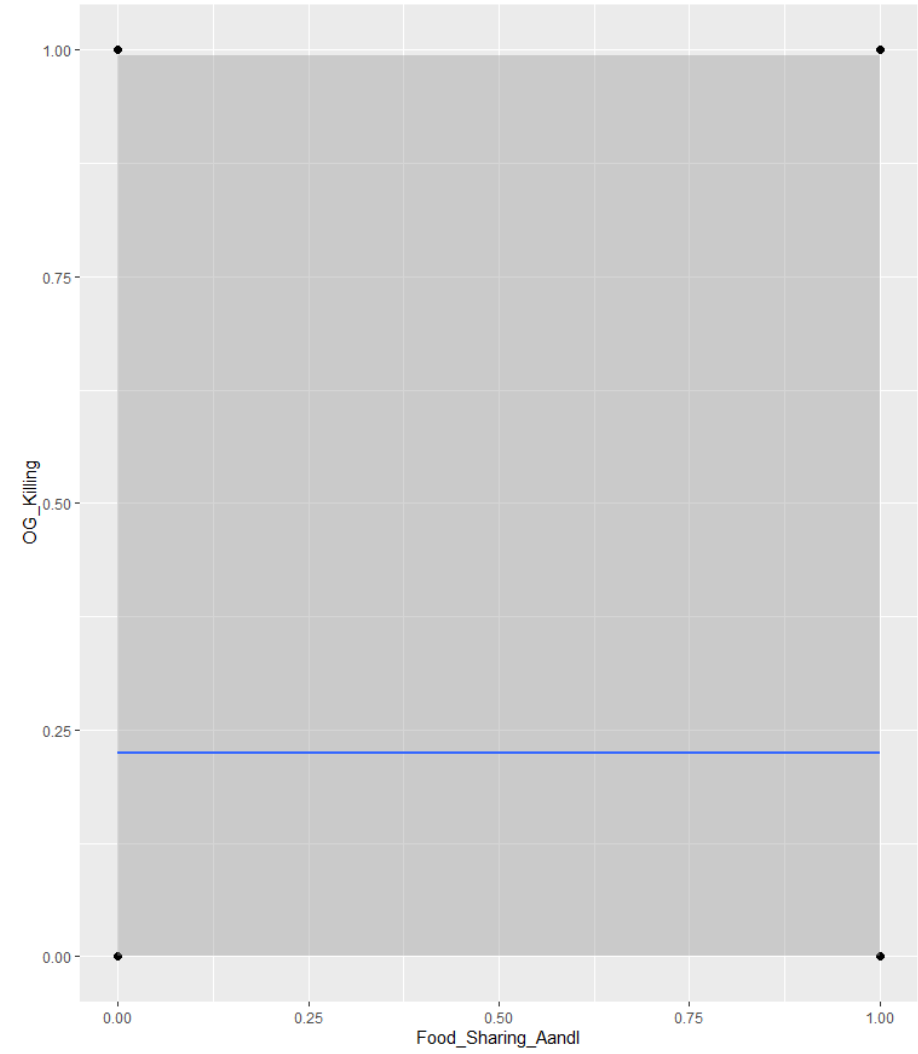
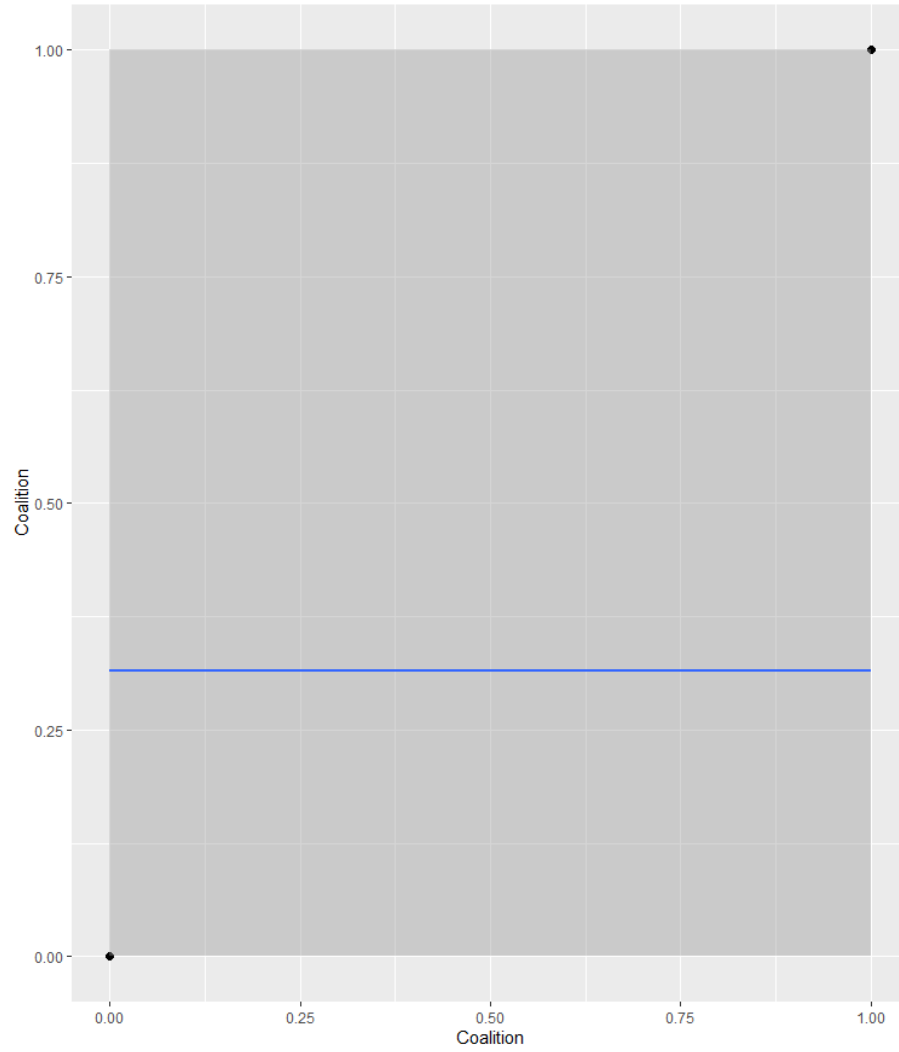
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGKilling_Intercept	-2.74	3.68	-12.16	3.68	1.00	4485	2331
IGKilling_Intercept	-5.43	5.57	-18.31	5.02	1.00	7104	7718
Coalition_Intercept	-0.51	8.41	-17.41	16.74	1.00	11001	12533
OGKilling_Coalition	1.82	1.60	-0.42	5.97	1.00	5084	2743
IGKilling_Coalition	5.02	2.81	0.78	11.59	1.00	6591	10151
Coalition_Food_Sharing_AandI	-0.85	3.56	-8.12	6.65	1.00	12107	11661

Draws were sampled using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

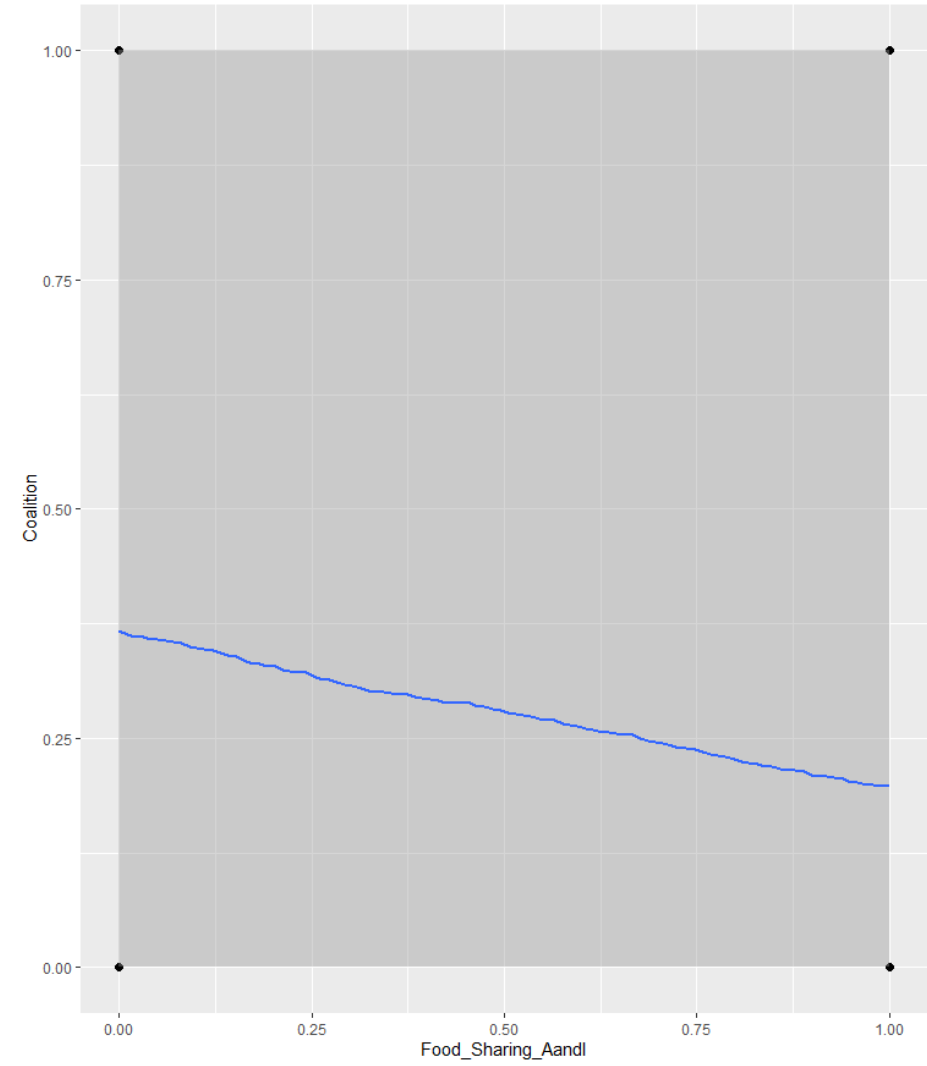
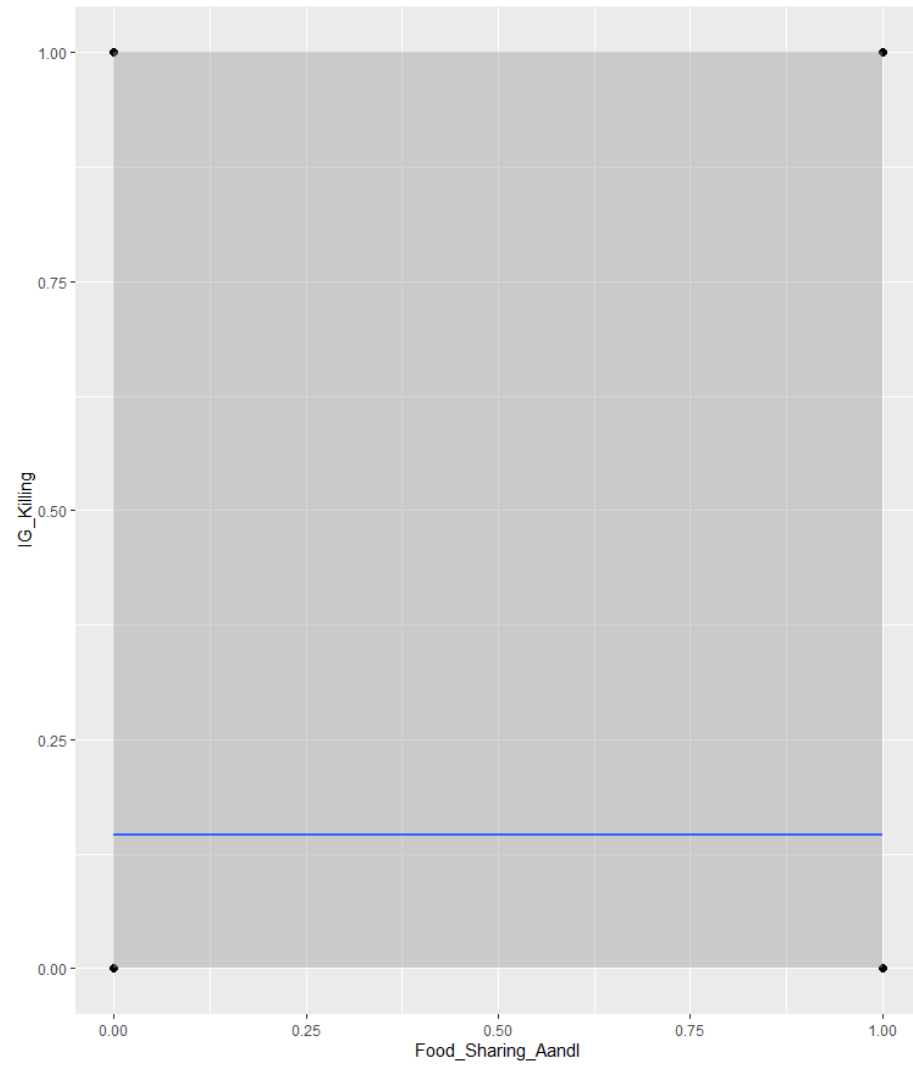
	Estimate	Est.Error	Q2.5	Q97.5
R2OGKilling	0.2971293	0.1977743	0.03665754	0.8159126
R2IGKilling	0.5314115	0.2169217	0.12137661	0.9084291
R2Coalition	0.8594159	0.1098664	0.57899377	0.9963998

*Plot, Conditional effects, PP checks*

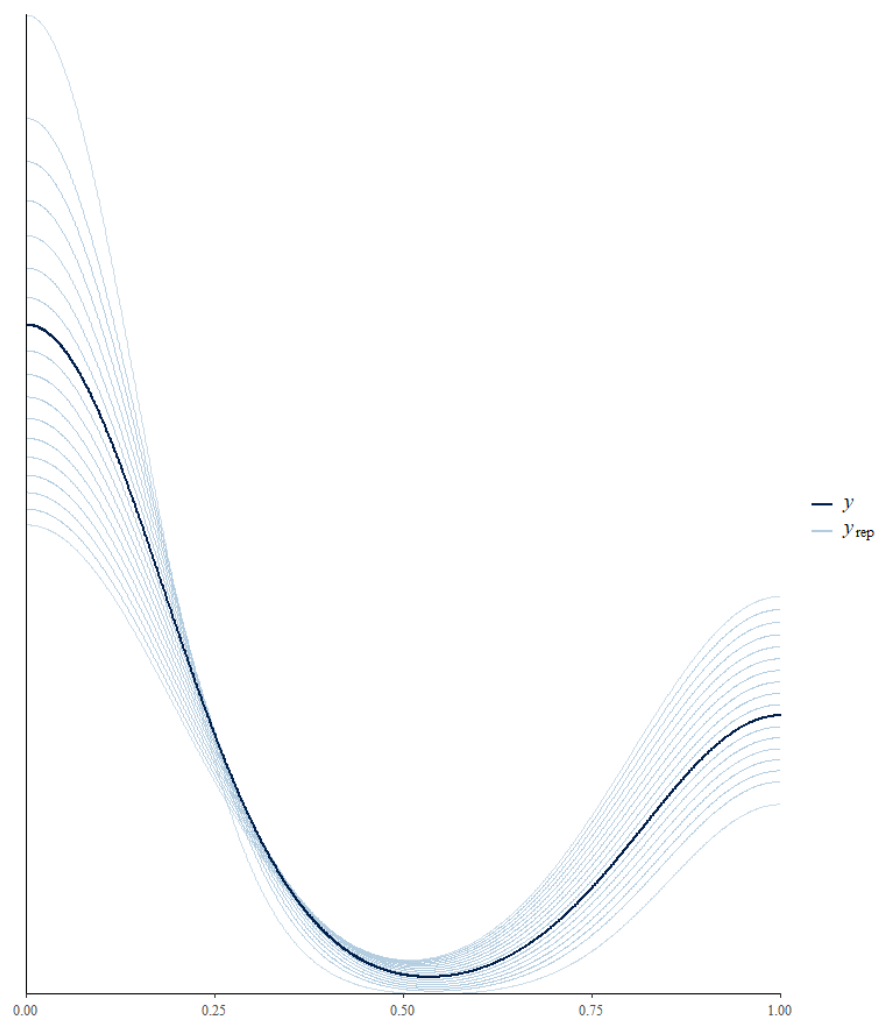




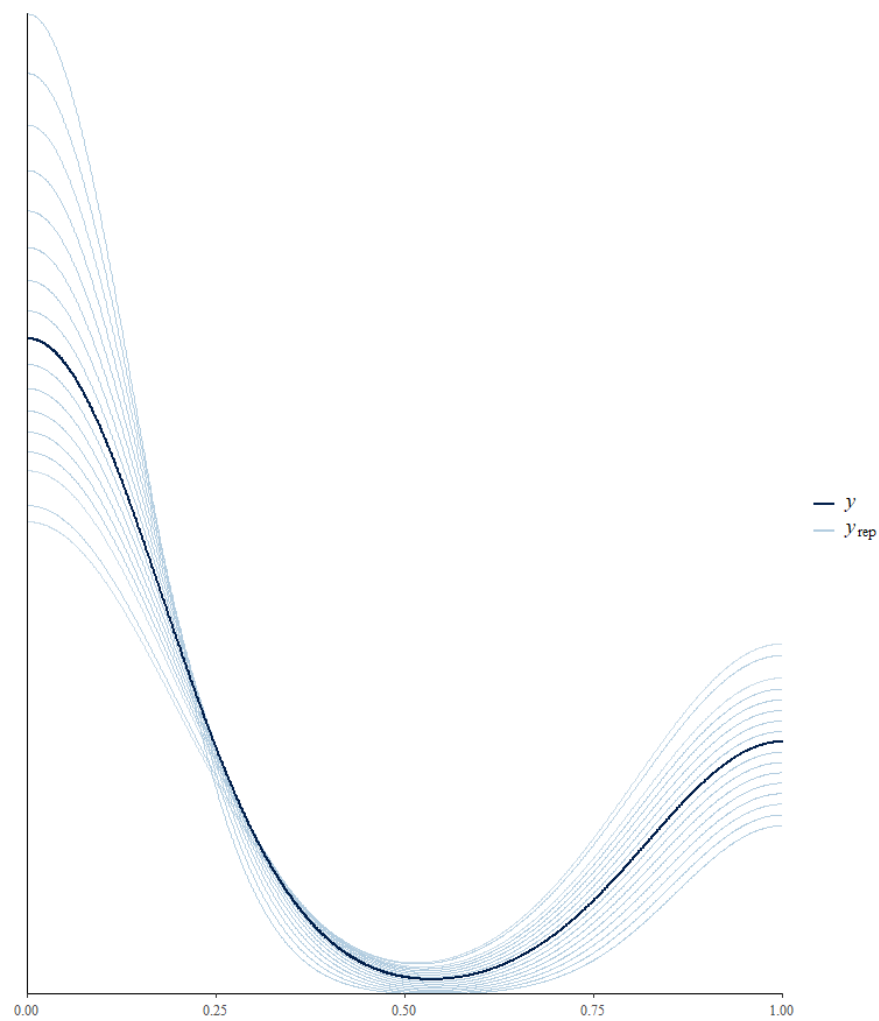




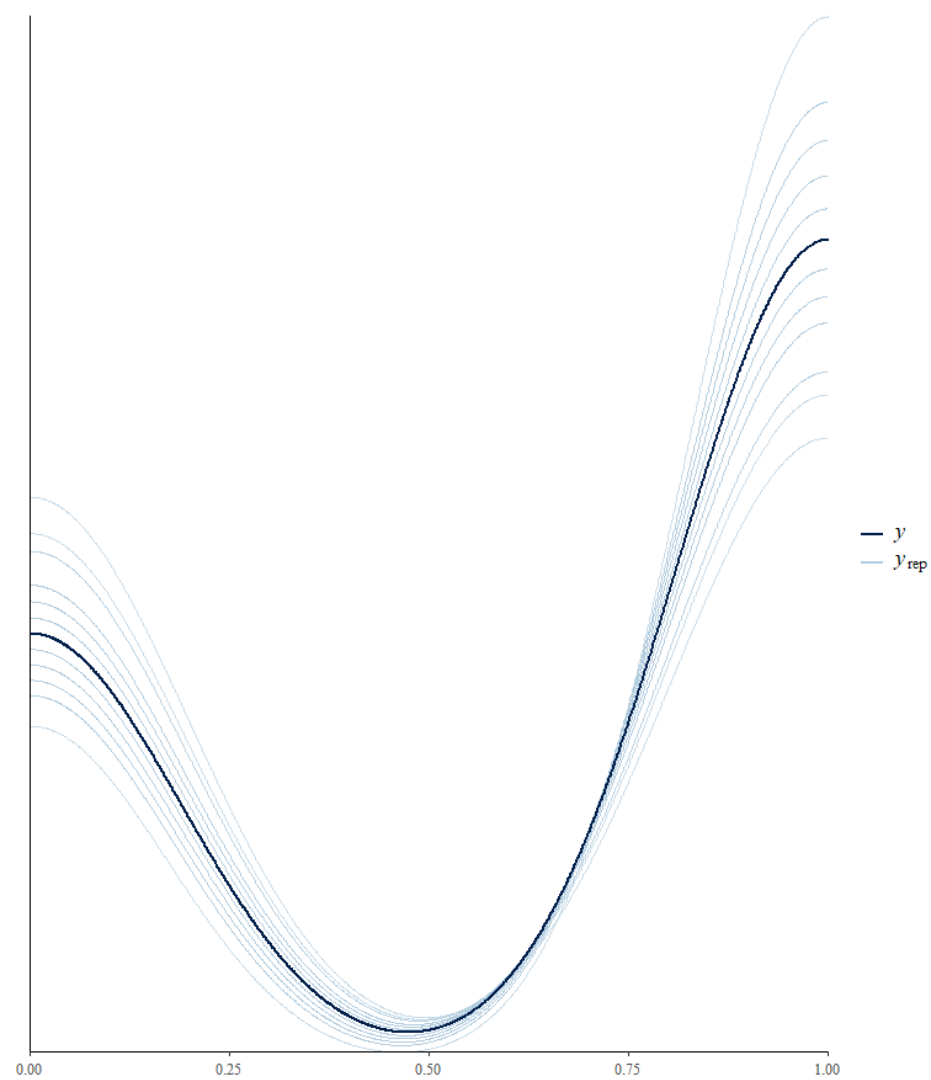
OG Killing



IG Killing



Coalition



*5F.3 Model C(iii) Infanticide and grooming*

```
> summary(Coalitioninf3G, waic= T); bayes_R2(Coalitioninf3G)
```

```
Family: MV(bernoulli, bernoulli)
```

```
Links: mu = logit
```

```
mu = logit
```

```
Formula: Infanticide ~ Coalition + (1 | gr(SpeciesTree, cov = A))
```

```
Coalition ~ Grooming + (1 | gr(SpeciesTree, cov = A))
```

```
Data: dataG (Number of observations: 68)
```

```
Draws: 4 chains, each with iter = 9000; warmup = 4500; thin = 1;
```

```
total post-warmup draws = 18000
```

Group-Level Effects:

~SpeciesTree (Number of levels: 68)

	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Infanticide_Intercept)	3.10	3.29	0.13	11.19	1.00	1183	1268
sd(Coalition_Intercept)	6.38	7.93	0.95	24.59	1.00	5694	6277

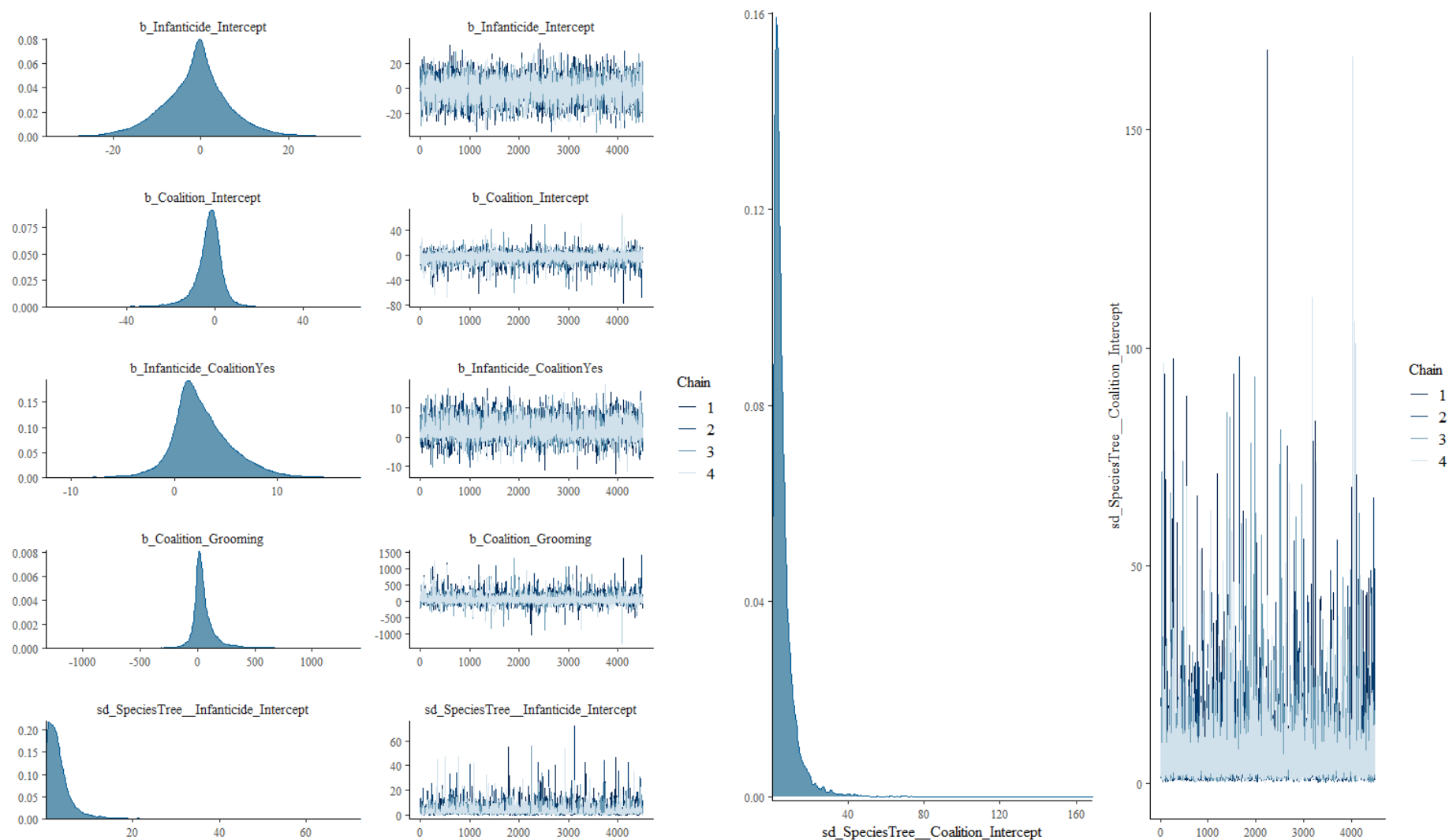
Population-Level Effects:

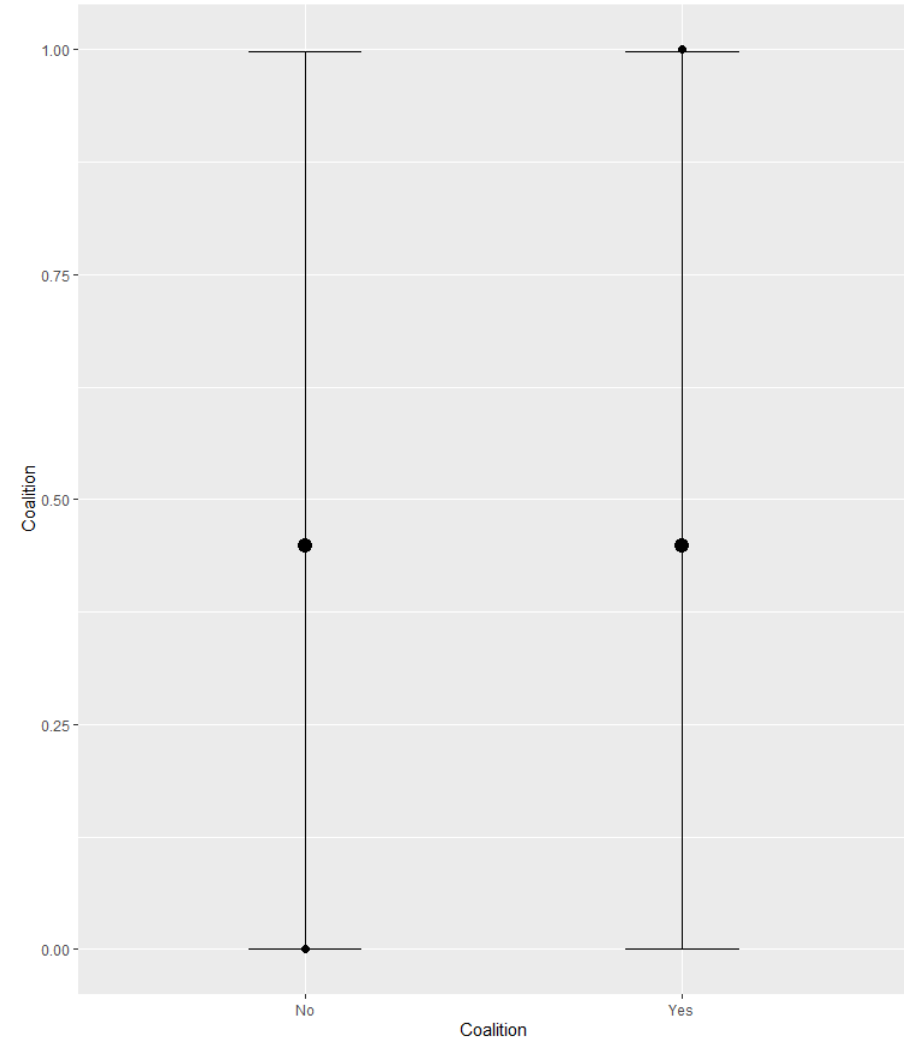
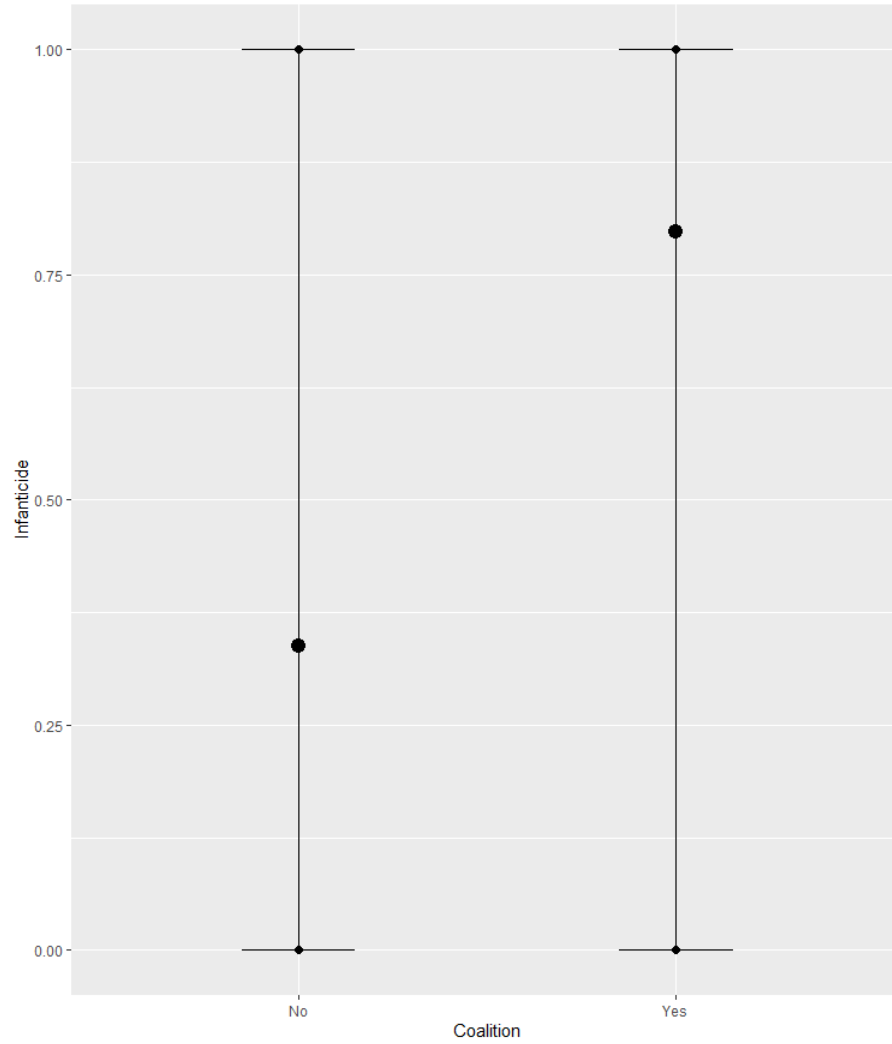
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Infanticide_Intercept	-1.06	7.54	-17.15	14.40	1.00	10756	10553

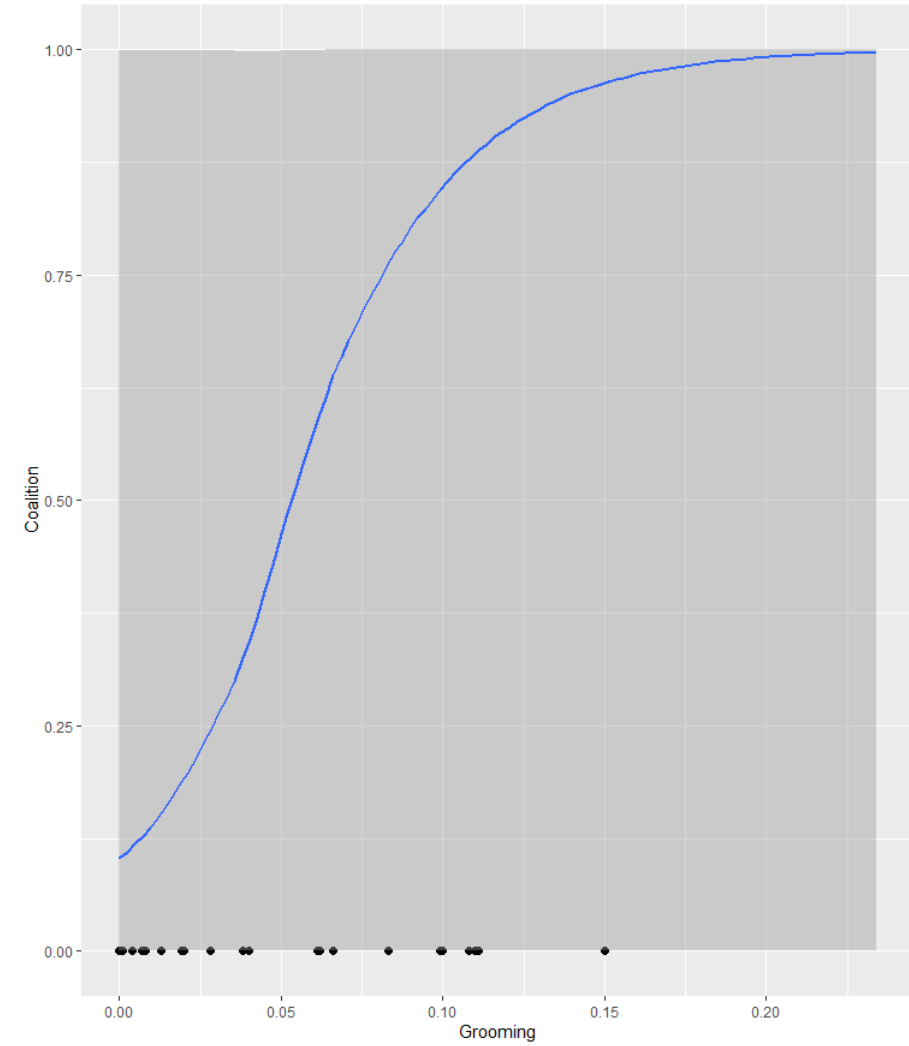
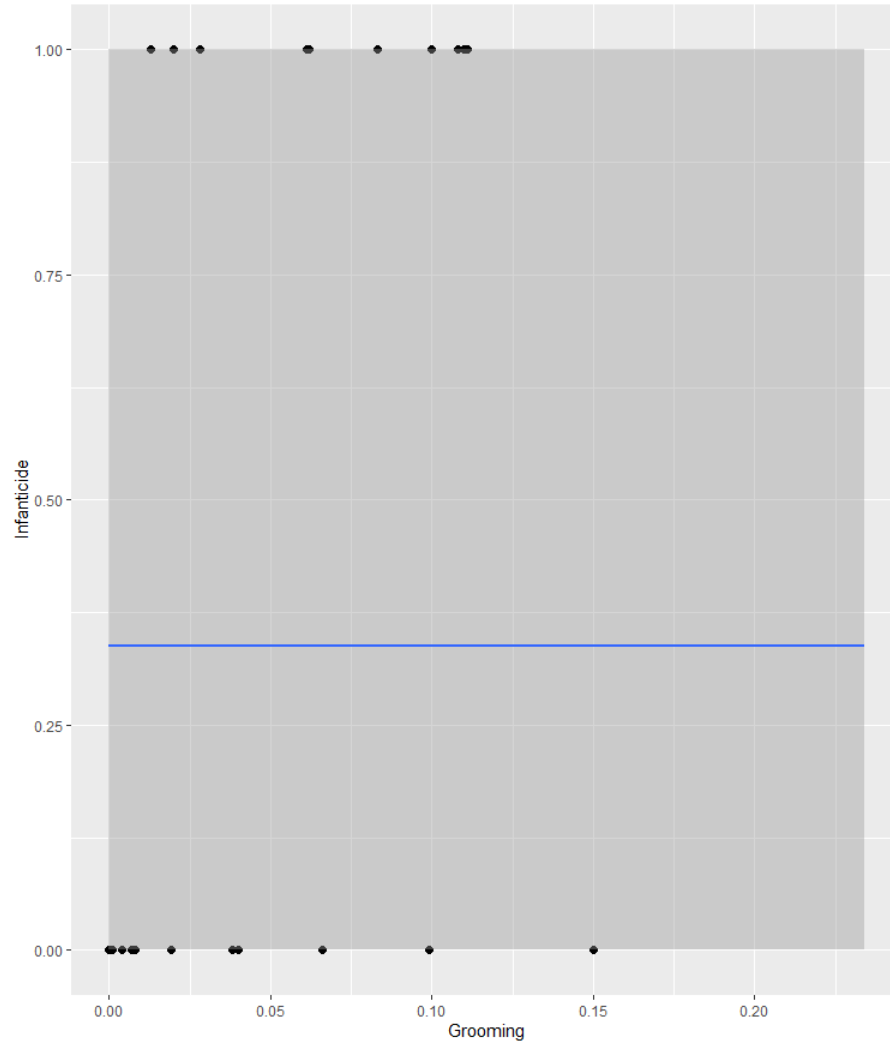
Coalition_Intercept	-2.93	7.31	-19.78	8.24	1.00	7302	5440
Infanticide_CoalitionYes	2.70	2.86	-2.42	9.17	1.00	6851	10327
Coalition_Grooming	54.04	130.27	-112.51	369.23	1.00	6844	4943

Draws were sampled using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
R2Infanticide	0.7035203	0.22408871	0.1322058	0.9758522
R2Coalition	0.8841506	0.09571788	0.6460721	0.9992525

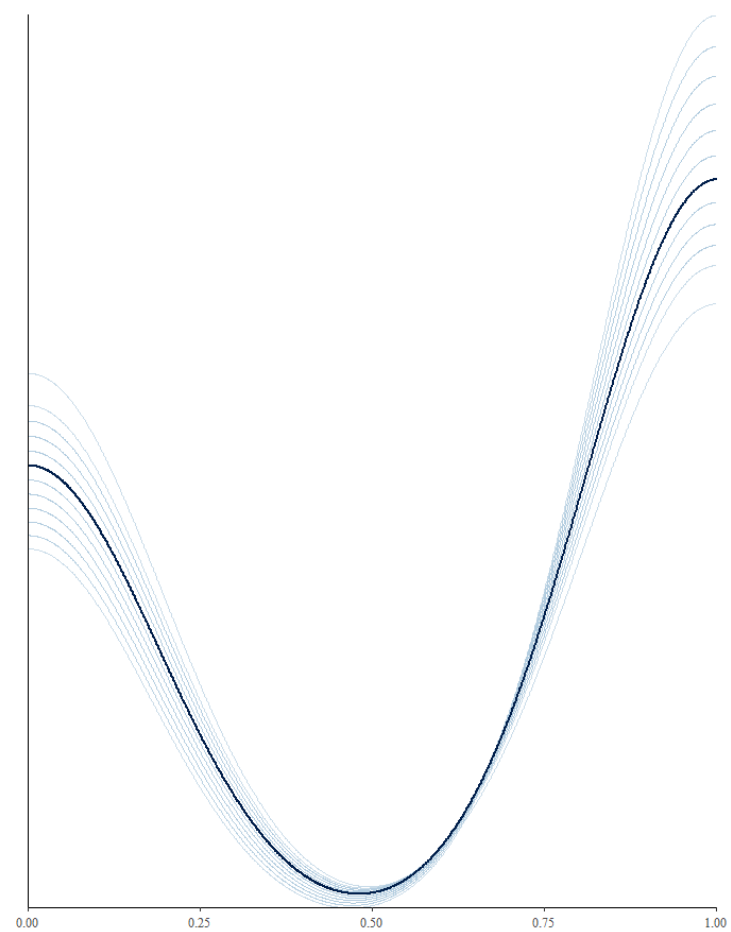
*Plot, Conditional effects, PP checks*



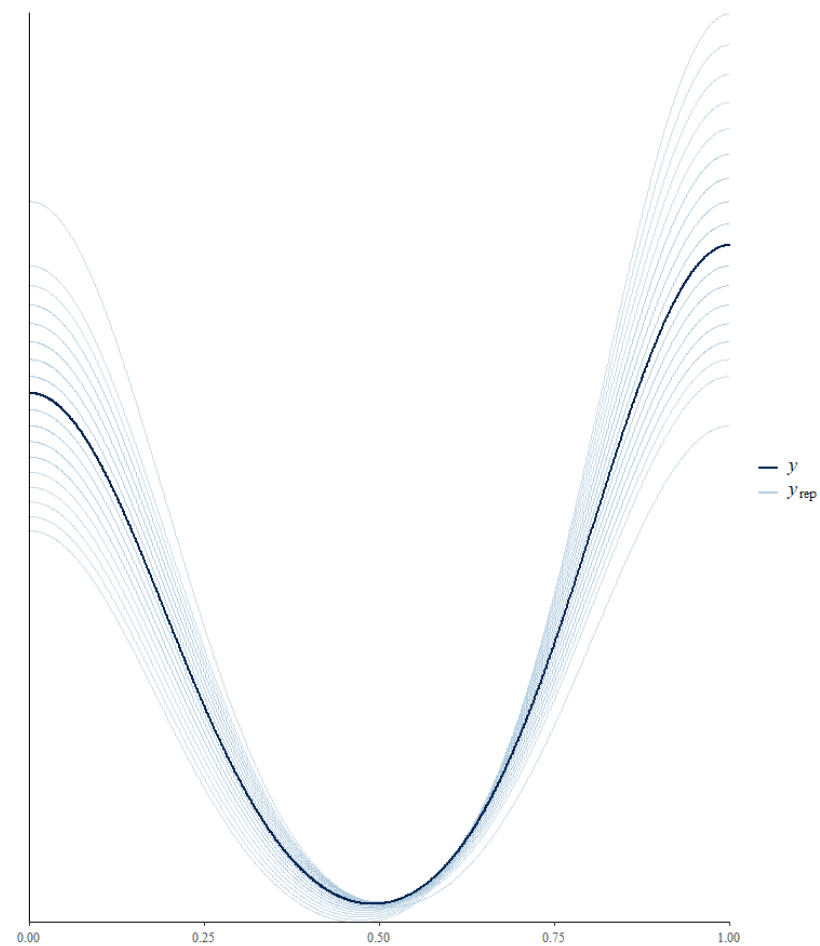




Coalition



Infanticide



*5F.4 Model C(iv) Infanticide and food-sharing*

```

> summary(Coalitioninf3F, waic= T); bayes_R2(Coalitioninf3F)
Family: MV(bernoulli, bernoulli)
Links: mu = logit
       mu = logit
Formula: Infanticide ~ Coalition + (1 | gr(SpeciesTree, cov = A))
        Coalition ~ Food_Sharing_AandI + (1 | gr(SpeciesTree, cov = A))
Data: data1 (Number of observations: 61)
Draws: 4 chains, each with iter = 9000; warmup = 4500; thin = 1;
       total post-warmup draws = 18000

Group-Level Effects:
~SpeciesTree (Number of levels: 61)

```

	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Infanticide_Intercept)	2.53	2.91	0.14	9.50	1.00	1347	1869
sd(Coalition_Intercept)	6.19	7.32	0.74	24.49	1.00	4457	4290

```

Population-Level Effects:

```

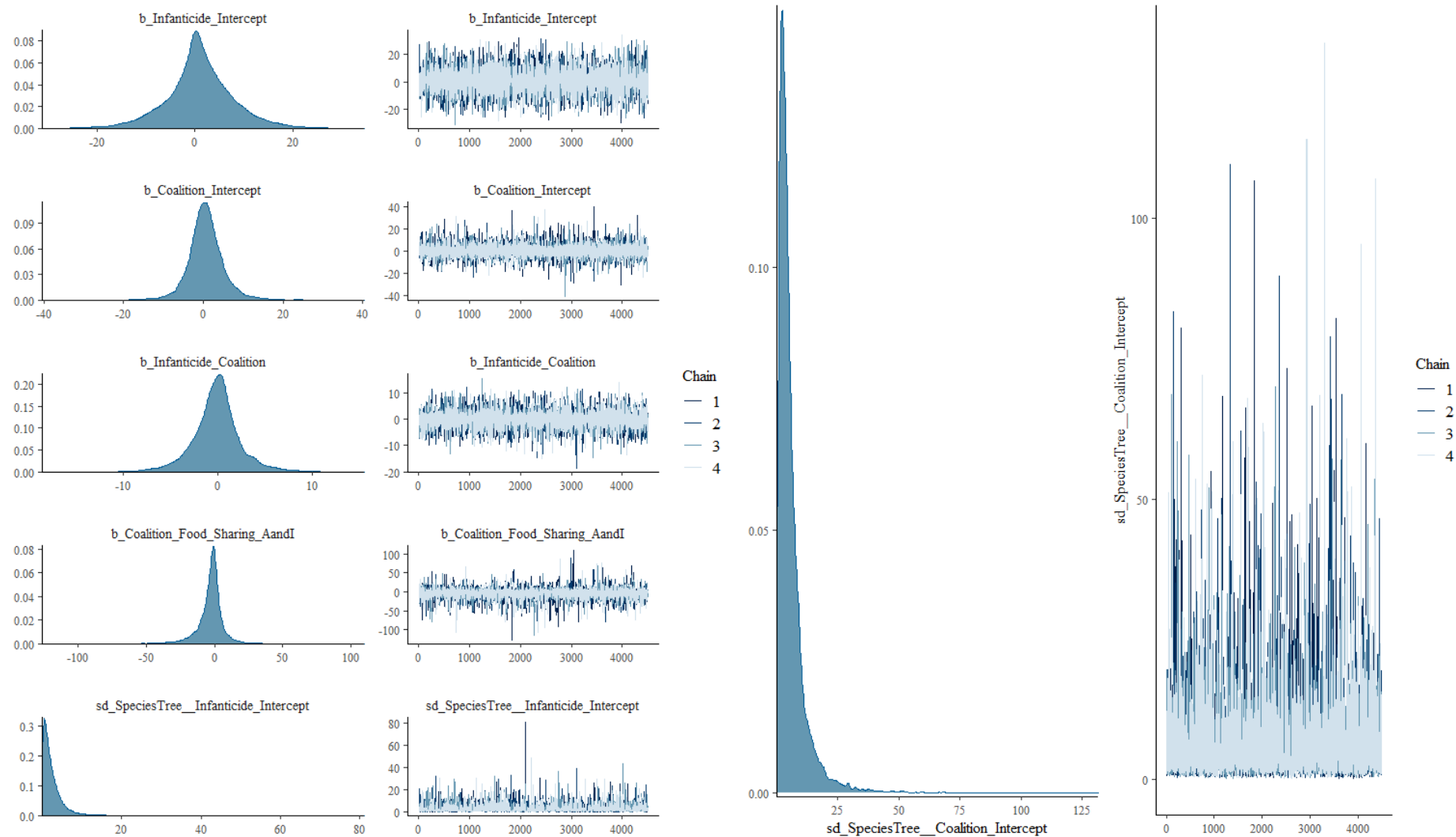
	Estimate	Est.Error	1-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Infanticide_Intercept	1.00	7.00	-13.79	15.91	1.00	9303	8346

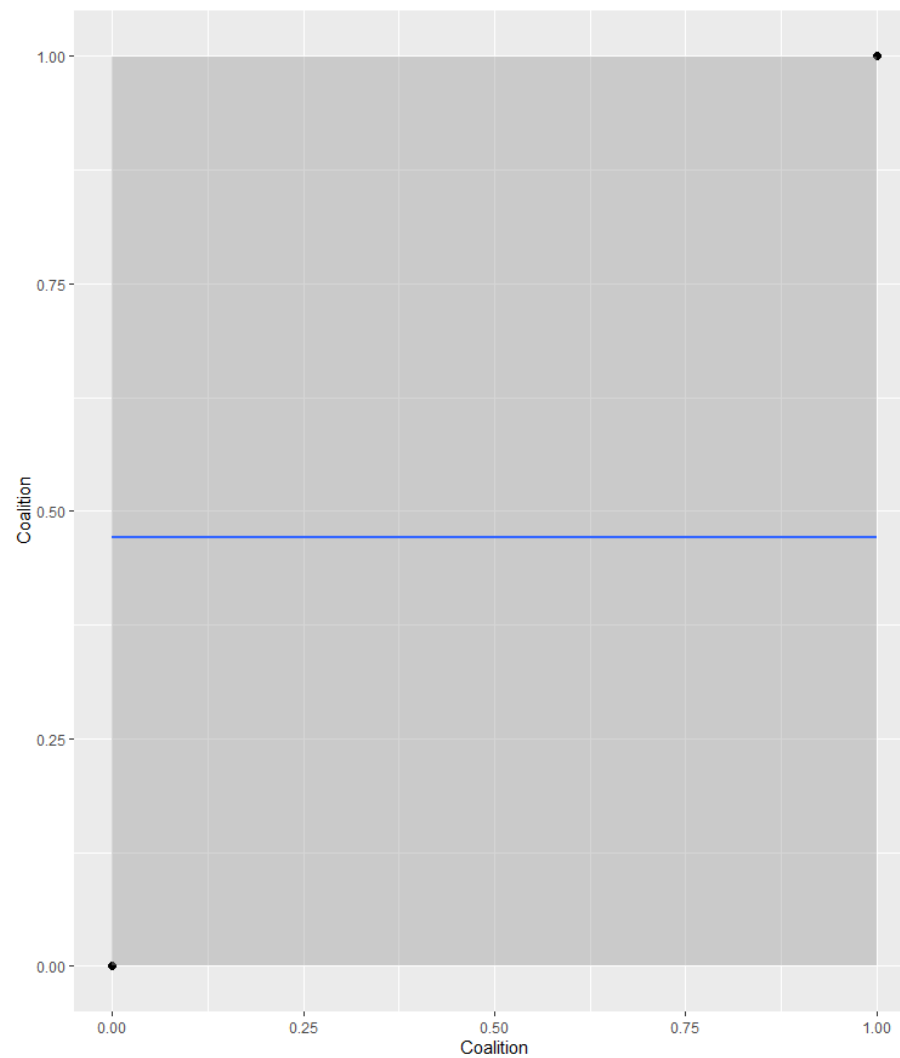
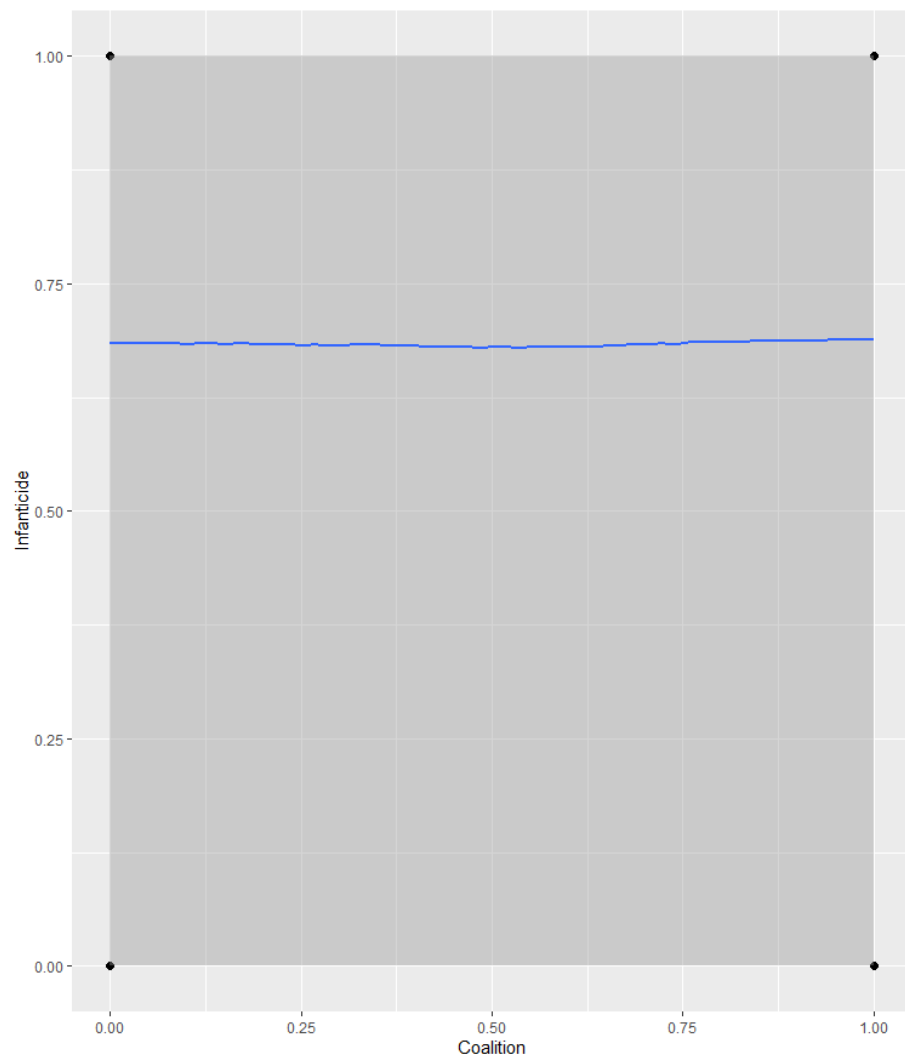
Coalition_Intercept	0.75	4.84	-8.50	11.26	1.00	8855	6261
Infanticide_Coalition	-0.16	2.61	-5.79	5.43	1.00	10283	7629
Coalition_Food_Sharing_AandI	-3.17	12.01	-30.92	16.65	1.00	6311	5822

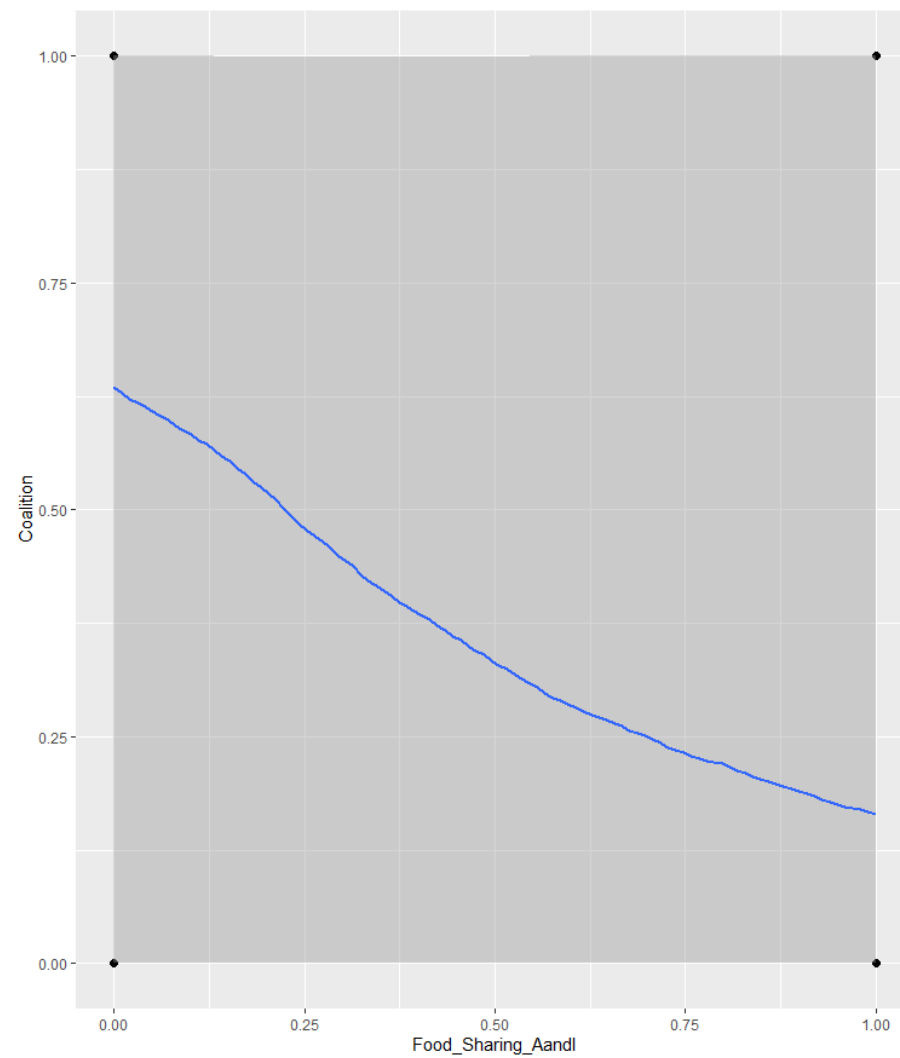
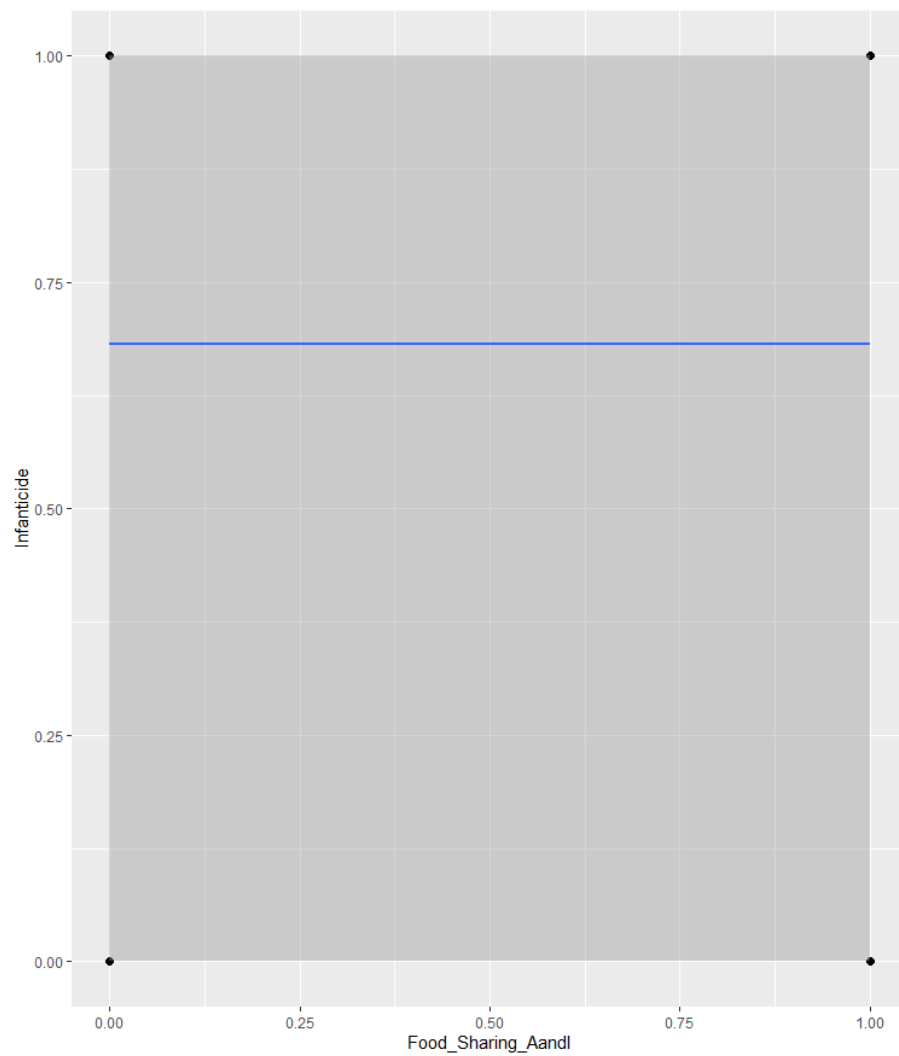
Draws were sampled using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
R2Infanticide	0.6339369	0.2279354	0.1133110	0.9502116
R2Coalition	0.8750552	0.1151754	0.5690842	0.9996307

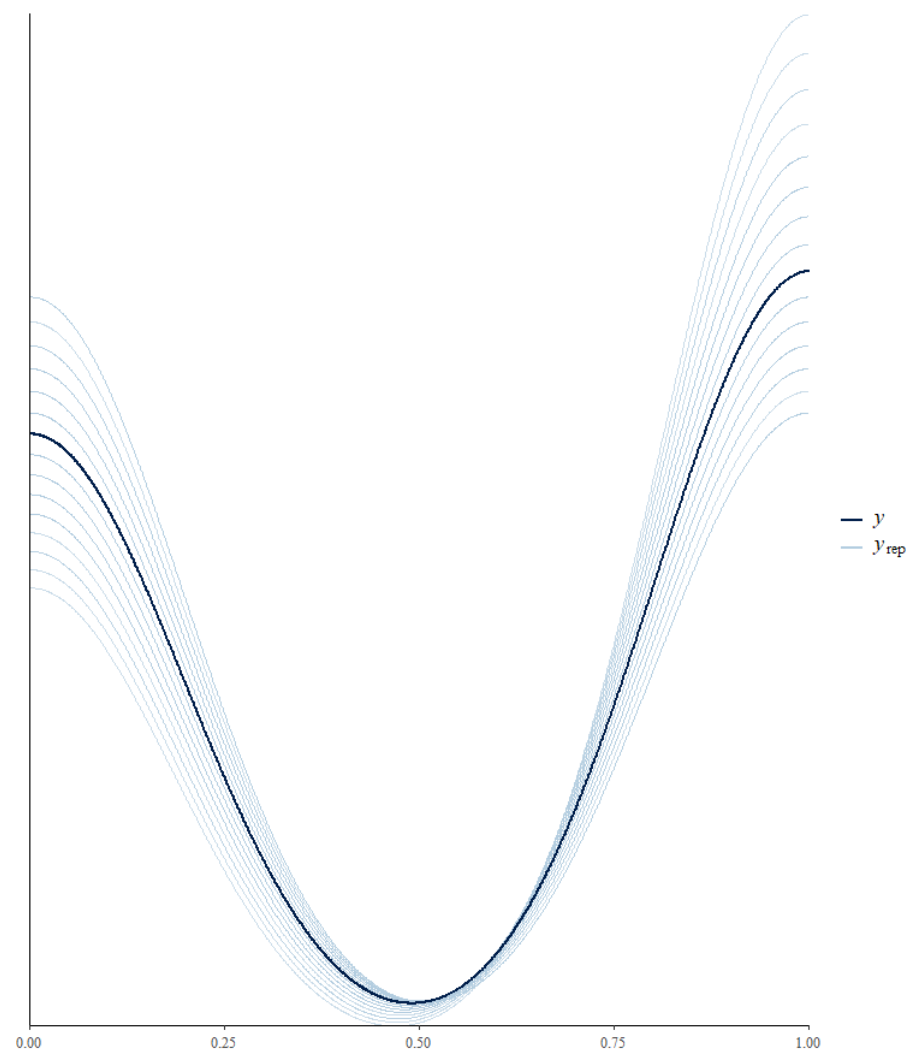
*Plot, Conditional effects, PP checks*



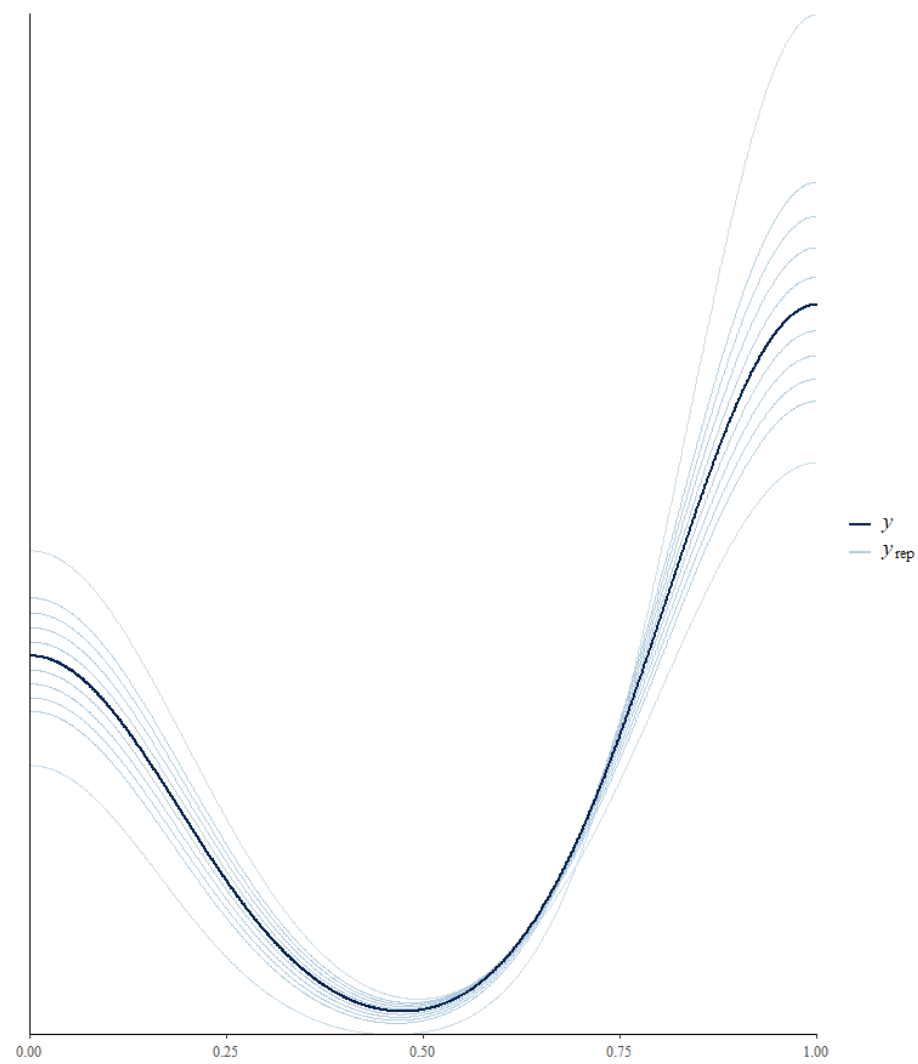




Infanticide



Coalition



*5F.5 Model C(v) Non-lethal aggression and grooming*

```

> summary(Coalitionagg3G, waic= T); bayes_R2(Coalitionagg3G)

Family: MV(zero_one_inflated_beta, hurdle_gamma, bernoulli)

Links: mu = logit; phi = identity; zoi = identity; coi = identity
       mu = log; shape = identity; hu = identity
       mu = logit

Formula: OG_Aggression ~ Coalition + (1 | gr(SpeciesTree, cov = A))
        IG_Aggression ~ Coalition + (1 | gr(SpeciesTree, cov = A))
        Coalition ~ Grooming + (1 | gr(SpeciesTree, cov = A))

Data: dataG (Number of observations: 68)

Draws: 4 chains, each with iter = 8000; warmup = 4000; thin = 1;
       total post-warmup draws = 16000

Group-Level Effects:
~SpeciesTree (Number of levels: 68)

```



	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGAggression_Intercept)	0.09	0.08	0.00	0.29	1.00	2163	1432
sd(IGAggression_Intercept)	0.27	0.11	0.11	0.53	1.00	2576	3303
sd(Coalition_Intercept)	6.19	7.42	0.95	23.36	1.00	5407	5533

## Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGAggression_Intercept	-0.46	0.66	-1.89	0.73	1.00	8394	5176
IGAggression_Intercept	-2.12	1.51	-5.24	0.88	1.00	9918	8722
Coalition_Intercept	-2.86	6.66	-18.83	8.06	1.00	7958	5372
OGAggression_CoalitionYes	-0.16	0.37	-0.85	0.62	1.00	9420	4468
IGAggression_CoalitionYes	-0.07	0.61	-1.27	1.11	1.00	16420	13338
Coalition_Grooming	53.27	114.45	-108.54	347.14	1.00	6929	4508

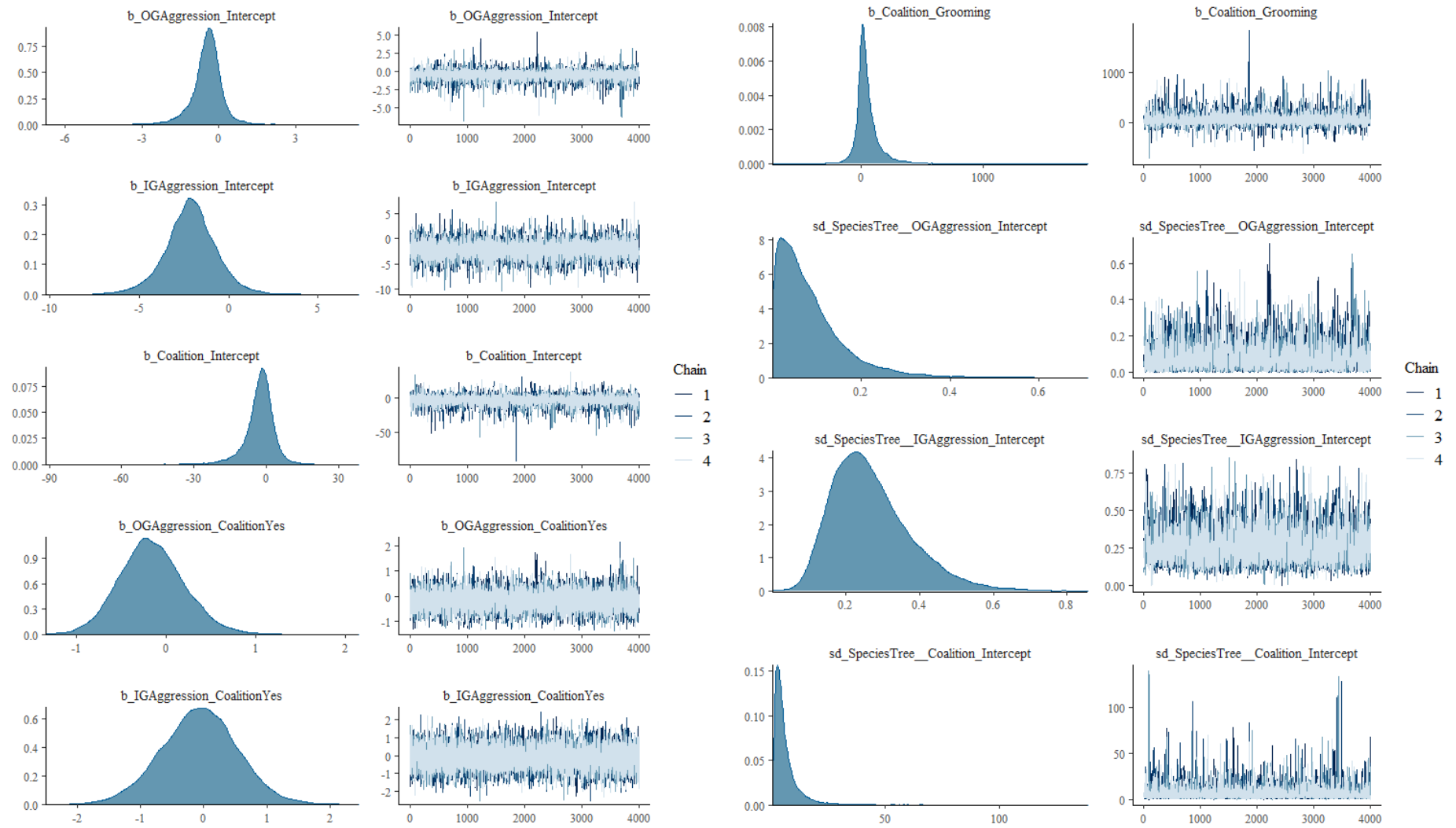
## Family Specific Parameters:

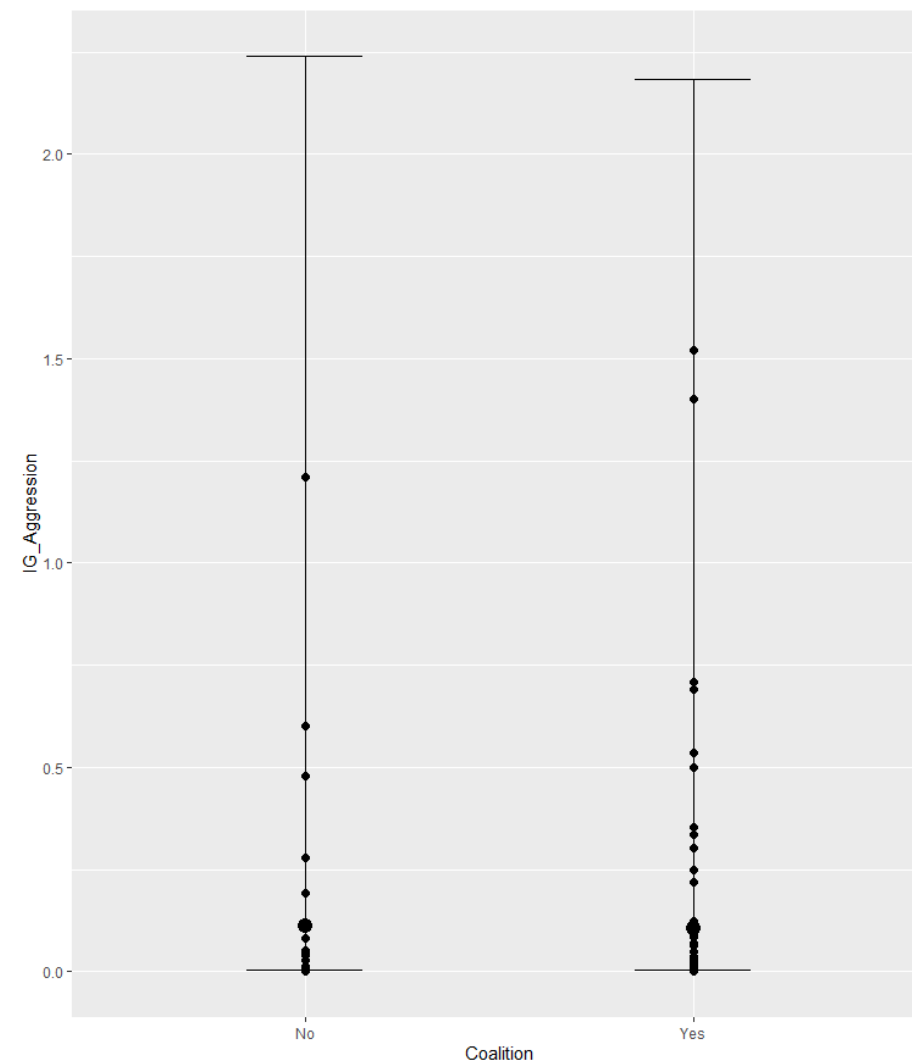
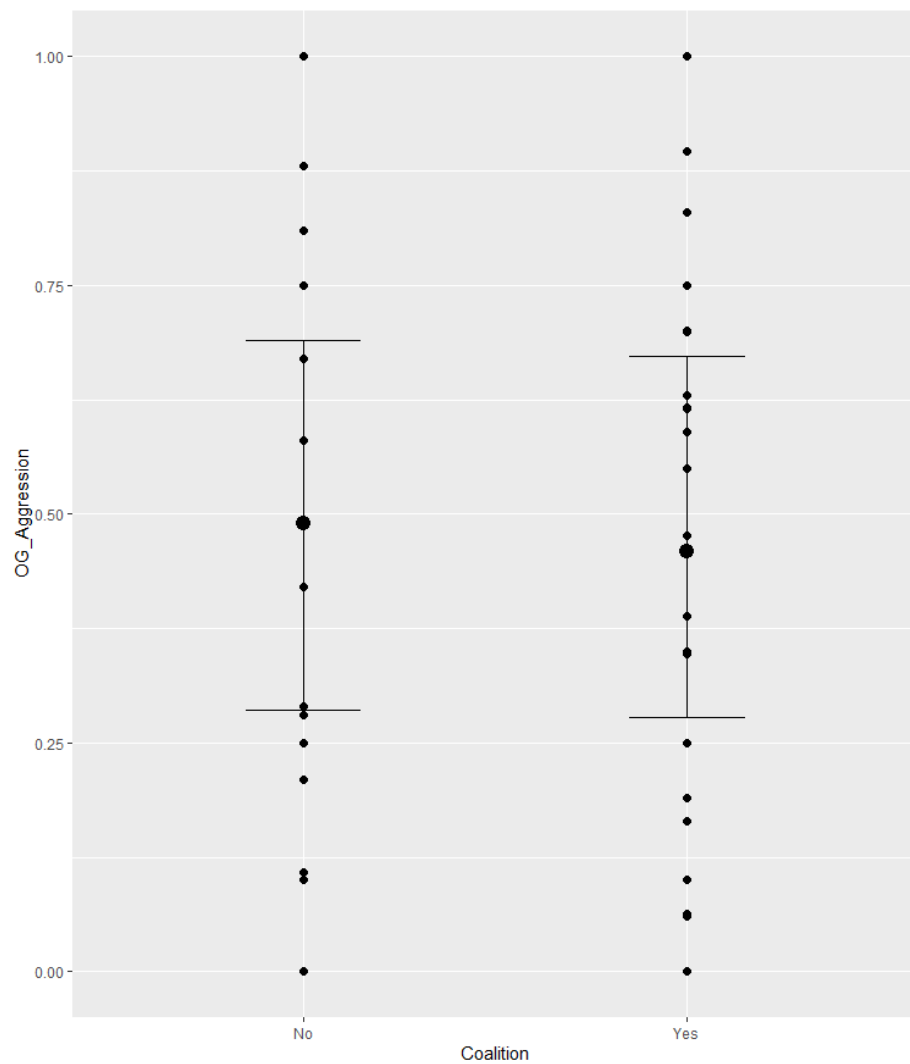
Estimate Est.Error l-95% CI u-95% CI Rhat Bulk\_ESS Tail\_ESS

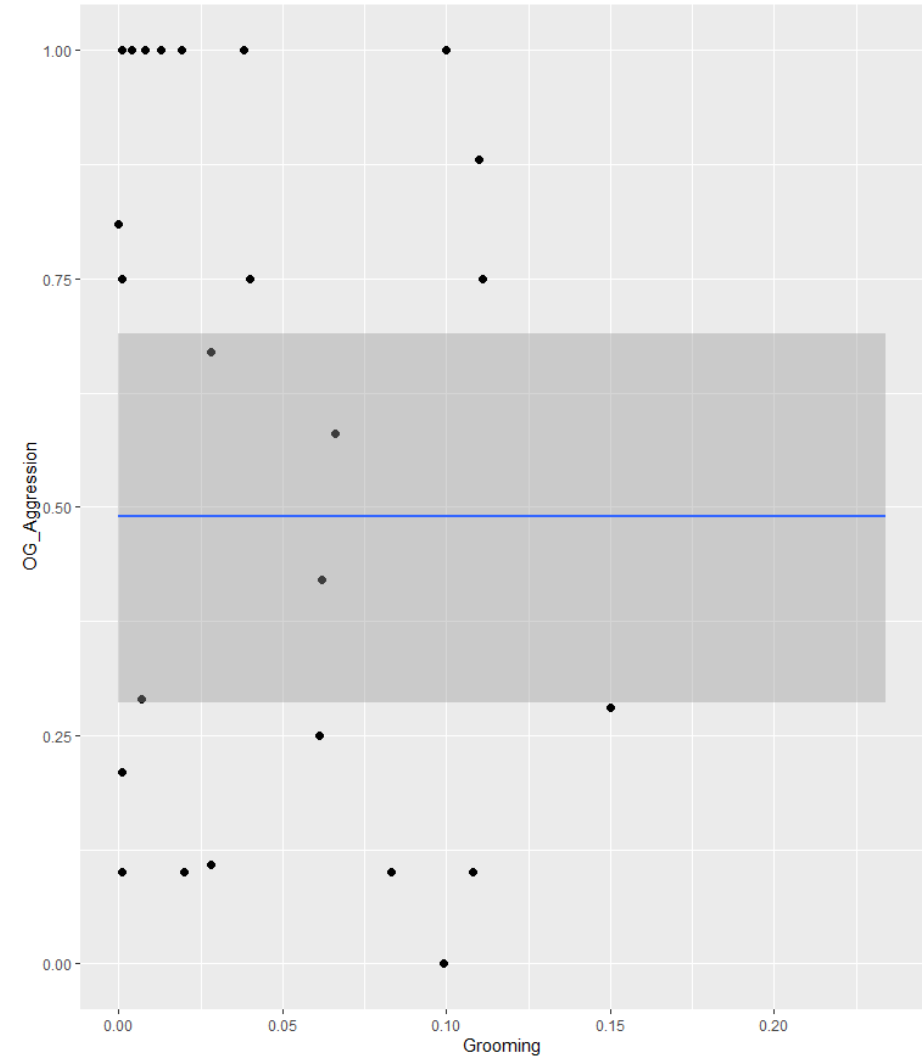
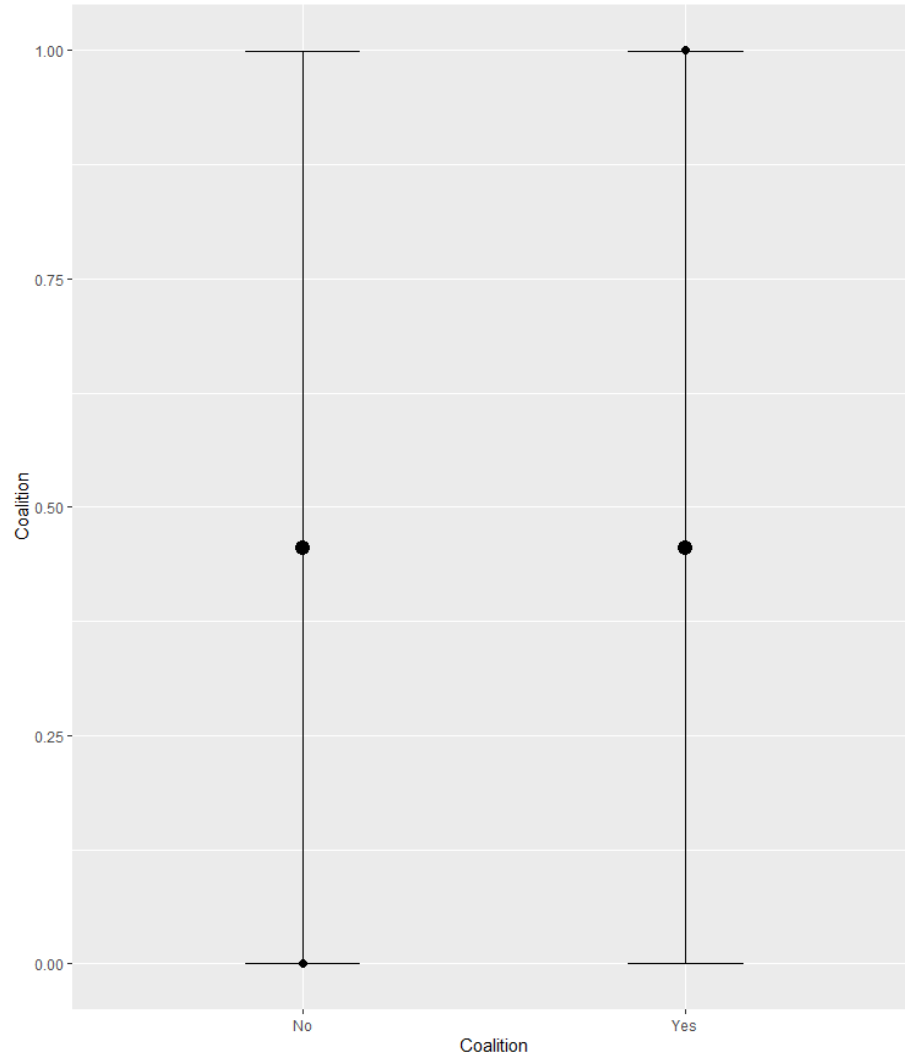
phi_OGAggression	3.08	1.42	1.89	5.50	1.00	2903	1642
zoi_OGAggression	0.29	0.05	0.19	0.40	1.00	35982	10704
coi_OGAggression	0.71	0.10	0.51	0.88	1.00	33373	10130
shape_IGAggression	0.48	0.10	0.33	0.72	1.00	4504	4881
hu_IGAggression	0.07	0.03	0.02	0.14	1.00	33849	11383

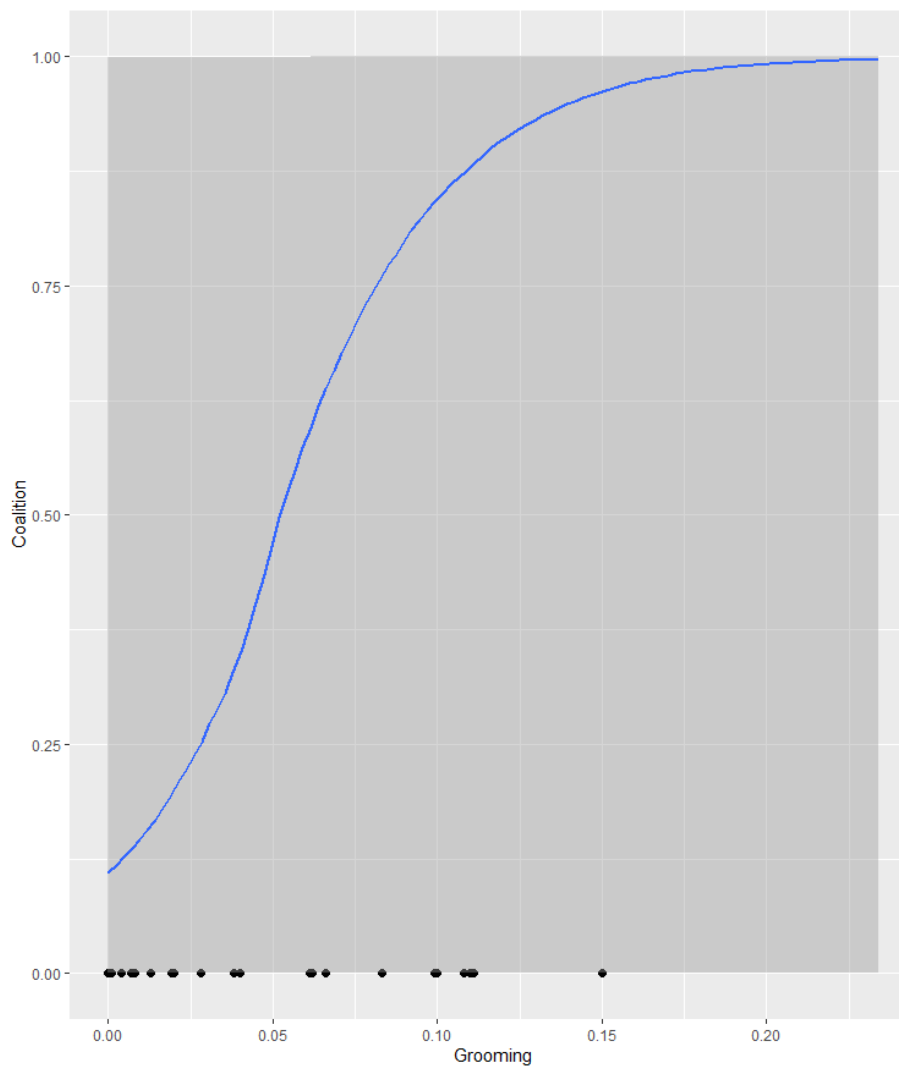
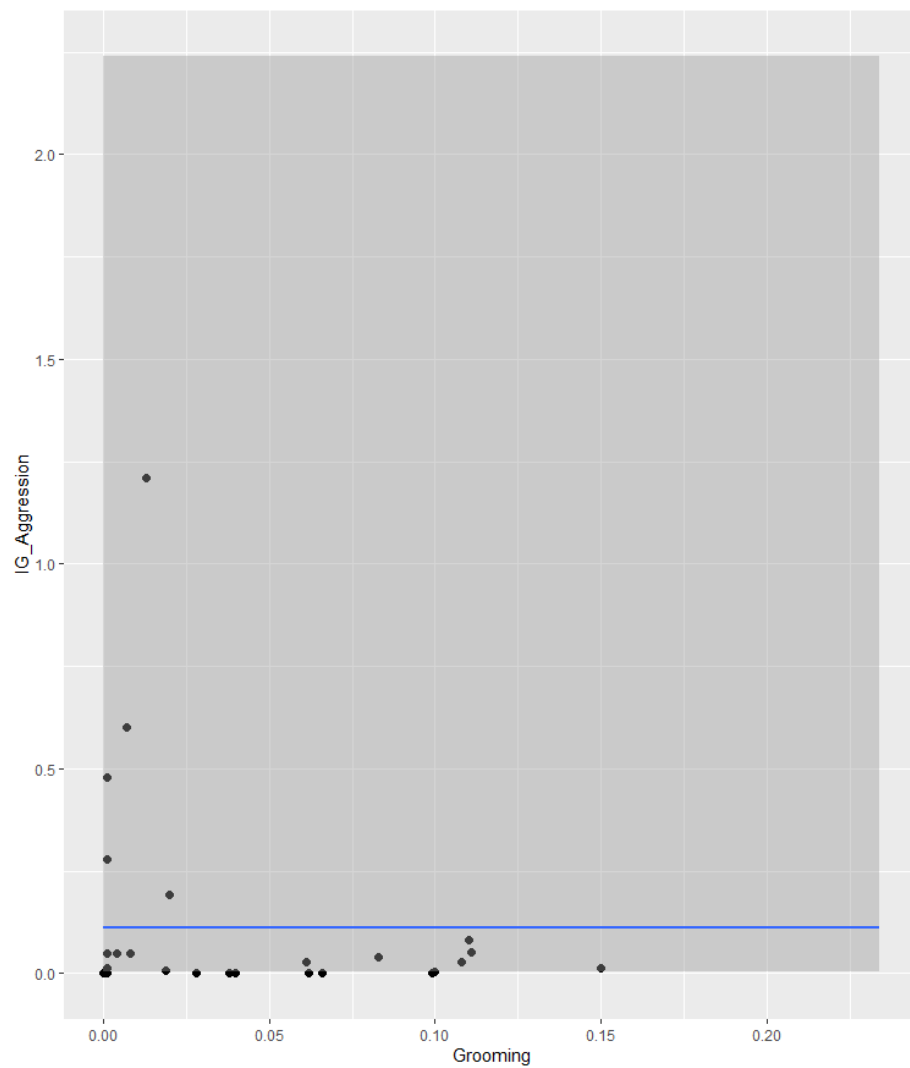
Draws were sampled using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
R2OGAggression	0.03937015	0.04326640	0.0009105448	0.1606113
R2IGAggression	0.34595648	0.15511556	0.0718800456	0.6316202
R2Coalition	0.88283064	0.09677391	0.6413335882	0.9992485

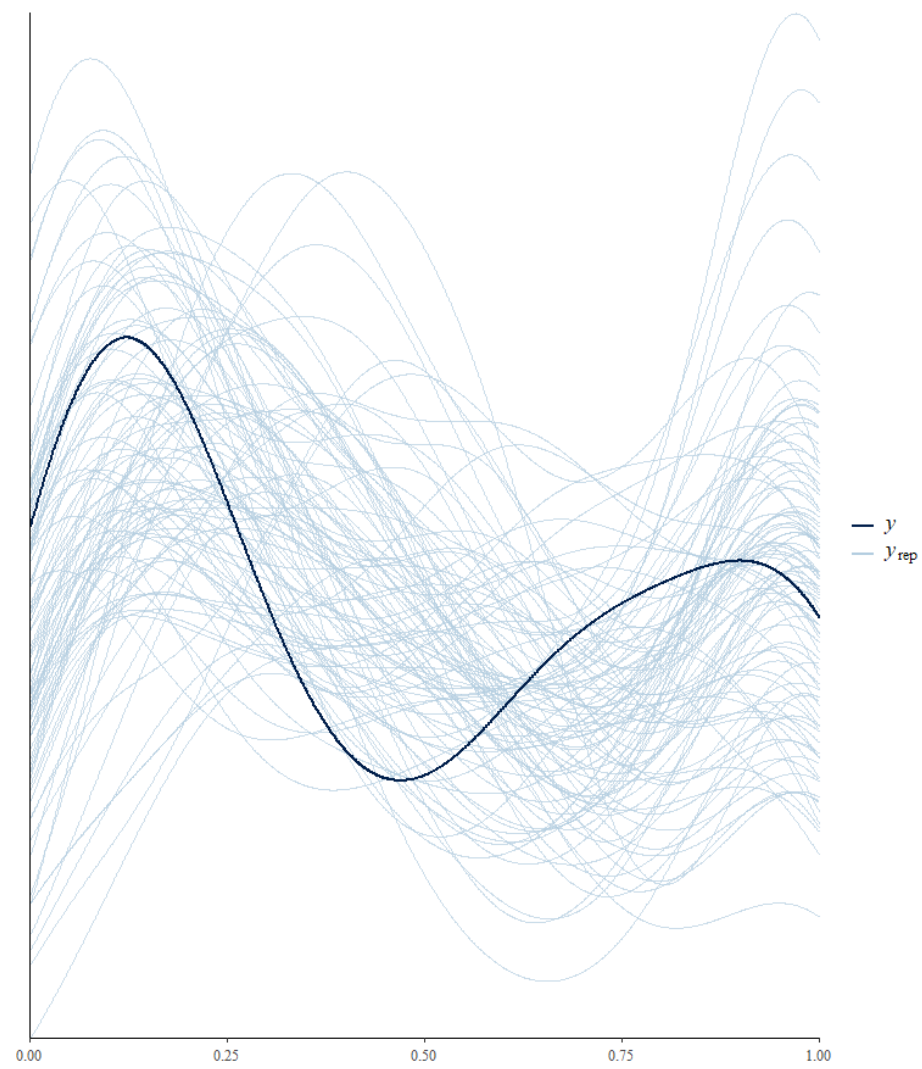
*Plot, Conditional effects, PP checks*







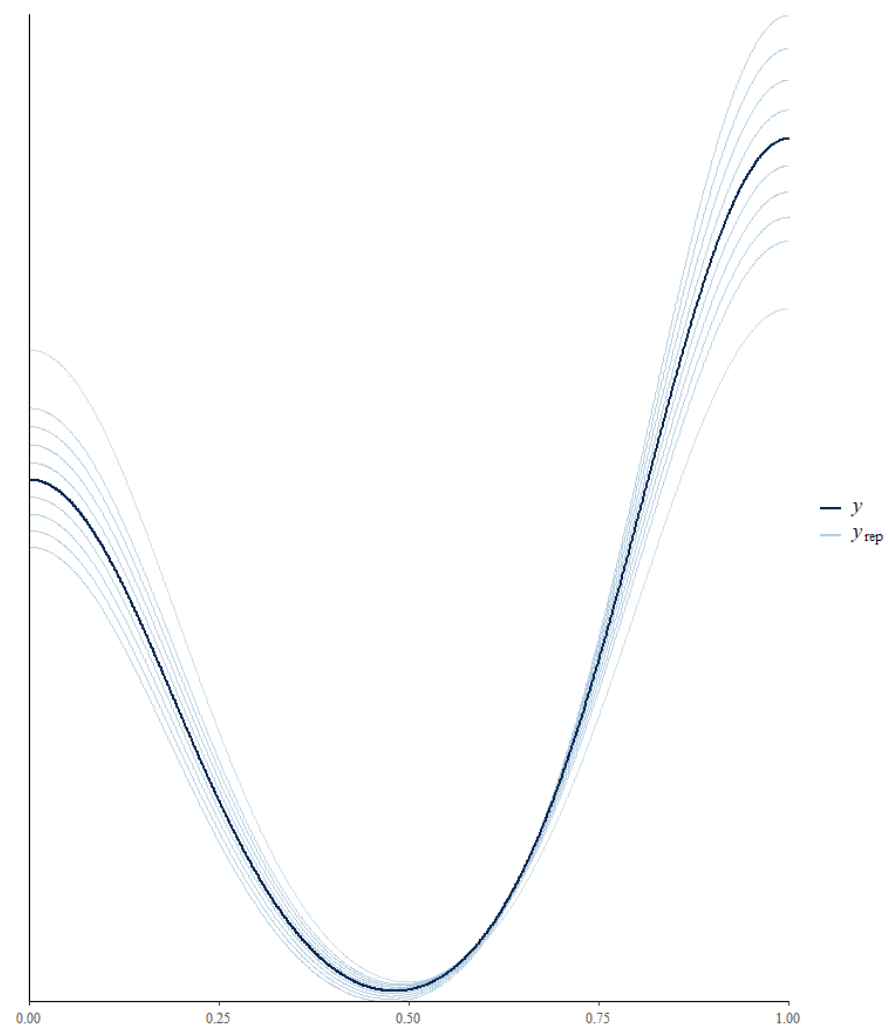
OG Aggression



IG Aggression



Coalition





*5F.6 Model C(vi) Non-lethal aggression and food-sharing*

```

> summary(Coalitionagg3F, waic= T); bayes_R2(Coalitionagg3F)
Family: MV(zero_one_inflated_beta, hurdle_gamma, bernoulli)
Links: mu = logit; phi = identity; zoi = identity; coi = identity
       mu = log; shape = identity; hu = identity
       mu = logit
Formula: OG_Aggression ~ Coalition + (1 | gr(SpeciesTree, cov = A))
        IG_Aggression ~ Coalition + (1 | gr(SpeciesTree, cov = A))
        Coalition ~ Food_Sharing_AandI + (1 | gr(SpeciesTree, cov = A))
Data: data1 (Number of observations: 61)
Draws: 4 chains, each with iter = 9000; warmup = 4500; thin = 1;
       total post-warmup draws = 18000

```

Group-Level Effects:

~SpeciesTree (Number of levels: 61)

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(OGAggression_Intercept)	0.08	0.06	0.00	0.22	1.00	3610	4546
sd(IGAggression_Intercept)	0.26	0.08	0.13	0.45	1.00	4780	6775
sd(Coalition_Intercept)	6.29	7.59	0.73	25.74	1.00	4066	4159

## Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGAggression_Intercept	-0.24	0.57	-1.43	0.89	1.00	11168	8354
IGAggression_Intercept	-2.29	1.43	-5.17	0.52	1.00	9757	9676
Coalition_Intercept	0.80	5.13	-8.87	12.08	1.00	6519	4185
OGAggression_Coalition	-0.43	0.38	-1.18	0.31	1.00	24907	13368
IGAggression_Coalition	-0.47	0.61	-1.69	0.70	1.00	14496	14368
Coalition_Food_Sharing_AandI	-3.72	13.93	-37.04	16.63	1.00	5398	3709

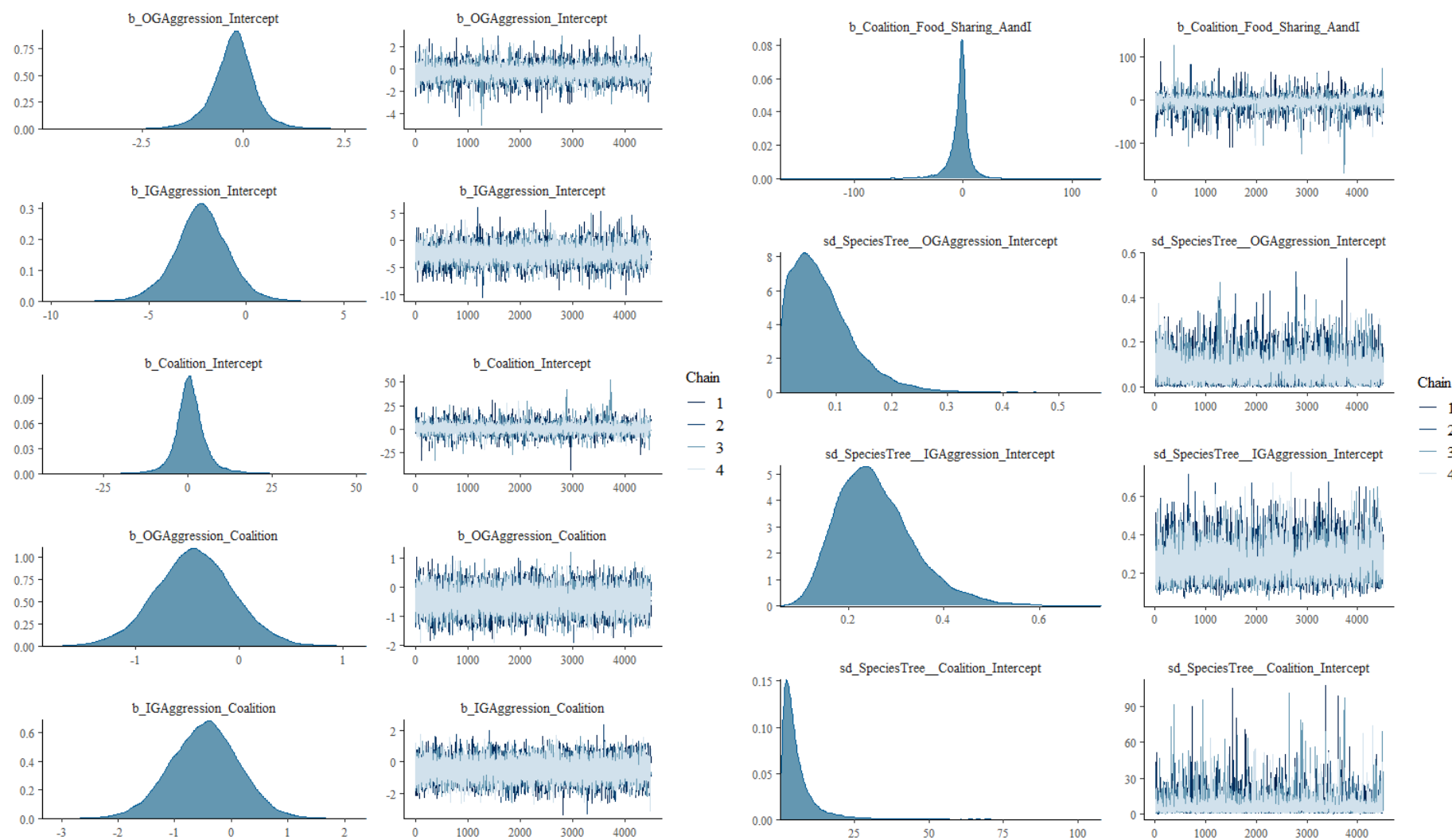
## Family Specific Parameters:

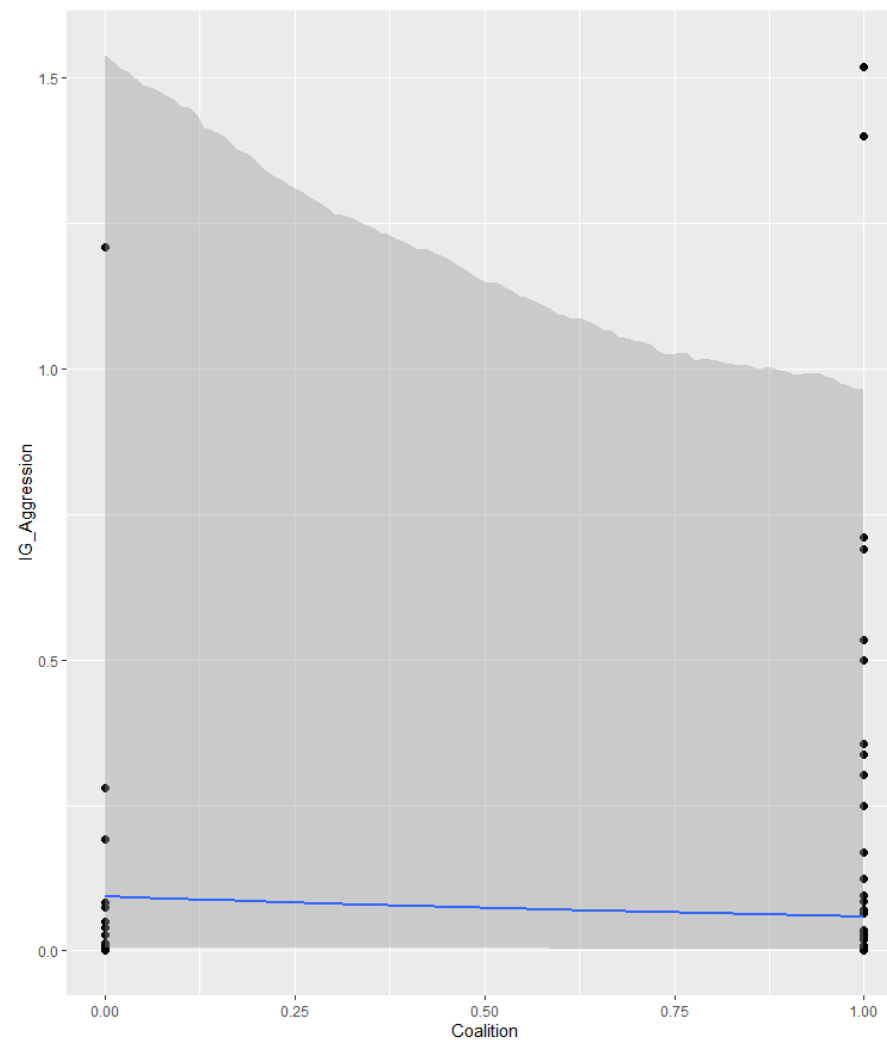
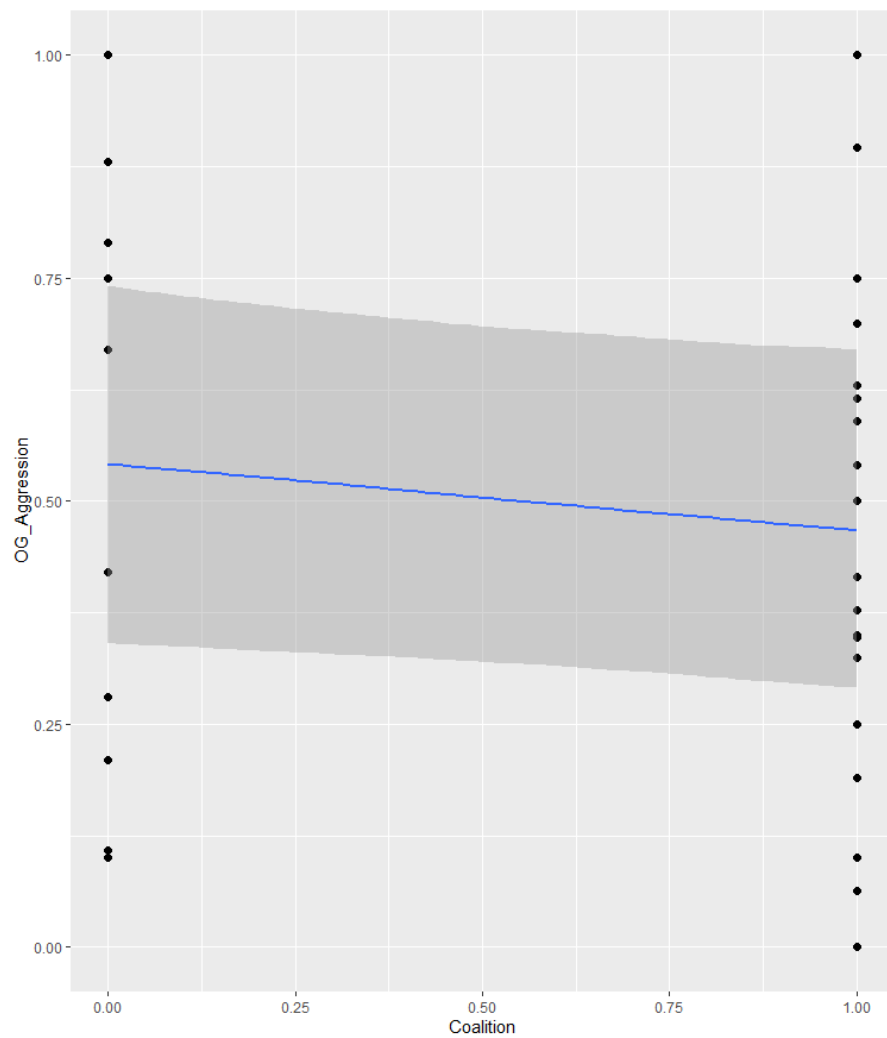
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
phi_OGAggression	3.00	0.74	1.92	4.62	1.00	8118	7871
zoi_OGAggression	0.25	0.05	0.16	0.37	1.00	33265	13431
coi_OGAggression	0.82	0.09	0.62	0.96	1.00	31639	11322
shape_IGAggression	0.62	0.13	0.41	0.92	1.00	7736	8799
hu_IGAggression	0.08	0.03	0.03	0.15	1.00	32117	12144

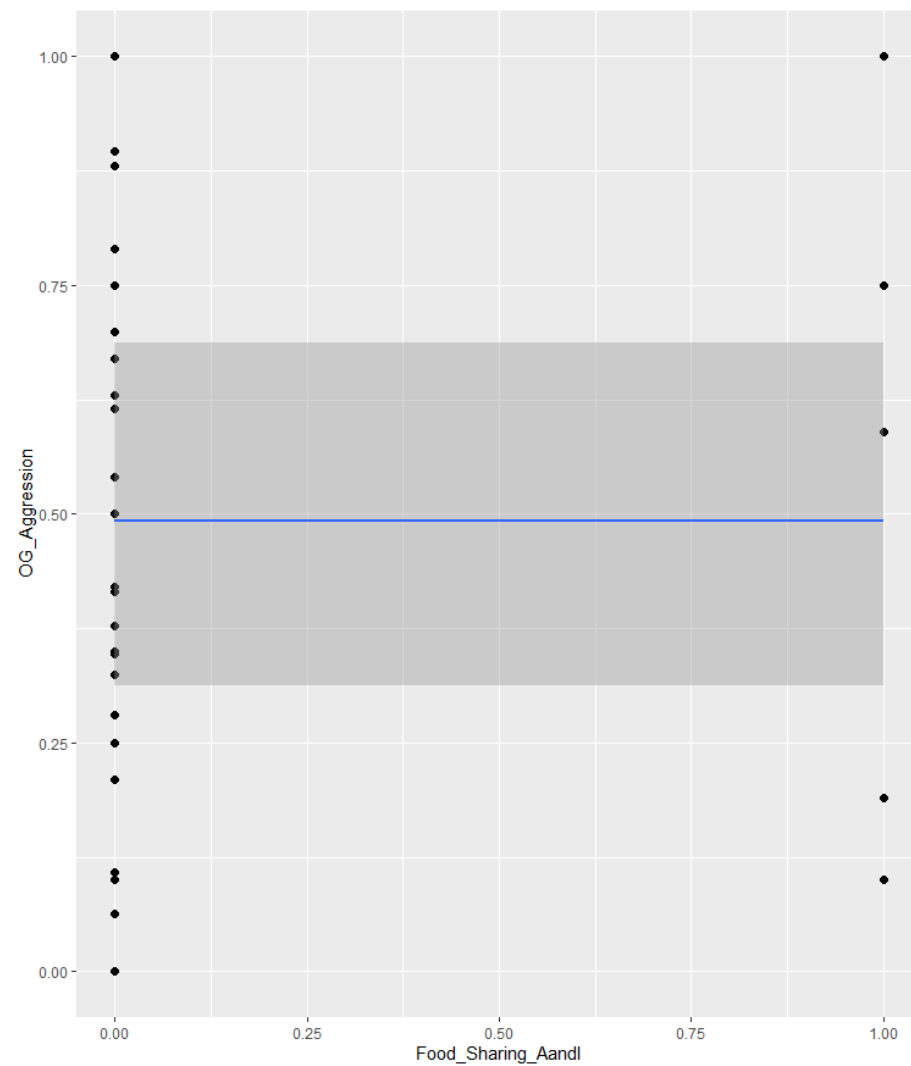
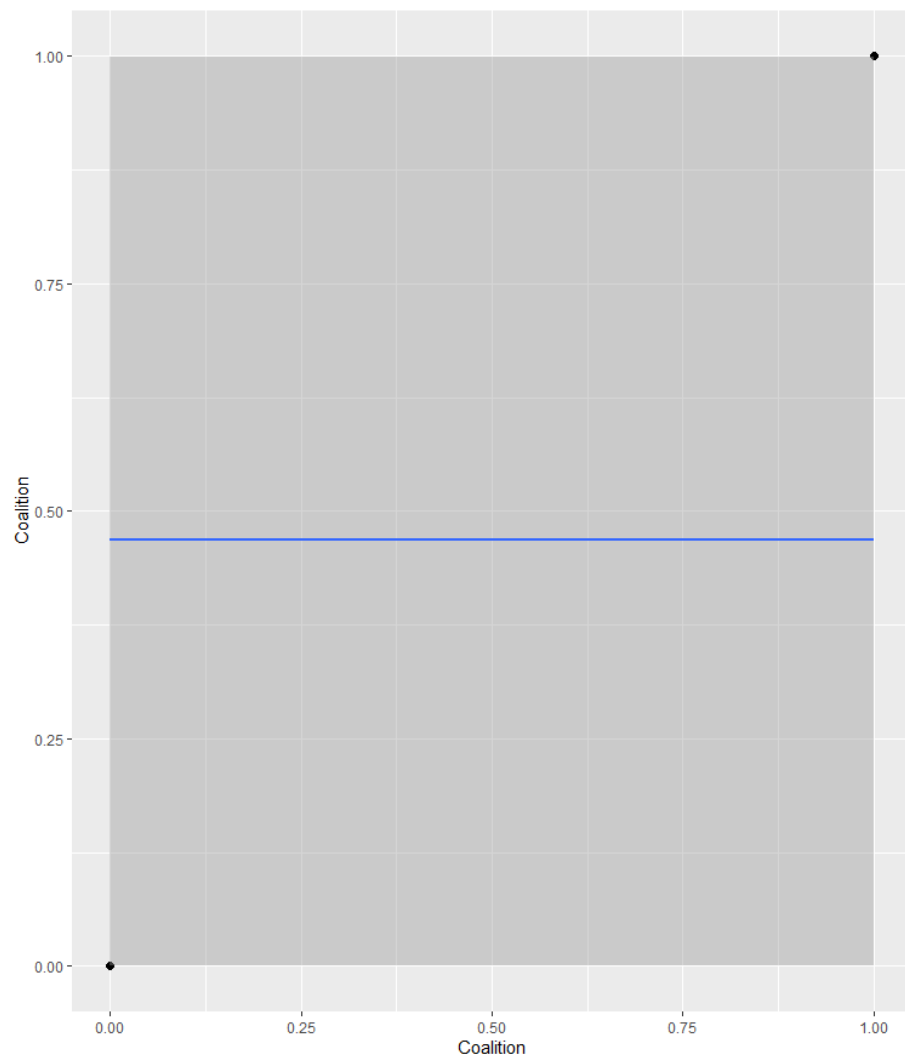
Draws were sampled using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

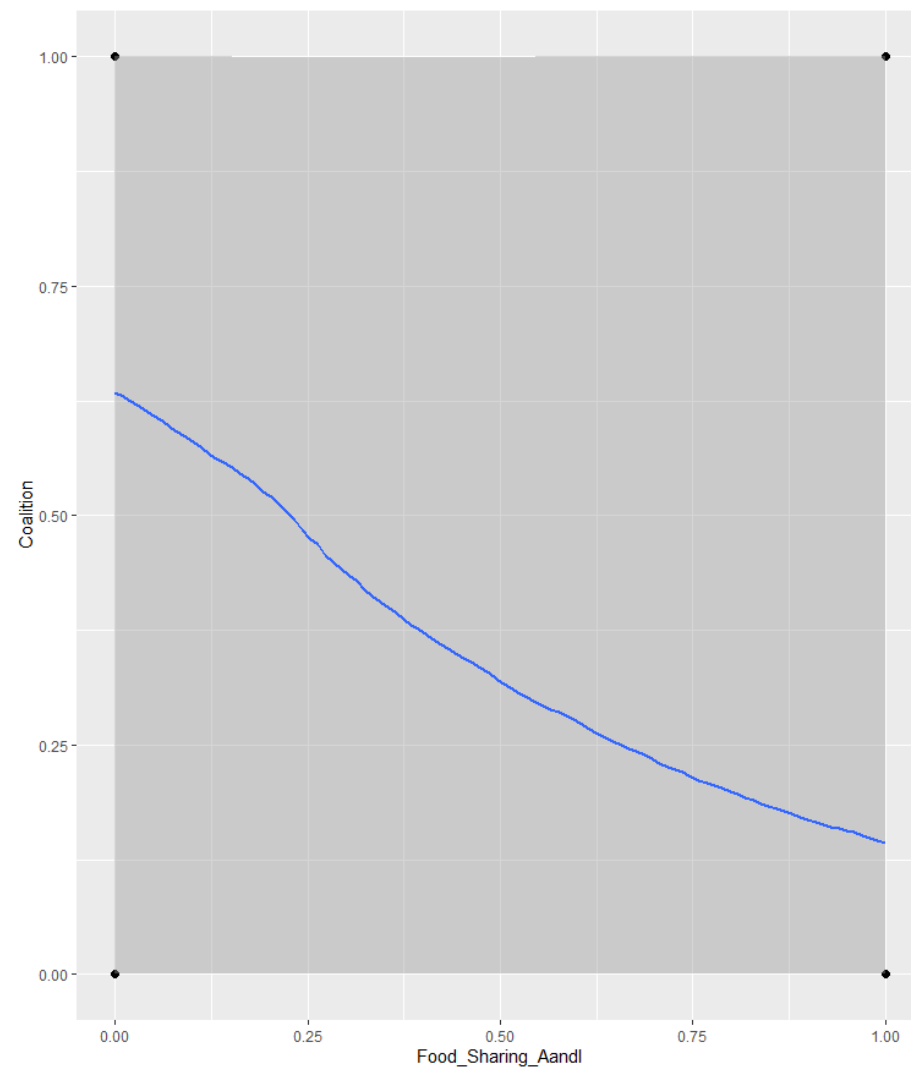
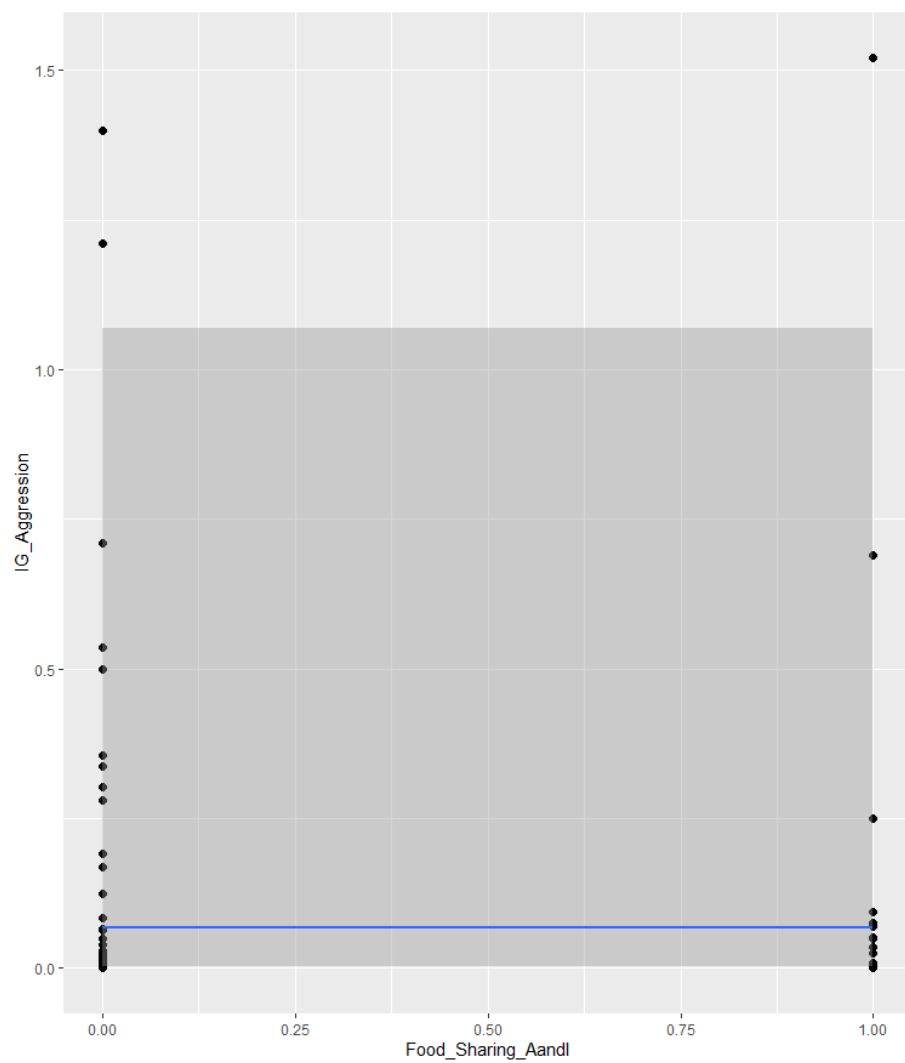
Estimate	Est.Error	Q2.5	Q97.5
----------	-----------	------	-------

R2OAggression	0.05339968	0.04496044	0.001962789	0.1686101
R2IGAggression	0.33269650	0.14376383	0.094249753	0.6195949
R2Coalition	0.87261243	0.11654660	0.559949614	0.9997052

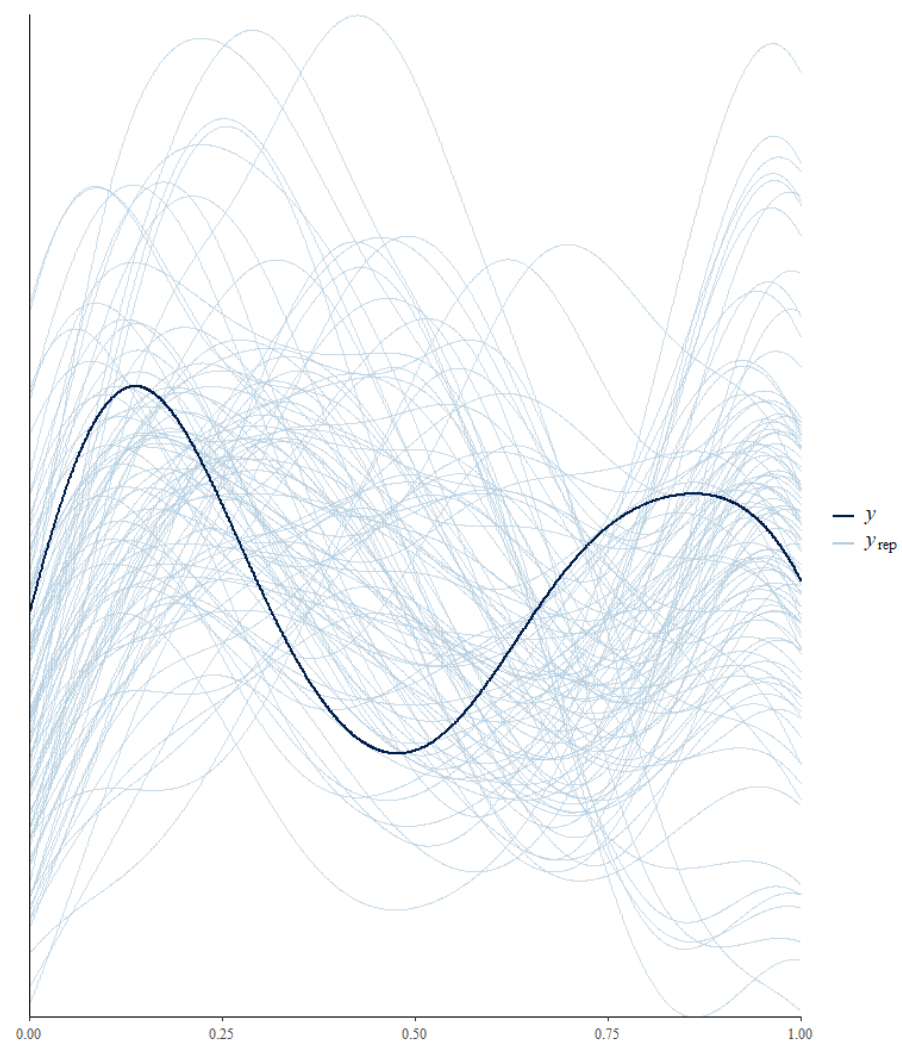
*Plot, Conditional effects, PP checks*



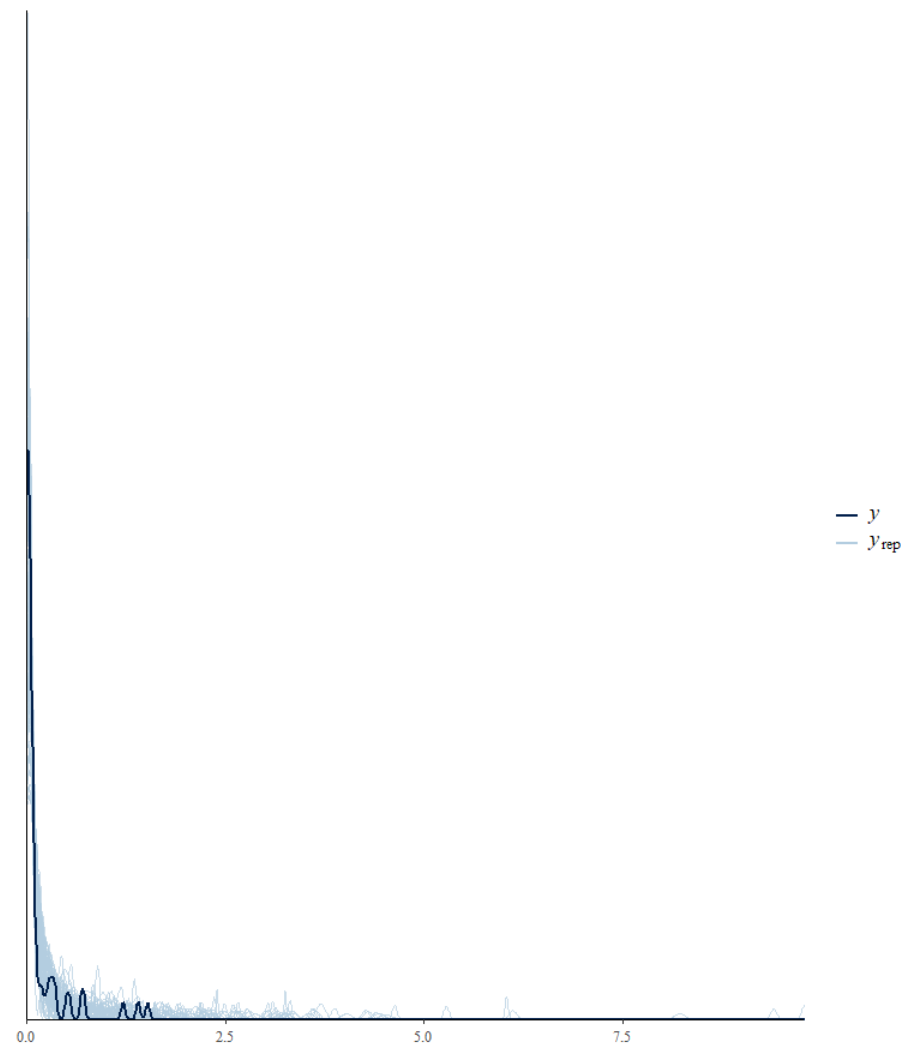




OG Aggression

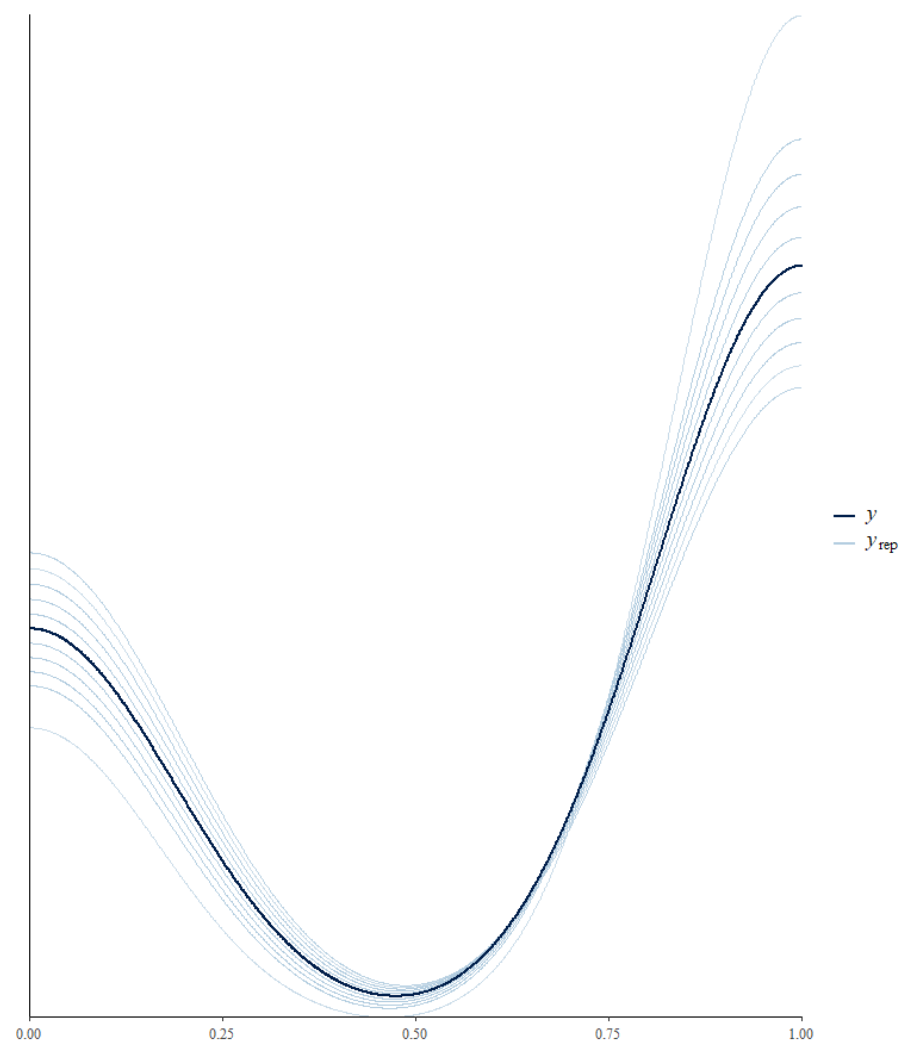


IG Aggression





Coalition



## Appendix 5G – Model D - Grooming correlations with inter and intragroup non-lethal aggression

*5G.1 Model D(i) - Specification and output*

```
brm(mvbind(Intergroup aggression, Intragroup aggression, Grooming) ~ 1+ (1|p|gr(SpeciesTree, cov = A))
```

```
> summary(fitaggA, waic= T); bayes_R2(fitaggA)
```

```
Family: MV(zero_one_inflated_beta, hurdle_gamma, gaussian)
```

```
Links: mu = logit; phi = identity; zoi = identity; coi = identity
```

```
mu = log; shape = identity; hu = identity
```

```
mu = identity; sigma = identity
```

```
Formula: OG_Aggression ~ 1 + (1 | p | gr(SpeciesTree, cov = A))
```

```
IG_Aggression ~ 1 + (1 | p | gr(SpeciesTree, cov = A))
```

```
Grooming ~ 1 + (1 | p | gr(SpeciesTree, cov = A))
```

```
Data: dataG (Number of observations: 68)
```

```
Samples: 4 chains, each with iter = 6000; warmup = 3000; thin = 1; total post-warmup samples = 12000
```

```
Group-Level Effects:
```

```
~SpeciesTree (Number of levels: 68)
```

```
Estimate Est.Error l-95% CI u-95% CI Rhat
```

```
Bulk_ESS Tail_ESS
```

# APPENDICES

sd(OAggression_Intercept)	0.07	0.07	0.00	0.24	1.00
2091 1793					
sd(IGAggression_Intercept)	0.24	0.10	0.10	0.48	1.00
2846 3999					
sd(Grooming_Intercept)	0.01	0.00	0.00	0.01	1.00
2302 4177					
cor(OAggression_Intercept,IGAggression_Intercept)	-0.03	0.47	-0.86	0.83	1.00
2273 4769					
cor(OAggression_Intercept,Grooming_Intercept)	-0.01	0.46	-0.84	0.84	1.00
1848 3500					
cor(IGAggression_Intercept,Grooming_Intercept)	0.37	0.35	-0.35	0.93	1.00
3469 7006					

## Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OAggression_Intercept	-0.48	0.46	-1.51	0.46	1.00	4736	3884
IGAggression_Intercept	-2.37	1.19	-4.87	-0.07	1.00	5912	6481
Grooming_Intercept	0.05	0.04	-0.03	0.13	1.00	6220	5995

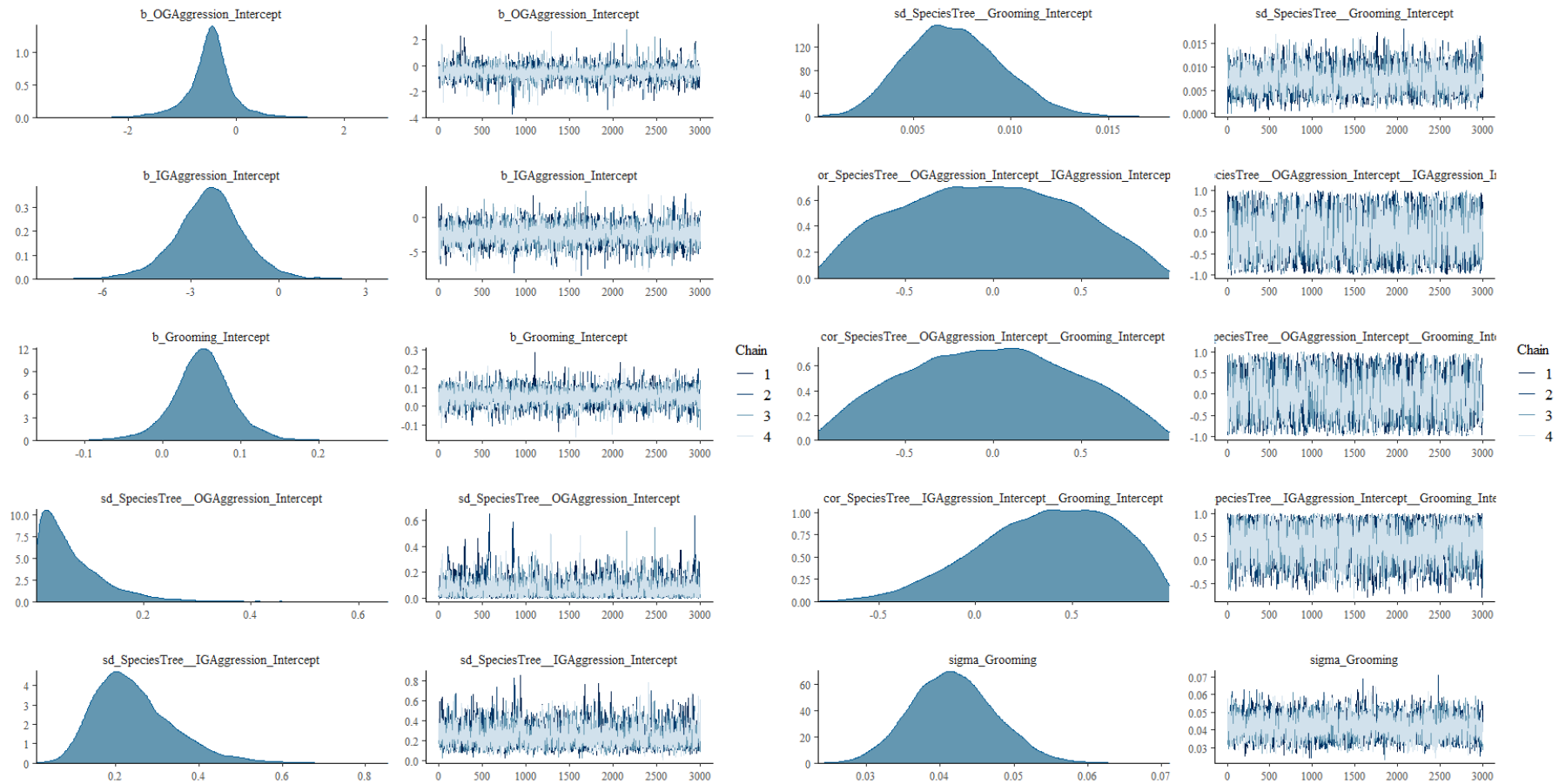
## Family Specific Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
phi_OAggression	2.90	1.05	1.84	4.70	1.00	3257	1857

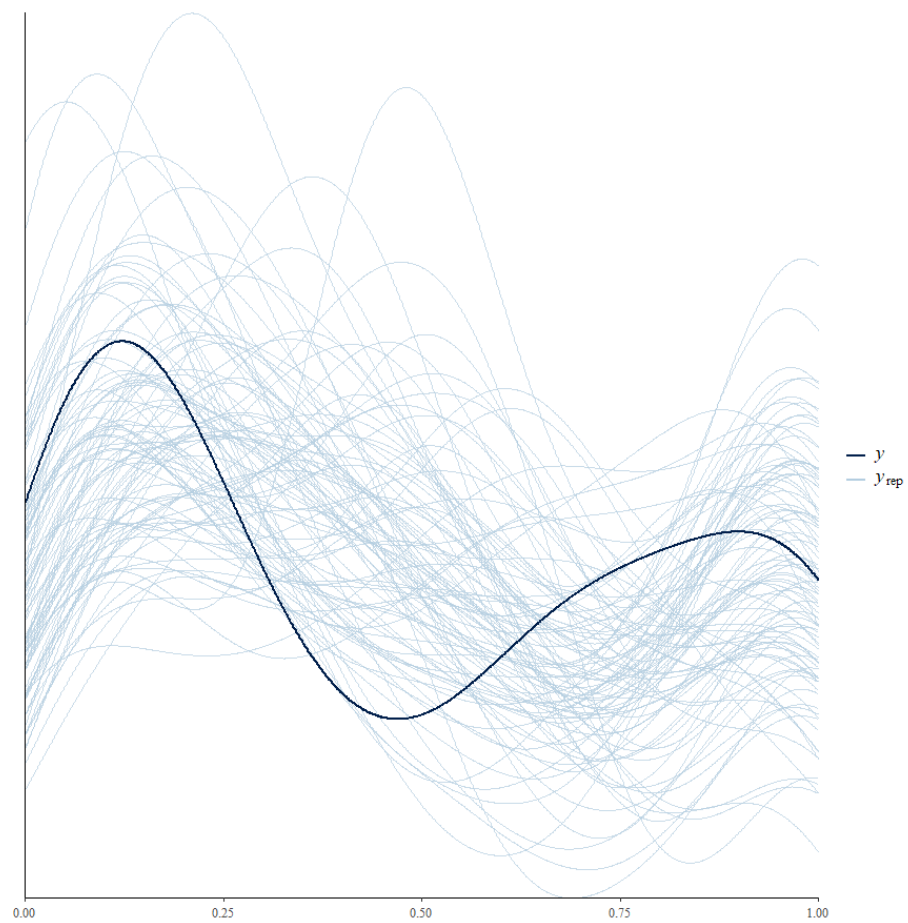
zoi_OGAggression	0.29	0.05	0.19	0.39	1.00	19667	7707
coi_OGAggression	0.71	0.10	0.51	0.88	1.00	18251	7621
shape_IGAggression	0.47	0.09	0.32	0.67	1.00	4962	4771
hu_IGAggression	0.07	0.03	0.02	0.14	1.00	17751	7782
sigma_Grooming	0.04	0.01	0.03	0.05	1.00	2985	5434

Samples were drawn using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

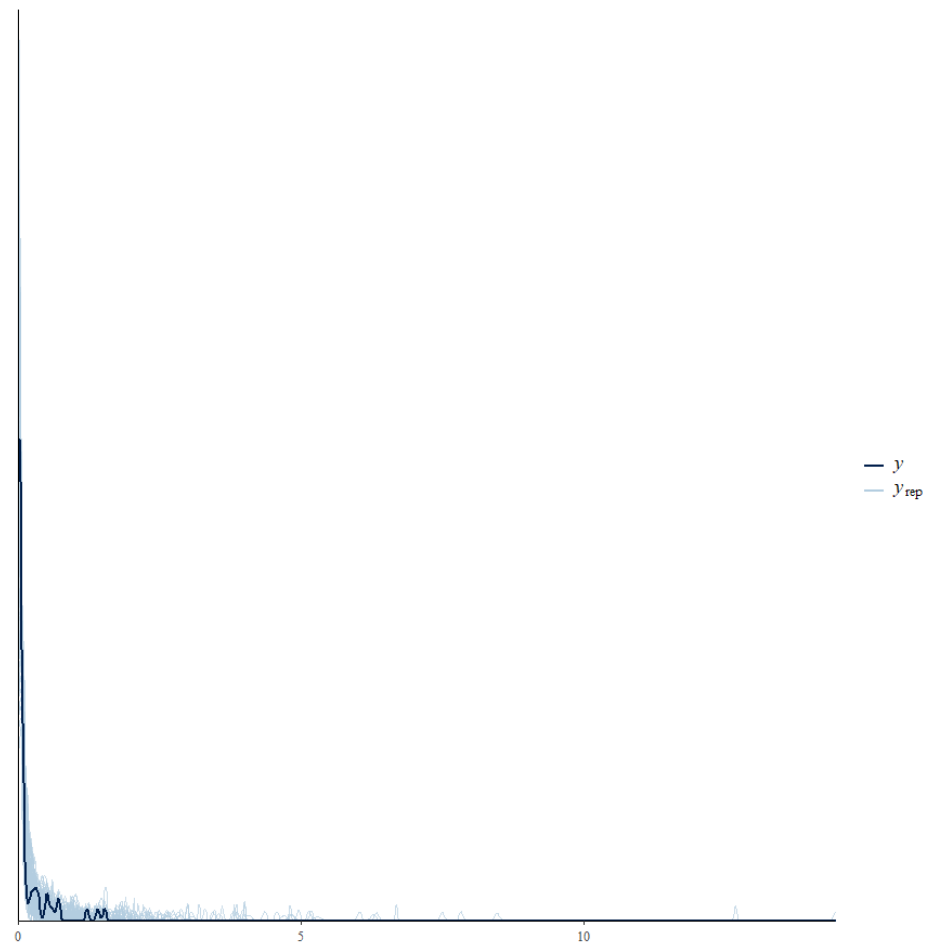
	Estimate	Est.Error	Q2.5	Q97.5
R2OGAggression	0.02411145	0.03609164	2.283764e-05	0.1232872
R2IGAggression	0.32365709	0.16243200	5.494742e-02	0.6295655
R2Grooming	0.37300781	0.14159526	8.871933e-02	0.6271526

*Plots, Conditional effects, PP checks*

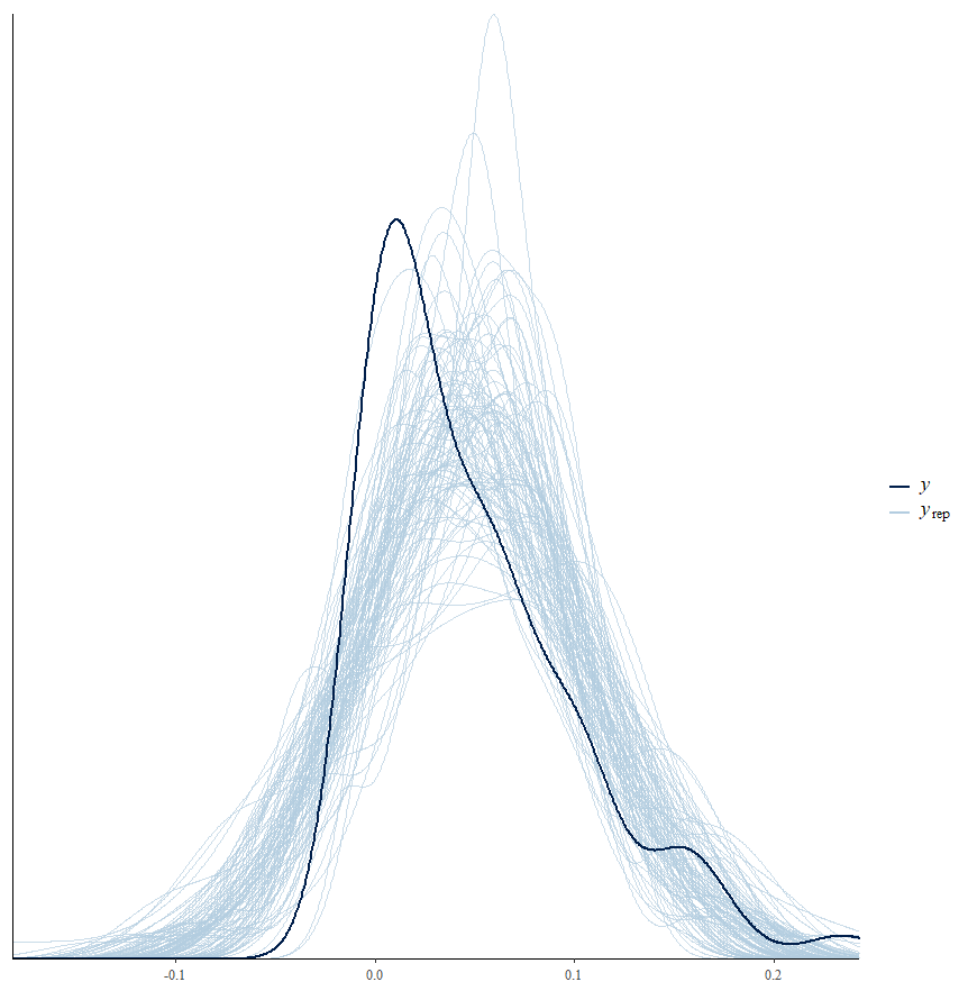
Intergroup aggression



Intragroup aggression



## Grooming



## Appendix 5H – Model E – Using the ‘Time-social’ variable

*5H.1 Model E(i) Specification and output for time-social and intergroup lethal aggression and infanticide*

```
> summary(fitsocialA, waic= T); bayes_R2(fitsocialA)
Family:  MV(bernoulli, bernoulli)
Links:   mu = logit
         mu = logit
Formula:  OG_Killing ~ Time_Social + (1 | p | gr(SpeciesTree, cov = A))
          Infanticide ~ Time_Social + (1 | p | gr(SpeciesTree, cov = A))
Data:     dataF (Number of observations: 77)
Draws:    4 chains, each with iter = 9000; warmup = 4500; thin = 1; total post-warmup draws = 18000
```

## Group-Level Effects:

```
~SpeciesTree (Number of levels: 77)
```

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat
Bulk_ESS Tail_ESS					
sd(OGKilling_Intercept)	0.87	1.41	0.03	4.12	1.00
1505 4414					
sd(Infanticide_Intercept)	0.32	0.42	0.01	1.18	1.00
2344 2824					



```

cor(OGKilling_Intercept,Infanticide_Intercept)    0.53    0.44    -0.66    0.98 1.00
4310      6375

```

## Population-Level Effects:

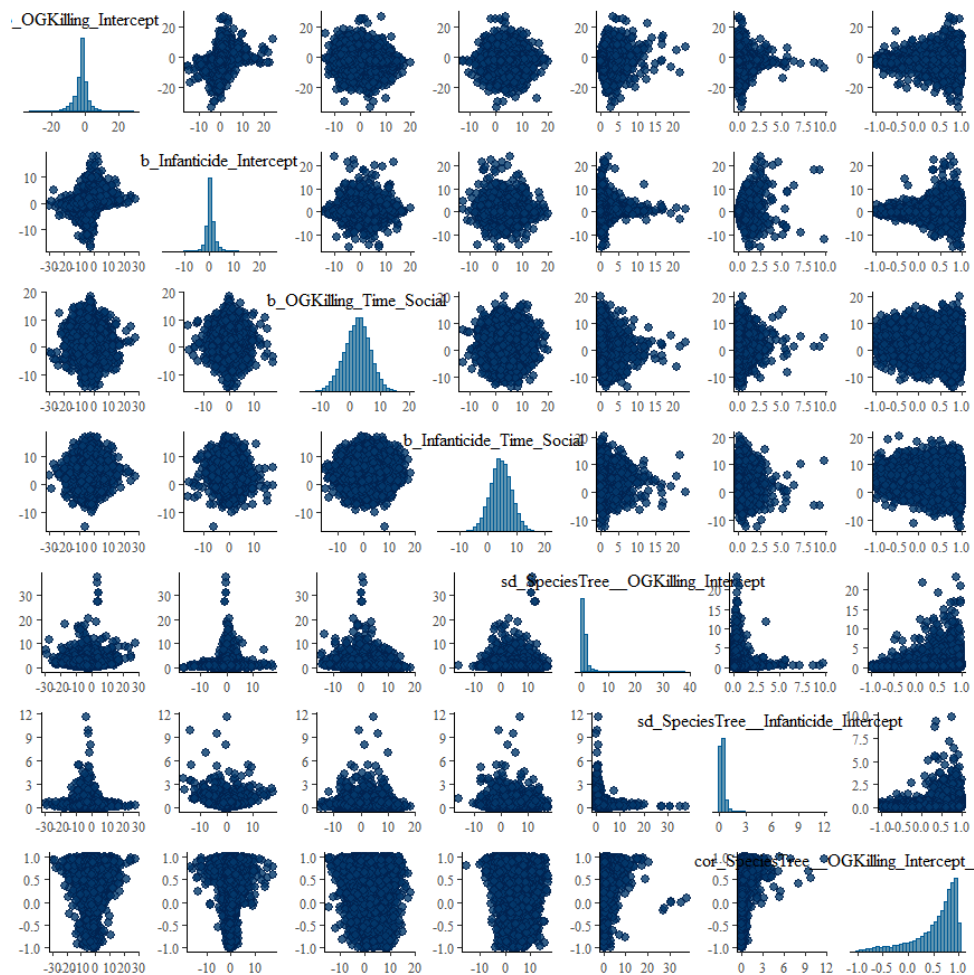
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
OGKilling_Intercept	-2.50	3.94	-11.48	5.50	1.00	8206	6465
Infanticide_Intercept	0.23	2.03	-3.41	4.47	1.00	7978	5411
OGKilling_Time_Social	2.17	4.40	-6.84	10.54	1.00	14899	11782
Infanticide_Time_Social	4.41	3.77	-3.07	11.78	1.00	30971	12149

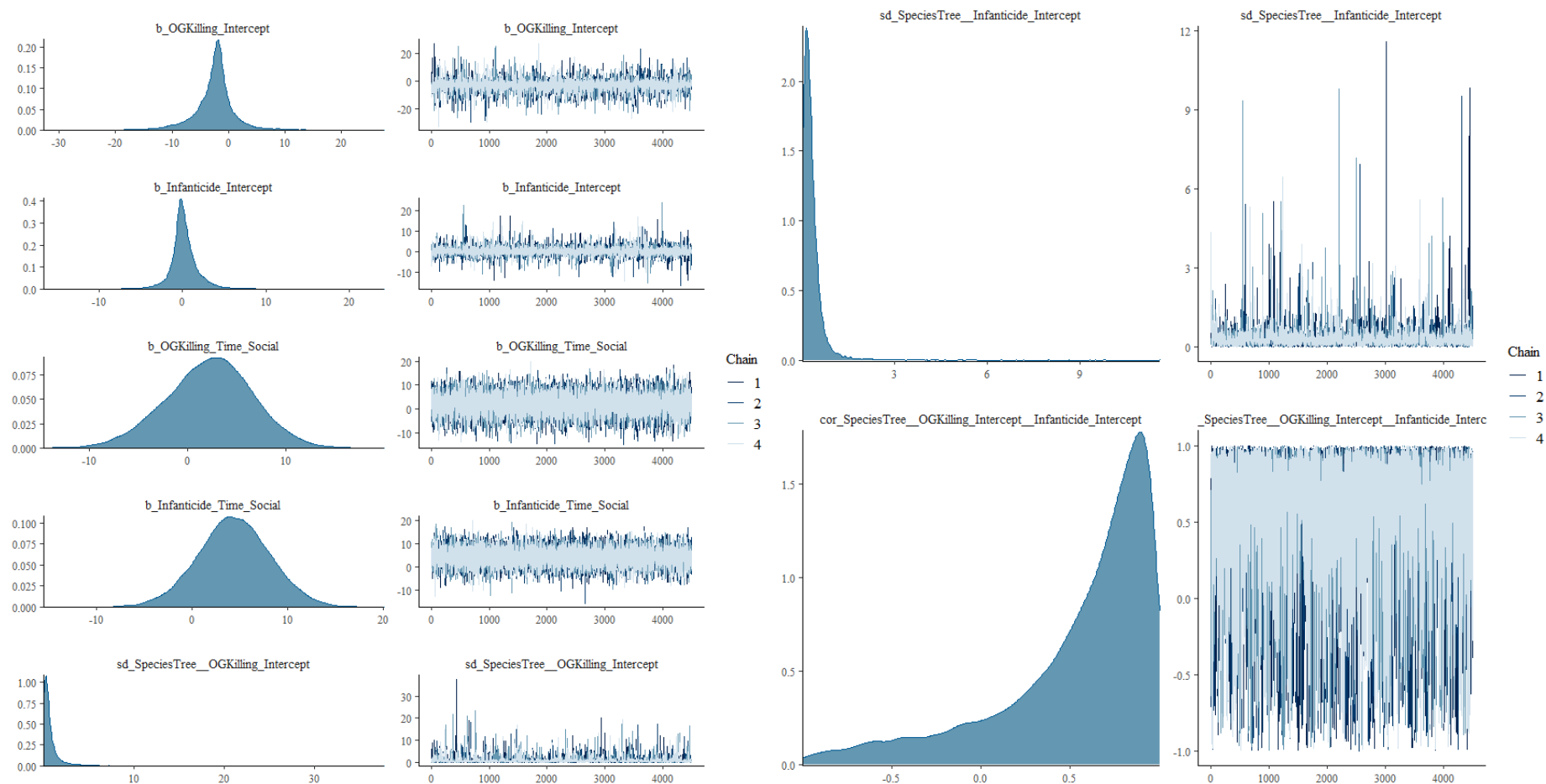
Draws were sampled using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

	Estimate	Est.Error	Q2.5	Q97.5
R2OGKilling	0.3258821	0.2183526	0.01649016	0.8299094
R2Infanticide	0.1893587	0.1401935	0.01154136	0.5449356

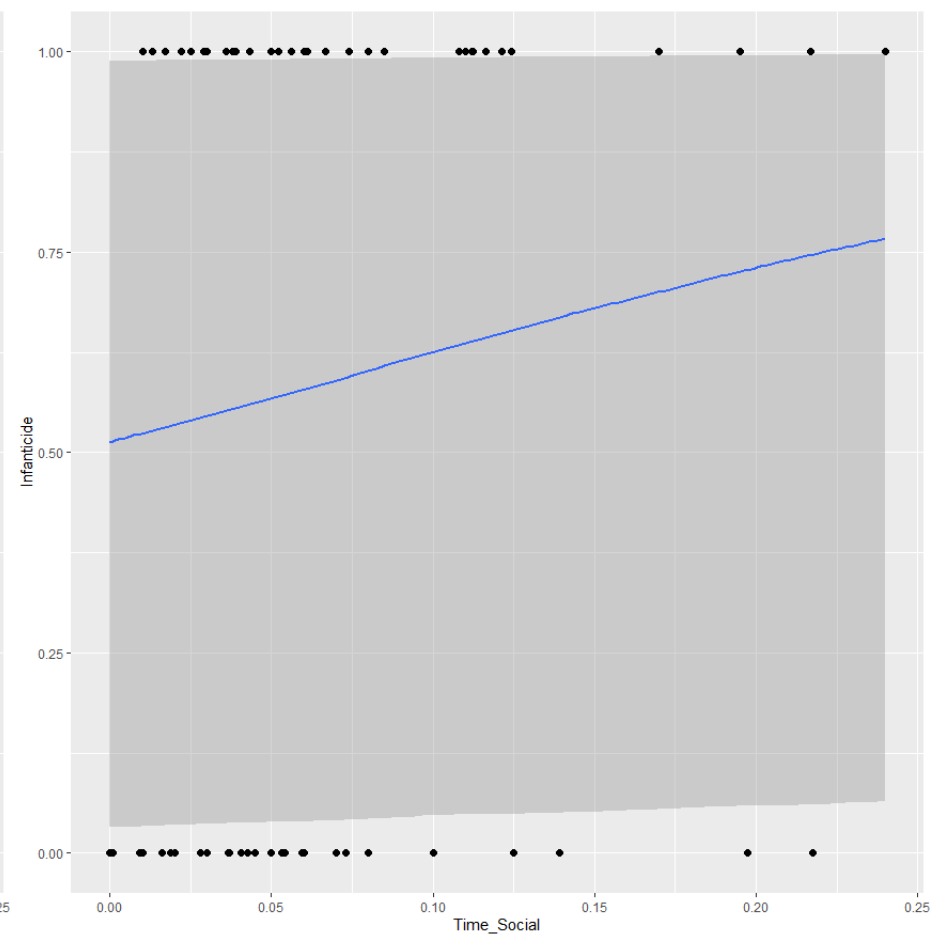
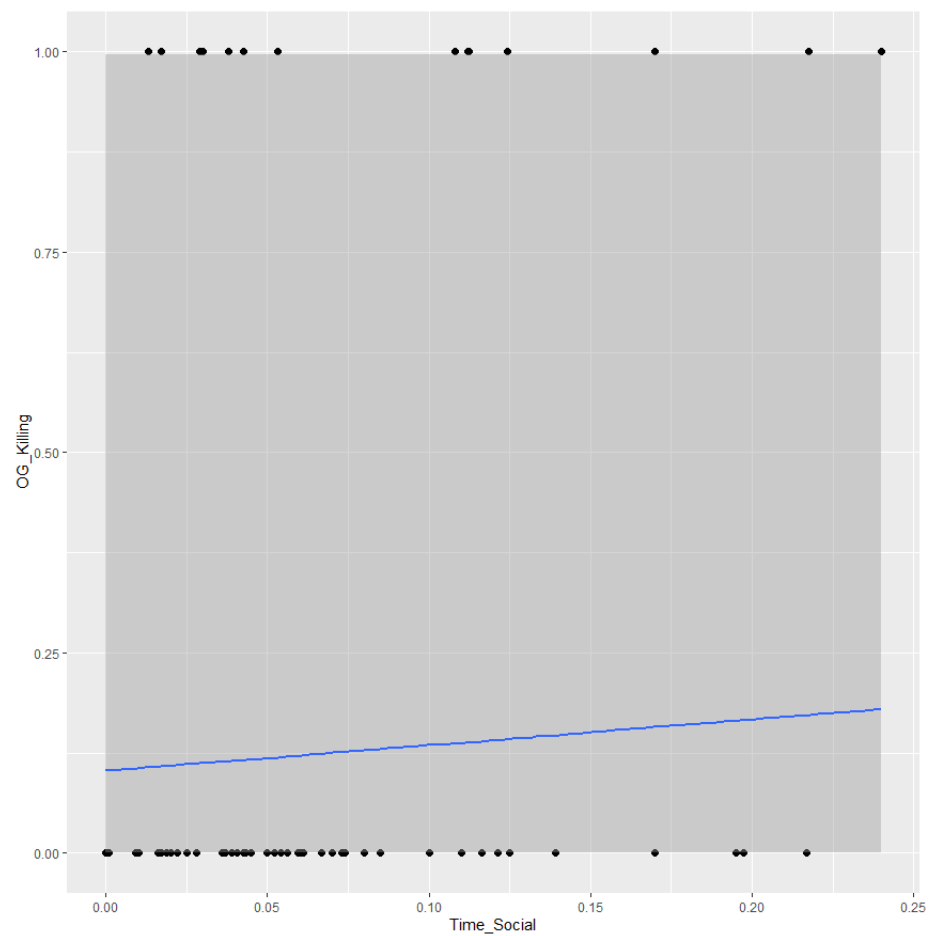
*Plots, Conditional effects, PP checks*

Pairs plot

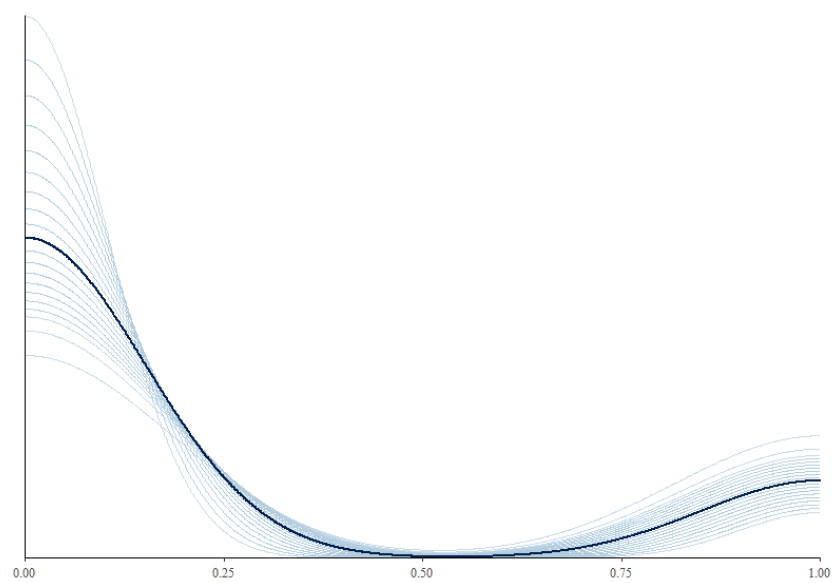




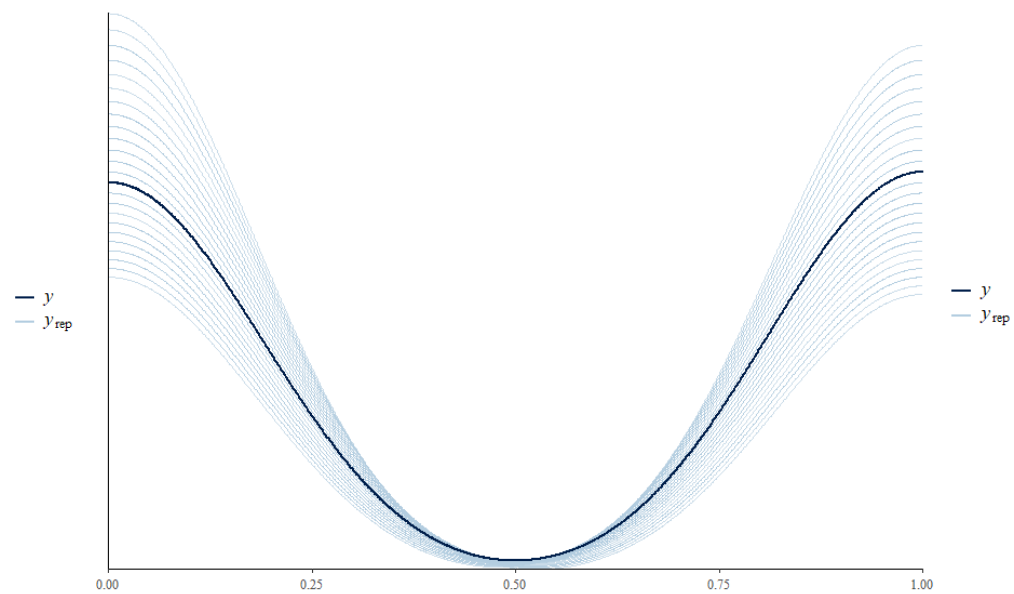
## Conditional plots



PP check – OG Killing



PP check – Infanticide



*5H.2 Model E(ii) Specification and output for time-social and intergroup aggression (non-lethal)*

```
> summary(fitsocial, waic= T); bayes_R2(fitsocial)
```

```
Family:  zero_one_inflated_beta
```

```
Links:  mu = logit; phi = identity; zoi = identity; coi = identity
```

```
Formula:  OG_Aggression ~ Time_Social + (1 | p | gr(SpeciesTree, cov = A))
```

```
Data:  dataF (Number of observations: 77)
```

```
Draws:  4 chains, each with iter = 7000; warmup = 3500; thin = 1; total post-warmup draws =
14000
```

Group-Level Effects:

```
~SpeciesTree (Number of levels: 77)
```

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
sd(Intercept)	0.08	0.06	0.00	0.23	1.00	2524	4265

Population-Level Effects:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	-0.78	0.52	-1.91	0.28	1.00	7066	5324
Time_Social	4.03	2.91	-1.76	9.74	1.00	16236	10342

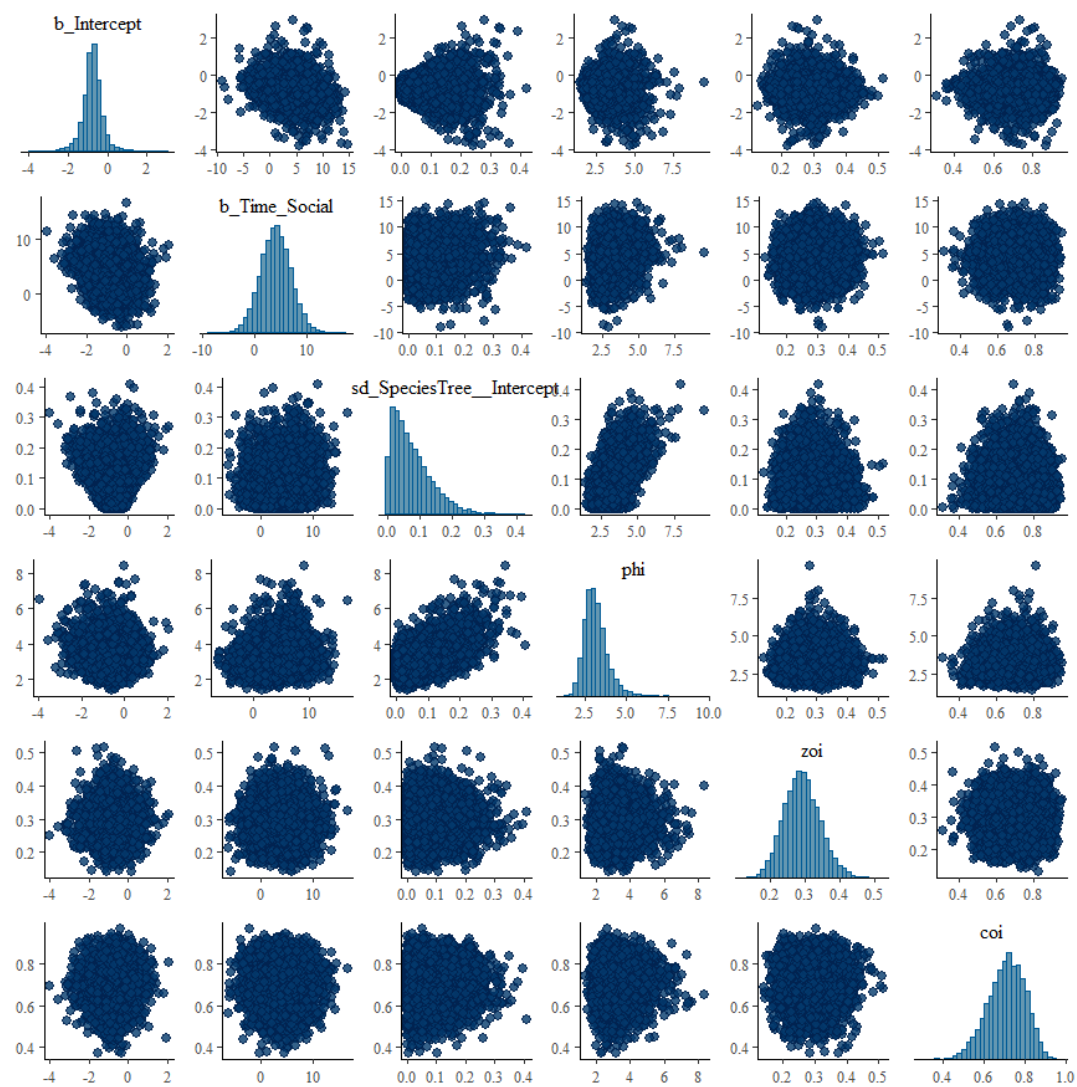
## Family Specific Parameters:

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
phi	3.15	0.72	2.04	4.88	1.00	5537	6168
zoi	0.29	0.05	0.20	0.40	1.00	21900	9615
coi	0.71	0.09	0.52	0.87	1.00	22757	9125

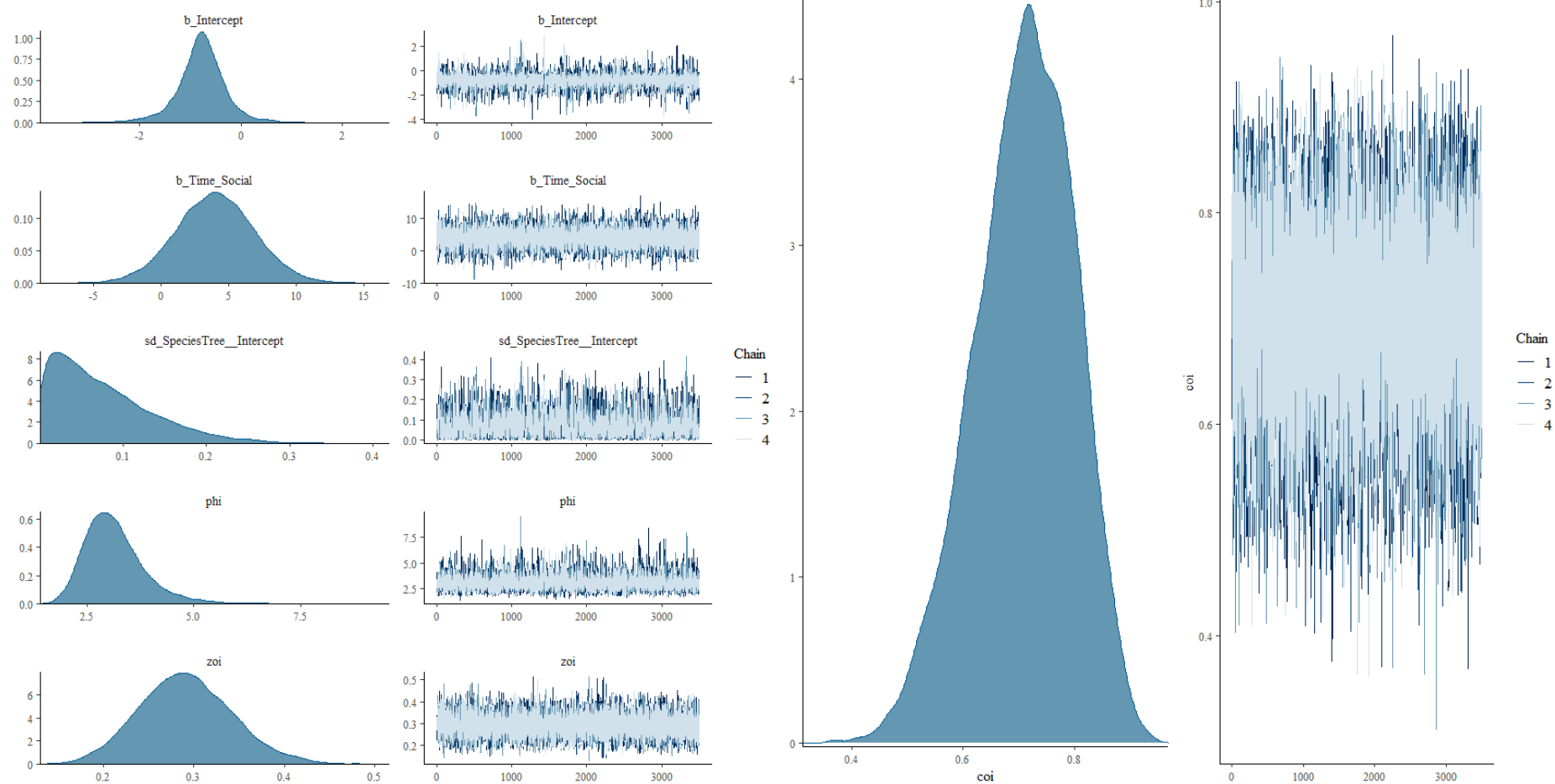
Draws were sampled using sampling(NUTS). For each parameter, Bulk\_ESS and Tail\_ESS are effective sample size measures, and Rhat is the potential scale reduction factor on split chains (at convergence, Rhat = 1).

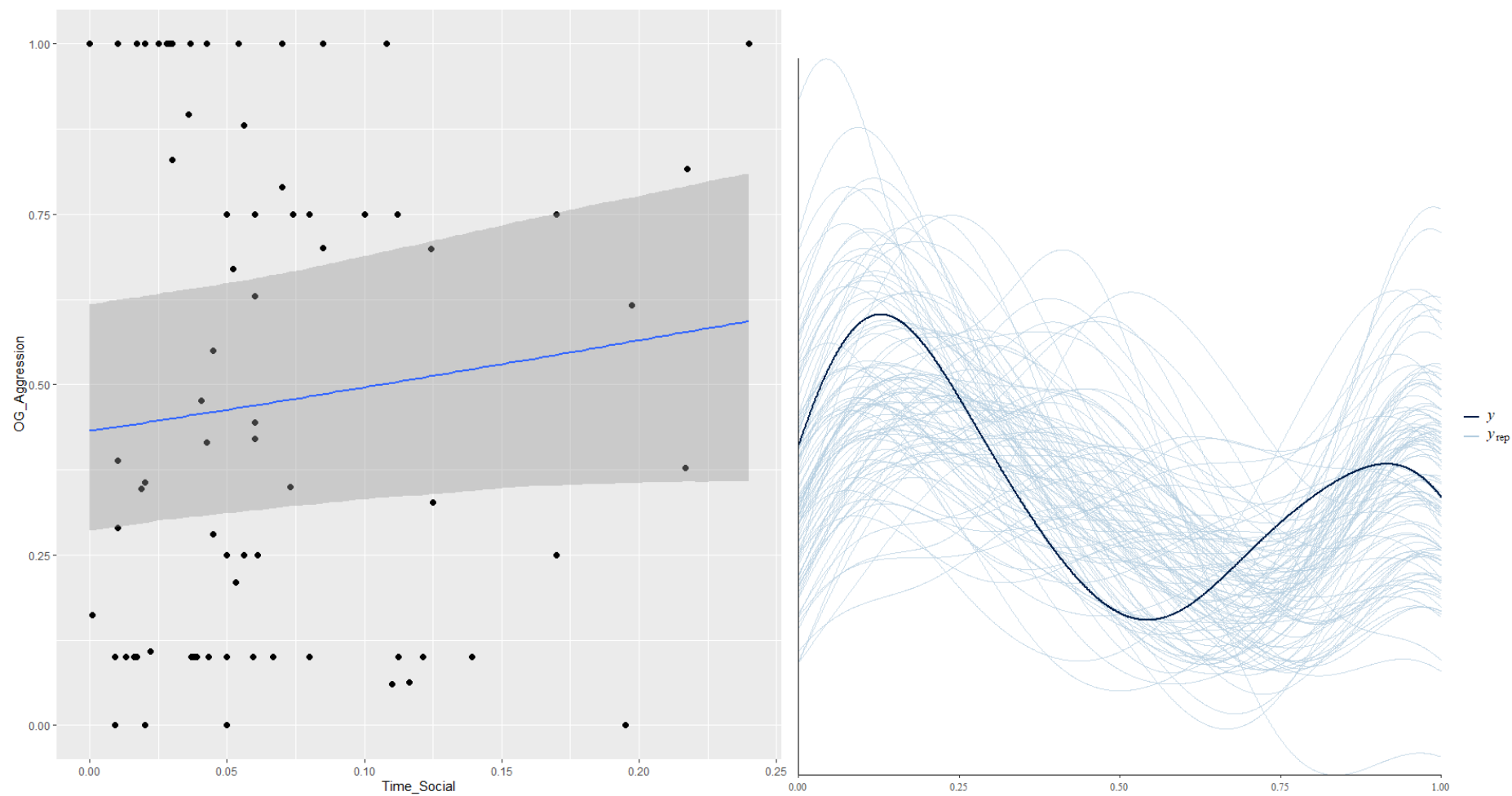
	Estimate	Est.Error	Q2.5	Q97.5
R2	0.03945624	0.03320922	0.001856556	0.1278605

*Plots, Conditional effects, PP checks*









## Appendix 5I – Model F - Mixed model for lethal aggression

*5I.1 Model F(i) Specification and output*

```

> summary(fitMixed1, waic= T); bayes_R2(fitMixed1)
Family: MV(bernoulli, bernoulli, bernoulli)
Links: mu = logit
       mu = logit
       mu = logit
Formula: IG_Killing ~ Grooming + Food_Sharing_AandI + Coalition + (1 | p | gr(SpeciesTree, cov =
A))
        OG_Killing ~ Grooming + Food_Sharing_AandI + Coalition + (1 | p | gr(SpeciesTree, cov =
A))
        Infanticide ~ Grooming + Food_Sharing_AandI + Coalition + (1 | p | gr(SpeciesTree, cov
= A))
Data: dataA (Number of observations: 46)
Draws: 4 chains, each with iter = 6000; warmup = 3000; thin = 1;
       total post-warmup draws = 12000

Group-Level Effects:
~SpeciesTree (Number of levels: 46)

```

	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat
Bulk_ESS Tail_ESS					
sd(IGKilling_Intercept) 697 1914	1.02	1.17	0.02	4.04	1.00
sd(OGKilling_Intercept) 786 2194	2.05	2.94	0.04	9.85	1.01
sd(Infanticide_Intercept) 2963 2019	4.40	4.07	0.50	14.45	1.00
cor(IGKilling_Intercept,OGKilling_Intercept) 1526 1597	0.43	0.39	-0.56	0.95	1.00
cor(IGKilling_Intercept,Infanticide_Intercept) 944 1329	0.31	0.37	-0.50	0.90	1.00
cor(OGKilling_Intercept,Infanticide_Intercept) 1638 1774	0.43	0.32	-0.34	0.91	1.00

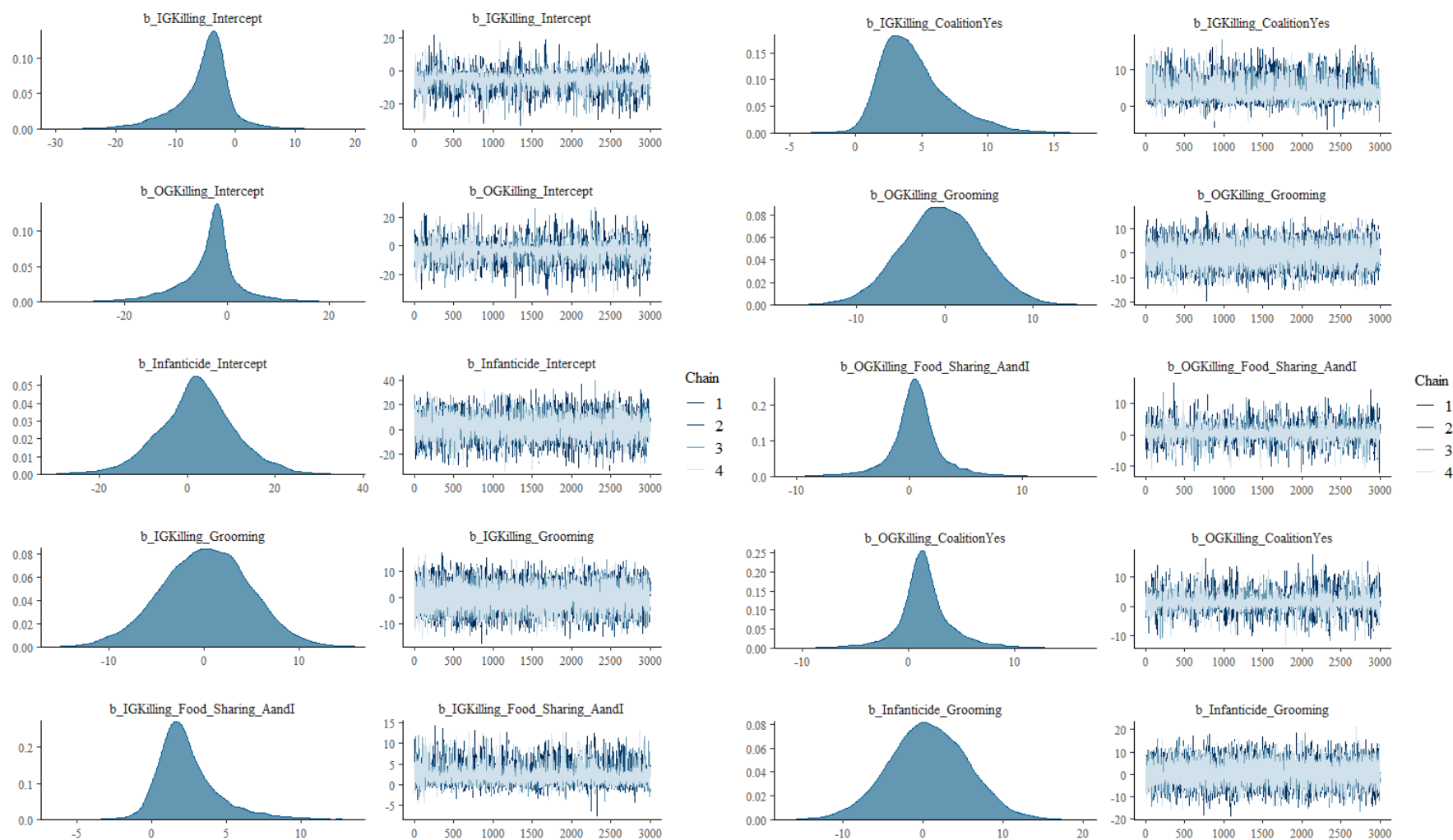
## Population-Level Effects:

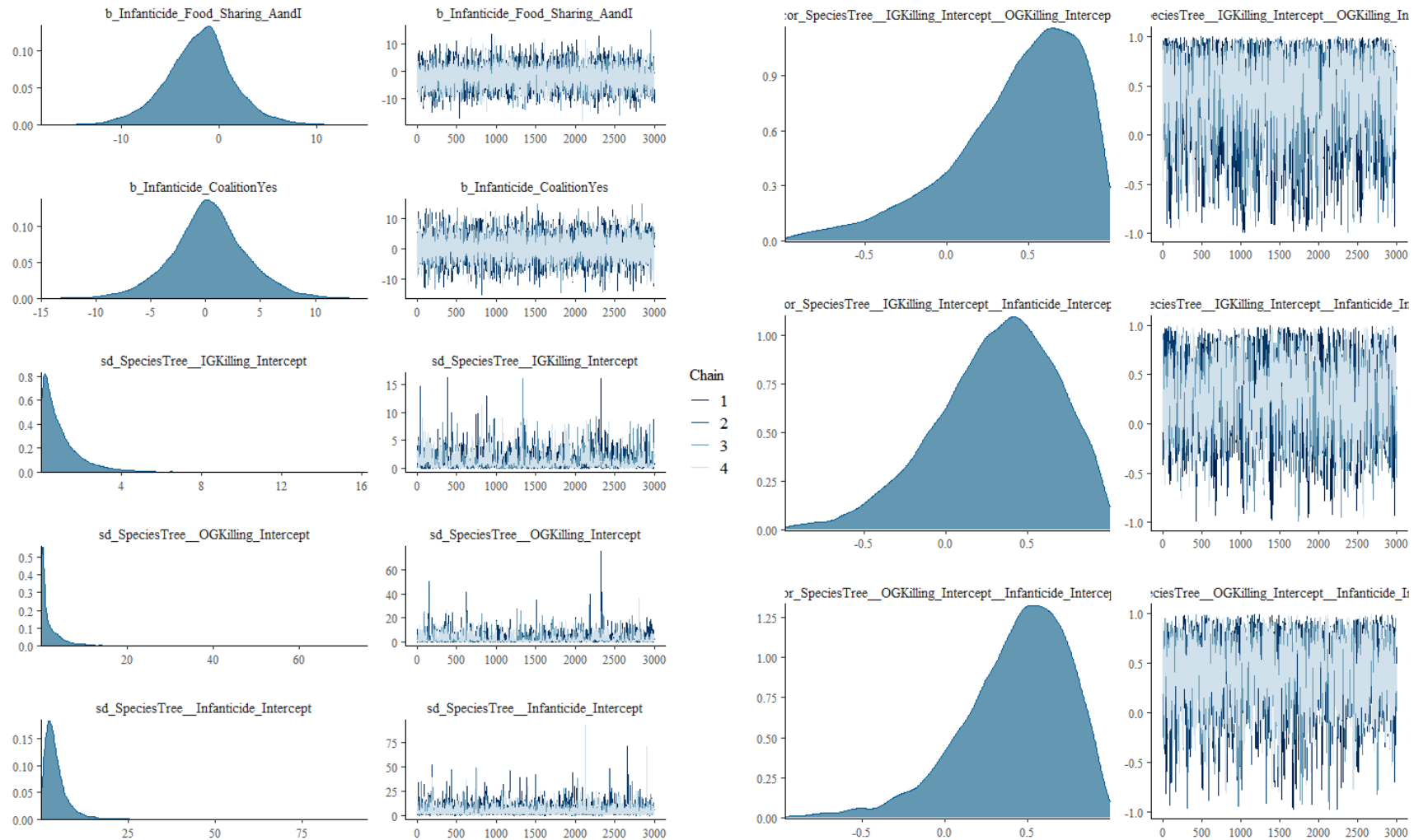
	Estimate	Est.Error	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
IGKilling_Intercept	-5.36	4.82	-17.08	3.14	1.00	3849	3616
OGKilling_Intercept	-3.37	5.86	-16.99	8.75	1.00	4841	3785
Infanticide_Intercept	2.18	8.69	-15.54	19.91	1.00	8551	8659
IGKilling_Grooming	0.17	4.60	-9.02	9.00	1.00	14009	8899
IGKilling_Food_Sharing_AandI	2.41	2.07	-0.62	7.75	1.00	3485	4170

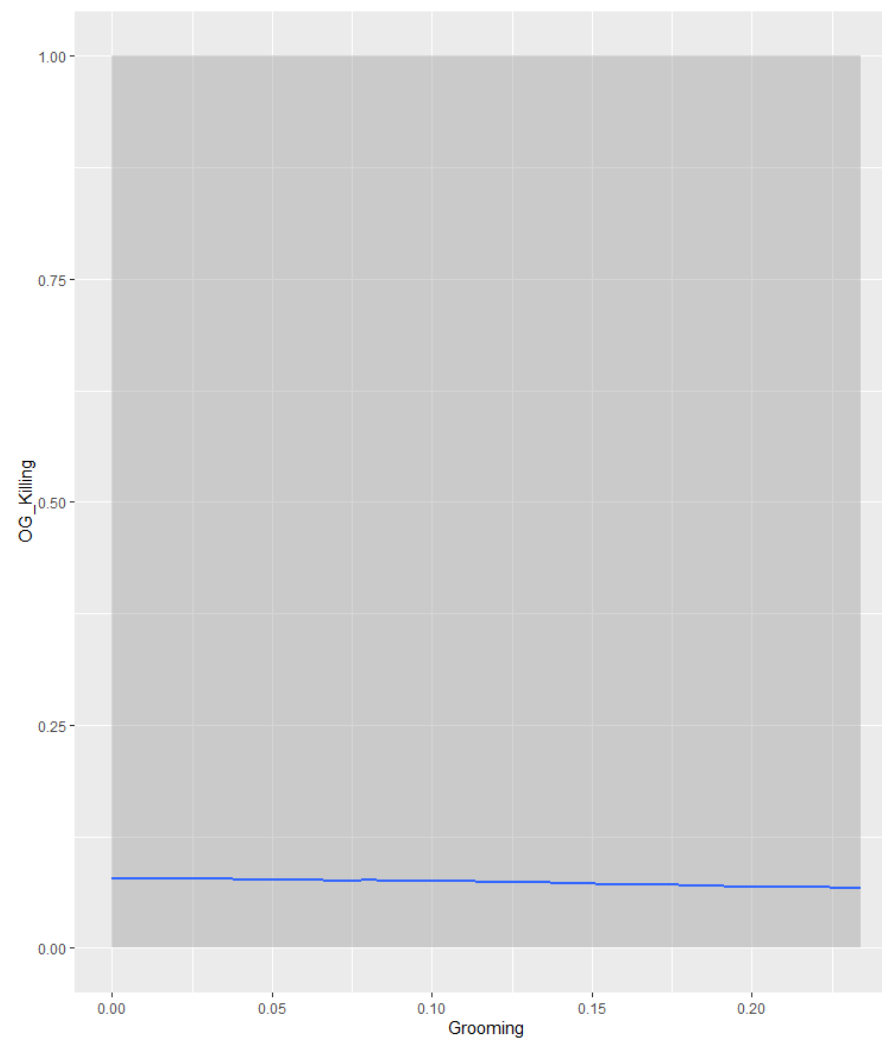
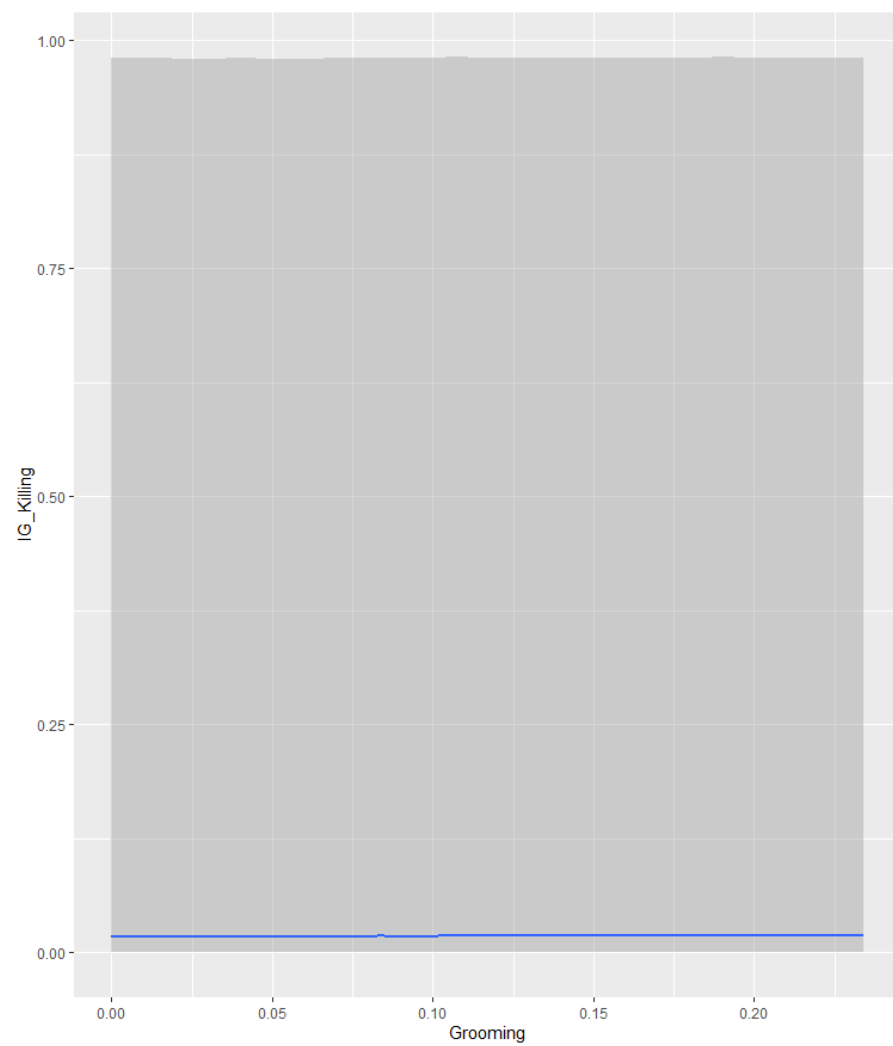
IGKilling_CoalitionYes	4.48	2.67	0.61	10.89	1.00	3193	4584
OGKilling_Grooming	-0.43	4.50	-9.29	8.35	1.00	16134	8283
OGKilling_Food_Sharing_AandI	0.52	2.32	-4.63	5.55	1.00	5783	3496
OGKilling_CoalitionYes	1.52	2.61	-3.92	7.64	1.00	6195	3971
Infanticide_Grooming	0.67	4.91	-9.03	10.21	1.00	15361	8595
Infanticide_Food_Sharing_AandI	-2.02	3.51	-9.28	5.18	1.00	8783	7143
Infanticide_CoalitionYes	0.29	3.51	-6.92	7.39	1.00	8753	7638

Draws were sampled using `sampling(NUTS)`. For each parameter, `Bulk_ESS` and `Tail_ESS` are effective sample size measures, and `Rhat` is the potential scale reduction factor on split chains (at convergence, `Rhat` = 1).

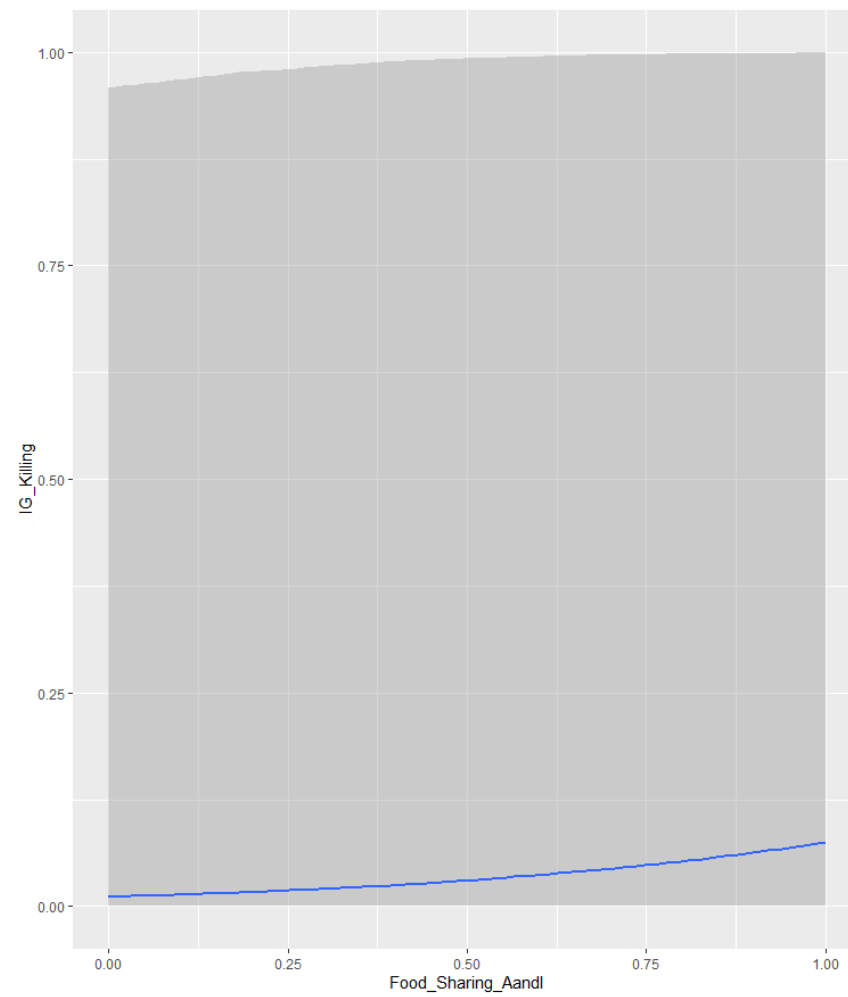
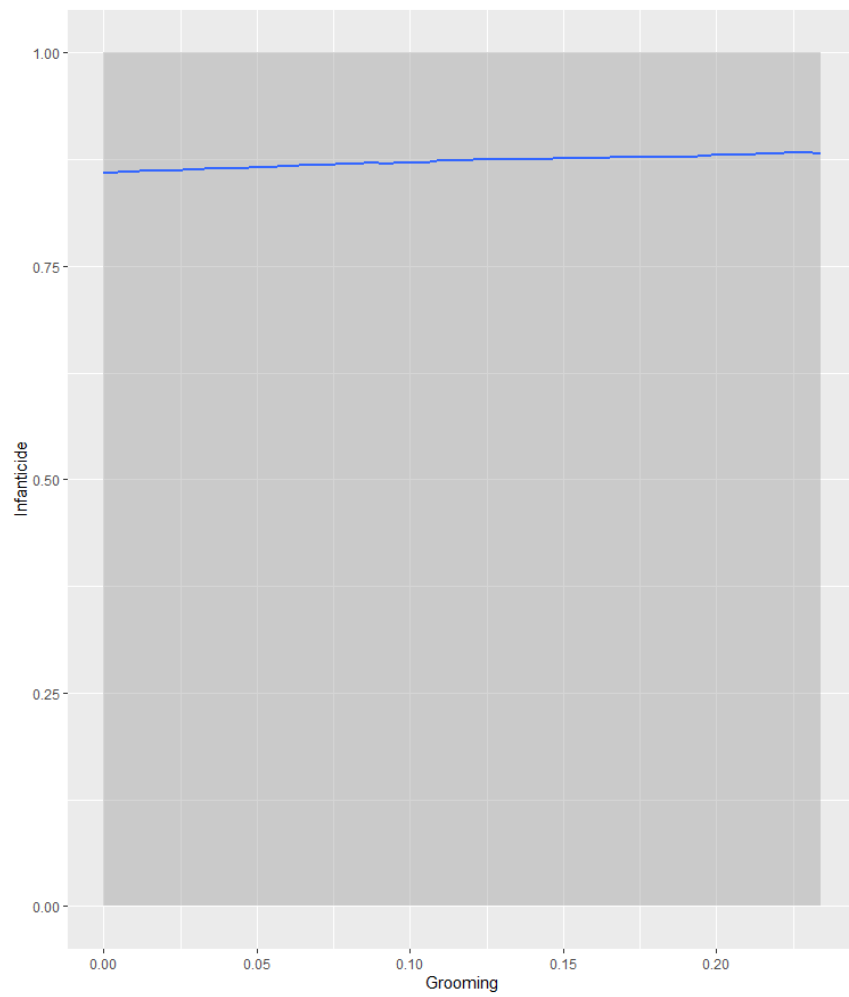
	Estimate	Est.Error	Q2.5	Q97.5
R2IGKilling	0.4930946	0.2044592	0.15535811	0.8948952
R2OGKilling	0.4980963	0.2715908	0.07178065	0.9682309
R2Infanticide	0.7969213	0.1652893	0.35545560	0.9958181

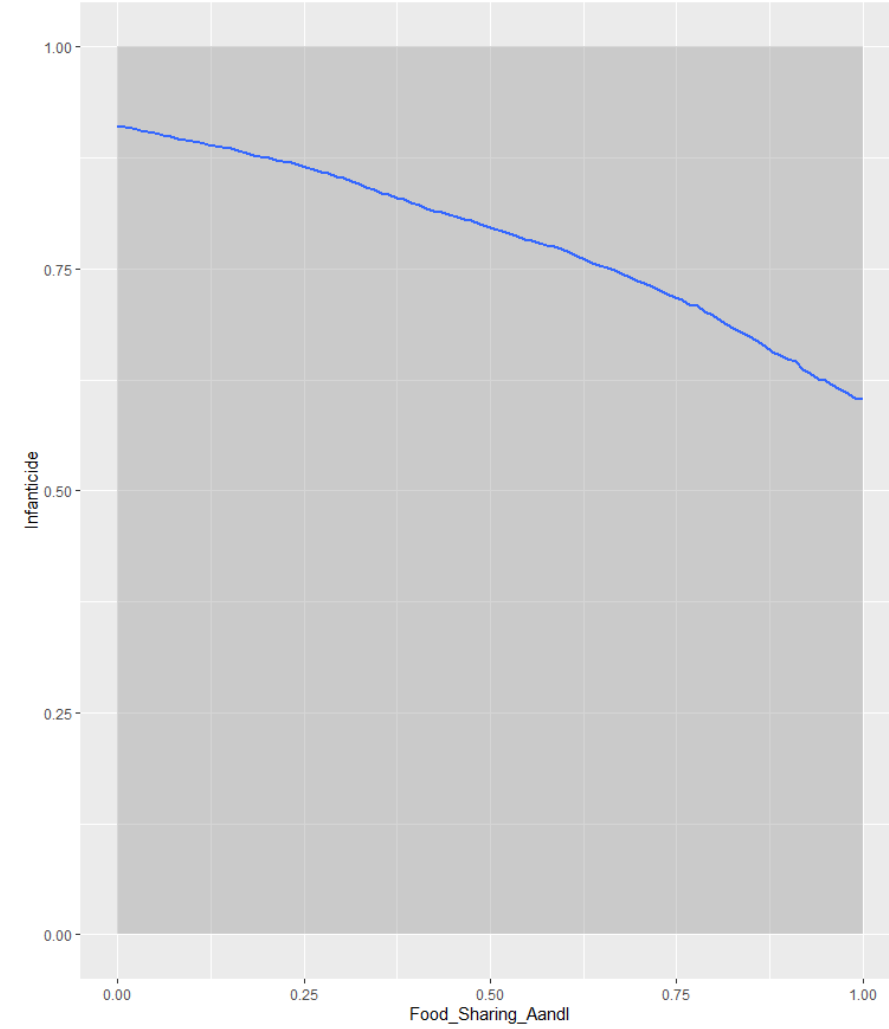
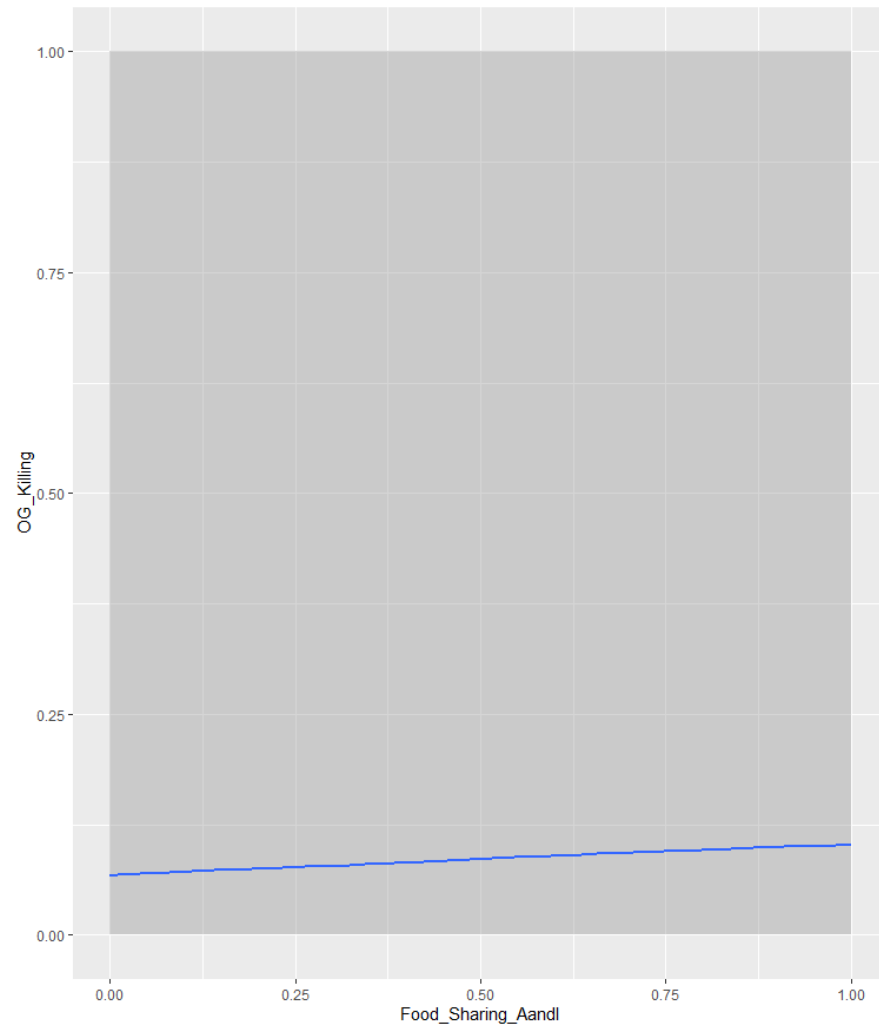
*Plots, Conditional effects, PP checks*

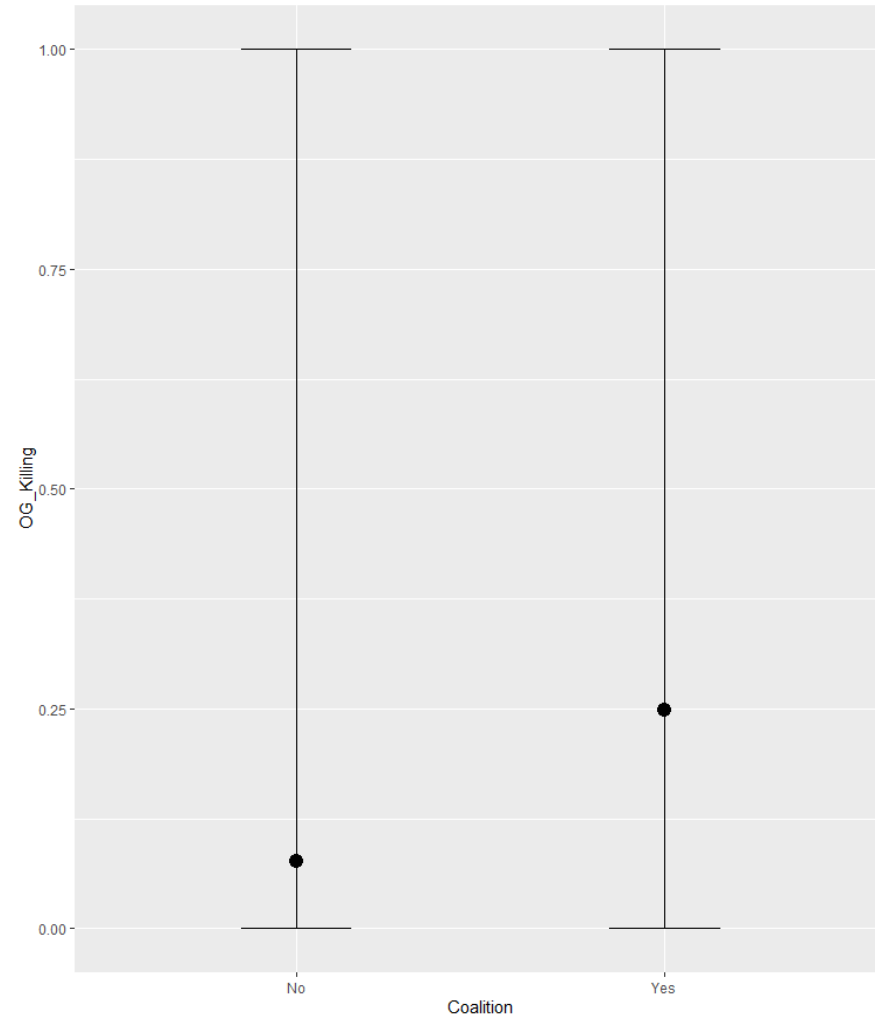
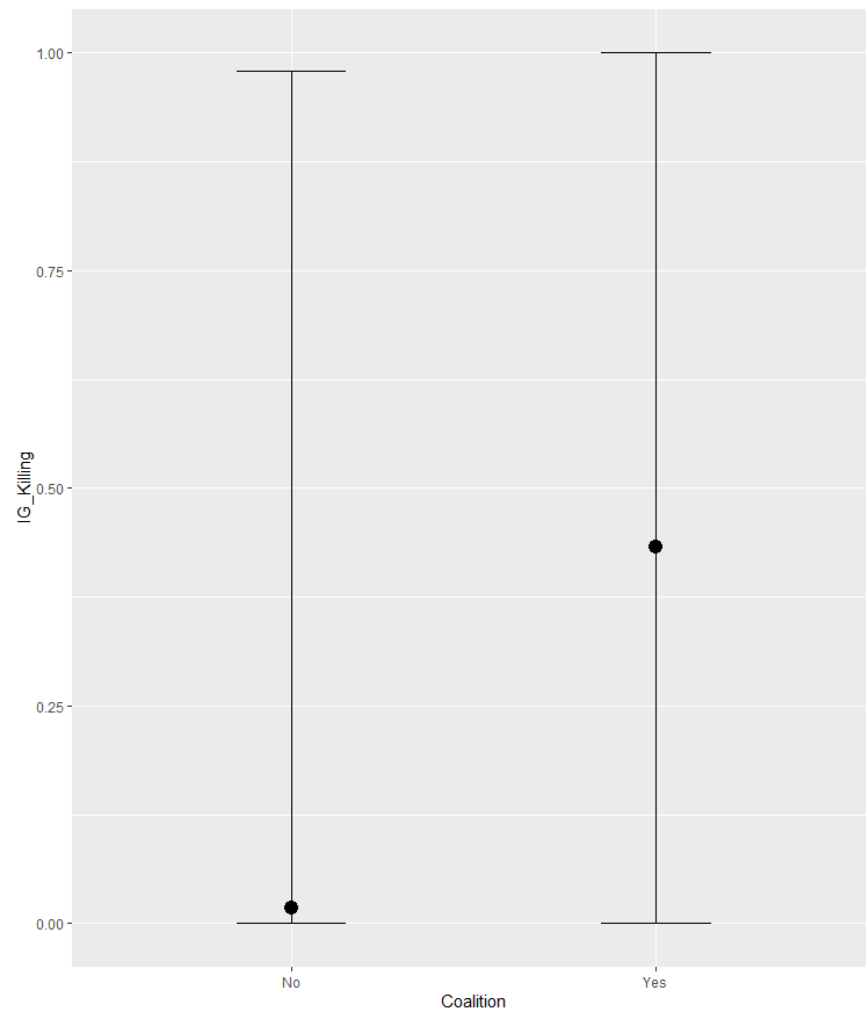


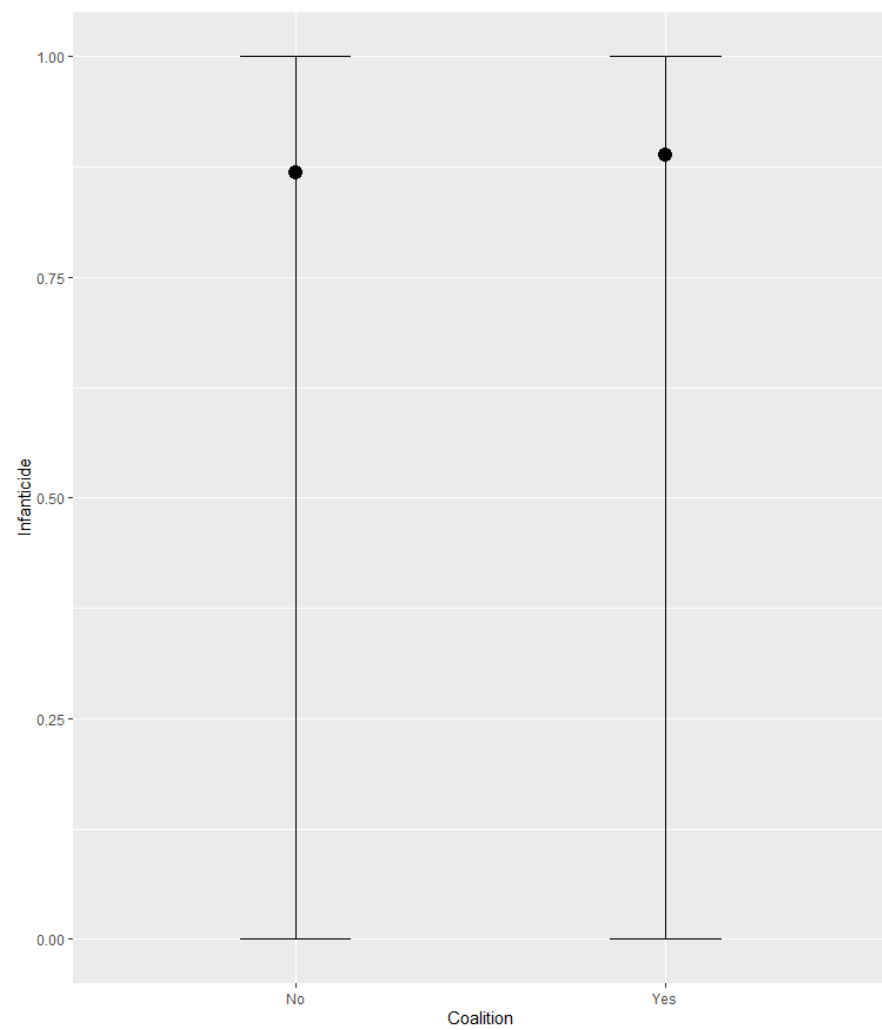




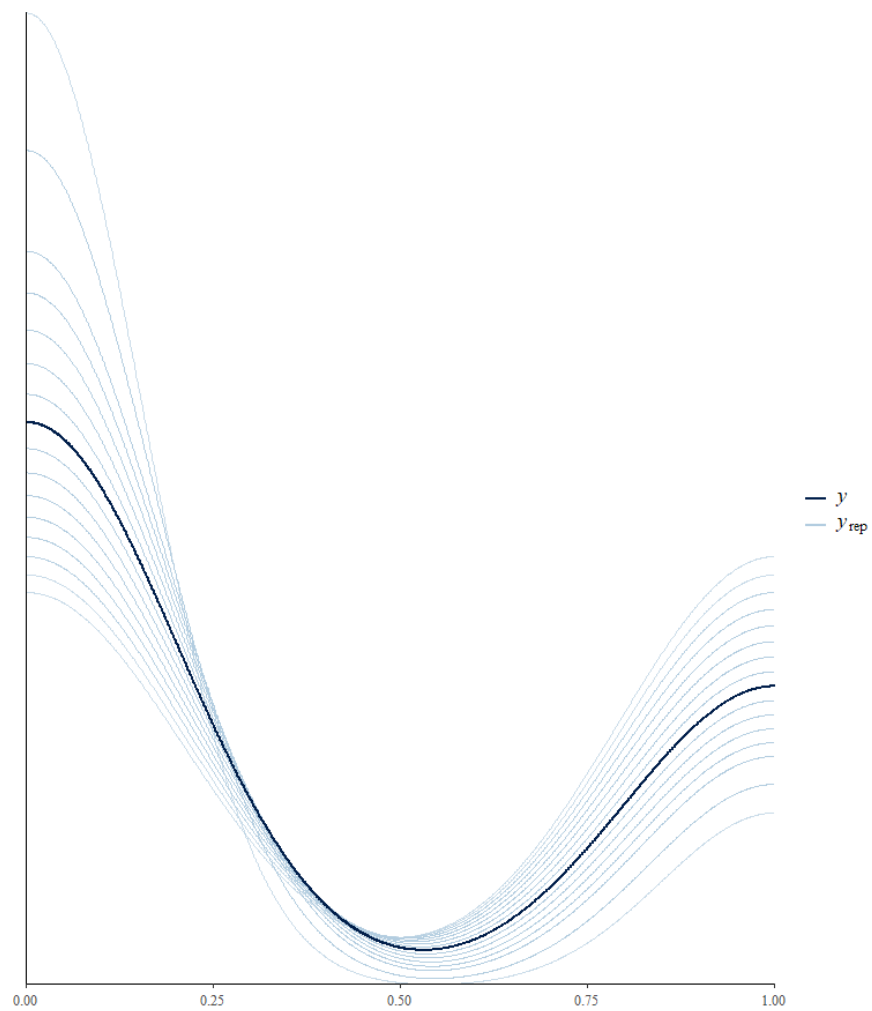




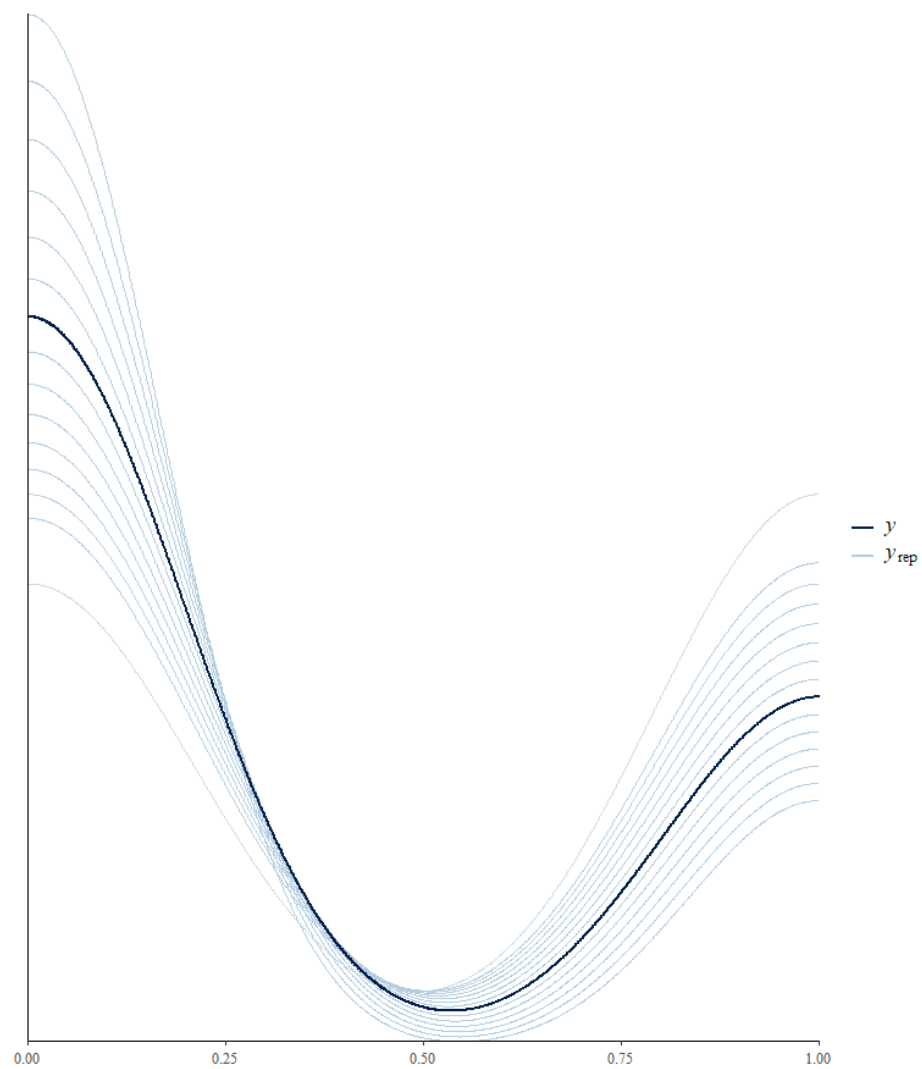




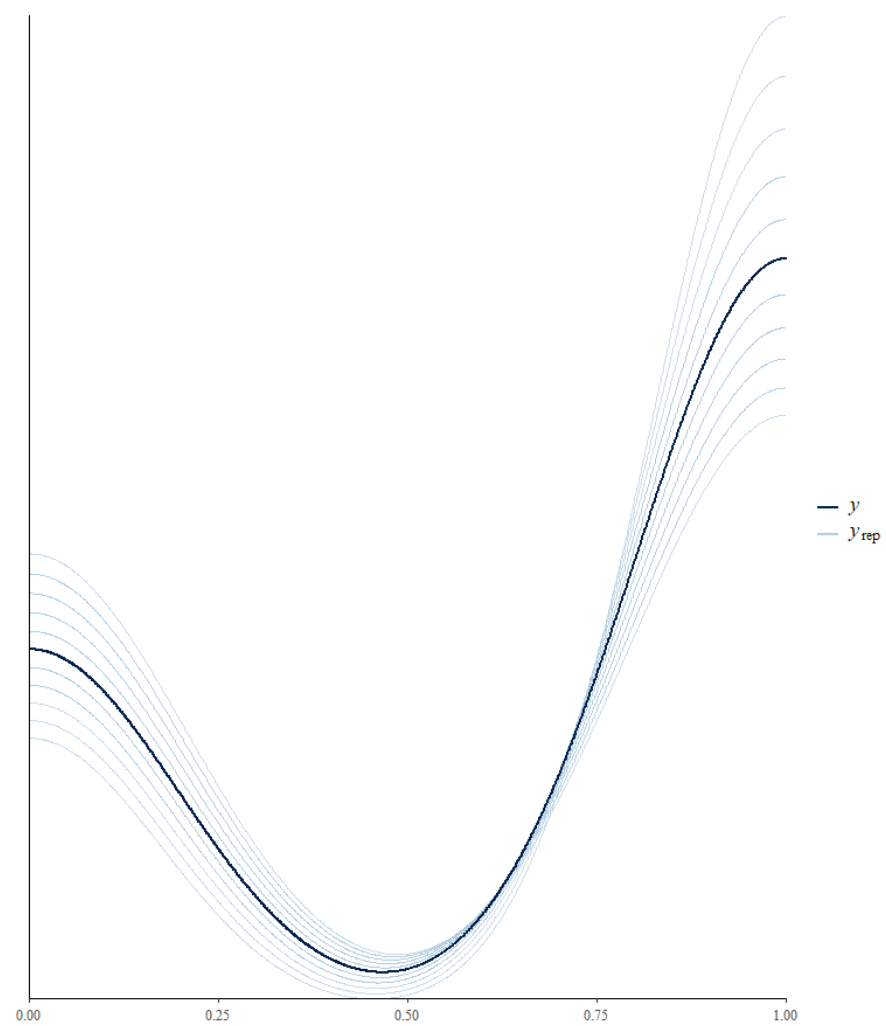
OG Killing



IG Killing



## Infanticide



## APPENDICES – RESEARCH OUTPUTS

## Appendix 6A - 2021 Postgraduate Showcase 2021 (Presentation)



UNIVERSITY OF  
LINCOLN  
THE DOCTORAL SCHOOL



2021  
POSTGRADUATE  
SHOWCASE

Wednesday  
24th February 2021




## Presentations



**Samantha Wakes**  
School of Psychology

*The evolutionary history of primate aggression*

Aggression towards conspecifics is a widespread phenomenon in many species. Diverse in its presentation, aggression can be displayed by both young or old individuals, within and between groups, and with attackers operating alone or in coalitions. Occurrences relating to non-human and human primates has spawned research into the ultimate and proximate factors involved in human aggression and warfare, including the evolutionary roots of this behaviour.

Previously it has been suggested that human lethal violence does in part have a phylogenetic aspect. However, studies have not tested whether violence is a single trait or split into many traits each with a different history and function. In our study, we focus on primates to analyse whether five different forms of aggression (i.e., intergroup, and intragroup aggression, intergroup and intragroup killing, and infanticide) show correlated evolution or whether they follow unique evolutionary paths.

A comparative analysis utilising a Bayesian multivariate approach was carried out on 104 species and sub-species extracted from our dataset. Early results indicate that evolution explains between 8-60% the unique aggression types with clear positive correlations between the three lethal aggression types. Our study suggests that aggression is a multi-faceted trait; each type of aggression seems to have a distinct evolutionary history and potentially be driven by different socio-ecological conditions.

## Appendix 6B - Postgraduate Showcase 2022 (Poster)



Samantha Wakes  
School of Psychology

#### Heterogeneity of aggression: The evolution of human aggression types

##### Objective

Aggression can be observed in many social species and may be considered as a uniform or pluriform phenomenon. Recently Gómez et al., (2016) provided evidence of aggression having an evolutionary basis when considering the single facet of lethal aggression as a pooled measure. This research aimed to explore different aggression types, both lethal and non-lethal, to identify their evolutionary history.

##### Methods

A species level comparative database was constructed containing data on intergroup aggression, intragroup aggression, intergroup lethal aggression, intragroup lethal aggression, and infanticide. Using the Bayesian brms package (Bürkner, 2017) a multivariate analysis was run on 104 primate species and sub-species to identify any correlations between aggression types and the phylogenetic influence.

##### Results

Strong/moderate correlations were found between intragroup and intergroup killing (0.67; 95% CI = 0.24-0.94), intragroup killing and infanticide (0.61; 95% CI = 0.08-0.93) and intergroup killing and infanticide (0.66; 95% CI = 0.13-0.94). No significant correlations were found between the other aggression types. Further, a substantial amount of the total variability for intragroup (60.6%) and intergroup killing (47.7%) could be explained by phylogeny, with moderate amounts explaining intra-group aggression (26.9%) and infanticide (25.3%).

##### Conclusions

The findings of this study suggest that aggression forms are distinct rather than a homologous behaviour, with phylogeny explaining high/moderate variance in four or five aggression types. To follow will be an investigation to identify the additional factors impacting on each aggression type, particularly intergroup aggression.





# The evolution of human aggression types

Samantha J Wakes <sup>1</sup>

Supervisors: Bonaventura Majolo, Marcello Ruta, Erik Willems (University of Zurich)



## 1. Objective

Aggression can be observed in many social species such as birds, humans, and primates. Recently Gómez *et al.*, (2016) provided evidence of aggression having an evolutionary basis when considering the single facet of lethal aggression as a pooled measure. However, is aggression one type of behaviour or are there different forms, and do these evolve uniquely? This research aimed to explore five potentially different aggression types seen in primates; intergroup aggression, intragroup aggression, intergroup lethal aggression, intragroup lethal aggression, and infanticide. As humans closest relatives, studying non-human primates can help in understanding human evolution and specifically the evolution of human aggression types.

## 2. Methods

A species level comparative database was constructed containing data on five different aggression types. Using the Bayesian brms package (Bürkner, 2017) a multivariate analysis was run on 104 primate species and sub-species (figure 1) to identify any correlations between aggression types and the phylogenetic influence.

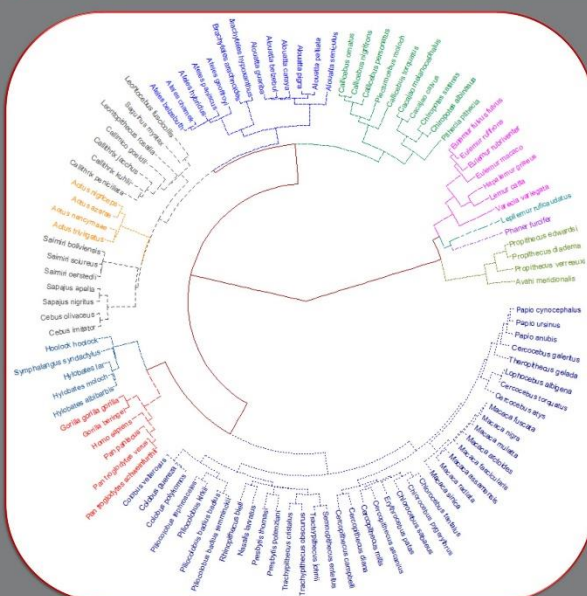


Figure 1:  
Phylogenetic tree showing the evolutionary relationships among the 104 primate species used within the study. The colours used indicate the species within the 11 family group included in the analysis.

## 3. Results

Analysis found **strong/moderate correlations between;**

- intragroup and intergroup killing (0.67; 95% CI = 0.24-0.94).
- intragroup killing and infanticide (0.61; 95% CI = 0.08-0.93).
- intergroup killing and infanticide (0.66; 95% CI = 0.13-0.94).

No significant correlations were found between the other aggression types.

Further, **a substantial amount of the total variability** for intragroup (60.6%) and intergroup killing (47.7%) can be **explained by phylogeny**, with moderate amounts explaining intra-group aggression (26.9%) and infanticide (25.3%).



## 4. Conclusions

The findings of this study suggest that aggression forms are different rather than a homologous behaviour, with phylogeny explaining high/moderate variance in four or five aggression types. To follow, an investigation is required to identify the additional factors impacting on each aggression type, particularly intergroup aggression.

## 5. References

- Bürkner, P. (2017) brms: An R package for Bayesian multilevel models using Stan. *Journal of statistical software*, 80 (1) 1-28.  
Gómez, J.M., Verdú, M., González-Megías, A. and Méndez, M. (2016) The phylogenetic roots of human lethal violence. *Nature*, 538 (7624) 233-237.

## Appendix 6C - EHBEA poster presentation April 2022

**PROGRAMME OVERVIEW: 19<sup>th</sup> – 22<sup>nd</sup> April 2022**

All times are in Central European Summer Time (CEST)

Day 0 – Tue 19 April					
	Start	End	Speaker	Location	Details
Conference opening	13.45	14.00	Colleran; McElreath	Zoom via Gathertown	
Plenary 1: Jenny Tung	14:00	15:00	Tung	Zoom via Gathertown	The long arm of early life: biological embedding in wild baboons
Break	15:00	15:20		Gathertown	
Single 1	15:20		Lidborg	Zoom via Gathertown	Do more masculine men have better quality partners?
	15:40		Skirgård		Does political complexity predict the number of languages in Remote Oceania?
	16:00		Foster		Systematic review and meta-analysis of the effects of predictors of cooperation on loan repayment in microfinance groups
	16:20		Jones		The Dark Secret of Our Success
Break	16:40	17:00		Gathertown	
Posters 1	17:00	19:00	Basava; Boon-Falleur; Chen; Costello; Duffy; Farkas; Fišerová; Frankowska; Galasinska-Grygorczuk; Glynatsi; Goodman; Hicks; Jacobs; Lee; Lie-Panis; Malaei; McAleavey; Mokos; Motes Rodrigo; Onohara; Pal; Pawlowski; Pettay; Power; Ready; Richerson; Rossetti; Russell; Schleihuf; Siekiera; Sobchuk; Stucky; Teramoto; Trzeciakowska; Varas Enriquez; Vitzthum; Wakes; Winters; Youngblood	Gathertown	See Abstract Booklet for titles
Event: Early career mixers	19:00	21:00		Gathertown	PhD student event coordinated by Jasmine Calladine. Postdoc event coordinated by Elena Miu.

**Wakes SJ\*, Ruta M, Willems EP, Majolo B**

University of Lincoln, 07101945@students.lincoln.ac.uk

Posters 1, Yellow Room: 17:00 to 19:00 Tuesday 19.04.2022

**Heterogeneity of aggression: The evolution of human aggression types**

**Objective:** Aggression can be observed in many social species and may be considered as a uniform or pluriform phenomenon. Recently Gómez et al., (2016) provided evidence of aggression having an evolutionary basis when considering the single facet of lethal aggression as a pooled measure. Our research aimed to explore different aggression types, both lethal and non-lethal, to identify their evolutionary history.

**Methods:** We constructed a species level comparative database containing data on intergroup aggression, intragroup aggression, intergroup lethal aggression, intragroup lethal aggression, and infanticide. Using the Bayesian brms package (Bürkner, 2017) a multivariate analysis was run on 104 primate species and sub-species to identify any correlations between aggression types and the phylogenetic influence.

**Results:** We found strong/moderate correlations between intragroup and intergroup killing (0.67; 95% CI = 0.24-0.94), intragroup killing and infanticide (0.61; 95% CI = 0.08-0.93) and intergroup killing and infanticide (0.66; 95% CI = 0.13-0.94). No significant correlations were found between the other aggression types. Further, a substantial amount of the total variability for intragroup (60.6%) and intergroup killing (47.7%) can be explained by phylogeny, with moderate amounts explaining intra-group aggression (26.9%) and infanticide (25.3%).

**Conclusions:** The findings of our study suggest that aggression forms are distinct rather than a homologous behaviour, with phylogeny explaining high/moderate variance in four or five aggression types. To follow, an investigation is required to identify the additional factors impacting on each aggression type, particularly intergroup aggression.