



# MONASH University

**Planting the seeds of a Tree of Death: A new approach, supporting information, test cases, and a national-scale study of population mortality structures from animal-marking records**

Shane M Baylis  
MSc., BSc.

A thesis submitted for the degree of Doctor of Philosophy at  
Monash University in 2017  
Faculty of Science, School of Biological Sciences

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## Abstract

*The primary purpose of this thesis is to build, test, and use a model of age-specific mortality for wild populations of marked animals, using data from a centralised animal-marking scheme. The development of such a modelling approach has been a long-held goal in ecology, and the applications of such a model extend throughout ecology and related disciplines, including evolution, animal behaviour, conservation, and gerontology. Here, we present a non-parametric, continuous-time model of age-specific population mortality designed for use with a national bird-banding dataset. We separately consider a 'panmictic' (i.e., assuming no geographic structuring in recapture probability) and 'geographic' (i.e., modelling recapture probability for individuals within discrete marking-locations) version of our model, and extend it to potentially include observations of live animals as well as recoveries of dead animals. For the 'panmictic' model, we provide mortality estimates using the model for twelve species of seabirds, and we compare our estimates to a priori expectations of survival and published estimates of survival for each species. For the 'geographic' model, we provide mortality estimates using the model for five bird species, chosen for their divergent live-histories and interactions with potential observers. Within this set of five species, we also provide comparisons between our fitted models and a priori expectations of survival and published estimates of survival for each species. We use the 'geographic' version of our modelling approach to generate population mortality structure estimates for sixty species of free-living wild birds from the Australian Bird and Bat Banding scheme dataset, and we analyse this set of mortality structures against life-history variables thought to be predictive of survival and senescence. Our set of population mortality estimates from Australian data is the largest collection of population mortality estimates for free-living wild birds in the world, and our modelling approach may be used on international bird-banding datasets, offering an unprecedented level of insight into mortality processes in wild populations. A potential limitation for any analyses of data from marked animals is mark-loss. Because bird-bands are lost through a process of physical wear during their time on an animal, models of mark loss informed by observations of physical deterioration of worn bands can be used to inform models of population mortality structures. Here, we provide a set of empirical measurements of band wear-rates, and use these measurements to correct for band-loss in our models. We conclude by proposing a vision for future work, with an ultimate target of a 'Tree of Death' – a phylogenetic tree linked to data on population mortality structures, useful for informing models of the evolution of life-histories and the rate-of-change in survival and senescence rates through evolutionary history.*

## Publications during enrolment

Baylis, S. M., de Lisle, M., & Hauber, M. E. (2014). Inferring maximum lifespan from maximum recorded longevity in the wild carries substantial risk of estimation bias. *Ecography* 37:770-780. doi: 10.1111/ecog.00507.

Hodgson, J. C., Baylis, S. M., Mott, R., Herrod, A., & Clarke, R. H. (2016). Precision wildlife monitoring using unmanned aerial vehicles. *Scientific Reports* 6:22574. doi: 10.1038/srep22574.

Manna, T., Cooper, C., Baylis, S., Shawkey, M. D., Waterhouse, G.I.N., Grim, T., & Hauber, M. E. (2016). Does the House Sparrow *Passer domesticus* represent a global model species for egg rejection behavior? *Journal of Avian Biology* doi: 10.1111/jav.01193.

## Thesis including published works declaration

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

This thesis includes 0 original papers published in peer reviewed journals and 2 submitted publications. The core theme of the thesis is the estimation of population mortality structures in wild populations of animals, using data from central animal-marking datasets. The ideas, development and writing up of all the papers in the thesis were the principal responsibility of myself, the student, working within the School of Biological Sciences under the supervision of Rohan Clarke and Paul Sunnucks.

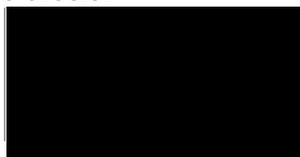
The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers and acknowledges input into team-based research.

In the case of Chapters 1 and 4, my contribution to the work involved the following:

Thesis Chapter	Publication Title	Status	Nature and % of student contribution	Co-author name(s) Nature and % of Co-author's contribution*	Co-author(s), Monash student Y/N*
1	A model for first-estimates of species-specific, age-specific mortality from centralised band-recovery databases	Submitted	Concept, modelling, validation, and manuscript preparation 80 %	1) Rohan Clarke, input into manuscript 10 %	No
				2) Paul Sunnucks, input into manuscript 10 %	No
4	Estimates of wear rates in metal bird bands from the archives of a national banding scheme	Submitted	Concept, data collection, statistical analysis, and manuscript preparation 70 %	1) Rohan Clarke, input into manuscript 5 %	No
				2) Paul Sunnucks, input into manuscript 5 %	No
				3) Michelle Van, input into manuscript, data collection 10 %	Yes
				4) Naomi Clarke, data collection 5 %	No
				5) David Drynan, data collection 5 %	No

I have renumbered sections of submitted or published papers in order to generate a consistent presentation within the thesis.

Student signature:



Date: 23-03-2017

## Acknowledgements

I would like to offer two types of acknowledgements: acknowledgements for those who helped me to achieve work, and acknowledgements for those who helped me to remain motivated, interactive, and generally not a hermit. I am exceptionally fortunate that my supervisors, Rohan and Paul, are worthy of both sorts of acknowledgement. Between them, they have provided support and encouragement, necessary criticism, knowledgeable specialist contacts, social events, excuses to head off critter-hunting, and immense subject-matter expertise.

My partner, Nancy, also falls into both acknowledgement-camps. Throughout the PhD, she has offered tireless assistance in day-to-day practicalities and an absurd capacity to provide work in the field, the lab, the conference-hall, and the densely-packed back-rooms of natural-history museums. She has been a constant enabling force behind my plans.

My parents, Leone and John, although based in another country, have offered unwavering enthusiasm for my project on the occasions I have had the opportunity to explain it to them. My labmates and lab-tech, situated at a more convenient distance, have offered their critiques on the many occasions I've borrowed their ears to test my explanations, conference presentations, or manuscripts at varying stages of completion. The enthusiasm, and the critiques, have been incredibly valuable.

I received financial support during my PhD from the Holsworth foundation (for research costs and conference attendance), the VW company (for attendance at a Spring School in Landscape Genetics), the Pacific Seabirds Group (for attendance at their annual conference in Juneau, Alaska), and from the Federal Government of Australia (for my living costs).

Finally, the dataset that made this thesis possible represents an immense amount of work by the Australian bird-banding community over the past sixty-five years. I have had access to this immensely valuable data through the Australian Bird and Bat Banding scheme, with specific help from David Drynan and Naomi Clarke.

*Shane Baylis*





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# General Introduction

In many areas of biology, researchers have reason to be concerned with 'vital rates': rates of birth and death by members of a population. A conservation manager may need to know the birth and death rates for a population to predict the range of population-growth to be expected over time; an evolutionary biologist may need similar data to assess the fitness cost of, say, migrating to a new habitat; a gerontologist may assess the change in survival-rates with increasing age (i.e., *survival* senescence), or the relationship between survival senescence (as just defined) and reproductive senescence (i.e., the change in number of offspring produced per year with increasing age); a fisheries stock-manager may need to know what proportion of newly-hatched fry will survive to a harvestable age-class.

In this thesis, I consider death-rates: annual adult mortality (i.e., the proportion of all members of a population who, having reached a birthday in an adult age-class, do not survive to their next birthday), first-year mortality (i.e., the proportion of all members of a population who, having been born, hatched, or fledged, do not survive to their first birthday), juvenile mortality (i.e., the proportion of all members of a population who, having been born or having reached a birthday below their age at first-breeding, do not survive to their next birthday), and survival senescence (i.e., the annual change in adult survival-rates for each one-year increase in age). Equivalently and interchangeably, I discuss survival, the complement of mortality. More generally, I discuss mortality structures, which describe the proportion of a population surviving as a function of age, and from which survival and senescence rates may be calculated.

## **Estimation of mortality structures: two analytical ‘camps’**

In my discussion of the models used to estimate mortality and senescence rates, I make a distinction between two major sets of goals that underpin two general classes of modelling approach, and are viable at different phylogenetic scales. In the first, research questions are asked at the scale of individual-level differences within a species. For instance, a researcher may ask how an indicator of body-condition correlates with age and risk of death, and use these observed relationships to test hypotheses of trade-offs acting within individuals to maximise their fitness despite senescence (e.g., Bérubé et al. 1999). Research questions like this necessitate the collection of individual-based, long-term monitoring datasets, with monitoring regimes often following stringent experimental designs (e.g., Loison et al, 1999 considers five populations monitored for between 12 and 22 years). This first modelling approach may be broadly termed the 'longitudinal approach', as in Nussey et al. (2008).

In the second major set of goals, research questions are asked at the scale of sets of species or populations, for evolutionary comparisons, or for broad phylogenetic coverage *per se*. For instance, a researcher may ask whether species expressing a specific behaviour show reduced adult survival, or slower survival senescence than species that do not express that specific behaviour (e.g., Beauchamp 2009). Equally, estimates of survival and senescence over a broad phylogenetic range may be of interest to any researcher studying any species within that range, and works that collect natural-history data for many species are often highly cited precisely because of their utility to field biologists. Analyses addressing evolutionary questions frequently require datasets covering many species, and frequently do not need individual-level data within each species: the species, rather than the individual, is the unit of comparison in many such analyses. Many evolutionary-scale analyses use comparatively simple proxies of vital rates within species, despite serious limitations and biases in such proxies (see *Approaches to estimating survival and senescence parameters over a broad phylogenetic range*, below).

There is no ‘hard’ distinction between the modelling approaches that may be used to answer individual-species level questions and the modelling approaches that may be used to answer evolutionary comparative questions. I argue that evolutionary comparative analyses of survival and senescence based on purpose-built long-duration capture-mark-recapture experiments are the ideal approach. However, this ideal may be prevented by pragmatic limitations – long-term intensive monitoring studies are difficult and expensive to conduct, and as a result, there are comparatively few such studies, while broad phylogenetic coverage is desirable for its own sake, and necessary for evolutionary comparative analyses. Because the need for accurate, unbiased

estimates of population mortality structures over a broad phylogenetic range is unmet, researchers may be forced to turn to critically limited and biased estimates. An estimation tool that provides unbiased estimates of population mortality structures, over a broad phylogenetic range, would overcome many of the limitations of evolutionary comparative analyses of vital rates.

### **The Tree of Death, and its place in evolutionary analysis**

If estimates of population mortality structures are available over a broad phylogenetic range, and the evolutionary relationships between species are well-known, it is possible to place changes in population mortality into a detailed evolutionary context. Throughout this thesis, I use the term ‘the Tree of Death’ to describe the patterns of change in population mortality parameters between related species, through evolutionary time. Using a Tree of Death, it will be possible to investigate the rates of change of population mortality parameters and to map out their evolutionary history. For instance, we could ask how quickly (in generations) a population can evolve from having high adult survival rate (say, 95% annual survival) to supporting a low annual survival rate (say, 50% annual survival), without going extinct in the process (cf. Evans et al. 2012 for a comparable analysis on the evolution of body size). Population survival parameters like annual adult survival, first-year survival, and survival senescence are unlikely to be independent of each other through evolutionary time. A Tree of Death is a necessary tool for examining how survival parameters coevolve.

### **Approaches to estimating population mortality structures over a broad phylogenetic range**

In order to estimate survival and senescence parameters across a broad phylogenetic range, several approaches have been used. First, life-table analyses have seen some use for unmarked wild populations. For some populations, individuals may be aged on sight (for instance, in Dall sheep, individuals may be aged by inspecting annuli present on the horns – see Hemming 1969). In populations where individuals may be aged by sight, a random sample of individuals from that population will reveal successively fewer individuals with each increase in age-class, consistent with the number of animals dying between each pair of successive age-classes (e.g., Promislow 1991). Similar life-tables may be derived from recovered animal carcasses for which the age-at-death can be determined (e.g., Monson et al. 2000; Erikson et al. 2006).

In some situations, the life-table approach applied to populations of unmarked animals can give

accurate estimates of mortality-rates between age-classes. Life-table approaches assume that the age of an individual can be accurately determined, and that the probability of recovering a carcass or sighting a live individual is independent of the age of the individual, which may not be true for all populations or species. Critically, the technique is potentially biased by variation in birth-rates: in the terminology of the rest of this thesis, the relative *Availability* of observations at different age-classes is not accounted for, generally because the relative *Availability* of different age-classes is unknown. To illustrate, consider a population where the mortality-structure is constant (i.e., the proportion of individuals that survive to age  $a + 1$ , given that they survived to age  $a$ , is constant for all time  $t$ , though the proportional survival from  $a$  to  $a + 1$  may differ for differing values of  $a$ ). If the birth-rate exceeds the death-rate in the population (i.e., the population is growing), the death-rate calculated by life-table methods can be biased upwards: population growth results in relatively larger numbers of young individuals, so the difference between the number of individuals in adjacent age-classes (and therefore the calculated mortality-rate between those age-classes) is increased. In this case, there are more *Available* individuals in lower age-classes, and the *Availability* of any given age-class is the number of individuals that could potentially have been observed in that age-class, in the absence of deaths. I note that the term *Availability* has two definitions in the discrete-time population-mortality literature. Mine matches that of Bellrose & Chase (1950), but the term is also used in the mark-recapture literature to denote 'available for capture', especially in cases where an individual may move out a study area and therefore become 'unavailable' (e.g., Kendall et al. 1997).

A variant on the life-table approach is to construct life-tables for populations of captive animals (e.g., Kohler et al. 2006). Captive populations of animals have several survival advantages over their wild counterparts: food is not generally in limited supply, predation risks are managed through exclusion, and disease risks are managed by veterinarians and people skilled in captive animal management. Some authors have argued that mortality in captive populations will, therefore, mainly reflect patterns of physiological decline (sometimes termed 'intrinsic mortality'), rather than stochastic causes-of-death which may occur at any age (sometimes termed 'extrinsic mortality'), and have argued that data from captive animals is preferable for estimating senescence-rates (e.g., Wilkinson & South 2002). Conversely, animals held in captive populations are susceptible to a range of diseases that are rare in free-living populations (e.g., Snyder et al. 1996; Wyss et al. 2013); management decisions in a captive setting may not be species-agnostic (e.g., members of charismatic species may be more likely to receive costly life-extending veterinary interventions than members of less-charismatic species); and members of long-established captive populations show evolutionary adaptation to captive conditions

(Frankham 2007). Finally, Tidière et al. (2016) report that captive conditions affect survival-rates and senescence-rates differently for species with 'fast' life-histories (i.e., high mortality-risk and high reproductive output) compared to 'slow' life-histories (i.e., low mortality-risk and low reproductive output). Species with a 'fast' live history see a greater delay in the onset of senescence in captivity relative to the wild than do species with a 'slow' life-history, and species with a 'fast' life-history also see a greater increase in survival-rates in captivity relative to the wild than do species with a 'slow' life-history. Considering the effects of diseases associated with captivity, human decision-making in captive management settings, evolutionary adaptation to captivity, and reports of differences in the effects of captivity on survival between major groups of organisms, I see no reason to assume that a species' patterns of survival or senescence in captivity accurately reflect that species' patterns of survival or senescence of the wild. Rather, I consider that survival and senescence in the wild and in captivity are essentially different subjects, with different potential applications, and data on one should not be treated as informative on the other.

Another approach widely used to estimate survival and senescence rates across a wide phylogenetic range is to take the maximum recorded longevity (MRL) within each species as a proxy of survival and senescence rates. MRLs are reported to be tightly correlated with senescence rates within species (e.g., Ricklefs 2010). A subset of Maximum Recorded Longevities are derived from captive records, and some studies exclusively use longevity records from captive populations (reviewed in Baylis et al. 2014). The limitations previously discussed for life-tables derived from captive records also apply to MRLs derived from captive records, so I argue that MRLs from captive populations are, at best, informative on mortality structures in captive populations, and are not necessarily informative on mortality structures in the wild.

Despite correlating with measured survival and senescence rates, MRLs are widely considered a dubious source of data on inter-species differences in mortality structures (see Botkin & Miller 1974; Arnold 1988; Duncan 1988; Krementz et al. 1989; Reznick et al. 2002; Sandercock 2003; Moorad et al. 2012; Baylis et al. 2014). MRLs are by definition an extreme, potentially outlying, record within each species. The expected value of the maximum recorded longevity is a complex function of sample size and age-specific survival-rates that does not provide a reliable proxy to annual survival rate (Krementz et al. 1989; Sandercock 2003). As a proxy of 'true' maximum longevity (and by extension, of senescence), MRLs are always biased downward relative to 'true' maximum longevity, and are further biased by sample size, adult survival-rates, and whether a species is typically observed alive or dead (Krementz et al. 1989; Moorad et al. 2012; Baylis et

al. 2014). Moreover, these biasing factors correlate with life-history variables reported to affect survival and senescence rates (Baylis et al. 2014). In light of the marked deficiencies of MRLs as a proxy of survival or senescence, Moorad et al. (2012) proposed a set of univariate alternatives to MRLs aimed at isolating inter-species differences in longevity that were less biased by sample size than were MRLs, with better robustness to sampling error. The set of univariate longevity measures was validated against population-mortality structures estimated for captive zoo and aquarium populations. Univariate alternatives to MRLs that are less biased by sample size and less prone to sampling error represent an improvement over direct use of MRLs. However, MRLs are also biased by inter-species differences in recapture types (i.e., whether members of a species are typically observed alive or recovered dead), the specific mortality structure, and interactions between recapture type, mortality structure, and sample size (Baylis et al. 2014), and it is not clear that the alternatives proposed by Moorad et al. (2012) are any less affected by those biases. Moreover, any univariate measure of longevity must necessarily estimate only one aspect of a mortality structure, rather than estimating the shape of the mortality structure as a whole. Therefore, the alternatives to MRLs proposed by Moorad et al. offer only a partial solution to the many weaknesses of MRLs as a measure of mortality structures between species.

In light of their many shortcomings, I am very sceptical of the utility of MRLs as a proxy of survival or senescence rates between species, especially in cases where data from captive populations are used to infer mortality parameters in the wild, or *vice versa*.

### **Data availability for animals in the wild, over a broad phylogenetic range**

One specific new opportunity for attempting to estimate mortality-rates and senescence-rates in the wild is in the recent availability of data resulting from the adoption of open-access data policies. Animal-handling activities are legally controlled at a national level in many regions, and regulatory bodies frequently oversee the collection and archiving of banding data. For instance, bird-banding in Australia is regulated by the Australian Bird and Bat Banding Scheme (ABBBS), which also holds records of banding, resighting, and recovery events starting in 1953 (ABBBS, 2017a). To organise data at the continental scales over which many animals range, animal marking schemes may also coordinate activities internationally, as in the case of EuRing, which coordinates bird-banding activities through multiple national-level banding schemes within Europe (European Union for Bird Ringing 2017), the North American Bird Banding Program, which coordinates bird-banding throughout North America (North American Bird Banding Program 2016). International coordination of animal marking efforts also exists for some non-

Avian taxa: for example, Atlantic sea-turtle tagging efforts are coordinated through the Archie Carr Center for Sea Turtle Research (Archie Carr Center, 2014).

Recently, the ABBBS instituted an open-access data policy: banding data held by the ABBBS is now available to researchers on request. It was this open-access data policy that prompted my interest in designing a mortality-estimation tool for use with national-scale datasets. Similarly, much or all of the data held in the North American Bird Banding Program databases became open-access in 2016, following Executive Order 13642, which directed an open data policy for data collected by US Government employees and agencies (Obama 2013). There is therefore a new incentive to develop models that accurately estimate population mortality-structures from the datasets held by national banding-schemes.

### **Challenges for estimation of mortality structures over a broad phylogenetic range using national mark-recapture data**

Compared to datasets collected in structured experimental designs, the datasets maintained by national banding schemes have some unique properties. In general, mark-recapture datasets held for each species within a national banding scheme are of long duration (see Appendix 3.2, this thesis). Within the dataset for each species, marking and recapture efforts may be carried out by multiple organisations, at multiple locations, with differing research goals, and the overall structure of marking and recovery effort in time and space is chaotic. Although the time, place, and species of all marking events is recorded, the discrete observation attempts required for many interval-based models (e.g., Seber 1982) cannot be rigorously defined, as there are few if any requirements to report capture attempts that result in no captures of a given species, or attempts at resighting an animal without handling it.

Mark-loss is a potential problem with any analysis of data from marked animals (Botkin & Miller 1974). Many early mark-recapture models simply assumed that mark-loss did not occur (e.g., Seber 1982), but more recent models have accounted for mark-loss by double-marking a subset of the marked population and assuming that marks are lost independently (e.g., Cowen & Schwarz 2006), or by equipping some of the marked population with a permanent mark that can never be lost (e.g., a tattoo – see Laake et al. 2014). For many species in national-scale mark-recapture datasets, double-banded or permanently-marked subsets of the marked population do not exist, so models that correct for mark-loss using double-marked or permanently-marked records cannot be used to estimate mortality or senescence in these species. Analysing the physical condition of worn animal tags offers an alternative approach to the estimation of mark-

loss, as bird-bands deteriorate by abrasion during their time on the animal (see Ludwig 1967; 1981). Further, archives of worn bands are available for many species, as bands recovered from dead animals are frequently sent in to banding schemes as part of the recovery-reporting procedure. For instance, in the Australian Bird and Bat Banding Scheme the recommended reporting technique for any band discovered on a dead animal involves mailing the physical band to the banding scheme's office in Canberra, where recovered bands are routinely archived (ABBBS, 2017b).

Movement of individuals presents an analytical challenge for analyses of survival in wild animals, as animals that move outside areas of active study may become unobservable by researchers. In general, we believe that our method is likely to be more robust to movement than many other CMR modelling approaches, but acknowledge that movement is conceptually and practically difficult to correct for. Our model, as applied in Chapter 1 and as used in Chapter 3, uses only dead recoveries of marked animals. In ring-recovery models, survival estimates are often considered to be unaffected by emigration, because few animal-marking projects explicitly aim to make recoveries of dead animals during animal-capturing operations and because dead animals are frequently recovered outside areas and times of active animal-marking (Burnham 1993; Frederiksen & Bregnballe 2000; Kendall et al. 2013). Our basic model assumes the probability of a dead recovery depends on time-specific research effort, and our advanced model in Chapter 2 and 3 has dead-recovery probabilities dependent on time- and location-specific recapture effort. Our approach is therefore more conservative than comparable approaches in this regard. We recognise that ours is not a complete solution to the potential problem of animal movement for estimates of survival (see Chapter One for situations that could still violate our model assumptions), but we suggest that dead-recovery models are unlikely to be strongly biased by time- and location-specific recapture effort, because for most species, most recoveries of dead animals do not happen during animal-marking efforts.

### **An outline of the main chapters**

In this thesis, I present four 'paper' chapters. In the first, I describe a basic model to estimate population mortality structures for species in a national bird-banding dataset. The basic model accounts for inter-annual differences in research effort, the 'availability' of individuals to be observed at each age-class, and mark-loss from banded animals. This first model is 'panmictic': it treats the marked population as a single unit with probabilities of recovery, given death, shared by all members of the marked population, and does not use data from animals observed alive. I demonstrated the use of this model on a set of 12 species of seabirds, because the wide-ranging

habits of seabirds make the 'panmictic' assumption more realistic for these taxa than for many other bird species, and because seabirds are often observed as beach-cast dead animals, resulting in relatively high numbers of dead recoveries for each species. I validated the model against simulated datasets, and against published estimates of survival-rates for the twelve seabird species.

In the second chapter, I present extensions of the basic model, allowing individuals from within geographic subdivisions within the marked population to have their own probability of recovery, given death, and allowing data from animals observed alive to inform the model. The inclusion of data from live observations of marked animals required the assumption that location-specific sampling effort affected the probability of observation of dead animals in the same way that it affected the probability of observation of live animals and, in practice, this assumption resulted in biologically unreasonable mortality models. I demonstrated the use of the geographically-explicit model on a set of five species chosen to be widely divergent in movement biology and in their interactions with potential observers. This set of five species served as a test for modelling large numbers of species over a wide phylogenetic range, which is the ultimate research aim of this thesis. I validated the model against simulated datasets and against published estimates of survival-rates for the five species.

In the third chapter, I present analyses from a set of fitted mortality-structure models for 60 avian species monitored within the Australian Bird and Bat Banding Scheme. From each fitted model, I extracted estimates of annual adult survival, annual first-year survival, and annual survival senescence, and I analysed this set of survival and senescence estimates against each other, and against life-history parameters reported to predict inter-species variation in survival and senescence. The set of 60 species is the largest dataset of mortality and senescence-rates ever collected for free-living wild birds. Unlike other published inter-species comparisons, my tests do not rely on ambiguous proxies of survival and senescence such as MRLs, and do not make any use of data from captive populations. My analyses are therefore powerful (i.e., have a large sample-size and small expected error – see simulations in Chapter 1 and Chapter 2) and specific (i.e., I have isolated estimates of annual survival and survival senescence, which is not possible in MRL-based analyses without external estimates of annual survival) compared to other inter-species comparisons of survival and senescence.

In the fourth chapter, I present analyses of wear rates of metal bands worn by birds in Australia, separately for species and band-designs. My dataset of band wear-rates covers a wide range of species and band-designs, and species were included in the sample on the basis of their inclusion

in the ABBBS archive, rather than out of prior concern at the wear-rate of their rings. Using this dataset, I test the hypothesis that the published literature tends to feature a disproportionately high number of rapid wear-rate estimates, which could result from researchers choosing to draw attention to poorly designed bands by conducting and publishing wear-rate studies. I use the empirical measurements of band wear-rates from this chapter to inform the band-loss model in Chapter 3.

Finally, I discuss the central findings of each chapter and the opportunities for further developments of the techniques presented in this thesis. I close by presenting the 'Tree of Death' as a high-level scientific output that is rendered achievable by this work.

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# Chapter One

## *A model for first-estimates of species-specific, age-specific mortality from centralised band-recovery databases*

### ABSTRACT

Population mortality curves, otherwise known as lifetime distribution functions, can be indispensable in many areas of ecology and environmental management including population viability and stock management analyses, disaster-recovery monitoring, and fundamental evolutionary biology. Yet available modelling tools are often unable to estimate population mortality curves from commonly-available datasets because these datasets fail to meet stringent experimental-design requirements. Here, we present a new method for estimating population mortality curves from records of marked individuals found dead. Such data are increasingly accessible in some of the largest biological data sets, such as continent- or nation-wide marking-and-recovery schemes for birds and other animals. The method accounts for known biases in availability by age-class, variable monitoring effort through time, and mark-loss. We show that our modelling approach generates accurate estimates of population mortality structure across a range of populations differing in marking histories, true mortality curves, monitoring regimes, and mark-loss rates. Our approach can be applied to multiple species or groups at a time, and can provide estimates of adult, immature, and first-year survival rates, required by predictive modelling applications such as Population Viability Analyses. Our approach is also capable of estimating apparent senescence rates for each population, and facilitates evolutionary analyses of life history traits. For example, our method is potentially useful for exploring the evolution of senescence or for inter-group comparisons of mortality rates where groups that differ by environment may be identified within mark-recovery records. To demonstrate the efficacy of this method we present fitted population mortality curves for a suite of seabird species represented in a national mark-recapture database and estimates of first-year survival rate, immature survival rate, annual adult survival rate, and apparent senescence rate derived from those curves.

## INTRODUCTION

The frequency distribution of ages-at-death for a species or population is a key piece of demographic information. If it can be accurately modelled, this distribution is central to estimates of population growth trajectories, breeding success-rates necessary for species persistence or harvesting-rate supportable by a population, the effect of senescence or aging on population structure, and many other parameters of interest to ecologists, conservation managers, fishery stock managers, and evolutionary theorists (Ricker 1975, pp 29-73; Traill et al. 2007; Baylis et al. 2014; Pierson et al. 2015).

If accurate, unbiased estimates of mortality parameters are available across many populations or species, these can be used for inter-population or inter-species demographic comparisons. Some authors have built databases of mortality structures for multiple species (e.g. Promislow, 1991; Loison et al. 1999). However, these analyses have generally considered only a limited number of species for which the authors have been able to access high-cost population actuarial datasets, many of which have used transversal life-table approaches, and so relied on assumptions such as zero population growth in order to estimate mortality structure. More recently, others have derived multi-species datasets of mortality curve estimates derived from long-running studies which relax many restrictive assumptions about the population under study. The number of species available for these analyses is limited by the substantial cost of data-collection, which limits the comparisons which can be made across populations, phylogeny, and environmental conditions (see Jones et al. 2008; Nussey et al. 2013).

Perhaps because of the difficulty and expense of obtaining population-mortality structure estimates for multiple species, many authors have used maximum recorded longevity (MRLs) within each species as an estimate of the maximum age an individual may attain, or as a proxy of annual adult survival rate (see Møller 2006; Baylis et al. 2014). A method that accurately estimates population mortality curves for multiple species from existing databases could considerably increase the number of species and populations available for comparisons, and allow comparisons to investigate multiple parameters such as adult survival rates, senescence rates, maximum plausible longevity, and juvenile mortality rates for each species. Population mortality structure models can also be used to parameterise predictive models of population persistence under specific situations, such as Population Viability Analyses (Beissinger and Westphal, 1998), which require accurate estimates of population parameters such as annual survival rates and survival to breeding age. Those parameters may be estimated from population mortality curves coupled with information from standard reference-works.

## **Data available for estimating survival parameters of wild populations**

National-level animal-marking schemes are a major data source for inference of survival parameters between populations. Animal-marking schemes may differ from each other in their data collection practices, data handling approaches, and data-access rules. Here we consider the information included in mark-recapture records in the Australian Bird and Bat Banding Scheme database (ABBBS, 2015) as an example of a national animal-marking database. If similarly-structured data are available within other banding schemes (e.g., the member-nations' datasets within EURING – see European Union for Bird Ringing 2017, and the dataset held by the United States Geological Survey – see North American Bird Banding Program 2016), our modelling approach should generalise to those schemes' datasets.

### ***Marking***

Each marked animal is recorded. Records may be assumed to contain information on the unique band number used to mark the animal, the species marked, the date the animal was marked, the location at which the mark was applied, the type(s) of mark applied, the method used to catch the animal, the status of the mark at the time of release (e.g., 'Animal was alive with the band'), the identity of the bander responsible for the marking project, and the specific banding project under which the animal was marked. Additional data may be available on the age of the animal (and how it was aged), the sex of the animal (and how it was sexed), and the time of day at which the animal was marked.

In contrast to datasets collected for the express purpose of estimating population mortality structures, marking in centralised mark-recapture datasets is carried out by multiple independent parties. Marking may occur over an extended time-period, or as a one-off event. A given researcher on a given animal-marking day might only mark individuals of one species, several species, or every animal captured. Researchers may deliberately bias their capture efforts towards a given species (e.g., by providing song-playback near their points of capture) or away from a given species (e.g., by setting nets in areas where species of interest are particularly active, and away from species which are not of interest). For most species, marking occurs at multiple locations. In the ABBBS dataset, each marking event is assigned to a 'locode', which is a study-site as defined by a researcher. Each locode may be viewed as a categorical location (i.e., individuals are 'from' the locode in which they were marked, and are more likely to be observed as a result of research effort at the same locode than at any other locode). Locode descriptions also often contain a lat/long position, which in principle allows continuous analyses of animal movement to inform models of recapture probability.

### ***Recapture and recovery***

Recapture and recovery records may be submitted to the ABBBS by anyone who has observed or recovered an ABBBS band or an animal marked with an ABBBS band. We consider two classes of mark-recovery: those recoveries made by researchers in the course of animal-capture for marking ('Marking observations'), and those recoveries made by people not involved in marking at the time (e.g., animals encountered by beach-patrol schemes, hunters, or members of the public willing to report a banded animal encountered opportunistically – collectively 'Non-marking observations'). Researchers who mark animals are encouraged to submit their observations of marked animals at the same time as they annually report the new bands that they have applied, so marking observations may not be reported for  $\leq 12$  months after the time of observation. The information requested with marking observations mirrors the information submitted with new band applications. Non-marking observations are encouraged either by post or through the ABBBS web portal. The ABBBS requests information on the unique band ID recovered, the species observed, any additional tags found on the animal, the date of observation, the method by which the animal was observed, whether the animal was alive or dead at the time of the observation, the location of the observation, and contact details for the person submitting the report. An unknown proportion of observations go unreported for both marking observations and non-marking observations.

### **Modelling approaches**

Much effort has been spent on model designs for datasets of marked-and-recaptured, marked-and-recovered, or marked-and-resighted animals (see Table 1.1). The model designs may be coarsely grouped according to whether they consider discrete or continuous time, and whether the model considers an open, closed, or combined open and closed ('Robust Design') population.

We have four major concerns with using interval-based, unitary-population models (see Table 1.1) to model population mortality structure from national-level databases:

1. *Quantification of recapture effort*: the data in national-scale band-recovery datasets are spread over a wide temporal range across many banding locations. In many year/location combinations, there are zero observations for a given species. Because there is no requirement for users to submit data to the ABBBS if they have attempted to capture animals for marking but failed to capture any animals, it is impossible to distinguish true zeroes (i.e., no marked animals were observed, despite effort) from an absence of observation effort; moreover, discontinuous monitoring effort makes

survival parameters inestimable in many interval-based techniques (Table 1.1). In our dataset, the number of animals recovered dead in a year correlates strongly with the number of animals banded in a year, presumably partly because researchers marking animals tend to mark in locations where their species of interest exists at high density, and tend to look for dead animals while they are on-site. Because we cannot unambiguously assign monitoring intervals with a consistent duration or unambiguously decide whether a given population was or was not monitored during a time-interval, we cannot use interval-based analysis techniques such as the Jolly-Seber (JS), Brownie, or Robust Design models (see Table 1.1).

2. *Spatial heterogeneity in catchability*: individual marked animals are marked at many marking locations, which may violate the assumption of a unitary population. Modelling approaches for handling heterogeneity in observability exist within interval-based techniques (Table 1.1), but interval-based techniques are ruled out by the chaotic structure of marking effort in national-scale databases.
3. *Mark loss*: there are well-developed models for mark-loss within JS models, but these rely on a portion of the marked population being double-marked (Table 1.1; Laake et al. 2014). For many of the species we wish to model, there is no double-marked segment of the population.
4. *Instantaneousness of marking and/or recapture events*: both marking and recapture events are chaotically-distributed over time, potentially ranging from field-studies in which there is only one marking-day, through to studies where researchers spend months at a time in the field attempting to mark and observe animals. For each species, there are potentially many years in which marking does not occur. Therefore, for this dataset, we cannot use techniques which assume instantaneous marking and/or monitoring events, such as the JS, Robust Design, Brownie, or similar models.

**Table 1.1:** Established modelling approaches for the estimation of population mortality structures from marked animals, with descriptions of the populations of marked animals for which they act as a model.

<b>Model name</b>	<b>Citations</b>	<b>Population parameters estimated</b>	<b>Populations to which the model is suited</b>
Composite Dynamic Model	Bellrose and Chase (1950); Deevey Jr. (1947)	Time-specific and age-specific survival	Demographically-stationary populations with a long history of marking and consistently non-zero likelihood of observation, or a random sample of animals from a demographically-stationary population ageable post-mortem by physical features
Mark-recovery models	Brownie (1985)	Time-specific survival, potentially through multiple age-classes defined from discrete marking times	Unitary populations in which individuals are captured and marked over a short time-period at regular intervals, from which animals are recovered dead in continuous time
Jolly-Seber Model	Seber (1982)	Survival, population size, births, and deaths at discrete time points summarising intervals	Unitary populations in which a sample of individuals are captured at random once per long period
Extensions to the Jolly-Seber Model	Pollock et al. (1990); Pledger et al. (2003); Cowen and Schwarz (2006)	Survival, population size, births, and deaths at discrete time points summarising intervals	Unitary populations sampled each long period, possibly with heterogeneous recapture probabilities or mark-loss
“Robust design” Model	Pollock (1982)	Survival, population size, births, and deaths at discrete time points summarising intervals	Unitary populations multiply-sampled within short periods (the 'closed population'), repeated each long period (the 'open population')
Combination Models	Kendall et al. (2013); Burnham (1993); Catchpole (1998); Barker (1997)	Survival, population size, births, and deaths at discrete time points summarising intervals	Unitary populations multiply-sampled on a regular basis, with incidental recoveries made outside the regular monitoring events

## Scope

In this paper, we present a model which utilises the dataset collected by the Australian Bird and Bat Banding Scheme, with an expectation that our modelling process may also be applicable to other banding schemes' datasets. Our aim with this model is to estimate population mortality structures for all species which have a recorded history of marking and recapture in centralised schemes, within the limitations of those datasets. We do not present our models as an alternative to JS models, Cormack-Jolly-Seber (CJS) models, or other models based on Robust Design or the integration of Robust Design and recovery data. Rather, we present our models as an alternative to MRLs, containing all of the information in MRLs and also providing a first estimate of population mortality structure, while remaining unaffected by the sample-size, recapture-type, and population-mortality curve biases which affect MRLs. Compared to capture-recapture models, our approach is cruder, but presents the important advantage of returning accurate estimates in situations where CR models' assumptions are strongly violated and data are too sparse for CR models.

Here, we develop an open-population, continuous-time model with the aim of estimating population mortality structures from data held for all species in a large, centrally-managed band-recovery database. We have chosen to develop an open-population model for obvious reasons (a mortality-structure model obviously must allow for the death of individuals). We have chosen a continuous-time model because centrally-managed datasets have many contributors working at many locations according to schedules determined by their own research requirements, so splitting into discrete marking and/or recapture periods (as in Burnham 1993; Catchpole 1998) was not well-supported by the data structure. Further, animal trapping attempts where no animals were captured may not be recorded, so it is not possible in principle to distinguish between zero effort and zero recaptures despite effort. We have chosen a panmictic model as a first-attempt solution, but note that our model may be applied to subsets of national-scale datasets, so a discrete-space form of our model can potentially be achieved by estimating location-specific parameters separately for individual marking locations. A continuous-space form of our model is also conceivable, as the key requirement for a continuous-space form of our model is a continuous-space estimate of observation probability, which could plausibly be generated from band-application records. We hope to extend our model to a continuous-time, continuous-space framework in future work. However, the panmictic and discrete-space versions of our model may be of use in cases with very high movement and extremely limited movement, respectively.

## METHODS

### Modelled mortality curves

Our model takes a sample of individuals marked as nestlings or newborns and with known ages-at-death (i.e., individuals recovered freshly dead), and uses the proportion of the sample that has died by each age to estimate this proportion in the population. Because there are biases that we expect to affect the probability of a given recovery-at-death being made, it is necessary to model those biases and re-weight each record according to its probability of being observed under the model.

Our model accounts for three major potential biases: ‘Availability’, ‘Intensity’ and ‘Mark-loss’. ‘Availability’ is, for each potential age-at-death, the proportion of the marked animals that could have achieved that age. Note that this usage contrasts with ‘Availability for capture’ in discussions of analyses which account for heterogeneous capture probabilities of individuals: for our model ages-at-death, rather than individuals at each discrete time-point, are differentially ‘Available’ (cf. Pledger et al., 2003). We correct for differences in Availability by up-weighting observations of deaths at ages that relatively few of the marked animals could have attained. For example, in an animal species that was first marked twenty years ago, and in which ten individuals per year have been marked, the oldest possible recorded age-at-death is twenty years, and only five percent of the marked animals could have achieved that age, whereas ninety-five percent of all marked animals could have been observed dying at one year of age. The assumption of zero population growth, found in composite dynamic models (see Table 1.1) is unnecessary in our model because all deaths are drawn from a known set of births and weighted accordingly by the correction for differences in availability by individuals. If uncorrected, differences in Availability would result in younger ages-at-death being over-represented in the model.

‘Intensity’ is the effect of research effort on the annual probability of observation within a species. We correct for variation in Intensity using, for each year, the predicted value of a constrained linear model fit between the number of animals marked in a year and the number of animals observed in a year, expressed as a proportion of the value for the year with the most intense study. We reason that researchers marking animals are also likely to report recoveries of dead, marked animals. We also reason that research projects often occur for sets of sequential years, separated by many years from the next research project on a species. Linear models were constrained to have an intercept  $\geq 0.1$ , and a slope  $\geq 0$  – i.e., even under no active study, species were assumed to have an observation-rate of at least one individual per 10 years, and increasing study intensity could not decrease the probability of observation of an individual dying in a year. These restrictions are

admittedly ad-hoc. They serve to prevent our algorithm from fitting zeroes for recapture probability in some years, and therefore giving infinite weight to any individual recovered in those years, as otherwise happens on some small datasets. Nevertheless, we consider them reasonable: if individuals of marked species were truly observed at a rate less than one individual per ten years, we would not have a dataset to analyse, and if increasing animal-marking effort truly caused a reduction in the absolute number of animals observed, scientists would presumably have stopped marking animals. If studies involve marking and observing animals for sets of contiguous years, then failing to account for differences in Intensity would result in over-representation of short-lived (e.g., less than, say, half a typical study-duration) relative to longer-lived individuals.

‘Mark-loss’ is any loss of marks from marked animals that renders them individually unrecognisable. In seabirds, which are marked with leg bands, we correct for Mark-loss as a function of time. We modified Ludwig's (1981) 'General Model of Band Loss' into a lognormal distribution of mark-loss times. Following Ludwig (1967), we used 65% band-wear as the likely band-loss point (i.e., the point at which 65% of the band's original mass has been lost to wear; but see also Ludwig 1981, Hatch and Nisbet 1983 and Ludwig et al. 1996 for discussion of estimates of band loss-points in different species). Not all seabird species have published wear-rate estimate for their bands available in the literature. For species with no available estimate, we inferred a likely wear-rate from published studies of comparable species (Table 1.2 and Appendix 1.1). With slight modification, this approach is transferrable to other animals (e.g. tagged fish and mammals). Failure to account for Mark-loss would result in an under-representation of long-lived individuals in the model.

If the interval between the first marking of a species and the end of the monitoring period exceeds the maximum longevity of the species (see *Assumptions and limitations of the fitted models*, below), then:

$$W_a = 1/(C_x / \max(C)) \quad [1]$$

$$W_i = 1/(I_y / \max(I)) \quad [2]$$

$$W_b = 1/(1 - L_y) \quad [3]$$

$$W_{aib} = W_a W_i W_b \quad [4]$$

$$W_{aib} = (1/(C_x / \max(C)))(1/(I_y / \max(I)))(1/(1 - L_y)) \quad [4a]$$

where:

$W_a$  is the weighting resulting from differences in Availability,

$W_i$  is the weighting resulting from differences in Intensity,

$W_b$  is the weighting resulting from differences in Mark-loss,

$W_{aib}$  is the combined weighting for an individual observation,

$C_x$  is the number of individuals that could have been recorded dying at age  $x$ . If all marked individuals were marked as nestlings, this is the sum of those marked  $\geq x$  years ago,

$\max(C)$  is the maximum value of  $C_x$  over all potentially-observed ages. If all marked individuals were marked as nestlings, this equals  $C_1$ ,

$I_y$  is the fitted Intensity, i.e., the predicted number of recaptures in the year that datapoint  $y$  was recovered, based on the number of animals marked in that year,

$\max(I)$  is the maximum value of  $I_y$  over all values of  $y$

$L_y$  is the probability of band-loss before reaching the age of observed datapoint  $y$ .

Ludwig (1981) gives the standard deviation of band wear-rates tended as one-third of the mean wear-rate across a range of band-types, and notes that 95 – 97 % of measured wear-rates were within two standard deviations of the mean, implying an approximately Normal distribution of observed band wear-rates. Individual bands are lost when 65% of a band's starting mass has been lost to wear (Ludwig, 1981).  $L_y$  is therefore the value of a cumulative log-Normal distribution evaluated at the age of datapoint  $y$ , with location parameter  $\mu = \ln(65 / r)$  and scale parameter  $\sigma = 0.333 \ln(\mu)$ , where  $r$  is the species-specific band-wear rate given in Table 1.2.

Once  $W_{aib}$  has been calculated for each observation, the weighted observations are used to estimate a mortality curve. The proportion of the population that has died by age  $x$  is estimated as the sum of all  $W_{aib}$  scores for animals which died at an age less than  $x$ , divided by the sum of all  $W_{aib}$  scores. Our approach is therefore similar to the Horvitz-Thompson approach used in some animal abundance estimation (Borchers et al. 1998; Buckland et al. 2010), in that the probability (relative to a 'most observable' state, in our case) of observing each datapoint is estimated, and that estimate is used to correct the dataset for under-representation of some classes of datapoints.

**Table 1.2:** Band wear-rates for seabirds used in model-fitting. Each wear-rate is an estimate of the proportion of mass lost by a band per year, estimated from published band wear-rate measurements groups of similar birds. Band metal is the current recommended band metal for each species, as recorded in ABBBS (2000). Band-metal codes: Aluminium – Al; Stainless Steel – SS; Incoloy – In. For full details of band wear-rate estimation and data sources relevant to the estimates, see Appendix 1.1. Taxonomy follows Gill and Donsker (2015).

Latin	Common	Wear rate	Group	Band metal
<i>Thalassarche cauta</i>	Shy Albatross	0.42%	Albatrosses	SS
<i>Macronektes giganteus</i>	Southern Giant Petrel	1.15%	Fulmarine Petrels	SS
<i>M. halli</i>	Northern Giant Petrel	1.15%	Fulmarine Petrels	SS
<i>Puffinus pacificus</i>	Wedge-tailed Shearwater	0.68%	Shearwaters	SS
<i>P. tenuirostris</i>	Short-tailed Shearwater	0.68%	Shearwaters	SS
<i>Pelagodroma marina</i>	White-faced Storm Petrel	0.43%	Storm Petrels	In
<i>Morus serrator</i>	Australasian Gannet	1.38%	Large Birds	SS
<i>Sula dactylatra</i>	Masked Booby	1.38%	Large Birds	SS
<i>Chroicocephalus novaehollandiae</i>	Silver Gull	4.10% Al; 1.40% SS	Small Gulls	Al or SS
<i>Larus dominicanus</i>	Kelp Gull	1.74%	Large Gulls	SS
<i>L. pacificus</i>	Pacific Gull	1.74%	Large Gulls	SS
<i>Thalasseus bergii</i>	Crested Tern	0.25%	Terns	In

### Model validation

We tested the behaviour of our weighting and curve-fitting approaches by Monte Carlo simulation, generating simulated populations, simulating data-collection from those populations, and estimating mortality curves using our weighting method. The basic simulated populations were designed to represent a well-studied animal species with a large number of total recoveries and relatively simple population dynamics. Modifications to the basic simulation were made to simulate less well-studied populations with different relationships between marking and recovery rates, reduced opportunities to recover dead, marked animals, different underlying mortality structures, and different species-monitoring histories. Our basic simulated population (Fig 2 A1; Table 1.3 A1) represents a good dataset, similar to our real-world dataset for the Short-tailed Shearwater: banding history exceeds maximum plausible longevity by a wide margin, band wear-rates are low, and the total number of observations is fairly large. The modifications to the basic simulation test how our model performs with lower-quality data and where the model assumptions are not met.

The basic simulated population had a sixty-four year marking history (matching the duration of bird-banding in our real-world dataset), 2.22% mean annual mark-wear rate (mass loss), and mark-loss occurred when 65% of the initial mark-mass was lost. Individuals were marked during studies. The number of studies initiated in a given year was a Poisson-distributed ( $\lambda = 0.4$ ) variable, and studies had a Poisson-distributed ( $\lambda = 3$  years) duration, so it was possible for several studies to start in the same year, or for a new study to begin while others were ongoing. Studies marked a

variable, uniformly-distributed (min = 1, max = 100) number of animals per year, and were also major sources of mark-recoveries. During the year in which the greatest numbers of animals were marked, an animal dying was set to have a recovery probability of 40% from research recovery, and an animal's probability of discovery owing to research effort was linearly related to the amount of research effort in that year, so an animal dying in a year with no research effort had a 0% probability of being recovered as a result of research effort. Independently of research effort, the basic probability of recovery of a dead animal from non-research activity was set to 10%. So, an animal dying in the most intensely-studied year had a combined probability of discovery of 46% - four percent of the animals dying in that year were discovered both as a result of research effort and by casual observers, 36% were discovered only as a result of research effort, 6% only by casual observers, and 54% were undiscovered. Conversely, an animal dying in a year where no studies were underway had a 10% probability of discovery – the 10% recovery-probability from non-research effort was the only source of recoveries for animals dying in those years.

We tested the method's robustness to high rates of mark-loss, incorrectly-assumed rates of mark-loss (i.e., mismatch between the real rates of mark-loss for a species and the rate used in the model), differences in true mortality-curve shape (Figure 1.1, and see lines A, C, D and E in Baylis et al. 2014 for formal definitions of the curves used), and reductions in numbers of observed individuals by three mechanisms: reductions in the time interval between the date of first marking in a species and the present day, reduced annual probability of study-initiation, and reduced numbers of animals marked per study-year. We generated estimates of Root Mean Squared Error (RMSE) and bias of our estimates at five, ten, and fifteen years of age for each set of simulated populations based on 500 simulation iterations.

The *R* script used to generate the simulations and confidence intervals is included as Appendix 1.10 to facilitate further testing of our model's robustness to violations of its assumptions, or fits applied to unusual datasets.

### **Fitting curves for a selection of species**

Records of marking and recovery dates were collected from the ABBBS database if they met the following conditions:

- 1) Record was of a member of a seabird Family; and
- 2) Record was of an individual marked as an unfledged young, with exact marking and recovery dates known, and

- 3) Record's recovery data indicated a beachwashed or 'found dead, cause unknown' recovery, and did not indicate that the bird was a skeleton, dried out corpse, or partially decomposed.

Species were selected for further analysis if there were > 20 records from that species. This is an arbitrary cut-off: we expected fitted models with ~ 20 individuals to be inaccurate for at least some estimated parameters, and chose to include these as examples of our model's performance on data-poor species. Twelve seabird species were represented by > 20 records in the ABBBS data.

Annual adult survival rates (i.e., for animals at or above the age of first breeding for their species), annual immature (i.e., for animals between zero and the age of first breeding) survival rates, first-year (i.e., aged between zero and one years) survival rates and senescence rates were estimated from our fitted curves for each species. Published estimates of adult survival, first-year survival, and survival senescence were also sought for each species by searching Web of Science for [species' Latin name] AND mort\*, [species Latin name] AND surv\*, and [species Latin name] AND senesc\*.

Additional graphs were generated of the  $W_a$ ,  $W_i$ ,  $W_b$ , and  $W_{aib}$  corrections for each species through time, to determine typical ranges, variances, and structures of these variables, and for use in model-validation. For each species, the corrected mortality curve, uncorrected mortality curve, and two-parameter Weibull (Weibull, 1951; Therneau, 2015) fitted-models from corrected and uncorrected data were generated. Additionally for each species, diagnostic plots were generated showing  $C_x$  and the relationship between annual numbers marked and recovered.

## RESULTS

### Model validation

In most simulated populations with known mortality curves, our modelling approach generates accurate estimates of the true, underlying population mortality curves (Figure 1.1; Table 1.3) with minimal bias (Table 1.3). This was true across varying mean sample sizes, differing true shapes of mortality curves, and differing band wear-rates, although for obvious reasons, the accuracy increased with increasing sample size (Table 1.3, row D cf. Table 1.3, A1) and decreased with increasing band wear-rates (Table 1.3, row A). When model assumptions were met, observed bias of the estimates was low in our simulations (between one-tenth and one-fifth of RMSE). The degree of bias increased with high band wear-rates and when sample-sizes were reduced by reducing the banding-history, study-initiation rate, or number of animals marked per study year (Table 1.3, rows A and D). Incorrectly-assumed band wear-rates could positively or negatively bias

fitted mortality-rates (Table 1.3, row B). Populations where the juvenile mortality-rates were high relative to adult mortality-rates appear to have reduced bias relative to populations where juvenile mortality-rates are low relative to adult mortality-rates (Table 1.3, Row C).

### **Fitted curves for selected species**

For the 12 species for which we fitted curves, all weighted survival curves estimated higher survival to each age relative to unweighted mortality curves (Figure 1.1), unsurprisingly indicating that modelled datapoints for older individuals tend to be weighted more highly than datapoints from younger individuals. Species differed in their marking histories and patterns of recaptures through time, and weights applied to datapoints for each species differed accordingly. Total weightings ( $W_{aib}$ ) were clearly more influenced by *Availability* and *Intensity* than by *Mark-loss*, indicating a relatively minor effect of mark-loss on our estimates of mortality for these species. There was no clear pattern across species whether *Availability* and *Intensity* was more heavily weighted. Diagnostic plots of *Availability*, *Intensity*,  $W_a$ ,  $W_i$ ,  $W_b$ , and  $W_{aib}$  for all species are presented in Appendix 1.3 – 1.8.

Estimated annual adult survival, immature survival, first-year survival, and senescence rates from our models and published sources are presented for each species in Table 1.4. The oldest age-class in the dataset was close to the maximum observable age-at-death (i.e., the age at which ‘Availability’ = 0) for three species – Kelp Gull, Northern Giant Petrel, and Shy Albatross (Figure 1.2; Appendix 1.3). For these three species, the critical assumption that marking history exceeds maximum longevity may not hold. For Kelp Gull, Northern Giant Petrel and Shy Albatross, peak  $W_{aib}$  scores were also markedly higher than for other species (~70 – 100 vs < 30 for all other species except Masked Booby, see Appendix 1.5), driven largely by high  $W_a$  values, indicating large numbers of recoveries at age-classes with low ‘Availability’. For the Masked Booby, the  $W_{aib}$  peak is largely driven by high  $W_i$  points (see Appendix 1.7), indicating that some individuals were recaptured in years where a hypothetical dead individual has a very low probability of being observed because of low researcher-effort. Estimated age-specific death-rates from our senescence model are presented for all ages after the age at first breeding in Appendix 1.9.

In every species where our model assumptions are met (i.e., excluding Kelp Gull, Northern Giant Petrel, and Shy Albatross), estimated first-year survival rates are lower than estimated immature survival rates and estimated immature survival rates are lower than estimated adult survival rates (Table 1.4, Section A). Estimated adult survival rates are generally high, as would be expected for seabirds, and are close to the estimates of adult survival available in literature sources in all species where our model assumptions are met (Table 1.4, Section A). Estimates of apparent senescence are broadly consistent between species. Most species show positive apparent senescence, although

it is noteworthy that the three smallest species, with the highest rates of annual adult mortality (White-faced Storm Petrel, Silver Gull, and Crested Tern) all have negative apparent senescence in our estimates (Table 1.4, section A).

In general, we should expect survival and senescence rates to be similar in closely-related species. We have three sets of closely-related species in our data where our model assumptions are met: two Shearwaters (Wedge-tailed and Short-tailed Shearwater), two Sulids (Australasian Gannet and Masked Booby), and two gulls (Silver Gull and Pacific Gull). In these sets, the shearwaters are of similar mass (475 g and 546 g), as are the Sulids (2700 g and 2190 g), but the two gulls have very different body-masses (264 g and 1040 g; all masses are mean female masses from Garnett et al. 2015). It is noteworthy that our estimates of all three survival rates and senescence are nearly equal for the two Shearwater species and the two Sulid species. Within the gulls, all three survival rates are higher for the larger species, as would be expected from the long-established pattern that members of larger species tend to live longer (Promislow, 1993).

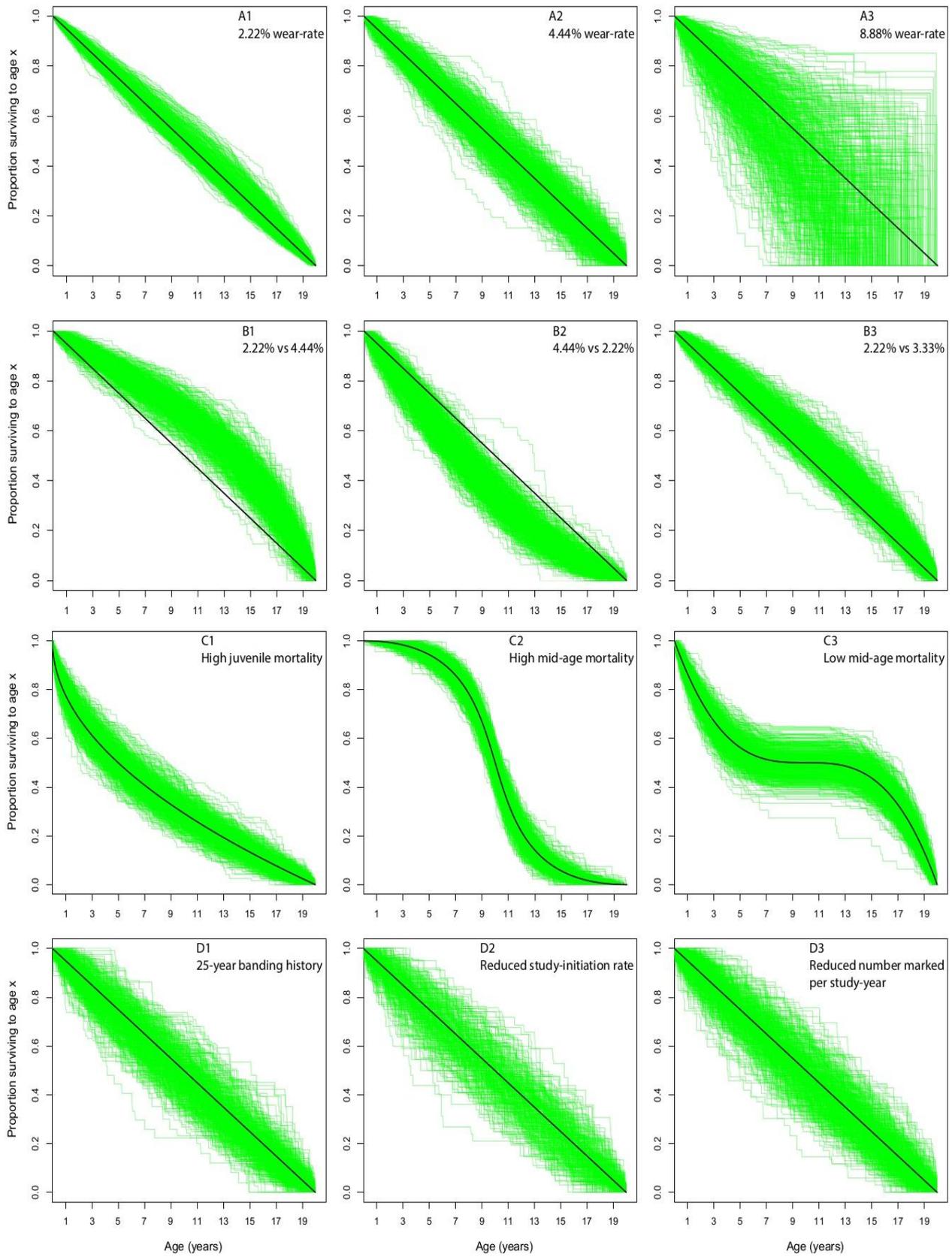


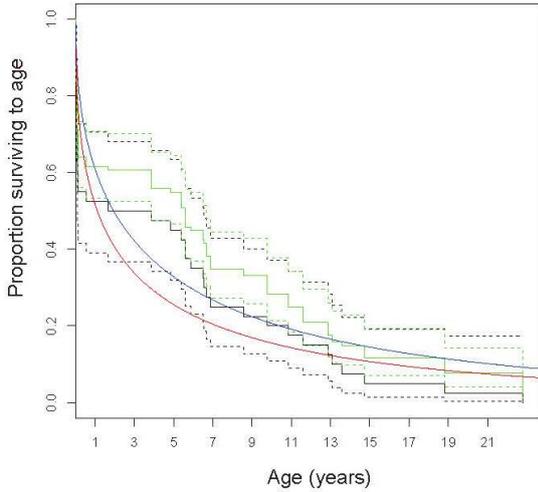
Figure 1.1: (facing page).

**Figure 1.1:** Plots of fitted mortality structures, with and without correction by weighting, and the true underlying mortality structures used in simulation modelling. In each case, the green lines represent the estimated proportion of all individuals which survive to age  $x$  in each of 500 simulated populations, with weighting; the red line represents a random mortality structure without weighting (i.e., if all data points in the set were assumed to represent a random sample of all deaths); the black line represents the true underlying mortality structure in the data. Unless otherwise noted, the defining terms for the simulations are: 64 year history of marking; 20 year true maximum longevity; simulated data had a band wear-rate of 2.22% per annum; 65% mass-loss cut-off for band loss; 2.22% annual band-wear was assumed during model-fitting 65% mass-loss was the assumed band loss point; the number of animals marked in total is the sum of all annual marking events, where annual study-initiation probability is a Poisson-distributed variable with  $\lambda = 0.4$ , study-duration is a Poisson-distributed variable with  $\lambda = 3$  years, annual sample-size (i.e., number of animals marked) in a study is a Uniformly-distributed variable with a minimum of 1 and a maximum of 50; the probability of being found dead for an individual dying during the year with the most intense study is 40%, the probability of any given individual being found dead in the absence of any study is 10% (so an individual dying in the most intensely-studied year has a 46% chance  $((40\% + 10\%) - (40\% * 10\%))$  of discovery). With these parameters, an average simulated population is represented by  $118 \pm 42$  (SD) band-recoveries (Table 1.2). Series A represents departure from these conditions by increasing mark-loss rate. Figure A1 represents 2.22% annual band-wear both in data-generation and model-fitting, A2 represents 4.44% annual band-wear, and A3 represents 8.88% annual band-wear. Series B represents differences between real band wear-rates and modelled band wear-rates. In B1, the real wear-rate is 2.22%, but the model assumes a wear-rate of 4.44%, in B2 the real wear-rate is 4.44% but the model assumes a wear-rate of 2.22%, in B3 the real wear-rate is 2.22% but the model assumes a wear-rate of 3.33%. Series C represents different underlying mortality structures, with C1 having high juvenile mortality, C2 having high juvenile survival, high middle-age mortality, and high old-age-survival, and C3 having high juvenile mortality, high middle-age survival, and high old-age mortality. Series D represents differing numbers of total recaptures, with D1 having a reduced history, of only 25 years of mark-recaptures, D2 having reduced study-initiation probability (annual study-initiations are Poisson-distributed with  $\lambda = 0.1$ ), and D3 having reduced numbers of animals marked per study-year (numbers marked per study-year are Uniformly-distributed with a minimum of one and a maximum of 15).

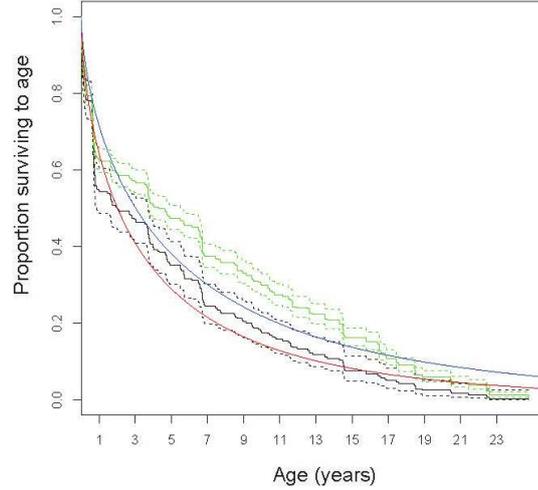
**Table 1.3:** Estimates of error and bias for each simulated population presented in Figure 1.1 (previous page). For each set of simulated populations, the table presents the Root Mean Squared Error (RMSE) and bias of the estimate at five, ten, and fifteen years of age. Proportions are based on a maximum of 500 simulated populations, each with total sample size set by the banding history. For each set of simulated populations, the number of populations in the set and number of recoveries in each population is given as  $N$  ( $n \pm SD$ ), where  $N$  is the number of populations in the set,  $n$  is the mean number of recoveries in a population, and  $SD$  is the standard deviation of the number of recoveries per population. If a simulation had no band-recapture records (i.e., if no studies were initiated, or if none of the marked individuals were discovered dead), or if our model-fitting algorithm failed for a simulation, then that simulation was excluded from the RMSE and bias calculations.

<b>A1 500 (115 ± 40)</b>			<b>A2 499 (93 ± 31)</b>			<b>A3 492 (51 ± 18)</b>		
Age	RMSE	bias	Age	RMSE	bias	Age	RMSE	bias
5	0.049	-0.008	5	0.049	-0.009	5	0.129	-0.047
10	0.056	-0.007	10	0.065	-0.012	10	0.227	-0.093
15	0.052	-0.004	15	0.069	-0.011	15	0.241	-0.095
<b>B1 500 (117 ± 40)</b>			<b>B2 499 (89 ± 31)</b>			<b>B3 500 (120 ± 40)</b>		
Age	RMSE	bias	Age	RMSE	bias	Age	RMSE	bias
5	0.092	0.085	5	0.110	-0.095	5	0.053	0.033
10	0.174	0.166	10	0.164	-0.153	10	0.085	0.065
15	0.188	0.176	15	0.133	-0.125	15	0.089	0.071
<b>C1 500 (126 ± 46)</b>			<b>C2 500 (119 ± 41)</b>			<b>C3 499 (117 ± 39)</b>		
Age	RMSE	bias	Age	RMSE	bias	Age	RMSE	bias
5	0.054	0.001	5	0.024	-0.002	5	0.056	-0.005
10	0.049	0.001	10	0.054	-0.006	10	0.057	-0.006
15	0.038	0.001	15	0.026	-0.002	15	0.057	-0.002
<b>D1 427 (49 ± 21)</b>			<b>D2 276 (38 ± 17)</b>			<b>D3 442 (38 ± 13)</b>		
Age	RMSE	bias	Age	RMSE	bias	Age	RMSE	bias
5	0.076	-0.021	5	0.087	-0.017	5	0.078	-0.015
10	0.088	-0.027	10	0.096	-0.011	10	0.093	-0.015
15	0.077	-0.021	15	0.085	-0.013	15	0.078	-0.009

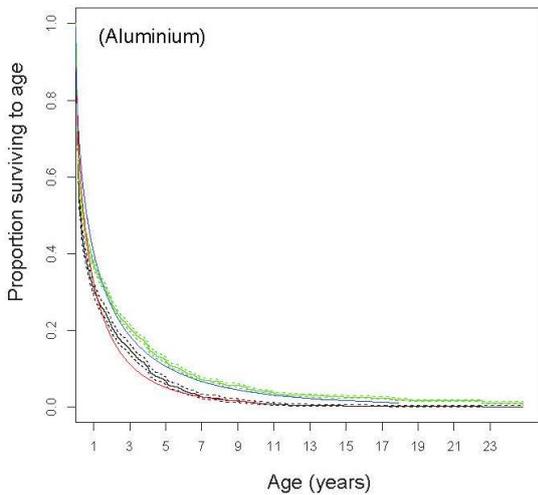
**Wedge-tailed shearwater (*Ardenna pacifica*)**



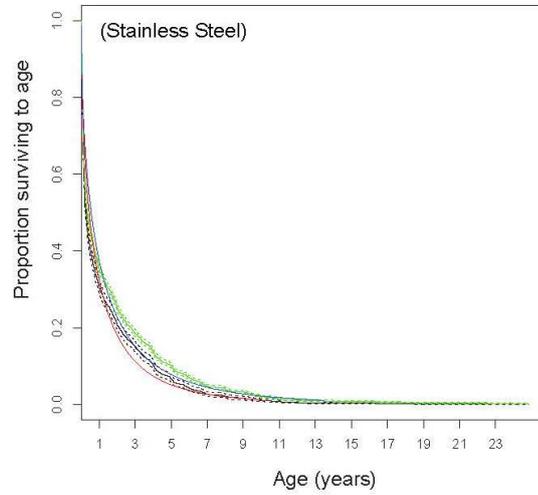
**Short-tailed shearwater (*Ardenna tenuirostris*)**



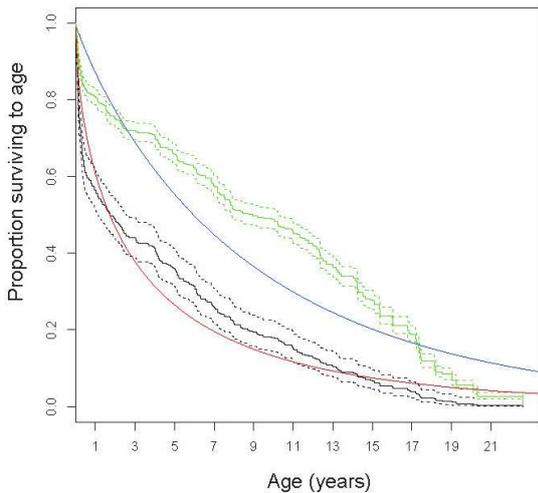
**Silver gull (*Chroicocephalus novaehollandiae*)**



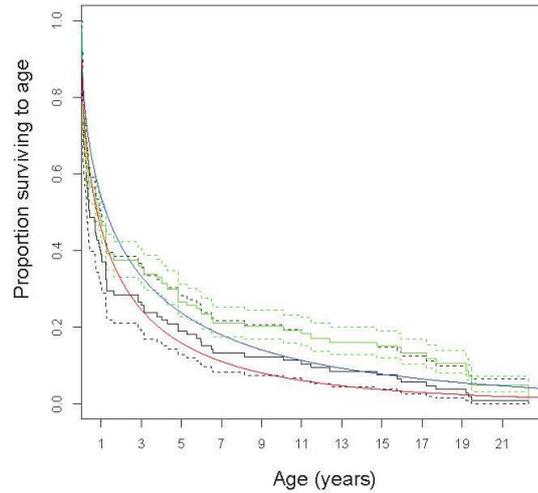
**Silver gull (*Chroicocephalus novaehollandiae*)**



**Kelp gull (*Larus dominicanus*)**



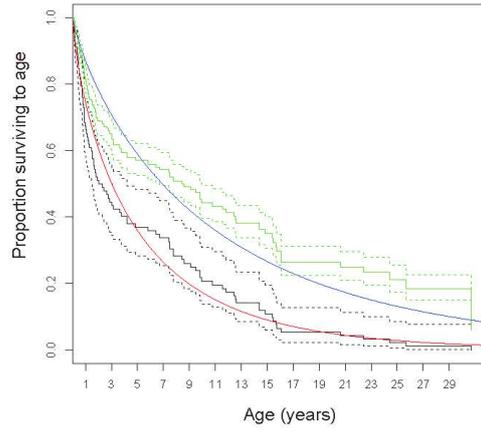
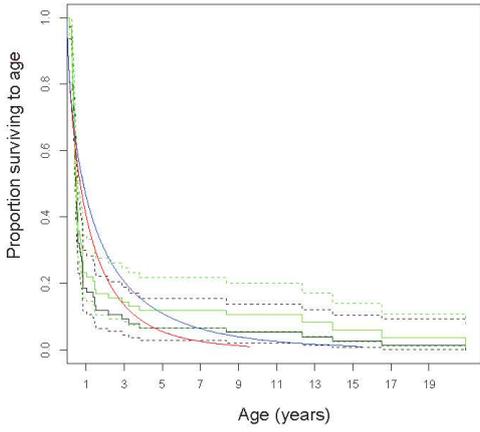
**Pacific gull (*Larus pacificus*)**



**Figure 1.2:** Individual species' fitted curves and Weibull fits. Green lines are weighted model data and their associated confidence intervals, representing the estimated proportion of all individuals which survive to age  $x$ . Black lines are the mortality curves which would be estimated from the available dataset under the assumption that recorded deaths are a truly representative sample of all deaths for that species – i.e., the proportion of individuals estimated to survive to age  $x$  without applying our modelling technique applied to the data. Red and blue lines are Weibull model-fits for the modelled species mortality data using our technique weighted data and not using our technique, respectively.

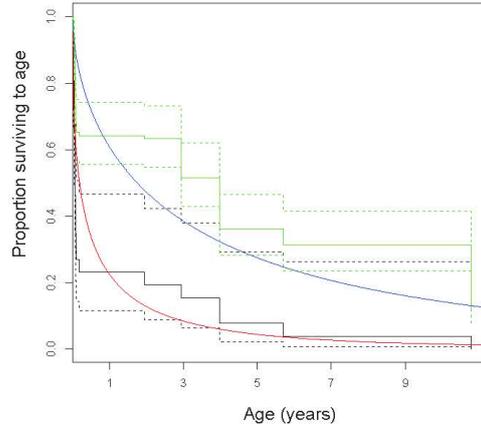
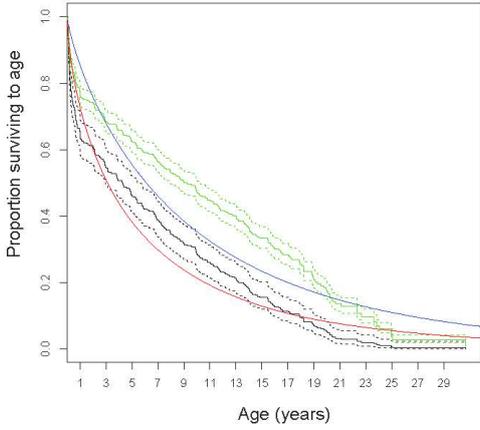
**Southern giant petrel (*Macronectes giganteus*)**

**Northern giant petrel (*Macronectes halli*)**



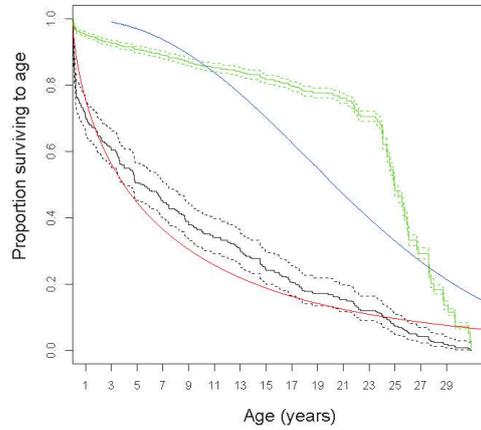
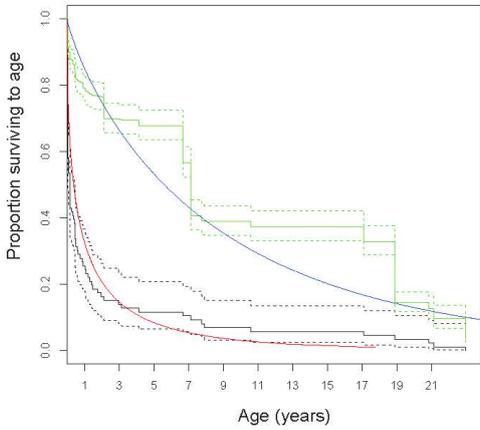
**Australasian gannet (*Morus serrator*)**

**White-faced storm petrel (*Pelagodroma marina*)**

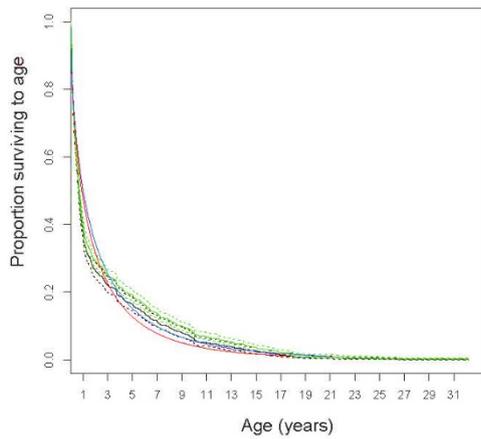


**Masked booby (*Sula dactylatra*)**

**Shy albatross (*Thalassarche cauta*)**



**Greater crested tern (*Thalasseus bergii*)**



**Figure 1.2: continued.**

**Table 1.4** (following pages): Estimates of annual adult survival, annual immature survival, first-year survival, and senescence for the species modelled in this MS, as well as estimates of those parameters taken from the literature (where available). Section A: species where the maximum recorded longevity in our data was not close to the banding history for that species (Appendix 1.3). For Silver Gull, the “SS bands” and “AI Bands” estimates are made under the assumption that all birds were banded with stainless steel bands or aluminium bands, respectively. Section B: species where the maximum recorded longevity in our data was close to the banding history for that species (Appendix 1.3). Our model’s assumptions may be violated for the species in Section B. For our models, an ‘adult’ is defined as an individual in an age-class equal to or older than the youngest record of breeding for that species; an ‘immature’ is defined as an individual in any age-class younger than the youngest record of breeding for that species; and first-year survival is defined as the survival rate from the time of banding as a nestling to one year after banding as a nestling. Estimates of annual adult survival, annual immature survival, and first-year survival are n-weighted estimates from our fitted models, and SE estimates for these parameters were generated by bootstrapping. Estimates of senescence rate are taken from a logit model of mortality rate in response to age-class after the age at first breeding using the `glm()` function in R. For senescence models, fitted estimates of numbers surviving were rounded to the nearest integer to allow model-fitting, and the final two age-classes were excluded to minimise the bias expected from terminating the data series at an age-class with 100% observed mortality. The values for ‘senescence rate’ are the expected change in log-odds of mortality for a one-year increase in age: larger absolute numbers indicate a larger proportional change in mortality-rate with increasing age, negative numbers indicate negative apparent senescence, and positive numbers indicate positive apparent senescence. Estimated mortality rates for each adult age-class are also presented visually in Appendix 1.9. Notes for literature references: Estimates from populations marked with ‘§’ were not presented numerically in the source material, so numbers were taken visually from figures. AFB: Age at First Breeding. NR: no records of survival estimates for this species. NE: no estimate of this parameter in this source. <sup>1</sup> The source of the estimates in Skira (1991) is not described in detail, and may be summaries from the same dataset as presented in Bradley et al. (1989). <sup>2</sup> Voisin (1988) presents estimates of 7.7 % and 8.3 % as the ‘mean annual mortality rate’ for adult Northern Giant Petrel and Southern Giant Petrel, respectively, but these are *absolute* mortality rates: a figure of 7.7 % indicates that, from a starting cohort of 100, an average of 7.7 individuals die each year until all individuals in the cohort are dead. This contrasts with the commonly-presented *relative* mortality rates, where a figure of 7.7 % indicates that for each age-class, an average of 7.7 % of the individuals which survived to enter the age-class did not survive to enter the subsequent age-class. Mortality rates presented here for Southern Giant Petrel and Northern Giant Petrel are relative mortality rates, calculated from raw data in Table 14 in Voisin (1988). Significance codes:  $P = 0 - 0.001$ : ‘\*\*\*’;  $P = 0.001 - 0.01$ : ‘\*\*’;  $P = 0.01 - 0.05$ : ‘\*’;  $P = 0.05 - 0.1$ :

Table 1.4: Continued.

Species	Citation	Population	Annual adult survival rate (bootstrap SE)	Annual immature survival rate (bootstrap SE)	First-year survival rate (bootstrap SE)	Apparent senescence rate (SE)
<b>Section A</b>						
Southern Giant Petrel	This study (N = 75) Voisin (1988)	ABBS dataset (1963 – 2013). AFB taken to be 4 years (Voisin 1988)	0.813 (0.023)	0.421 (0.087)	0.228 (0.054)	0.095 (0.080)
Wedge-tailed Shearwater	This study (N = 40) NR	Ile de la Possession (1966, 1968, and 1969 cohorts) <sup>2</sup> ABBS dataset (1959 – 2009). AFB taken to be 4 years (Szabo, 2013)	0.799 0.868 (0.031)	NE 0.869 (0.043)	NE 0.673 (0.086)	NE 0.027 (0.049)
Short-tailed Shearwater	This study (N = 278) Skira (1991) <sup>1</sup>	ABBS dataset (1958 – 2014). AFB taken to be 4 years (Bradley et al. 1989). Male adults at first year of breeding Female adults at first year of breeding Male adults at ninth year of breeding Female adults at ninth year of breeding Male adults at eighteenth year of breeding Female adults at eighteenth year of breeding Juveniles	0.886 (0.009) 0.922 ± 0.015 0.984 ± 0.018 0.934 ± 0.021 0.924 ± 0.023 0.837 ± 0.019 0.844 ± 0.018	0.845 (0.019) NE	0.667 (0.036)	0.088 *** (0.017) NE
White-faced Storm Petrel	Bradley et al. (1989)	Fisher Island adults 1 – 5 years after first breeding Fisher Island adults 6 – 10 years after first breeding Fisher Island adults 11 – 15 years after first breeding Fisher Island adults 16 – 20 years after first breeding Fisher Island adults 21 – 25 years after first breeding Fisher Island adults 26 – 30 years after first breeding ABBS dataset (1958 – 1984). AFB taken to be 4 years from Madeiran Storm Petrel data (Bried & Bolton, 2005)	0.918 ± 0.007 0.925 ± 0.009 0.882 ± 0.015 0.914 ± 0.019 0.830 ± 0.037 0.800 ± 0.077 0.840 (0.149)	0.759 (0.136)	0.637 (0.160)	-1.167 (0.620)
Australasian Gannet	This study (N = 316) NR	ABBS dataset (1955 - 2013) AFB taken to be 3 years (Ismar, 2013)	0.921 (0.007)	0.884 (0.014)	0.780 (0.026)	0.078 *** (0.011)
Masked Booby	This study (N = 86) NR	ABBS dataset (1962 - 2012) AFB taken to be 3 years (O'Neill et al., 1996)	0.903 (0.045)	0.880 (0.059)	0.792 (0.080)	0.098 *** (0.025)
Silver Gull (SS bands)	This study (N = 2559)	ABBS dataset (1953 – 2013). AFB taken to be 2 years from Red-billed Gull data (Mills 2013)	0.743 (0.015)	0.467 (0.013)	0.372 (0.012)	-0.027* (0.012)
Silver Gull (AI bands)	This study (N = 2559) NR	ABBS dataset (1953 – 2013). AFB taken to be 2 years from Red-billed Gull data (Mills 2013)	0.808 (0.029)	0.487 (0.016)	0.388 (0.015)	-0.074 *** (0.008)

Table 1.4: Continued.

<b>cont'd)</b> <b>Species</b>	<b>(cont'd)</b> <b>Citation</b>	<b>(cont'd)</b> <b>Population</b>	<b>(cont'd)</b> <b>Annual</b> <b>adult survival rate</b> <b>(bootstrap SE)</b>	<b>(cont'd)</b> <b>Annual</b> <b>immature survival</b> <b>rate (bootstrap SE)</b>	<b>(cont'd)</b> <b>First-year</b> <b>survival rate</b> <b>(bootstrap SE)</b>	<b>(cont'd)</b> <b>Apparent</b> <b>senescence rate</b> <b>(SE)</b>
Pacific Gull	This study (N = 105) NR	ABBS dataset (1961 – 2013). AFB taken to be 4 years from Kelp Gull data (Crawford et al., 2000)	0.891 (0.025)	0.704 (0.045)	0.489 (0.053)	0.044 (0.036)
Crested Tern	This study (N = 1299) NR	ABBS dataset (1955 – 2013). AFB taken to be 2 years (Higgins and Davies, 1996)	0.857 (0.012)	0.502 (0.020)	0.403 (0.020)	-0.013 (0.010)
<b>Section B</b>						
Shy Albatross	This study (N = 313) Alderman et al. (2011)	ABBS dataset (1960 – 2014). AFB taken to be 5 years (Brothers et al. 1997) Albatross Island, Australia, from the paper's own model Albatross Island, Australia, from a multi-state CMR model Albatross Island, Australia, 2 § 1981 1982 1983 1984 1985 1986 1987 1988 1990 1992 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002	0.953 (0.002) 0.941 0.961	0.980 (0.005) NE	0.953 (0.012)	0.254*** (0.015) NE
Northern Giant Petrel	This study (N = 92) Voisin (1988)	ABBS dataset (1967 – 2013). AFB taken to be 5 years (Voisin 1988)	0.932 (0.016)	0.885 (0.027)	0.815 (0.046)	-0.004 (0.024)
Kelp Gull	This study (N = 366) Altwegg et al. (2007)	Ile de la Possession (1966, 1968, and 1969 cohorts) ABBS dataset (1977 – 2012). AFB taken to be 4 years (Crawford et al., 2000) Multiple colonies from the species' African range <sup>2</sup> Lambert's Bay, 1999 – 2006	0.812 0.898 (0.007) 0.84 (CI: 0.77 – 0.89) 0.84 (CI: 0.78 – 0.89)	NE 0.912 (0.010) NE	NE 0.811 (0.017) 0.44 (CI: 0.35 – 0.54)	NE 0.165*** (0.015) NE

## DISCUSSION

Our modelling technique produces accurate, repeatable estimates of population mortality structure with minimal bias, under limitations that affect real-world datasets including mark-loss, variable recapture effort, and differing potential availability of age-classes for recapture. Our technique has immediate implications for researchers who require an estimate of the population mortality structure for their species of interest and researchers wishing to make comparisons of the mortality structures of groups of marked individuals. Real-world examples include people wishing to estimate the effect of predator removal on mortality structures within a species (e.g., Almany and Webster 2006), or to estimate evolutionary trajectories of mortality structures between species (e.g., Jones et al. 2014).

Our technique has considerable advantages over existing techniques for estimating population mortality structures. Compared to the meta-analysis technique of Promislow (1991) and the large-scale targeted data-collection of studies such as Loison et al. (1999), a mortality structure may be estimated for more species, using data that are already collected. Compared with the use of MRLs to estimate population mortality parameters, our technique gives a direct estimate of the *complete* mortality curve, rather than estimating a single parameter of it. Researchers may estimate multiple scalar parameters from each species mortality curve as we have done, or use function regression techniques (e.g., Yen et al. 2014) to compare the curves.

Our method should not suffer from the recapture number, recapture type, and curve biases that affect MRL analyses. However, as with all modelling techniques, our method makes assumptions about the nature of the data, and a failure to meet these assumptions could affect the interpretation of fitted models.

### **Assumptions and limitations of the fitted models**

#### **1) *Duration of marking-history for modelled species***

Of the existing modelling procedures outlined in Table 1.1, our modelling process bears the most similarity to the Composite Dynamic family of models: the key assumption of both is that the distribution of ages or age-classes at which deaths are observed or disappearances are seen to occur mirrors the distribution of deaths or disappearances in the population. From this, a death curve is constructed based on the cumulative proportion of all observed deaths at each age or age-class.

Composite Dynamic models have been critiqued for their unreasonable assumptions, chiefly the assumption of 100% mortality in the final year of monitoring, and the assumption that recapture probabilities are constant through time or time-intervals (Burnham and Anderson, 1979). Our modelling process does not assume that recapture probabilities are constant through time – time-variability is instead assumed to be driven by the structure of sampling effort, which is recorded in band-application data and estimated in the  $W_i$  parameter. Our modelling process does not assume 100% mortality in the final year of monitoring, but makes the related assumption that the time interval between the first marking of a species and the present day exceeds the maximum possible longevity for that species. In national-level mark-recapture datasets, the interval between first-marking and the present day is commonly 50+ years (see Appendix 1.3). We consider 50+ years is likely to exceed the maximum plausible longevity of many species. As a coarse test of this assumption for a particular species, we can compare the duration of species' banding-histories with the maximum recorded longevity for that species: if the interval between first marking and the present day is very close to the maximum recorded longevity, the assumption that the interval between first marking and the present day exceeds the species' true maximum longevity is likely violated. In our analysis, we used three points of evidence to conclude that the true maximum longevity of the Shy Albatross exceeded the marking history for this species – a tiny proportion of all bands applied to this species were applied >33 years ago and our estimated mortality curve ended at approximately 33 years (see Appendix 1.3); other *Thalassarche* albatrosses have maximum recorded longevitys of between 37 and 47.2 years (AnAge database, build 13, Tacutu et al. 2013); and we observed many fitted points in our model with excessively high  $W_a$  values. We predict that fitted curves for this species will tend to extend to greater ages as death records continue to be reported, and the marking history approaches and exceeds the true maximum longevity for this species.

## 2) ***Independence of datapoints with respect to age-at-death***

Our model assumes that, apart from the biases modelled by  $W_a$ ,  $W_i$ , and  $W_b$ , marked animal carcasses are discovered at a rate that is independent of age-at-death. The validity of this assumption needs to be considered for each species. For instance, species may be resident in unmonitored sites, in which case they are expected to have a lower probability of detection (Schmutz et al. 1994). If this occurs at a specific age, then this would generate a bias in our model where the period of residence away from the monitored area should be under-represented in recorded deaths, and hence the modelled death-rate in those age-classes should under-estimate the true death-rate. Of the species covered in our dataset, the

Shy Albatross is sedentary around breeding colonies as an adult (from  $\sim 5$  years of age), but ranges widely before that age (Brothers et al. 1997). Hence, the fitted model for the Shy Albatross may be affected by differing levels of observability by age-class, and if similar patterns of movement occur in other species, they may also be affected. Our weighting calculations summarise each year as a separate age-class, so under the current version of  $W_i$ , species that show annual migration between two areas should not be affected by within-year differences in catchability so long as the age-structure of deaths is equal across the two areas.

### 3) *Variance of estimates at high ages-at-death*

We consider the increasing variances of mortality rate estimates at higher ages, as well as at time- or age-ranges in the model with low probability of recapture, to be a shortcoming in our fitted models. This appears unavoidable, because the root cause is a lack of data in the affected time- or age-ranges. Estimates of mortality structure for the many species where detailed, well-designed longitudinal study data are unavailable are a key output of our modelling process. For those comparisons, a degree of noise in individual species-models may be statistically tolerable. For estimates for single species, users should remain aware of the volatility of model-estimates at high age-classes.

### 4) *Population dynamics and the population under study*

We consider that there are two reasonable sets of assumptions that researchers might make about mortality structures in the population under study. The first is that mortality structures are a fixed attribute of each species, and that other than the effects of ‘Availability’, ‘Intensity’, and ‘Mark-loss’, the sampled individuals represent a random sample of ages-at-death for that species. In that case, the fitted model estimates the mortality structure for the species under study. The second possible set of assumptions is that mortality structures are variable within each species, either through time or geographically. In that case, the fitted model estimates the mortality structure of the population for which the researcher’s dataset is a random sample other than the effects of ‘Availability’, ‘Intensity’, and ‘Mark-loss’.

## **Regarding Heterogeneity**

Population heterogeneity is a concern in many animal-recapture models. We consider that for the purposes of estimating mortality structures, two sorts of heterogeneity are potentially concerning:

- 1) Heterogeneous survival rates between, e.g., sexes, migrants and residents, or surviving animals vs. already-dead animals (i.e., the ‘individual quality’ effect, where the

mortality-risk curve for each individual does not match the mortality-risk curve for the population as a whole – see Fox et al. 2006; Lescroël et al. 2009)

- 2) Heterogeneous recapture probabilities between animals, e.g., animals whose core territory is near vs. far from areas of intense capture effort; trap-shy vs. trap-happy animals; or animals belonging to one migratory group or another, where migratory routes differ in monitoring intensity.

Our model assumes that the duration of banding history should exceed the true maximum longevity for that species. If that assumption is met, our fitted models are unaffected by the first type of heterogeneity, as deaths may be observed in proportion to their rate of occurrence right up until the age at which all individuals are dead.

To account for the second form of heterogeneity, we must make one further assumption: that mortality structures are consistent across animals with differing probabilities of being observed. However, if there is a difference in the survival curves of, e.g., residents vs migrants, then this heterogeneity will be correctly modelled (i.e., the curve will correctly describe the marked population as a whole) if the relative probability of observing residents vs. migrants may be estimated and accounted for. This specific possibility is discussed in the section ‘*Spatially explicit recapture effort*’, below.

### **Diagnostics of the fitted models**

Our weighting procedure is essentially a model of the probability of observing each observed point. A potential diagnostic, which we used to identify issues with our Northern Giant Petrel, Kelp Gull, and Shy Albatross datasets, is to examine the distribution of weights used for each species. One should not expect to see many points with high weights, as by definition, they have high weights because they should be rare. It is not a simple matter to suggest what number of highly-weighted points is suspicious, or how highly-weighted a point should be in order to be considered suspicious, as our variable of interest (the true longevity structure of a species) should cause variation in the number and distribution of high-weighted points. However, if the sum of all  $W_{aib}$  values for a species exceeds the total number of marks applied to that species, then we may conclude that model assumptions are violated. An intuitive explanation is presented in the supplementary material, Appendix 1.2.

We consider it prudent, in any analysis using this technique, to make available graphs of  $W_a$ ,  $W_i$ ,  $W_b$ , and  $W_{aib}$  by year of mark recovery for each species (see Appendix 1.4 – 1.8), to facilitate critical examination of the model by reviewers and readers.

Estimated mark loss accounts for only a small proportion of the  $W_{aib}$  score for most of the species analysed in our dataset (see Appendix 1.8). However, it is possible that estimates of band-wear rates enter the literature primarily when researchers notice distressingly high rates of wear in the bands applied to their study species, and write articles to advocate for harder or better-fitting bands (Appendix 1.1; Table 1.1). If this is the case, then our estimated band-wear rates will over-estimate true rates of band-wear. This potential bias could be remedied by taking a selection of worn bands from marked animals, regardless of the age of the tag and its degree wear, and using the wear-rates on these tags to parameterise our band wear-rate estimates (Ludwig, 1967).

### **Fitted Curves and their Interpretations**

Every species showed some degree of elevated mortality risk in early life, compatible with a learning period, although it could also be explained as a bias whereby individuals that die young are more likely to be observed dead, because the researchers who marked them are more likely to be still present at the marking site. On the assumption that studies mark and check for marked individuals, adding a geographic term to research effort should reduce the risk of such a bias, as the research effort correction will be more accurately assigned to individuals that the research is likely to observe.

Several of the species in our model show apparent senescence in survival (Promislow 1991; Gaillard et al. 1994; Nussey et al. 2008; reviewed in Nussey et al. 2013). In order to show apparent senescence in analyses such as ours, survival senescence must be sufficiently strong to overcome the effect of 'demographic heterogeneity' on apparent senescence. Demographic heterogeneity describes the phenomenon where the probability of death per unit time for a population may decline with increasing age, even if all individuals within that population have increasing probabilities of death per unit-time. The unit-time probability of death appears to decline because the lowest-quality individuals (which have high annual risks of death relative to high-quality individuals) die earlier than high-quality individuals. Depending on the degree of variation in individual quality, this effect may cancel out or reverse trends in 'apparent senescence' (defined as changes in per unit-time probability of death for all remaining members of a cohort over increasing age, Nisbet 2001; Nussey et al. 2008). The ability to estimate differences in apparent senescence rates among large groups of species is an important feature of our model, and a complement to existing studies (see Nussey et al. 2013).

## **Related Models and Future Directions**

Our model of encounters is based on a continuous-time framework with a coarsely-estimated time-specific recapture effort, and a panmictic population. We consider that finer-grained estimation of time-specific recapture effort (e.g., using day-specific effort estimates), the inclusion of data from animals resighted alive, and removing the assumption of panmixia would greatly increase the utility of our models. We propose a version of our model that includes geographic structure and uses data from live resightings in Chapter 2 of this thesis.

### **Time-specific recapture effort**

In our model, the  $W_i$  estimator is somewhat incongruous: we have a continuous time response (density of recaptures through time) modelled with a very coarse temporal resolution (annually). This incongruity is not a necessary feature of our model, and can be done away with by estimating  $W_i$  on a daily rather than annual basis, provided that mark-applications are recorded against specific days. We have not done so here solely because we did not consider mortality-rate estimates would be accurate at temporal scales smaller than one year (because of periodic movements, in some species), and so did not request marking-data summarised at daily resolution. Daily-summary data allow more accurate assignment of relevant effort to each recapture record, allowing a reduction in noise in the estimation of the  $W_i$  estimator. The related problem of population-size estimation in continuous-time data has been considered at some length (e.g., Becker 1984; Becker and Heyde 1990; Yip, Fong, and Wilson 1993; Wilson and Anderson 1995; Wilson and Collins 1992), but the extension of this work into population-mortality estimation has received little attention.

### **Spatially explicit recapture effort**

Our model of seabird populations assumes panmixia in the  $W_i$  and  $W_a$  estimates, which limits the number of species to which our model may be reasonably applied. A major complication to database-scale estimation of mortality structures stems from the fact that marking locations may be so close as to be essentially sampling the same population as each other, or so far as to sample completely disconnected populations. We consider that there are two viable alternatives to the assumption of panmixia.

First, one could treat each location of marking as a separate population, and estimate  $W_a$  and  $W_i$  separately for ‘populations’ comprised of animals marked at each location. This approach makes the most sense for sedentary species, where the probability of observing a marked individual is essentially unaffected by research effort at any location other than the one at which it was marked.

Such a model would result in location-specific overall weightings, but would need to be adjusted to compensate for different numbers of recaptures of animals marked at different locations (i.e., without adjustment, an animal recaptured in the most intensely-studied year in a location where few animals were marked, would have a  $W_i$  of 1, equal to the weight given to an animal recovered in the most intensely-studied year at a location where many animals were marked, so animals from smaller projects would not disproportionately affect the fitted model).

Second, one could estimate  $W_i$  over a continuous-time geographic surface informed by spatio-temporal marking and recapture activity, and estimate the probability of an observation of an individual by its relative probability over the surface. Theory concerning spatially-explicit capture-recapture for population-density estimation (SECR) has been developed over the past decade (see Efford 2004; Efford et al. 2004; Borchers and Efford 2008; Efford, Borchers and Byrom 2009; Efford and Fewster 2013), allowing the estimation of recapture probabilities over a two-dimensional spatial surface. If it is possible to estimate a recapture-probability spatial surface using this or a similar method, then  $W_i$  could be made location-specific as well as time-specific. A continuous-space, continuous-time modelling approach has been applied to estimates of population density by Borchers et al. (2014).

### **Modellable species groups**

Birds are often used as a model system for tagged-animal analyses, but they are not the only group on which these analyses may be used. For our model, the only fundamental requirements are that individuals must be uniquely recognisable at birth and at death to allow ages-at-death to be inferred, that records must be kept of the total number of individuals marked through time, that the interval between the first banding of a species and the present must exceed the species' maximum plausible longevity, and that marked animal carcasses are discovered at a rate that is independent of age-at-death after availability, intensity, and mark loss are accounted for. Other species-groups may fulfil these criteria, for instance marked salmonids (Gilbreath et al. 1976), cetaceans individually recognised from scarring or colouration patterns (Constantine et al. 2012; but see Carroll et al. 2016 for a caveat of this technique for estimates including juvenile age-classes), sea-turtles, reptiles and amphibians recognised by permanent marks (Spellerberg, 1977; Balazs, 1999; Waudby and Petit 2011), and any mammal species that may be tagged (Diefenbach and Alt, 1998). Individual-precision genetic identification of individuals may allow this technique to be used without requiring the invasive marking of individuals (see Waits et al. 2001; Banks et al. 2003a,b; Efford et al. 2009), as genomic approaches can yield cost-effective, unambiguous recognition of individuals (Ringler et al. 2015; Woodruff et al. 2015; Szabolcsi et al. 2014).

Seabirds are unusual in that they are very commonly marked as nestlings and observed freshly dead. Many species' typical mark-recoveries feature individuals resighted alive (see Baylis et al. 2014), so extending the technique to handle live recaptures would substantially increase the number of species that it is possible to model, and provide greater sample-sizes for species that it is already possible to model. Extending our model to include live recoveries could be achieved using standard techniques for censored observations in modelling approaches such as Cox's Proportional Hazards modelling (Cox, 1972).

### **Concluding remarks**

Population-mortality curves are a key piece of demographic, and therefore ecological and evolutionary, data. Traditional demographic modelling techniques have made restrictive assumptions that have limited the number of species to which population-mortality curves could be fitted. Our model uses extensive but chaotically-structured national-scale mark-recapture databases to deliver accurate first-estimates demographic structures for a wide range of species, which opens up potential avenues for further research into the populations, conservation, and evolution of species. We have identified as potential challenges to our model geographic structure of recovery probability, marking histories shorter than species' maximum longevitys, and over-estimated mark loss-rates. However, in time, marking histories for all species will lengthen beyond species' maximum longevitys, geographic structuring of discoveries of dead individuals is a problem that can potentially be solved by incorporating geographic information from relatively short-term GPS studies, and over-estimates of mark wear-rates can be corrected by careful observations of worn tags or marks. We believe that this model has great potential utility in providing estimates of important biological parameters from the data stored in central animal-marking databases. As central animal-data repositories increasingly adopt open-data policies, there are many advantages to be gained from developing and using data-analysis methods which provide biologically-relevant interpretations of these datasets.

### **ACKNOWLEDGEMENTS**

The authors would like to thank Steve Beissinger, Rachel Fewster, and four anonymous referees for their comments on various drafts of this manuscript; David Drynan and the Australian Bird and Bat Banding Scheme for making available the ABBBS database under a Creative Commons Author Attribution license; and the many researchers who contributed data to the ABBBS dataset. These analyses could not have been possible without the combined efforts of researchers and database managers over several decades. This research was supported by the Australian Federal Government's Australian Postgraduate Awards scheme and the Holsworth Wildlife Research Endowment Fund.

## DATA ACCESSIBILITY

The data analysed in this manuscript were provided by the Australian Bird and Bat Banding Scheme (ABBBS) under a Creative Commons Author Attribution license. All R scripts generated for this manuscript are available as supplementary materials, Appendices 1.10 and 1.11. Appendix 1.10 includes script for simulating populations and for fitting curves to the datasets generated from those simulated populations, and Appendix 1.11 is the script that generates fitted curves for real-world datasets.

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## Chapter Two

### *A broadly-applicable modelling approach for first-estimates of species mortality curves from public-submission datasets*

#### ABSTRACT

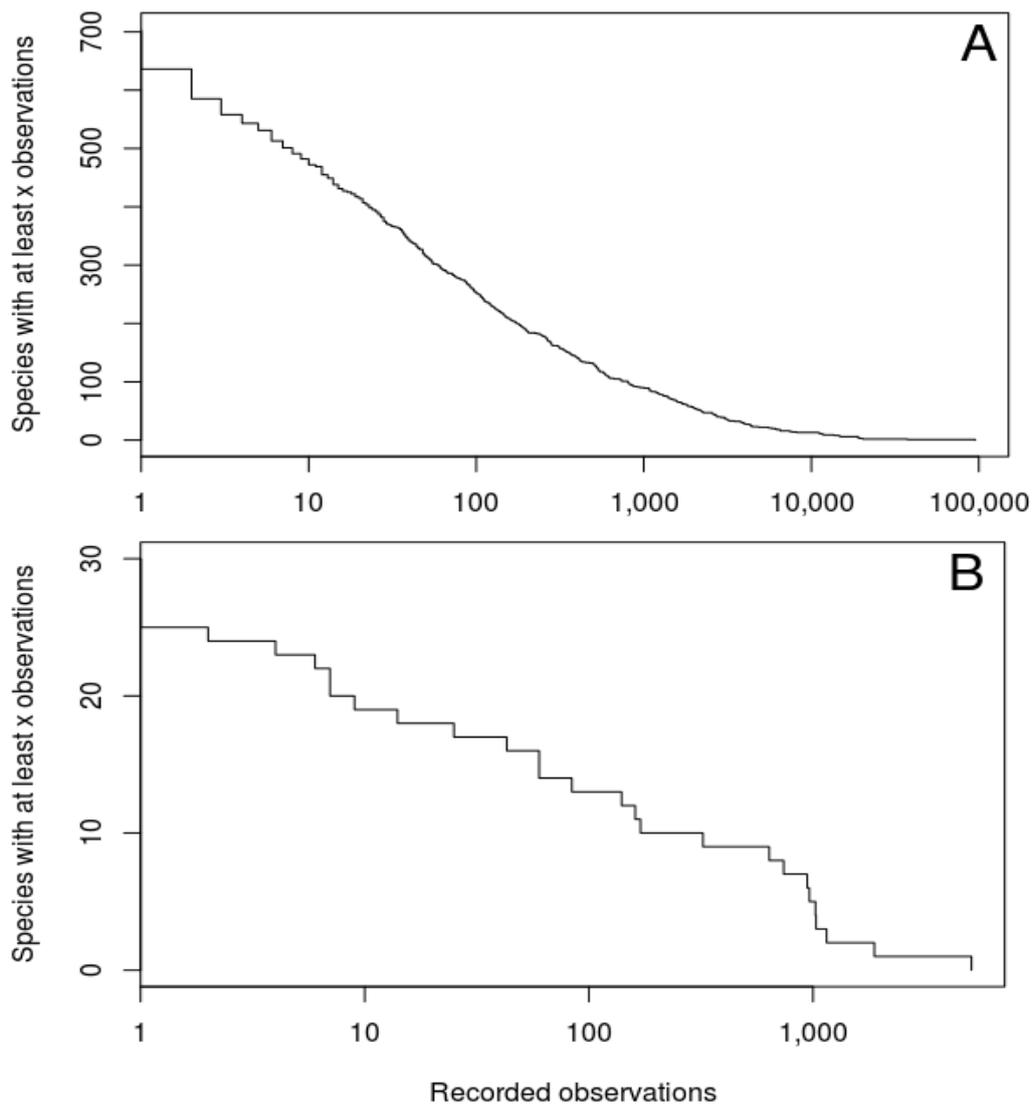
National and international mark-recapture data-repositories are increasingly adopting open-data policies. There is an increasing need for researchers to develop methods which generate meaningful biological estimates from these large, sometimes haphazardly-organised databases. Here, we present a model for estimating population mortality structures from national mark-recapture datasets, employing both data from animals recovered freshly dead and animals observed alive, given research effort approximated from complete records of band-applications at a national scale. Our model specifically handles geographic structure of marking activity, whereas similar methods have required the assumption of equal probability of observation across animals marked at different marking locations. Further, our model is robust to the effects of mark-loss and variable research effort through time and space. We test our model against simulated datasets, and present fitted models for five species of birds, using data from a national scale mark-recapture dataset. Finally, we present an analysis of the number of species for which it is possible to estimate mortality curves using this modelling approach.

## INTRODUCTION

Estimates of population mortality structure, commonly approximated through parameters such as annual or seasonal adult survival, juvenile survival, and senescence, are widely useful. Applications exist in ecology (e.g., Brodie et al. 2013; Erikstad et al. 2013), evolutionary biology (e.g., Bell et al. 2004; Cox & Cresswell 2014; Székely et al. 2014), conservation biology (Cox et al. 2014; Woodruff et al. 2016), and physiology and medicine (e.g., Nussey et al. 2014). Only limited numbers of species and populations have had their mortality structures estimated in detail. For instance, in studies considering senescence components of mortality structures, Nussey et al. (2013) describe birds as an uncommonly well-studied phylogenetic group, yet they can find senescence estimates for representatives of only 58 of 2209 avian genera. Similarly, Székely et al. (2014) note that they could find sex-specific estimates of adult mortality rates for only 187 of the approximately 10,000 species of birds in a systematic literature review.

A widely-applicable method for estimation of population mortality estimates from national-scale mark-recapture datasets has been a long-held goal in ecological modelling (see for instance Møller 1993), and a range of modelling approaches exist for demographic inference from observations of marked animals. However, no approach has yet provided a basis for general-purpose first-estimates of population mortality structures across the diverse set of free-living wild species typically contained in national-scale mark-recapture databases. Analyses of patterns in mortality rates across large sets of species in the wild have therefore considered either Maximum Recorded Longevity (MRL) data (which is biased as a proxy of mortality rates or survival senescence – see Baylis et al., 2014), or meta-analysis of the much smaller subset of species for which dedicated population-demography studies have been conducted (e.g., Nussey et al. 2013; Székely et al. 2014).

Mark-recapture and mark-recovery data exist for thousands of species in national-scale mark-recapture databases (ABBBS; see Figure 2.1). There is much value to be gained from inferring population mortality structures from the data contained in national-scale mark-recapture databases. These analyses can provide increased phylogenetic depth for comparative analyses, can allow inter-population survival comparisons without requiring a dedicated long-running demographic study for each population, and can allow detailed study of the relationships between life-history variables and survival parameters. Further, temporal sub-models could allow analyses of trends in survival structure, presenting the possibility of natural experiments to estimate the effects of specific events (such as a large oil spill) or long-running shifts in environmental conditions (such as climate change) on population mortality structures.



**Figure 2.1:** A summary of the data available in the ABBBS dataset, broken down by number of recapture and recovery records for each species, separately for avian species (A) and bat species (B). Data are as summarised at the ABBBS website at June 2016, and include repeat observations of the same individual

Here, we selectively sample from the Australian Bird and Bat Banding Scheme (ABBBS) database. The ABBBS database is ultimately appealing for analyses because it covers a wide taxonomic and temporal range, banders are obliged to report the time, place, and species against every band applied to an animal (so numbers of marked animals are confidently known), and the data are open-access. Many other national bird-banding schemes exist, and these may offer comparable data structures. In that case, our proposed analyses can be repeated on the datasets held by these other national banding schemes.

As a model national mark recapture database, the ABBBS dataset contains > 570,000 band-resighting, band-recovery, and band-recapture (collectively, 'encounter') records from > 3.2 million marked individuals across > 700 species of birds in 85 Families, and > 14,000 band-resighting,

encounter records from > 46,000 marked individuals across 31 species of bats in 6 Families (ABBBS, 2016). The ABBBS dataset represents a small proportion of the total phylogenetic and geographic diversity covered in the world's national-scale mark-recapture datasets: the EuRing database (covering data from national schemes throughout Europe) recorded its ten-millionth encounter in 2012 (EuRing, 2012), and has presumably continued to accumulate encounter records since then. The North American Bird Banding Program (covering data through multiple national schemes in North America) dataset is similar in volume to the EuRing dataset, containing over nine million encounter records from more than fifty million marked birds (BBL, 2016).

An extensive body of existing theory has been developed around modelling population trends from experiments, with some degree of experimental design underlying the data-collection process (Lindberg, 2010; Kendall et al. 2012). Existing theory therefore makes powerful, flexible inference possible at experimental scales, but is not optimised for wide-scale, multiple-species inference of the sort required to gain insights from national-scale datasets. Here, we use a composite-dynamic model coupled with survey-analysis tools to estimate species-specific mortality structures from recapture and recovery records across multiple discrete populations in national-scale mark-recapture databases, while addressing some of the limitations of popular modelling approaches. In a previous paper, we have used a similar approach in estimation from recoveries of freshly-dead animals only, in exceptionally mobile species where an individual's recovery may occur at effectively any point in the species' range (Chapter 1). This previous 'panmictic' model was primarily viable for populations of seabirds, which range very widely, and for which marking-location is therefore not strongly predictive of death-location. As such, this study is a generalisation of the functionally-panmictic, recoveries-only model, useful across a broader suite of species. The models we present here may be applied over a much broader range of species than the model presented in Chapter One. Increased species-coverage for population mortality models is desirable for its own sake, and will increase the statistical power of tests of survival and senescence models.

Formally, this study considers those species whose movement is sufficiently limited that populations marked at one marking location may be treated as independent from populations marked at another marking location. This assumption relates to our  $W_{il}$  estimator, which fits a linear relationship between research effort and the number of recoveries in a year, independently for each marking location. If animals move sufficiently far that their probability of recovery in a year is impacted by research effort at a marking location other than the one at which they were marked, then a model that also includes an effect of nearby research effort would be more appropriate here. Such a model is mentioned as a possibility in Chapter 1.

A 'hard' test that could be used to check whether recapture effort at one site could influence recapture probabilities for individuals marked at another site is to compare the distance between any two banding locations and the maximum distance between banding and recovery location recorded for that species. If the maximum distance travelled is less than the distance between any pair of marking locations, movement between sites can be ignored as a bias in  $W_{it}$ . Because the extreme movement record is generally an outlying event, we suggest that this 'hard' test is very conservative, but could be applied in future models.

We validate our model by testing it against simulated data and by comparing published estimates to our own for each species.

## METHODS

### Data

Data were collated from the Australian Bird and Bat Banding Scheme (ABBBS) for five species: Bar-tailed Godwit (*Limosa lapponica*), Eastern Yellow Robin (*Eopsaltria australis*), Superb Blue Wren (*Malurus cyaneus*), Satin Bowerbird (*Ptilonorhynchus violaceus*), and Pacific Black Duck (*Anas superciliosa*). These species were selected to cover a diverse range of mark-recapture techniques used by researchers, and a range of movement strategies by the animals, including a hunted species, a species typically captured by cannon-netting, a species principally observed for behavioural research via colour-marks, a very small species commonly captured by mist-net, and a medium-sized species commonly captured by mist-net (Table 2.1). The final set of species was also influenced by institutional factors: in the School of Biological Sciences at Monash University, the Peters lab works closely with fairy-wrens, the Sunnucks lab has an ongoing study of Eastern Yellow Robins, and members of the Clarke lab frequently work with waders. For these species, we could easily find researchers with relevant applied field experience to discuss the models and their outputs.

For each species, data were collected on every individual that had been marked and recaptured at least once, and all marking events for that species. The collected data for marked-and-recaptured animals included (for each animal): date of marking, date of last observation, whether or not the animal was alive at the time of its last observation, location of marking (described as a single locode), species, and band number. We also collated an 'effort' dataset, which summarised, for each species, the total number of animals marked each year in each marking-location.

### Statistical methods

Statistical methods followed our method for estimating mortality curves from panmictic populations (Chapter 1). This was modified to model location-specific recapture probabilities and to, in principle, admit data from animals recaptured alive in addition to recovery records from dead animals.

Location-specific recapture probabilities were modelled by modifying the  $W_a$  and  $W_i$  parameters to location-specific versions of themselves (henceforth,  $W_{al}$  and  $W_{il}$ , respectively). Weightings according to availability and intensity are therefore equal across sites for a hypothetical individual which is recovered on the most intensely-monitored year at its own site, and of the age-class with the most marked individuals at its own site. Observations and weightings were pooled across

multiple sites, and this pooled dataset was used to estimate the mortality curve for the species. Our modelling approach for  $W_{at}$  formally assumes complete isolation between sites – if inter-site movement occurs, our approach here will not account for the possibility that an individual marked at one location may be captured at another location. Nevertheless, the set of species modelled here was selected to include some species with long-distance movements as a partial test of model behaviour in species which violate the isolation of populations from different marking sites.

**Table 2.1:** Capture and resighting methods for the five species in this paper. *Marking methods* and *Resighting methods* list any method used in  $\geq 1\%$  of all marking events or resightings in the ABBBS dataset as at March 11, 2016. N is the number of sightings or resightings, with the percentage of all sightings for the species in parentheses. Multiply-resighted animals are counted multiple times in this table. For the Bar-tailed Godwit we excluded resighting records which did not allow the animal's band number to be determined (e.g., sightings of leg-flags by colour only, which allow identification to a cohort but not as an individual). *Movement* summarises each species' movement patterns, as reported in Garnett *et al* (2015).

<b>Species</b>	<b>Marking methods</b>	<b>N</b>	<b>Resighting methods</b>	<b>N</b>	<b>Movement</b>
Pacific Black Duck	Probably trapped device unknown:	19071 (72.3%)	Probably trapped device unknown:	2832 (34.0%)	Locally dispersive;
	Trapped in cage trap:	3000 (11.4%)	Shot for sport/food:	2635 (31.6%)	locally nomadic;
Superb fairy-wren	Nestling hand raised (abandoned, orphaned, or nest destroyed):	1272 (4.8%)	Colour marking sighted in field (band no. inferred):	1514 (18.2%)	irregular international dispersal
	Trapped with cannon net:	108 (4.2%)	Trapped in cage trap:	588 (7.0%)	
	Trapped in clap trap/net, sprung trap, etc.:	456 (1.7%)	Found dead, cause unknown:	137 (1.6%)	
	Trapped in mist net:	407 (1.5%)	All other methods:	635 (7.6%)	
	Captive bird (was from wild):	333 (1.3%)			
	Trapped by hand or with handheld net:	280 (1.0%)			
Bar-tailed Godwit	All other methods:	446 (1.7%)			
	Trapped with cannon net:	23514 (94.0%)	Trapped with cannon net:	2949 (74.2%)	Total international migrant
	Trapped in mist net:	658 (2.6%)	Readable band/flag/neck col sighted in field, number on standard band inferred:	739 (18.6%)	
	Probably trapped device unknown:	649 (2.6%)	Colour marking sighted in field (band no. inferred):	95 (2.4%)	
All other methods:	189 (0.8%)	All other methods:	191 (4.8%)		
Satin Bowerbird	Trapped in cage trap:	4394 (75.6%)	Trapped in cage trap:	3565 (92.0%)	Locally dispersive;
	Trapped in mist net:	789 (13.6%)	Trapped in mist net:	200 (5.2%)	nomadic partial migrant;
	Trapped, device unknown:	466 (8.0%)	All other methods:	108 (2.8%)	no international migration
	All other methods:	167 (2.9%)			
Eastern Yellow Robin	Trapped in mist net:	22470 (52.1%)	Trapped in mist net:	13387 (91.0%)	Locally dispersive;
	Probably trapped device unknown:	14660 (34.0%)	Hand caught at roost or nest:	584 (4.0%)	no local migration;
	Hand caught at roost or nest:	3045 (7.1%)	Trapped by hand or with handheld net:	455 (3.1%)	no international migration
	Trapped by hand or with handheld net:	2329 (5.4%)	All other methods:	293 (2.0%)	
	Caught at nest by hand, or with handheld net:	503 (1.2%)			
	All other methods:	93 (0.2%)			
Eastern Yellow Robin	Trapped in mist net:	10732 (50.4%)	Trapped in mist net:	6421 (98.4%)	Locally dispersive;
	Probably trapped device unknown:	9944 (46.7%)	All other methods:	107 (1.6%)	no local migration;
	Trapped by hand or with handheld net:	397 (1.9%)			no international migration
	All other methods:	214 (1.0%)			

For location sub-model analyses to be valid, only locations at which the marking history exceeds the marked species' maximum longevity may be included in the final analysis: if records are included from locations where the marking history does not exceed the species' maximum longevity, the final model is expected to under-estimate survival to old age-classes. Similarly, our modelling approach for  $W_{il}$  assumes complete isolation: if inter-site movement occurs, our approach here will not capture the increased probability of recapture of individuals that were marked at one site due to increased monitoring effort at another site.

Because the weightings for each individual resighting are standardised within their site of marking, each site which meets the sub-model assumptions contributes to the final model in proportion to the number of animals that were recovered from that site – directly pooling weighted points would result in essentially random contributions from each sub-model. Our approach is optimal if population mortality structure does not differ between sites, or if an estimate of the mean population mortality structure within a species is desirable.

In the absence of published estimates of wear-rates for the five species modelled here, wear-rates were taken to be 0.42 % / annum, a value typical of published estimates for albatrosses, shearwaters, and storm petrels. In Chapter 1, we found that  $W_b$  values were almost always 1 with very small variance, even in species fitted with fast-wearing bands. Hence, inter-species variability in true band-wear rates is unlikely to substantially impact our fitted models.

### **Fitting final species survival curves: four approaches**

Here, we define variations in *intensity* as spatial and temporal variation in researcher effort that results in spatial and temporal differences in the probability of a marked individual being observed. We define variations in *availability* as the different numbers of animals that can be observed as members of each age-class, based history of animal-marking for a species (i.e., in a species first marked ten years in the past, animals are *available* to be observed in all age-classes under the eleven-year age class, and similarly, younger age-classes generally have higher *availability* than older age-classes). We define *band-loss* as the loss of bands from banded birds resulting from abrasion of the band during its time on the animal.

For a dataset of recovery events from a panmictic population unaffected by individual, age-specific, or temporal variations in *intensity*, *availability*, or *band-loss* the non-parametric maximum likelihood estimate of the mortality curve is the empirical distribution recognisable as the simplest form of the Kaplan-Meier estimate (Kaplan & Meier, 1958). In our related model (Chapter 1), which considered recoveries of freshly-dead animals from within functionally-panmictic populations, we therefore used Kaplan-Meier curves with observations weighted by  $W_{aib}$

to estimate population mortality structures within each species. Here we have considered four approaches to estimating species survival curves from weighted observations, and attempted all of them. The exact algorithms used in each case are available in MEMOIR v 0.92 (and above). We predominantly present results based on the non-parametric estimator, excluding live resightings, as these are the least biased estimates, but we present an example of fitted models to data for each technique in order to highlight their potential uses.

#### ***Nonparametric estimator, excluding live resightings***

One possible approach is to exclude live resightings and fit individual Kaplan-Meier models for each locode, then pool these models for an estimate across all locations (see Figure 2.4A). In this case, each locode's model is equivalent to a species model in Baylis et al (2016). It is desirable to have the better-studied locations contribute more to the final model than the less-studied locations, and this is achieved by weighting the contribution of each sub-model by the number of datapoints informing that sub-model. This approach is unaffected by censoring, and robustly incorporates data from multiple locations into the final model. Because data from live resightings are not used, the final estimate is expected to be less precise than a model that also includes information from live resightings.

#### ***Nonparametric estimator, including live resightings***

A second approach is to employ Kaplan-Meier estimation using the standard technique to account for right-censoring within each population (Kaplan and Meier 1958; Therneau, 2015; see Figure 2.4B). This will result in accurate, unbiased estimates of the survival curve if censoring is non-informative, and non-informative censoring is most likely when there are few or no multiply-resighted individuals in the population. Where the assumption of noninformative censoring is violated, the resulting estimation bias can be severe (see Figure 2.4B).

#### ***Parametric estimator, excluding live resightings***

For species where data are too sparse for non-parametric estimators to give useful estimates, or where a parametric estimate is desired for other reasons, a parametric model may be fit to weighted data. Standard parametric survival models include the two-parameter weibull, the exponential, the gaussian, the logistic, the lognormal, and the log-logistic. For all of these models, the R package 'Survival' provides model-fitting tools incorporating weighted, possibly censored, data (Therneau, 2015).

When live recaptures are excluded, parametric sub-models which incorporate observation weightings are unbiased and accurate under the standard assumptions of such models (Figure

2.4C). Importantly, the species mortality-curve should come from a distribution which can be accurately approximated by the parametric model in use. In the case of our simulated populations, the two-parameter Weibull clearly over-estimates survival in young age-classes, under-estimates survival through middle-age, and over-estimates survival in old age-classes, but these biases would be less pronounced in populations experiencing approximately Weibull-distributed mortality. Pooling sub-models is achieved by weighting model predictions across all sub-models by the number of datapoints informing that sub-model, as for the non-parametric examples.

### ***Parametric estimator, including live resightings***

A final approach is to use a parametric estimator for each location's sub-model, and include live resightings (Figure 2.4D). This approach is subject to bias from informative censoring, as for the non-parametric estimator including live resightings. However, full models generated from parametric sub-models were substantially less affected by informative censoring than full models generated from non-parametric sub-models in our simulations (contrast Figure 2.4a and 4b with 4c and 4d). Pooling sub-models is achieved in the same way as for parametric estimators excluding live resightings.

### **Internal Validation**

To prevent errors associated with our modifications to the established model, we tested the modified model against simulated datasets with differing mark-recapture histories and population mortality structures between populations. Specifically, we generated datasets where animals had differing probabilities of being observed alive or dead (i.e., we increased or decreased the probability that an animal would be observed, given that it was alive, relative to the probability that an animal would be observed, given that it had recently died), datasets differing in the number of banding-locations, datasets differing in the number of animals banded per banding-event, and datasets differing in the clustering of marking-events (i.e., the probability of an animal-marking study being initiated in a given year was modified, but the long-run average number of animals marked per year was held constant by increasing or decreasing the number of animals marked per study).

### **Cross-validation**

The five species selected have published estimates of population-mortality available. We searched the published literature for reports of annual adult survival-rate, annual juvenile survival-rate, and survival senescence rate, and compared the published estimates to own for each species.

## RESULTS

### Internal Validation

Estimated mortality-curves for simulated datasets were closely related to the underlying population mortality-structures, though the amount of error differed substantially between simulated populations, and in one extreme case (the simulations with the greatest number of marking-locations included in any set of simulations), the simulation provided no datasets where our algorithm's requirements for inference were met (Table 2.2, Figure 2.2 B2). There were simulations in which models incorporating live recaptures had a large estimated bias relative to RMSE, apparently caused by informative censoring (Figure 2.4). Parametric models were also biased by their parametric constraints (Figure 2.4).

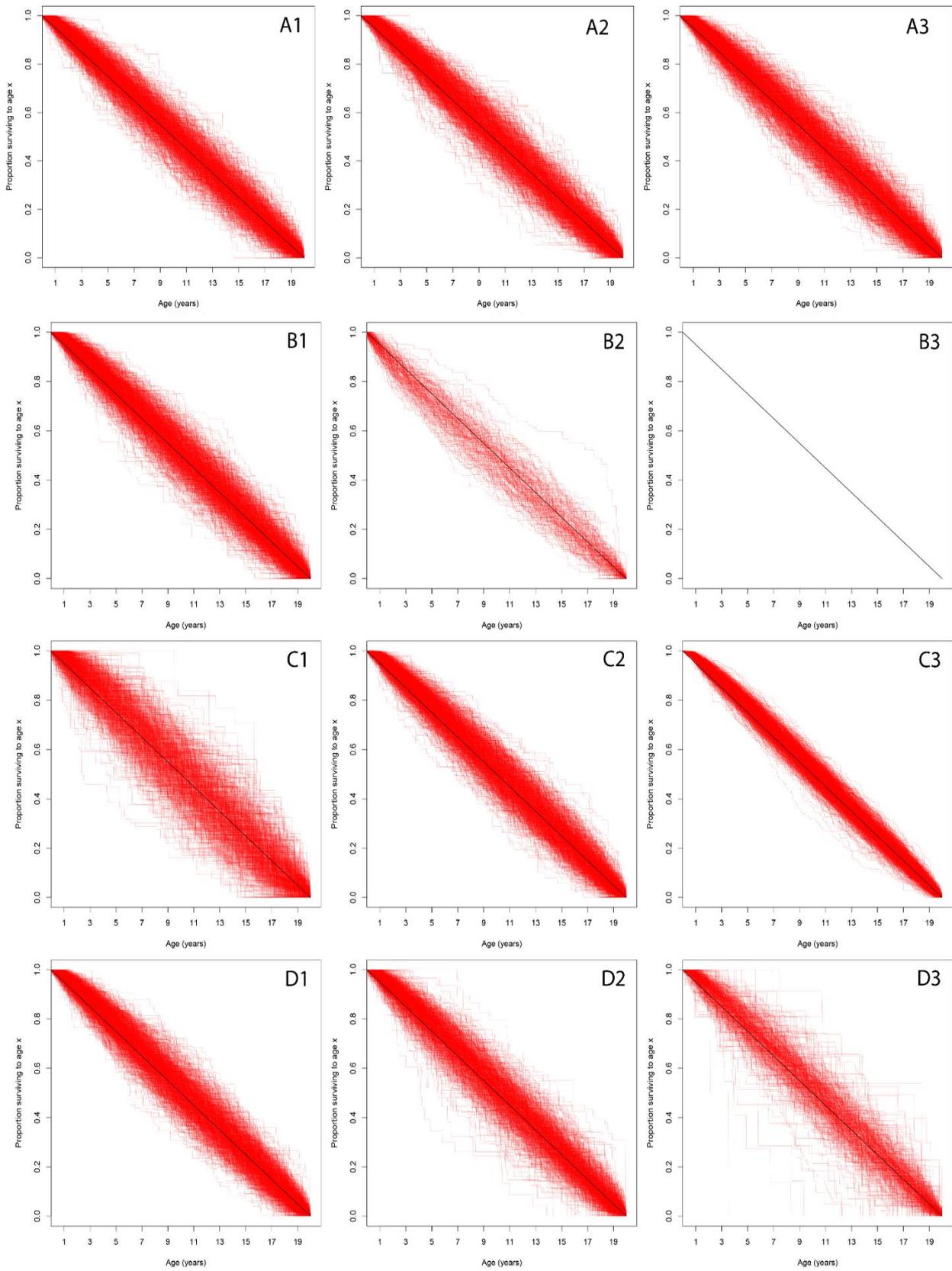
### Species mortality-curve estimates and cross-validation

The estimated mortality-curves for all five species are smooth curves, with elevated mortality-risk in juvenile age-classes. For all species except the Bar-tailed Godwit, fitted mortality curves are very close to the unweighted mortality-curve estimate, indicating fairly small age-related differences in estimated *availability*, *intensity*, and *band-loss*. For the Bar-tailed Godwit, relatively heavily-weighted observations of older individuals, likely a result of adjustment for *mark-loss* and *availability* resulted in a marked divergence between the weighted and unweighted curve. Fitted mortality curves for each species are presented as Figure 2.3.

A comparison of estimated annual adult survival, annual juvenile survival, and annual senescence rates from this study and from published sources is presented in Table 2.3. For annual adult survival estimates and juvenile survival estimates, error estimates are provided by bootstrapping, and for survival senescence estimates, error estimates are provided from a logit model of proportional survival as a function of age. Modelled juvenile mortality, annual adult survival, and senescence rates closely follow published rates for these species, falling within the range of published estimates in nearly all cases. For the Eastern Yellow Robin, estimated annual adult survival is at the lower end of the range of estimates from other sources, which we suspect to be caused by a specific shortcoming in estimating mortality this species' mortality-curve exclusively from dead recoveries (see Discussion).

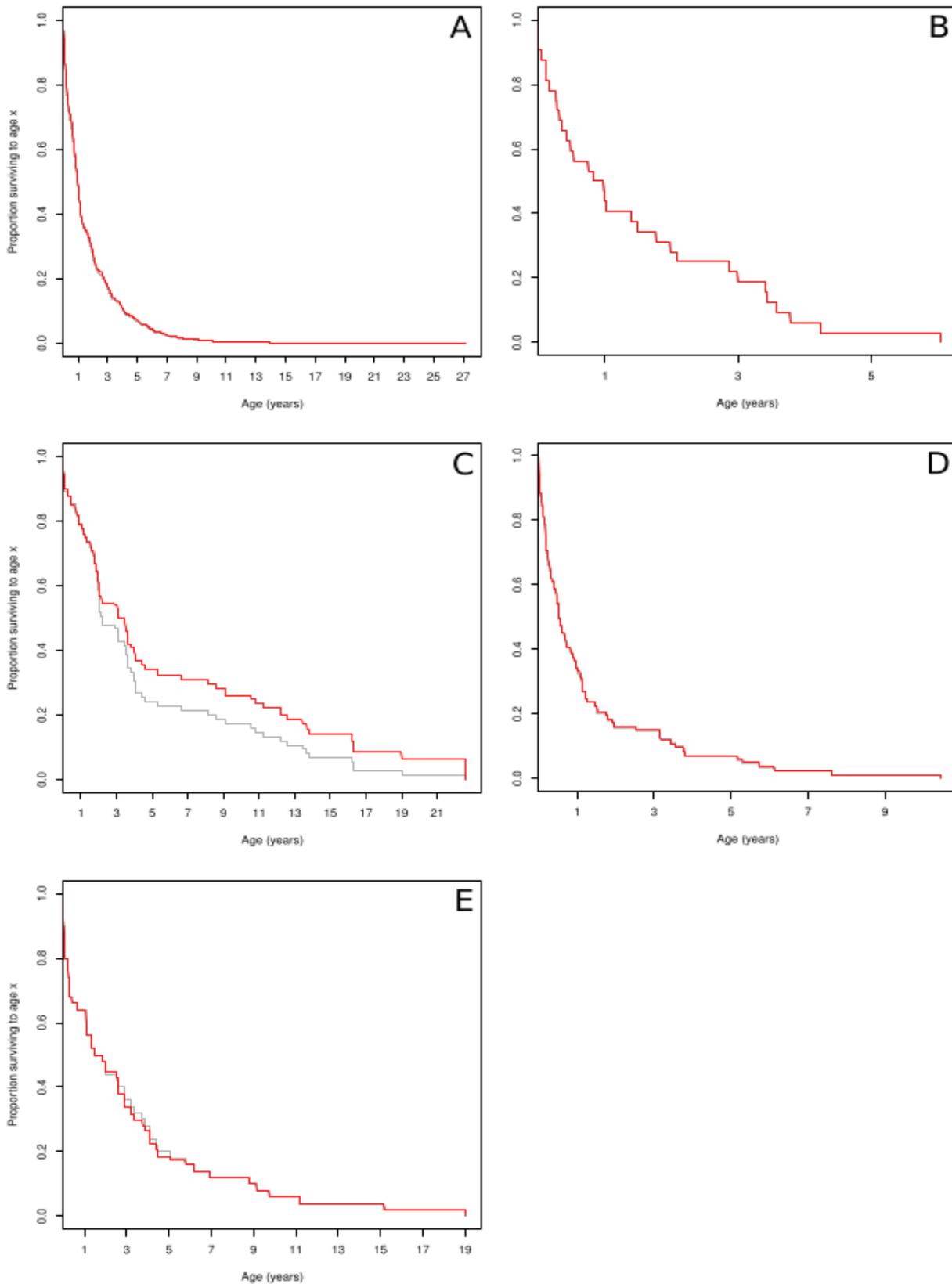
**Table 2.2:** Degrees of confidence for each simulated population presented in Figure 2.2. For each set of simulated populations, the table presents the Root Mean Squared Error (RMSE) and bias of the estimate at five, ten, and fifteen years of age. Proportions are based on a maximum of 1000 simulated populations, each with total sample size set by the banding history. For each set of simulated populations, the number of populations in the set and number of recoveries in each populations are given as  $N (n \pm SD)$ , where  $N$  is the number of populations in the set,  $n$  is the mean number of recoveries in a population, and  $SD$  is the standard deviation of the number of recoveries in a population. If a simulation had no band-recapture records (i.e., if no studies were initiated, or if none of the marked individuals were discovered dead), or if the `MEMOIR.fit` algorithm failed for a simulation, then that simulation was excluded from the proportion calculation.  $N$  and  $SD$  are the mean and  $SD$  of the number of individuals recaptured in each simulation, with populations with zero recaptures excluded.

<b>A1 931 replicates</b>			<b>A2 923 replicates</b>			<b>A3 924 replicates</b>		
Age	RMSE	bias	Age	RMSE	bias	Age	RMSE	bias
5	0.068	0.048	5	0.074	0.055	5	0.072	0.052
10	0.071	-0.040	10	0.069	-0.031	10	0.072	-0.034
15	0.068	-0.057	15	0.067	-0.056	15	0.069	-0.056
<b>B1 994 replicates</b>			<b>B2 173 replicates</b>			<b>B3 0 replicates</b>		
Age	RMSE	bias	Age	RMSE	bias	Age	RMSE	bias
5	0.071	0.051	5	0.059	-0.016	5	NA	NA
10	0.070	-0.036	10	0.099	-0.075	10	NA	NA
15	0.066	-0.054	15	0.078	-0.062	15	NA	NA
<b>C1 734 replicates</b>			<b>C2 957 replicates</b>			<b>C3 987 replicates</b>		
Age	RMSE	bias	Age	RMSE	bias	Age	RMSE	bias
5	0.090	0.051	5	0.071	0.055	5	0.062	0.055
10	0.102	-0.031	10	0.066	-0.031	10	0.048	-0.035
15	0.087	-0.060	15	0.064	-0.053	15	0.056	-0.053
<b>D1 959 replicates</b>			<b>D2 828 replicates</b>			<b>D3 427 replicates</b>		
Age	RMSE	bias	Age	RMSE	bias	Age	RMSE	bias
5	0.071	0.053	5	0.078	0.056	5	0.092	0.054
10	0.068	-0.033	10	0.075	-0.029	10	0.091	-0.035
15	0.066	-0.055	15	0.071	-0.052	15	0.076	-0.057

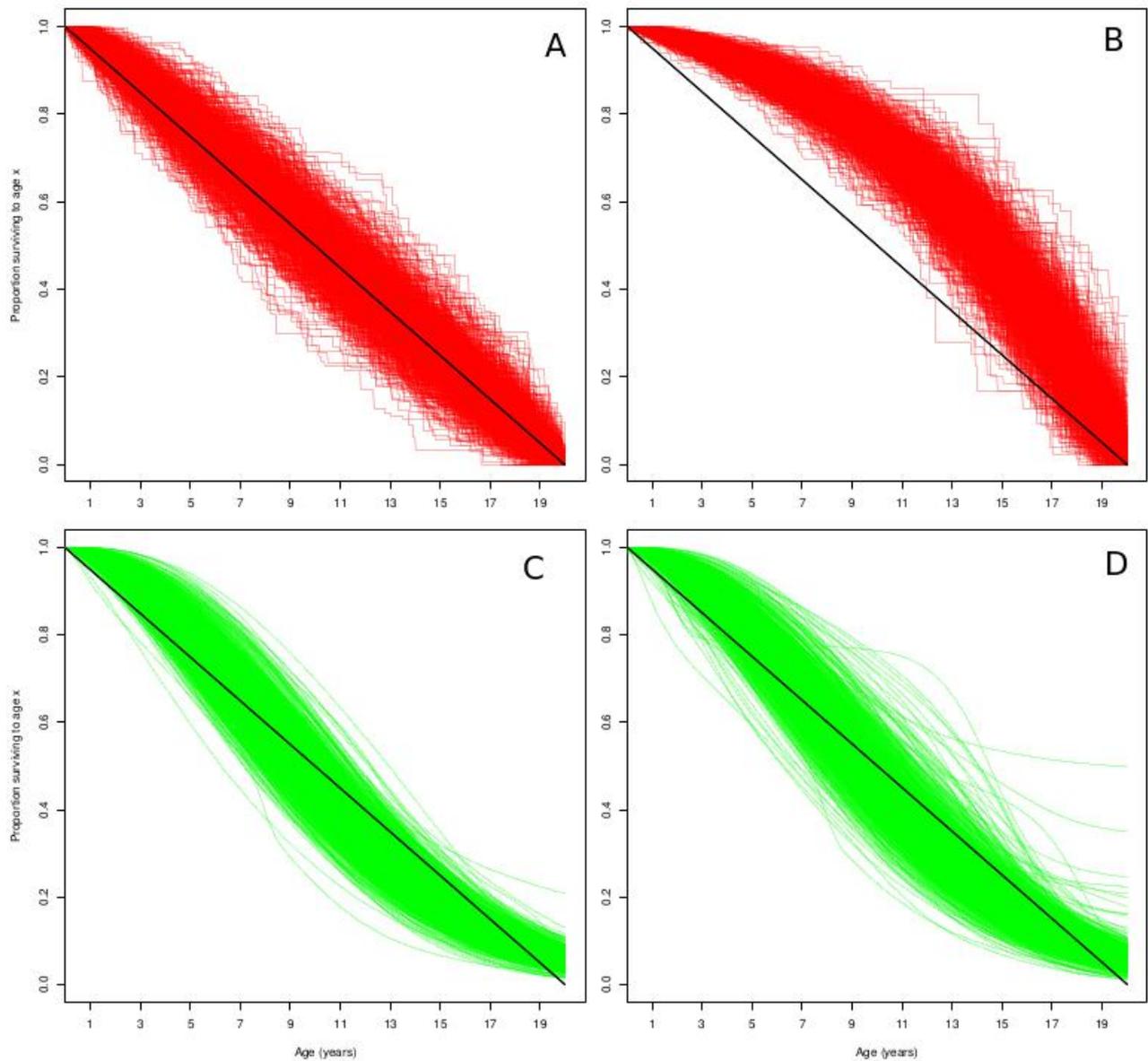


**Figure 2.2:** (facing page).

**Figure 2.2:** Plots of fitted mortality structures and the true underlying mortality structures used in simulation modelling. In each case, the red lines represent the fitted mortality structures from 1000 simulated populations, and the black line represents the true underlying mortality structure in the data. Unless otherwise noted, the defining terms for the simulations are: 64 year history of marking; 20 year true maximum longevity; simulated data had a band wear-rate of 2.22% per annum; 65% mass-loss cut-off for band loss; 2.22% annual band-wear was assumed during model-fitting 65% mass-loss was the assumed band loss point; the number of animals marked in total is the sum of all annual marking events, where annual study-initiation probability is a Poisson-distributed variable with  $\lambda = 0.4$ , study-duration is a Poisson-distributed variable with  $\lambda = 3$  years, annual sample-size (i.e., number of animals marked) in a study is a Uniformly-distributed variable with a minimum of 1 and a maximum of 50; the probability of being found dead for an individual dying during the year with the most intense study is 40%, the probability of any given individual being found dead in the absence of any study is 10% (so an individual dying in the most intensely-studied year has a 46% chance  $((40\% + 10\%) - (40\% * 10\%))$  of discovery). New default settings (specific to the geographically-explicit model including observations of live animals) are: an animal that is alive in a year when a study is undertaken at its site of marking has a 50 % probability of being observed (i.e., setting `liveRecapDeflator` in `MEMOIR.sim` = 0.5), and zero otherwise, and animal marking potentially occurs at 5 locations (but may occur at fewer than five in a given simulation if no studies are stochastically initiated at a location). Simulations in Series A differ in the maximal probability of resighting an animal in a year when it is marked and alive (setting `liveRecapDeflator` in `MEMOIR.sim`): A1 has `liveRecapDeflator` set to 0.2, in A2 it is set to 0.5, and in A3 it is set to 0.8. Simulations in Series B differ in the number of different marking-locations included in the model, when the probability of a study being initiated in each year in each marking-location is equal between marking-locations (setting `locs` in `MEMOIR.sim`): B1 includes 3 marking-locations, B2 includes 10 marking-locations, and B3 includes 30 marking-locations. Simulations in Series C differ in the relative marked-population size at each site: all simulations include 5 marking-locations, but in C1 each active study marks between 1 and 20 individuals per year, in C2 each active study marks between 1 and 60 individuals per year, and in C3 each active study marks between 1 and 180 individuals per year (setting `catchSize` in `MEMOIR.sim`). Simulations in Series D differ in the proportion of all marking events which occur at each marking event (by modifying both `batchProb` and `catchSize` while keeping the long-run mean number of marked animals constant): in D1 the probability of a new study starting at each site in each year is 0.5, and each study marks a maximum of 40 individuals per year of operation, in D2 the probability of a new study starting at each site in each year is 0.2 and each study marks a maximum of 100 individuals per year of operation, and in D3 the probability of a new study starting at each site in each year is 0.05 and each study marks a maximum of 400 individuals per year of operation.



**Figure 2.3:** Fitted mortality curves for the five species modelled in this study. Grey lines represent a simple composite dynamic model of population mortality structure – i.e., it assumes that sightings or recoveries of animals at each age represent a truly random sample across all age-classes. Red lines represent MEMOIR-weighted pooled mortality-curve models fit using Kaplan-Meier fits for location sub-models, excluding live recaptures. A: Pacific Black Duck; B: Eastern Yellow Robin; C: Bar-tailed Godwit; D: Superb Fairy-wren; E: Satin Bowerbird.



**Figure 2.4:** Fitted models from 1000 simulated populations, each with a maximum of five banding locations. A: Non-parametric maximum likelihood estimates for sub-models (weighted Kaplan-Meier), excluding live resightings; B: Non-parametric maximum likelihood estimates for sub-models (weighted Kaplan-Meier), including live resightings; C: Parametric (two-parameter Weibull) estimates for sub-models, excluding live resightings; D: Parametric (two-parameter Weibull) estimates for sub-models, including live resightings. Data for this figure are the same as in Figure 2.2, subplot A3. Simulation A3 was chosen because it clearly showed the the informative censoring bias in non-parametric fits; other simulations were affected by this bias to a lesser degree.

## DISCUSSION

Our method generates accurate, repeatable estimates of population mortality structures for multiple species, using data which are recently open-access and currently under-utilised. Where estimates of annual adult survival or annual juvenile survival were available for two or more populations of a species, our estimates for mean annual adult survival and mean annual juvenile survival were generally within the range of estimates available in the literature for populations of that species (Table 2.3). We therefore consider that our estimates are accurate approximations to the true, underlying population parameters, with accuracy comparable to that of widely-used modelling approaches which underlie published estimates. Our estimation approach could readily be adjusted to provide sex-specific, location-specific, or other covariate-specific estimates of survival rates within species, simply by subsetting datasets before analysis.

There is a theoretical reason to suspect that our estimate of the annual survival rates for the Eastern Yellow Robin is an under-estimate of the true rate: for this species, there were no sites for which more than one marked animal was recovered dead. In this situation, the MEMOIR algorithm provides no effective weighting, as points cannot be weighted relative to other points within any of the location-specific sub-models. In MEMOIR weighting, we expect records of older individuals should be more highly-weighted than records of younger individuals: within each location,  $W_b$  is constrained to increase with age;  $W_a$  can only increase with increasing age; and if marking activity tends to occur at a site in blocks of contiguous years (as in the research effort of a single PhD project, or at a lab-group's recurring study site for a long-running project), then research effort should generally be lower with increasing temporal distance from a given animal's time of marking – which should tend to inflate  $W_i$  for older records as well. Note that this proposed structure for  $W_i$  assumes that differences in  $W_i$  by age are mainly driven by studies ending. If, for instance, long-running studies tend to become larger with time, or if within a study, researchers get better at sighting individuals through time,  $W_i$  may have a different structure. Without effective weighting, we would generally expect the estimated survival rates to be biased downward relative to the true survival rates.

Nevertheless, our estimate of the annual adult survival rate for the Eastern Yellow Robin is within the range of published adult survival-rate estimates for populations of this species (Table 2.3). In section *A live-resightings-only estimator of mortality for MEMOIR-weighted data*, we discuss an estimation approach not based on the Kaplan-Meier estimator, which may be useful for species like the Eastern Yellow Robin, where live recaptures and resightings are much more common than observations of dead animals.

**Table 2.3:** Our estimates of annual adult survival, juvenile mortality, and senescence rate for the five species in our data, with estimates from the literature for comparison. Estimates are presented for each population and sub-population analysed in each source. If estimates for annual adult survival rate or annual juvenile survival rate were presented as mortality rates in the source material, these have been converted for presentation here. NS = no study was found which estimated these parameters for this species. NE = not estimated. Dead records are based on fits generated in MEMOIR v 0.93, using development versions `MEMOIR.fit()`, `MEMOIR.simplotter()`, and `MEMOIR.survrates()` between v 0.93 and v 0.94. All estimates from this study are from mark-recoveries of dead individuals only. \* Tidemann (2004) included loss of eggs in calculations of first-year mortality, which may explain the discrepancy between their first-year mortality estimate and ours. + Cockburn et al. also present data for females, which is identical to Russell et al. (2007) Canberra Botanic Gardens population. We suspect these two papers use a partially-overlapping dataset. (EAAF = East-Asian Australasian Flyway)

<b>Species</b>	<b>Citation</b>	<b>Population</b>	<b>Annual adult survival rate (bootstrap SE)</b>	<b>First-year survival rate (bootstrap SE)</b>	<b>Senescence rate (SE)</b>
Pacific Black Duck	This study	ABBBS dataset (1953 - 2015)	0.61 (0.04 SE)	0.51 (0.05 SE)	-0.09 (0.01 SE)
	Halse et al. (1993)	All, SW Australia, 1968 – 1975	0.63 (SE 0.04; range 0.32 – 0.97)	0.56 (SE 0.06; range 0.31 – 1.00)	NE
		Males, SW Australia, 1969 – 1975	0.67 (SE 0.04; range 0.30 – 1.00)	NE	NE
		Females, SW Australia, 1969 – 1975	0.63 (SE 0.06; range 0.37 – 0.79)	NE	NE
Caithness et al. (1991)	Males, Auckland Acclimatization District, NZ, 1957 – 1974.	0.55 (SE 0.04)	0.38 (SE 0.04)	NE	
	Females, Auckland Acclimatization District, NZ, 1957 – 1974.	0.55 (SE 0.12)	0.49 (SE 0.11)	NE	
Bar-tailed Godwit	This study	ABBBS dataset (1961 - 2015)	0.88 (0.03 SE)	0.80 (0.04 SE)	-0.07 (0.03 SE)
	Piersma et al. (2016)	Birds using the EAAF, 2007	0.90 (CI: 0.84 – 0.94)	NE	NE
		2008	0.90 (CI: 0.87 – 0.93)	NE	NE
		2009	0.93 (CI: 0.90 – 0.95)	NE	NE
		2010	0.89 (CI: 0.86 – 0.91)	NE	NE
		2011	0.80 (CI: 0.77 – 0.83)	NE	NE
		2012	0.71 (CI: 0.68 – 0.74)	NE	NE
Satin Bowerbird	This study	ABBBS dataset (1970 - 2015)	0.80 (0.06 SE)	0.71 (0.08 SE)	-0.06 (0.07 SE)
	NS	NS	NE	NE	NE
Superb Fairy-wren	This study	ABBBS dataset (1955 – 2015)	0.62 (0.06 SE)	0.36 (0.06 SE)	-0.29 (0.10 SE)
	Tidemann (2004)	Canberra Booligal	0.66	0.12 *	NE
			0.25	0.03 *	NE
	Russell et al. (2007)	Canberra, AUS, 1988 – 2007 (Canberra Botanic Gardens) & 2003 – 2005 (Campbell Park).			
		Breeding females with helpers	0.78	NE	NE
		Breeding females without helpers	0.67	NE	NE
	Cockburn et al. (2008b) +	Canberra Botanic Gardens 1988 – 2007	0.70	NE	NE
Breeding males with helpers		0.70	NE	NE	
	Males without helpers				
Eastern Yellow Robin	This study	ABBBS dataset (1956 - 2015)	0.58 (0.07 SE)	0.52 (0.10 SE)	-0.04 (0.21 SE)
	Zanette (2000)	Females in small fragments	0.742 (SE = 0.067)	NE	NE
		Females in large fragments	0.667 (SE = 0.105)	NE	NE
	Debus (2006)	Imbota Nature Reserve, Armidale, AUS	0.78 (SE = 0.15)	NE	NE
		Breeding males (2000 – 2001)	0.46 (SE = 0.14)	NE	NE
		Breeding males (2001 – 2002)	0.89 (SE = 0.11)	NE	NE
		Breeding females (2000 – 2001)	0.73 (SE = 0.14)	NE	NE
		Breeding females (2001 – 2002)			

Of the four final curve-fitting techniques, the non-parametric estimate excluding live recaptures was the most consistently accurate and unbiased in our simulations (Figure 2.4). We suspect that the bias in the non-parametric estimate including live recaptures results from informative censoring in the simulated data. If this is the case, then a potential standard solution is to interval-censor the Kaplan-Meier fits (as in Thurneau, 2015), but at present, we lack the real-world data to test this solution: records of every sighting for each individual would be required, rather than the most recent record for each individual. Interestingly, parametric survival-estimates seem far less affected by informative censoring than non-parametric estimates (Figure 2.4).

To our knowledge, our estimates represent the first published estimates of survival senescence rates for all five species, the first published estimates of the juvenile survival rate for Eastern Yellow Robin, Bar-tailed Godwit, and Satin Bowerbird, and the first published estimate of adult survival rate for the Satin Bowerbird. One notable exception to the tight agreement between our modelled mortality rates and previously-published mortality rates is in the estimated juvenile survival-rate for Superb Blue Wrens. The estimate of survival-rate published in Tidemann (2004) is presented as “% nesting success (survival after a year)”, indicating that the estimate in Tidemann (2004) may have included loss of eggs or un-fledged young. In contrast, our estimate makes use exclusively of dead recoveries of marked animals, so losses of eggs and deaths that occur before an individual is large enough to band do not count towards our estimates of juvenile mortality.

### **Potential non-independence of estimates from cross-validation**

Because the studies we have used for cross-validation mostly occurred in Australia, and all bird-marking studies in Australia are required to submit data to ABBBS, our dataset contains at least some records from individuals included in our cross-validation studies. The shared individuals imply a degree of non-independence between our fitted mortality models and the analyses used as cross-validation. We do not believe that the use of shared individuals will have an analytically-important impact on our findings: our models are based entirely on observations of dead animals, whereas the studies we cite for cross-validation are predominantly based on observations of live animals, and therefore independent from our analyses. The only species for which data from dead recoveries has been used in cross-validation papers is the Pacific Black Duck. Of the two studies we cross-reference for Pacific Black Duck survival estimates, one (Caithness et al. 1991) took place in New Zealand, and is therefore independent from our study. The other (Halse et al. 1993) included 1459 band recoveries from Pacific Black Ducks, all from before 1978. A high proportion of these are likely to be from individuals marked as adults and therefore not included in our study (68% of bands were recorded as being applied to adults), but the exact number of recoveries from

individuals marked as pulli in Halse et al. (1993) is uncertain. Our study uses data from 7248 recovered individuals. If we conservatively assume that all 1459 of the recovered bands in Halse et al. (1993) are also in our sample, this represents 20% of datapoints shared between the two studies. We therefore consider our findings to be largely independent of those in Halse et al. (1993).

### **Future directions: potential modifications to the $W_{il}$ estimator**

In our weighting scheme, the  $W_{il}$  estimator estimates the relative probability that an individual within the set of individuals marked at a given marking-location will be observed. In our existing implementations of the weighting scheme, the  $W_{il}$  estimator only takes information on research intensity within the same locode: an individual's probability of being observed is modelled as depending only on research effort at the exact location that it was marked. If inter-location movement occurs, observation probability may in reality be influenced by research activity at locations other than an individual's marking location.

In the ABBBS dataset, marking locations are recorded as 'locodes'. Each locode is marking-location as defined by the researcher submitting data. Locodes differ in their level of geographic precision: some researchers may, for instance, define any duck caught near a given lake as being in the same locode, whereas another researcher may define a separate locode for each breeding territory in which they sample. Many locodes have a recorded geographic location in decimal degrees format, which opens the possibility of using geographically-explicit analyses, either by summarising banding effort near to the location that each individual was marked in a series of distance bins, or as a continuous surface. Instead of basing the  $W_{il}$  estimate on a model of the form:

$$\text{recovered} \sim a + \text{beta} * \text{banded} + \text{error} \quad [1]$$

we could employ an alternate form, for instance:

$$\begin{aligned} \text{recovered} \sim a + \text{beta} * \text{banded} + \text{beta}_2 * \text{banded}_{0\_10} \\ + \text{beta}_3 * \text{banded}_{10\_20} + \text{error} \end{aligned} \quad [2]$$

where `recovered` is the sum of animals recaptured and resighted at the active locode during the time-period in question, `beta`, `beta_2`, and `beta_3` are estimated parameters, `banded` is the number of animals banded at the active locode during the time-period in question, `banded_0_10` is the number of animals banded between zero and ten kilometres from the locode in question (excluding those banded at the locode in question) during the time-period in question, `banded_10_20` is the number of animals banded between ten and twenty kilometres from the locode in question during the time-period in question, and `error` is random error.

With these versions of the  $W_{il}$  estimator, the recapture probability for an individual in a time-period may vary according to research effort in nearby banding locations, in addition to its own location of banding. Depending on the specific form of model chosen, these modifications to the  $W_{il}$  estimator allow the final model to vary from functionally-panmictic (as in Chapter 1), through to completely geographically discrete.

### **Future directions: a live-resightings-only estimator of mortality for MEMOIR-weighted data**

Problems of using the Kaplan-Meier estimator for final within-location mortality-curve estimation include the amount of noise in estimates when there are few observations of dead individuals, and the fact that the estimator does not respond to differing densities of live observations between observations of dead individuals. Our pooled models rely on individual-location models containing sufficient observations of freshly-dead individuals for datapoints to be weighted relative to each other, but for some species (e.g., in our data, the Eastern Yellow Robin), there may be few or no locations from which  $> 1$  dead observations were made. In these cases our model reduces to an unweighted panmictic model through the pooling process. In the specific case of the Eastern Yellow Robin, multiple recaptures have been made at many of the sites at which the species was banded, so a model based on live resightings would not reduce to an unweighted functionally-panmictic model as our model has. For species like this, or species where there are no observations of freshly-dead animals, an estimate of mortality structure using only live observations would be useful as a primary estimate of the mortality-curve. For species where live resightings are highly numerous compared to dead observations, or in cases where there are at most one dead recovery per location (e.g., in our data, the Eastern Yellow Robin), a live-resightings estimate of mortality structure could also serve as useful cross-validation for estimates made from dead recoveries only. Because dead recoveries are often made by chance observation, survival models based on dead recoveries are often considered robust to the potential biasing effects of animals moving outside the sampling area. Therefore, a comparison of a live-only and dead-only model for the same species could help to quantify any bias in estimates of survival arising from animals moving out of the sampling area.

A further advantage of having separate estimates from recaptures and recoveries is that models based on recaptures are often considered to be biased by the confounding of permanent emigration and mortality, and therefore only estimate 'apparent survival' (e.g., Francis & Saurola, 2002), whereas models based on recoveries are considered to reflect true survival. Within our modelling framework, we have proposed a version of the  $W_{il}$  estimator which could capture detectable inter-site movements, and therefore minimise the effect of permanent emigration on the estimated survival curve (see section *Potential modifications to the  $W_{il}$  estimator*). Since the bias from

confounding permanent emigration and mortality is unidirectional (i.e., the bias can only cause an under-estimate of survival), over a suite of species, models based on recoveries can be used to assess the effectiveness of  $W_{it}$  estimators at modelling-out the effects of emigration on observability.

A live-resightings model could be built as follows: consider the set of all live observations of individuals from a population in which all marked individuals were marked more than that species' maximum longevity ago (i.e., all marked individuals are now dead), for which there has been constant survey-effort across time, for which observability for a given survey-effort does not change with age or time, and for which there is no mark-loss. Assume that death-curves are a fixed attribute of the species, and hence any highly-observable individuals have the same death-curve as less-observable individuals, or equivalently, assume that all individuals are equally observable.

Given a sufficiently large number of observations of marked animals, the number of observations of animals in any age interval is proportional to the number of animals surviving to occur within that age-interval. If we make the simplifying assumption of linearity of death within each age-interval, then where:

$n_{(a < \text{Age} < a+1)}$  is the number of observations of live individuals between age  $a$  and age  $a + 1$ ,  
 $d$  is a density parameter whose value is constant across all values of  $a$ ,  
 $s_{(a + 0.5)}$  is the estimated proportion of the population surviving at  $a + 0.5$ ,

we can state:

$$n_{(a < \text{Age} < a+1)} \sim d * s_{(a + 0.5)} \quad [3]$$

which provides an immediate estimate of relative survival at the midpoint of each age-interval. This calculation and reasoning is essentially identical to classic composite-dynamic mortality-curve estimation techniques (e.g., Bellrose & Chase, 1950), which have been criticised for assuming that recovery probabilities are constant through time, for assuming that negligible numbers of marked animals remain alive when the data are analysed, and that age-specific mortality rates are constant through time (Burnham & Anderson 1979).

For sets of observations from populations where a subset of individuals were marked more than the species' maximum longevity ago, where survey effort has been non-constant, or which experience mark-loss (i.e., most species' data in national-scale mark-recapture datasets), the `MEMOIR.fit()` algorithm provides weightings to account for under-representation owing to variation in *availability*, *intensity*, and *mark-loss*, as defined in Chapter 1. MEMOIR weighting does not formally account for differences in death-rates between years, but in MEMOIR analyses of a typical national-scale animal-marking dataset, animals marked in many different years are

included in the model, which will serve to smooth out effects of year-specific death-rates if they occur. A MEMOIR-weighted composite dynamic model can therefore be used to estimate interval-based mortality structures exclusively from national-scale mark-resighting and mark-recapture data.

## **Applications**

MEMOIR-based analyses of survival may be used to inform decisions at the level of individual species, populations within species, collections of species under differing environmental conditions, or broad-scale evolutionary, global geographic, or ecological hypothesis-testing. In order to inform those decisions, users will need to be able to access the outputs of MEMOIR-based estimates for a broad suite of species, populations in diverse geographic areas, or populations existing under a variety of environmental conditions. To that end, we intend to perform MEMOIR-based analyses for every species in the ABBBS dataset for which sufficient data exist to give reasonable predictions. If the necessary assumptions of MEMOIR-based analysis can be made of the data held by the North American Bird Banding Program, EURING, or other international datasets, the large set of mortality estimates arising from analyses of these datasets could also provide substantial benefits to researchers across many disciplines in biology.

## **ACKNOWLEDGEMENTS**

The authors would like to thank David Drynan and the ABBBS for making public the data used in this paper, and the Australian bird-banding community for collecting this data. This work was supported by the Australian Postgraduate Awards (APA) scheme and by the Holsworth Wildlife Research Endowment Fund.

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## Chapter Three

### *Survival and survival senescence in wild birds: analyses over a broad taxonomic range from national banding scheme data*

#### ABSTRACT

Patterns of death are predicted to vary widely between populations and species, in response to physiological, ecological, and evolutionary pressures. Practical factors have limited the number of species for which complete death-curves are available in wild settings, and have limited the range of age-classes through which changes in death-rates have been modelled. With few exceptions, studies investigating life-history parameters predicted to influence mortality and senescence rates have therefore relied on maximum recorded longevity data, which are noisy and substantially biased, have relied heavily on data from captive populations, whose mortality and senescence structures may differ from populations of the same species in wild settings, or have had limited sample-size and therefore relatively low power. Here, we present analyses of a set of population-mortality models for sixty avian species, from data collected in a national bird-banding scheme. We demonstrate that the 'fast-slow life-history continuum' accounts for much of the variance in adult survival rates, first-year survival rates, and senescence rates between species. We show that phylogeny and measures of sociality (implied by colonial nesting and cooperative breeding) are significantly predictive of adult survival rates, but that residual brain-mass and migratory status do not usefully predict adult survival, first-year survival, or senescence.

## INTRODUCTION

Population mortality-rate parameters, such as annual adult survival rates, survival to breeding age, and annual survival-senescence rate, are core population biology measures, central to questions of conservation, evolution, and ecology. The structure of mortality rates through age-classes varies widely between species (Jones et al. 2008; Jones et al. 2014). It is therefore a goal of ecologists and evolutionary biologists to detect relationships between survival rate parameters and morphological, physiological, behavioural, and ecological variables across species, and to develop theories to explain these relationships. There is an extensive literature of published work on this topic, proposing diverse explanatory models for survival and survival senescence (e.g., Deevey Jr. 1947; Promislow 1991; King 1996; Loison et al. 1999; Wasser & Sherman 2010; Healy et al. 2014; Delhaye et al. 2016). Survival rates between two ages are simple to define: they represent the proportion of individuals who, having survived to a particular age, die before reaching a subsequent specified age. In contrast, senescence may be defined as a complex process potentially involving declines in reproductive output, physiological condition, or survival rate with increasing age (e.g., Marsh & Kasuya 1986; Williams et al. 2006; Nussey et al. 2013; Hassall et al. 2015). Here, we refer only to *survival* senescence, defined as change in annual adult survival rate with increasing age, not senescence in reproductive ability or physiological condition.

Many published reports are based on 'maximum recorded longevity' (MRL) datasets. MRL datasets are relatively noisy, have biases that correlate with the explanatory variables (Baylis et al. 2014), and cannot be directly replicated owing to the impossibility of collecting an independent instance of a species' maximum recorded longevity. Further, MRLs are a single value per species, confounded on juvenile mortality, adult mortality, and senescence, and therefore do not allow investigation of the relationships between survival and senescence rates.

Another approach to determining predictors of survival is to fit population mortality models to observed populations of animals, and analyse differences in population mortality model parameters between species or groups of species, for either wild or captive populations. Survival and senescence parameters may be markedly different in captivity and in the wild (Tidière et al. 2016), and there may be correlates of survival parameters that cannot be observed in captive populations - for instance, a study considering only captive populations would necessarily be blind to effects of long-distance migration on survival, because being a captive individual and being an individual who takes part in long-distance migration are mutually exclusive. We therefore draw an important distinction between survival and senescence *in free-living animals* and survival and senescence *in captivity*, as the patterns and processes differ between the two.

Ricklefs (2010) presents extensive model-based analyses of survival and senescence, covering some 260 species of birds, mammals, reptiles, and amphibians, including wild-living populations of 55 species. Nevertheless, Ricklefs (2010) does not present data for free-living wild birds – although he held data for four wild avian populations, these were the minority of his avian dataset, and so were excluded from analyses to ensure data consistency. Conversely, Jones et al. (2008) present an analysis of data from free-living animals, including senescence estimates for twelve species of birds and eight species of wild mammals. In a meta-analysis of the published literature on senescence, Nussey et al. (2013) provide reports of 'evidence consistent with senescence' in 175 species of birds, mammals, 'other vertebrates', and invertebrates, including evidence consistent with *survival* senescence in 48 species of free-living birds. Together, these numbers suggest that relatively low availability of fitted mortality models for free-living wild birds still presents a limitation to studies of the relationships between life-history parameters and survival rates in these animals.

Despite relatively restricted data, some general relationships between survival and senescence rates, and other life-history parameters, are widely reported. For instance, animals with a larger body-size, lower maximum fecundity and a longer generation time and slower basal metabolic rate will tend to have higher adult survival rates and slower survival-senescence rates than animals of smaller body-size, with higher maximum fecundity, longer generation times, and faster basal metabolic rate – a pattern termed the 'fast-slow life-history continuum' (Jones et al. 2008; Ricklefs 2010). Additional factors have been proposed as explanatory variables for inter-species differences in survival rate and senescence parameters, including migration (e.g., Møller 2006), sociality (e.g., Blumstein & Møller 2008), sexual size dimorphism (Searcy & Yasukawa 1981), and relative brain mass (e.g., Ricklefs & Scheuerlein 2001). Conversely, inter-species differences in life-history factors such as growth rates and provisioning patterns have been explained as a consequence of inter-species differences in age-specific mortality risk (Martin 2015).

Here, we employ the MEMOIR (Baylis et al. *this work*) modelling technique to estimate annual adult survival rates, annual first-year survival rates, and annual adult survival-senescence for multiple species monitored under a national-level bird-banding scheme. We present analyses of the relationships between survival and senescence estimates and life-history variables proposed as correlates of survival or senescence in published studies. Specifically, we present analyses of annual first-year survival, annual adult survival, and annual survival senescence, their relationships with each other, and their relationships with life-history parameters outlined in the previous paragraph, including body mass (average, average male, and average female),

male:female body-mass ratio, relative brain mass, clutch size (mean, minimum, and maximum), egg diameter, migratory status (i.e., international migrant or not), and three measures of sociality (cooperative breeding status, feeding aggregation status, and colonial nesting status). We present data for sixty species, with minimal crossover to other published analyses: Ricklefs (2010) contains survival rate estimates for seven of our species, but solely for captive populations of those species, the dataset of Jones et al. (2008) contains a senescence rate estimate for one of our species, and the meta-analysis of Nussey et al. (2013) contains data for four of our species. Therefore, our dataset represents an independent dataset for all hypotheses tested. Our aim is to provide estimates of the relationships between adult survival, first-year survival, and survival senescence in the wild, and to attempt to replicate a set of published correlations between survival parameters and life-history variables. In cases where published sources have used MRLs as a proxy of a survival variable (e.g., of senescence, or of 'lifespan'), we aim to show what specific survival parameter (if any) is correlated with the life-history variable under study.

## **METHODS**

### **Data**

Data were collected from the Australian Bird and Bat Banding Scheme (ABBBS) dataset. The ABBBS is the central government scheme responsible for organisation of bird banding and issuing of approved bird bands for research, and holds data on bird banding throughout Australia from 1953 onwards. Data were included in our analyses if:

- 1) they were for a species within Class Aves
- 2) at least ten marked individuals from that species had been recovered freshly dead

Data were collected for each marked individual on its date of banding, date of last resighting, recovery, or recapture, state at last observation (alive or dead), and location of banding. For each location where a species had been marked, data were collected on the total number of animals marked at that location for each year from the first year of banding for that species.

All estimates of survival parameters were generated using R version 3.2.2 (R Core Team, 2015), with additional packages 'survival' (Therneau 2015), 'devtools' (Wickham & Chang 2015), and 'MEMOIR' (Chapter 2). Data were taken from the ABBBS dataset for individuals marked as pulli or as juveniles and recovered freshly dead. MEMOIR models were fitted to subsets of these data using 'locode' as a unique location-of-marking identifier and these sub-models were weighted according to sample-size and pooled into a combined model, as described in Chapter 2, for all species with ten or more dead recoveries.

Bird bands come in multiple designs, differing in size, shape, and the metal used to manufacture the band, and the use of several differing band designs within a species presents a potential confound to the MEMOIR model of band wear-rates (see Chapter One and Chapter Two). Band-metal, specifically, determines a large proportion of the variability in band wear-rates within species (see Chapter Four). There were some species in our dataset where individuals had been marked with one of multiple different band metals, and the metal used in each band was not identifiable for all individuals. Therefore, for species which had been marked with multiple band-metals, multiple models were fitted to check for consistency in parameter-estimates from models which assumed a different band-metal. Discrepancies in parameter-estimates between models for different band-metals were small: the mean absolute difference between estimated first-year survival rates assuming two different band-metals was 0.4 %, and the mean absolute difference between adult survival rate estimates assuming two different band-metals was 0.3 % (see Appendix 3.2). For multiple-species comparisons, we used point-estimates from models that assumed that the band-metal currently recommended by the ABBBS had been used for all banding events. In cases where multiple band-metals are currently recommended by the ABBBS, we used point-estimates from models that assumed that the harder band-metal was used for all banding events.

Sixty species from 48 genera met the requirements of this modelling approach (see Appendix 3.2). For those species, we investigated the relationships between first-year survival rates, adult survival rates, and senescence parameters using linear quadratic modelling, employing AIC for model-selection. The estimated survival and senescence parameters for the modelled species, along with the band-metal used in their model, are presented in Table 3.1.

Life-history and taxonomy data for all our species were available from Garnett et al. (2015). We collected data on Hackett coarse clade (a coarse phylogenetic grouping based on the avian phylogeny in Hackett et al. 2008, split as defined in Garnett et al. 2015), morphology (average body mass, male average body mass, female average body mass, and brain mass residual), and breeding biology (average clutch size, minimum clutch size, maximum clutch size, and egg diameter – note that in our data, egg diameter correlates extremely tightly with egg length ( $R^2 = 0.975$ ), so we have kept diameter as a single measure of ‘egg size’), three proxies of sociality (cooperative breeding status, nest aggregation and feeding aggregation status), and movement biology (total migration status). We also calculated the mean male:female body mass ratio from data in Garnett et al. (2015). These variables were selected on the basis of published literature suggesting an association between the variable and survival.

**Table 3.1:** Estimated first-year survival, annual adult survival, and survival senescence parameters for the sixty species. A blank line is left between each Hackett Coarse Clade. Taxonomy follows Gill and Donsker (2017).

Scientific Name	Common Name	Metal	First-year Survival	Adult Survival	Survival Senescence
<i>Anseranas semipalmata</i>	Magpie Goose	SS	0.644	0.951	-0.219
<i>Cereopsis novaehollandiae</i>	Cape Barren Goose	SS	0.282	0.709	-0.297
<i>Cygnus atratus</i>	Black Swan	ML	0.434	0.761	-0.215
<i>Tadorna tadornoides</i>	Australian Shelduck	SS	0.636	0.631	-0.085
<i>Chenonetta jubata</i>	Australian Wood Duck	SS	0.11	0.428	-0.839
<i>Anas castanea</i>	Chestnut Teal	SS	0.304	0.533	-0.392
<i>A. superciliosa</i>	Pacific Black Duck	SS	0.457	0.613	-0.112
<i>Eudyptula minor</i>	Little Penguin	SS	0.39	0.861	-0.143
<i>Pelagodroma marina</i>	White-faced Storm-Petrel	ML	0.412	0.818	-0.333
<i>Diomedea exulans</i>	Wandering Albatross	ML	0.876	0.841	-0.052
<i>Thalassarche melanophris</i>	Black-browed Albatross	SS	0.555	0.852	-0.147
<i>T. cauta</i>	Shy Albatross	SS	0.901	0.939	0.065
<i>Macronectes giganteus</i>	Southern Giant-Petrel	SS	0.379	0.894	-0.259
<i>M. halli</i>	Northern Giant-Petrel	SS	0.755	0.894	-0.003
<i>Fulmarus glacialisoides</i>	Southern Fulmar	SS	0.25	0.667	-20.143
<i>Ardenna pacifica</i>	Wedge-tailed Shearwater	SS	0.676	0.901	-0.053
<i>A. tenuirostris</i>	Short-tailed Shearwater	SS	0.62	0.88	-0.024
<i>Phaethon rubricauda</i>	Red-tailed Tropicbird	SS	0.516	0.848	-0.621
<i>Threskiornis molucca</i>	Australian White Ibis	SS	0.542	0.796	-0.044
<i>T. spinicollis</i>	Straw-necked Ibis	SS	0.263	0.798	-0.301
<i>Bubulcus ibis</i>	Cattle Egret	AM	0.443	0.779	-0.139
<i>Ardea alba</i>	Great Egret	AM	0.231	0.571	-1.43
<i>Pelecanus conspicillatus</i>	Australian Pelican	SS	0.205	0.532	-0.637
<i>Morus serrator</i>	Australasian Gannet	SS	0.614	0.913	-0.035
<i>Sula dactylatra</i>	Masked Booby	SS	0.31	0.863	-0.206
<i>S. leucogaster</i>	Brown Booby	SS	0.277	0.779	-0.365
<i>Microcarbo melanoleucos</i>	Little Pied Cormorant	SS	0.277	0.316	-0.362
<i>Phalacrocorax fuscescens</i>	Black-faced Cormorant	SS	0.588	0.786	-0.105
<i>P. sulcirostris</i>	Little Black Cormorant	SS	0.553	0.583	0.112
<i>P. varius</i>	Pied Cormorant	SS	0.415	0.717	-0.231
<i>P. carbo</i>	Great Cormorant	SS	0.614	0.66	-0.164
<i>Anhinga novaehollandiae</i>	Australasian Darter	SS	0.417	0.767	-0.309
<i>Pandion cristatus</i>	Eastern Osprey	SS	0.477	0.88	-0.202
<i>Accipiter fasciatus</i>	Brown Goshawk	SS	0.148	0.556	-1.609
<i>Haliastur sphenurus</i>	Whistling Kite	SS	0.357	0.737	-0.489
<i>Gallirallus sylvestris</i>	Lord Howe Woodhen	SS	0.768	0.933	-0.133
<i>Tribonyx mortierii</i>	Black-tailed Native-hen	SS	0.847	0.804	-0.165
<i>Haematopus longirostris</i>	Australian Pied Oystercatcher	SS	0.693	0.874	-0.046

**Table 3.1:** continued.

Scientific Name	Common Name	Metal	First-year Survival	Adult Survival	Survival Senescence
<i>Chroicocephalus novaehollandiae</i>	Silver Gull	SS	0.365	0.703	-0.205
<i>Larus dominicanus</i>	Kelp Gull	SS	0.633	0.894	-0.013
<i>L. pacificus</i>	Pacific Gull	SS	0.345	0.88	-0.205
<i>Hydroprogne caspia</i>	Caspian Tern	SS	0.671	0.914	-0.109
<i>Thalasseus bergii</i>	Crested Tern	IN	0.392	0.886	-0.157
<i>Dacelo novaeguineae</i>	Laughing Kookaburra	SS	0.595	0.839	-1.004
<i>Falco berigora</i>	Brown Falcon	SS	0.612	0.853	-0.037
<i>F. peregrinus</i>	Peregrine Falcon	SS	0.498	0.776	-0.169
<i>Platycercus elegans</i>	Crimson Rosella	SS	0.47	0.624	-0.471
<i>Menura novaehollandiae</i>	Superb Lyrebird	SS	0.364	0.778	-0.452
<i>Malurus cyaneus</i>	Superb Fairy-wren	AY	0.396	0.635	-0.658
<i>Sericornis frontalis</i>	White-browed Scrubwren	AY	0.357	0.483	-0.616
<i>Gymnorhina tibicen</i>	Australian Magpie	SS	0.52	0.782	-0.216
<i>Strepera graculina</i>	Pied Currawong	SS	0.267	0.2	0.087
<i>Grallina cyanoleuca</i>	Magpie-lark	AY	0.457	0.182	NA
<i>Corvus mellori</i>	Little Raven	SS	0.405	0.695	-0.28
<i>C. coronoides</i>	Australian Raven	SS	0.375	0.4	-0.46
<i>Corcorax melanorhamphos</i>	White-winged Chough	SS	0.602	0.82	-0.072
<i>Hirundo neoxena</i>	Welcome Swallow	AY	0.202	0.78	-1.311
<i>Zosterops lateralis</i>	Silvereye	AY	0.456	0.448	-0.399
<i>Sturnus vulgaris</i>	Common Starling	AY	0.385	0.789	-0.188
<i>Turdus merula</i>	Common Blackbird	AY	0.288	0.535	-0.403

## Analyses

All analyses of life-history attributes and their relationships with survival parameters were conducted in R version 3.2.2 (R Core Team 2015). We conducted exploratory analyses to identify relationships between our three derived death-curve parameters (annual first-year survival rate, annual adult survival rate, and annual adult survival-senescence) and taxonomic, morphological, behavioural, breeding biology, and movement biology data. For each life-history parameter, a separate linear model was constructed testing for a relationship between the value of that life history parameter and the estimated survival parameter, across all species in our dataset. We also tested for a relationship between phylogeny (i.e., Hackett coarse clade) and survival parameters. The values of survival parameters may be phylogenetically constrained, and phylogenetic effects may give an appearance of correlation between life-history parameters and

survival through the non-independence of datapoints from related species. We therefore separately fitted each linear model, including Hackett coarse clade as a random-intercepts effect using package 'lme4' (Bates et al. 2015), to check reported relationships' robustness to phylogenetic corrections.

## RESULTS

Across all sixty bird species modelled, adult survival, first-year survival, and senescence were all significantly correlated in pair-wise linear-quadratic contrasts (Table 3.2, Figure 3.1). Among the set of Hackett coarse clades for which more than one species was sampled (49 species; 10 clades), Hackett coarse clade significantly predicted estimates of annual adult survival (ANOVA  $F_{9,39} = 2.71$ ,  $P = 0.015$ ) and annual first-year survival (ANOVA  $F_{9,39} = 2.19$ ,  $P = 0.044$ ), but not annual adult survival-senescence (ANOVA  $F_{9,38} = 0.37$ ,  $P = 0.942$ ).

**Table 3.2:** Model-summaries of relationships between adult survival rate, first-year survival rate, and annual senescence parameters. Each line represents the lowest-AIC model relating one survival parameter to another, of the form  $Y_i = \beta_0 + \beta_1 x_i + \beta_2 x_i^2$  or  $Y_i = \beta_0 + \beta_1 x_i$ , with the standard error of each model term presented in brackets following the term. Statistical significance is coded for each contrast as '.' if  $0.1 > P > 0.05$ , '\*' if  $0.05 > P > 0.01$ , '\*\*' if  $0.01 > P > 0.001$ , and '\*\*\*' if  $0.001 > P > 0$ .

Y, x	$\beta_0$ (SE)	$\beta_1$ (SE)	$\beta_2$ (SE)
First-year survival, Adult survival	0.540 (0.180) **	-1.132 (0.598) .	1.336 (0.475) **
Survival senescence, Adult survival	0.405 (0.496)	-3.460 (1.584) *	3.216 (1.216) *
Survival senescence, First-year survival	-1.423 (0.216) ***	3.821 (0.906) ***	-2.688 (0.882) **

Some life-history variables in our dataset showed tight collinearity (Appendix 3.1), but as our analyses considered each life-history variable independently, we present each correlation as an independent relationship, rather than an integrated model. At least one survival parameter was significantly predicted by each of body mass (species' average, average female, and average male), cooperative breeding, and feeding aggregation in models including phylogeny as a random effect (Table 3.3). In every case where there was a statistically significant correlation between a survival parameter and a life-history variable, the sign of the correlation was the same for all three survival parameters with that life-history variable, implying a shared pattern across all three survival parameters (Table 3.3). Similarly, at least one survival parameter was significantly predicted by body mass (as average female), body mass dimorphism, clutch size (mean, minimum, and maximum), egg diameter, and migration status, and colonial nesting status in models not including phylogeny as a random effect (Table 3.4). Note that we consider phylogenetic correction (i.e., as in Table 3.3) necessary for valid inference in this analysis, and we have chosen to present an analysis without such correction as direct replications of published

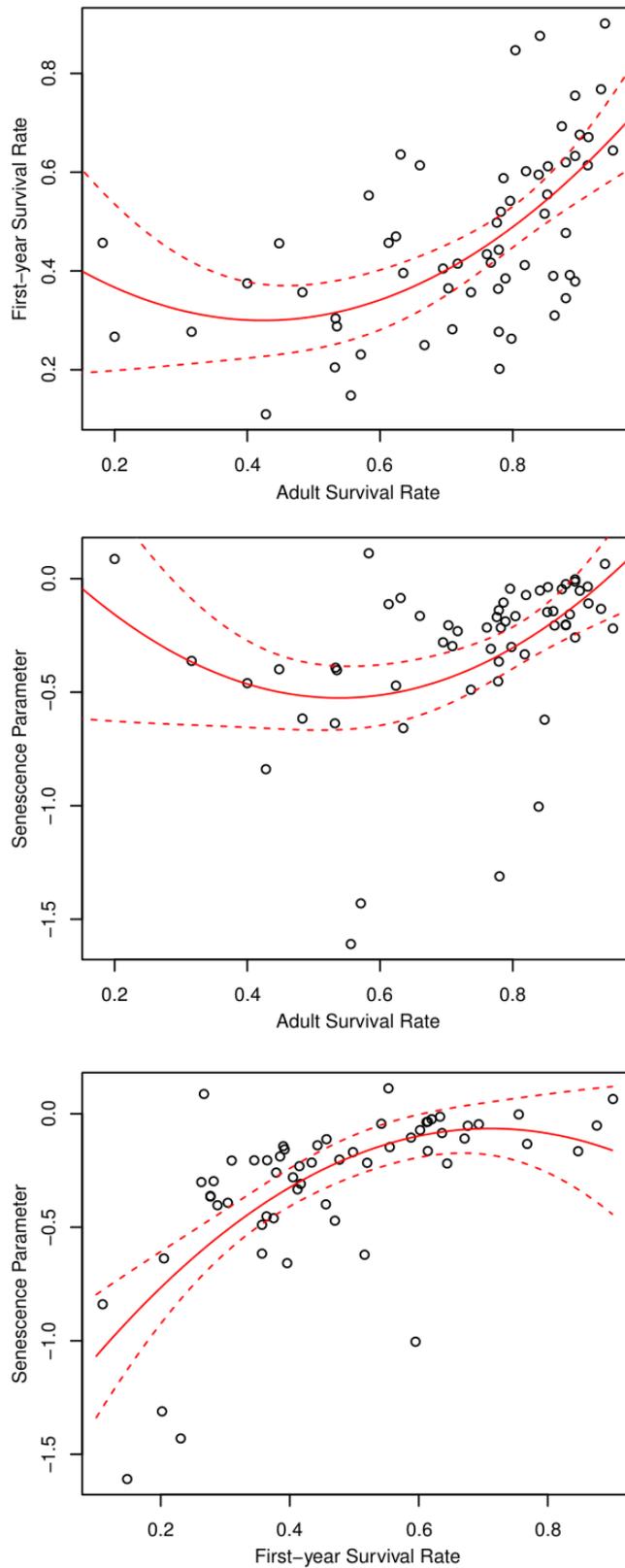
studies in which phylogenetic corrections have only occasionally been applied (reviewed in Baylis et al. 2014). With the exception of body mass dimorphism and cooperative breeding, in every case where there was a statistically significant correlation between a survival or senescence parameter and a life-history variable, the sign of the correlation was the same for all three survival parameters with that life-history variable (Table 3.3; Table 3.4).

**Table 3.3:** Model coefficients and estimate standard errors for explanatory models including phylogenetic adjustments (i.e., models of the form  $Y_i = a + C_i + \beta x_i + \varepsilon_i$ , where  $C_i$  is the Clade effect for observation  $i$ , and  $\beta x_i$  is the effect of the explanatory variable for observation  $i$ ). Values for all explanatory variables except for Male : Female body mass ratio were taken directly from Garnett et al (2015). Values for Male : Female body mass ratio were computed from 'Male body mass average' and 'Female body mass average' values, also from Garnett et al. (2015). Values for Male : Female body mass ratio range from 0.54 to 1.43 in our data. Values for brain mass residual are defined in the source material as 'Brain mass controlling allometrically for body mass relative to a regression of brain mass on body mass for all Australian birds'. In our data, values of brain mass residual range from -0.39 to 0.26. Total-migrant status, cooperative breeding status, feeding aggregation status, and colonial nesting status are each binary variables scored as zero or one. Statistical significance is coded for each contrast as '.' if  $0.1 > P > 0.05$ , '\*' if  $0.05 > P > 0.01$ , '\*\*' if  $0.01 > P > 0.001$ , and '\*\*\*' if  $0.001 > P > 0$ .

	Adult survival	First-year survival	Survival senescence
Avg. body mass (kg)	0.026 (SE = 0.016)	0.037 (SE = 0.016) *	0.028 (SE = 0.031)
Avg. female body mass (kg)	0.032 (SE = 0.020)	0.051 (SE = 0.019) *	0.040 (SE = 0.039)
Avg. male body mass (kg)	0.022 (SE = 0.015)	0.033 (SE = 0.015) *	0.027 (SE = 0.029)
Male : Female body mass ratio	-0.200 (SE = 0.189)	0.201 (SE = 0.193)	0.441 (SE = 0.352)
Brain mass residual	-0.043 (SE = 0.279)	-0.066 (SE = 0.287)	0.385 (SE = 0.504)
Mean clutch size	-0.042 (SE = 0.021) .	0.008 (SE = 0.023)	-0.027 (SE = 0.038)
Maximum clutch size	-0.003 (SE = 0.011)	0.012 (SE = 0.012)	-0.003 (SE = 0.020)
Minimum clutch size	-0.036 (SE = 0.018)	-0.003 (SE = 0.019)	-0.021 (SE = 0.032)
Egg diameter (mm)	0.005 (SE = 0.003) .	0.005 (SE = 0.003) .	0.005 (SE = 0.005)
Total-migrant status	0.007 (SE = 0.067)	0.004 (SE = 0.070)	0.002 (SE = 0.117)
Cooperative breeding status	0.395 (SE = 0.089) ***	0.220 (SE = 0.103) *	0.086 (SE = 0.199)
Feeding aggregation status	0.096 (SE = 0.058)	0.033 (SE = 0.062)	0.254 (SE = 0.099) *
Colonial nesting status	0.184 (SE = 0.093) .	0.096 (SE = 0.095)	0.028 (SE = 0.171)

**Table 3.4:** Model coefficients and estimate standard errors for explanatory models excluding phylogenetic adjustments (i.e., models of the form  $Y_i = a + \beta x_i + \varepsilon_i$ , where  $Y_i$  is the value of the response variable for observation  $i$ , and response variables are Adult survival, first-year survival, or survival senescence,  $\beta x_i$  is the effect of the explanatory variable for observation  $i$ ). Explanatory variables are defined as in Table 1. Statistical significance is coded for each contrast as '.' if  $0.1 > P > 0.05$ , '\*' if  $0.05 > P > 0.01$ , '\*\*' if  $0.01 > P > 0.001$ , and '\*\*\*' if  $0.001 > P > 0$ .

	Adult survival	First-year survival	Survival senescence
	0.025 (SE = 0.013) .	0.026 (SE = 0.013)	0.043 (SE = 0.026)
	0.044 (SE = 0.018) *	0.044 (SE = 0.017)	0.059 (SE = 0.033) .
	0.022 (SE = 0.013) .	0.020 (SE = 0.013)	0.031 (SE = 0.024)
Male : Female body mass ratio	-0.056 (SE = 0.135)	0.118 (SE = 0.129)	0.489 (SE = 0.236) *
Brain mass residual	-0.232 (SE = 0.175)	-0.101 (SE = 0.180)	-0.040 (SE = 0.354)
Mean clutch size	-0.029 (SE = 0.010) **	-0.011 (SE = 0.011)	-0.015 (SE = 0.021)
Maximum clutch size	-0.013 (SE = 0.006) *	-0.006 (SE = 0.006)	-0.006 (SE = 0.012)
Minimum clutch size	-0.030 (SE = 0.014) *	-0.011 (SE = 0.015)	-0.026 (SE = 0.029)
Egg diameter (mm)	0.005 (SE = 0.001) ***	0.004 (SE = 0.002) *	0.008 (SE = 0.003) *
Total-migrant status	0.066 (SE = 0.055)	0.064 (SE = 0.055)	0.126 (SE = 0.111)
Cooperative breeding status	0.062 (SE = 0.074)	0.106 (SE = 0.070)	-0.118 (SE = 0.144)
Feeding aggregation status	0.084 (SE = 0.050) .	0.046 (SE = 0.051)	0.147 (SE = 0.099)
Colonial nesting status	0.165 (SE = 0.044) ***	0.055 (SE = 0.049)	0.150 (SE = 0.094)



**Figure 3.1:** Relationships between the three survival parameters modelled, with fitted models as defined in Table 3.3 (solid red lines),  $\pm 1.96$  SE (dashed red lines). Top: first-year survival as a function of adult survival; middle: senescence parameter as a function of adult survival; bottom: senescence parameter as a function of first-year survival.

## DISCUSSION

One of the clearest signals in our analyses is the correlation between sociality and adult and first-year survival. In principle, sociality could be causally linked to inter-species differences in adult and first-year survival in many ways. Colonial nesters, flocking species, and cooperative breeders could receive survival advantages from group predator-detection or predator-saturation effects (e.g., Roberts 1996); socially-foraging species could forage more efficiently and therefore have decreased starvation risk relative to solitary species (e.g., Fernández-Juricic et al. 2004); or large groups may be able to socialise some risks by developing social interactions where well-off individuals assist other group-members (e.g., Carter & Wilkinson 2013). Alternatively, social species could have their survival reduced by factors such as greater competition for food (e.g., Stahl et al. 2001), greater risk of disease transmission (e.g., Tella 2002) or greater risks from conflict between individuals (e.g., Ramos 2003). Equally, greater longevity could cause the development of complex social interactions (e.g., Kerth 2008). Finally, apparent correlations between sociality and survival may arise from collinearity with other, actually-causal, relationships (i.e., relationships of the type proposed in Blumstein & Møller 2008).

Sociality has a mixed history of being reported to correlate with longevity and senescence in birds. Blumstein & Møller (2008) studied North American birds, and noted a correlation between senescence (proxied by MRLs) and sociality (indicated by cooperative care for offspring). However, they proposed that the correlation was an artefact of collinearity between sociality, body size, survival rate, and the age at first reproduction, rather than a link between sociality and senescence. Beauchamp (2009) studied North American birds, and reported no correlation between longevity (proxied by MRLs) and flocking (indicated by maximum recorded foraging group size). Munshi-South and Wilkinson (2005) studied parrots, and reported a correlation between lifespan (proxied by MRLs) and sociality (indicated by communal roosting). Wasser & Sherman (2010) studied birds from multiple regions, and reported a correlation between senescence (proxied by MRLs) and sociality (indicated by colonial nesting and/or cooperative breeding). Finally, Beauchamp (2014) studied birds from multiple regions, and reported a correlation between sociality (indicated by cooperative breeding) and adult survival rate, but not between sociality and longevity (proxied by MRLs).

From the considerations outlined in the previous paragraphs, we consider the theory around the correlation between sociality and survival in wild species to be flexible: any particular observed relationship between survival and sociality can be smoothly explained in terms of current theory. We also observe that it is fairly simple to collect a large set of life-history parameters to analyse

against any set of survival and senescence estimates: in our analyses, all life-history variables were collected from a single reference dataset. Therefore, it would be easy to test an array of different models of life-history and its relationship to survival. If very different observations can easily fit into existing theory, many explanatory models are testable, research is not pre-registered, and null-hypothesis significance testing is used to decide which effects are publishable, researchers can conduct exploratory analyses until they find a model that returns a statistically significant result, and report that result. These exploratory analyses are expected to have low replicability and to overstate effect sizes (Ioannidis 2005; Loken & Gelman 2017). A research culture that encourages publication of such exploratory analyses probably caused the low replicability of published findings in psychological science (termed the ‘Replication Crisis’ – see Open Science Collaboration 2015). We expect the same mechanism may cause low reproducibility of published findings in evolutionary ecology. Further, we expect that analyses conducted using MRLs will produce spurious correlations through the biases associated with MRL data (Baylis et al. 2014). Therefore, in our interpretation of the results, we treat published reports of correlations between life-history variables and survival parameters as speculative, and we present our own analyses as independent attempts at replicating those published correlations.

In our data, sociality (by all three measures: colonial nesting, flocking, and cooperative breeding) was estimated to be positively correlated with adult survival, first-year survival, and survival senescence. In the cases of cooperative breeding and adult survival, cooperative breeding and first-year survival, and flocking and senescence, the positive correlations were statistically significant. Our findings most directly replicate those of Beauchamp (2014): both studies found a significant positive correlation between adult survival and sociality, and both used cooperative breeding to indicate sociality. Additionally, we have demonstrated a positive correlation between first-year survival and cooperative breeding.

If we consider our point-estimates for effects, we find a general agreement between our data and the 'fast-slow life-history continuum' (as in Jones et al. 2008; Ricklefs 2010). Our adult survival rates are estimated to correlate positively with first-year survival rates, and both adult and first-year survival rates correlate positively with body-mass (regardless of whether average body-mass, female body-mass, or male body-mass is used), and adult survival rates correlate negatively with fecundity measured by clutch-size (regardless of whether mean, maximum, or minimum is used). Although our correlation point-estimates consistently align with the predictions of the fast-slow life-history continuum, not all of these point-estimates are significantly different from zero. Notably, the correlations between adult survival rates and body

mass are not significantly different from zero, and nor are the correlations between adult survival and fecundity, or the correlations between first-year survival and fecundity. We interpret our results as showing agreement with the fast-slow life history continuum, albeit with relatively low statistical power. Our work is the first to demonstrate that the fast-slow life-history continuum also predicts differences in first-year survival rates between species in the wild.

Other reported correlations between life-history variables and survival or senescence were not found in our analyses. Firstly, long-distance migration has been suggested to negatively correlate with senescence, and has been reported as negatively associated with senescence (as proxied by MRLs adjusted for effort, survival rate, and body mass: Møller 2006), whereas we find no significant correlation between migration status and juvenile survival, adult survival, or annual survival senescence. Our survival and senescence estimates are not biased by sampling effort, and we estimate survival and senescence separately. For a more direct comparison to the tests in Møller (2006), we repeated the analyses presented in Table 3.4 using residuals from a model of adult-survival, first-year survival, or survival senescence predicted by body mass as our response variable. Migratory status was not a significant predictor of body-mass-adjusted adult survival, first-year survival, or survival senescence (adult survival:  $t_{56} = 0.70$ ,  $P = 0.487$ ; first-year survival:  $t_{56} = 0.75$ ,  $P = 0.456$ ; survival senescence:  $t_{56} = -1.765$ ,  $P = 0.083$ ). We therefore suggest that the original finding that senescence correlates with migratory activity may have been a chance correlation.

Similarly, residual brain mass (i.e., brain mass standardised for body-mass) has been hypothesised to be negatively associated with senescence, and reported to be negatively correlated with rate of senescence in long-lived mammals (Promislow 1991, but see Gaillard et al. 1994), whereas we find no significant correlation between residual brain mass and adult survival, first-year survival, or annual survival senescence. We note that, although our findings contrast with the initial findings reported by Promislow, Gaillard et al. (1994) presented a more robust re-analysis of Promislow's (1991) dataset, in which they found no evidence of a correlation between brain mass and survival. Our findings on the relationship between senescence and brain mass in birds are therefore in keeping with the re-analysis of the Promislow (1991) data on brain mass and senescence in mammals.

On survival senescence, our results appear to contradict the finding of Ricklefs (2010): across species, our senescence estimates are positively correlated with adult survival (Table 3.2; Figure 3.1), whereas Ricklefs reports a negative correlation between senescence and adult survival. The apparent contrast between our findings and Ricklefs' could be driven by differing models and

definitions of senescence, and comparing the two sets of analyses will require additional data. Specifically, Ricklefs' analyses calculate senescence as a derived rate-of-aging starting at the age at first breeding for each species, based on an underlying Weibull mortality model. In contrast, our analyses use an underlying logit model of age-specific mortality, and we calculate senescence as the change in log-odds of mortality per year of increasing age, starting at the second year of life. At present, we lack data on age at first breeding for many of the species in our dataset, so cannot replicate Ricklefs' analyses directly. A contrast between Ricklefs' findings and ours could arise if species with high adult-survival rates also show an extended learning-period compared to species with low adult-survival. In that case, our survival rate estimates will be averaging over several years' data for long-lived species where survival rate increases with increasing age (because of ongoing learning and mild or non-existent senescence), as well as the years where additional learning-effects are minimal, but senescence continues. If learning effects are larger than senescence effects, and continue longer in long-lived than short-lived species, learning effects could reverse apparent trends in survival rate with age across species in our model.

The dataset on which our analyses are based is not a completely random sample of all bird species, and we would therefore urge caution in inferring relationships across all birds from our data. Specifically, we were only able to fit MEMOIR models to species for which there were a sufficiently large number of recoveries of freshly-dead animals that had been marked as pulli. Our dataset is almost certainly biased by these restrictions. For instance, our dataset is likely to be biased towards larger-bodied species as these can more easily be found and recovered, and biased against species that live in dense bush. Because Passerines, for instance, are generally smaller than non-Passerines, we also expect our dataset to include biases against Passerines as a phylogenetic group. We caution that the relationships we report are correlations, not experimental interventions. We also caution that collinearity exists between life-history variables we have investigated, and collinearity can alter the estimated correlation coefficients when multiple variables are included in a model. Our estimates of correlations between life-history variables and survival parameters are therefore presented as replication attempts, rather than an attempt to build a full model of the effect of life-history variables on survival.

The range of relationships between survival, senescence, and life-history proposed in the literature highlights the advantage of estimating survival and senescence using MEMOIR models, rather than MRLs. MEMOIR models can be used to estimate annual survival and senescence separately, can be used to generate estimates for a wide range of species, and are not biased by the recapture number, recapture type, and death-curve biases which plague MRLs

(Baylis et al. 2014). We therefore recommend MEMOIR models as a superior replacement for MRLs in analyses of comparative survival and senescence among groups of species. The fact that we have been able to derive a sizeable survival and senescence rate dataset from a single national-level bird-banding database strongly implies that our methods may be used to generate several large, independent survival and senescence rate datasets from international banding databases, allowing detailed replication of the analyses presented here.

## ACKNOWLEDGEMENTS

The authors would like to thank David Drynan and the Australian Bird and Bat Banding Scheme for making available the data for this paper. We give our thanks to the many researchers who have contributed to these datasets. This work was supported by the Australian Postgraduate Awards (APA) scheme and by the Holsworth Wildlife Research Endowment Fund.

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## Chapter Four

### *Estimates of wear rates in metal bird bands from the archives of a national banding scheme*

#### ABSTRACT

Bird-banding using numbered metal rings around the tibia or tarsi of marked birds, has been a widespread and common method of individual identification for many years. Studies that use data from recaptured banded birds are often forced to assume that band-loss is negligible, yet band wear-rates differ markedly between band sizes, band metals, and species in the relatively few cases where wear-rates have been determined. Additionally, it is plausible that the existing literature on band-wear estimates is upwardly-biased relative to the true distribution of wear-rates across species and band metals. Using routinely archived returned bands from a national banding database over the years 1963 to 2005, we present wear-rate estimates of bands applied to 173 avian species, five band-metals, and a total of 236 species / band-size / band-metal combinations. Band wear-rates are generally well-explained by band-metal and species functional-group, but we find some individual species with highly divergent wear-rates from others in their functional group. We also find that the published literature on band wear-rates provides, on average, more rapid estimates of wear for a given metal-type than our analyses. We suggest that publication biases favouring the publication of rapid wear-rate estimates may drive the contrast between estimated wear-rates in our analyses and the published literature.

## INTRODUCTION

Animal-marking is central to animal studies that require free-living animals to be uniquely identifiable. Datasets of observations of marked animals are used to infer core ecological patterns and processes including population sizes, birth and death rates, migration, breeding behaviour, and territorial structure. Studies that rely on marked animals being individually recognisable can be biased by loss of marks or, in the case of uniquely-numbered marks such as bird bands, band-wear that results in marks becoming unreadable while still on the animal (Coulson & White, 1955).

Animal marking is frequently organised at a national or international level by national banding schemes such as the United States Geological Survey Bird Banding Laboratory (BBL), EuRing, or the Australian Bird and Bat Banding Scheme, who often provide bands and recommend band-types to be used for each species. National banding schemes generally aim to recommend bands that will survive for the entire lifespan of the animal to which they are applied, with consideration also given to factors such as ease of application of the band. Published estimates of band wear-rates are disproportionately common in a small number of taxa – most estimates are for species of seabirds and waterfowl (collectively, waterbirds), and studies of other taxa are almost absent from the literature (Table 4.1). Band-wear rates may vary systematically between groups of birds – for instance, bands may generally wear more rapidly on seabirds than on bush-birds, owing to the corrosive nature of seawater (Laque, 1975). For many taxa, there is little empirical support for the idea that bands tend to outlast the animals to which they are applied. Similarly, some population-structure estimates perform a correction for expected band-loss inferred from observed band-wear (e.g., Ludwig, 1981). The lack of wear-rate estimates across many taxa limits the ability of researchers to make inferences about population structure for these taxa.

Of the published estimates of band-wear documented in Table 4.1, many identify bands applied to a species as having unacceptably high wear-rates, likely to result in a substantial proportion of bands wearing out while the animals is still alive. Some authors have investigated wear-rates across diverse taxa, presumably to investigate how wear-rates differ between these groups (e.g., Harris 1980), whereas the preparation and publication of other papers appears to be motivated by the author's observation of high band wear-rates in their study species (e.g., DuWors et al., 1987; Harris, 1964). Therefore, the published literature overall probably presents a biased sample of wear-rates, tending to contain more records of fast-wearing bands than of slow-wearing bands.

**Table 4.1:** Species on which band wear-rates have been reported in the published literature. Note that seabirds and waterfowl account for nearly all of the published reports, and that most studies report on Aluminium bands. Band metal codes: AM, Aluminium; AY, Alloy; IN, Incoloy; ML, Monel; SS, Stainless Steel; T, Titanium.

<i>Latin name</i>	<i>Common name</i>	<i>Source</i>	<i>AM</i>	<i>SS</i>	<i>IN</i>	<i>ML</i>	<i>T</i>
<i>Branta canadensis</i>	Canada Goose	Ludwig (1981)	2.27 %				
<i>Anser brachyrhynchus</i>	Pink-footed Goose	Harris (1980)	1.30 %				
<i>Aix sponsa</i>	Wood Duck	Ludwig (1981)	2.64 %				
<i>Anas platyrhynchos</i>	Mallard	Ludwig (1981) Harris (1980)	4.46 % 6.00 %				
<i>A. crecca</i>	Eurasian Teal	Harris (1980)	2.00 %				
<i>A. carolinensis</i>	Green-winged Teal	Ludwig (1981)	3.28 %				
<i>Melanitta fusca</i>	White-winged Scoter	DuWors et al. (1987)	2.73 %				
<i>Bucephala clangula</i>	Common Goldeneye	DuWors et al. (1987)	8.40 %				
<i>Phoebastria immutabilis</i>	Laysan Albatross	Ludwig et al. (1996)	2.42 %				
<i>P. nigripes</i>	Black-footed Albatross	Ludwig et al. (1996)	1.40 %				
<i>Hydrobates pelagicus</i>	European Storm Petrel	Harris (1980)	8.50 %				
<i>Fulmarus glacialis</i>	Northern Fulmar	Anderson (1980)	4.76 % 5.26 % 3.64 %			0.54 % 0.26 % 0.91 % 0.90 %	
<i>Ardenna tenuirostris</i>	Short-tailed Shearwater	Wooller et al. (1985)				1.20 %	
<i>Puffinus puffinus</i>	Manx Shearwater	Harris (1964)	8.90 %				
<i>Podiceps nigricollis</i>	Eared Grebe	Jehl (1990)	9.8 % 5.4 %				
<i>Sula bassana</i>	Gannet	Harris (1980)	4.00 %				
<i>Phalacrocorax aristotelis</i>	European Shag	Harris (1980)	5.20 % 3.40 %				
<i>P. carbo</i>	Great Cormorant	Harris (1980)	1.00 % 1.00 %				
<i>Haematopus ostralegus</i>	Eurasian Oystercatcher	Harris (1980)	2.00 %				
<i>Rissa tridactyla</i>	Kittiwake	Harris (1980) Coulson & White (1955)	8.60 % 8.60 %				
<i>Chroicocephalus novaehollandiae</i>	Silver Gull	Wooller & Wooller (1998)	4.10 %	1.40 %			
<i>C. ridibundus</i>	Black-headed Gull	Harris (1980) Coulson & White (1955)	3.40 % 4.60 %				

**Table 4.1:** continued.

<i>Latin name</i>	<i>Common name</i>	<i>Source</i>	<i>AM</i>	<i>SS</i>	<i>IN</i>	<i>ML</i>	<i>T</i>
<i>Leucophaeus atricilla</i>	Laughing Gull (female)	Dolbeer & Belant (1994)	7.60 %				
	Laughing Gull (male)		6.80 %				
<i>Larus delawarensis</i>	Ring-billed Gull	Ludwig (1967)	9.55 %			4.30 %	
			7.86 %				
		Ludwig (1981)	10.57 %				
			7.59 %				
<i>L. marinus</i>	Great Black-backed Gull	Harris (1980)	3.80 %				
<i>L. dominicanus</i>	Dominican Gull	Fordham (1967)	4.90 %				
<i>L. argentatus</i>	Herring Gull	Ludwig (1967)	7.50 %			1.62 %	
		Coulson (1976)				3.80 %	
		Harris (1980)	3.80 %				
		Ludwig (1981)	5.29 %		1.29 %	1.96 %	1.36 %
<i>L. fuscus</i>	Lesser Black-backed Gull	Coulson (1976)				2.20 %	
		Harris (1980)	3.50 %				
<i>Hydroprogne caspia</i>	Caspian Tern	Ludwig (1967)	3.13 %			9.61 %	
			1.63 %				
		Ludwig (1981)	3.04 %			4.45 %	
			2.38 %				
			2.22 %				
<i>Thalasseus elegans</i>	Elegant Tern	Collins (2007)	4.95 %				
<i>Onychoprion fuscatus</i>	Sooty Tern	Bailey et al. (1987)	0.57 %				
<i>Sterna dougallii</i>	Roseate Tern	Hatch & Nisbet (1983a)	6.30 %				
<i>S. hirundo</i>	Common Tern	Hatch & Nisbet (1983b)	6.62 %		0.58 %		
			4.08 %				
		Ludwig (1981)	5.42 %				
			Nisbet & Hatch (1988)	5.45 %		0.25 %	
<i>S. paradisaea</i>	Arctic Tern	Hatch & Nisbet (1983a)	0.90 %				
			0.91 %				
<i>Fratercula arctica</i>	Atlantic Puffin	Harris (1980)	3.96 %		3.24 %		
					1.80 %		
					8.04 %		
					1.92 %		
<i>Aeronautes saxatalis</i>	White-throated Swift	Collins (1973)	5.50 %				
<i>Coloeus monedula</i>	Jackdaw	Harris (1980)	3.60 %				
<i>Corvus coronoides</i>	Australian Raven	Rowley (1966)			7.20 %		
<i>Turdus migratorius</i>	American Robin	Ludwig (1981)	3.37 %				
<i>Molothrus ater</i>	Brown-headed Cowbird	Ludwig (1981)	6.85 %				

Wear-rates between bands are generally considered to follow an approximately Normal distribution (Ludwig 1981; Hatch and Nisbet 1983), and bands have been modelled as being lost either at a set proportion of their initial mass (Ludwig 1981), or uniformly over a range of proportions of their starting mass (Hatch and Nisbet 1983). An unbiased reference-set of band wear-rates may be used to inform and improve band-type recommendations, and inform studies using band-wear to correct for the effects of band-loss. Here, we present such a reference-set using routinely-archived worn bands for the Australian Bird and Bat Banding Scheme over the years 1963 to 2005, covering 173 species over a wide taxonomic range, in the hope that this reference-set will be useful for future models of the demography of marked populations. We also present analyses aimed at quantifying the likely publication bias in published estimates of band wear rates.

### **Band collections available for comparison**

The Australian Bird and Bat Banding Scheme (ABBBS) has maintained a collection of worn bands and unworn bands as part of its standard operations since the 1960s. This collection consists of three types of band: retained, returned, and worn. *Retained* bands were archived at the ABBBS shortly after manufacture: commonly, the first ten bands were kept from a string of bands to provide a basis for comparison of wear-rates. Efforts were made by the ABBBS to ensure that the stock of retained bands was reasonably representative of the range of bands issued by the ABBBS, but some gaps exist in this archive. *Returned* bands were issued to bird-banders, but were never used in a banding study, and were subsequently returned to the ABBBS. The stock of *returned* bands is complementary to the stock of *retained* bands, by representing additional prefixes.

*Worn* bands were applied to a bird and worn in the wild for some period of time, then removed from the wearer and returned to the ABBBS. In most cases, these bands were recovered from dead birds. In our analyses, we specifically avoided bands whose return was motivated by their state of wear (e.g., bands taken from a banded animal and replaced with another band), because such decisions by bird-banders to remove bands would result in a biased sample of bands being returned to the ABBBS.

### **Terminology**

'Bands' are individual numbered metal rings designed as permanent marks for free-living wild birds. Bands are distributed on 'strings', which are sets of bands with band-numbers in a continuous sequence. Each band has a prefix, a size, and a metal. Prefix, size, and metal type

were shared by all bands within a string, and our individual 'types' of bands for this analysis are defined as a unique combination of prefix, size, and metal.

## **METHODS**

### **Sample selection**

*Retained* and *returned* bands were collected for all band types available in the archive. Not all band types were represented by specimens in either the *retained* or *returned* archive. For such bands, we lack data from which to estimate the mass of bands at the time of application. *Worn* bands were archived according to the species on which they were worn. The number of worn bands available per species was highly variable, and a small number of species accounted for most of the worn bands available.

*Retained* and *returned* bands were selected for weighing by the following criteria: a sample of three *retained* bands from each available string was selected, to a maximum of ten strings, giving thirty bands per type. If fewer than ten strings had been retained for a band type, strings were sampled from the stock of *returned* strings until ten strings had been sampled. These bands were used to estimate the starting mass of bands at the time that they were applied to birds.

For a set of band sizes where there were many *retained* and also many *returned* strings available, a sample of three bands from each of ten strings was taken from both the *retained* and *returned* stock. In this sample, an effort was made to select band-sizes over the range of sizes issued by the ABBBS. These samples were used to test for any systematic differences in mass between the *retained* and *returned* stock, which could result from abrasion during transport to the bird-bander, and time in their supplies.

*Worn* bands were selected for weighing, based on the species to which they had been applied. For each species, all bands were weighed unless there were > 100 bands available for that species, in which case every N<sup>th</sup> band was selected, such that the total number of sampled bands was approximately 100.

## Sample preparation and weighing

Selected bands were gently brushed with a soft-bristled toothbrush in distilled water with a mild detergent, immersed in absolute ethanol, rinsed in distilled water and allowed to air-dry on absorbent paper to ensure that the recorded weight of the band was not influenced by foreign matter. Dried bands were weighed to the nearest 0.0001 g on a Mettler AE260 scientific balance, and the band-number for each weighed band was recorded.

For each weighed band, data on the band's metal type, size, prefix, the species the band was applied to, and the number of days the band was on the bird were taken from the ABBBS database.

## Statistical analyses

Analyses focused on four issues in sequence: first, whether bands experienced experimentally-relevant amounts of wear while issued to bird-banders but not applied to birds; second, what the starting mass was for bands of each type; third, the rate at which bands of each type lost mass during wear on each species of bird and the amount of wear that resulted in band-loss for each band type on each species; and fourth, whether the wear-rates for a given metal-type reported in the literature differed systematically from the wear-rates estimated in our analyses.

All statistical modelling and hypothesis testing was carried out in *R* version 3.2.2 (R Core Team, 2015). For the first question, we constructed a linear model of band mass as a function of the band's *retained* or *returned* status, with the band's type and string as blocking factors. For the second, we constructed a three-way (size x metal x prefix) table of vectors of masses for each band type, and investigated the table for dimensions in which it could be collapsed (e.g., if all unworn bands of one size and metal type were of approximately equal weight regardless of prefix, we could collapse the table in the prefix dimension, and treat all bands of the same size and metal type as though they had the same starting mass).

For the third question, we modelled the mass of *worn* bands (as a proportion of the starting mass of bands of their type) as a function of the number of days they had been worn on a bird. For bands experiencing particularly rapid mean wear-rates, linear modelling may provide an underestimate of the true wear-rate, as rapidly-wearing individual bands may wear out and be lost from the bird, and therefore not enter our sample. Such a bias is in principle detectable (see Appendix 4.1), and we have identified cases where it appears our sample may be affected by this bias.

In band-type / species combinations for which fewer than four worn bands were available, we were unable to reliably fit a linear model to our data. Therefore, we also calculated the mass lost per year for each band, and we report the mean mass lost per year for the bands in our sample as an alternative measure of the wear-rate for each band-type / species combination.

We investigated the fourth question using linear models with each wear-rate estimate weighted by the log of the number of observed bands informing that estimate. Bands issued by the ABBBS are made of Aluminium, 'Alloy' (a Magnesium-Aluminium alloy), 'Monel' (a Copper-Nickel alloy), 'Incoloy' (a Nickel-Chromium alloy), or Stainless Steel (details from the Australian Bird Banders' Manual - Commonwealth of Australia, 1989). Because the chemical composition of bands is sometimes ambiguous in the literature, bands were grouped into 'soft bands' (Aluminium and Alloy bands), Monel bands, and 'hard bands' (Stainless Steel and Incoloy bands) for these comparisons. In general, Alloy bands are primarily used on small to medium Passerines, and Incoloy bands are used on shorebirds, Stainless Steel bands are used on seabirds, raptors, parrots, and most waterfowl. Aluminium and Monel bands have largely been replaced by the use of other metals. Monel has been replaced by stainless steel in nearly all cases owing to problems with 'crevice attack', in particular on species that inhabit tropical marine environments (Commonwealth of Australia, 1989).

## RESULTS

### Comparability of Retained and Returned reference-bands

On average, returned bands were 0.15 % heavier than retained bands of the same type in our sample, and the contrast between the two groups was not statistically significant ( $T_{1298} = 0.229$ ,  $P = 0.819$ ). For all analyses of wear-rates, unworn masses of each band-type were therefore estimated from a pooled dataset of retained and returned bands.

### Starting masses of each band-type

Unworn bands were weighed for each combination of band-metal, size, and prefix for which reference-bands were available, to provide an estimate of the starting (unworn) mass of our worn-bands dataset. The estimated unworn mass for bands of each combination of band-metal, size, and prefix is presented in Table 3.

### Wear-rates and band loss-points

Band wear-rates were variable between species (see Table 4.2; Appendix 4.2), so we opted against pooling our analyses across species within band-type; however, between-metal differences in wear rates were generally large compared to between-species differences in wear-rates. Alloy bands consistently showed high wear-rates in comparison to Stainless bands, and Monel and Aluminium bands showed highly variable wear-rates (see Figure 4.1; Figure 4.2). Differences in band wear-rates within metal-types appear to be largely explainable as differences between species or functional group (Appendix 4.2), but wear-rates of Monel bands applied to Short-tailed Shearwaters (*Ardenna tenuirostris*) also correlated tightly with prefix (Appendix 4.2).

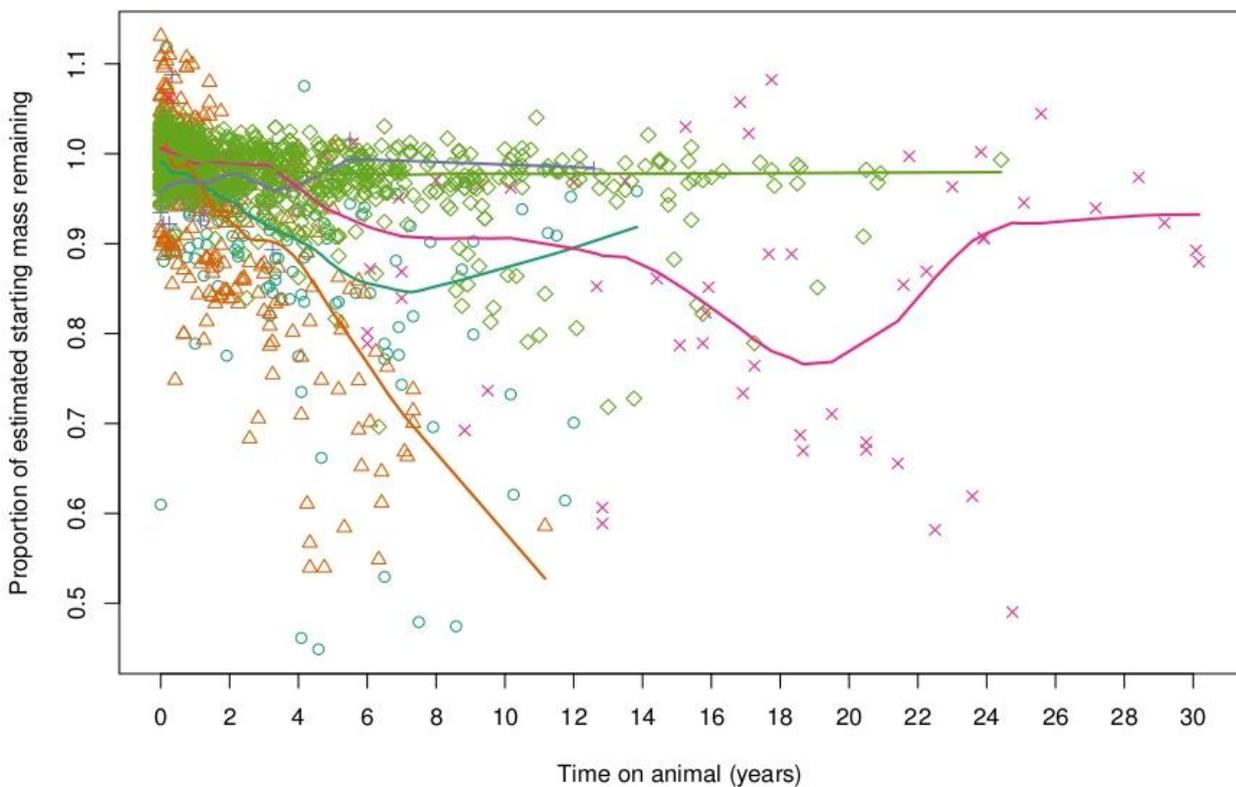
Band wear-rates are largely explained by band-metal, and in general, wear-rates estimated in our study converge to a metal-specific wear-rate with low inter-species variability at large sample-sizes (see Figure 4.2). Bands of a given metal-type applied to some functional groups of birds have wear-rates that are clearly distinct from those of other functional groups. In general, bands on Passerines appear to wear more quickly than bands on most other functional groups across a range of band-metals, however, within Aluminium bands, bands on ducks, geese, and swans, and seabirds also showed an elevated apparent wear-rate (Appendix 4.2).

Some species-specific wear-rates were evident within functional-group / metal-type combinations. For instance, stainless steel bands on Kelp Gulls (*Larus dominicanus*) wear much more rapidly than stainless steel bands on other seabirds, and stainless steel bands on Pacific

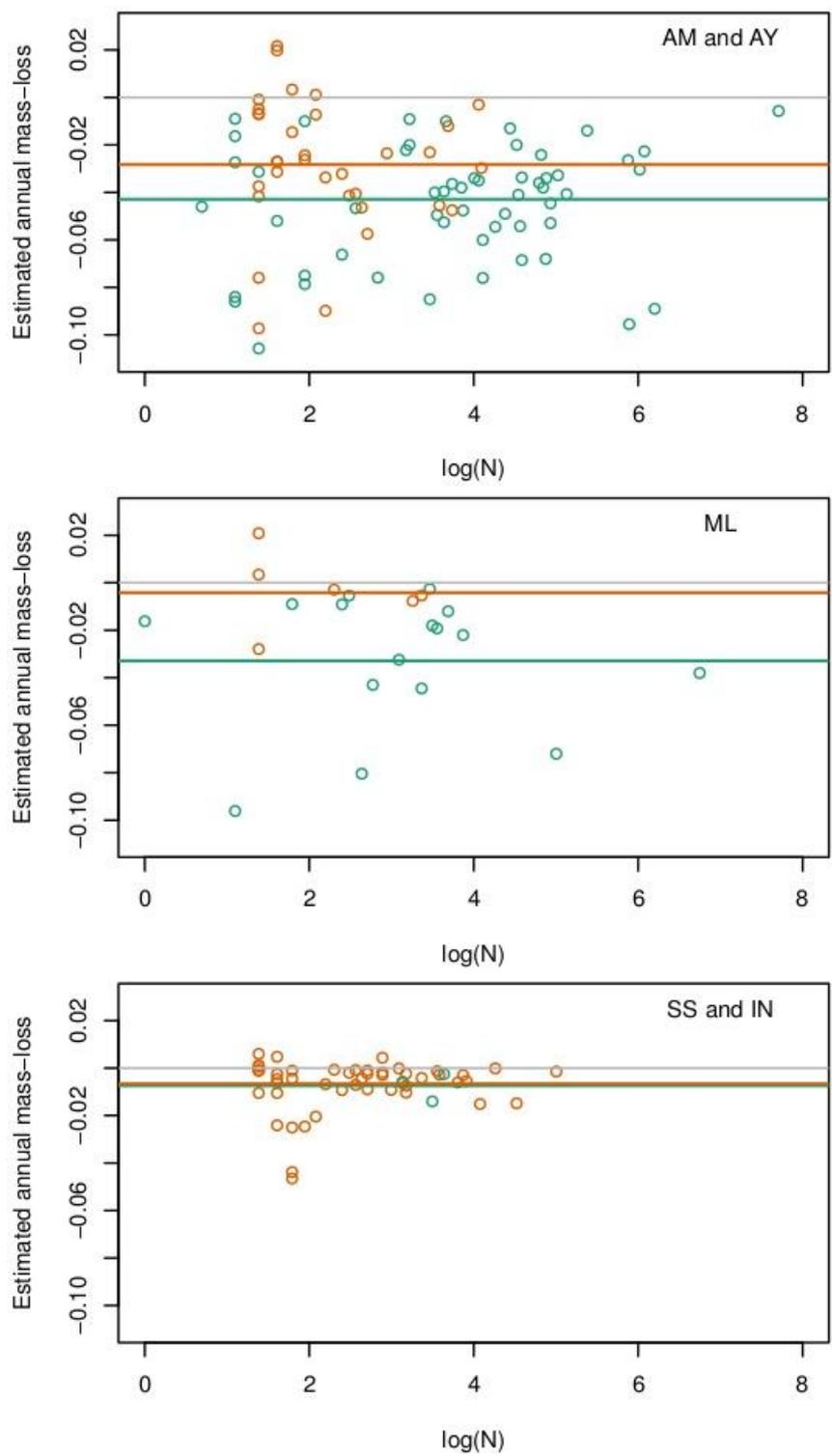
Gulls (*L. pacificus*) may also wear relatively rapidly (see Appendix 4.2).

### Contrasts with existing literature

Annual proportional wear across all three metal-types examined was on average higher for bands reported in the literature than for bands reported in this study. The contrast in reported wear-rates by data-source was statistically significant for soft bands and Monel bands, but not for hard bands (AM / AY: 1.30 %,  $t = 2.233$ ,  $P = 0.028$ ; ML: 2.87 %,  $t = 2.262$ ,  $P = 0.036$ ; SS / IN: 0.11%,  $t = 0.233$ ,  $P = 0.817$ ; Figure 4.2). If we assume that the distribution of true wear-rates across the avian community is roughly consistent across geographic regions, this implies selective reporting of rapidly-wearing bands in the literature when compared to our analyses.



**Figure 4.1:** Band mass as a proportion of estimated starting mass through increasing age for all weighed bands, coloured by metal type. Teal circles indicate Aluminium bands, orange triangles Alloy bands, purple plus-marks Incoloy bands, pink cross-marks Monel bands, and green diamonds Stainless Steel bands. A Lowess smoothed-line is given for each metal-type, indicating the central tendency of the sample's remaining mass through increasing age. Note that heterogeneous wear-rates (e.g., between species) prevent simple interpretations of wear-rates from Lowess lines. For instance, Monel bands appear to fall into three groups: those that wear rapidly (approximately 3% / year), those that wear at a medium rate (approximately 1.7% / year), and those that show negligible wear (approximately 0.3% / year). As each group drops out of the sample in sequence (presumably through wear-related band-loss making the bands irretrievable), the Monel Lowess line shows a corresponding wavy function. Some general patterns may nevertheless be seen: Aluminium bands appear to have heterogeneous wear-rates; Alloy bands show homogeneous, fairly rapid, wear; Stainless bands appear to wear only minimally, but with some heterogeneity in wear-rates that may be species-specific.



**Figure 4.2:** Funnel plots of estimated wear-rates against (log) sample-size, split by metal-type for estimates reported in the literature (green) and from this study (orange). All estimates from this study are derived from linear modelling (i.e., they equal parameter  $\beta$  in Table 4.2, not parameter  $\mu$ ). Because of ambiguity in metal-identification in the literature, Aluminium (AM) and Alloy (AY) bands, and Stainless Steel (SS) and Incoloy (IN) bands, are presented together, but Monel (ML) is presented in its own subfigure. Horizontal lines denote the (log) N-weighted mean reported wear rate for bands in the literature (green) and this study (orange).

**Table 4.2:** Estimated band wear-rates, percentage mass-loss of band-loss, and parameters of a log-normal band-loss curve for species marked with differing bands. Band sizes are as described in Commonwealth of Australia (1989). Taxonomy follows Gill & Donsker (2015).  $\mu$ : mean wear-rate, estimated as the mean of individual band-wear rates in the sample, where individual band-wear is assessed against the mean unworn mass of bands of that type;  $\beta$ : estimated annual wear-rate from linear modelling of mass against time spent on animal (for band-type / species combinations with  $N > 3$  only); SE: estimated standard error of annual  $\beta$ ;  $P$ : P-value for the hypothesis-test of  $\beta = 0$ ;  $N$ : the number of weighed bands used in the analysis for the band-type / species combination.

<i>Latin name</i>	<i>Common name</i>	<i>Size</i>	$\mu$	$\beta$	<i>SE</i>	<i>P</i>	<i>N</i>
<b>Aluminium Bands</b>							
<i>Chenonetta jubata</i>	Australian Wood Duck	10	0.097	-0.023	0.004	0.000	19
<i>Anas superciliosa</i>	Pacific Black Duck	11	0.017	-0.030	0.004	0.000	60
<i>Nycticorax caledonicus</i>	Nankeen Night Heron	11	0.136				2
<i>Bubulcus coromandus</i>	Cattle Egret	10	0.100	-0.003	0.001	0.014	58
<i>Ardea alba</i>	Eastern Great Egret	11	-0.001				1
<i>Ardea intermedia</i>	Intermediate Egret	10	0.067	-0.005	0.002	0.085	4
<i>Sula dactylatra</i>	Masked Booby	13	0.004	0.020	0.036	0.621	5
<i>Microcarbo melanoleucos</i>	Little Pied Cormorant	11	-0.021				1
<i>Aquila audax</i>	Wedge-tailed Eagle	15	-0.004				1
<i>Accipiter fasciatus</i>	Brown Goshawk	10	0.002				1
<i>Haliastur sphenurus</i>	Whistling Kite	11	-0.012				2
<i>Chroicocephalus novaehollandiae</i>	Silver Gull	8	0.061	-0.037	0.061	0.600	4
<i>Thalasseus bergii</i>	Crested Tern	7	0.051	-0.023	0.003	0.000	32
<i>Spilopelia chinensis</i>	Spotted Turtle-Dove	8	-0.017				2
<i>Spilopelia senegalensis</i>	Laughing Turtle-Dove	7	-0.012				2
<i>Ocyphaps lophotes</i>	Crested Pigeon	8	-0.014	-0.015	0.003	0.005	6
<i>Leucosarcia melanoleuca</i>	Wonga Pigeon	10	0.099				2
<i>Geopelia humeralis</i>	Bar-shouldered Dove	8	-0.035				3
<i>Ninox novaeseelandiae</i>	Southern Boobook	11	-0.009				1
<i>Podargus strigoides</i>	Tawny Frogmouth	10	0.003				1
<i>Todiramphus sanctus</i>	Sacred Kingfisher	5	0.002				2
<i>Gliciphila melanops</i>	Tawny-crowned Honeyeater	2	-0.077				1
<i>Phylidonyris novaehollandiae</i>	New Holland Honeyeater	3	0.035				3
<i>Philemon corniculatus</i>	Noisy Friarbird	7	0.038				1
<i>Melithreptus lunatus</i>	White-naped Honeyeater	2	0.033				1
<i>Acanthagenys rufogularis</i>	Spiny-cheeked Honeyeater	5	0.022				1
<i>Anthochaera carunculata</i>	Red Wattlebird	7	0.048	-0.026	0.004	0.001	7
<i>Caligavis chrysops</i>	Yellow-faced Honeyeater	2	0.013				3
<i>Manorina flavigula</i>	Yellow-throated Miner	5	0.037	-0.027	0.014	0.155	5
<i>Gavicalis virescens</i>	Singing Honeyeater	3	0.017				1
<i>Ptilotula penicillata</i>	White-plumed Honeyeater	2	-0.039	-0.031	0.001	0.000	5
<i>Sericornis frontalis</i>	White-browed Scrubwren	2	0.031				3
<i>Pomatostomus superciliosus</i>	White-browed Babbler	5	0.126				2
<i>Strepera versicolor</i>	Grey Currawong	10	0.025	-0.076	0.034	0.156	4
<i>Pachycephala rufiventris</i>	Rufous Whistler	3	0.072				1
<i>Colluricincla harmonica</i>	Grey Shrike-thrush	5	0.049				3

Table 4.2: continued.

<i>Latin name</i>	<i>Common name</i>	<i>Size</i>	$\mu$	$\beta$	<i>SE</i>	<i>P</i>	<i>N</i>
	<b>Aluminium Bands</b>						
<i>Rhipidura threnothorax</i>	Sooty Thicket-Fantail	2	0.025				1
<i>Symphysia trivirgatus</i>	Spectacled Monarch	2	0.003				1
<i>Corvus bennetti</i>	Little Crow	10	0.062				1
<i>Corvus coronoides</i>	Australian Raven	10	0.042				2
<i>Struthidea cinerea</i>	Apostlebird	7	0.082				1
<i>Eopsaltria australis</i>	Eastern Yellow Robin	2	0.000				2
<i>Acridotheres tristis</i>	Common Myna	7	0.055				2
<i>Sturnus vulgaris</i>	Common Starling	5	0.042				3
<i>Passer domesticus</i>	House Sparrow	3	0.048				3
	<b>Alloy Bands</b>						
<i>Sternula albifrons</i>	Little Tern	4	0.131				1
<i>Onychoprion anaethetus</i>	Bridled Tern	6	0.005	-0.007	0.009	0.535	4
<i>Geopelia striata</i>	Peaceful Dove	6	-0.004				1
<i>Geopelia striata</i>	Peaceful Dove	5	-0.062	0.003	0.019	0.869	6
<i>Aegotheles cristatus</i>	Australian Owlet-nightjar	5	-0.085				1
<i>Todiramphus sanctus</i>	Sacred Kingfisher	5	-0.023				3
<i>Climacteris picumnus</i>	Brown Treecreeper	4	0.065				1
<i>Malurus lamberti</i>	Variiegated Fairy-wren	1	0.071				1
<i>Malurus cyaneus</i>	Superb Fairy-wren	1	0.107	-0.041	0.013	0.009	12
<i>Malurus melanocephalus</i>	Red-backed Fairy-wren	1	0.089				2
<i>Acanthorhynchus tenuirostris</i>	Eastern Spinebill	1	0.005	-0.034	0.006	0.001	9
<i>Lichmera indistincta</i>	Brown Honeyeater	1	0.123				2
<i>Lichmera indistincta</i>	Brown Honeyeater	2	-0.002	-0.001	0.011	0.940	4
<i>Phylidonyris pyrrhoptera</i>	Crescent Honeyeater	2	-0.190				1
<i>Phylidonyris novaehollandiae</i>	New Holland Honeyeater	3	0.039	-0.048	0.003	0.000	42
<i>Phylidonyris niger</i>	White-cheeked Honeyeater	3	0.078				2
<i>Melithreptus lunatus</i>	White-naped Honeyeater (Eastern)	2	0.034				3
<i>Melithreptus chloropsis</i>	White-naped Honeyeater (Western)	3	0.017				1
<i>Acanthagenys rufogularis</i>	Spiny-cheeked Honeyeater	5	-0.361				1
<i>Anthochaera chrysoptera</i>	Little Wattlebird	6	0.005	-0.090	0.048	0.102	9
<i>Anthochaera carunculata</i>	Red Wattlebird	6	-0.142				1
<i>Caligavis chrysops</i>	Yellow-faced Honeyeater	2	0.047	-0.007	0.024	0.791	4
<i>Manorina melanophrys</i>	Bell Miner	4	0.060				1
<i>Manorina melanocephala</i>	Noisy Miner	6	-0.175	-0.046	0.010	0.000	14
<i>Gavicalis virescens</i>	Singing Honeyeater	3	0.016	-0.007	0.006	0.269	8
<i>Ptilotula ornata</i>	Yellow-plumed Honeyeater	2	0.060				1
<i>Ptilotula penicillata</i>	White-plumed Honeyeater	3	0.052				1
<i>Ptilotula penicillata</i>	White-plumed Honeyeater	2	-0.054	-0.032	0.009	0.005	11
<i>Pardalotus punctatus</i>	Spotted Pardalote	1	0.045				1
<i>Pardalotus striatus</i>	Striated Pardalote	1	0.016				1
<i>Sericornis frontalis</i>	White-browed Scrubwren	2	0.033	-0.024	0.007	0.021	7
<i>Sericornis magnirostra</i>	Large-billed Scrubwren	1	-0.119				1

**Table 4.2:** continued.

<i>Latin name</i>	<i>Common name</i>	<i>Size</i>	$\mu$	$\beta$	<i>SE</i>	<i>P</i>	<i>N</i>
	<b><i>Alloy Bands</i></b>						
<i>Smicromnis brevirostris</i>	Weebill	1	0.688				2
<i>Acanthiza pusilla</i>	Brown Thornbill	1	0.033				2
<i>Acanthiza chrysorrhoa</i>	Yellow-rumped Thornbill	1	0.090				2
<i>Acanthiza lineata</i>	Striated Thornbill	1	0.016	-0.042	0.016	0.121	4
<i>Pomatostomus superciliosus</i>	White-browed Babbler	5	0.102	-0.097	0.008	0.007	4
<i>Psophodes olivaceus</i>	Eastern Whipbird	6	0.077	-0.027	0.026	0.368	5
<i>Artamus cinereus</i>	Black-faced Woodswallow	5	-0.154				1
<i>Artamus cyanopterus</i>	Dusky Woodswallow	4	-0.013				1
<i>Cracticus torquatus</i>	Grey Butcherbird	6	0.003				1
<i>Pachycephala pectoralis</i>	Golden Whistler	3	0.062				1
<i>Pachycephala occidentalis</i>	Western Whistler	3	0.016				1
<i>Colluricincla harmonica</i>	Grey Shrike-thrush	5	-0.054				2
<i>Oriolus sagittatus</i>	Olive-backed Oriole	6	0.088				1
<i>Rhipidura leucophrys</i>	Willie Wagtail	3	0.027				3
<i>Rhipidura albiscapa</i>	Grey Fantail	1	-0.046				3
<i>Grallina cyanoleuca</i>	Magpie-lark	6	0.029				3
<i>Eopsaltria australis</i>	Eastern Yellow Robin	2	0.066				1
<i>Eopsaltria griseogularis</i>	Western Yellow Robin	2	0.014				1
<i>Eopsaltria georgiana</i>	White-breasted Robin	2	-0.013				2
<i>Melanodryas cucullata</i>	Hooded Robin	2	-0.917				1
<i>Petroica boodang</i>	Scarlet Robin	1	0.066				2
<i>Hirundo neoxena</i>	Welcome Swallow	2	0.004	0.001	0.007	0.876	8
<i>Petrochelidon ariel</i>	Fairy Martin	1	0.276				1
<i>Zosterops lateralis</i>	Silvereye	1	0.053	-0.012	0.006	0.039	40
<i>Sturnus vulgaris</i>	Common Starling	6	0.007	-0.057	0.020	0.013	15
<i>Zoothera dauma</i>	White's Thrush	6	0.205				1
<i>Turdus merula</i>	Common Blackbird	6	0.076	-0.045	0.009	0.000	36
<i>Passer domesticus</i>	House Sparrow	3	0.026	-0.041	0.011	0.003	13
<i>Stagonopleura bella</i>	Beautiful Firetail	2	0.021				1
<i>Neochmia temporalis</i>	Red-browed Finch	2	0.000	0.022	0.037	0.600	5
<i>Neochmia temporalis</i>	Red-browed Finch	1	0.042				3
<i>Poephila personata</i>	Masked Finch	2	-0.008				1
<i>Taeniopygia bichenovii</i>	Double-barred Finch	1	0.087				3
<i>Carduelis carduelis</i>	European Goldfinch	2	0.004				2
	<b><i>Incoloy Bands</i></b>						
<i>Accipiter cirrocephalus</i>	Collared Sparrowhawk	7	0.113				1
<i>Charadrius ruficapillus</i>	Red-capped Plover	3	0.006				1
<i>Charadrius bicinctus</i>	Double-banded Plover	4	0.002				3
<i>Limosa lapponica</i>	Bar-tailed Godwit	7	0.351				3
<i>Arenaria interpres</i>	Ruddy Turnstone	5	0.010				1
<i>Calidris tenuirostris</i>	Great Knot	6	0.052	-0.002	0.006	0.704	5
<i>Calidris canutus</i>	Red Knot	5	0.014				3

**Table 4.2:** continued.

<b>Latin name</b>	<b>Common name</b>	<b>Size</b>	<b><math>\mu</math></b>	<b><math>\beta</math></b>	<b>SE</b>	<b>P</b>	<b>N</b>
<i>Calidris ruficollis</i>	Red-necked Stint	3	0.013	0.006	0.006	0.416	4
<i>Calidris ferruginea</i>	Curlew Sandpiper	4	0.027				1
<i>Thalasseus bergii</i>	Crested Tern	7	0.162				3
<i>Sternula albifrons</i>	Little Tern	4	0.015				1
<i>Sternula nereis</i>	Fairy Tern	4	0.001				1
<i>Sterna hirundo</i>	Common Tern	5	-0.004				1
<i>Todiramphus sanctus</i>	Sacred Kingfisher	5	0.249				1
<i>Philemon corniculatus</i>	Noisy Friarbird	7	0.033				1
<i>Anthochaera carunculata</i>	Red Wattlebird	7	-0.106				2
<i>Cracticus nigrogularis</i>	Pied Butcherbird	7	0.156				2
<i>Pachycephala pectoralis</i>	Golden Whistler	3	0.077				1
<i>Turdus merula</i>	Common Blackbird	6	0.022				1
<b>Monel Bands</b>							
<i>Cereopsis novaehollandiae</i>	Cape Barren Goose	14	0.003				1
<i>Cygnus atratus</i>	Black Swan	14	0.007	-0.005	0.001	0.000	29
<i>Pelagodroma marina</i>	White-faced Storm-Petrel	5	0.007				1
<i>Diomedea exulans</i>	Wandering Albatross	14	0.003	-0.003	0.001	0.001	10
<i>Ardenna pacifica</i>	Wedge-tailed Shearwater	16	0.033	-0.028	0.003	0.011	4
<i>Ardenna tenuirostris</i>	Short-tailed Shearwater	16	-0.003	-0.008	0.005	0.132	26
<i>Ardenna carneipes</i>	Flesh-footed Shearwater	16	0.010	0.003	0.006	0.623	4
<i>Phalacrocorax varius</i>	Pied Cormorant	14	0.007	0.021	0.031	0.570	4
<b>Stainless Steel Bands</b>							
<i>Anseranas semipalmata</i>	Magpie Goose	13	-0.004	-0.004	0.001	0.028	6
<i>Dendrocygna eytoni</i>	Plumed Whistling-Duck	10	0.005				1
<i>Cereopsis novaehollandiae</i>	Cape Barren Goose	15	-0.014	-0.003	0.000	0.000	36
<i>Tadorna tadornoides</i>	Australian Shelduck	12	0.066	-0.004	0.004	0.292	14
<i>Chenonetta jubata</i>	Australian Wood Duck	11	0.015				1
<i>Chenonetta jubata</i>	Australian Wood Duck	10	-0.070	-0.009	0.003	0.011	15
<i>Anas superciliosa</i>	Pacific Black Duck	11	0.035	-0.004	0.002	0.092	29
<i>Anas gracilis</i>	Grey Teal	9	0.067	-0.002	0.002	0.471	18
<i>Anas castanea</i>	Chestnut Teal	10	0.020				1
<i>Anas castanea</i>	Chestnut Teal	9	0.009	-0.025	0.009	0.039	7
<i>Biziura lobata</i>	Musk Duck	13	0.044				1
<i>Eudyptula minor</i>	Little Penguin	19	-0.004	-0.001	0.000	0.000	149
<i>Thalassarche melanophris</i>	Black-browed Albatross	12	0.019				1
<i>Thalassarche cauta</i>	Shy Albatross	13	0.005				1
<i>Macronectes giganteus</i>	Southern Giant-Petrel	13	-0.041				3
<i>Macronectes halli</i>	Northern Giant-Petrel	13	0.001				2
<i>Ardenna pacifica</i>	Wedge-tailed Shearwater	16	-0.001	-0.003	0.001	0.000	48
<i>Ardenna tenuirostris</i>	Short-tailed Shearwater	16	-0.006	-0.001	0.000	0.006	35
<i>Ardenna carneipes</i>	Flesh-footed Shearwater	16	-0.015	-0.006	0.001	0.016	5
<i>Threskiornis molucca</i>	Australian White Ibis	12	0.019	-0.010	0.001	0.000	24
<i>Threskiornis spinicollis</i>	Straw-necked Ibis	12	0.008	-0.005	0.002	0.070	5

**Table 4.2:** continued.

<i>Latin name</i>	<i>Common name</i> <b>Stainless Steel Bands</b>	<i>Size</i>	$\mu$	$\beta$	<i>SE</i>	<i>P</i>	<i>N</i>
<i>Platalea regia</i>	Royal Spoonbill	13	0.087	-0.001	0.001	0.390	4
<i>Nycticorax caledonicus</i>	Nankeen Night Heron	11	-0.002				2
<i>Ardea pacifica</i>	White-necked Heron	12	-0.016				1
<i>Morus serrator</i>	Australasian Gannet	13	0.006	0.000	0.001	0.896	71
<i>Sula dactylatra</i>	Masked Booby	13	0.008	-0.002	0.002	0.356	24
<i>Sula leucogaster</i>	Brown Booby	12	0.001	-0.001	0.001	0.523	13
<i>Phalacrocorax fuscescens</i>	Black-faced Cormorant	12	-0.009	-0.001	0.005	0.890	4
<i>Phalacrocorax fuscescens</i>	Black-faced Cormorant	13	0.001	-0.001	0.001	0.107	15
<i>Phalacrocorax varius</i>	Pied Cormorant	13	0.019	0.000	0.000	0.706	22
<i>Pandion cristatus</i>	Eastern Osprey	13	0.001				1
<i>Hieraaetus morphnoides</i>	Little Eagle	13	0.003				1
<i>Hydroprogne caspia</i>	Caspian Tern	9	0.011	0.005	0.023	0.847	5
<i>Aquila audax</i>	Wedge-tailed Eagle	15	0.003				3
<i>Accipiter novaehollandiae</i>	Grey Goshawk	12	-0.002				1
<i>Accipiter novaehollandiae</i>	Grey Goshawk	27	-0.608				1
<i>Accipiter fasciatus</i>	Brown Goshawk	11	0.331				1
<i>Accipiter fasciatus</i>	Brown Goshawk	9	-0.005	-0.025	0.008	0.040	6
<i>Accipiter fasciatus</i>	Brown Goshawk	10	0.053	-0.002	0.002	0.297	15
<i>Accipiter cirrocephalus</i>	Collared Sparrowhawk	9	0.520				1
<i>Circus approximans</i>	Swamp Harrier	11	-0.107	-0.010	0.006	0.212	4
<i>Milvus migrans</i>	Black Kite	11	0.016				1
<i>Haliastur sphenurus</i>	Whistling Kite	10	0.003				1
<i>Haliastur sphenurus</i>	Whistling Kite	11	0.003				3
<i>Haliaeetus leucogaster</i>	White-bellied Sea-Eagle	15	-0.001				1
<i>Gallirallus sylvestris</i>	Lord Howe Woodhen	10	0.018	-0.007	0.003	0.025	24
<i>Gallinula tenebrosa</i>	Dusky Moorhen	11	-0.010				2
<i>Fulica atra</i>	Eurasian Coot	10	0.002				1
<i>Grus rubicunda</i>	Brolga	13	0.008				1
<i>Haematopus longirostris</i>	Pied Oystercatcher	10	-0.008	-0.006	0.002	0.005	23
<i>Vanellus miles</i>	Masked Lapwing	8	0.126				1
<i>Numenius madagascariensis</i>	Far Eastern Curlew	10	-0.383				1
<i>Calidris tenuirostris</i>	Great Knot	6	0.084				2
<i>Chroicocephalus novaehollandiae</i>	Silver Gull	8	0.010	-0.007	0.004	0.141	13
<i>Larus pacificus</i>	Pacific Gull	11	-0.018	-0.006	0.001	0.000	45
<i>Larus dominicanus</i>	Kelp Gull	11	0.005	-0.015	0.001	0.000	92
<i>Spilopelia chinensis</i>	Spotted Turtle-Dove	8	0.005				1
<i>Ocyphaps lophotes</i>	Crested Pigeon	8	-0.051				3
<i>Scythrops novaehollandiae</i>	Channel-billed Cuckoo	11	0.010				1
<i>Tyto novaehollandiae</i>	Masked Owl	13	0.043				1
<i>Tyto delicatula</i>	Eastern Barn Owl	10	0.000				1
<i>Tyto delicatula</i>	Eastern Barn Owl	11	0.005				2
<i>Tyto delicatula</i>	Eastern Barn Owl	27	-0.197				1
<i>Ninox connivens</i>	Barking Owl	13	-0.008				1
<i>Ninox novaeseelandiae</i>	Southern Boobook	11	0.059	-0.007	0.013	0.617	9
<i>Ninox novaeseelandiae</i>	Southern Boobook	10	0.000				3

**Table 4.2:** continued.

<i>Latin name</i>	<i>Common name</i> <i>Stainless Steel Bands</i>	<i>Size</i>	$\mu$	$\beta$	<i>SE</i>	<i>P</i>	<i>N</i>
<i>Podargus strigoides</i>	Tawny Frogmouth	9	0.151				1
<i>Podargus strigoides</i>	Tawny Frogmouth	10	-0.113	-0.009	0.008	0.260	11
<i>Dacelo novaeguineae</i>	Laughing Kookaburra	20	0.009	-0.003	0.001	0.008	18
<i>Dacelo novaeguineae</i>	Laughing Kookaburra	9	0.077	0.004	0.002	0.033	18
<i>Falco cenchroides</i>	Nankeen Kestrel	8	-0.043				2
<i>Falco longipennis</i>	Australian Hobby	9	0.001				1
<i>Falco berigora</i>	Brown Falcon	11	0.000				3
<i>Falco berigora</i>	Brown Falcon	10	0.007	0.001	0.003	0.870	4
<i>Falco subniger</i>	Black Falcon	11	0.001				1
<i>Falco peregrinus</i>	Peregrine Falcon	12	0.018	-0.001	0.002	0.682	4
<i>Falco peregrinus</i>	Peregrine Falcon	27	-0.026	0.001	0.000	0.019	4
<i>Falco peregrinus</i>	Peregrine Falcon	11	-0.065	-0.046	0.013	0.022	6
<i>Eolophus roseicapillus</i>	Galah	20	0.069	-0.002	0.002	0.413	12
<i>Lophochroa leadbeateri</i>	Major Mitchell's Cockatoo	21	0.010				3
<i>Cacatua tenuirostris</i>	Long-billed Corella	21	0.008				1
<i>Cacatua sanguinea</i>	Little Corella	21	0.003				2
<i>Cacatua galerita</i>	Sulphur-crested Cockatoo	22	0.063				2
<i>Platycercus elegans</i>	Crimson Rosella	24	0.010	-0.001	0.001	0.286	10
<i>Platycercus elegans adalaidae</i>	Adelaide Rosella	24	0.007				1
<i>Platycercus eximius</i>	Eastern Rosella	24	0.027				3
<i>Barnardius zonarius</i>	Australian Ringneck	24	0.093				3
<i>Parvipsitta porphyrocephala</i>	Purple-crowned Lorikeet	24	0.017				1
<i>Trichoglossus haematodus</i>	Rainbow Lorikeet	25	-0.009	-0.005	0.003	0.048	50
<i>Trichoglossus chlorolepidotus</i>	Scaly-breasted Lorikeet	24	0.092	-0.001	0.010	0.918	6
<i>Glossopsitta concinna</i>	Musk Lorikeet	24	-0.006				2
<i>Pitta versicolor</i>	Noisy Pitta	6	0.014				1
<i>Ptilonorhynchus violaceus</i>	Satin Bowerbird	9	0.015	-0.024	0.006	0.025	5
<i>Anthochaera carunculata</i>	Red Wattlebird	7	0.046				1
<i>Manorina melanocephala</i>	Noisy Miner	6	0.011				1
<i>Gymnorhina tibicen</i>	Australian Magpie	9	0.060	-0.015	0.002	0.000	59
<i>Gymnorhina tibicen</i>	Australian Magpie	10	-0.216				1
<i>Strepera graculina</i>	Pied Currawong	9	0.031	-0.009	0.001	0.000	20
<i>Strepera fuliginosa</i>	Black Currawong	9	-0.002	-0.010	0.001	0.001	5
<i>Strepera versicolor</i>	Grey Currawong	9	0.011				1
<i>Corvus orru ceciliae</i>	Torresian Crow	10	0.024				1
<i>Corvus bennetti</i>	Little Crow	9	0.016				1
<i>Corvus mellori</i>	Little Raven	10	0.069	-0.044	0.005	0.001	6
<i>Corvus coronoides</i>	Australian Raven	10	-0.073	-0.020	0.001	0.000	8
<i>Corcorax melanorhamphos</i>	White-winged Chough	9	0.032				2

**Table 4.3:** Starting masses of each band type as used in this study, inferred from samples of unworn retained and returned bands from the ABBBS archives. Each line corresponds to a band 'type' for the purposes of our analyses. In each case, the estimated starting mass for a band-type was the median mass of unworn bands with the same metal type and prefix, except where there were no unworn bands of that metal type and prefix available, in which case the starting mass was taken to be the median across all unworn bands of the same size and metal type. Band details (Internal diameter, Height, and Gauge) are given from manufacturing specifications. Band metal codes: AM, Aluminium; AY, Alloy; IN, Incoloy; ML, Monel; SS, Stainless Steel. SDs are given for band type (Type SD), defined as unique combinations of band size, metal, and prefix, and for size / metal (Size / metal SD), defined as all unworn bands of a given size and metal. Type SD is not given for band-types which were not available in the sample of unworn bands. <sup>a</sup> Three anomalous sets of bands were detected: Size 8 Stainless Steel bands between 082 – 30000 and 082 – 71000 were apparently manufactured heavier than standard specification, so worn bands in this series had their starting mass measured from only the reference bands in the same series. Bands with prefix 082 from outside the 082 – 30000 – 082 - 71000 range did not occur in our sample of worn bands, so only this anomalous set is reported here. Little Penguin flipper bands between 190 – 08000 and 190 – 26000, and between 190 – 46000 and 190 – 96000, were apparently manufactured lighter than standard specification, so worn bands in these series had their starting mass measured only from reference bands in the same series. <sup>b</sup> For band size 24 in Stainless Steel there were no reference bands, but there were seven worn bands that had been on an animal for less than one month. Worn bands had their starting mass estimated as the median of those seven bands.

<i>Size</i>	<i>Prefix</i>	<i>Metal</i>	<i>Internal Diameter (mm)</i>	<i>Height (mm)</i>	<i>Gauge (mm)</i>	<i>Starting Mass (g)</i>	<i>Type SD (g)</i>	<i>Size / metal SD (g)</i>
1	013	AY		2	5.5	0.38	0.0429	0.0018
1	014	AY		2	5.5	0.38	0.0404	0.0018
1	015	AY		2	5.5	0.38	0.0393	0.0018
1	016	AY		2	5.5	0.38	0.0434	0.0018
1	017	AY		2	5.5	0.38	0.0423	0.0018
1	018	AY		2	5.5	0.38	0.0430	0.0018
2	020	AM				0.0625		0.0009
2	023	AY	2.3	5.5	0.38	0.0458	0.0063	0.0040
2	024	AY	2.3	5.5	0.38	0.0445	0.0024	0.0040
2	025	AY	2.3	5.5	0.38	0.0474	0.0009	0.0040
3	031	AM				0.1232	0.0015	0.0017
3	032	AY	2.8	5.5	0.5	0.0721	0.0019	0.0009
3	032	IN	2.8	5.5	0.35	0.1602	0.0071	0.0064
3	033	AY	2.8	5.5	0.5	0.0720	0.0006	0.0009
3	033	IN	2.8	5.5	0.35	0.1631	0.0030	0.0064
3	034	AY	2.8	5.5	0.5	0.0722	0.0004	0.0009
4	041	IN	3.3	5.5	0.35	0.1818	0.0047	0.0060
4	041	AY	3.3	5.5	0.5	0.0849	0.0017	0.0161
5	050	ML	4	5.5	0.35	0.3034	0.0020	0.0020
5	050	AM				0.2001	0.0045	0.0045
5	051	IN	4	5.5	0.35	0.2120	0.0063	0.0063
5	051	AY	4	5.5	0.5	0.1055	0.0022	0.0020
6	061	SS				0.6337	0.0253	0.0253
6	061	IN	4.5	5.5	0.35	0.2332	0.1269	0.1146
6	061	AY	4.5	7	0.5	0.1657	0.0088	0.0052
6	062	AY	4.5	7	0.5	0.1669	0.0017	0.0052
6	062	IN	4.5	5.5	0.35	0.2449	0.0032	0.1146
7	071	IN	5.5	7	0.56	0.6394		0.0234
7	071	SS				0.7780		0.0004
7	071	AM	5.5	7	0.7	0.2566		0.0016
8	080	AM	6.5	6.5	0.7	0.2991		0.0016
8	081	SS	6.5	6.5	0.7	0.7915		0.0277
8	082 <sup>a</sup>	SS	6.5	6.5	0.7	0.8649	0.0277	0.0277
9	091	SS	8	10	1	2.2317	0.0436	0.0436
10	100	AM	9.5	10	1	0.8762	0.0112	0.0112
10	100	SS	9.5	10	1	2.6605	0.0251	0.0279
10	100	SS	9.5	10	1	2.3885	0.0251	0.0279
10	101	SS	9.5	10	1	2.6135	0.0221	0.0279

**Table 4.3:** continued.

<b>Size</b>	<b>Prefix</b>	<b>Metal</b>	<b>Internal Diameter (mm)</b>	<b>Height (mm)</b>	<b>Gauge (mm)</b>	<b>Starting Mass (g)</b>	<b>Type SD (g)</b>	<b>Size / metal SD (g)</b>
11	110	AM	11	12	1	1.5148	0.0208	0.0208
11	110	SS	11	12	1	3.5824	0.0113	0.0274
11	111	SS	11	12	1	3.5303	0.0020	0.0274
12	121	SS	14	12	1	4.4809	0.1240	0.1240
13	131	SS	16	12	1	5.0861	0.1061	0.1894
13	131	AM	16	12	1.5	2.6029	0.0051	0.5011
14	140	ML	20	16		6.9101	0.0118	0.0118
15	150	AM				5.1206	0.0426	0.0426
15	150	SS	22	12	1	6.8919	0.1312	0.1312
16	160	ML		1		1.5798		0.0624
16	161	SS		1		1.0402		0.0191
19	190	SS				2.0322	0.0874	0.0874
19	190 <sup>a</sup>	SS				1.8829	0.0874	0.0874
19	190 <sup>a</sup>	SS				1.8550	0.0874	0.0874
20	200	SS	9	5	1	1.2612	0.0131	0.0131
21	210	SS	11	5	1	1.4780	0.0147	0.0147
22	220	SS	13	5	1	1.7555	0.0238	0.0238
24	240 <sup>b</sup>	SS	5.5	5	0.7	0.5560		0.0056
25	250	SS	6.5	5	1	0.9661	0.0040	0.0040
27	270	SS	12.5	12	1	3.8870	0.0197	0.0197

## DISCUSSION

Although band wear-rates can vary substantially between species, most variability in estimated band wear-rates is explained by the combination of band-metal and avian functional-group. Within Aluminium bands, functional-groups fall into two clusters of wear-rates: fast-wearing (Passerines, Seabirds, and Ducks, Geese, and Swans, approximately 3 % per year), and slow-wearing (Birds of Prey, Other Non-passerines, and Waders, Herons, and Ibises, approximately 0.5 % per year). Within Alloy bands, bands worn by Passerines make up nearly all our dataset. Alloy bands worn by Passerines in our dataset appear to wear at a slightly faster rate than Aluminium bands worn by Passerines (approximately 4 % per year, against approximately 3 % per year). Within stainless steel bands, functional-groups also fall into two clusters, although in this case, Passerines are the only group in the fast-wearing cluster (a wear rate of approximately 1.5 % per year), with Birds of Prey, Ducks, Geese, and Swans, Parrots, Rails, Seabirds, Waders, Herons, and Ibises, and Other Non-passerines all falling into a cluster with slow wear-rates (approximately 0.1 % per year) across those groups.

Soft-metal bands worn by gulls have previously been identified as having worryingly high loss-rates, presumably resulting from rapid wear of soft-metal bands on these species (Gaston et al. 2013). On that basis, Gaston et al. (2013) recommended the use of hard-metal bands for marking gulls and other long-lived seabirds. Based on our observed wear-rates for Aluminium bands, we echo the recommendation of Gaston et al. that hard-metal bands should generally be used for marking long-lived seabirds. However, within stainless steel bands applied to seabirds in our data, the wear-rate of bands on Kelp Gulls is exceptionally rapid, and the wear-rate of bands applied to Pacific Gulls also appears high compared to other seabirds (Table 2; Appendix 4.2). We contend that bands worn by large coastal gulls may be subject to such exceptionally abrasive conditions that even the use of hard-metal bands is unlikely to solve the problem of wear-related band-loss for this group.

Monel bands were unusual in that functional groups did not cleanly explain the variance in band wear-rates as they did for other metal-types. Monel bands on Ducks, Geese, and Swans showed consistently low wear-rates over the species in our dataset (approximately 0.3 % per year), but Monel bands on seabirds showed marked clustering in wear-rates both between and within species, correlating with band prefix. We speculate that within-species differences in wear-rates may have been driven by small differences in band-chemistry between manufacturing-batches, or on differences between the environment of the populations marked during the time each manufacturing-batch was being applied – for example, it is possible that bands with prefix 160 were mainly used while a large banding-project was under way in a temperate environment,

whereas bands with prefix 161 were mainly used while a large banding-project was underway in the tropics.

Our estimated wear-rates contrast strongly with previously published wear-rates. The N-weighted average wear-rates in the published literature are faster than the N-weighted wear-rates in our dataset for all band-metals (Figure 4.2). In this study, we have estimated wear-rates from every combination of band-type and species for which bands were available in a large national archive. Our data are nevertheless constrained to only those bands returned to the Banding Office, which may bias our sample against some species or species-groups. However, we see no reason to think that our sample should contain disproportionate numbers of rapidly-wearing versus slowly-wearing species / band-type combinations. We therefore suspect that the published literature as a whole represents a biased sample of measured band wear-rates. We can think of two mechanisms that would bias the published literature in this way. Firstly, there is a genuine need to identify rapidly-wearing bands so that more-suitable bands can be put into use, which provides an incentive to publish records of rapidly-wearing bands. Secondly, negative wear-rate estimates (i.e., estimates that imply that bands increase in mass while worn) can arise from sampling variation. Negative wear-rate estimates are clearly unrealistic, and presumably unpublishable, but there is no similar mechanism preventing publication of unrealistic rapid wear-rate estimates. This publication bias will also tend to bias the mean of published wear-rates towards more rapid estimates.

The impact of publication bias on reported wear-rates can be large: the N-weighted mean published mass loss-rate for soft-metal (Aluminium / Alloy) bands is 4.28 % per year, compared to our estimate of 2.98 % per year; for Monel bands it is 3.28 % per year, compared to our estimate of 0.42 % per year; and for hard-metal (stainless steel / Incoloy) bands it is 0.74 % per year, compared to our estimate of 0.65 % per year. We therefore urge caution in using previously published wear-rates to correct for wear-related band-loss: such models would be affected by publication-bias in the literature, and we present our analyses as an unbiased alternative to the published literature as a whole. We appreciate the need for future studies to provide estimates of band wear-rates for a variety of band designs and species, both to highlight cases where band-designs are insufficient, and to provide estimates of band wear-rates for modelling purposes. We suggest that future studies on band-wear should explicitly state whether the species and bands in their study-set were selected on the basis of prior concern over wear-rates, to allow 'typical' wear-rates to be estimated from meta-analyses without bias from studies of bands with unusually-rapid wear.

## ACKNOWLEDGEMENTS

The authors would like to acknowledge the many banders and members of the public who have contributed to the ABBBS archives by banding birds or returning worn bands. Ashley Herrod assisted with the weighing of the bands. This work was supported by the Holsworth Wildlife Research Fund and the Australian Government's Australian Postgraduate Awards (APA) scheme.

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## General Discussion

Population mortality structures underpin core processes in biology, and estimates of those structures underpin central biological theories. Population mortality structures, and their relationship with population birth-rates, determine whether populations are expanding or contracting, whether a gene, trait, or behaviour imposes a survival-cost or benefit, and whether a medical, conservation, or ecological-management intervention is effective in meeting its goals. Similarly, senescence is a key process leading to human mortality, and mortality in captive populations, and is a widely-reported yet little understood process amongst wild populations of animals (Nussey et al. 2013).

In this thesis, I have generated and tested a new method for estimating population mortality structures across multiple species or populations, employing as an example data from the Australian Bird and Bat Banding Scheme (ABBBS) database. Survival and senescence parameters, including annual adult survival, annual first-year survival, annual juvenile survival, and yearly survival senescence, can be simply calculated from population mortality structures. My method requires that animals have been marked at a very young age, that animals have been recovered freshly dead, and that records have been kept of the total number of animals marked per year, or, for geographically-explicit models, the number of animals marked per location per year. Internationally, many national-scale banding authorities hold datasets that meet these requirements, and in recent years, both the ABBBS dataset, and part or all of the North American Bird Banding Program dataset, have become open-access (Obama 2013). As open-access data policies become widespread – a trend that I hope continues – my modelling approach is clearly useful in modelling survival in the wild across a wide taxonomic and geographic range, and across a wide variety of organismal groups differing in life-history or management structures.

## Summary of core findings

In Chapter 1, I presented a new method for estimating population-mortality structures from national-scale mark-recovery datasets. I tested the method's robustness to variation in sample-size, variation in true population mortality-structures, variation in band wear-rates, variation in the history of banding in the simulated animal-marking scheme, and mis-specification of band wear-rates. I fitted population mortality models to a set of 12 seabird species, and compared annual juvenile survival rate, annual adult survival rate, and annual survival senescence rate parameters from the population mortality models to published estimates of those parameters. The seabird models served as a ground-truth test for my modelling process: it would have been implausible on an *a priori* biological basis to observe a low survival-rate for seabirds (which, as a group, are well-known to be long-lived – e.g., Clapp & Sibley 1966; Johnsen et al. 1994; Anderson & Apanius 2003; Fredriksen et al. 2008; Hennicke et al. 2012). Survival rates of adults are generally higher than survival rates of juveniles in birds (Siriwardena et al. 1998), so model estimates of higher juvenile survival than adult survival would also have been biologically implausible *a priori*. Similarly, very different mortality-curves for closely-related species would have indicated a probable failure of my model assumptions, as published estimates of survival rates often show a high degree of correlation with phylogeny (Ricklefs 2010).

When Chapter 1 was written, the analyses in Chapter 4 had not been carried out, so there was little empirical support for any particular assumed band wear-rate in my models. A small number of differences are apparent between the population mortality-estimates for species presented in both Chapter 1 and Chapter 3 (e.g., the apparent survival rate crash in elderly Shy Albatross in Chapter 1, which does not appear in the Chapter 3 model for the same species). These differences appear mainly to result from different assumed band wear-rates between the models. The estimated mortality structures in Chapter 3 are preferable to those in Chapter 1 wherever they are in conflict, as the structures in Chapter 3 are informed by empirical measurements of band wear-rates gathered in Chapter 4.

My simulations indicated that, when the model-assumptions were met, my models produce cumulative survival estimates that are accurate (i.e., have low error) across the range of age-classes, and accuracy is reasonably maintained under low sample-sizes, differing mortality-structures, rapid band wear-rates, and short banding-history. Similarly, bias was low (i.e., a small fraction of total error), even under low sample-sizes, differing mortality-structures, rapid band wear-rates, and short banding-history in my simulations, but mis-specification of band wear-rates caused appreciable bias (i.e., bias was a substantial proportion of total error). My models based on real seabird data gave estimates that closely matched my *a priori* expectations –

seabirds were estimated to have generally high adult survival-rates, juveniles showed elevated mortality relative to adults, and closely-related species generally (with the exception of juvenile mortality rates in Northern Giant-Petrel and Southern Giant-Petrel, of which the Northern Giant Petrel showed a distinct set of very highly-weighted points, indicating probable issues with model assumptions) showed very similar survival-rates.

The first version of the MEMOIR model, as presented in Chapter 1, has potential uses in populations of marked animals where individuals are commonly recovered dead, especially where individuals have been marked at only one location or where dead individuals are recovered with equal probability regardless of the location at which they were marked. Seabirds in international datasets may be a future subject for this form of model, but the lack of ability to handle geographic structure prevents this first form of the MEMOIR model from being widely useful, as many species have limited range-sizes, and hence have recovery-probabilities that are tightly linked to their location-of-marking. The first form of the MEMOIR model is not capable of including data from animals sighted alive, further restricting its potential use.

In Chapter 2, I extended the basic MEMOIR model outlined in Chapter 1 to handle geographic structure in marking and recapture effort, and to include observations from marked animals sighted or captured-and-released alive. I tested this form of the MEMOIR model with simulated datasets with variable structures of sampling effort, variable numbers of marking-locations, variable numbers of animals marked per marking-expedition, and variable peak-probabilities of observation for each dead individual offset by increased numbers of marked animals. I also used this method to estimate mortality-structures for five avian species selected for their diverse structures of interactions with researchers and observers. For four of the five species, there were studies of survival and/or senescence rates available in the published literature. The selection of these five species allowed similar proof-of concept testing to that described for Chapter 1, including checking for biological plausibility against general patterns in survival rates, and cross-validation of my models against the published literature.

My simulations indicated that MEMOIR models including geographic structure could generate accurate estimates of the cumulative probability of survival to any age-at-death for the marked population, and that these estimates displayed a low degree of bias. Because weightings of points within a geographic location's sub-model were weighed relative to each other, and mortality curves from each geographic sub-model were weighted relative to the number of observations informing the curve, models incorporating data from multiple locations sometimes failed, especially in cases where there were many locations and few observations per location. The proximate cause of these model failures was the possibility of geographic sub-models containing

very few datapoints, whereas 'panmictic' models and combined geographic models had a hard-coded minimum number of datapoints. Investigating minimum sample-sizes for sub-models within geographically explicit models is a potential avenue for improving the reliability of the MEMOIR algorithm.

Parameter-estimates for adult survival and juvenile-survival from my fitted models for the five species showed agreement with published estimates of the same parameters. For each species, except for Satin Bowerbird (for which no published estimates were available), my estimated value for adult survival-rate was within the range of published estimates for the same parameter. Published estimates of juvenile survival-rate were available only for the Pacific Black Duck, and again, my estimate fell within the range of published estimates for this species. The scarcity of published juvenile survival-rates, and absence of any published estimates of senescence rates even within the well-studied species we had selected, highlighted the lack of data on survival parameters in wild populations, and the ability of MEMOIR modelling to fill many of these gaps in the literature.

In Chapter 3, I presented fitted MEMOIR models, using only observations of dead animals and assuming geographic structure based on banding-locations, to a set of 60 species from the Australian Bird and Bat Banding Scheme dataset. For each species, I extracted the adult survival-rate, first-year survival rate, and senescence rate (collectively, 'survival parameters') from my fitted mortality structure model. I investigated relationships between survival parameters, and relationships between survival parameters and life-history variables.

My set of survival parameter estimates is the largest dataset of avian survival-rates and senescence-rates in the wild of which I am aware (see Ricklefs 2010; Nussey et al. 2013). Between-species analyses of my models provided support for the 'fast-slow life-history continuum' as a unifying structure that explains much of the inter-species variance in survival and senescence parameters. It is noteworthy that my model provides estimates of juvenile (or first-year) as well as adult survival rates, whereas the models used by some other authors (e.g., Ricklefs 2010) begin at approximately the age at first breeding for each species, and do not estimate juvenile survival. Correlations between juvenile survival and adult survival, and between juvenile survival and the fast-slow life-history continuum have been reported in some taxa (e.g., mammals – see Promislow & Harvey 1990), and the ability to test these relationships amongst many species is a potential advantage of my approach over widespread approaches that model mortality starting at sexual maturity. Finally, I provided evidence against the hypothesis that relative brain-mass or migration status are biologically-significant predictors of survival or senescence rates in birds, though these had previously been reported as predictors of survival or

senescence (brain size: Ricklefs & Scheuerlein 2001; migration: Møller 2006).

The analyses in Chapter 3 allow replication of published inter-species life-history studies: the scale of study necessary to independently reproduce a dataset equivalent to the set of maximum recorded longevities for all available species has provided a prohibitive barrier to independent reproduction of such studies. MEMOIR models allow comparatively simple replications: my findings in Chapter 3 may be used as an independent replication of relationships reported in the published literature, and may themselves be replicated in international mark-recapture datasets, such as those held by EURING or the North American Bird Banding Program. In this way, researchers may distinguish effects that are stable across geographic regions, taxa, or analytical approaches from effects that are not, and identify claimed effects that do not replicate in independent datasets.

Noisy data, open theoretical structures and the ability of researchers to test multiple explanatory models for their data tend to favour the publication of spurious correlations, leading to the 'replication crisis' (Ioannidis, 2005; Open Science Collaboration 2015; Loken & Gelman 2017). The expected replication crisis has recently been empirically confirmed in Psychology (Open Science Collaboration 2015). Noisy data, open theoretical structures, and the ability of researchers to test multiple explanatory models are also common features of empirical evolutionary ecology research, but the replication-rate of evolutionary ecology studies has yet to receive empirical assessment comparable with the assessment of Psychology. Using data from MEMOIR models, it would be feasible to attempt to replicate a large set of published life-history analyses. The analyses I presented in Chapter 3 quantified eight life-history variables that have previously been reported as predictors of specific survival-rate parameters in published literature (pooling the body-mass variables and the clutch-size variables). Two of these variables were not found to significantly predict any survival-rate parameter, and five were not found to significantly predict the survival-rate they had been claimed to predict in the initial publication. Analyses of a similar set of replications could be used as a pilot-study of the 'replication crisis' in evolutionary ecology.

In Chapter 4, I presented analyses of wear-rates of metal bird-banding rings, to use in estimates of the distribution of longevities of these rings when worn by birds. I also presented comparisons between my set of band wear-rate estimates and the set of wear-rate measurements available in the published literature, and demonstrated that, within a type of band-metal, wear-rates reported in the literature are more rapid than wear-rates in an exhaustive study, implying publication bias towards reporting faster-wearing bands.

The wear-rates I estimated in Chapter 4 informed the modelling undertaken in Chapter 3, and will be useful in MEMOIR modelling undertaken on other datasets. MEMOIR models are unusual compared to standard mark-recapture models that account for potential mark-loss, in that MEMOIR models do not require any portion of the population to be double-banded, but do require an accurate estimate of the band wear-rate and the amount of wear that results in bands being lost.

The published literature on band wear typically overstates the wear rate for worn bands. This finding is interesting primarily in that, although wear-related band-loss can be important, it seldom has a large effect on fitted mortality models. Few bands are worn for long enough for wear-related loss to occur, and accordingly, the weighting for band-loss was typically the smallest weighting in MEMOIR models.

### **General comments on national mark-recapture schemes**

Our analyses have relied extensively on data from a national-scale governmentally administered mark-recapture dataset. Two features of national-scale, governmentally administered data collection are of particular value for survival estimation: standardisation and centralisation. The national standardisation of band designs, of band application techniques, and of band-types used on each species has allowed us to treat these standardised variables as constant through time between multiple independent studies. Centralisation of data, and especially the requirement that every issued band is known to have either been applied to an animal (and if applied, the species of that animal) or has gone unused, has made the  $W_a$  estimator in our analyses possible: if these data had not been centralised, then estimating the number of marked individuals potentially available through each age-class would have been effectively impossible.

### **Future directions**

MEMOIR modelling, as developed and demonstrated in this thesis, presents many opportunities for future research. I have mentioned the possibility of using MEMOIR models as a pilot-study for the replication-rate of evolutionary ecology research. With a large set of models, it would be possible to estimate a replication-rate for an effect reported in the published literature, and to empirically establish the 'type M error rate' (i.e., the amount by which a typical published study over-estimates the magnitude of a reported effect, relative to an independent replication of the same effect, see Gelman & Carlin, 2014) in this region of the evolutionary ecology literature.

There is also considerable utility in having MEMOIR models for many taxa, to aid in research for individual species. For instance, a researcher following a specific population or species

expressing, say, an unusual behaviour may be interested in knowing the typical survival-rates for that species or other populations of that species, for comparison to their specific population. Similarly, a researcher planning a long-duration tracking study may wish to know their species' expected lifespan in advance of the study, so that they can plan to gather sufficient data to test their hypotheses, even with data-loss from some individuals in their study dying. In this case, advance knowledge of first-year or juvenile mortality-rates may be particularly useful: if juvenile mortality-rates are high, it may not be economically viable to suffer the loss of tracking equipment attached to juvenile birds, and so the equipment may be attached only to adults – or similarly, a researcher forewarned of high juvenile mortality may choose a less costly tracking device for juveniles compared to adults.

Another potential avenue for research lies in variability that is not explained by species, e.g., variability by sex within species, variability by geographic location within species, or variability by time or ecological 'treatment' within species. For instance, it has been proposed that survival-rates could vary by sex because of differential costs of reproduction, physiology, behaviour, or genetics, or as a consequence of heterogamety being sex-specific and the heterogametic sex being less robust (Donald, 2007; Jorgenson et al., 1997). In birds, adult sex ratios tend to be strongly male-biased despite equal sex-ratios at birth (Donald, 2007). The age-structure of sex-biased mortality is key data for determining which potential causal factors may plausibly explain sex-specific survival rates.

One particular avenue to which MEMOIR modelling may be suited is in detecting changes in demographic rates through time and space in harvested populations. Harvesting applies evolutionary selection against phenotypes that are 'desirable' for harvest: for instance, increasing mortality rates is expected to select for earlier sexual maturity, and hunting for impressive sexually-selected weapons such as tusks or antlers selects for reduced weapon size (Allendorf & Hard 2009). In populations that are harvested for food, body size is often used as a basis for selection, and this selective pressure can rapidly cause changes in mean body mass (Conover 2007; Conover et al. 2011). If harvested and unharvested populations exist for a species, MEMOIR models could be used to quantify the impact of harvesting pressure on population demography, including estimating selection pressure and demonstrating changes in survival senescence.

One might also investigate time-specific (i.e., chronological time, rather than age-related) effects on survival and senescence. Time-specific MEMOIR models are, at present, only very coarse, as each discrete time-class in a time-specific MEMOIR model would need to cover at least as many

years as the maximum longevity of the species under study. Nevertheless, one could define an event (for instance, an article of conservation legislation, an environmental disaster such as an oil spill, or the economic collapse of a fishery), divide a species' dataset into the set of animals marked at least one maximum-longevity before some event, those marked between one maximum-longevity before the event and the event, and those marked after the event. After discarding the group marked between one maximum-longevity before the event and the event, one could fit separate MEMOIR models to the data from animals marked after the event and the data from animals marked at least one maximum-longevity before the event, and check for differences in survival-rates between those two models. Comparisons of this form critically depend on the event occurring at least one maximum longevity in the past, as each time-period is an independent MEMOIR model, each requiring at least some of the marked animals to have reached their maximum possible longevity. For obvious reasons, comparisons of this form are more likely to be viable for species with a short maximum longevity and a long history of marking.

Similarly, researchers might use MEMOIR models to investigate geographic patterns in survival and senescence rates. For instance, Bergmann's Rule (Bergmann 1847) states that within genera, larger species are found in colder climates (or after Mayr 1956, that within *species*, larger individuals are found in colder climates). In empirical analyses of Bergmann's Rule, latitude has frequently stood in for hard data on temperature, with individuals from high latitudes assumed to exist in colder conditions. If we were to take Bergmann's Rule as a given, and also take the position that body-mass is causally linked to survival-rate, we might state the corollary, that within species, individuals from colder climates have a higher survival-rate than individuals from hotter climates. Such a corollary could be easily tested over a broad taxonomic base using MEMOIR models: with an initial dataset including many species, an analyst might split the data for each species into a high-latitude and low-latitude group, fit a MEMOIR model separately to each group, and analyse the set of between-group differences in survival and senescence-rates.

Finally, individuals moving out of a study area present an avenue for future research. In capture-mark-recapture studies with a single focal study area and where some individuals permanently emigrate from the study area, it is difficult to distinguish permanent emigrants from dead individuals and make unbiased estimates of survival rates (see Powell et al. 2000; Cilimburg et al. 2002; Gilroy et al. 2012). In Chapter 2, I proposed a version of the MEMOIR model that only uses data from live resightings of marked individuals. This live-resightings version of the MEMOIR model would have its estimates of survival affected by individuals moving away from the study area unless all resighting events are 'non-marking observations'. One plausible

scenario is that dead recoveries are all ‘non-marking observations’, and that live resightings are a mix of ‘marking observations’ and ‘non-marking observations’ or entirely ‘marking observations’, and some individuals permanently emigrate from the area in which ‘marking observations’ occur. In such a scenario, the ‘dead-only’ model (as applied in Chapter 3) will give an unbiased estimate of the true survival curve, but the ‘live-only’ model will be biased by permanent emigration, and a comparison of the two models can be used to estimate the bias associated with permanent emigration.

### **Ultimate aims for MEMOIR models: a vision for the Tree of Death project**

Finally, survival and senescence rates are parameters that undergo evolutionary change. The phylogenetic tree of birds is fairly well-established (Davis & Page 2014; Prum et al. 2015). By combining MEMOIR analyses over the datasets of multiple national banding schemes, we can therefore build up trees of mortality structures, and from these, estimate the rates of evolutionary change in survival and senescence in the wild. Trees like this will allow much more detailed testing of causal hypotheses – instead of asking whether a life-history variable is correlated with a survival or senescence parameter, causal questions can begin to be reasonably addressed, by assessing whether changes in a life-history parameter in evolutionary time generally precede changes in a survival or senescence variable, or vice versa. This 'Tree of Death' project, derived from the set of population mortality-curves for many species, will necessarily be a long-term, multi-stakeholder endeavour, tying together data from a wide array of field researchers, NGOs, and Government agencies from multiple countries.

Ultimately, a 'Tree of Death' for free-living wild animals is achievable only by combining the results of many long-duration, purpose-built capture-mark-recapture studies covering large numbers of species (i.e., the 'longitudinal approach' of Nussey et al. 2008), or through MEMOIR models. Long-duration capture-mark-recapture studies are expensive and difficult to conduct, and frequently take decades to produce senescence estimates. For many species, no long-duration capture-mark-recapture study has yet been initiated, but data suitable for MEMOIR analyses exist. Therefore, MEMOIR modelling currently represents the only viable approach for building a 'Tree of Death' with coverage of many species of free-living wild animals, and may remain the only viable option for the foreseeable future.

### **Conclusion**

I have presented, tested, and applied a novel method for estimating species-specific population-mortality curves based on publicly-available mark-recapture data, of the sort widely held in national banding schemes. My method has already delivered the largest set of first-year survival,

adult-survival, and senescence parameters for free-living wild birds, and using this dataset, I have tested a set of evolutionary hypotheses, and clarified the relationships between survival at different age-ranges, senescence, and life-history. By utilising open-access international datasets, my method can deliver population mortality structures and derived survival and senescence rate estimates for many more species. Survival and senescence parameters estimated through MEMOIR modelling have diverse implications in population biology, conservation, evolution, management, and gerontology. Access to fundamental population mortality parameters across many populations will provide valuable reference material, and core data for hypothesis generation and testing, for many years to come.

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# Appendix 1

## *Supplementary materials to Chapter 1 – A model for first-estimates of species-specific, age-specific mortality from centralised band-recovery databases*

### **Appendix 1.1:** Band-wear estimation.

We have defined seven groups for modelling of band-wear: Albatrosses, Fulmarine Petrels, Shearwaters, Storm Petrels, Small Gulls, and Large Gulls, and Large Birds. Albatrosses, Large Gulls, and Fulmarine Petrels are all also considered Large Birds. For modelling, we required an estimate of the wear-rate of bands of the metal type used in Australian banding studies on members of each group.

For species in groups with no recorded wear-rate of the required metal type, we inferred the likely wear-rate of that metal from the wear-rates for all other metal wear-rates recorded for that group in the literature. Wear-rates for Aluminium bands are by far the most common in the literature (see Table), so all inferences of wear-rates of specific metals are made via an estimate for the wear-rate of Aluminium bands. Inferred wear-rates were taken from the most-specific groups available. For instance, estimates of the wear-rates of both Aluminium and Stainless bands were available for Silver Gulls, so these estimates were used directly without inferring from other members of the Small Gulls group. Albatrosses are in both the Albatrosses group and the Large Birds group, so if an estimated wear-rate is required for a species of Albatross, data are taken from all Albatrosses for which there are data. By contrast, the Australasian Gannet is a member of the Large Birds group, because there are no published wear-rates on Sulids available. So, if an estimated wear-rate is required for the Australasian Gannet, data are pooled across all Large Birds.

For species with recorded wear-rates of both Aluminium and Stainless bands (Common Tern and Silver Gull), the mean wear-rate of stainless bands is 22% the wear-rate of Aluminium bands. For species with recorded wear-rates for both Aluminium and Incoloy bands (two datasets of Common Tern), the mean wear-rate of Incoloy bands is 5% the wear-rate of Aluminium bands. For species

with recorded wear-rates for both Aluminium and Monel bands (Ring-billed Gull and two datasets of Herring Gull), the mean wear-rate of Monel bands is 39% the wear-rate of Aluminium bands.

For species in groups with no recorded wear-rate for the required metal type, we inferred the likely wear-rate of the required metal from the observed metals. So, for instance, we required an estimate of the wear-rate of Stainless bands on Albatrosses, but the two observed wear-rates on Albatrosses were both Aluminium, at 1.40% and 2.42%. The mean wear-rate of Aluminium bands on Albatrosses is therefore 1.91%. Stainless bands wear at 22% the rate of Aluminium bands, so we estimate the annual wear-rate of stainless bands on Albatrosses as 0.42%. Similarly, only one wear-rate is observed for Shearwaters, of Monel bands, but we required an estimate of the wear-rate of Stainless bands on Shearwaters. The observed wear-rate of Monel bands on Shearwaters is 1.2%. Monel bands wear at 39% the rate of Aluminium bands, so our estimated wear-rate for Aluminium bands on Shearwaters is 3%. Finally, Stainless bands wear at 22% the rate of Aluminium bands, so our estimated band-wear rate for Stainless bands on Shearwaters is 0.68%.

**Appendix table 1.1.1:** Band wear-rates reported in the literature, used to infer band wear-rates for use in our modelling. Band-metal codes: Aluminium – Al; Stainless Steel – SS; Incoloy – In; Monel – Mo. A band wear-rate of 9.61% was also noted for Monel bands on Caspian Terns by Ludwig (1967), but this is approximately three times the wear-rate of softer aluminium bands on the same species in the same study. Ludwig (1967) notes that Monel bands corroded rapidly on Caspian Terns, and attributes the corrosion to the birds' habit of defecating on their own legs. We have chosen to omit the 9.61% wear-rate from our calculations because of its high leverage and because we suspect it does not represent typical wear-rates for this metal.

<i>Latin binomial</i>	<i>Common name</i>	<i>Band Metals</i>				<i>Group</i>	<i>Source</i>
		<b>Al</b>	<b>SS</b>	<b>In</b>	<b>Mo</b>		
<i>Phoebastria nigripes</i>	Black-footed Albatross	1.40%				Albatrosses; Large Birds	Ludwig et al. (1996)
<i>P. immutabilis</i>	Laysan Albatross	2.42%				Albatrosses; Large Birds	Ludwig et al. (1996)
<i>Fulmarus glacialis</i>	Northern Fulmar	5.26%				Fulmarine Petrels; Large Birds	Anderson (1980)
<i>Puffinus tenuirostris</i>	Short-tailed Shearwater				1.20%	Shearwaters	Wooller et al. (1985)
<i>Hydrobates pelagicus</i>	European Storm Petrel	8.50%				Storm Petrels	Harris (1980)
<i>Chroicocephalus ridibundus</i>	Black-headed Gull	3.40%				Small Gulls	Harris (1980)
<i>C. novaehollandiae</i>	Silver Gull	4.10%	1.40%			Small Gulls	Wooller & Wooller (1998)
<i>Rissa tridactyla</i>	Kittiwake	8.60%				Small Gulls	Harris (1980)
<i>Larus delawarensis</i>	Ring-billed Gull	9.55%			4.30%	Large Gulls; Large Birds	Ludwig (1967)
<i>L. argentatus</i>	Herring Gull	7.50%			1.62%, 3.80%	Large Gulls; Large Birds	Ludwig (1967); Coulson (1976)
<i>L. fuscus</i>	Lesser Black-backed Gull				2.20%	Large Gulls; Large Birds	Coulson (1976)
<i>Hydroprogne caspia</i>	Caspian Tern	3.13%				Terns	Ludwig (1967)
<i>Sterna hirundo</i> (size 3 bands)	Common Tern	5.42%	0.55%	0.25%		Terns	Hatch & Nisbet (1983); Nisbet & Hatch (1988)
<i>S. hirundo</i> (size 2 bands)	Common Tern	4.07%		0.25%		Terns	Nisbet & Hatch (1985); Nisbet & Hatch (1988)
<i>S. paradisaea</i>	Arctic Tern	0.90%				Terns	Hatch & Nisbet (1983)
<i>S. dougallii</i>	Roseate Tern	6.30%				Terns	Hatch & Nisbet (1983)
<i>Onychoprion fuscatus</i>	Sooty Tern	0.57%				Terns	Bailey et al (1987)

**Appendix 1.2:** An estimate of the expected ratio of  $N$  to  $\sum W_{aib}$  for model diagnostics.

In our modelling approach, each of the three weights,  $W_a$ ,  $W_i$ , and  $W_b$ , estimates the under-representation of points like the present point, relative to the situation expected to give the highest rate of observations. For example, the  $W_a$  value of a point is the odds of a point like the present one being missed because of low *Availability*, relative to the most-available point in the dataset. It follows that, in a hypothetical population where all marked individuals have died (say, a population where  $t = \infty$ ),

$$\sum W_a = N * \Pr(\text{dead} \cap \text{found})$$

with  $W_a = 1$  for all points. As we move back in time from  $t = \infty$ , we have fewer observations (as some points that will be observed have not yet been observed), and the  $W_a$  scores of points at under-represented ages increase to compensate for their absence. Thus, in a scenario with no band-loss and constant monitoring intensity,

$$E(\sum W_a) = N * \Pr(\text{dead} \cap \text{found})$$

for all  $t$ , given that the maximum value of  $t$  exceeds the maximum longevity of the species.

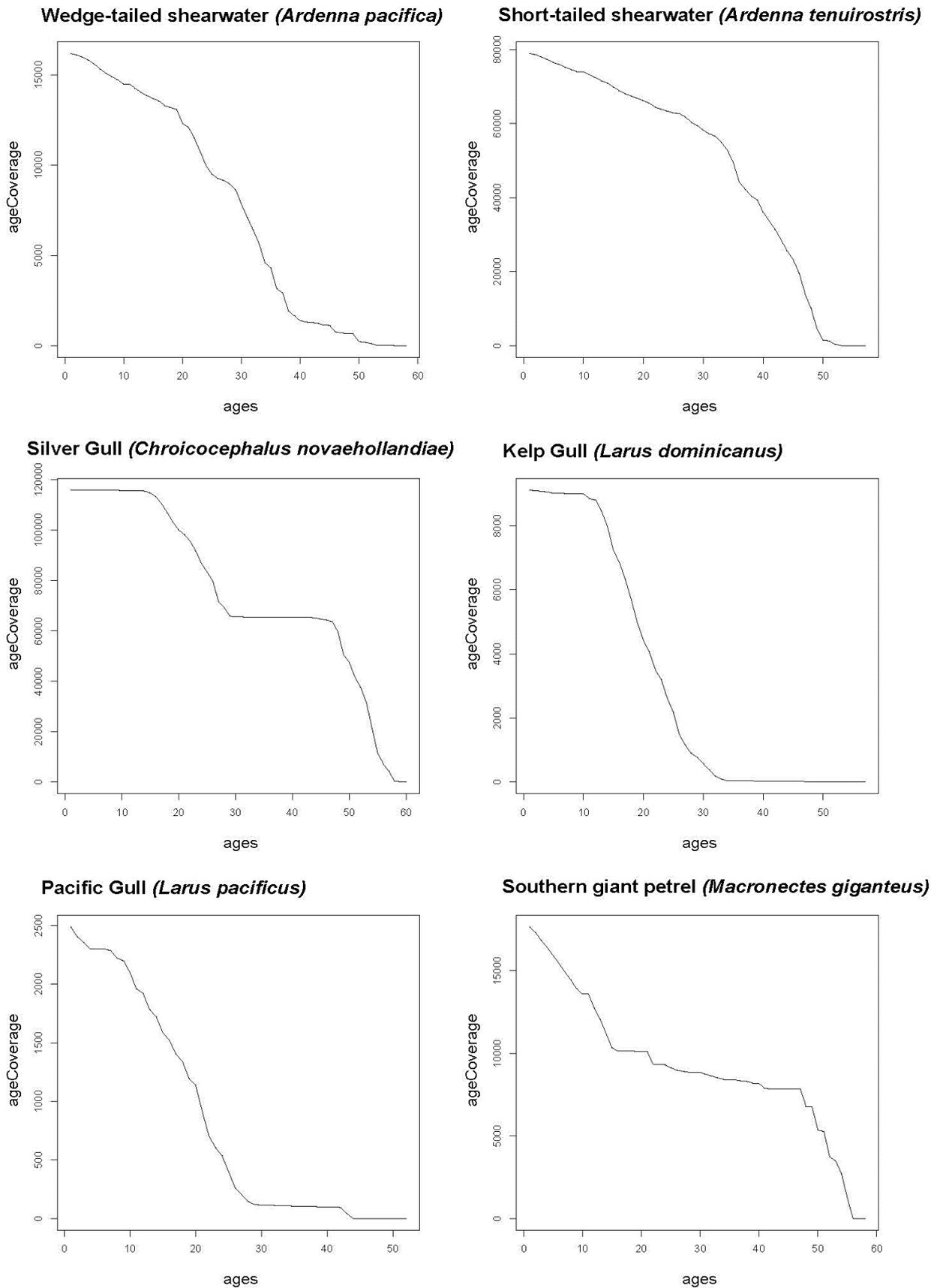
The structure of  $W_i$  and  $W_b$  is essentially the same as for  $W_a$  (i.e., increases in  $W_i$  and  $W_b$  serve to offset missing observations that are missing because of lower-intensity monitoring in some years and mark-loss in some age-classes), giving the general statement:

$$E(\sum W_{aib}) = N * \Pr(\text{dead} \cap \text{found})$$

For most plausible population-marking histories, the probability of a marked individual being found dead will be less than one, often much less. Therefore, if the sum of  $W_{aib}$  exceeds the number of individuals marked, there is probably something wrong with the fitted model and the model fit should be treated with suspicion. We suggest that researchers may be able to devise more-stringent tests based on their own estimates of  $\Pr(\text{dead} \cap \text{found})$  in their own study systems.

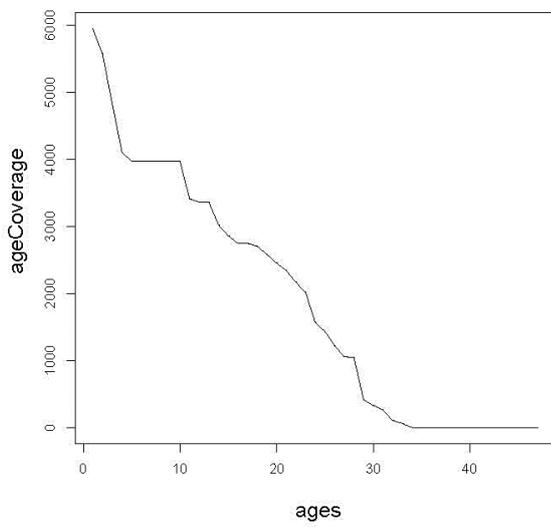
### Appendix 1.3: Availability curves for all modelled species.

**Appendix figure 1.3.1:** Curves denote the number of individuals in each species that could potentially have died at each age – i.e., for individuals marked as unfledged young,  $y$  equals the number of individuals marked  $\geq x$  years ago.

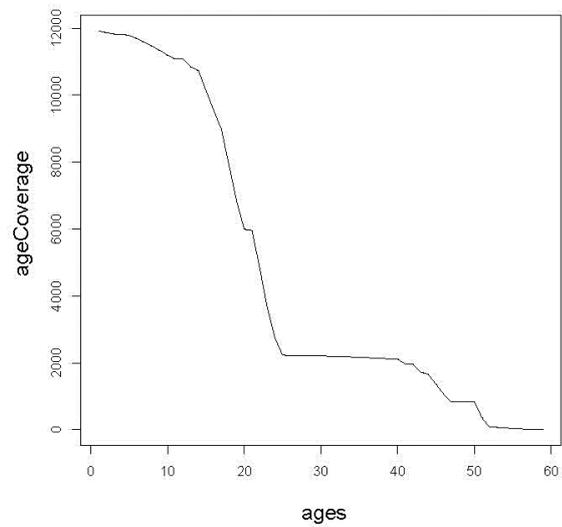


Appendix figure 1.3.1: continued.

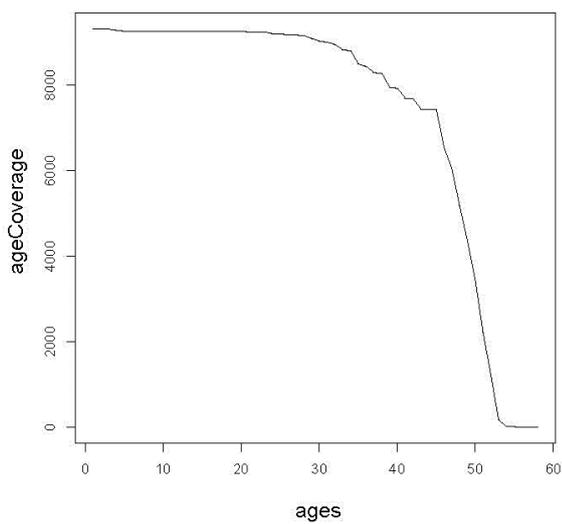
Northern giant petrel (*Macronectes halli*)



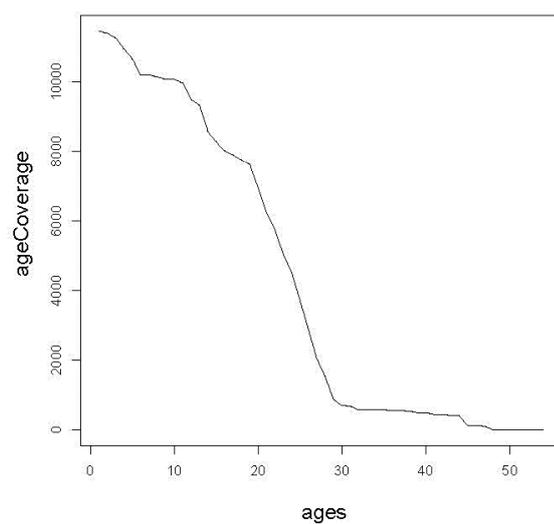
Australasian Gannet (*Morus serrator*)



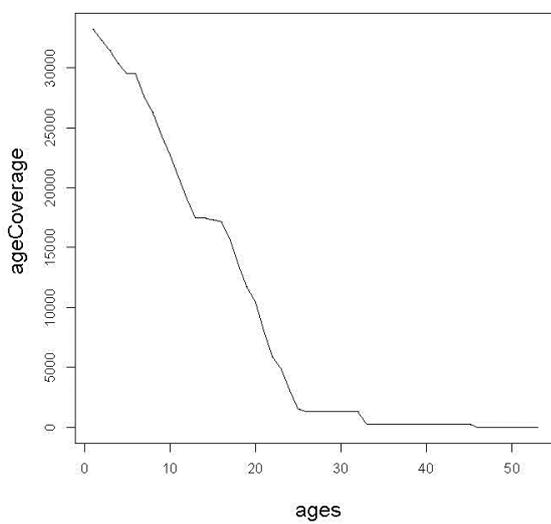
White-faced storm petrel (*Pelagodroma marina*)



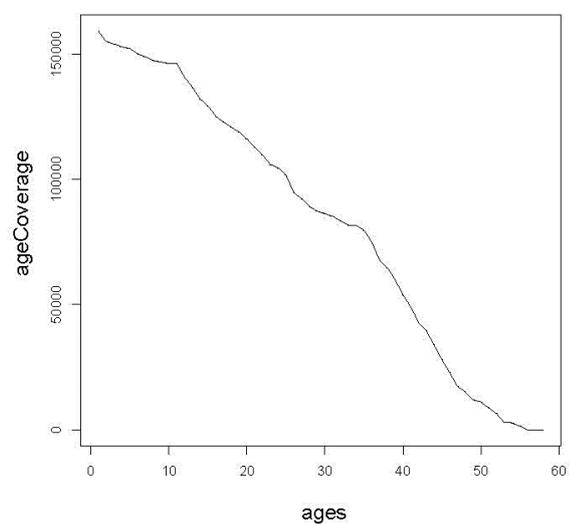
Masked Booby (*Sula dactylatra*)



Shy albatross (*Thalassarche cauta*)

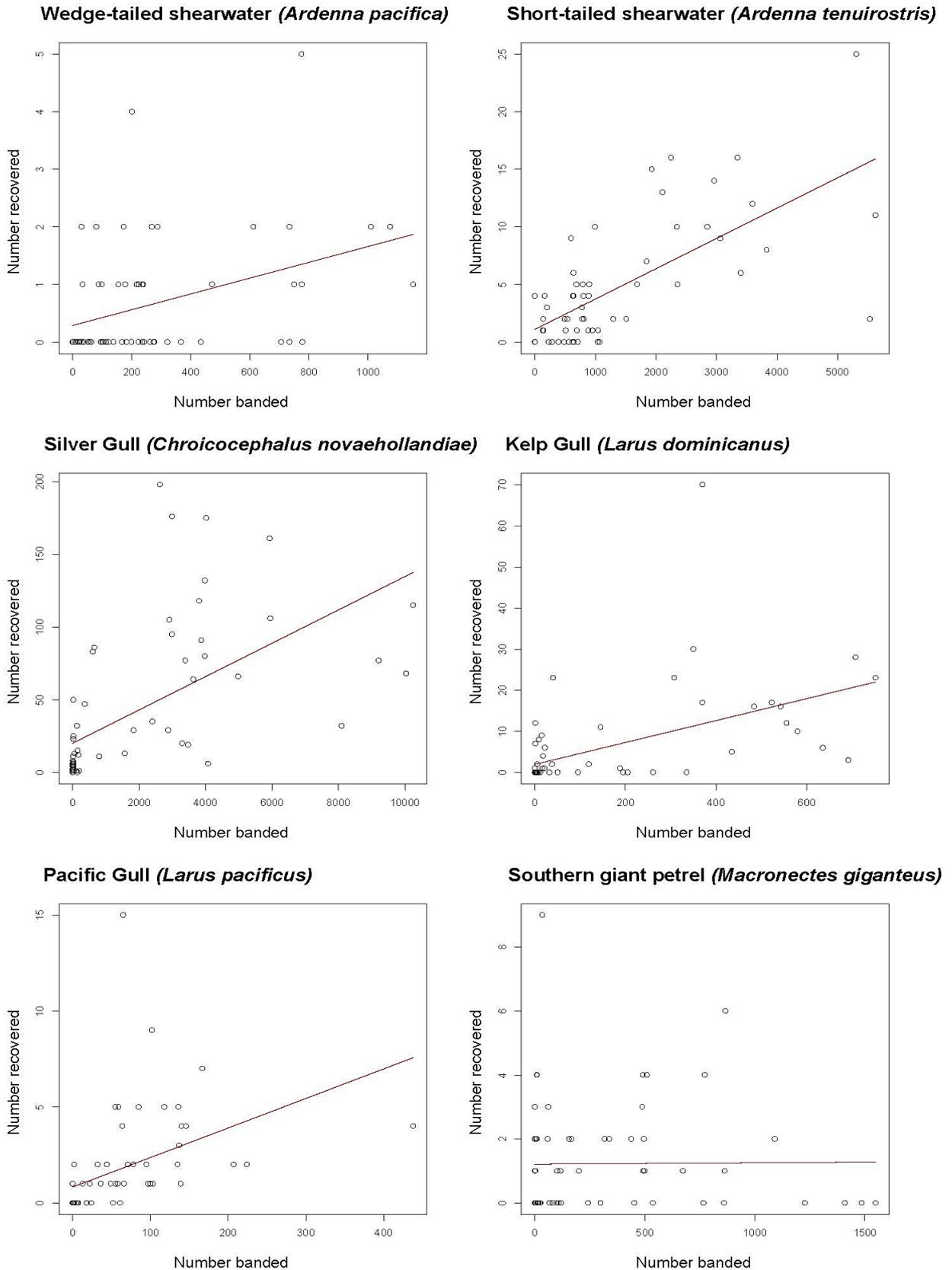


Crested tern (*Thalasseus bergii*)



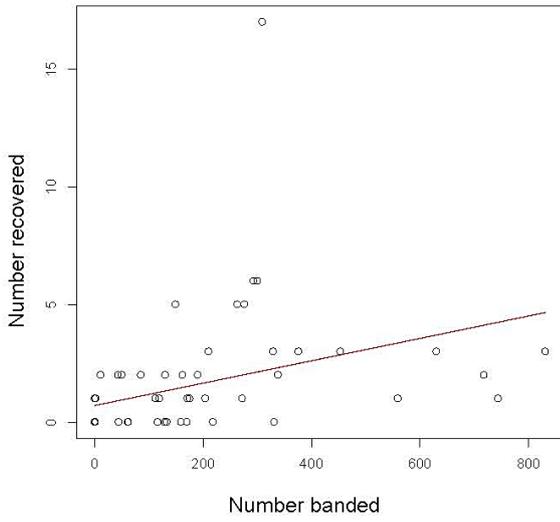
## Appendix 1.4: Intensity models for each modelled species.

**Appendix figure 1.4.1:** Each graph represents a linear model-fit between the number of individuals banded and recaptured in a year. Linear models are constrained so that their intercept and slope are both  $\geq 0$  - i.e., even with no study, the probability of a dead individual being found is  $> 0$ , and increasing study cannot decrease the probability of a dead individual being found.

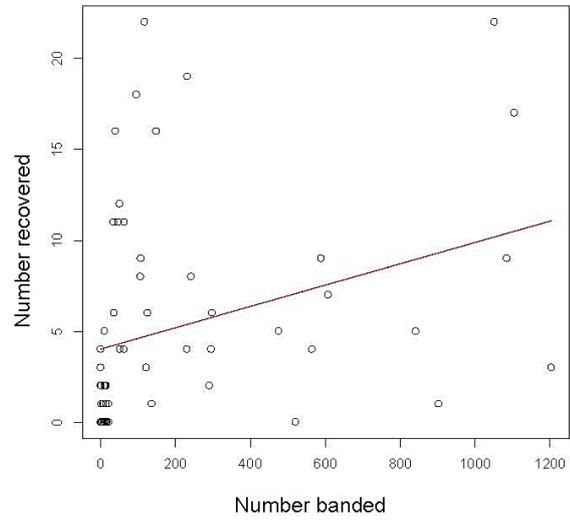


Appendix figure 1.4.1: continued.

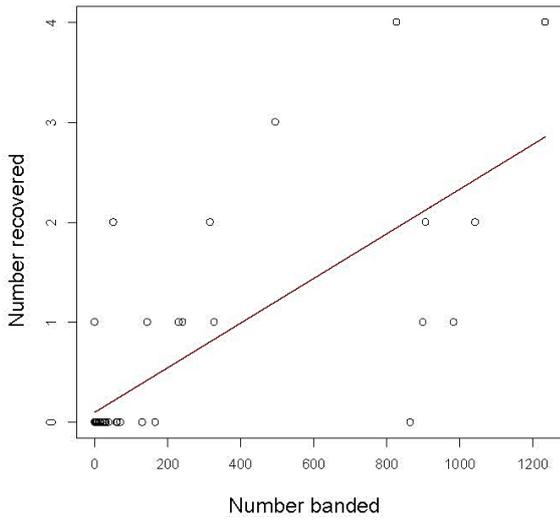
Northern giant petrel (*Macronectes halli*)



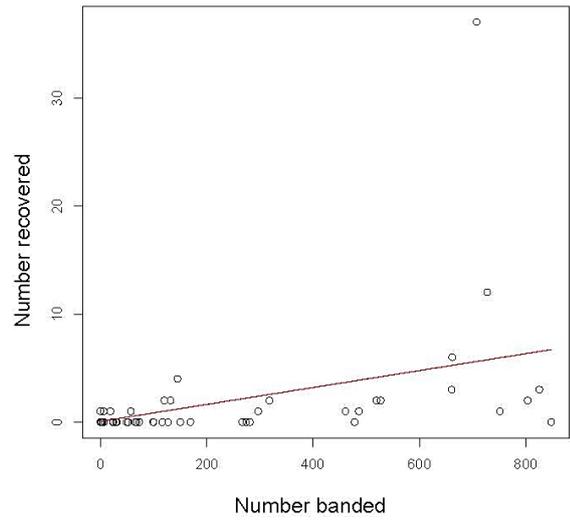
Australasian Gannet (*Morus serrator*)



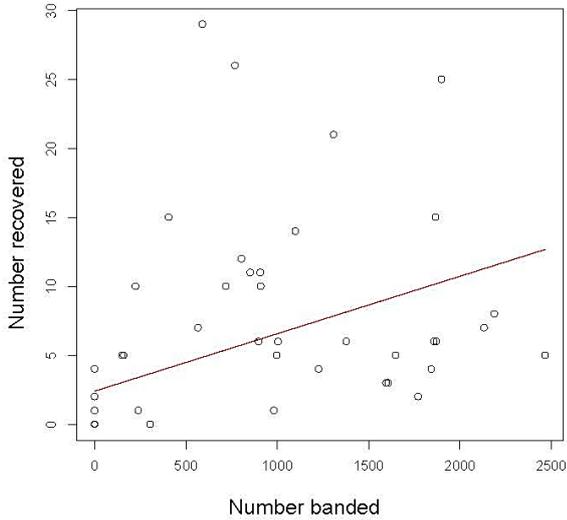
White-faced storm petrel (*Pelagodroma marina*)



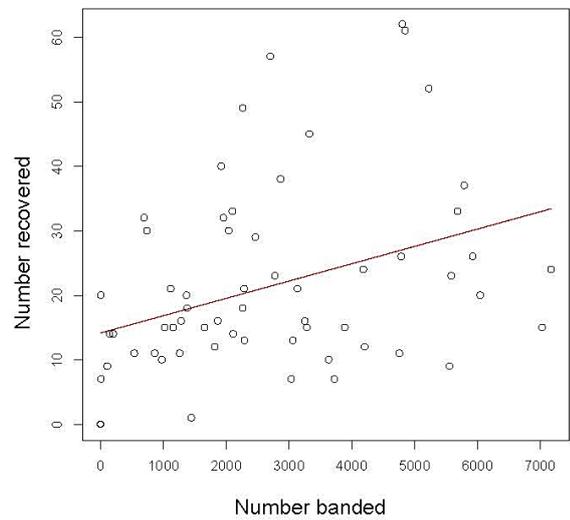
Masked Booby (*Sula dactylatra*)



Shy albatross (*Thalassarche cauta*)

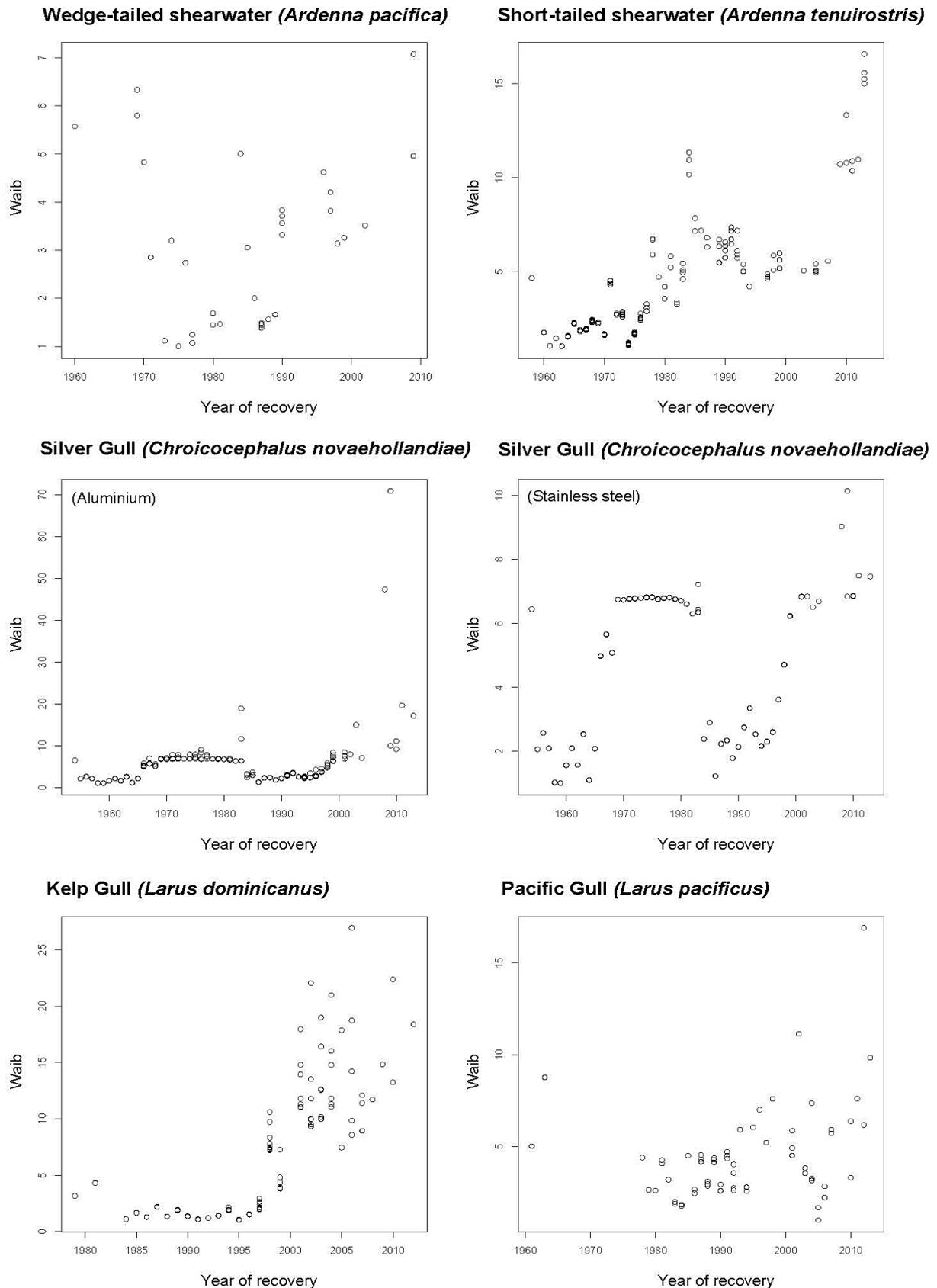


Crested tern (*Thalasseus bergii*)



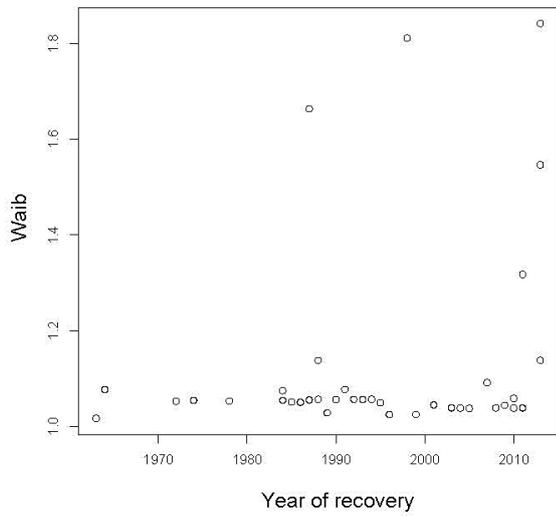
**Appendix 1.5:**  $W_{aib}$  fitted values for each modelled species.

**Appendix figure 1.5.1:** High  $W_{aib}$  scores denote individuals with a high combined  $W_a$ ,  $W_i$  and  $W_b$  score. Individuals with a very high  $W_{aib}$  score are considered to have a very low prior probability of discovery.

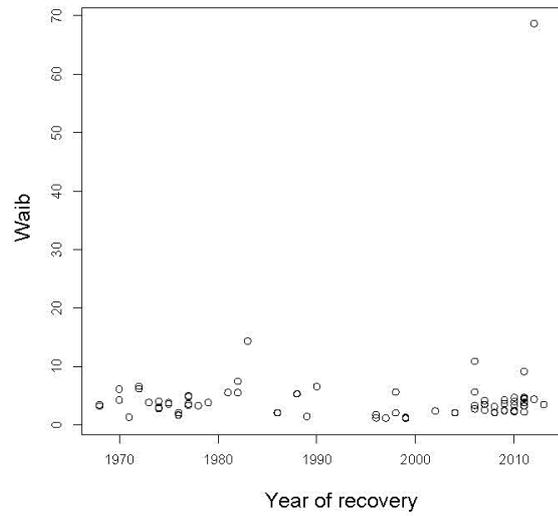


Appendix figure 1.5.1: continued.

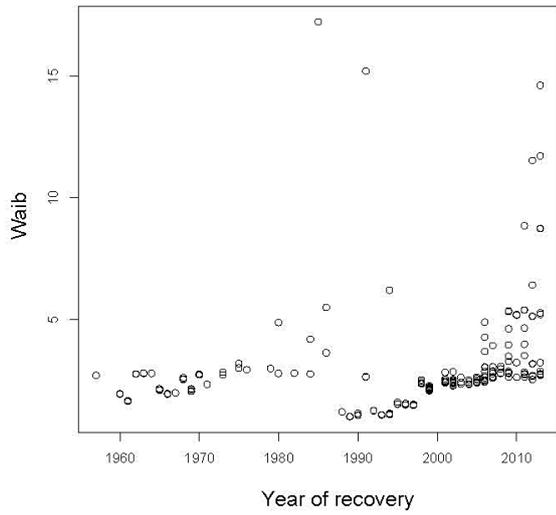
**Southern giant petrel (*Macronectes giganteus*)**



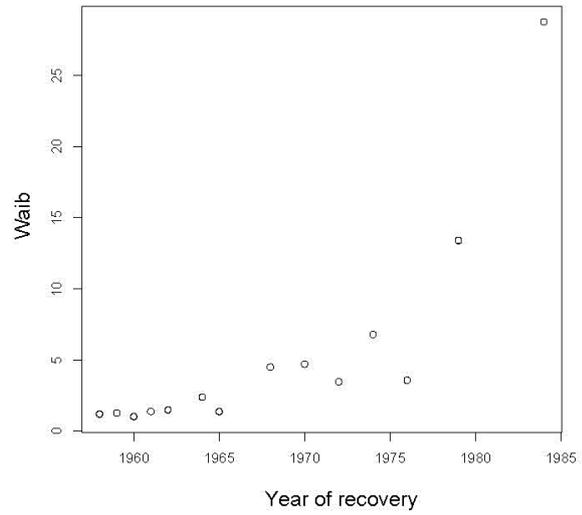
**Northern giant petrel (*Macronectes halli*)**



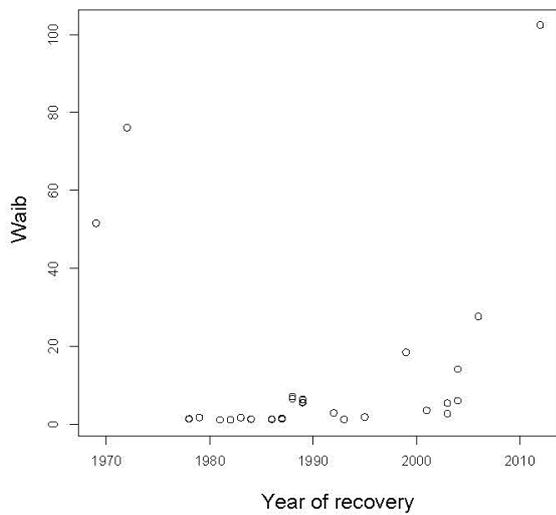
**Australasian Gannet (*Morus serrator*)**



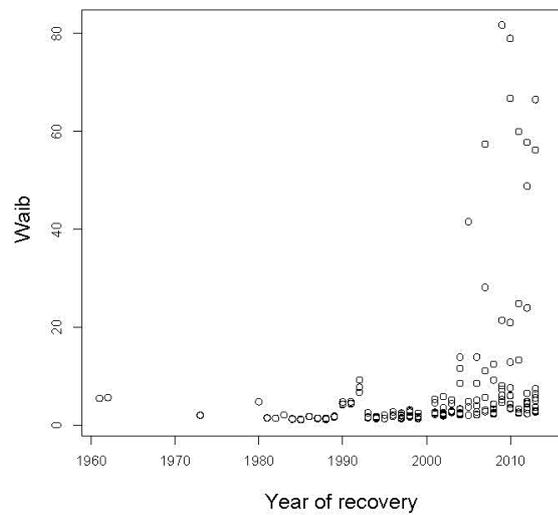
**White-faced storm petrel (*Pelagodroma marina*)**



**Masked Booby (*Sula dactylatra*)**

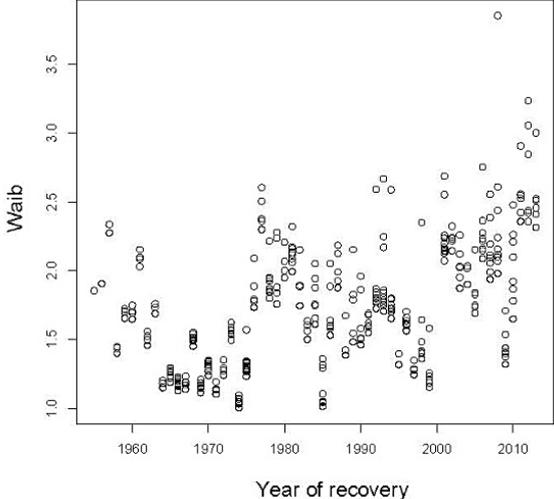


**Shy albatross (*Thalassarche cauta*)**



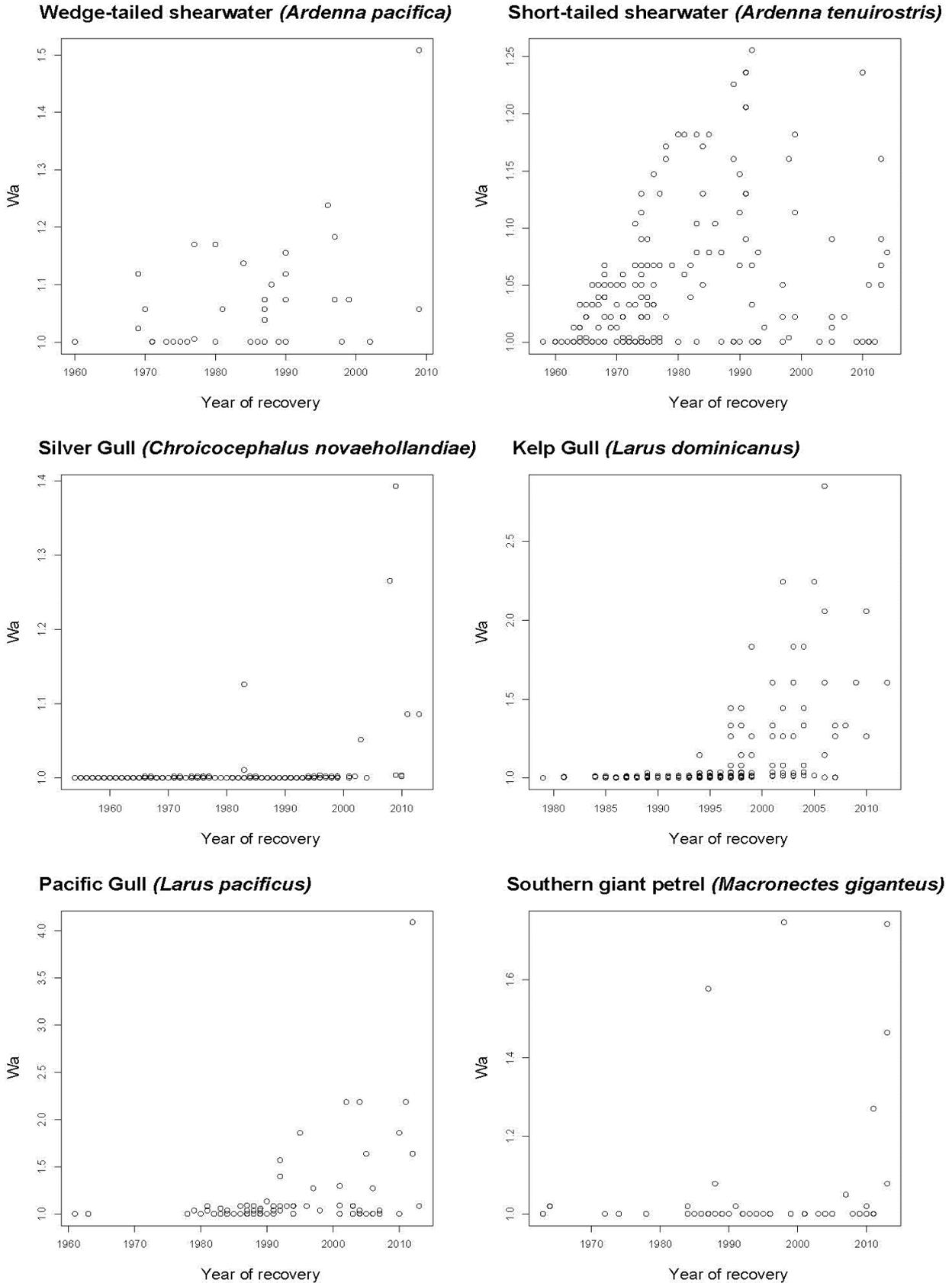
Appendix figure 1.5.1: continued.

Crested tern (*Thalasseus bergii*)



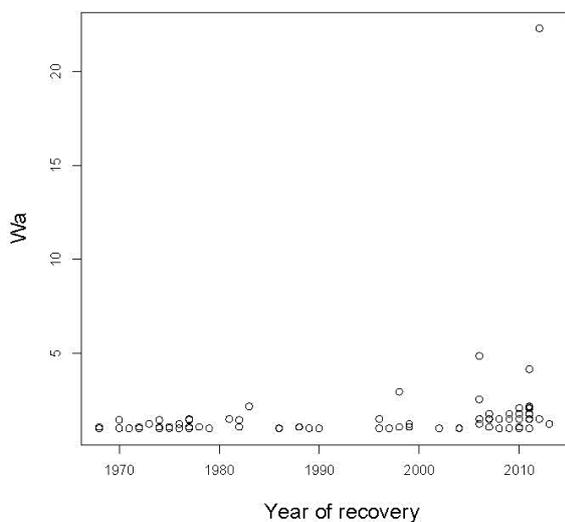
**Appendix 1.6:**  $W_a$  fitted values for all modelled species.

**Appendix figure 1.6.1:** High  $W_a$  values denote individuals found dead at an age that proportionally few of the marked population could have attained. Because all individual progress through all ages until their terminal age, individuals with high  $W_a$  scores are also individuals with a high age-at-death relative to other members of their species.

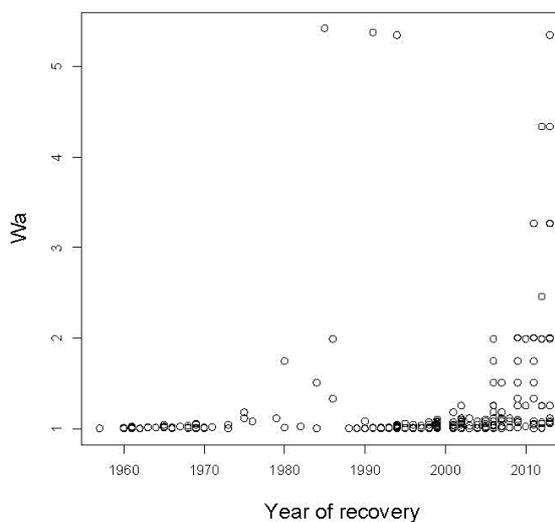


Appendix figure 1.6.1: continued.

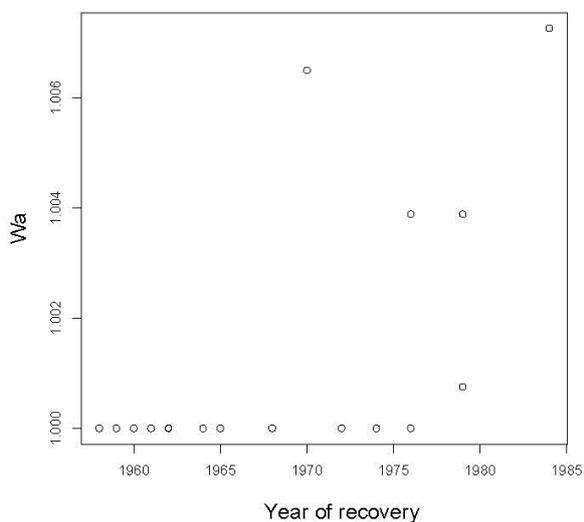
Northern giant petrel (*Macronectes halli*)



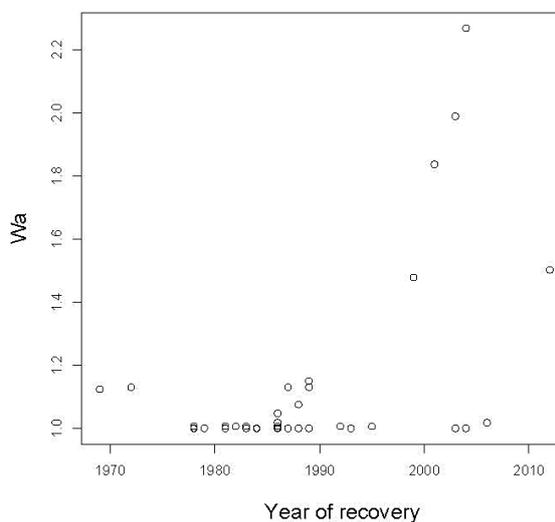
Australasian Gannet (*Morus serrator*)



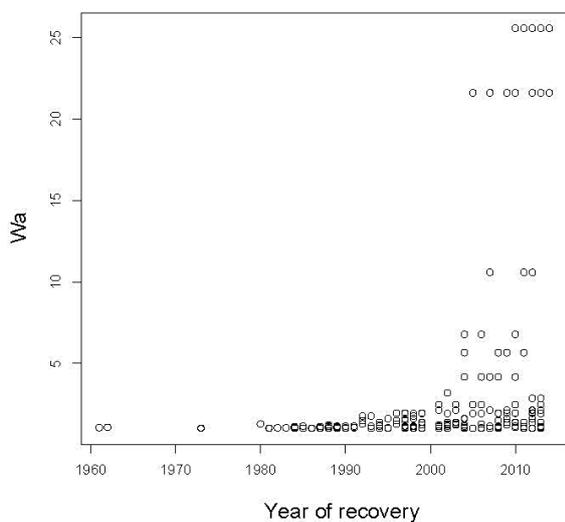
White-faced storm petrel (*Pelagodroma marina*)



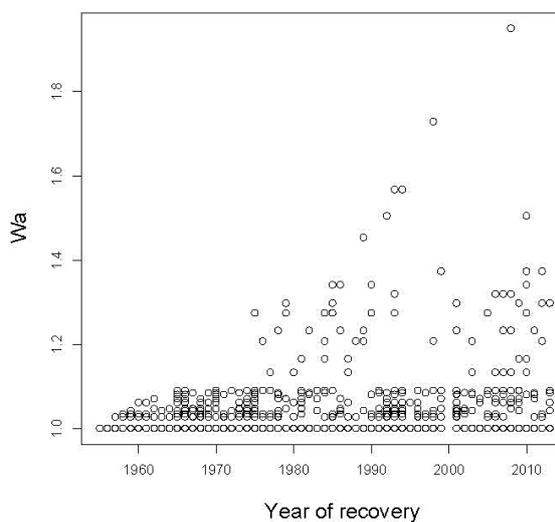
Masked Booby (*Sula dactylatra*)



Shy albatross (*Thalassarche cauta*)



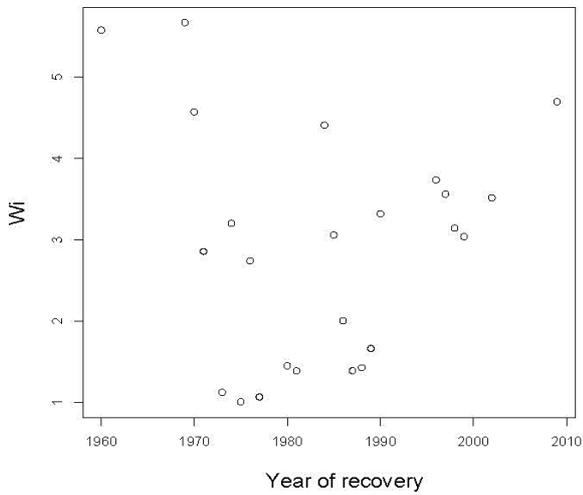
Crested tern (*Thalasseus bergii*)



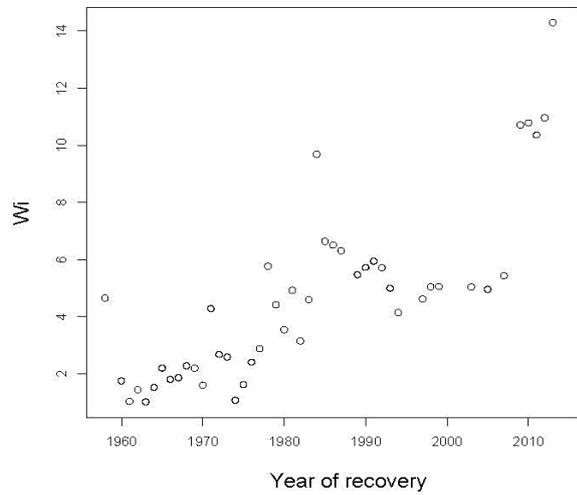
**Appendix 1.7:** Fitted  $W_i$  values for all modelled species.

**Appendix figure 1.7.1:** A high  $W_i$  value denotes an individual captured in a year when their species was not under intense study.

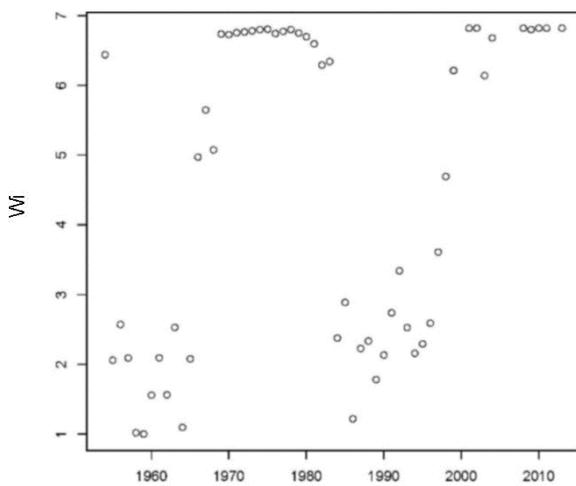
**Wedge-tailed shearwater (*Ardenna pacifica*)**



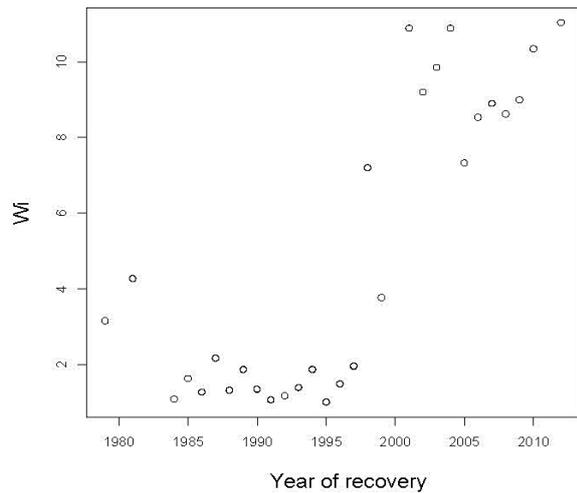
**Short-tailed shearwater (*Ardenna tenuirostris*)**



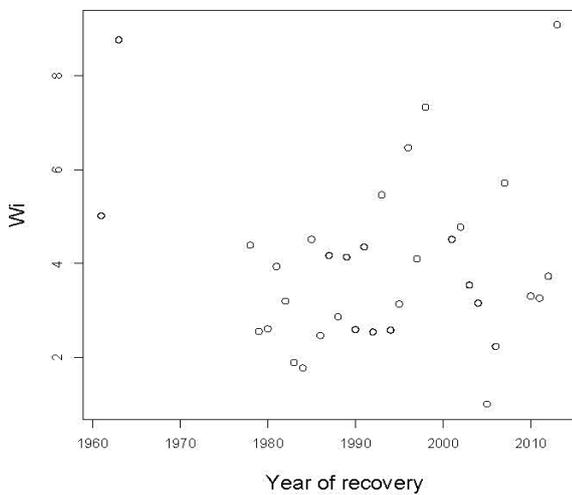
**Silver Gull (*Chroicocephalus novaehollandiae*)**



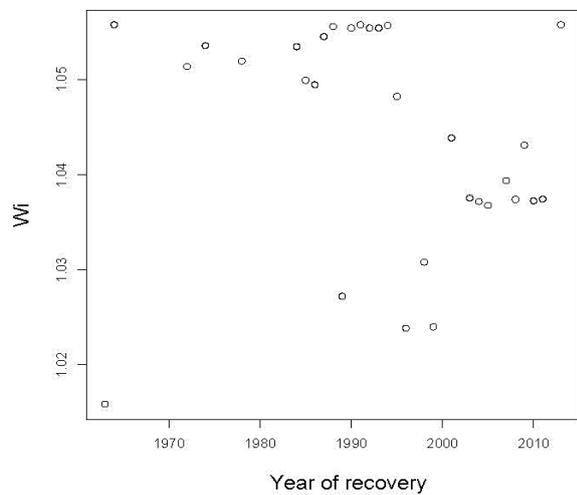
**Kelp Gull (*Larus dominicanus*)**



**Pacific Gull (*Larus pacificus*)**

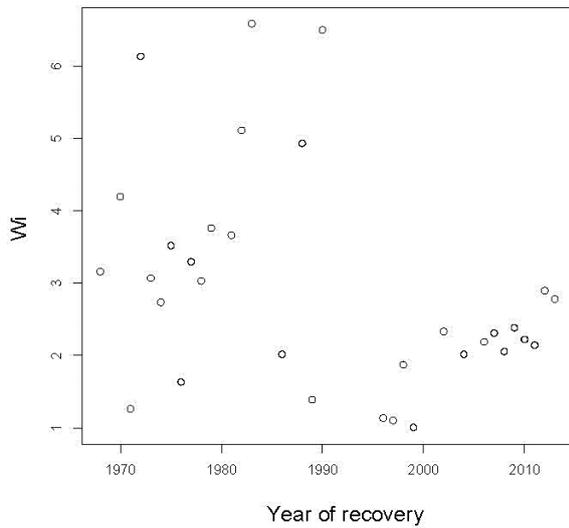


**Southern giant petrel (*Macronectes giganteus*)**

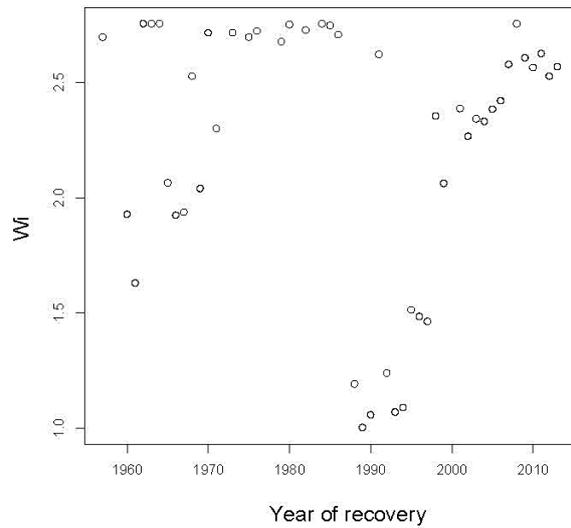


Appendix figure 1.7.1: continued.

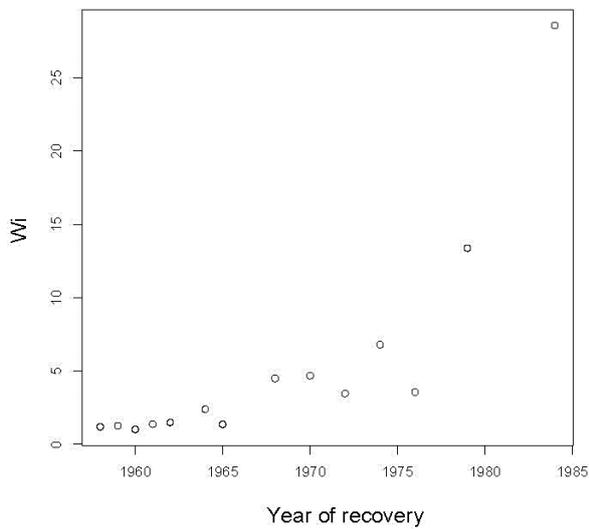
Northern giant petrel (*Macronectes halli*)



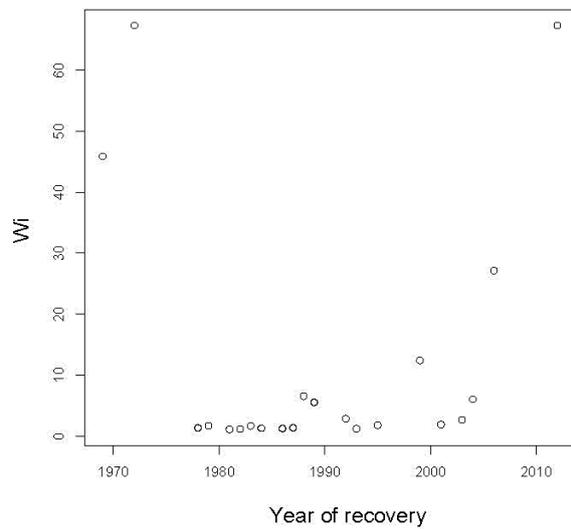
Australasian Gannet (*Morus serrator*)



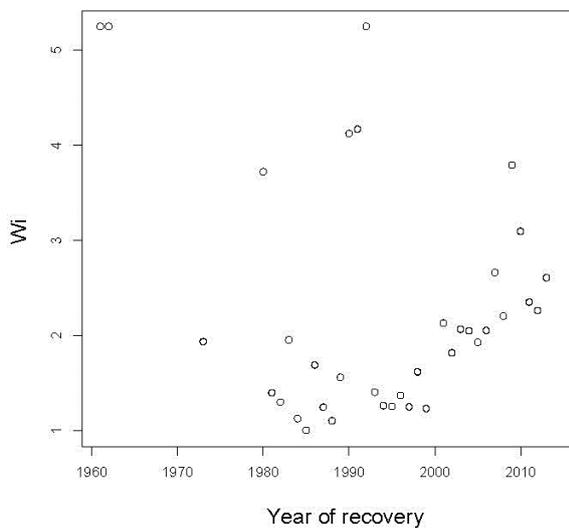
White-faced storm petrel (*Pelagodroma marina*)



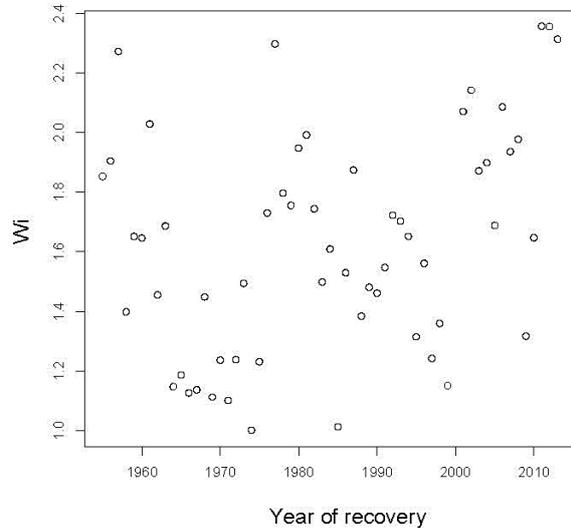
Masked Booby (*Sula dactylatra*)



Shy albatross (*Thalassarche cauta*)



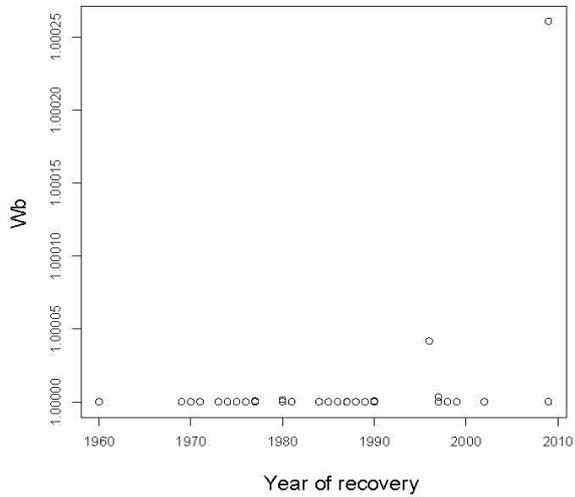
Crested tern (*Thalasseus bergii*)



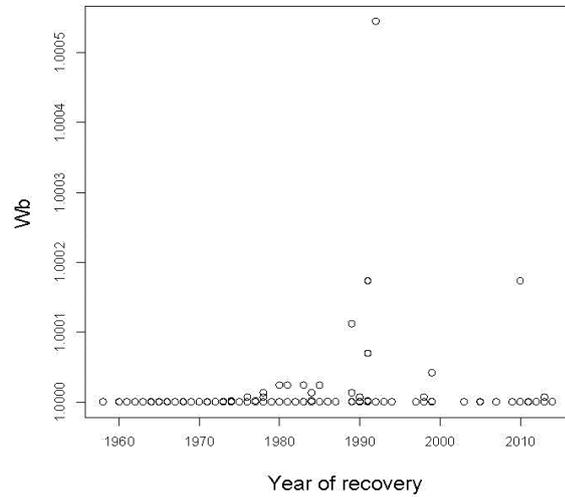
**Appendix 1.8:** Fitted  $W_b$  values for all modelled species.

**Appendix figure 1.8.1:** A high  $W_b$  value denotes an individual recovered at an age where it has a high modelled likelihood of band loss. It is noteworthy that fitted  $W_b$  values are generally very low. Axis labels are accurate to 5 decimal places, so White-faced Storm Petrel and Crested Tern  $W_b$  values, which round to 1, are all  $< 1.00001$ .

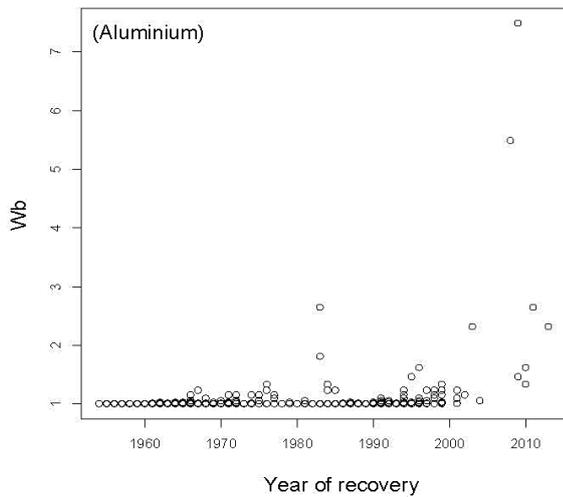
**Wedge-tailed shearwater (*Ardenna pacifica*)**



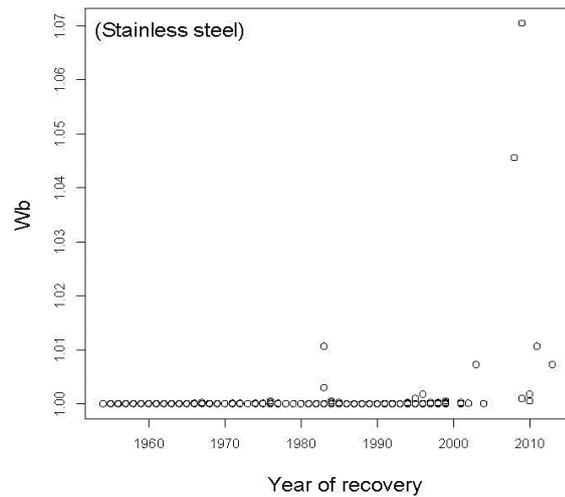
**Short-tailed shearwater (*Ardenna tenuirostris*)**



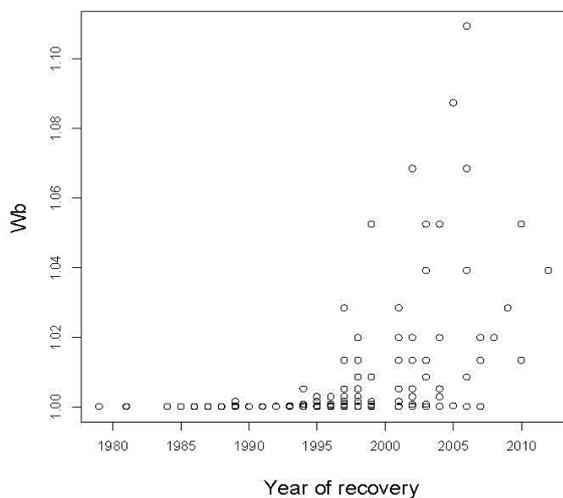
**Silver Gull (*Chroicocephalus novaehollandiae*)**



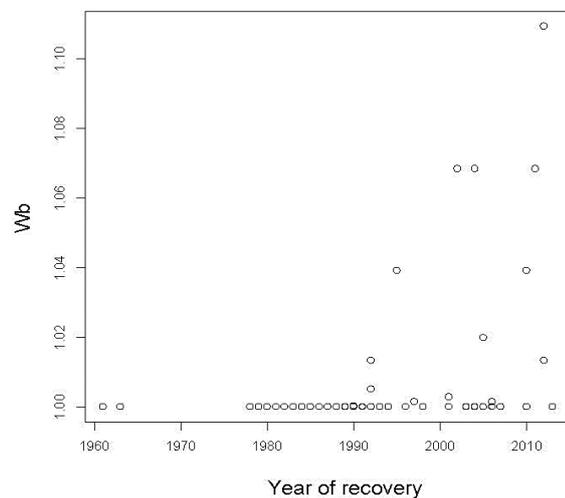
**Silver Gull (*Chroicocephalus novaehollandiae*)**



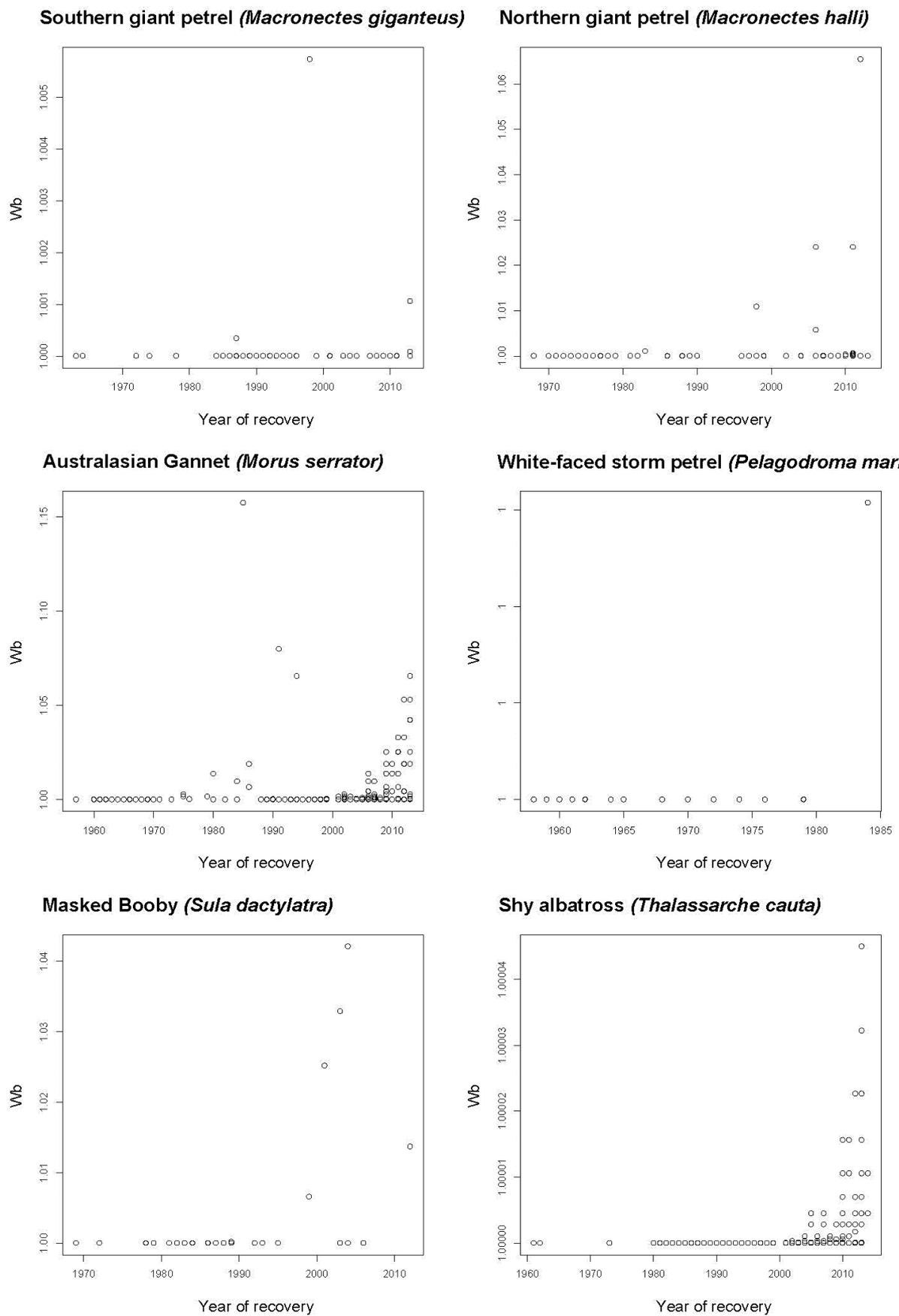
**Kelp Gull (*Larus dominicanus*)**



**Pacific Gull (*Larus pacificus*)**

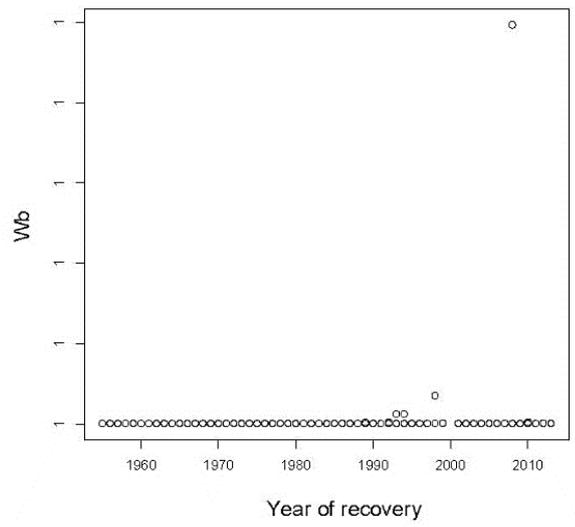


Appendix figure 1.8.1: continued.



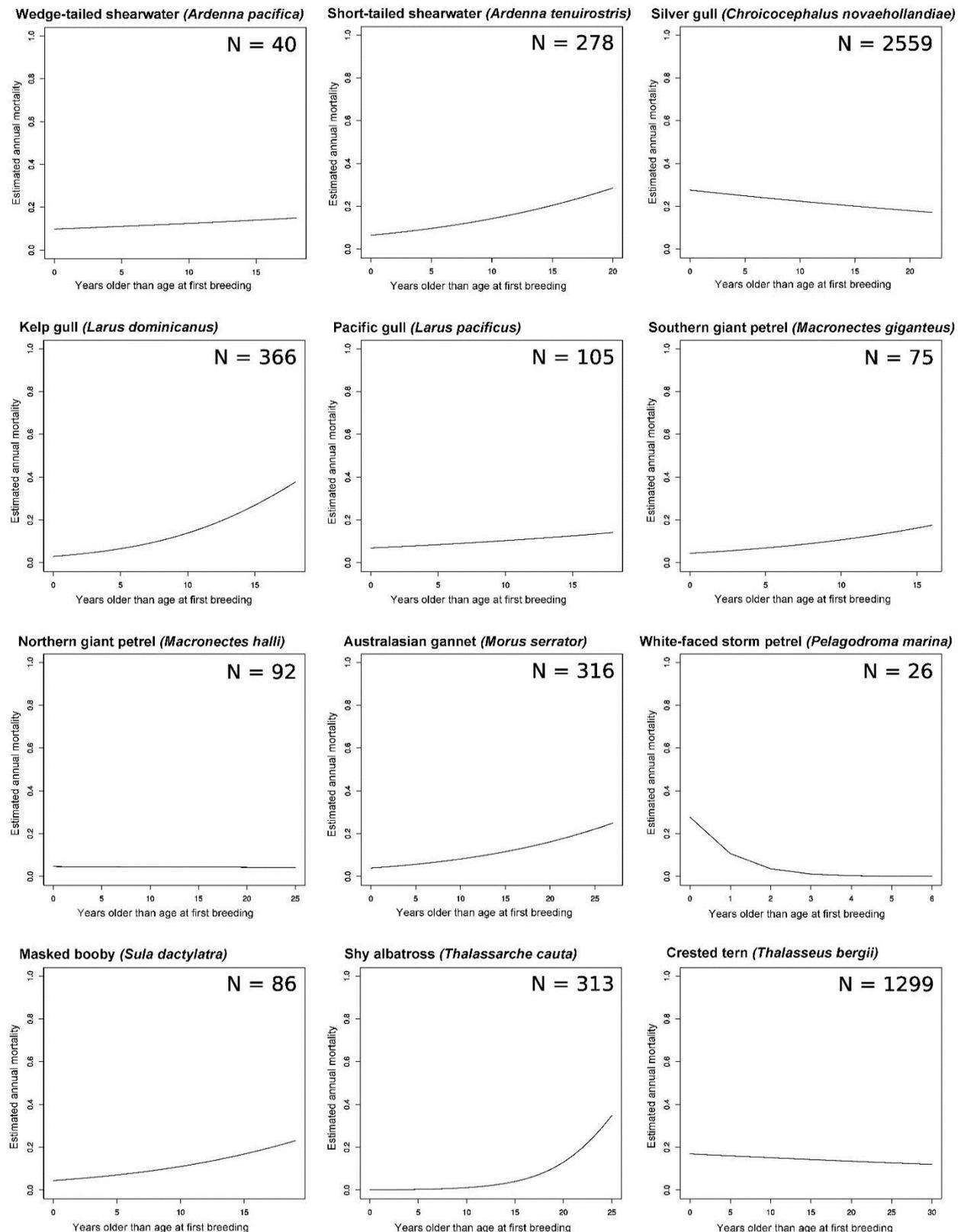
Appendix figure 1.8.1: continued.

Crested tern (*Thalasseus bergii*)



## Appendix 1.9: Estimated age-specific mortality-rates for the twelve species.

**Appendix figure 1.9.1:** Estimates are based on a binomial model, using the estimated number of animals surviving through each age-class rounded to an integer value and the number of animals entering each age-class rounded to an integer value as the  $p$  and  $N$  values, respectively. Data for these estimates were trimmed to between the species' age at first breeding and the species' maximum recorded age – 1, to generate models primarily reflecting senescence effects and to avoid the expected bias from the proportional survival at the maximum recorded age being constrained to equal zero.



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- Bailey, E. E., Woolfenden, G. E., Robertson Jr., W. B. (1987) Abrasion and loss of bands from dry tortugas sooty terns. *Journal of field ornithology*, 58, 413-424.
- Coulson, J. C. (1976) An Evaluation of the Reliability of Rings used on Herring and Lesser Black-backed Gulls. *Bird Study*, 23, 21-26.
- Hatch, J. J., & Nisbet, I. C. T. (1983) Band wear and band loss in Common Terns. *Journal of Field Ornithology*, 54, 1-16.
- Harris, M. P. (1980) Loss of weight and legibility of bird rings. *Ringing and migration*, 3, 41-49.
- Ludwig, J. P. (1967) Band loss - Its effect on banding data and apparent survivorship in the Ring-billed Gull population of the Great Lakes. *Bird-banding*, 38, 309-323.
- Ludwig, J. P., Summer, C. L., Auman, H. J., Colborn, T. L., Ludwig, F. E. & Diefenderfer, G. (1996) Band loss in North Pacific populations of Laysan Albatross (*Diomedea immutabilis*) and Black-footed Albatross (*D. nigipes*). *North American Bird Bander*, 20, 157-164.
- Nisbet, I. C. T., & Hatch, J. J. (1985) Influence of band size on rates of band loss by Common Terns. *Journal of Field Ornithology*, 56, 178-181.
- Nisbet, I. C. T., & Hatch, J. J. (1988) Durability of incoloy bands on Common Terns. *Colonial Waterbirds*, 11, 113-114.
- Wooller, R. D., Skira, I. J., & Serventy, D. L. (1985) Band wear on short-tailed shearwaters *Puffinus tenuirostris*. *Corella*, 9, 121-122.
- Wooller & Wooller (1998) Wear rates of aluminium and stainless steel leg bands on Silver Gulls. *Corella*, 22, 29-31.

## **Appendix 2**

### ***Supplementary materials to Chapter 2 – A broadly-applicable modelling approach for first-estimates of species mortality curves from public-submission datasets***

No supplementary materials.



## Appendix 3

### *Supplementary materials to Chapter 3 – Survival and survival senescence in wild birds: analyses over a broad taxonomic range from national banding scheme data*

#### Appendix 3.1: Correlations between life-history variables used in our model

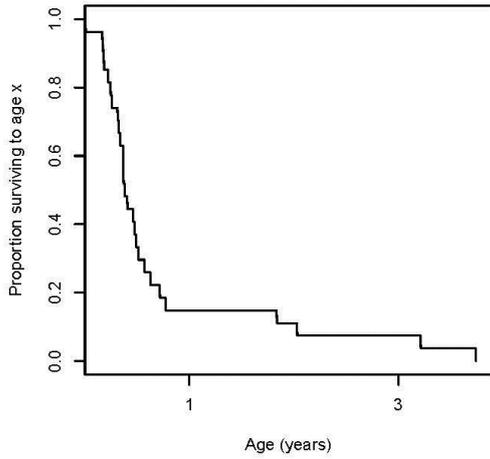
**Appendix table 3.1.1:** Correlation matrix between our explanatory variables. All values above |0.7| are presented in bold. 'Mass' is mean adult body mass; 'Mass (♂)' is mean body mass of adult males; 'Mass (♀)' is mean body mass of adult females; 'Mass (♂ / ♀)' is the mean body mass of adult males divided by the mean body mass of adult females; 'Brain residual' is the same as 'brain mass residual', defined in Table 1; 'Clutch' is the mean clutch-size; 'Clutch max' is the maximum recorded clutch size; 'Clutch min' is the minimum recorded clutch size; 'Egg diameter' is the mean diameter of eggs, in millimetres; 'Migrant', 'Cooperative breeding', 'Flocking', and 'Colonial nesting' are the species' total migration, cooperative breeding, flocking, and colonial nesting statuses, as defined in Chapter 3, Table 1.

	<i>Mass</i>	<i>Mass (♂)</i>	<i>Mass (♀)</i>	<i>Mass (♂/♀)</i>	<i>Brain residual</i>	<i>Clutch</i>	<i>Clutch max</i>	<i>Clutch min</i>	<i>Egg diameter</i>	<i>Migrant</i>	<i>Cooperative breeding</i>	<i>Flocking</i>
Mass (♂)	<b>0.997</b>											
Mass (♀)	<b>0.997</b>	<b>0.993</b>										
Mass (♂ / ♀)	0.375	0.422	0.335									
Brain residual	-0.084	-0.099	-0.093	-0.153								
Clutch	-0.166	-0.154	-0.167	0.113	-0.332							
Clutch max	-0.088	-0.072	-0.087	0.154	-0.376	<b>0.903</b>						
Clutch min	-0.110	-0.103	-0.106	0.067	-0.343	<b>0.785</b>	0.547					
Egg diameter	<b>0.857</b>	<b>0.849</b>	<b>0.862</b>	0.309	-0.147	-0.147	-0.099	-0.035				
Migrant	0.344	0.330	0.354	0.027	-0.104	0.043	0.106	0.048	0.392			
Cooperative breeding	-0.210	-0.198	-0.224	-0.013	0.088	0.111	0.150	-0.118	-0.335	-0.088		
Flocking	-0.001	0.012	-0.027	0.201	-0.108	0.081	0.131	-0.014	0.029	0.138	0.164	
Colonial nesting	0.477	0.488	0.480	0.418	-0.227	-0.379	-0.298	-0.300	0.537	0.301	-0.331	0.129

### Appendix 3.2: Model summary and diagnostic plots for all species modelled in Chapter 3.

The appendix is sorted first by band-metal, then by species. Species banded with more than one band-metal are presented once for each metal with which they were banded, and for each metal, the model assumes that all animals were banded only with that metal. Within each species' page, the species' common name, Latin name, annual adult survival rate, annual first-year survival rate, survival senescence rate, the sample-size used in computing the mortality structure ( $N$ ), the number of locations over which the species was banded ( $N$  locations), the Maximum Recorded Longevity / Maximum Possible Longevity (MRA / MPA), the proportions of all observations that are of freshly-dead animals (Prop. obs. dead), and the annual band wear-rate used in computing the mortality structure (Ann. wear-rate) are presented as text. Annual adult survival, annual first-year survival, and annual survival senescence are defined in the Chapter 3 main text.  $N$  is defined as the total number of observations for the species.  $N$  locations is defined as the number of unique locations ('locodes') at which the species was recorded as being banded. MRA / MPA is defined as the age of the oldest observed observation, as a fraction of the number of years between the first marking event for the species and the year at which the data were extracted from the ABBBS database. Prop. obs dead is equal to 1 for all species in this dataset, as observations from live animals were excluded from the models. Ann. wear-rate for each species was inferred from the modelling in Chapter 4, and is generally equal to the rate of wear for a metal-type worn by members of a functional group (as in Chapter 4), but where the wear-rate for a specific species / metal type combination was estimated by linear modelling in Chapter 4, we used that for models of that species / metal type combination. Five plots are presented for each species. In the top-left plot, the estimated species mortality curve is presented as a black line, and the unweighted mortality-structure (i.e., the mortality structure if observations were a truly random sample, unaffected by differences in *availability*, *intensity*, and *mark-loss*) is presented in grey. The species' *availability* curve is presented in the middle-left plot. *Availability* curves represent the number of marked individuals marked  $\geq x$  years ago, and therefore potentially observable dead at age  $x$ . The  $W_{aib}$  value for each observation within the species is presented against the year of observation in the middle-right plot. The data informing the  $W_i$  model for the species is presented in the bottom-left plot, with  $W_i$  calculated as a linear model of the relationship between the number of animals marked in a year (proxying the study *intensity*) and the number of animals recovered in that year, for each year between the year of first banding for the species and the year at which the data were extracted from the ABBBS database. In the bottom-right figure, the  $W_i$  value for each point is presented against the year of observation for that point.

Models for species marked with Aluminium bands,  
treating all observations as Aluminium-marked animals



**Brown Goshawk**

*Accipiter fasciatus*

Ann. adult surv. ~ 0.556 (SE = NaN )

Ann. Y1 surv. ~ 0.148 (SE = NaN )

Surv. senesc. ~ -1.609 (SE = 0.704 )

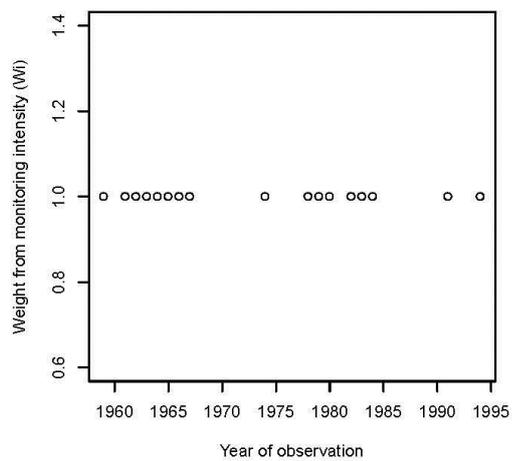
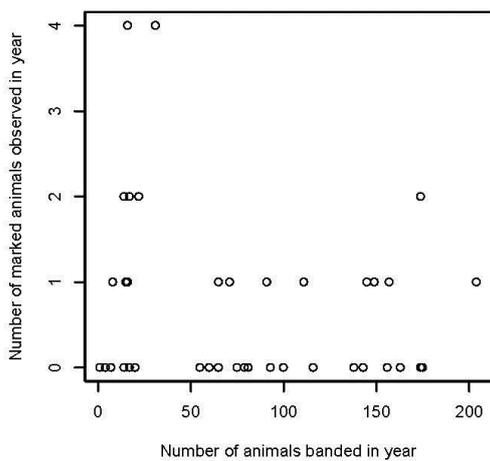
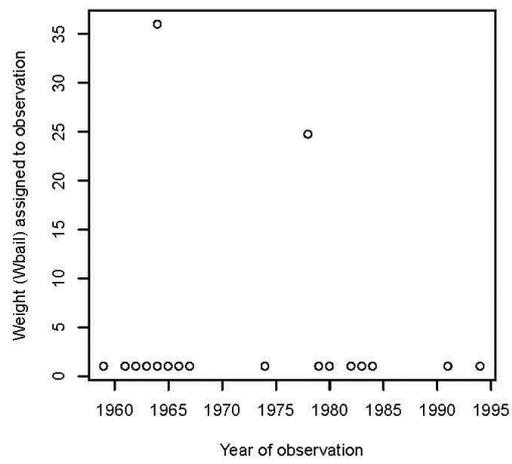
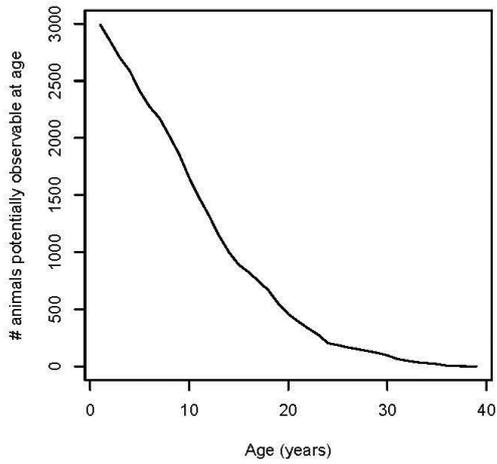
N = 27

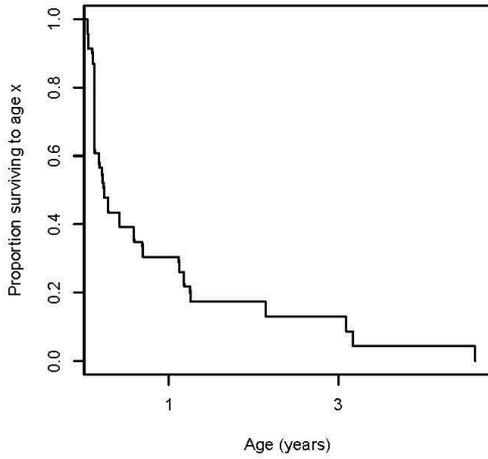
N locations = 19

MRA / MPA = 0.075

Prop. obs. dead = 1

Ann. wear-rate = 0.5 %





**Chestnut Teal**

*Anas castanea*

Ann. adult surv.  $\sim 0.533$  (SE = NA)

Ann. Y1 surv.  $\sim 0.304$  (SE = NA)

Surv. senesc.  $\sim -0.392$  (SE = 0.352)

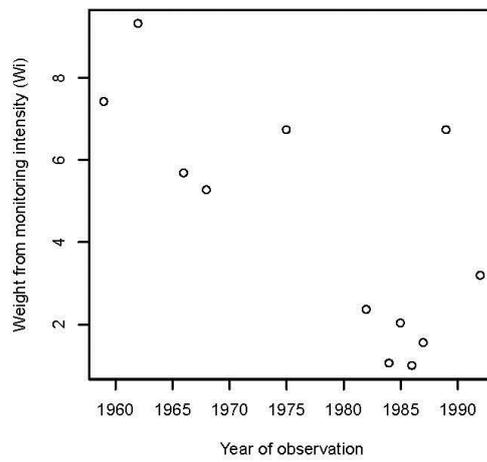
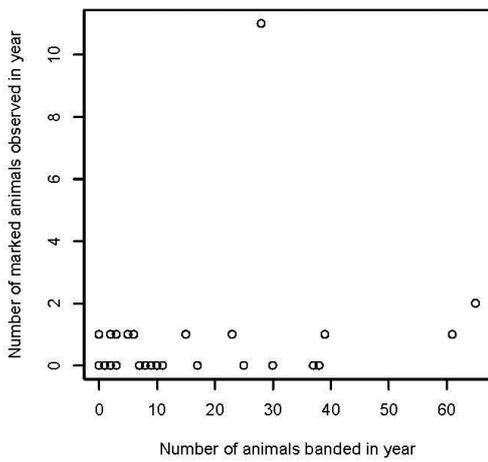
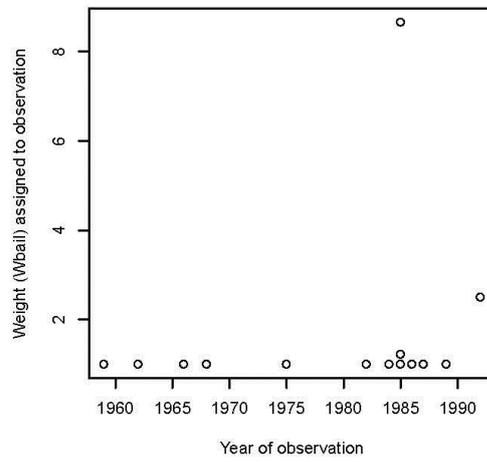
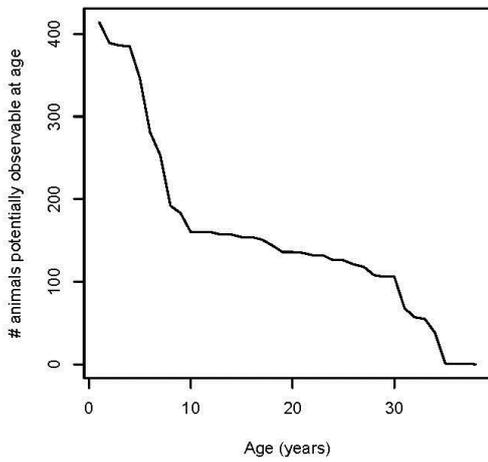
N = 23

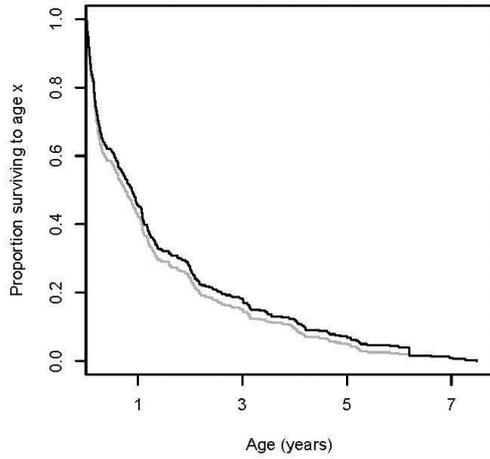
N locations = 12

MRA / MPA = 0.103

Prop. obs. dead = 1

Ann. wear-rate = 3 %





**Pacific Black Duck**

*Anas superciliosa*

Ann. adult surv.  $\sim 0.613$  (SE = NaN)

Ann. Y1 surv.  $\sim 0.457$  (SE = NaN)

Surv. senesc.  $\sim -0.112$  (SE = 0.051)

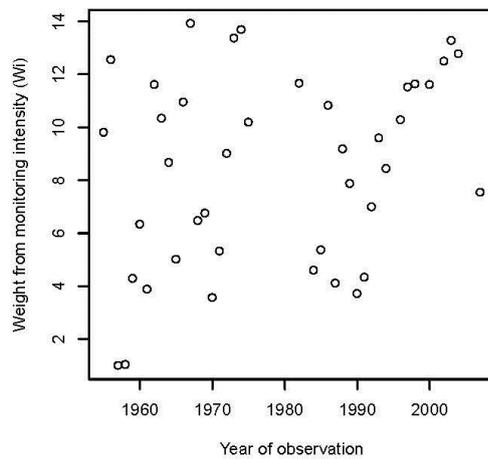
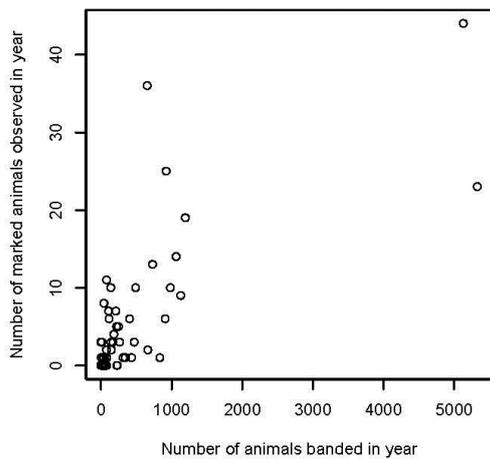
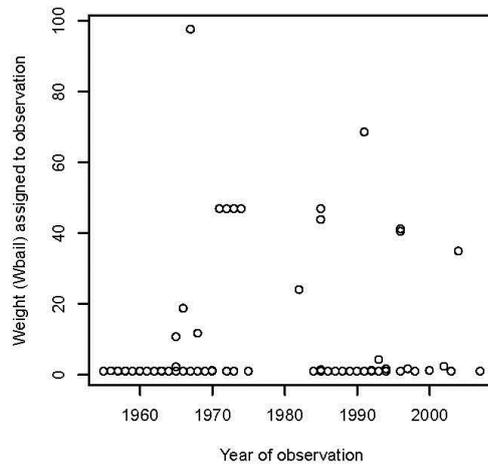
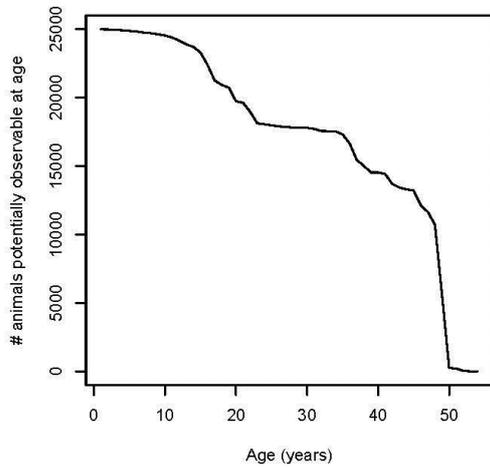
N = 314

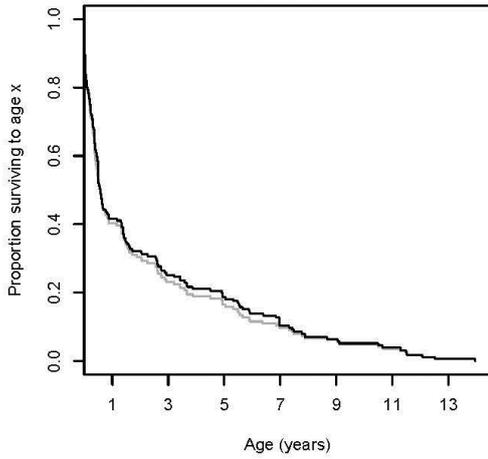
N locations = 38

MRA / MPA = 0.127

Prop. obs. dead = 1

Ann. wear-rate = 3 %





**Cattle Egret**

*Ardea ibis*

Ann. adult surv.  $\sim 0.779$  (SE = NA)

Ann. Y1 surv.  $\sim 0.443$  (SE = NA)

Surv. senesc.  $\sim -0.139$  (SE = 0.038)

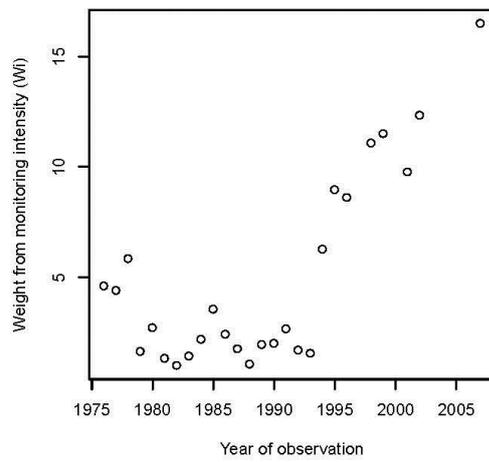
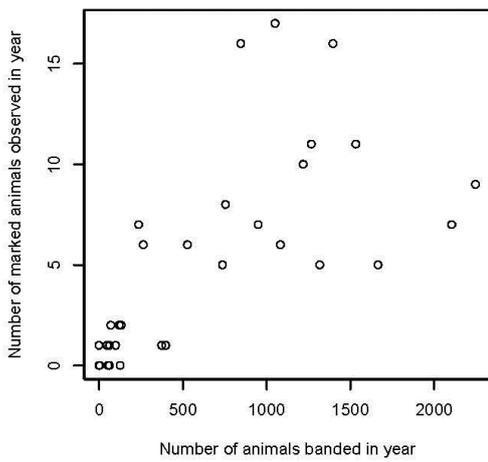
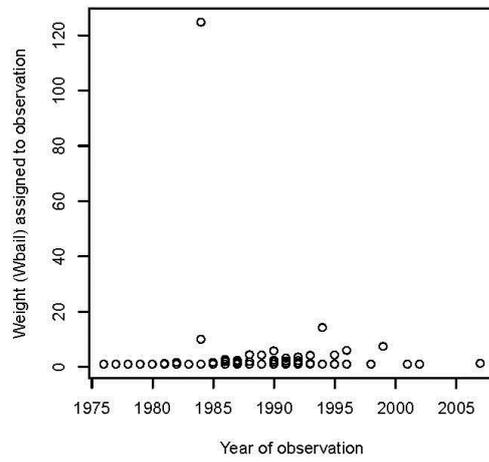
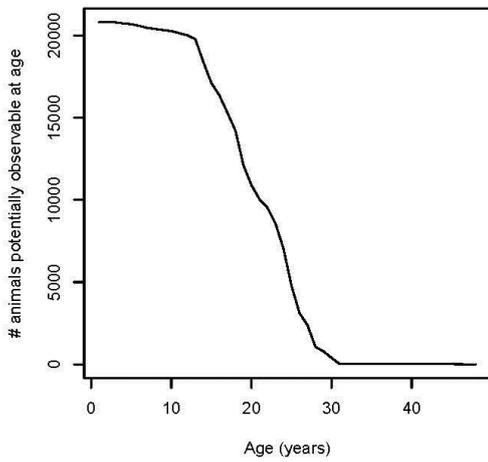
N = 164

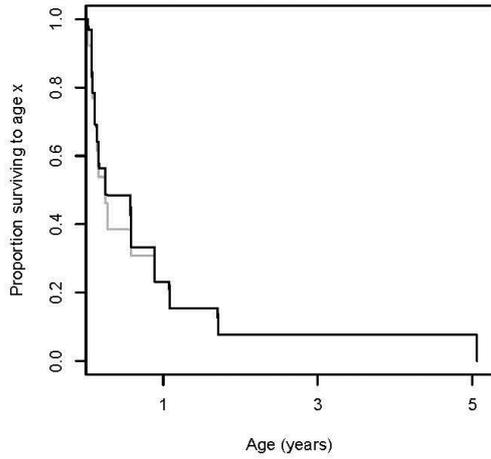
N locations = 27

MRA / MPA = 0.265

Prop. obs. dead = 1

Ann. wear-rate = 0.3 %





**Eastern Great Egret**

*Ardea modesta*

Ann. adult surv. ~ 0.571 (SE = NA )

Ann. Y1 surv. ~ 0.231 (SE = NA )

Surv. senesc. ~ -1.43 (SE = 0.825 )

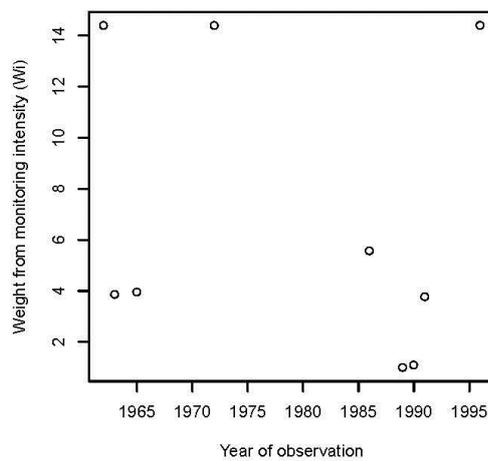
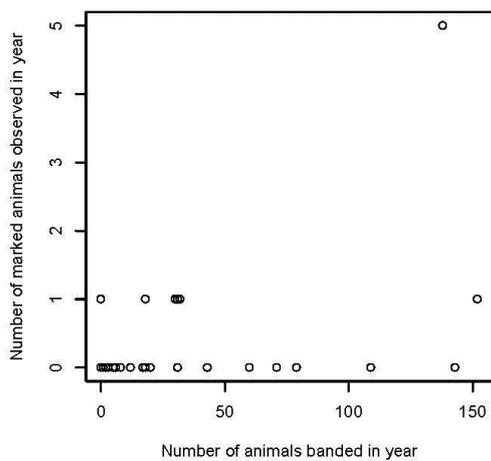
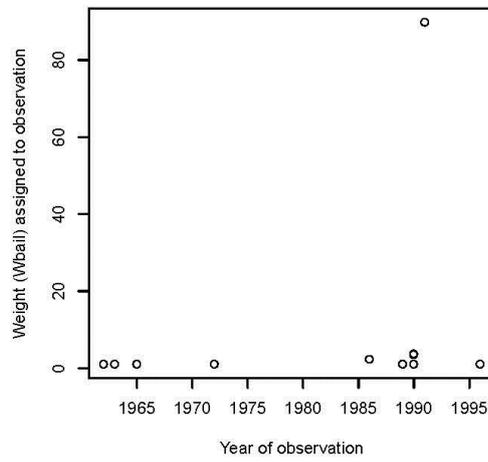
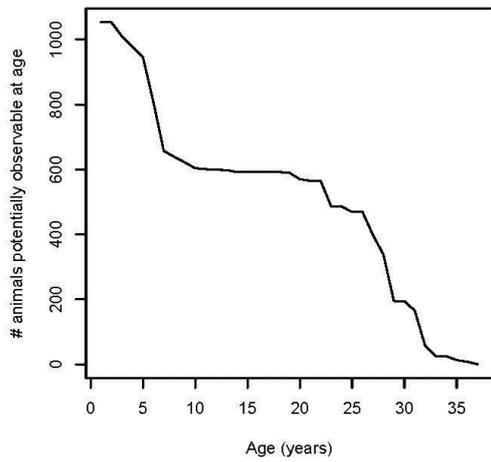
N = 13

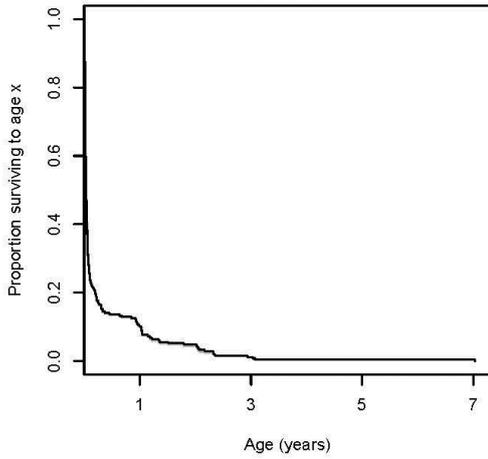
N locations = 8

MRA / MPA = 0.132

Prop. obs. dead = 1

Ann. wear-rate = 0.5 %





**Australian Wood Duck**

*Chenonetta jubata*

Ann. adult surv.  $\sim 0.428$  (SE = NA)

Ann. Y1 surv.  $\sim 0.11$  (SE = NA)

Surv. senesc.  $\sim -0.839$  (SE = 0.208)

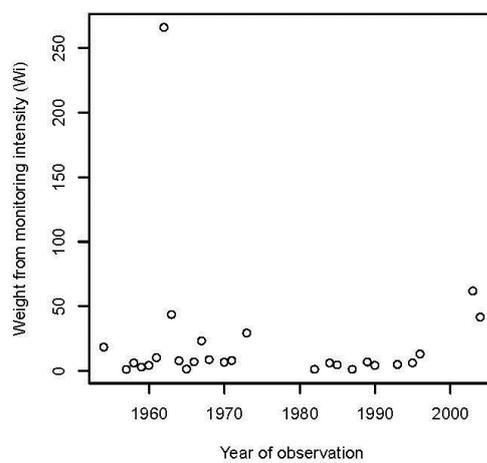
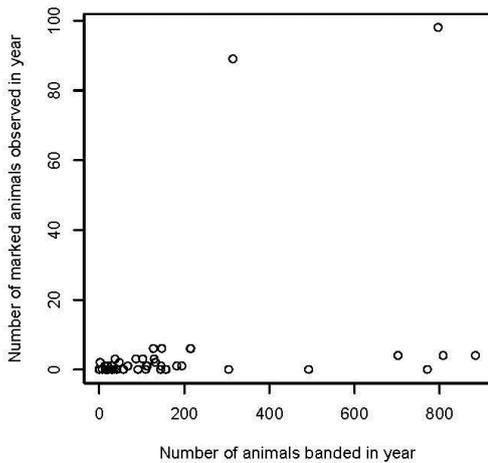
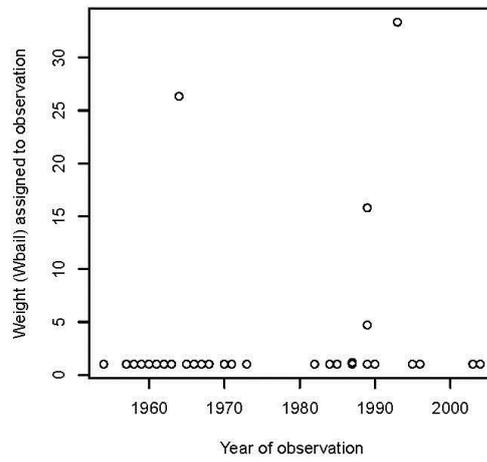
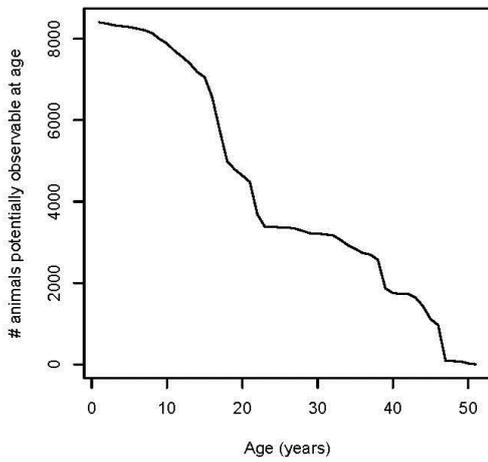
N = 252

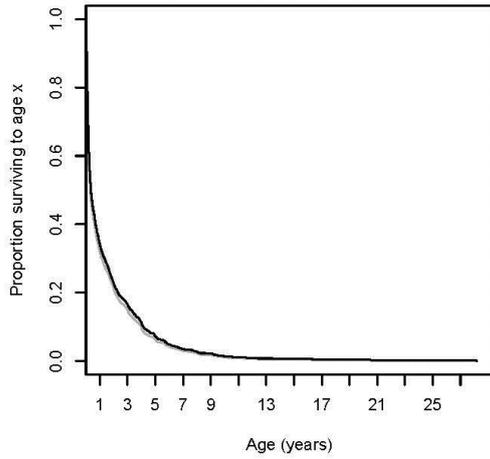
N locations = 24

MRA / MPA = 0.135

Prop. obs. dead = 1

Ann. wear-rate = 3%





**Silver Gull**

*Chroicocephalus novaehollandiae*

Ann. adult surv.  $\sim 0.717$  (SE = NA)

Ann. Y1 surv.  $\sim 0.366$  (SE = NA)

Surv. senesc.  $\sim -0.21$  (SE = 0.012)

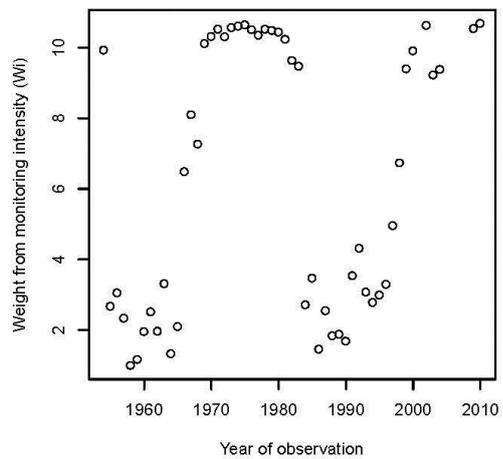
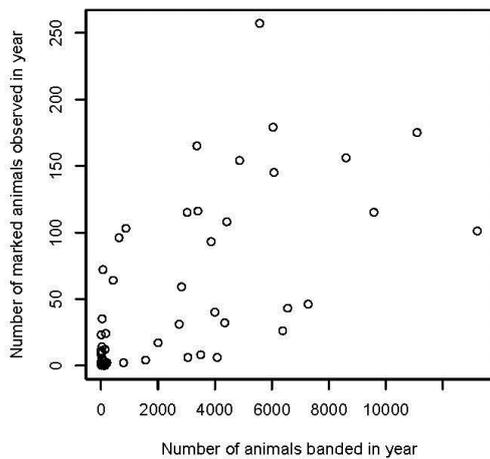
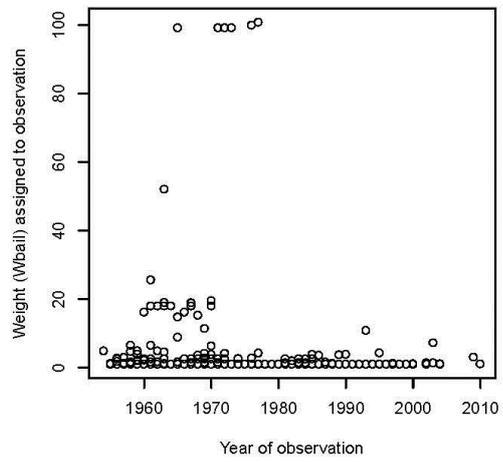
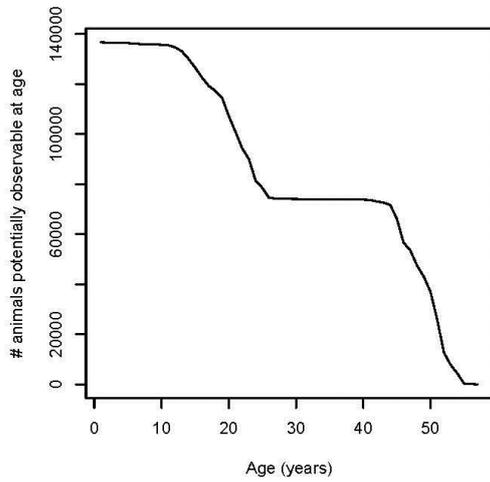
N = 2728

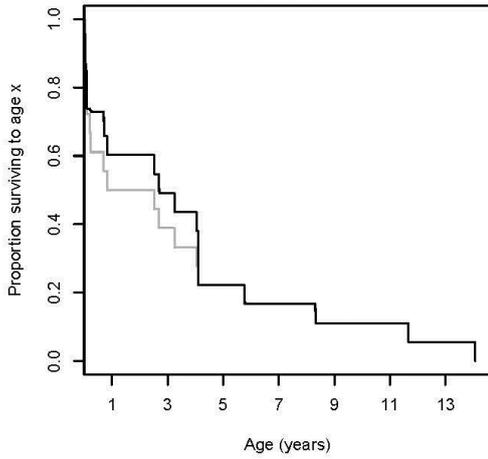
N locations = 151

MRA / MPA = 0.483

Prop. obs. dead = 1

Ann. wear-rate = 3 %





### White-winged Chough

*Corcorax melanorhamphos*

Ann. adult surv.  $\sim 0.82$  (SE = NA)

Ann. Y1 surv.  $\sim 0.602$  (SE = NA)

Surv. senesc.  $\sim -0.072$  (SE = 0.09)

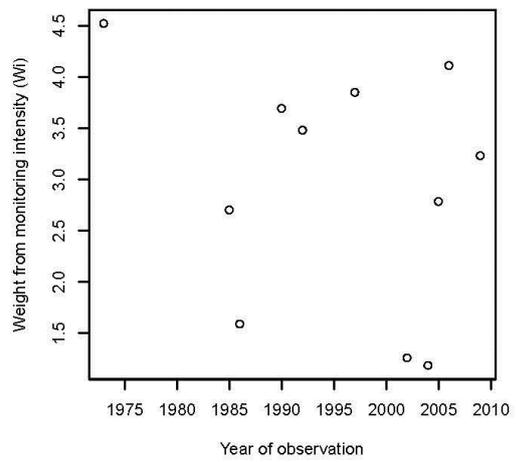
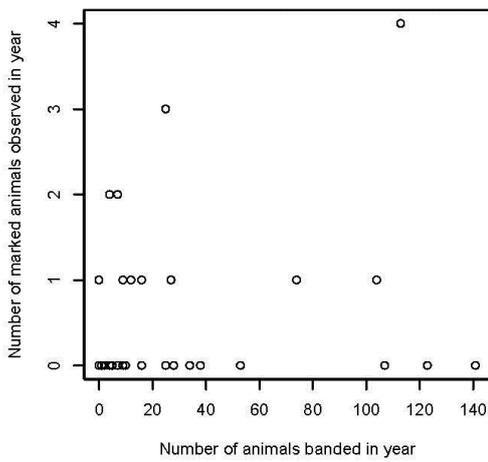
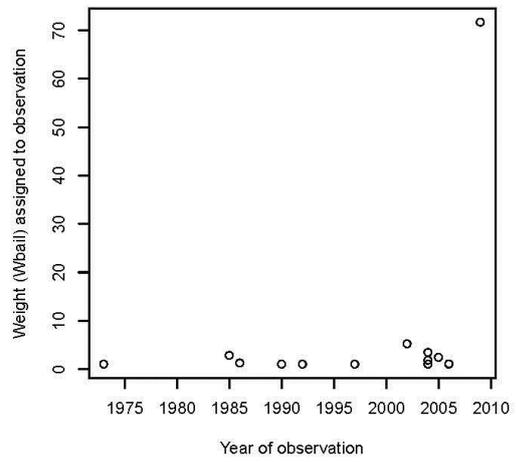
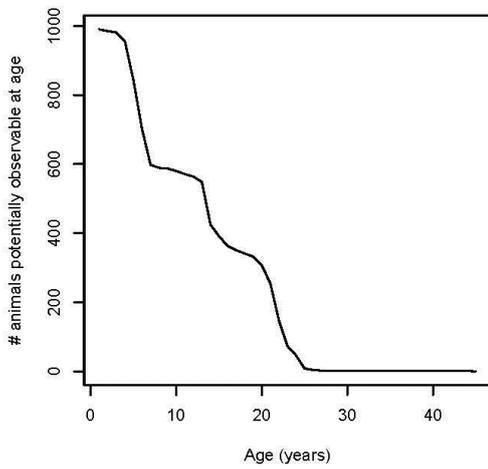
N = 18

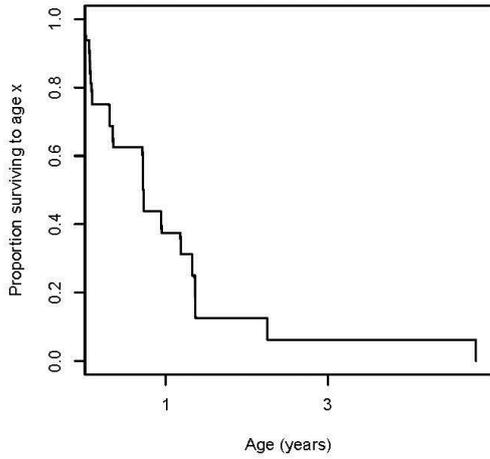
N locations = 9

MRA / MPA = 0.304

Prop. obs. dead = 1

Ann. wear-rate = 3%





**Australian Raven**

*Corvus coronoides*

Ann. adult surv.  $\sim 0.4$  (SE = NA)

Ann. Y1 surv.  $\sim 0.375$  (SE = NA)

Surv. senesc.  $\sim -0.46$  (SE = 0.517)

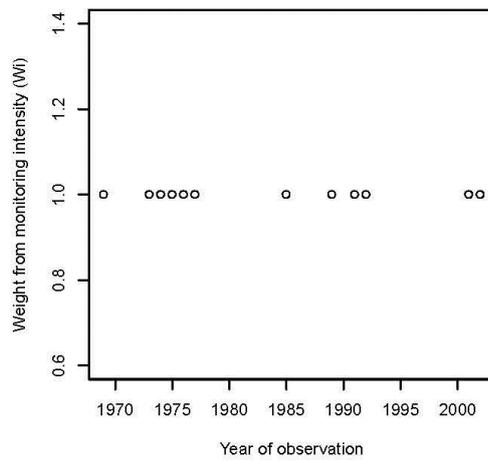
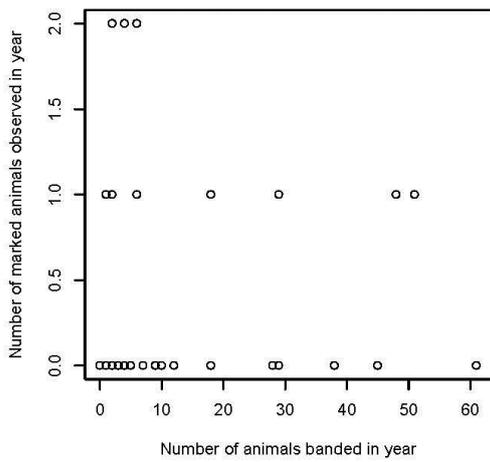
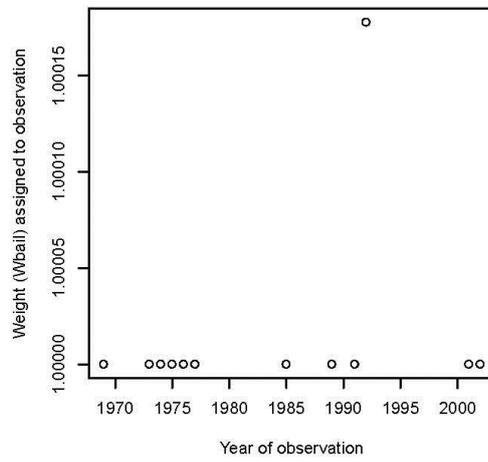
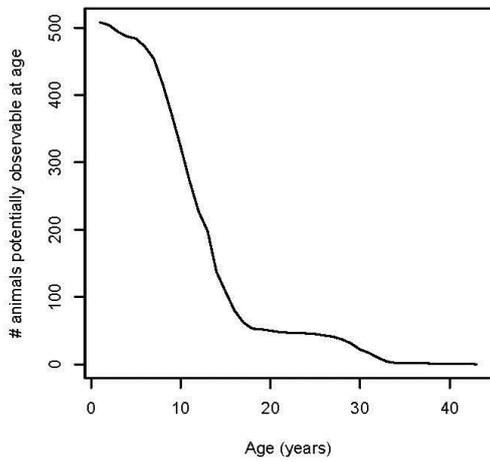
N = 16

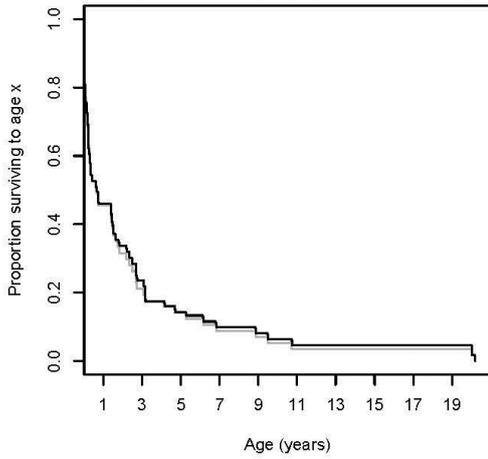
N locations = 12

MRA / MPA = 0.091

Prop. obs. dead = 1

Ann. wear-rate = 3 %





### Australian Magpie

*Cracticus tibicen*

Ann. adult surv.  $\sim 0.799$  (SE = NA)

Ann. Y1 surv.  $\sim 0.524$  (SE = NA)

Surv. senesc.  $\sim -0.241$  (SE = 0.064)

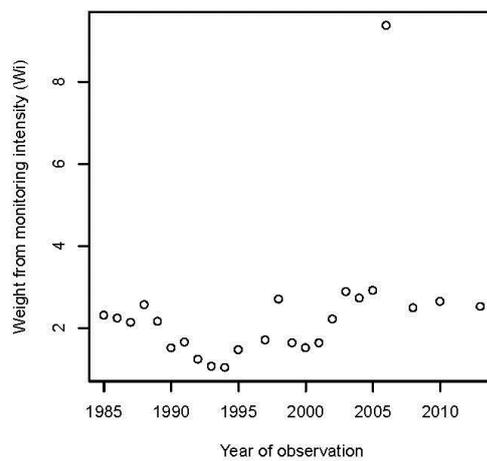
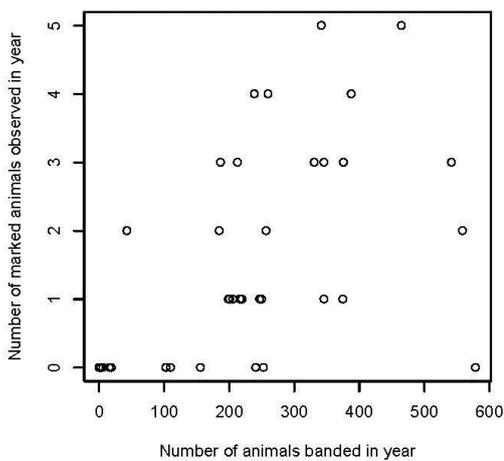
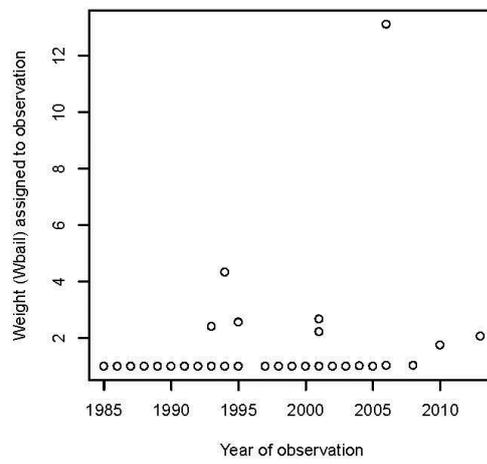
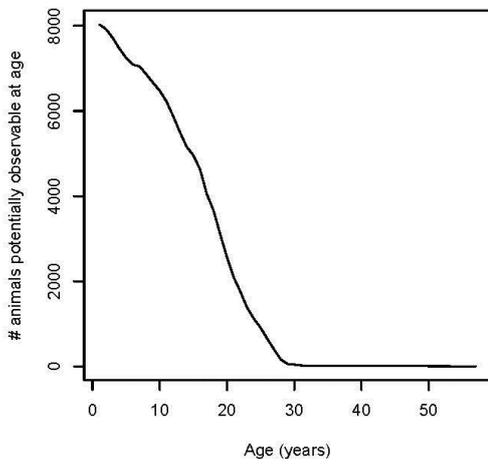
N = 57

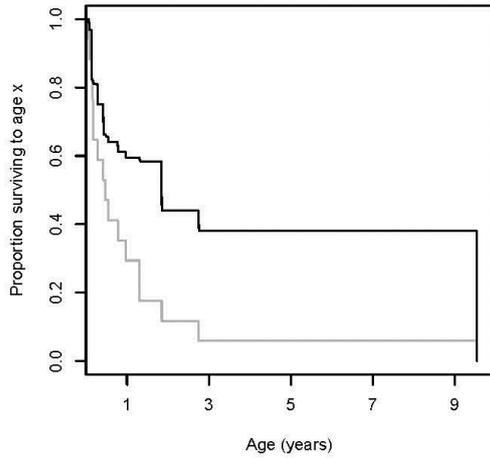
N locations = 30

MRA / MPA = 0.345

Prop. obs. dead = 1

Ann. wear-rate = 3 %





**Laughing Kookaburra**

*Dacelo novaeguineae*

Ann. adult surv. ~ 0.839 (SE = NA )

Ann. Y1 surv. ~ 0.595 (SE = NA )

Surv. senesc. ~ -1.004 (SE = 0.392 )

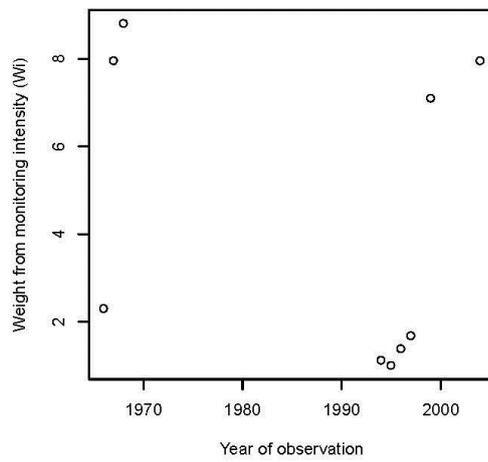
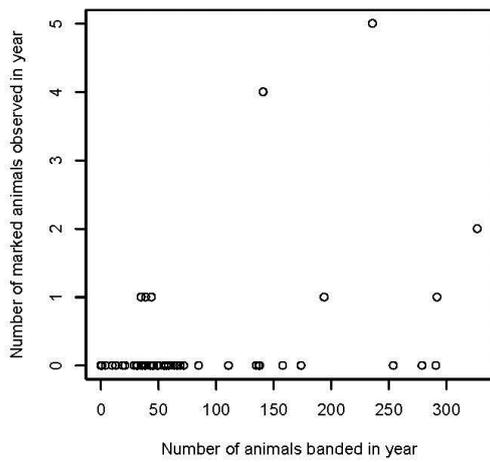
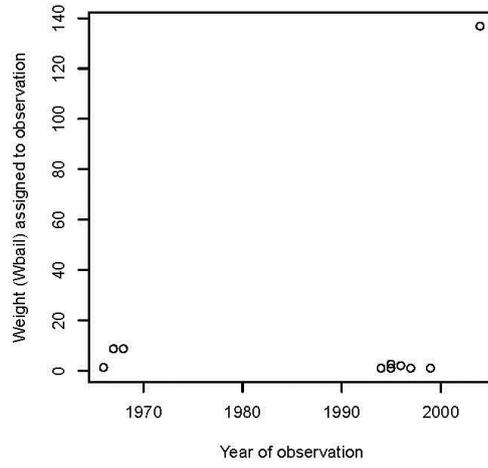
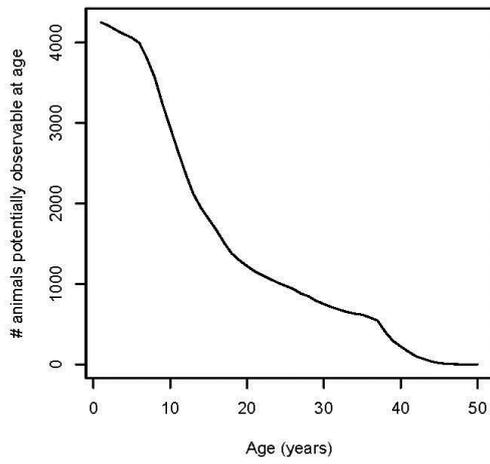
N = 17

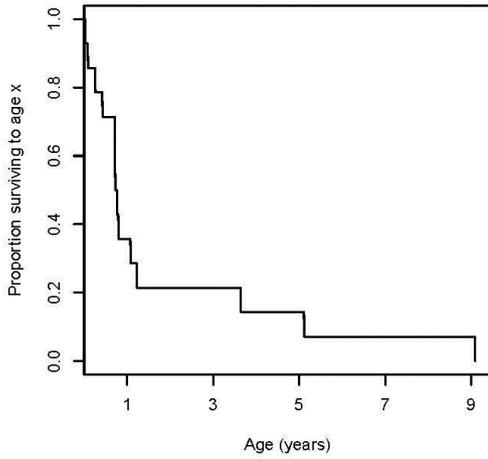
N locations = 5

MRA / MPA = 0.176

Prop. obs. dead = 1

Ann. wear-rate = 0.5 %





**Whistling Kite**

*Haliastur sphenurus*

Ann. adult surv.  $\sim 0.737$  (SE = NA)

Ann. Y1 surv.  $\sim 0.357$  (SE = NA)

Surv. senesc.  $\sim -0.489$  (SE = 0.248)

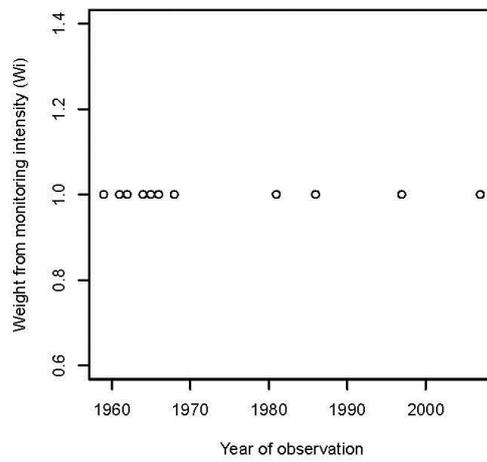
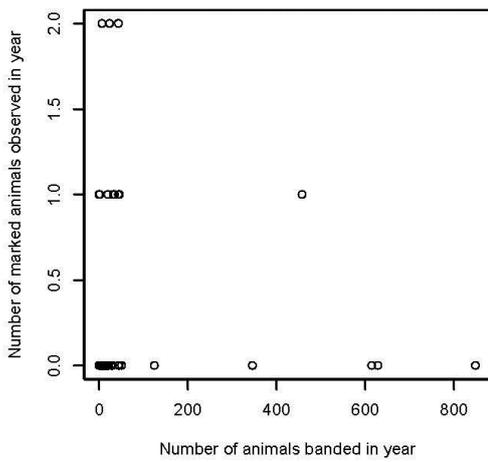
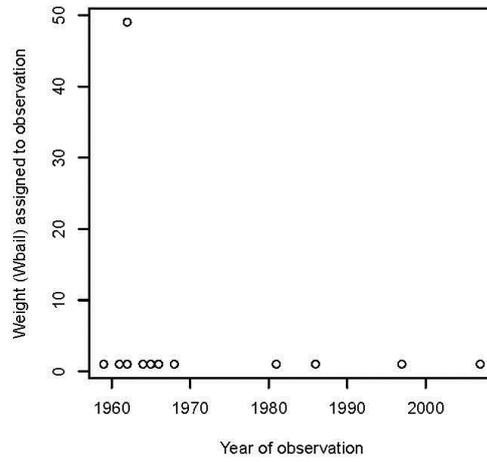
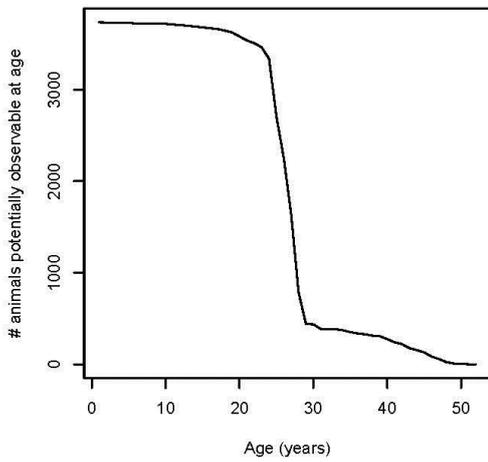
N = 14

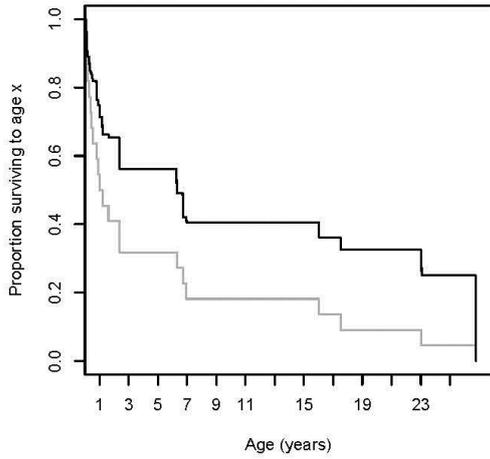
N locations = 14

MRA / MPA = 0.17

Prop. obs. dead = 1

Ann. wear-rate = 0.5 %





### Caspian Tern

*Hydroprogne caspia*

Ann. adult surv.  $\sim 0.934$  (SE = NA)

Ann. Y1 surv.  $\sim 0.748$  (SE = NA)

Surv. senesc.  $\sim -0.084$  (SE = 0.041)

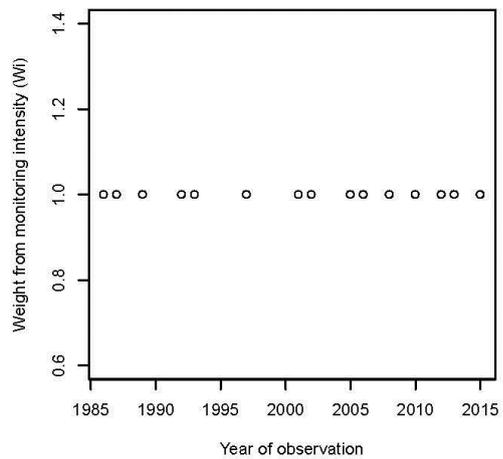
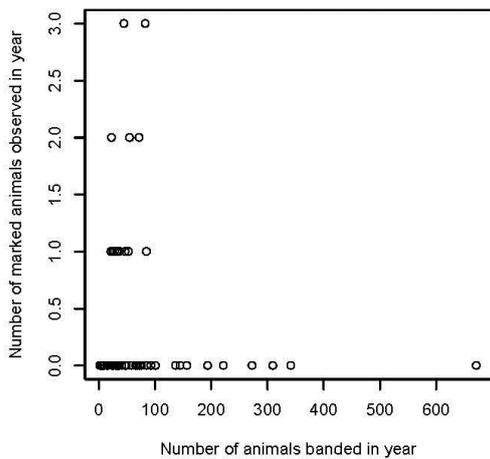
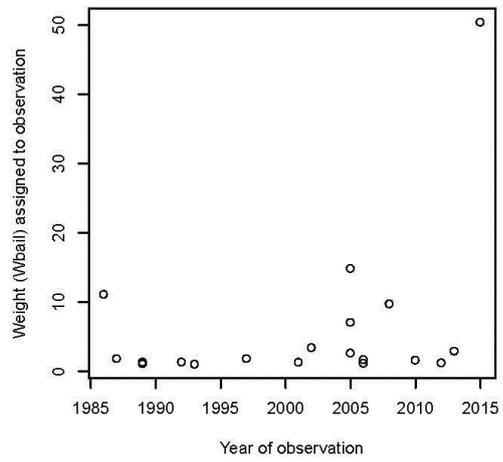
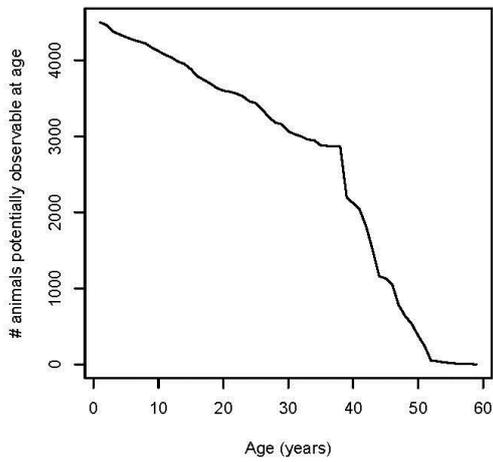
N = 22

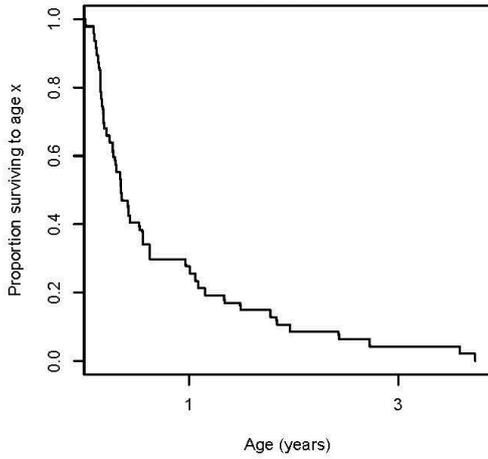
N locations = 4

MRA / MPA = 0.433

Prop. obs. dead = 1

Ann. wear-rate = 3 %





**Little Pied Cormorant**

*Microcarbo melanoleucos*

Ann. adult surv.  $\sim 0.316$  (SE = NA)

Ann. Y1 surv.  $\sim 0.277$  (SE = NA)

Surv. senesc.  $\sim -0.362$  (SE = 0.445)

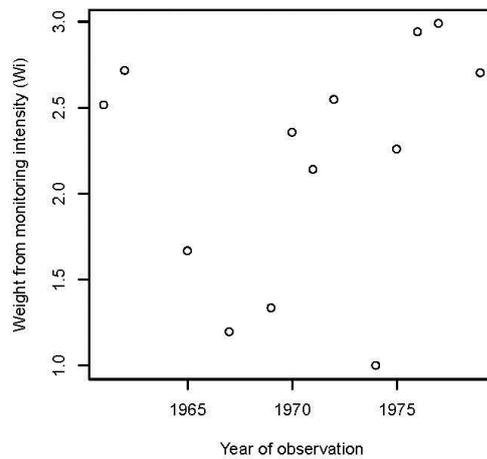
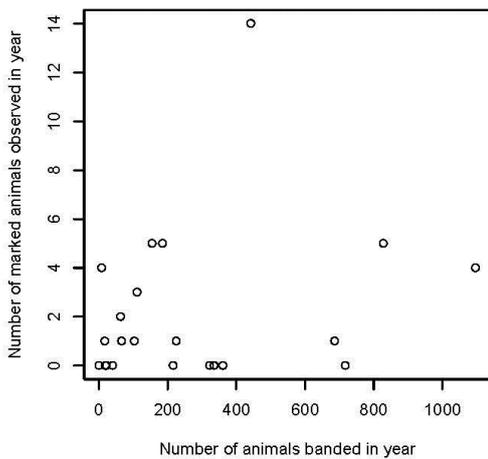
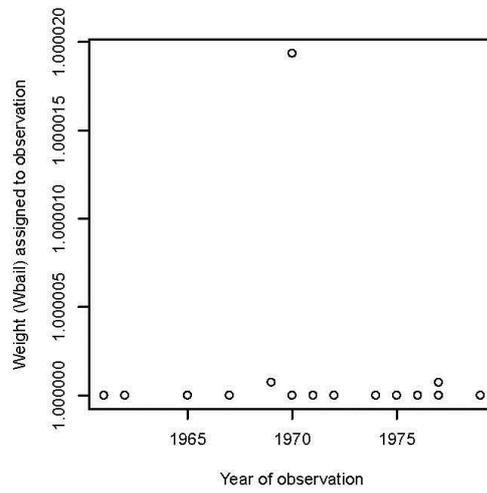
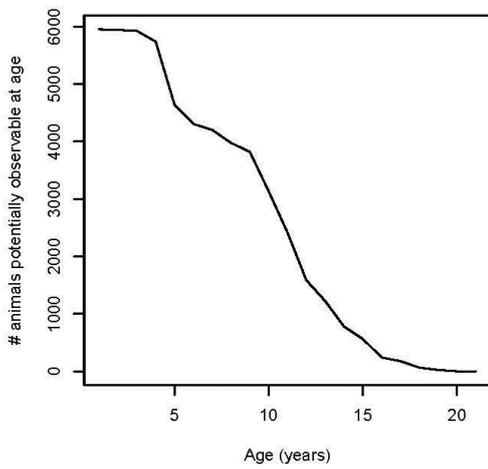
N = 47

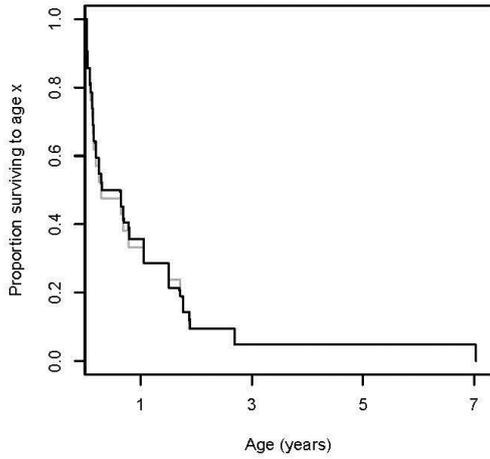
N locations = 16

MRA / MPA = 0.136

Prop. obs. dead = 1

Ann. wear-rate = 3 %





**White-browed Scrubwren**

*Sericornis frontalis*

Ann. adult surv.  $\sim 0.483$  (SE = NA)

Ann. Y1 surv.  $\sim 0.357$  (SE = NA)

Surv. senesc.  $\sim -0.616$  (SE = 0.343)

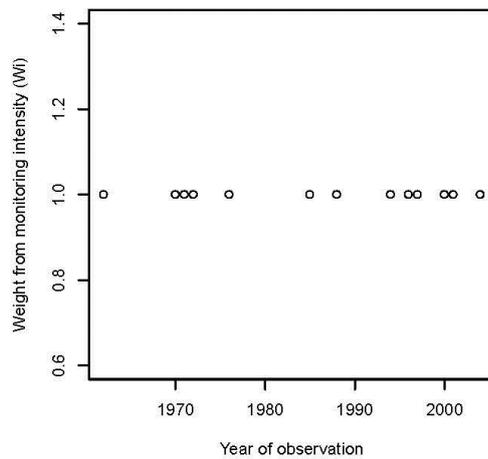
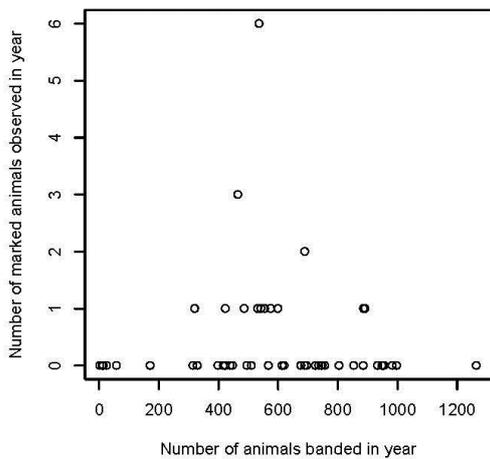
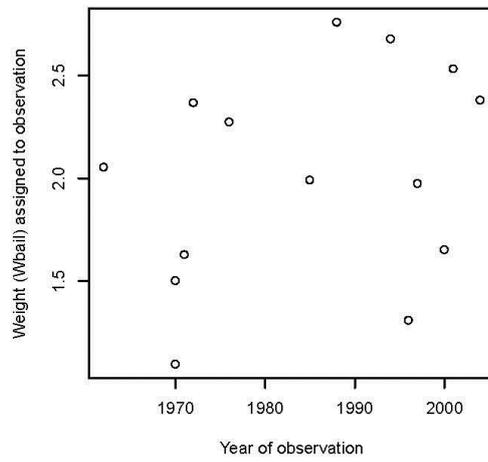
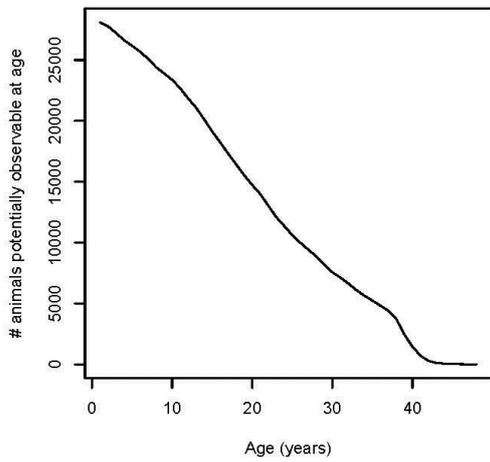
N = 21

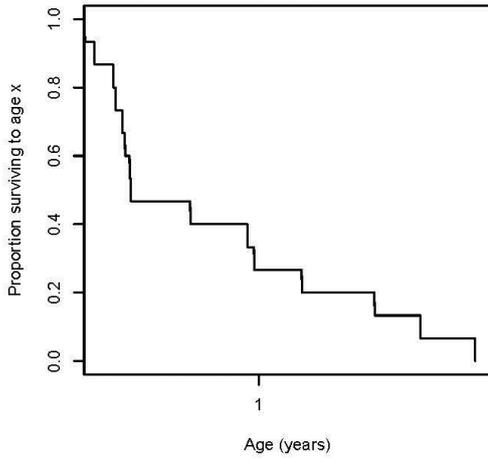
N locations = 5

MRA / MPA = 0.143

Prop. obs. dead = 1

Ann. wear-rate = 3 %





**Pied Currawong**

*Strepera graculina*

Ann. adult surv.  $\sim 0.2$  (SE = NA)

Ann. Y1 surv.  $\sim 0.267$  (SE = NA)

Surv. senesc.  $\sim 0.087$  (SE = 1.294)

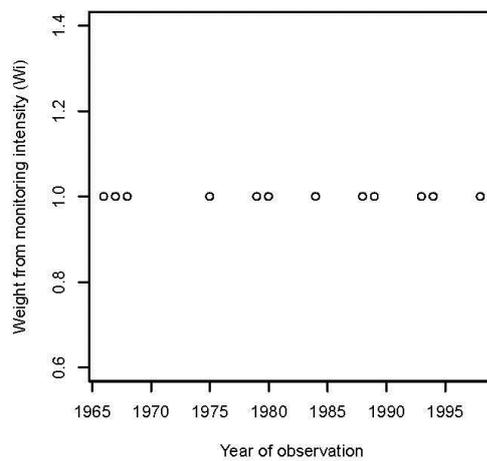
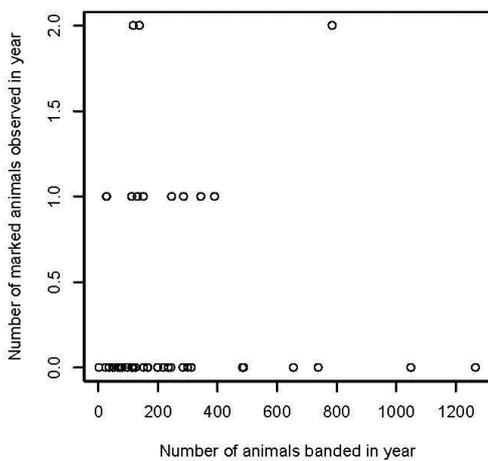
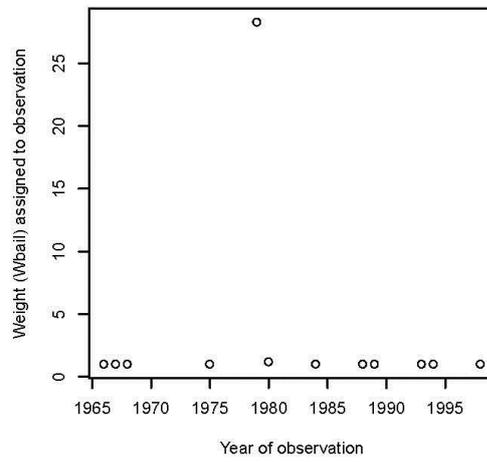
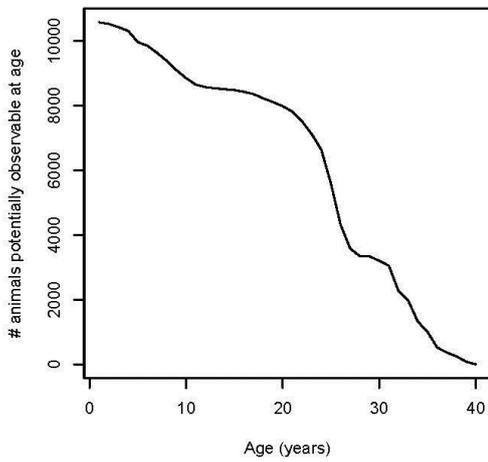
N = 15

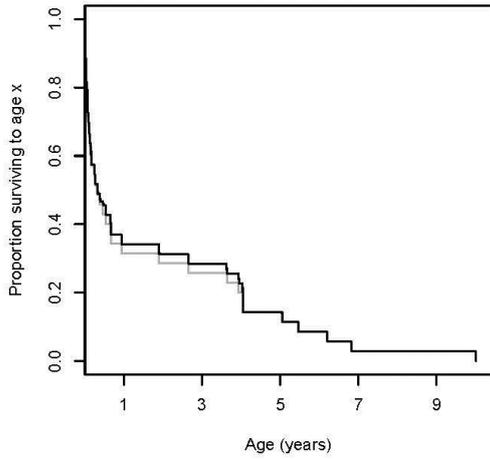
N locations = 13

MRA / MPA = 0.049

Prop. obs. dead = 1

Ann. wear-rate = 3 %





**Common Starling**

*Sturnus vulgaris*

Ann. adult surv. ~ NaN (SE = NA)

Ann. Y1 surv. ~ 0.385 (SE = NA)

Surv. senesc. ~ -0.188 (SE = 0.125)

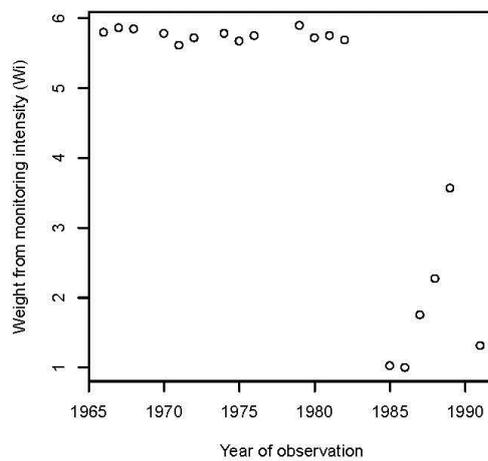
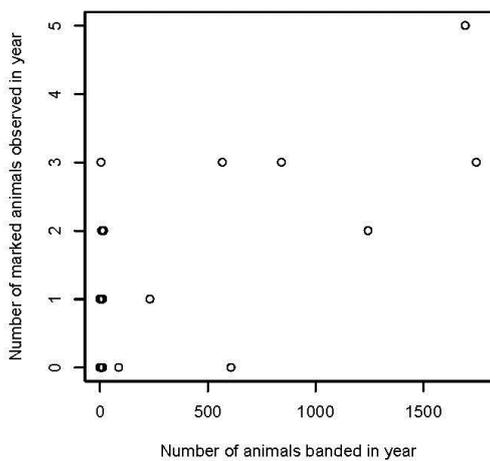
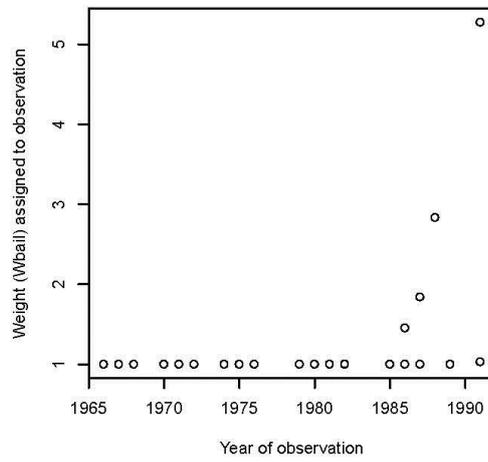
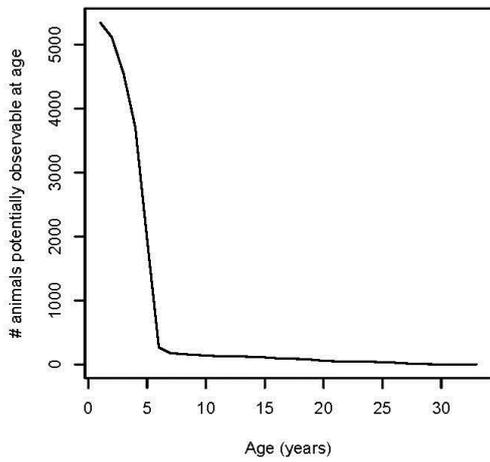
N = 35

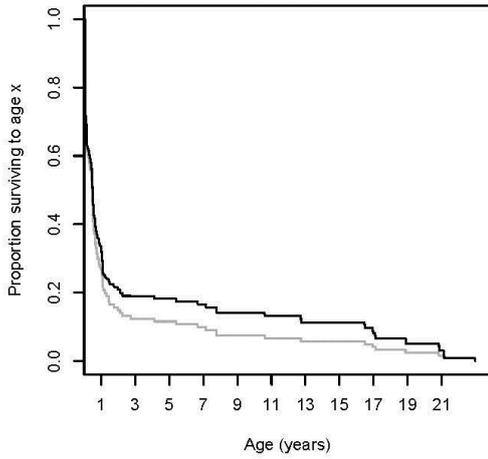
N locations = 14

MRA / MPA = 0.294

Prop. obs. dead = 1

Ann. wear-rate = 3 %





**Masked Booby**

*Sula dactylatra*

Ann. adult surv.  $\sim 0.883$  (SE = NA)

Ann. Y1 surv.  $\sim 0.336$  (SE = NA)

Surv. senesc.  $\sim -0.173$  (SE = 0.026)

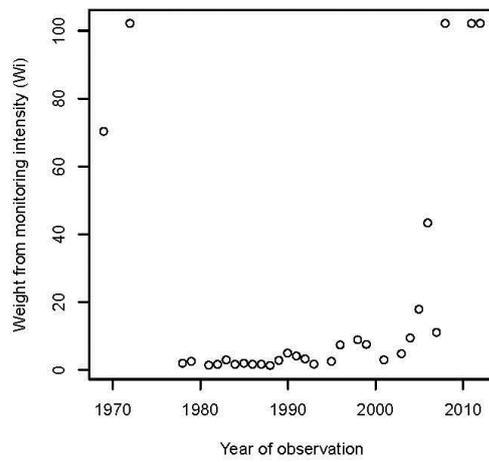
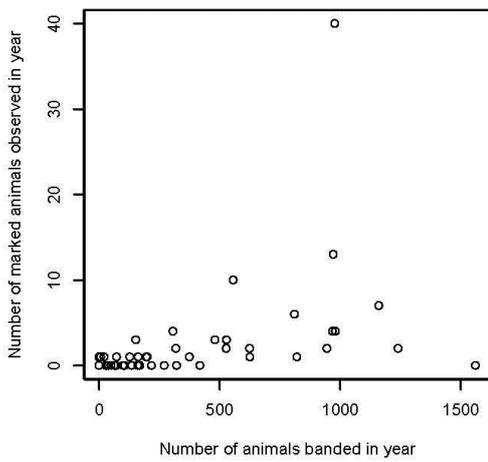
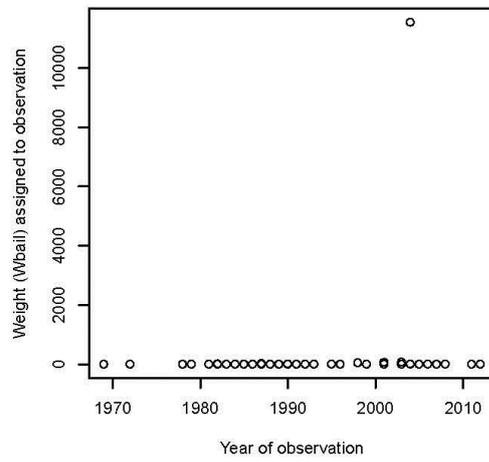
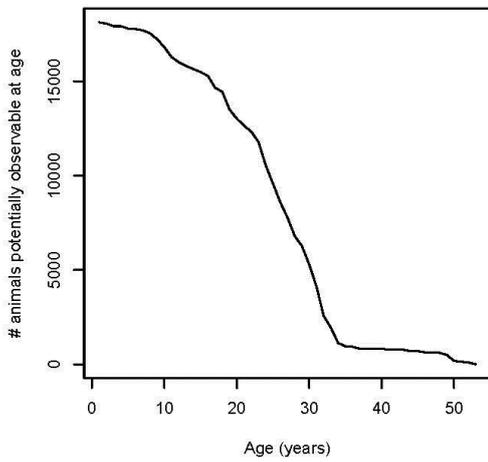
N = 121

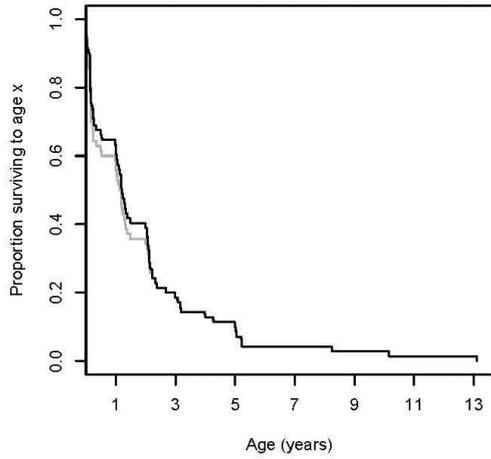
N locations = 17

MRA / MPA = 0.407

Prop. obs. dead = 1

Ann. wear-rate = 3 %





**Australian Shelduck**

*Tadorna tadornoides*

Ann. adult surv.  $\sim 0.631$  (SE = NA)

Ann. Y1 surv.  $\sim 0.636$  (SE = NA)

Surv. senesc.  $\sim -0.085$  (SE = 0.069)

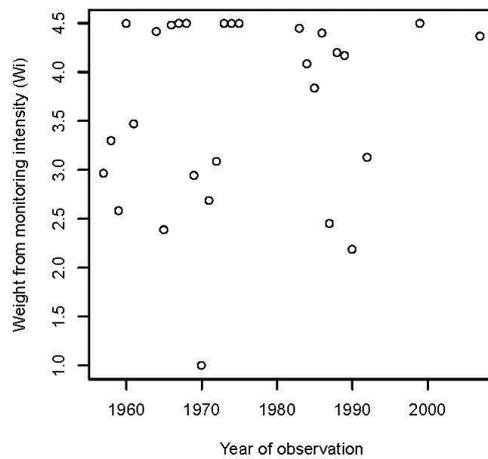
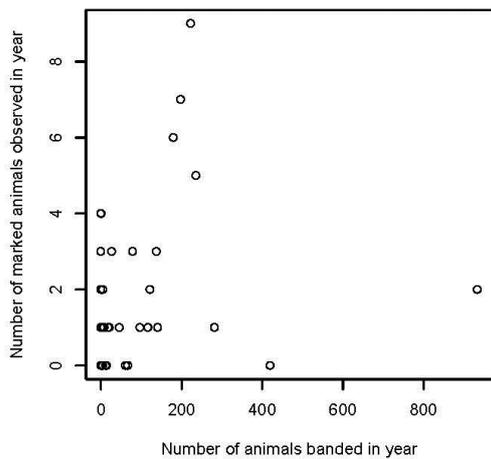
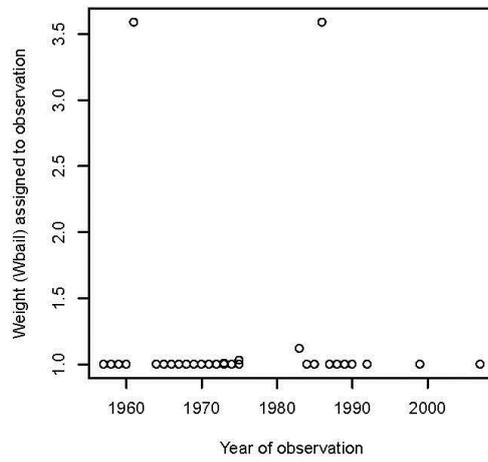
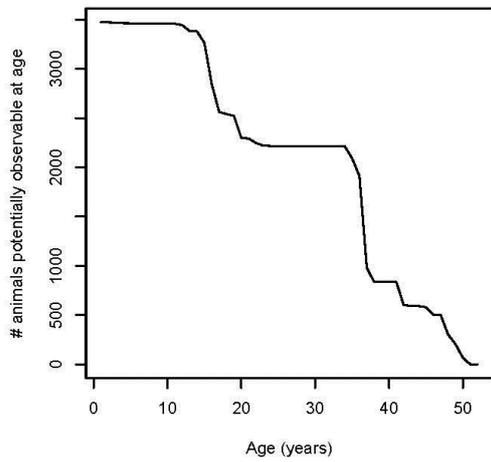
N = 70

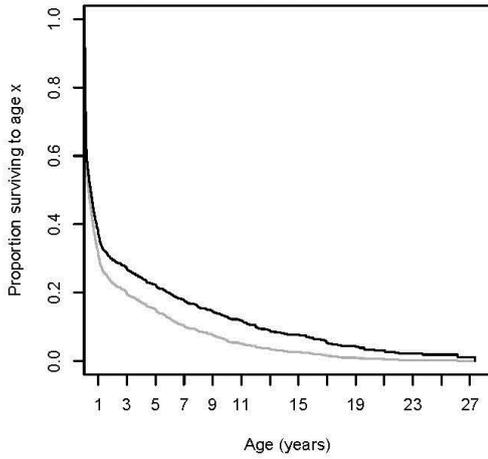
N locations = 12

MRA / MPA = 0.245

Prop. obs. dead = 1

Ann. wear-rate = 3 %





**Crested Tern**

*Thalasseus bergii*

Ann. adult surv.  $\sim 0.886$  (SE = NA)

Ann. Y1 surv.  $\sim 0.391$  (SE = NA)

Surv. senesc.  $\sim -0.157$  (SE = 0.008)

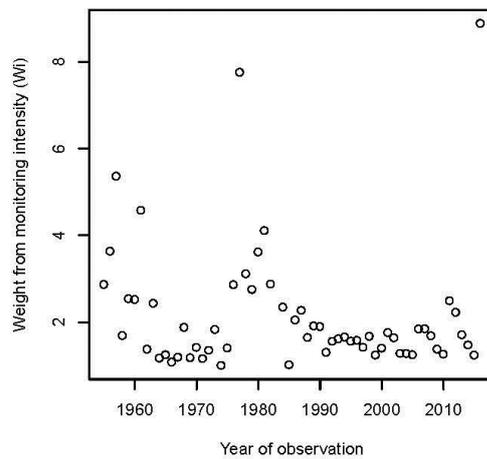
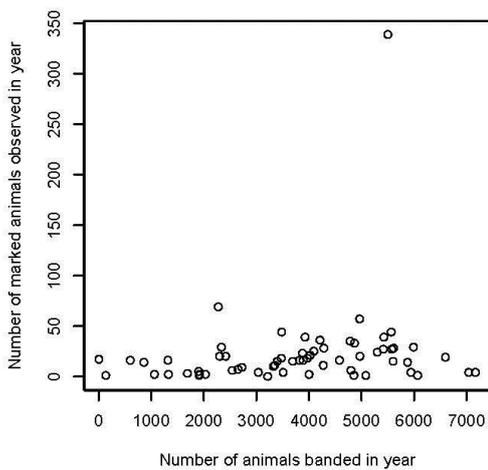
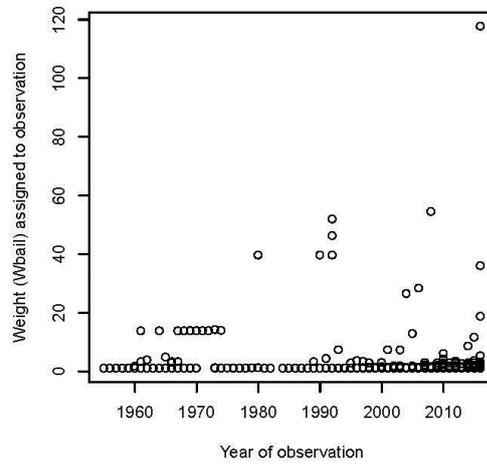
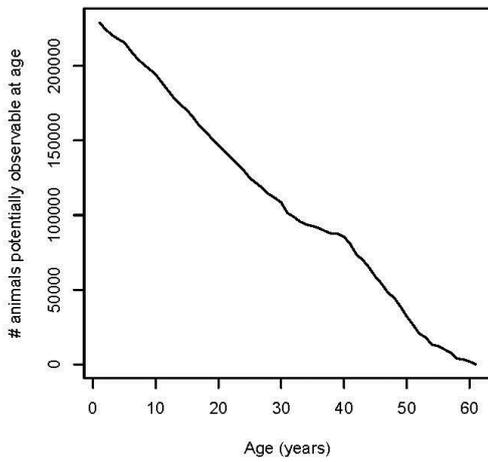
N = 1384

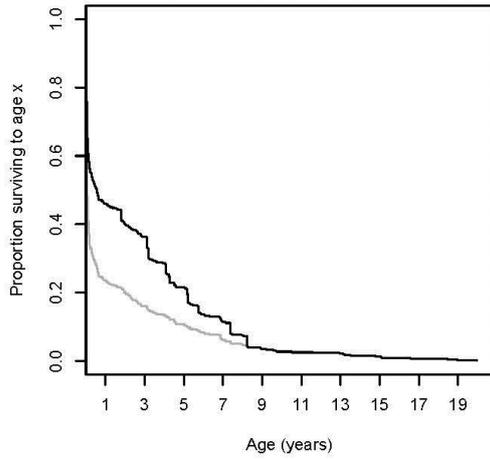
N locations = 48

MRA / MPA = 0.435

Prop. obs. dead = 1

Ann. wear-rate = 2.3 %





**Australian White Ibis**

*Threskiornis molucca*

Ann. adult surv.  $\sim 0.796$  (SE = NA)

Ann. Y1 surv.  $\sim 0.542$  (SE = NA)

Surv. senesc.  $\sim -0.044$  (SE = 0.019)

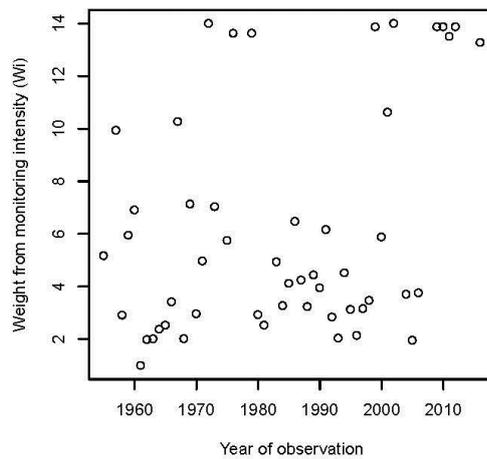
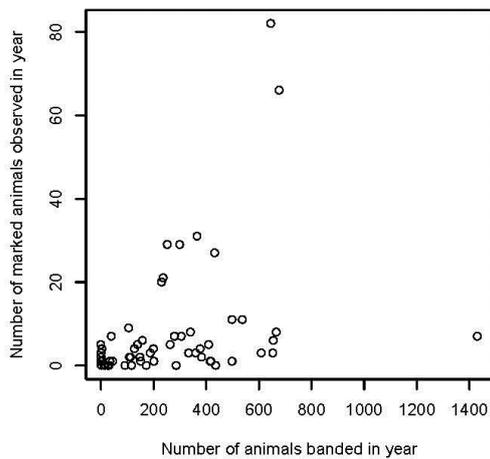
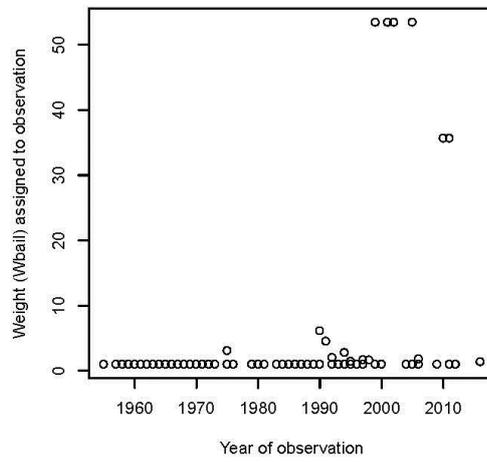
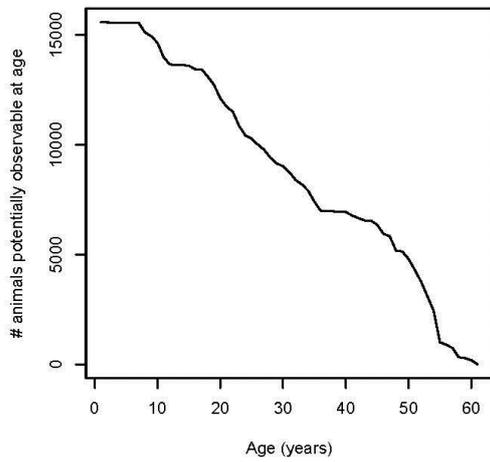
N = 469

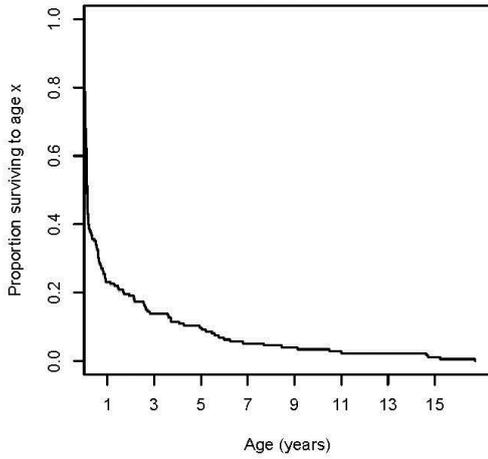
N locations = 29

MRA / MPA = 0.306

Prop. obs. dead = 1

Ann. wear-rate = 0.5 %





**Straw-necked ibis**

*Threskiornis spinicollis*

Ann. adult surv.  $\sim 0.798$  (SE = NA)

Ann. Y1 surv.  $\sim 0.263$  (SE = NA)

Surv. senesc.  $\sim -0.301$  (SE = 0.05)

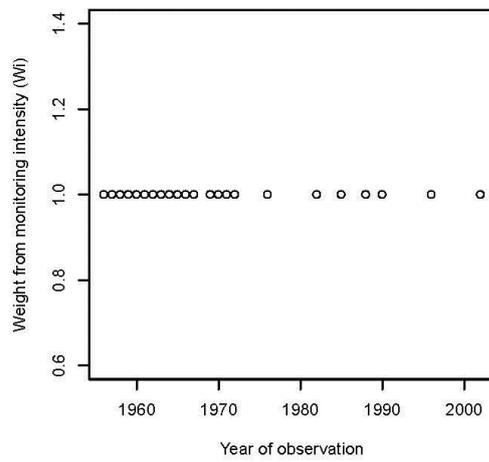
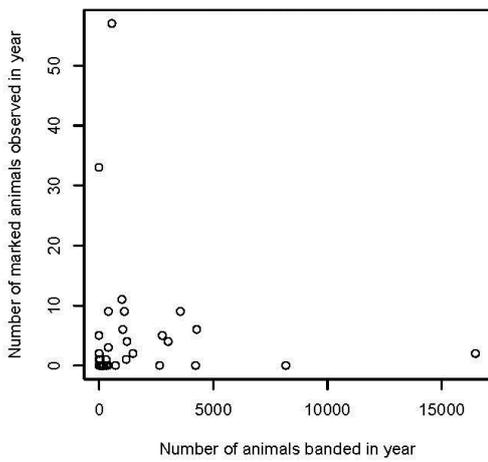
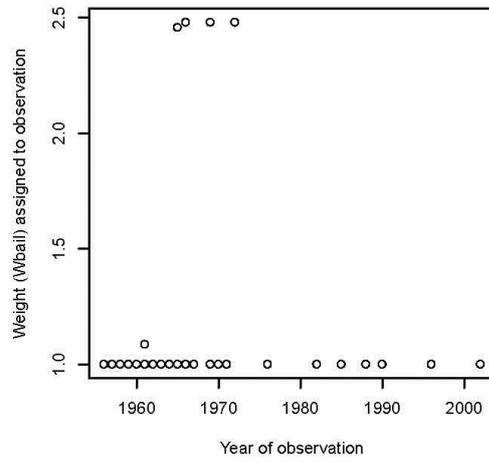
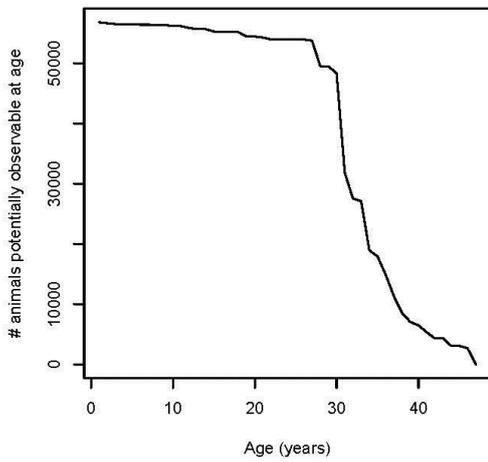
N = 175

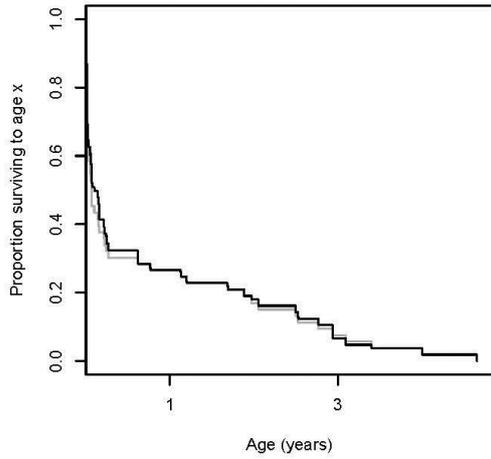
N locations = 26

MRA / MPA = 0.333

Prop. obs. dead = 1

Ann. wear-rate = 0.5 %





**Common Blackbird**

*Turdus merula*

Ann. adult surv.  $\sim 0.535$  (SE = NA)

Ann. Y1 surv.  $\sim 0.288$  (SE = NA)

Surv. senesc.  $\sim -0.403$  (SE = 0.261)

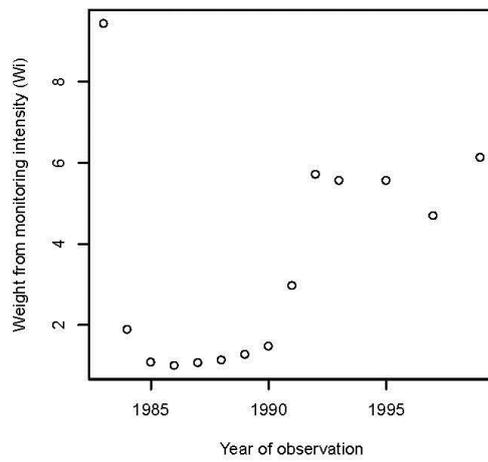
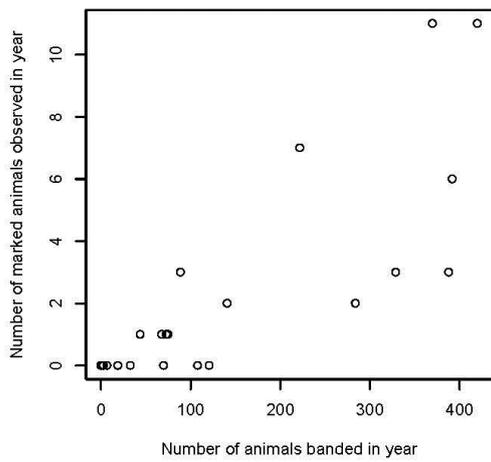
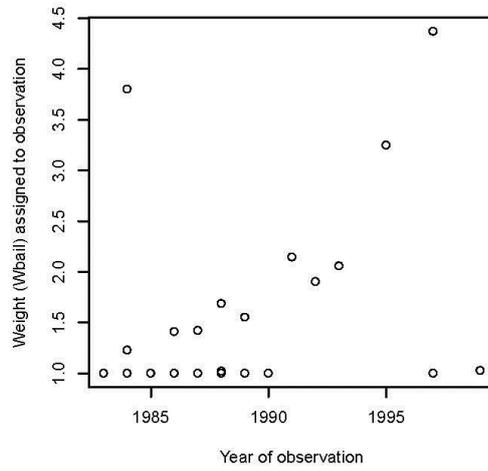
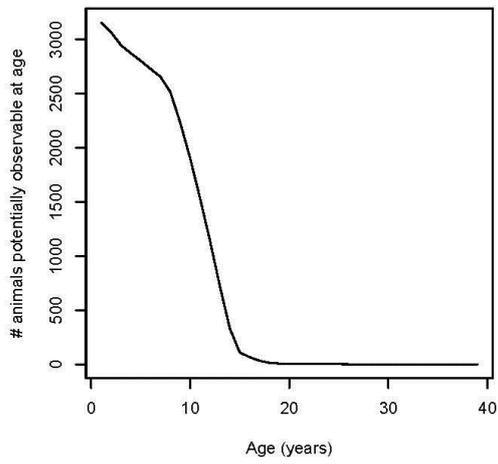
N = 53

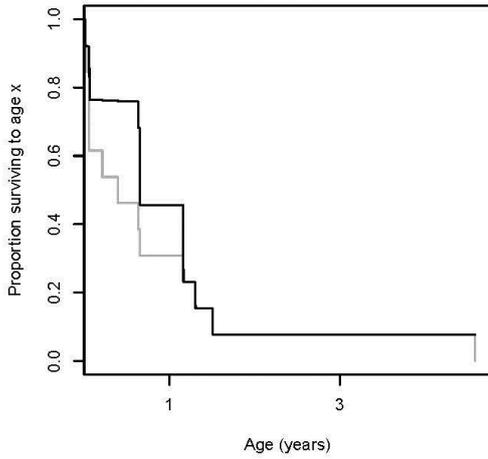
N locations = 15

MRA / MPA = 0.1

Prop. obs. dead = 1

Ann. wear-rate = 3 %





**Silvereye**

*Zosterops lateralis*

Ann. adult surv.  $\sim 0.448$  (SE = NA)

Ann. Y1 surv.  $\sim 0.456$  (SE = NA)

Surv. senesc.  $\sim -0.399$  (SE = 0.571)

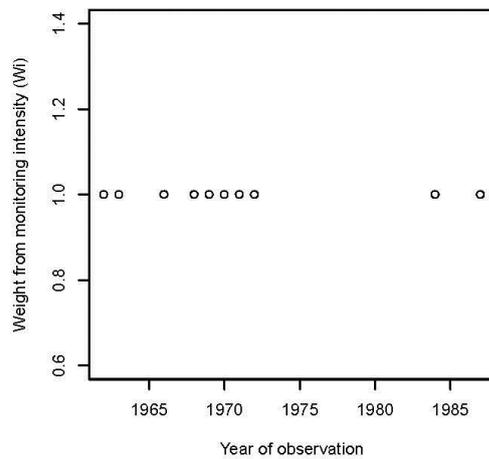
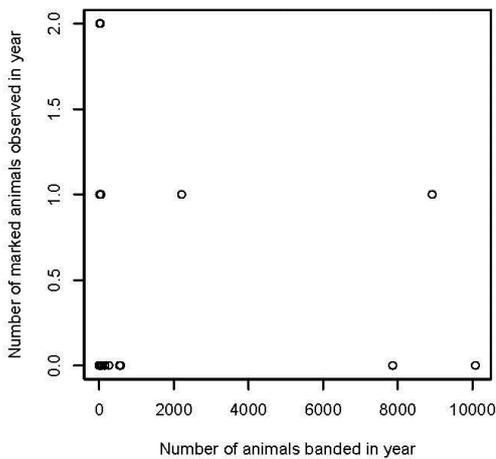
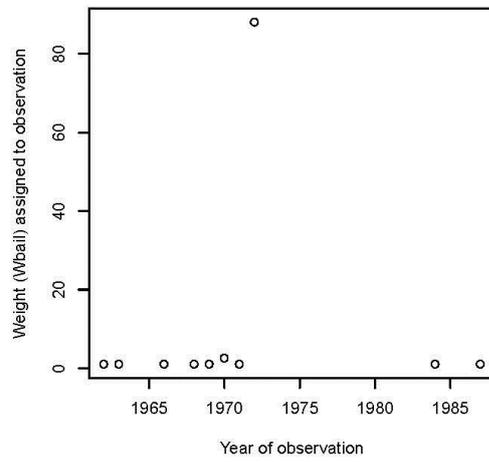
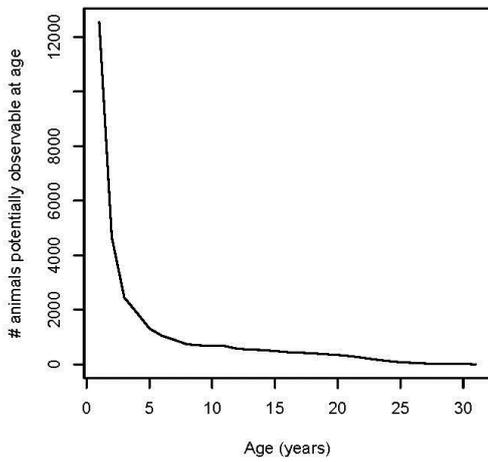
N = 13

N locations = 8

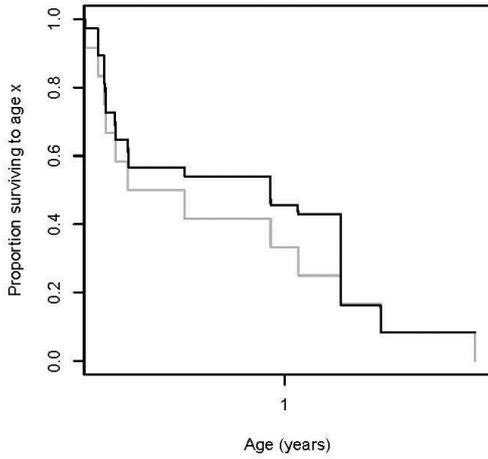
MRA / MPA = 0.125

Prop. obs. dead = 1

Ann. wear-rate = 3%



Models for species marked with Alloy bands,  
treating all observations as Alloy-marked animals



**Magpie-lark**

*Grallina cyanoleuca*

Ann. adult surv. ~ 0.182 (SE = NA)

Ann. Y1 surv. ~ 0.457 (SE = NA)

Surv. senesc. ~ NA (SE = 0.566)

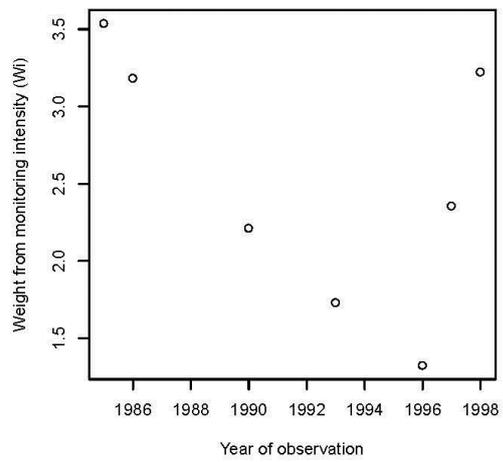
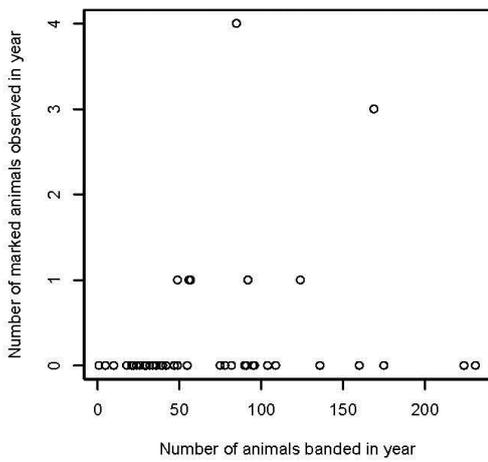
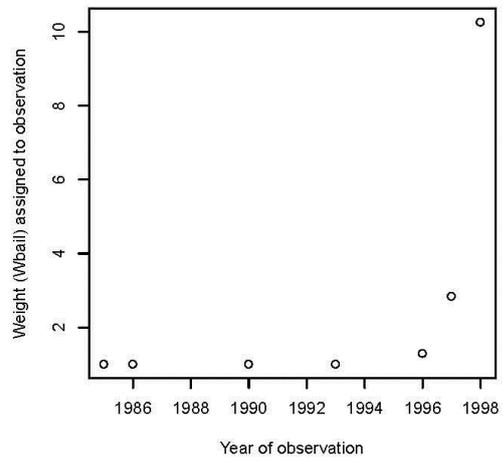
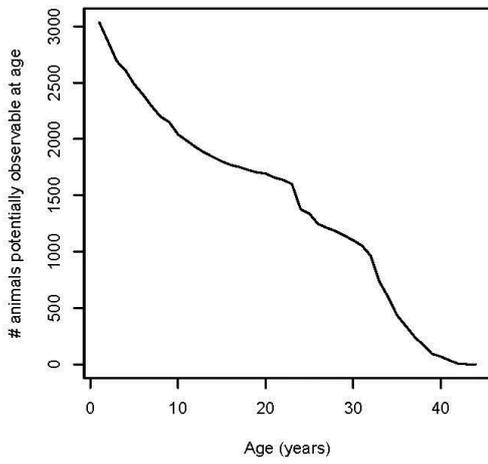
N = 12

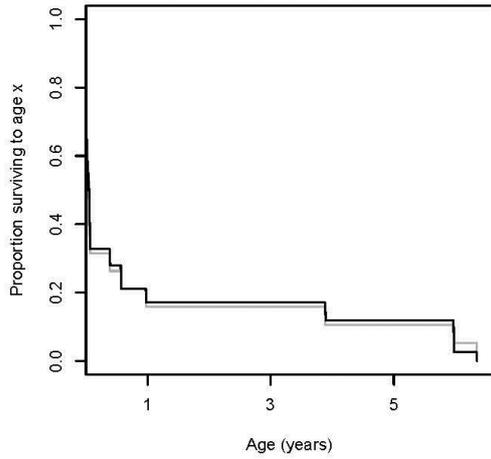
N locations = 5

MRA / MPA = 0.022

Prop. obs. dead = 1

Ann. wear-rate = 4%





**Welcome Swallow**

*Hirundo neoxena*

Ann. adult surv.  $\sim 0.78$  (SE = NA)

Ann. Y1 surv.  $\sim 0.202$  (SE = NA)

Surv. senesc.  $\sim -1.311$  (SE = 0.554)

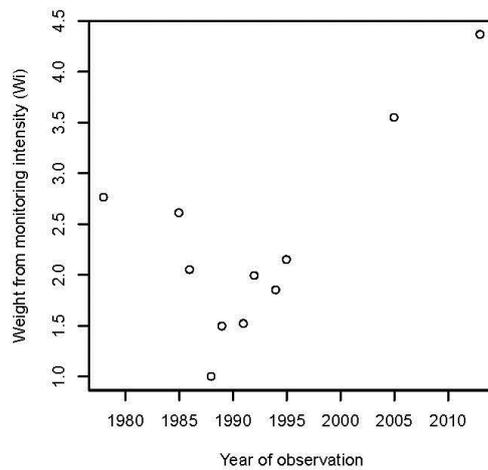
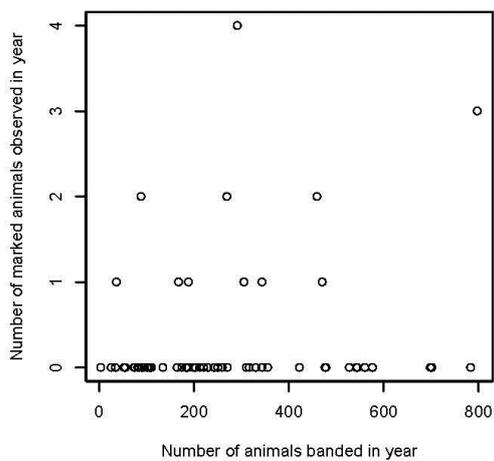
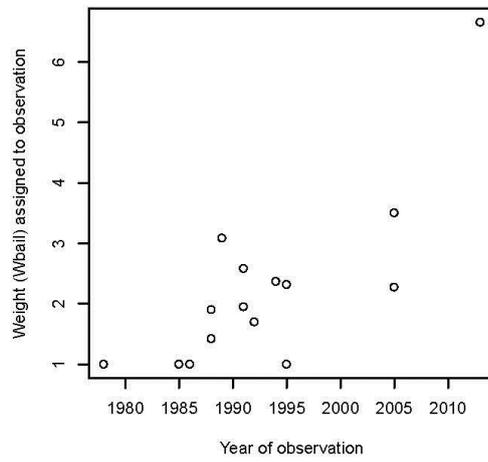
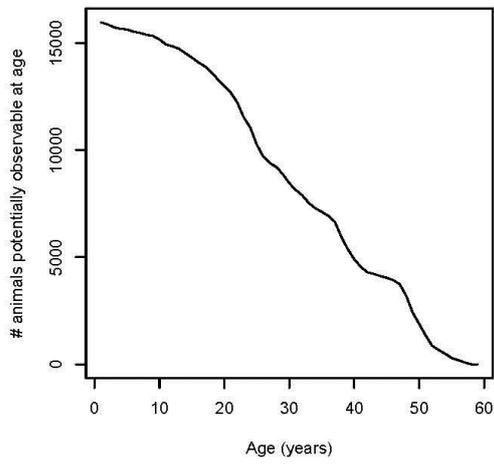
N = 19

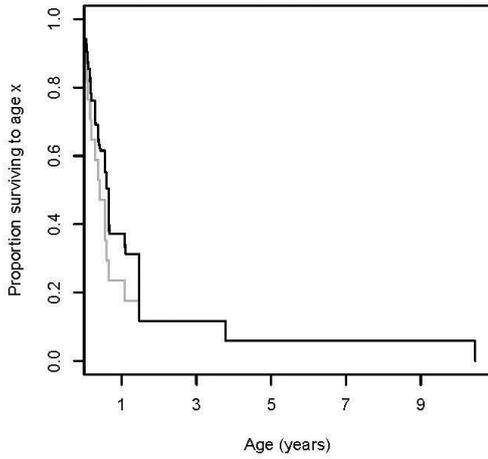
N locations = 8

MRA / MPA = 0.1

Prop. obs. dead = 1

Ann. wear-rate = 4 %





**Superb Fairy-wren**

*Malurus cyaneus*

Ann. adult surv.  $\sim 0.635$  (SE = NA)

Ann. Y1 surv.  $\sim 0.396$  (SE = NA)

Surv. senesc.  $\sim -0.658$  (SE = 0.326)

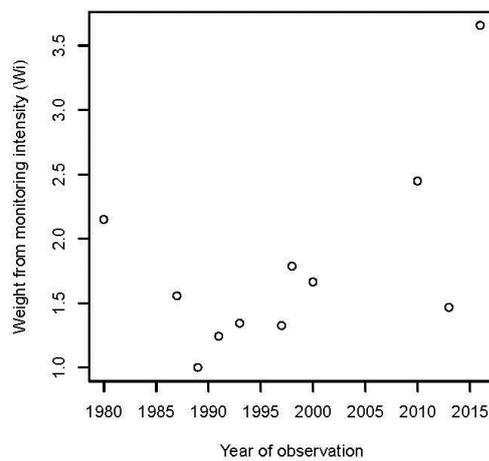
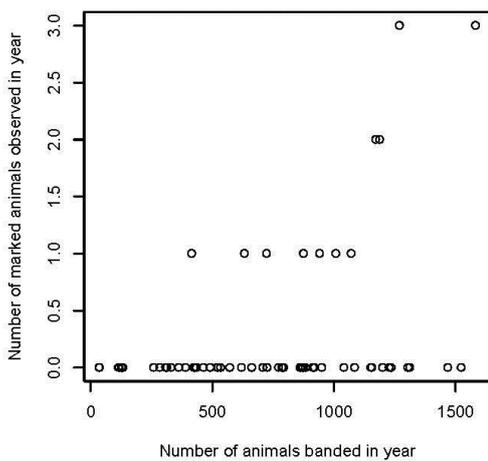
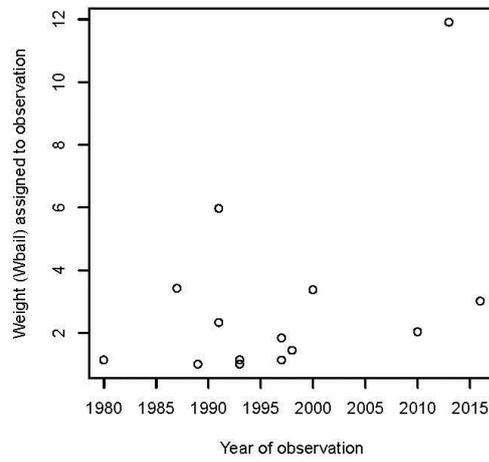
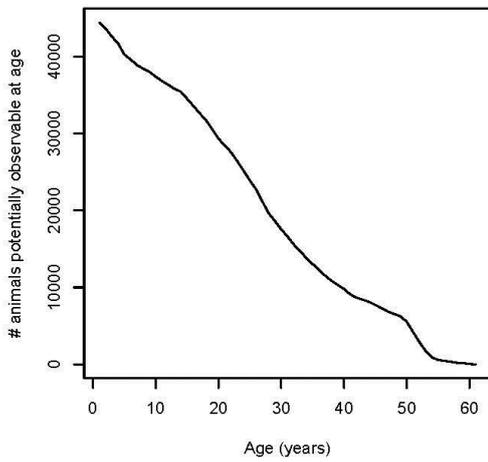
N = 17

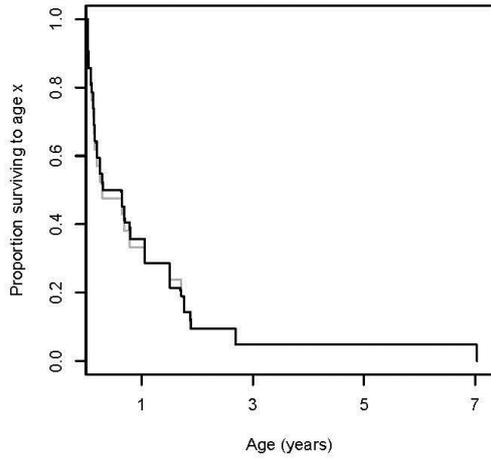
N locations = 8

MRA / MPA = 0.161

Prop. obs. dead = 1

Ann. wear-rate = 4%





**White-browed Scrubwren**

*Sericornis frontalis*

Ann. adult surv.  $\sim 0.483$  (SE = NA)

Ann. Y1 surv.  $\sim 0.357$  (SE = NA)

Surv. senesc.  $\sim -0.616$  (SE = 0.343)

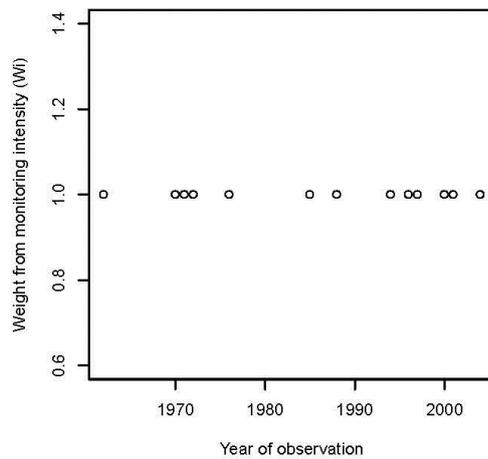
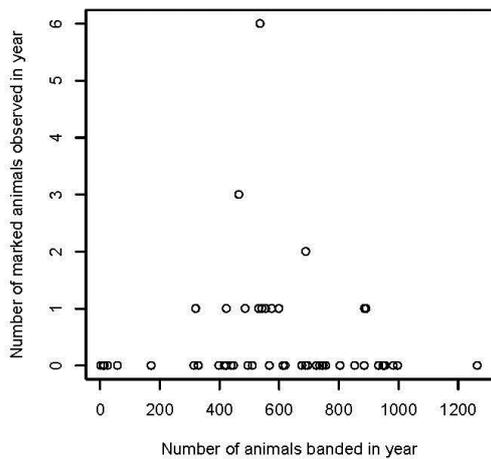
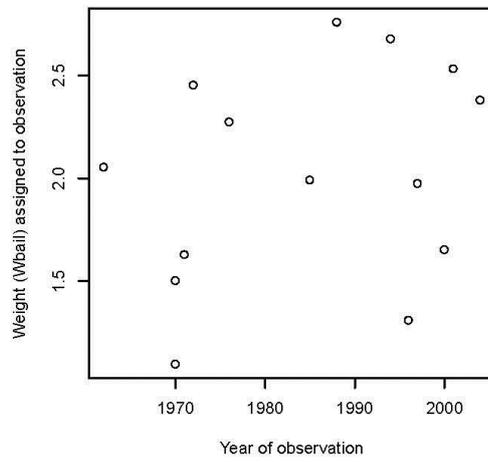
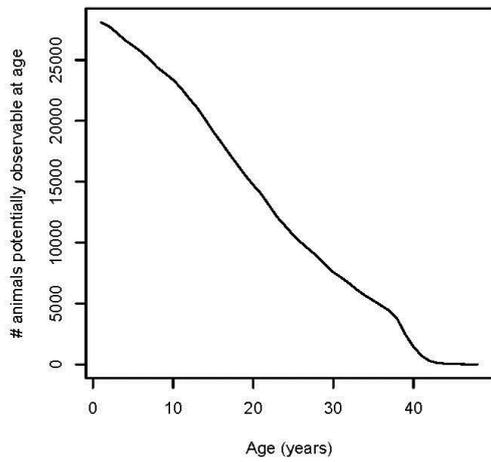
N = 21

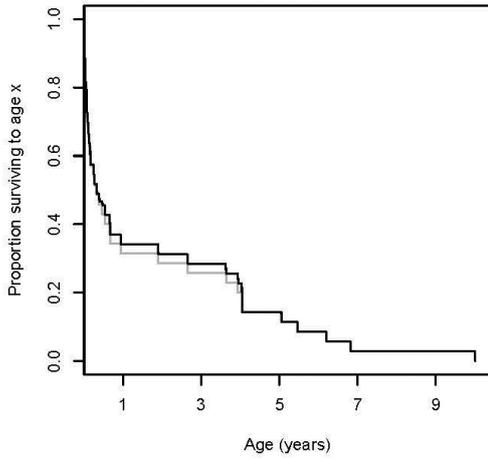
N locations = 5

MRA / MPA = 0.143

Prop. obs. dead = 1

Ann. wear-rate = 4 %





### Common Starling

*Sturnus vulgaris*

Ann. adult surv. ~ NaN (SE = NA)

Ann. Y1 surv. ~ 0.385 (SE = NA)

Surv. senesc. ~ -0.188 (SE = 0.125)

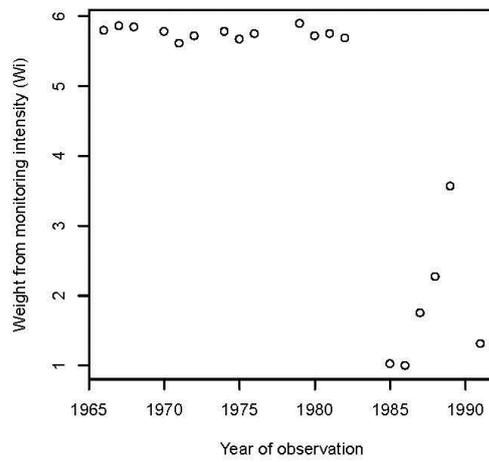
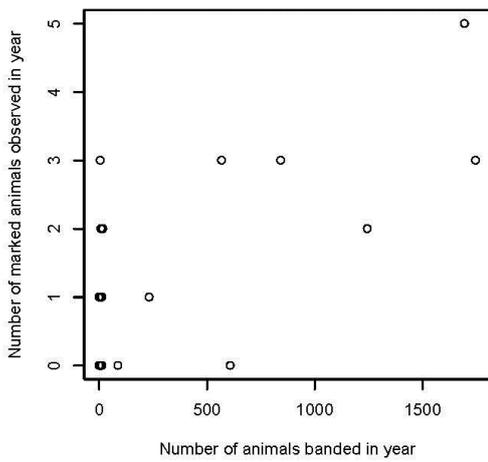
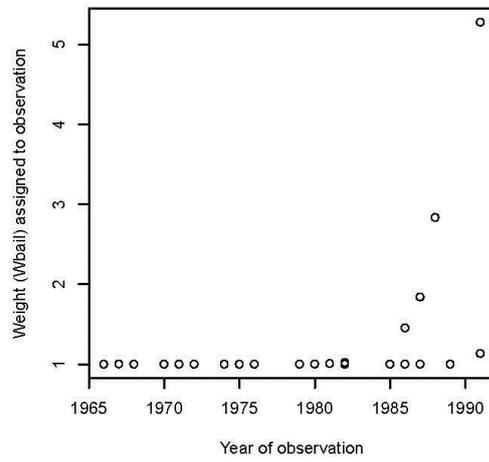
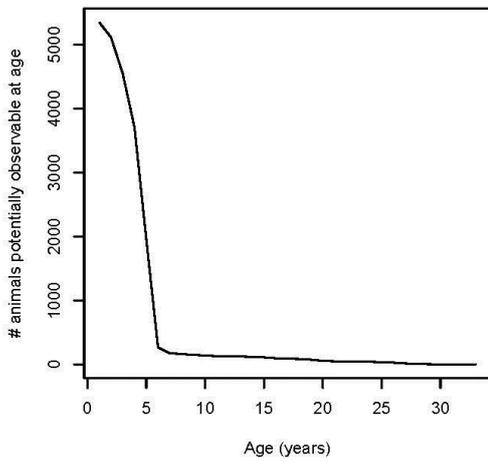
N = 35

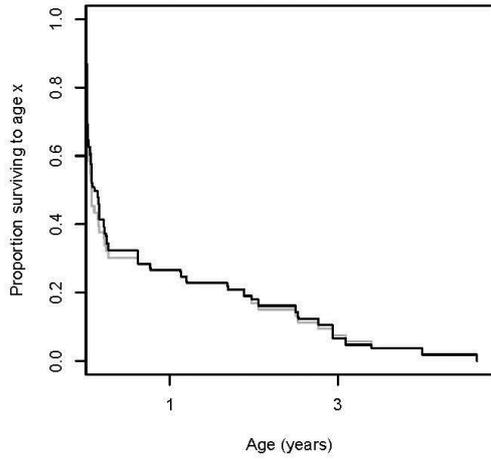
N locations = 14

MRA / MPA = 0.294

Prop. obs. dead = 1

Ann. wear-rate = 4%





**Common Blackbird**

*Turdus merula*

Ann. adult surv. ~ 0.535 (SE = NA )

Ann. Y1 surv. ~ 0.288 (SE = NA )

Surv. senesc. ~ -0.403 (SE = 0.261 )

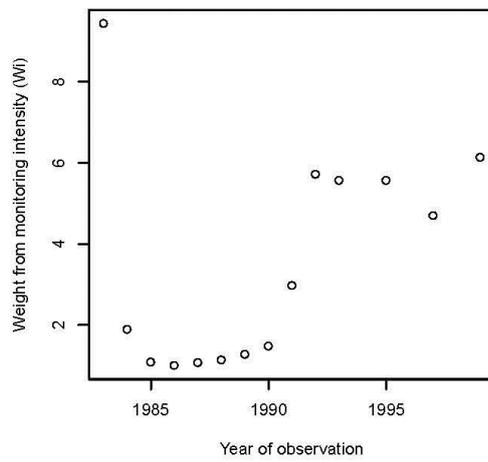
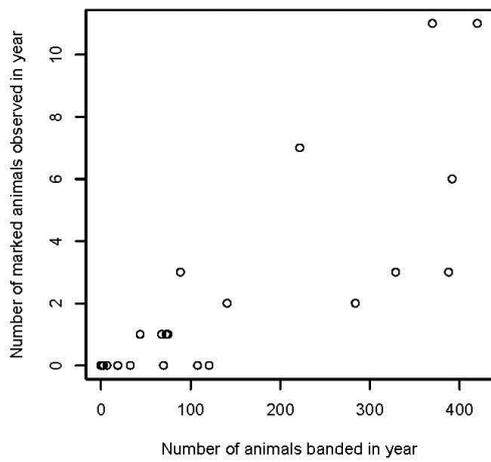
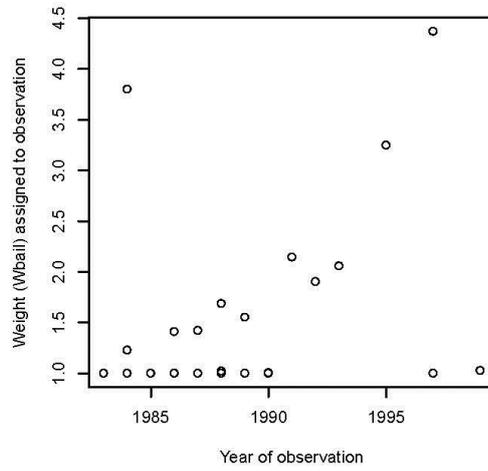
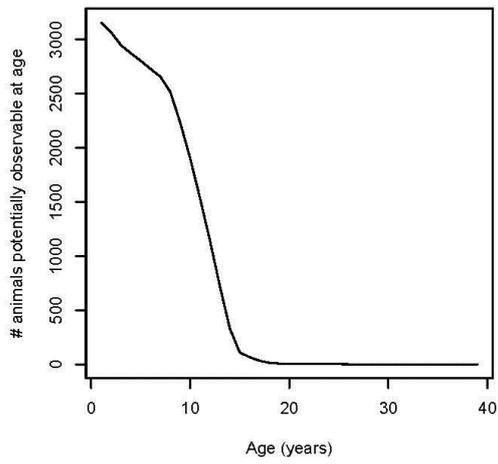
N = 53

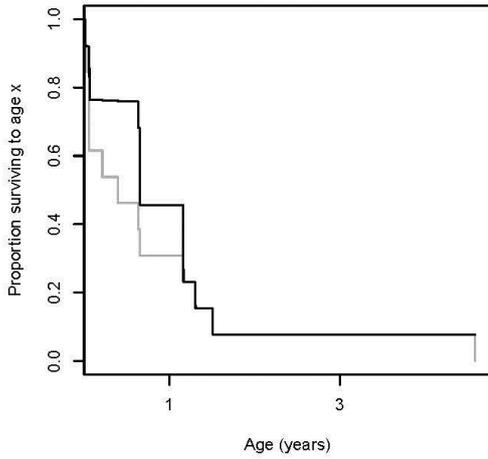
N locations = 15

MRA / MPA = 0.1

Prop. obs. dead = 1

Ann. wear-rate = 4.5 %





**Silvereye**

*Zosterops lateralis*

Ann. adult surv.  $\sim 0.448$  (SE = NA)

Ann. Y1 surv.  $\sim 0.456$  (SE = NA)

Surv. senesc.  $\sim -0.399$  (SE = 0.571)

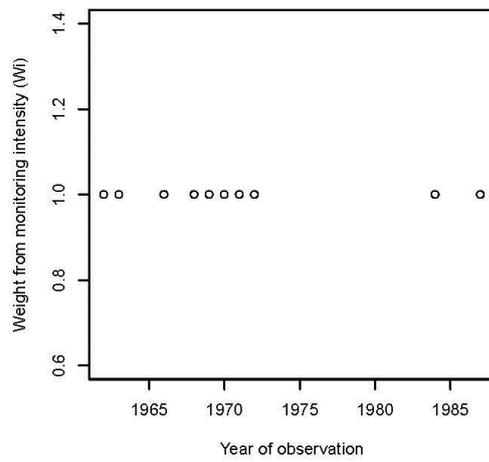
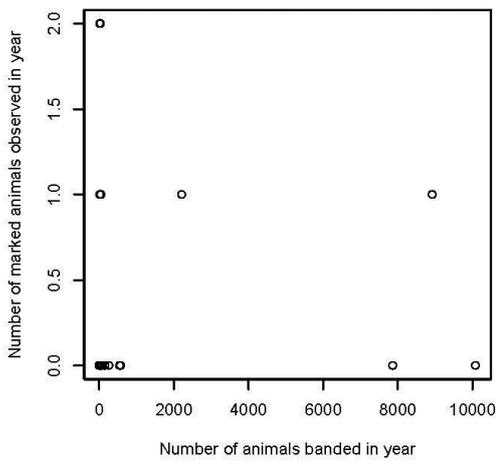
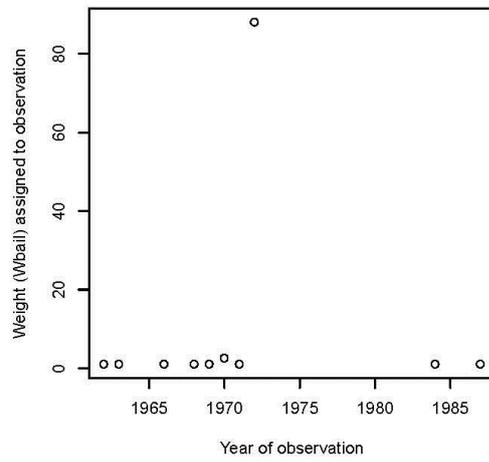
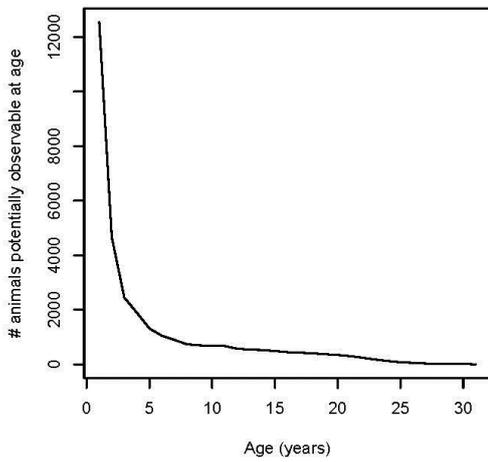
N = 13

N locations = 8

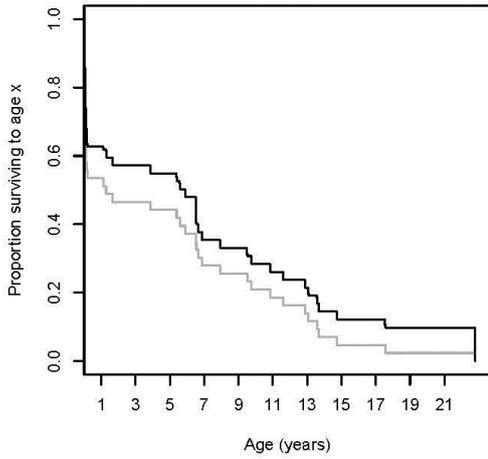
MRA / MPA = 0.125

Prop. obs. dead = 1

Ann. wear-rate = 1.2 %



Models for species marked with Monel bands,  
treating all observations as Monel-marked animals



**Wedge-tailed Shearwater**

*Ardenna pacifica*

Ann. adult surv.  $\sim 0.901$  (SE = NA)

Ann. Y1 surv.  $\sim 0.676$  (SE = NA)

Surv. senesc.  $\sim -0.053$  (SE = 0.037)

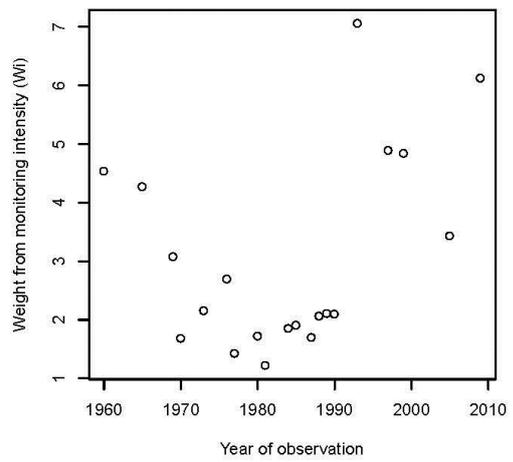
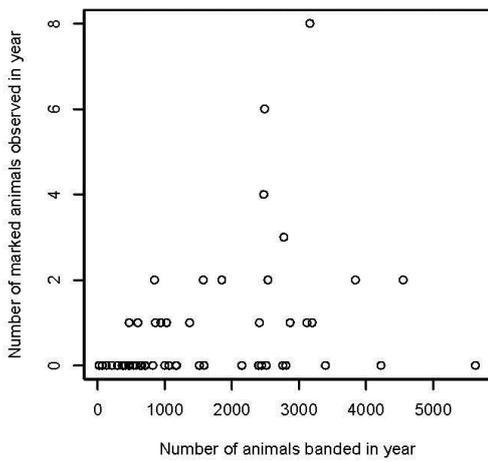
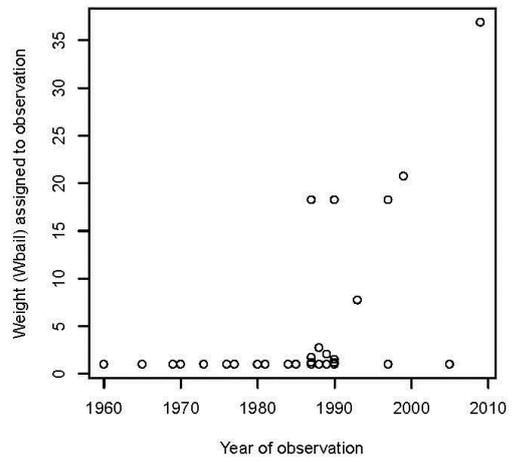
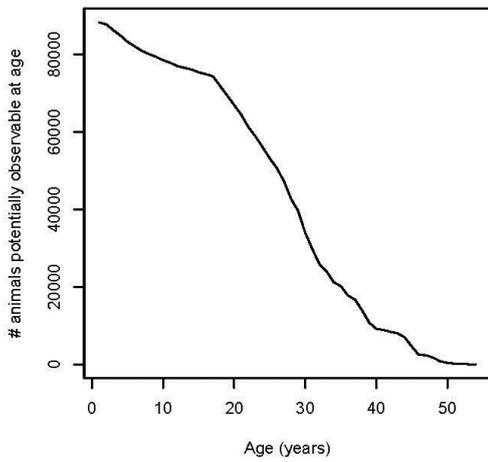
N = 43

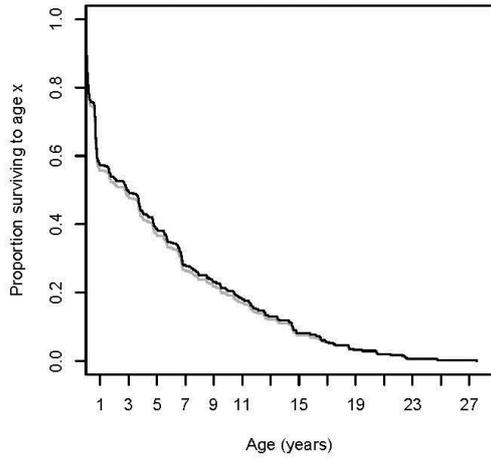
N locations = 18

MRA / MPA = 0.4

Prop. obs. dead = 1

Ann. wear-rate = 0.6 %





**Short-tailed Shearwater**

*Ardenna tenuirostris*

Ann. adult surv.  $\sim 0.88$  (SE = NA)

Ann. Y1 surv.  $\sim 0.62$  (SE = NA)

Surv. senesc.  $\sim -0.024$  (SE = 0.012)

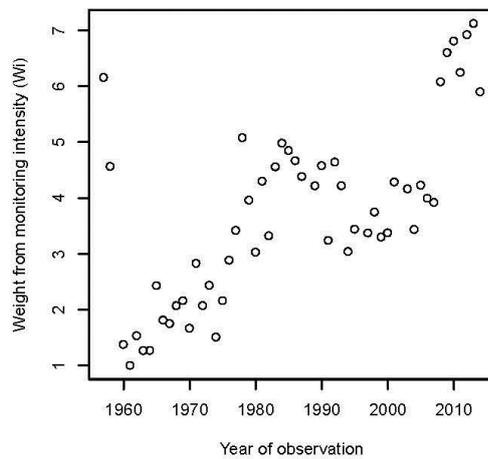
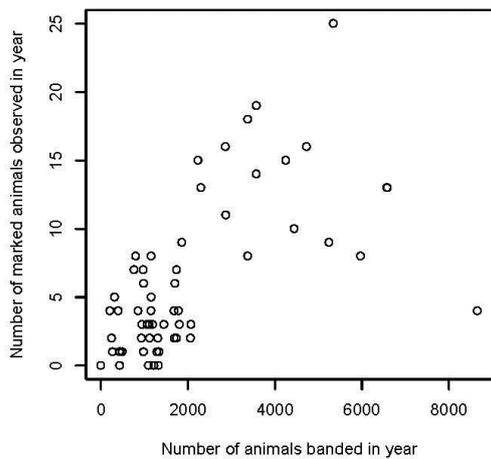
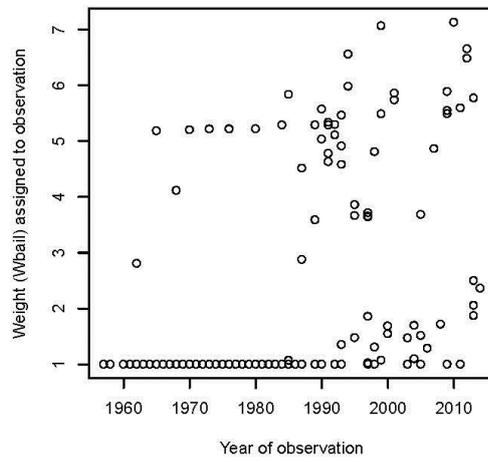
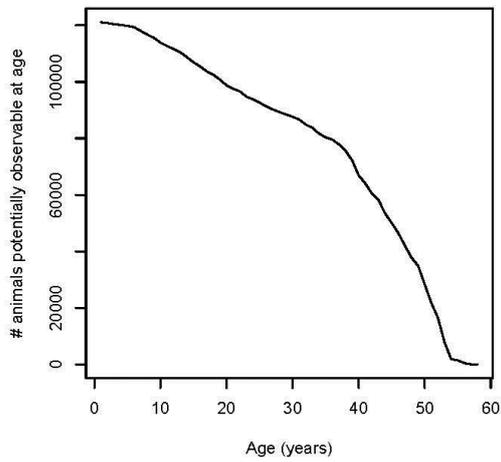
N = 361

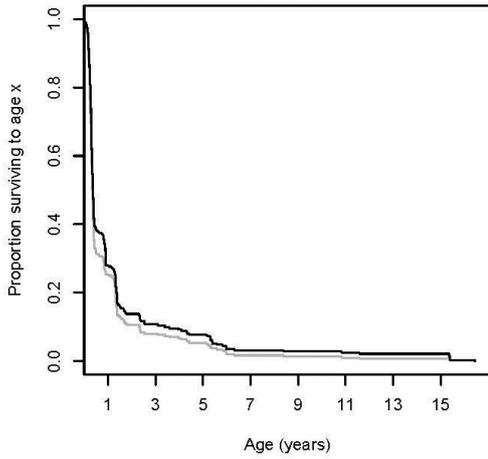
N locations = 26

MRA / MPA = 0.458

Prop. obs. dead = 1

Ann. wear-rate = 0.8 %





**Cape Barren Goose**

*Cereopsis novaehollandiae*

Ann. adult surv.  $\sim 0.709$  (SE = NA)

Ann. Y1 surv.  $\sim 0.282$  (SE = NA)

Surv. senesc.  $\sim -0.297$  (SE = 0.04)

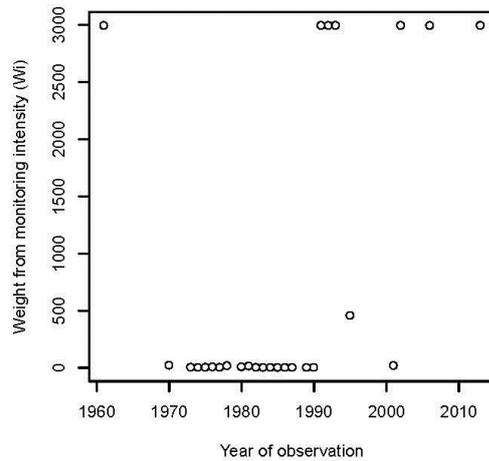
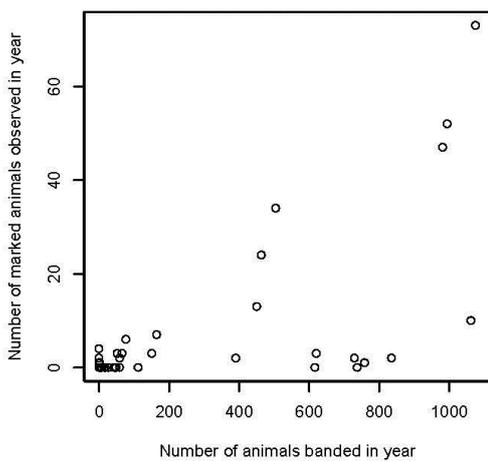
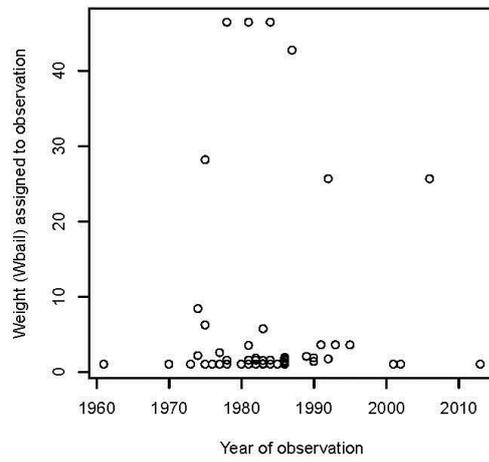
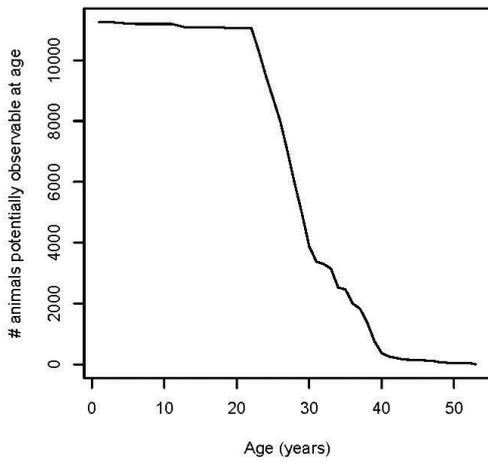
N = 300

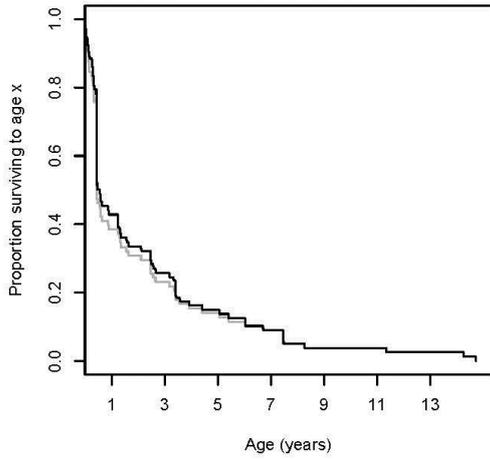
N locations = 30

MRA / MPA = 0.296

Prop. obs. dead = 1

Ann. wear-rate = 0.5 %





**Black Swan**

*Cygnus atratus*

Ann. adult surv.  $\sim 0.761$  (SE = NA)

Ann. Y1 surv.  $\sim 0.434$  (SE = NA)

Surv. senesc.  $\sim -0.215$  (SE = 0.063)

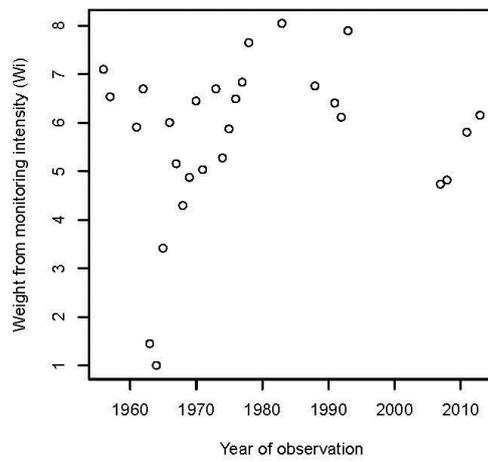
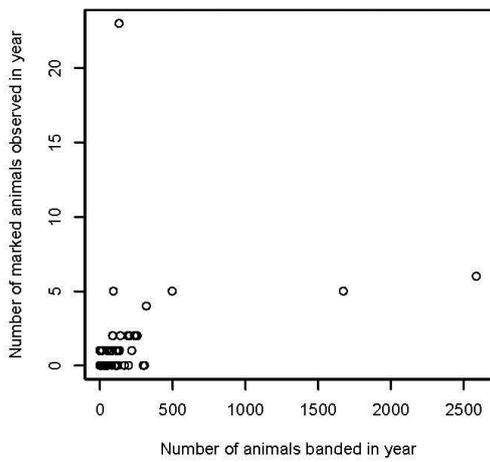
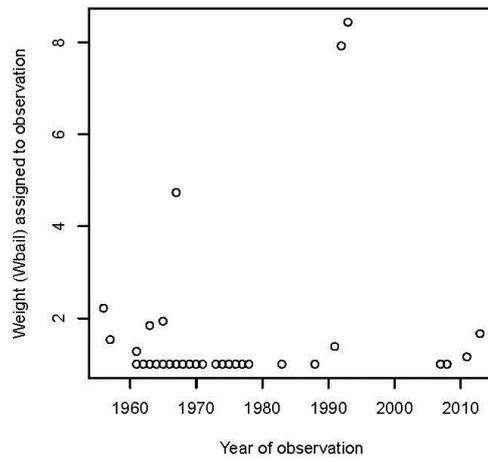
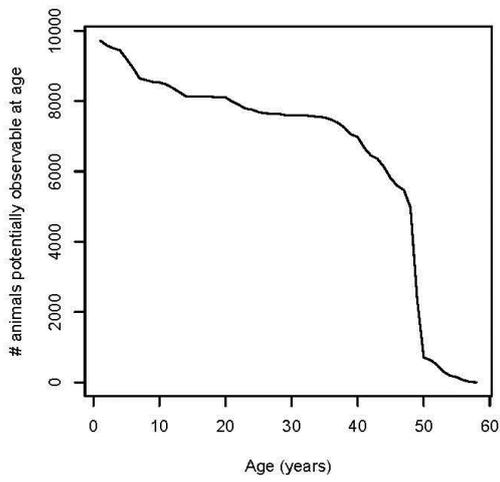
N = 78

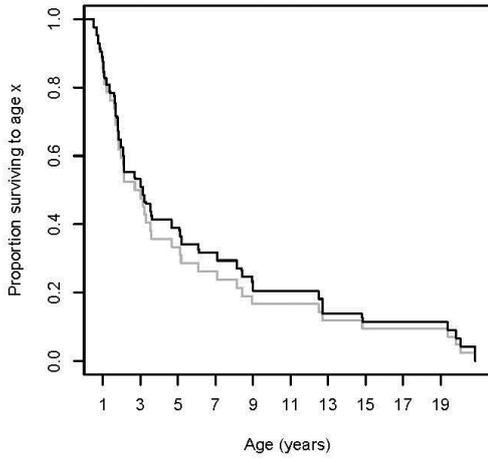
N locations = 19

MRA / MPA = 0.237

Prop. obs. dead = 1

Ann. wear-rate = 0.5 %





### Wandering Albatross

*Diomedea exulans*

Ann. adult surv.  $\sim 0.841$  (SE = NA)

Ann. Y1 surv.  $\sim 0.876$  (SE = NA)

Surv. senesc.  $\sim -0.052$  (SE = 0.036)

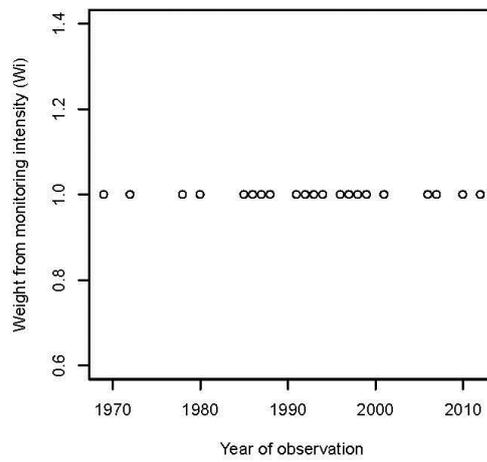
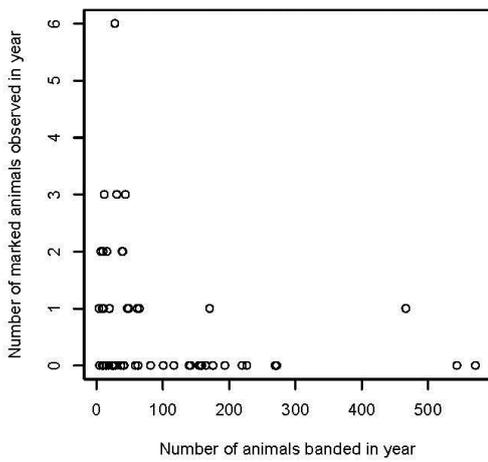
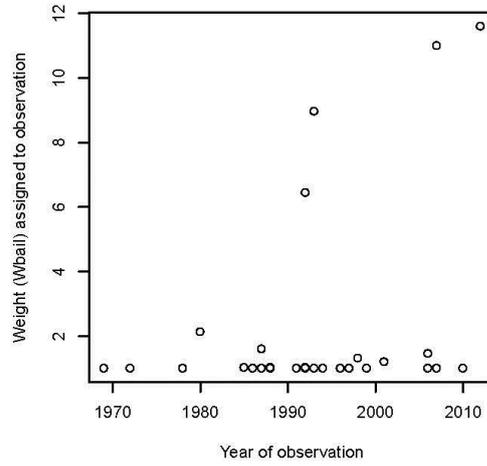
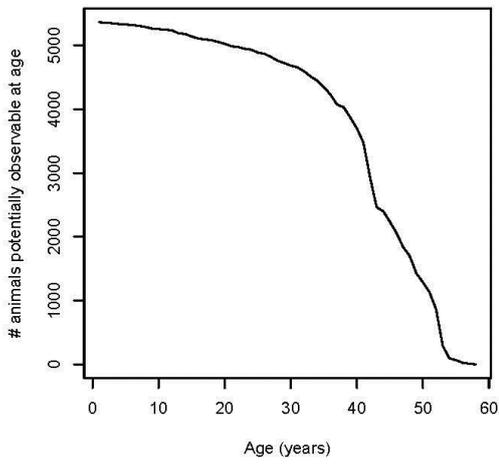
N = 42

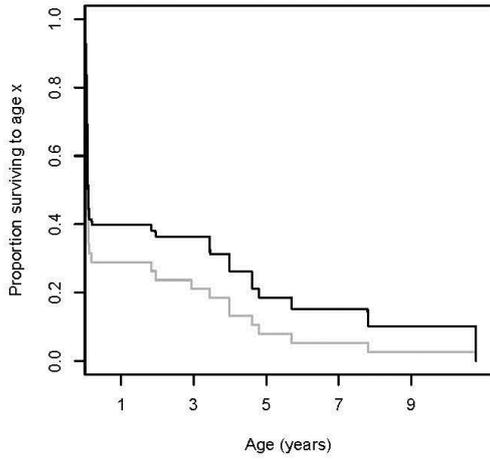
N locations = 15

MRA / MPA = 0.339

Prop. obs. dead = 1

Ann. wear-rate = 0.6 %





**White-faced Storm-Petrel**

*Pelagodroma marina*

Ann. adult surv.  $\sim 0.818$  (SE = NA )

Ann. Y1 surv.  $\sim 0.412$  (SE = NA )

Surv. senesc.  $\sim -0.333$  (SE = 0.108 )

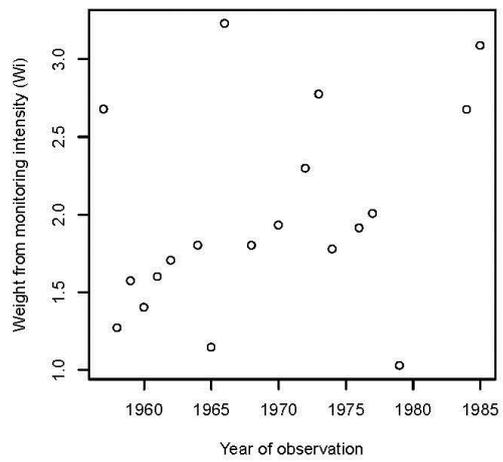
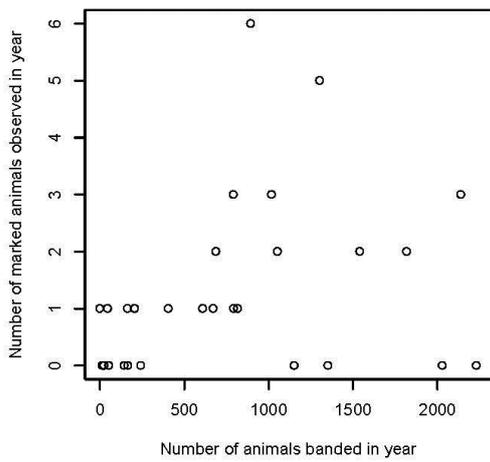
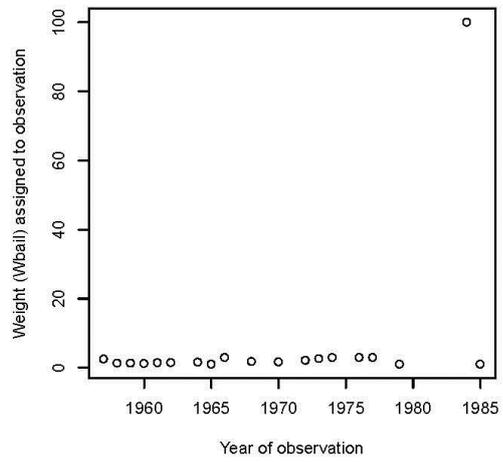
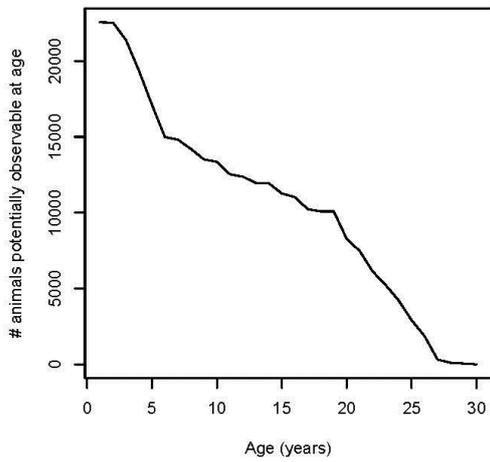
N = 38

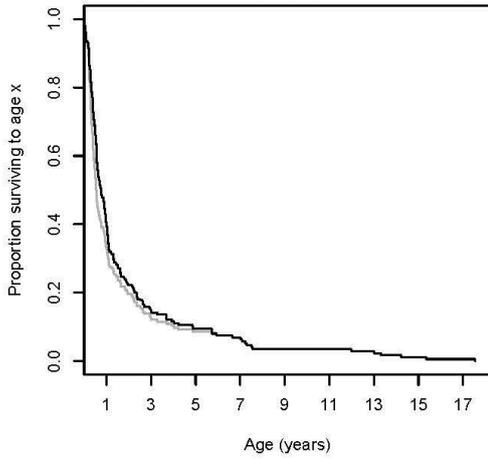
N locations = 3

MRA / MPA = 0.323

Prop. obs. dead = 1

Ann. wear-rate = 0.6 %





**Pied Cormorant**

*Phalacrocorax varius*

Ann. adult surv.  $\sim 0.717$  (SE = NA)

Ann. Y1 surv.  $\sim 0.415$  (SE = NA)

Surv. senesc.  $\sim -0.231$  (SE = 0.044)

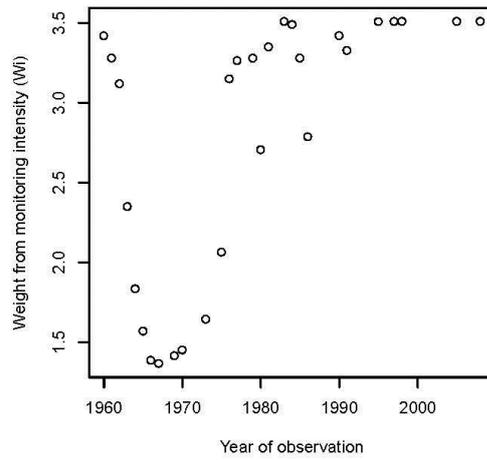
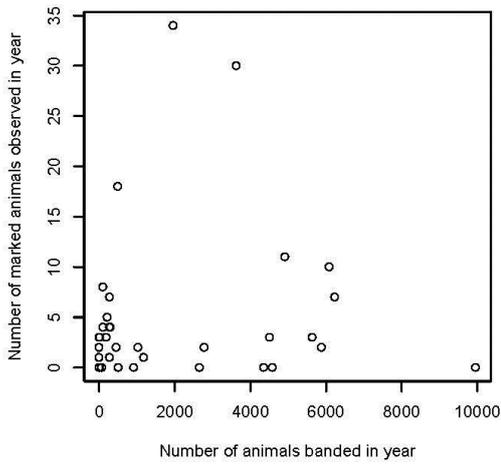
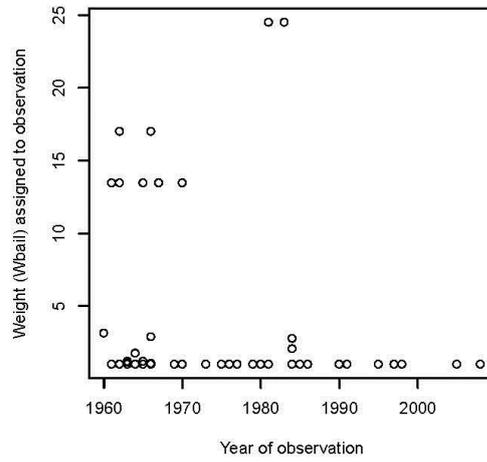
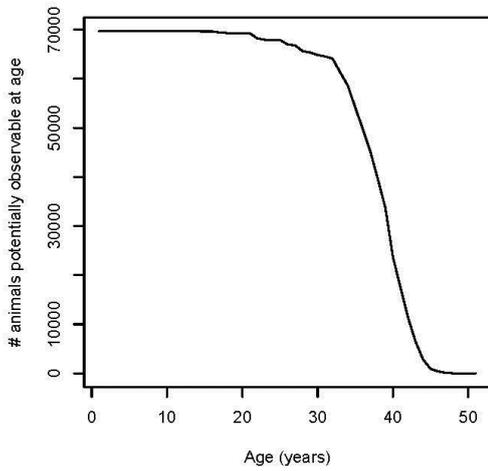
N = 174

N locations = 16

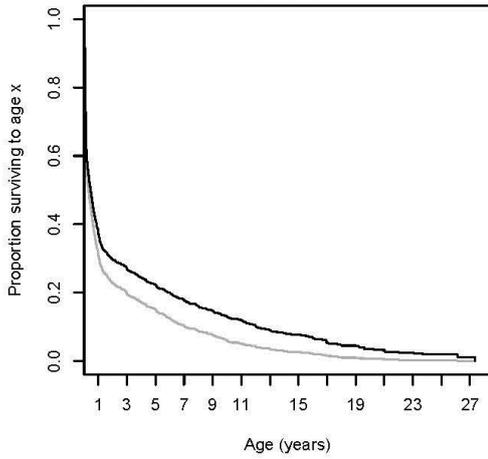
MRA / MPA = 0.327

Prop. obs. dead = 1

Ann. wear-rate = 0.6 %



Models for species marked with Incoloy bands,  
treating all observations as Incoloy-marked animals



**Crested Tern**

*Thalasseus bergii*

Ann. adult surv.  $\sim 0.886$  (SE = NA)

Ann. Y1 surv.  $\sim 0.392$  (SE = NA)

Surv. senesc.  $\sim -0.157$  (SE = 0.008)

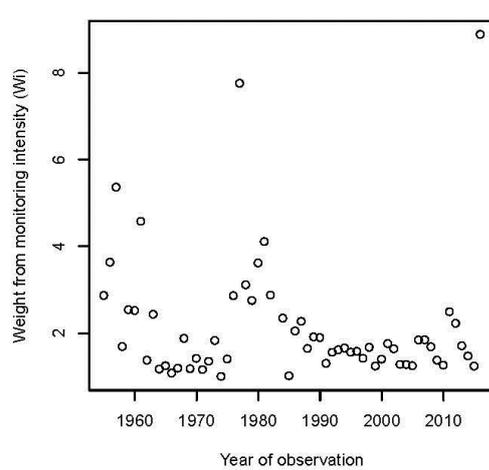
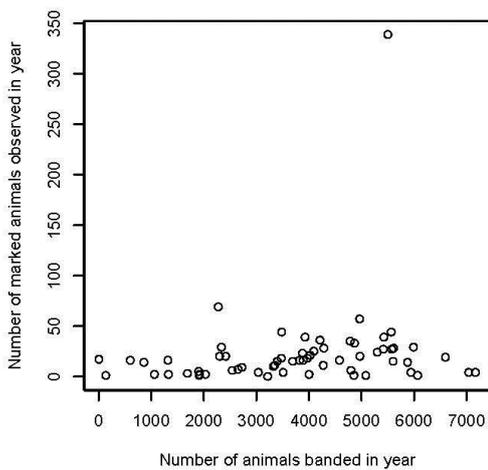
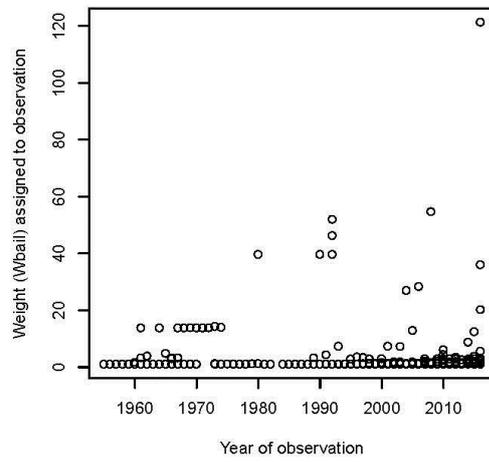
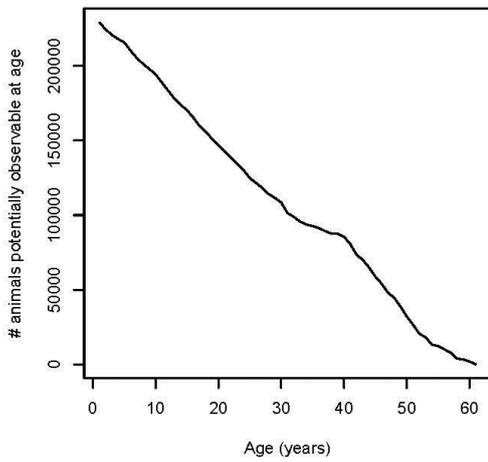
N = 1384

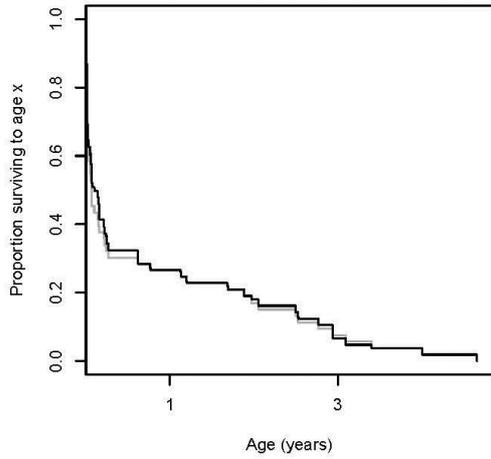
N locations = 48

MRA / MPA = 0.435

Prop. obs. dead = 1

Ann. wear-rate = 2.4 %





**Common Blackbird**

*Turdus merula*

Ann. adult surv.  $\sim 0.535$  (SE = NA)

Ann. Y1 surv.  $\sim 0.288$  (SE = NA)

Surv. senesc.  $\sim -0.403$  (SE = 0.261)

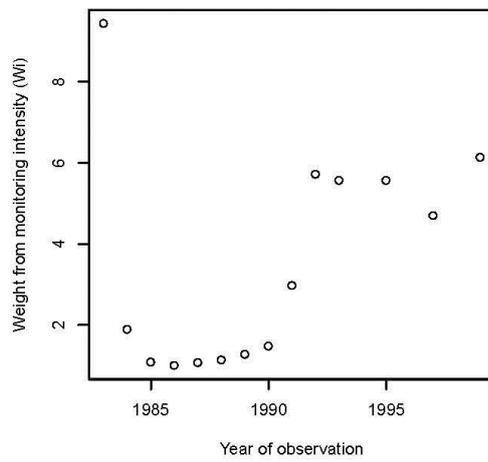
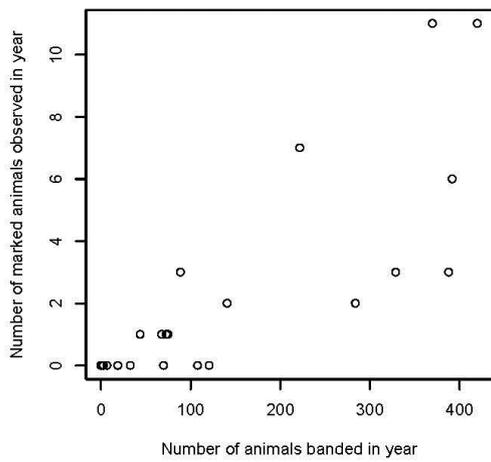
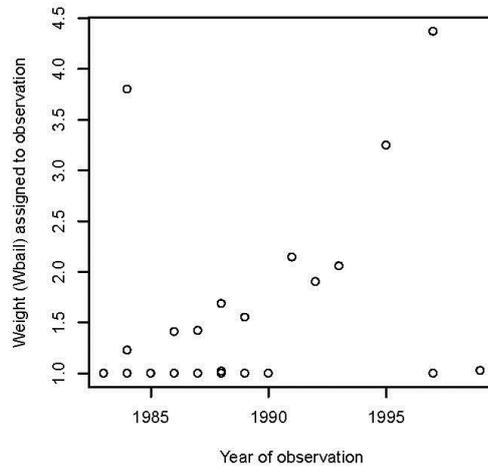
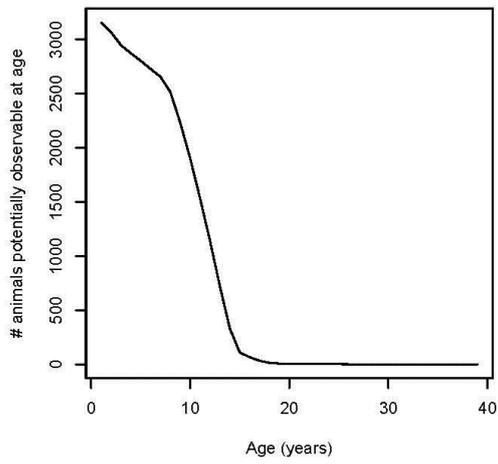
N = 53

N locations = 15

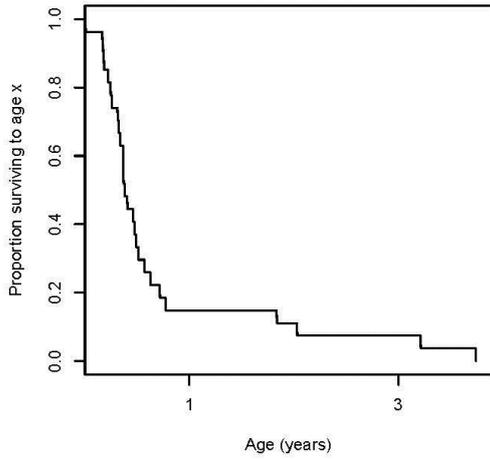
MRA / MPA = 0.1

Prop. obs. dead = 1

Ann. wear-rate = 2.4 %



Models for species marked with Stainless Steel bands,  
treating all observations as Stainless Steel-marked animals



**Brown Goshawk**

*Accipiter fasciatus*

Ann. adult surv. ~ 0.556 (SE = NaN)

Ann. Y1 surv. ~ 0.148 (SE = NaN)

Surv. senesc. ~ -1.609 (SE = 0.704)

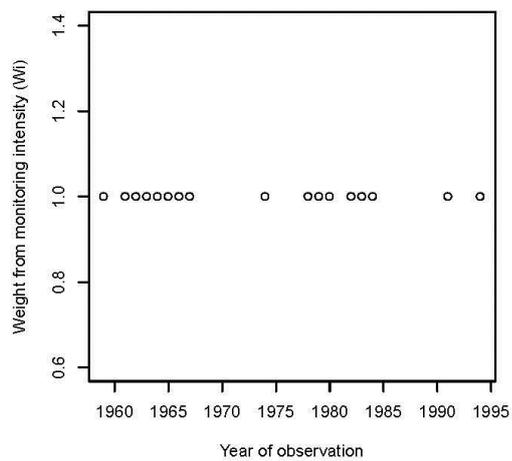
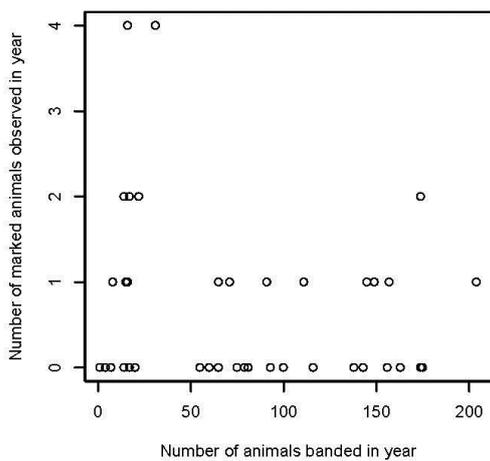
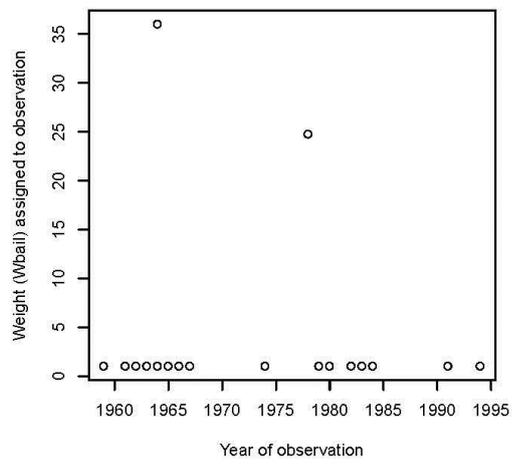
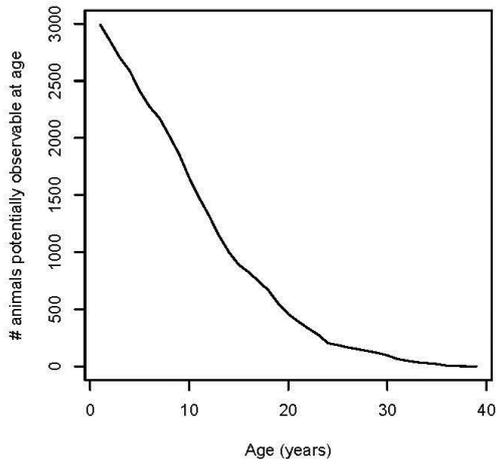
N = 27

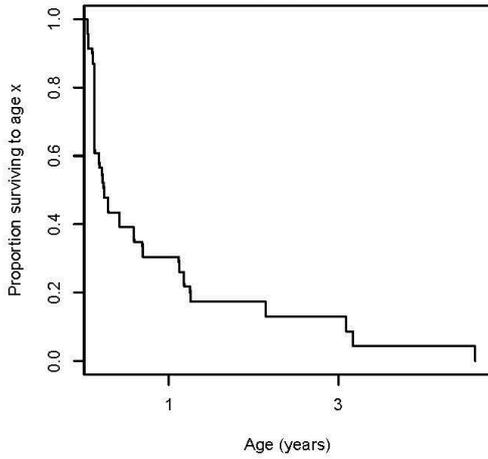
N locations = 19

MRA / MPA = 0.075

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Chestnut Teal**

*Anas castanea*

Ann. adult surv.  $\sim 0.533$  (SE = NA)

Ann. Y1 surv.  $\sim 0.304$  (SE = NA)

Surv. senesc.  $\sim -0.392$  (SE = 0.352)

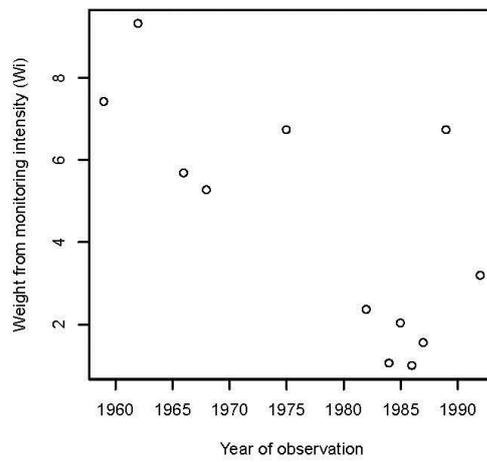
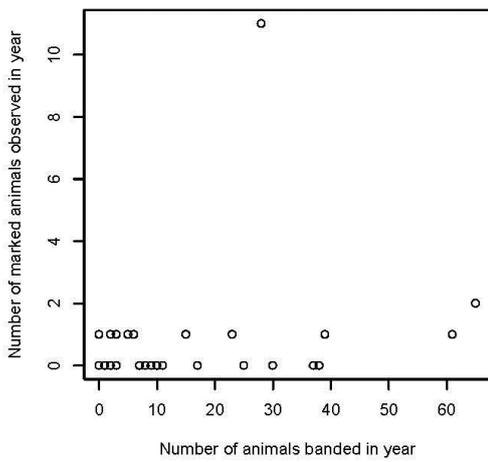
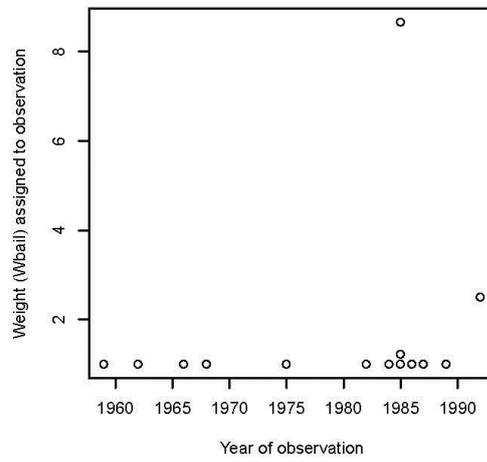
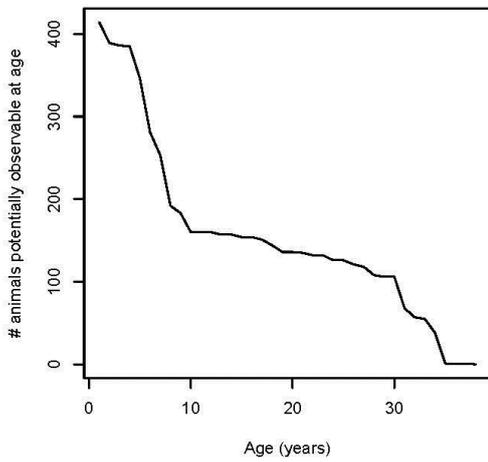
N = 23

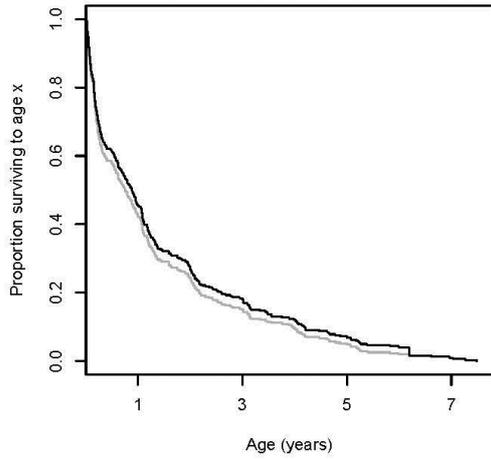
N locations = 12

MRA / MPA = 0.103

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Pacific Black Duck**

*Anas superciliosa*

Ann. adult surv.  $\sim 0.613$  (SE = NaN)

Ann. Y1 surv.  $\sim 0.457$  (SE = NaN)

Surv. senesc.  $\sim -0.112$  (SE = 0.051)

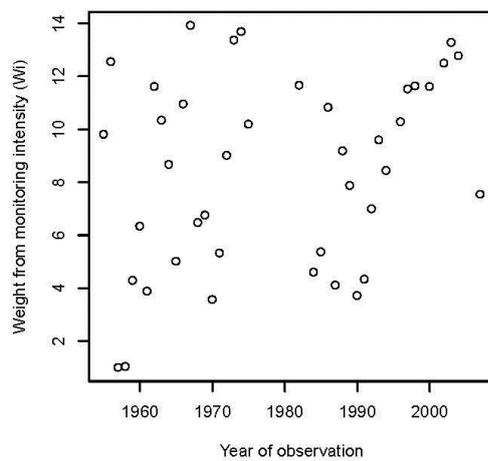
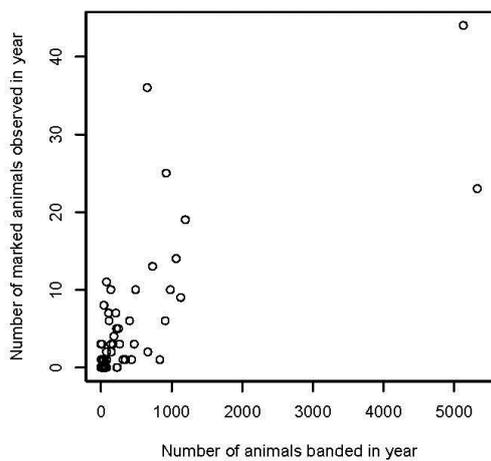
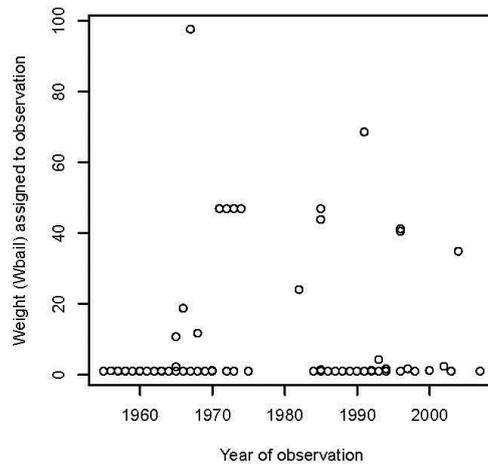
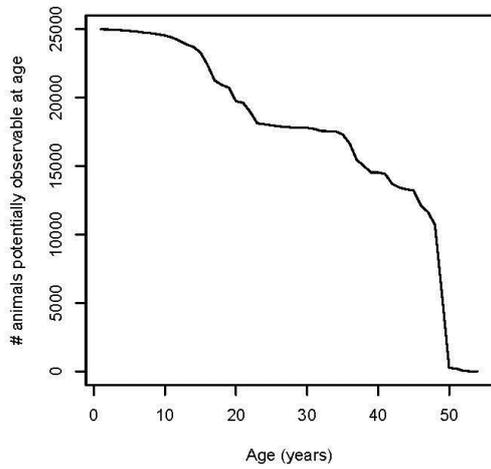
N = 314

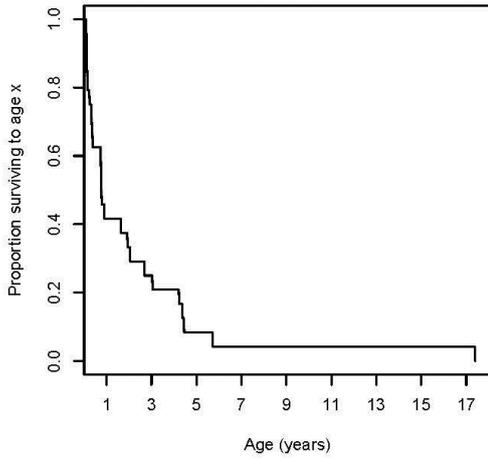
N locations = 38

MRA / MPA = 0.127

Prop. obs. dead = 1

Ann. wear-rate = 0.4 %





**Darter**

*Anhinga novaehollandiae*

Ann. adult surv.  $\sim 0.767$  (SE = NA)

Ann. Y1 surv.  $\sim 0.417$  (SE = NA)

Surv. senesc.  $\sim -0.309$  (SE = 0.136)

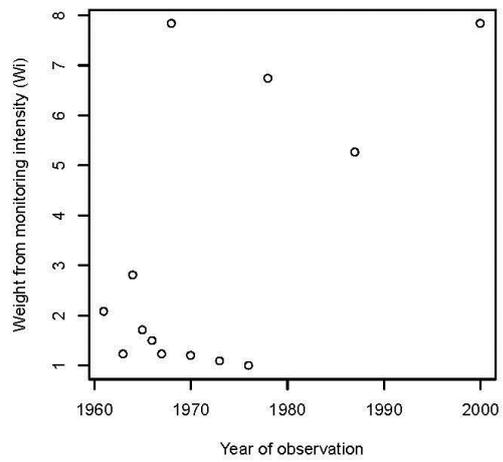
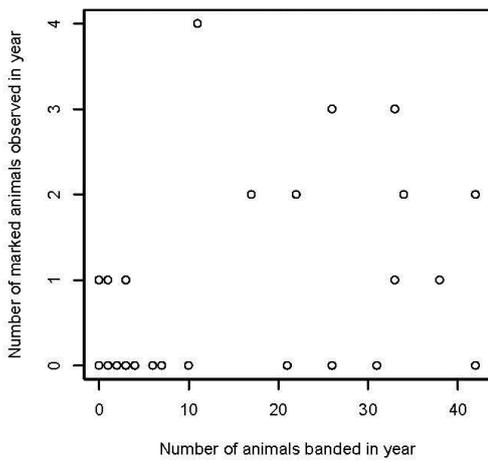
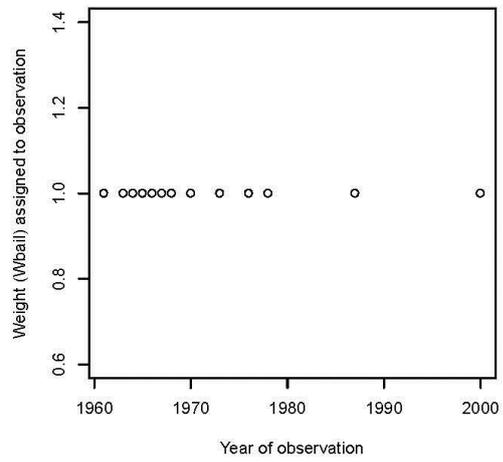
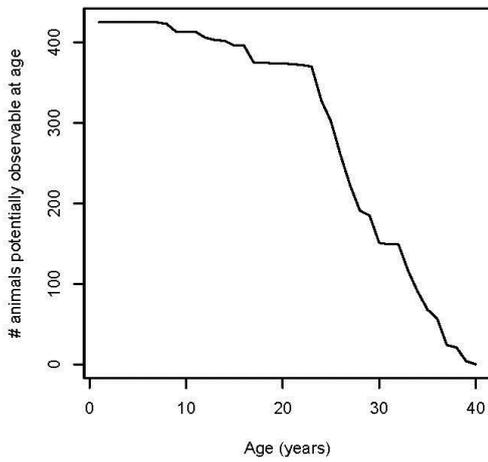
N = 24

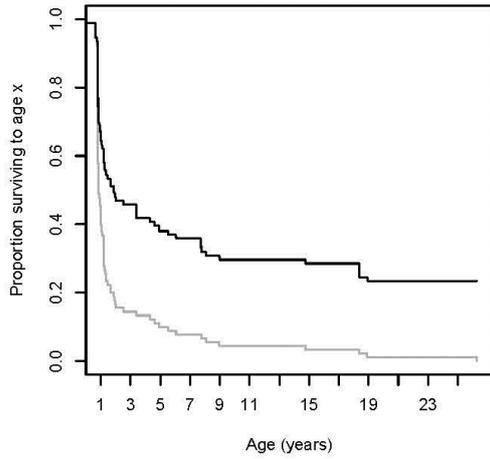
N locations = 11

MRA / MPA = 0.415

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Magpie Goose**

*Anseranas semipalmata*

Ann. adult surv.  $\sim 0.951$  (SE = NA)

Ann. Y1 surv.  $\sim 0.644$  (SE = NA)

Surv. senesc.  $\sim -0.219$  (SE = 0.033)

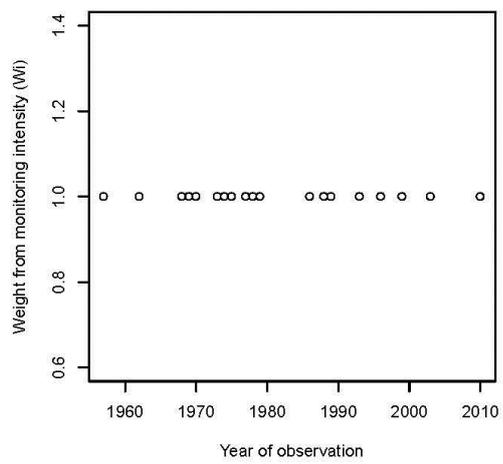
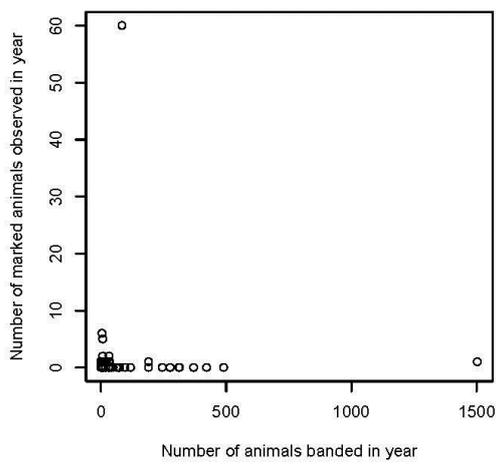
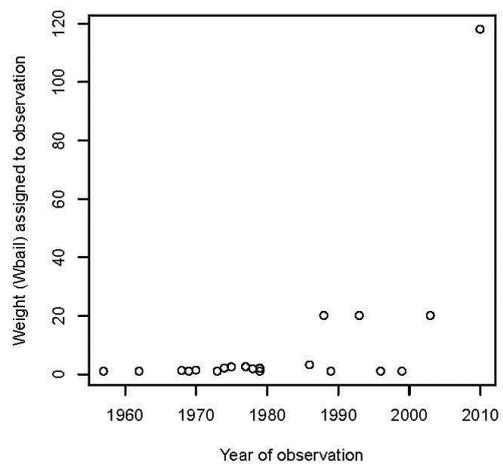
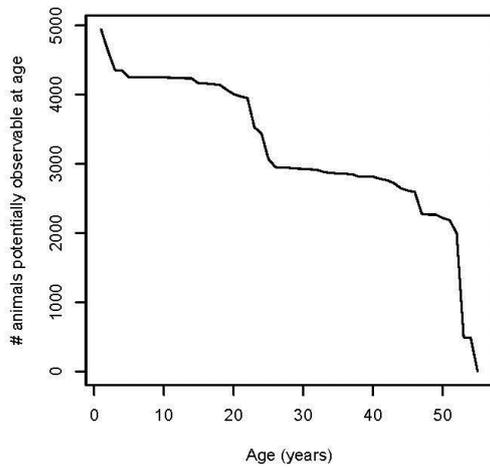
N = 90

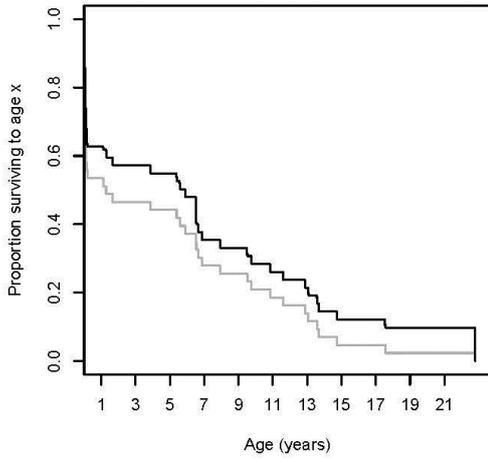
N locations = 8

MRA / MPA = 0.464

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Wedge-tailed Shearwater**

*Ardenna pacifica*

Ann. adult surv.  $\sim 0.901$  (SE = NA)

Ann. Y1 surv.  $\sim 0.676$  (SE = NA)

Surv. senesc.  $\sim -0.053$  (SE = 0.037)

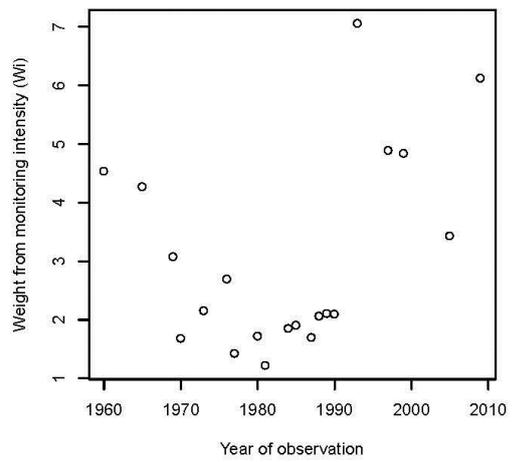
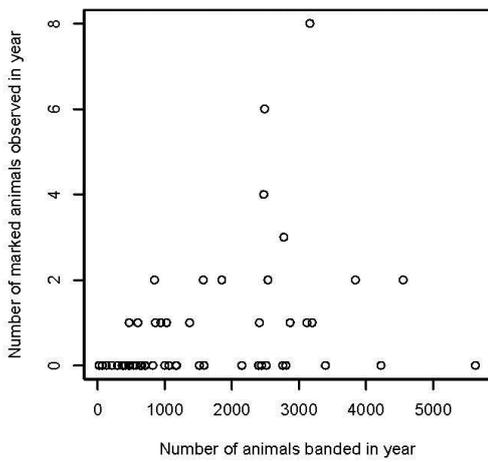
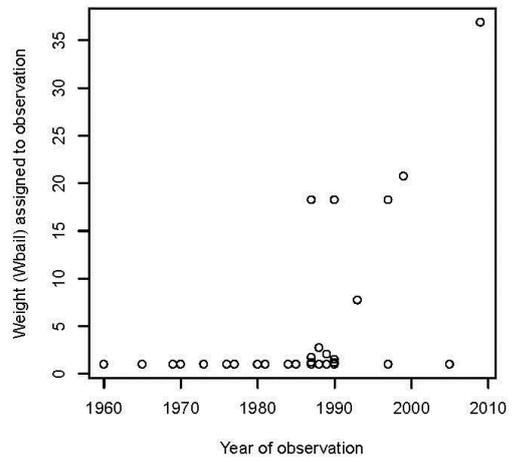
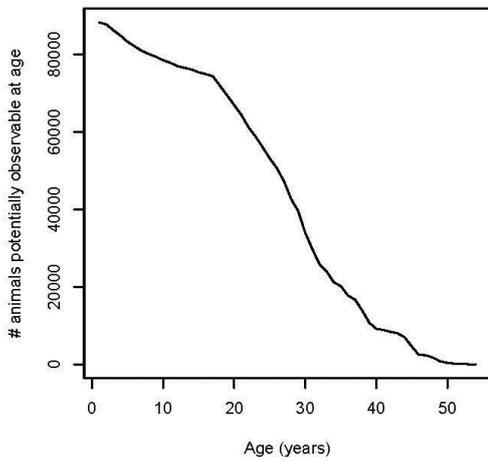
N = 43

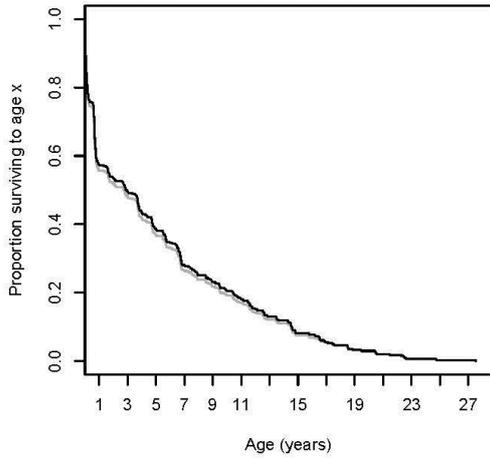
N locations = 18

MRA / MPA = 0.4

Prop. obs. dead = 1

Ann. wear-rate = 0.3 %





**Short-tailed Shearwater**

*Ardenna tenuirostris*

Ann. adult surv.  $\sim 0.88$  (SE = NA)

Ann. Y1 surv.  $\sim 0.62$  (SE = NA)

Surv. senesc.  $\sim -0.024$  (SE = 0.012)

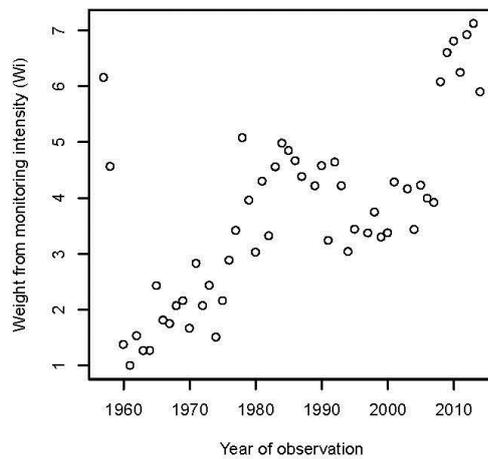
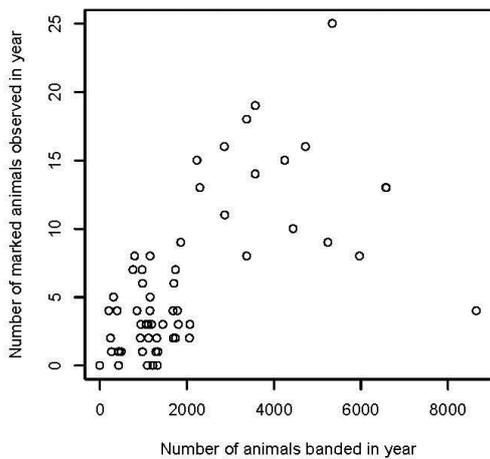
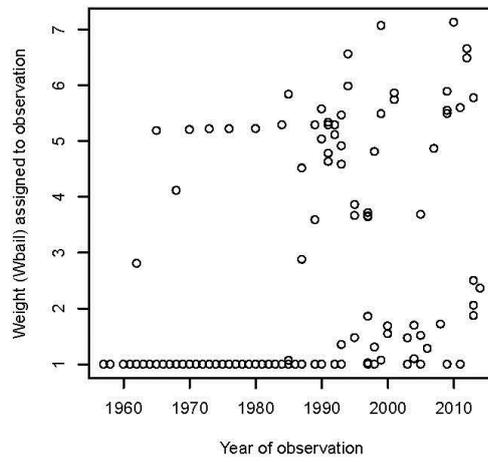
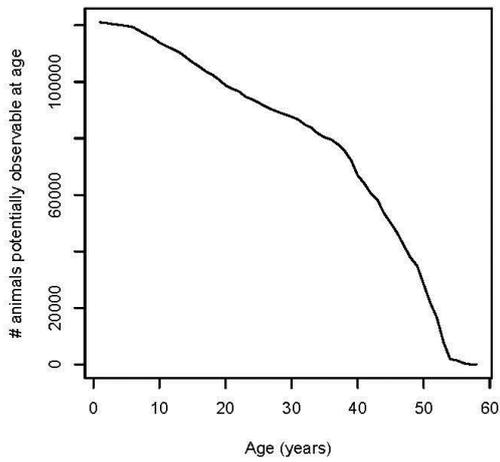
N = 361

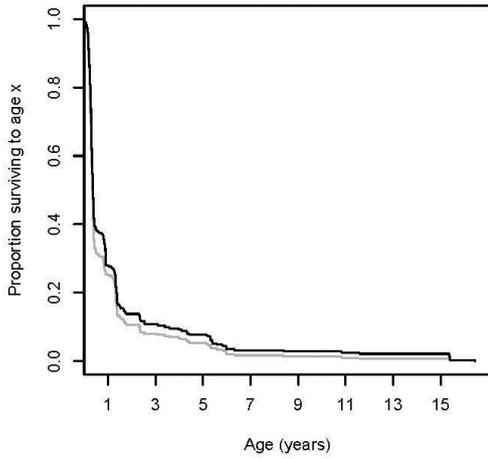
N locations = 26

MRA / MPA = 0.458

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Cape Barren Goose**

*Cereopsis novaehollandiae*

Ann. adult surv.  $\sim 0.709$  (SE = NA)

Ann. Y1 surv.  $\sim 0.282$  (SE = NA)

Surv. senesc.  $\sim -0.297$  (SE = 0.04)

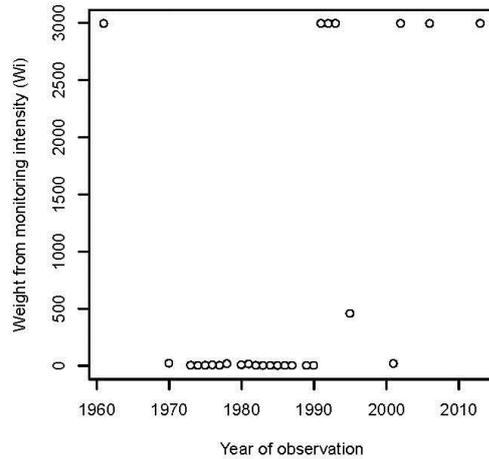
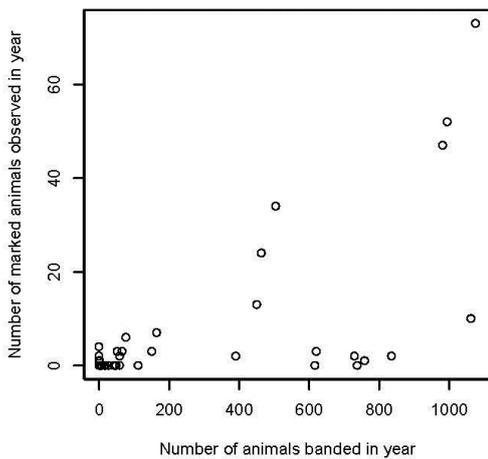
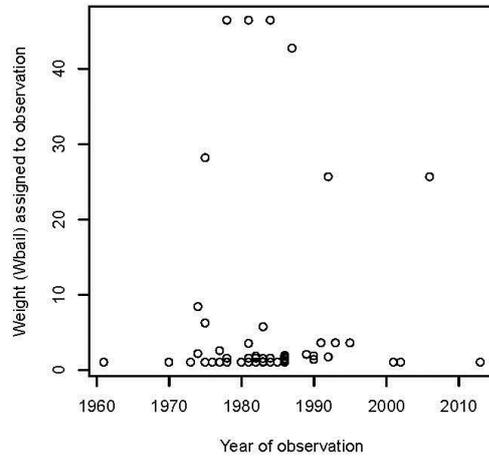
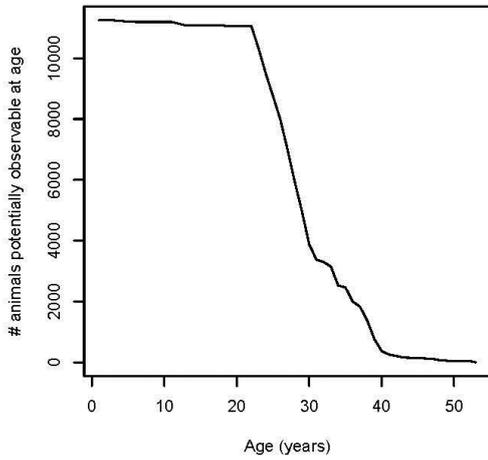
N = 300

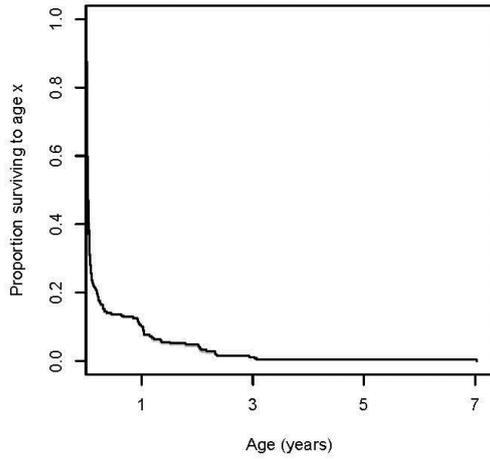
N locations = 30

MRA / MPA = 0.296

Prop. obs. dead = 1

Ann. wear-rate = 0.3 %





**Australian Wood Duck**

*Chenonetta jubata*

Ann. adult surv.  $\sim 0.428$  (SE = NA)

Ann. Y1 surv.  $\sim 0.11$  (SE = NA)

Surv. senesc.  $\sim -0.839$  (SE = 0.208)

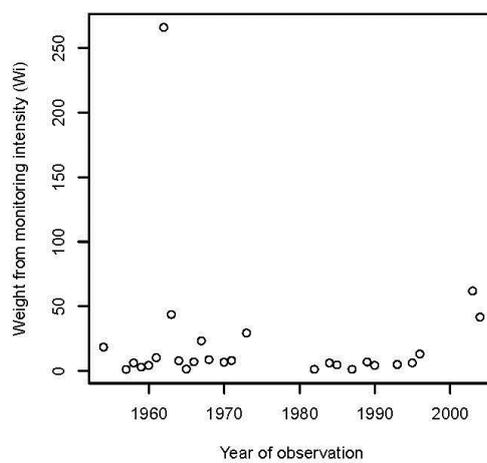
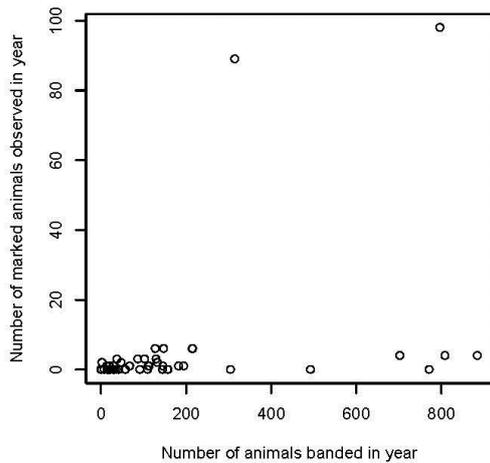
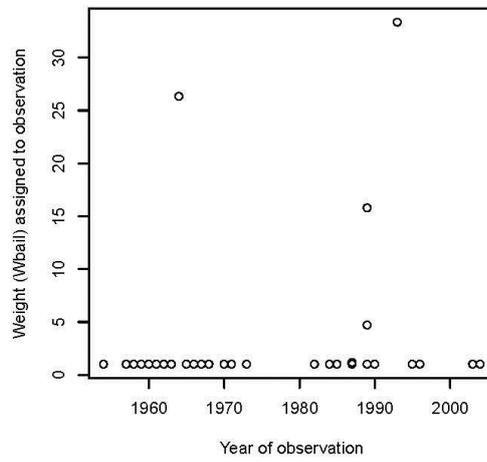
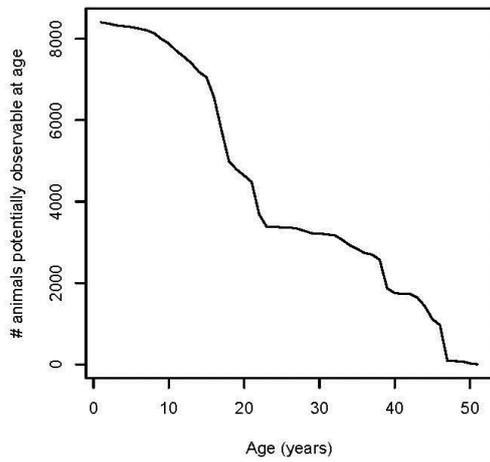
N = 252

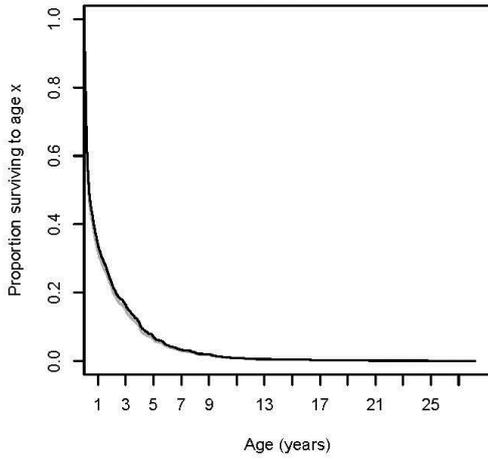
N locations = 24

MRA / MPA = 0.135

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Silver Gull**

*Chroicocephalus novaehollandiae*

Ann. adult surv.  $\sim 0.703$  (SE = NA)

Ann. Y1 surv.  $\sim 0.365$  (SE = NA)

Surv. senesc.  $\sim -0.205$  (SE = 0.013)

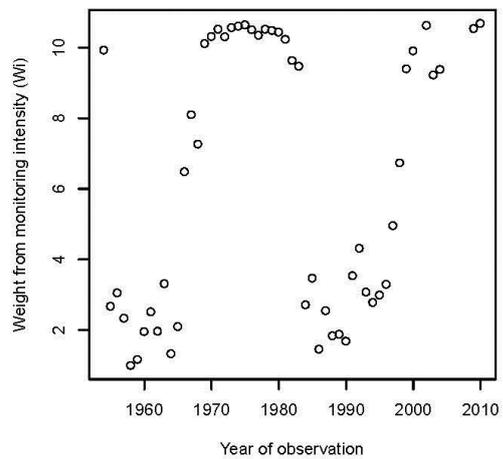
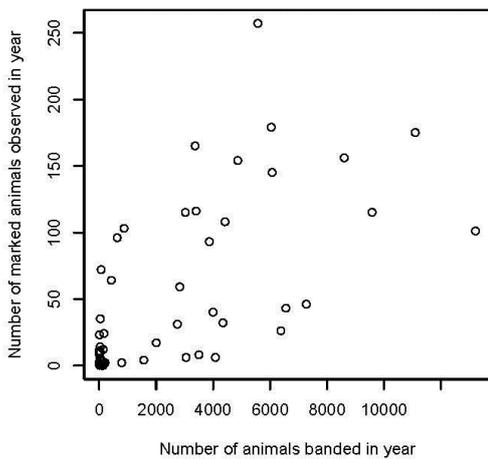
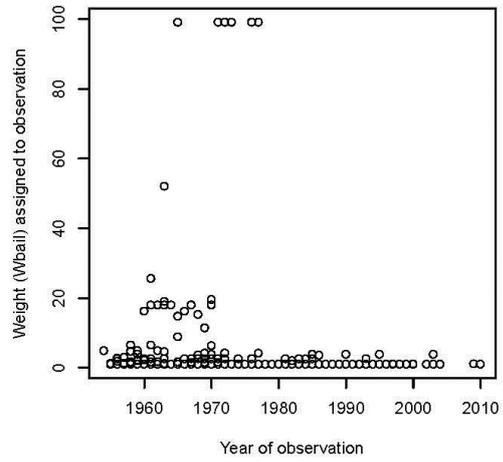
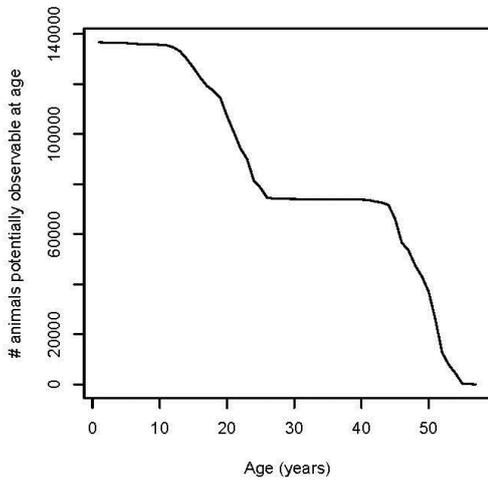
N = 2728

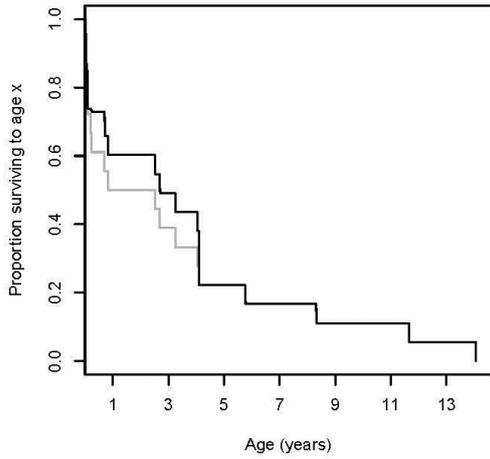
N locations = 151

MRA / MPA = 0.483

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





### White-winged Chough

*Corcorax melanorhamphos*

Ann. adult surv.  $\sim 0.82$  (SE = NA)

Ann. Y1 surv.  $\sim 0.602$  (SE = NA)

Surv. senesc.  $\sim -0.072$  (SE = 0.09)

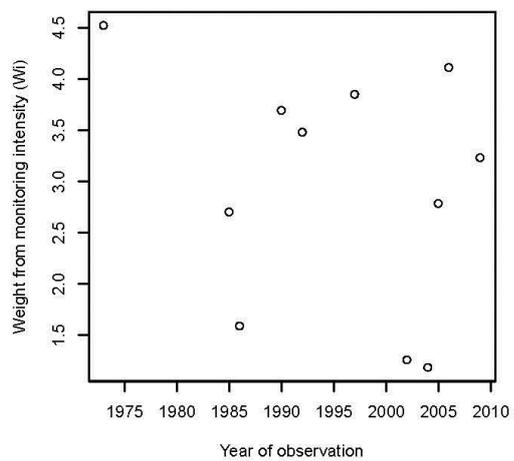
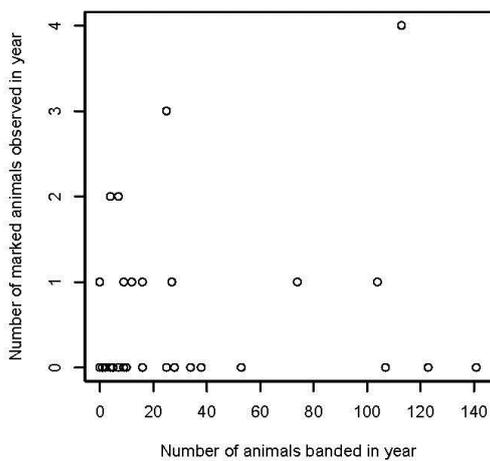
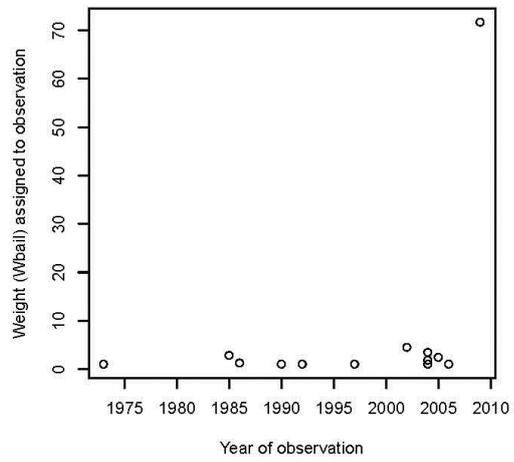
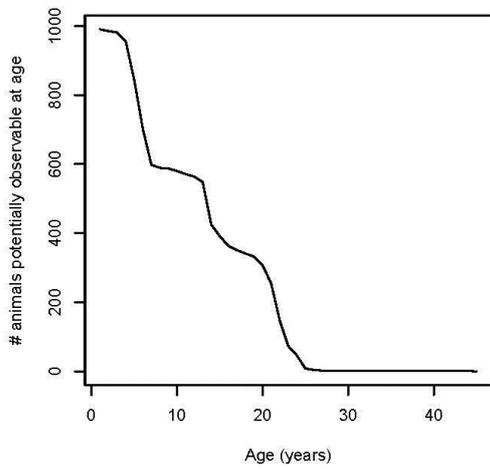
N = 18

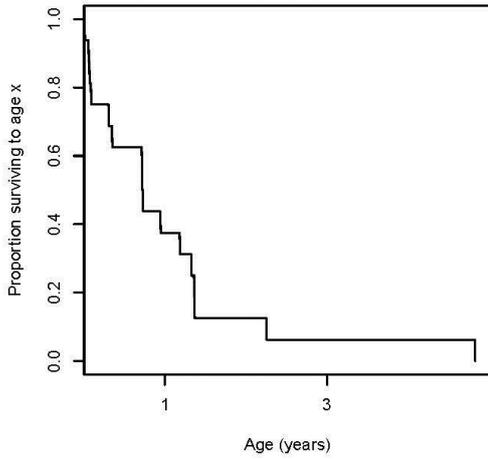
N locations = 9

MRA / MPA = 0.304

Prop. obs. dead = 1

Ann. wear-rate = 1.5 %





**Australian Raven**

*Corvus coronoides*

Ann. adult surv.  $\sim 0.4$  (SE = NA)

Ann. Y1 surv.  $\sim 0.375$  (SE = NA)

Surv. senesc.  $\sim -0.46$  (SE = 0.517)

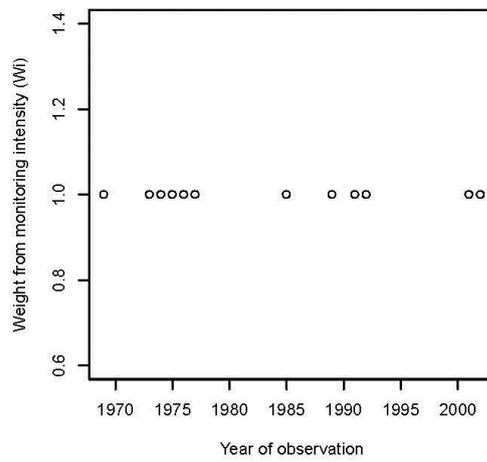
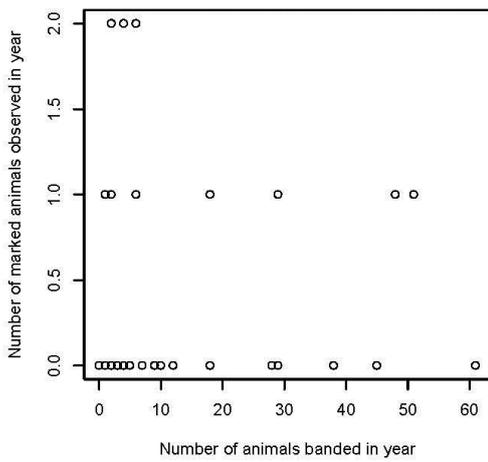
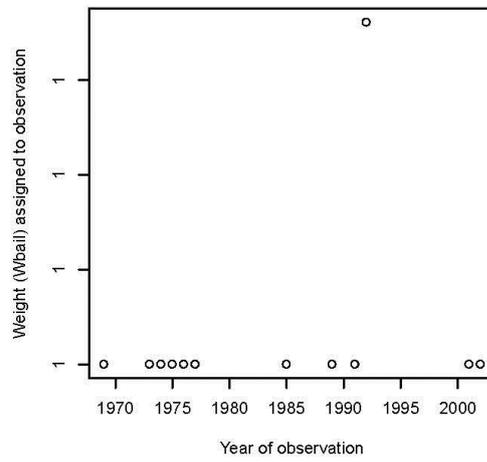
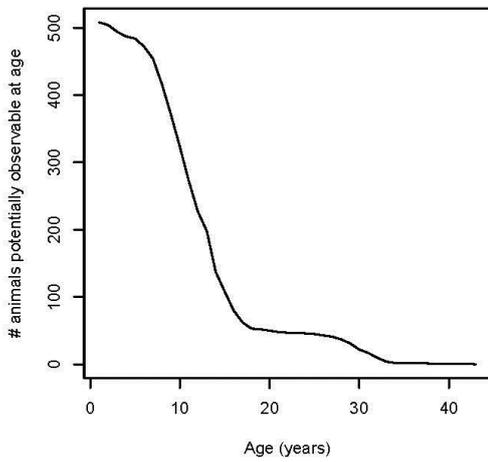
N = 16

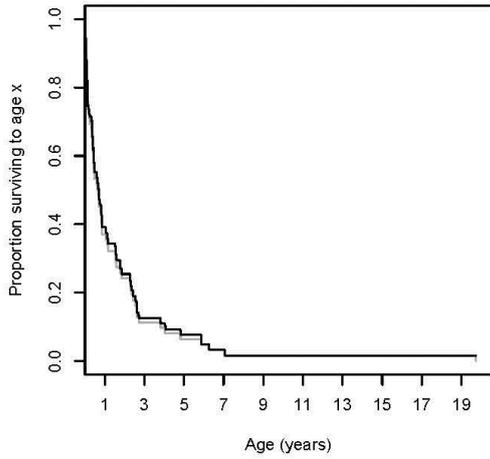
N locations = 12

MRA / MPA = 0.091

Prop. obs. dead = 1

Ann. wear-rate = 1.5 %





**Little Raven**

*Corvus mellori*

Ann. adult surv. ~ 0.695 (SE = NA )

Ann. Y1 surv. ~ 0.405 (SE = NA )

Surv. senesc. ~ -0.28 (SE = 0.092 )

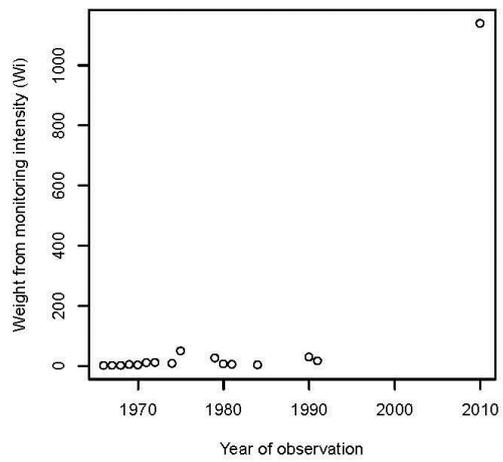
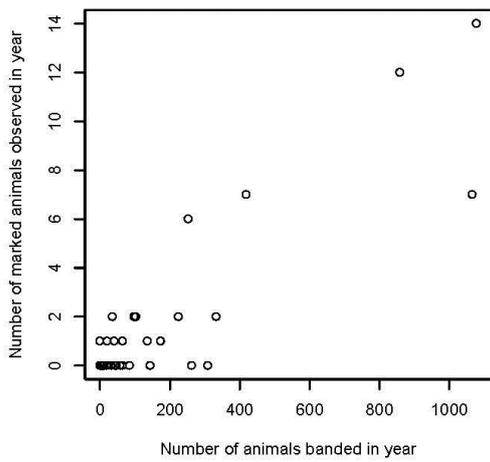
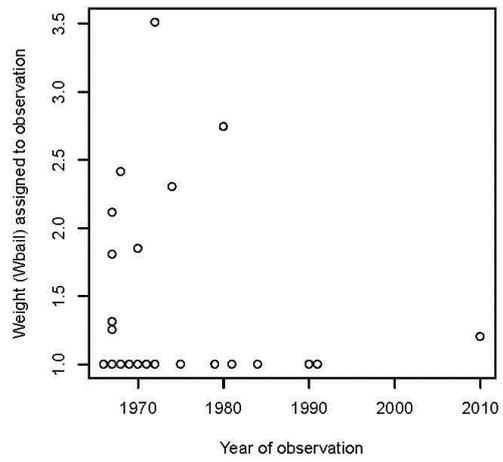
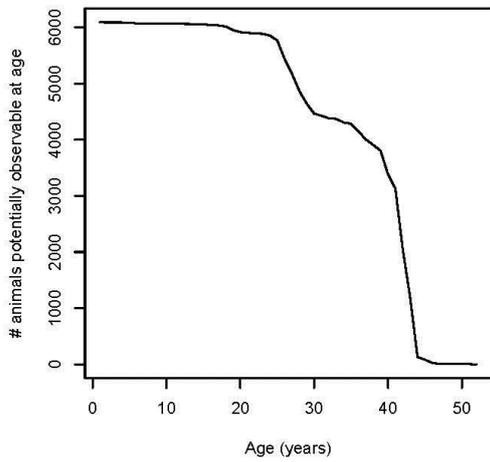
N = 62

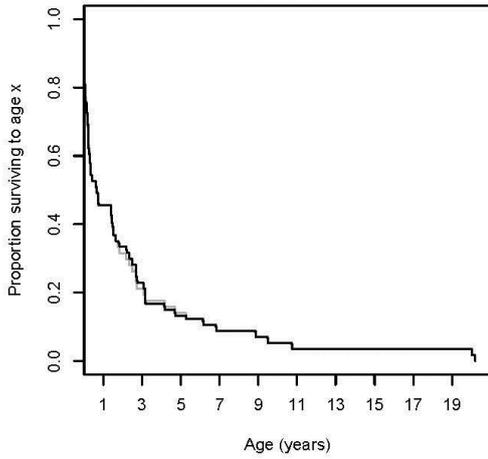
N locations = 21

MRA / MPA = 0.358

Prop. obs. dead = 1

Ann. wear-rate = 1.5 %





**Australian Magpie**

*Cracticus tibicen*

Ann. adult surv.  $\sim 0.782$  (SE = NA)

Ann. Y1 surv.  $\sim 0.52$  (SE = NA)

Surv. senesc.  $\sim -0.216$  (SE = 0.065)

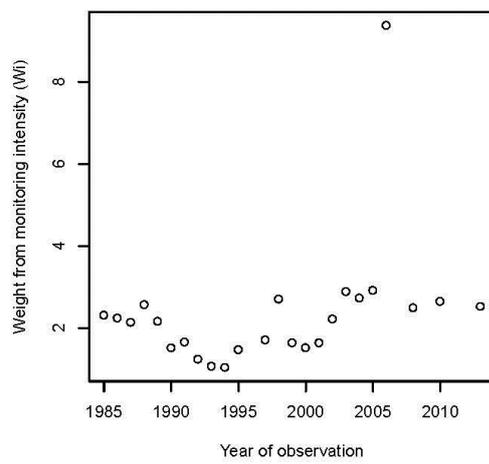
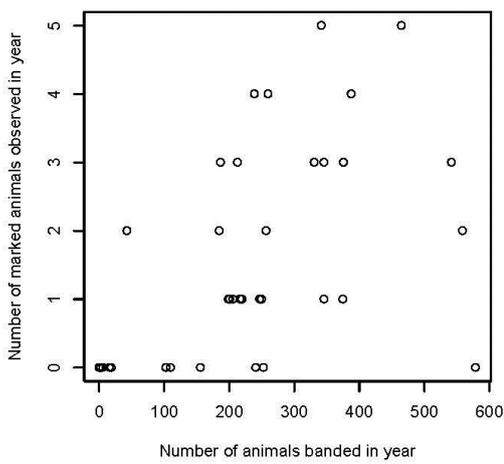
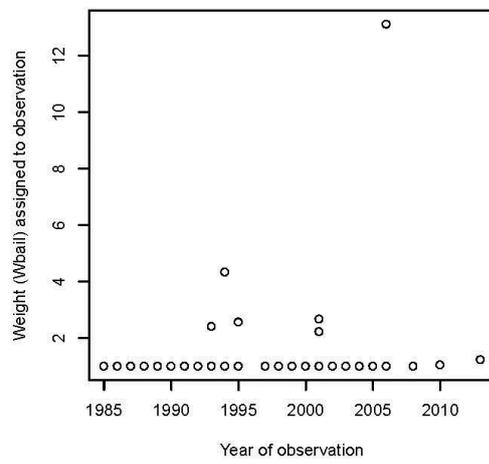
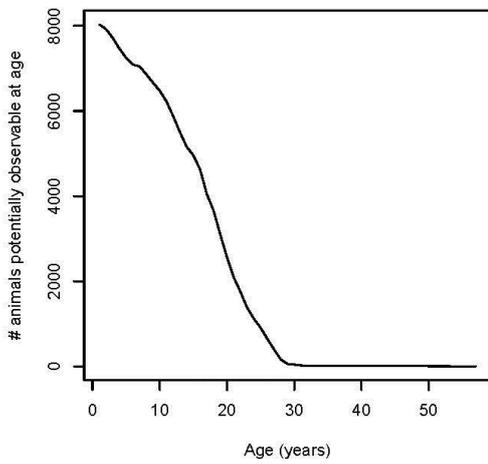
N = 57

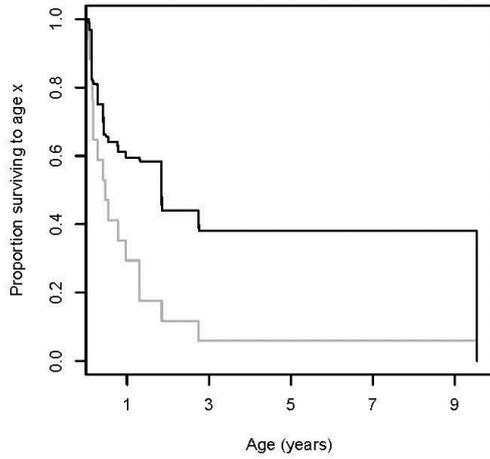
N locations = 30

MRA / MPA = 0.345

Prop. obs. dead = 1

Ann. wear-rate = 1.5 %





### Laughing Kookaburra

*Dacelo novaeguineae*

Ann. adult surv.  $\sim 0.839$  (SE = NA)

Ann. Y1 surv.  $\sim 0.595$  (SE = NA)

Surv. senesc.  $\sim -1.004$  (SE = 0.392)

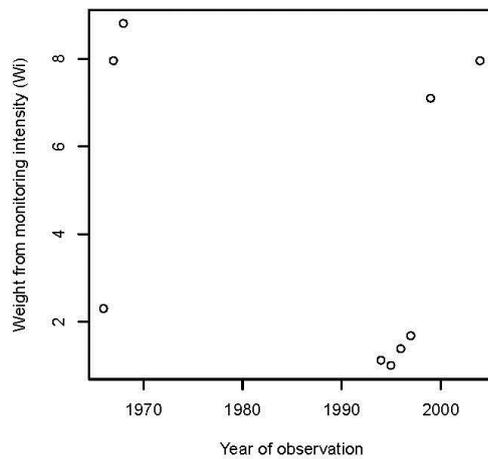
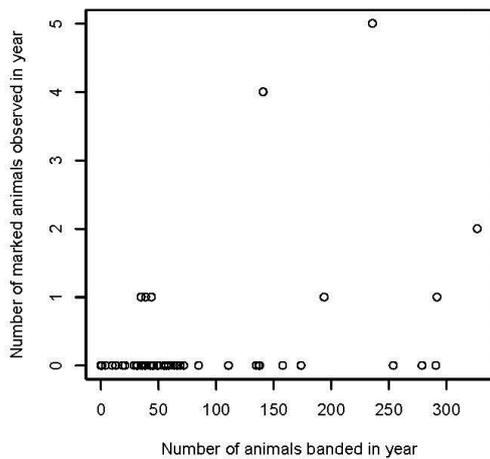
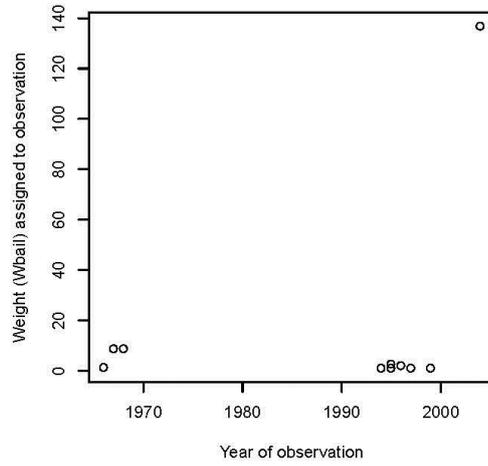
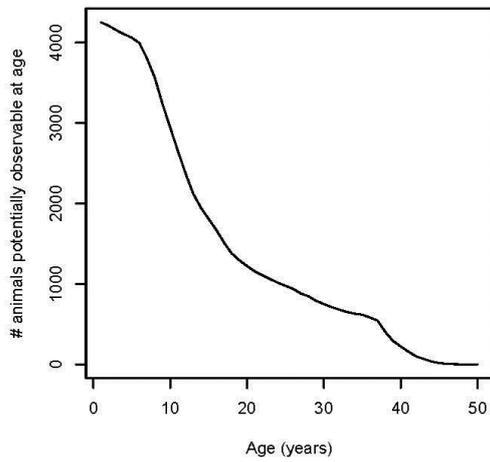
N = 17

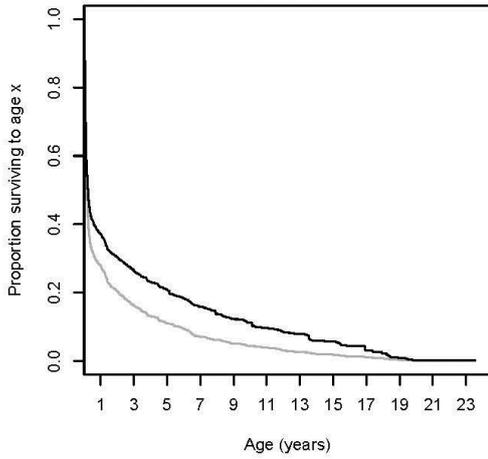
N locations = 5

MRA / MPA = 0.176

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Little Penguin**

*Eudyptula minor*

Ann. adult surv.  $\sim 0.861$  (SE = NA)

Ann. Y1 surv.  $\sim 0.39$  (SE = NA)

Surv. senesc.  $\sim -0.143$  (SE = 0.007)

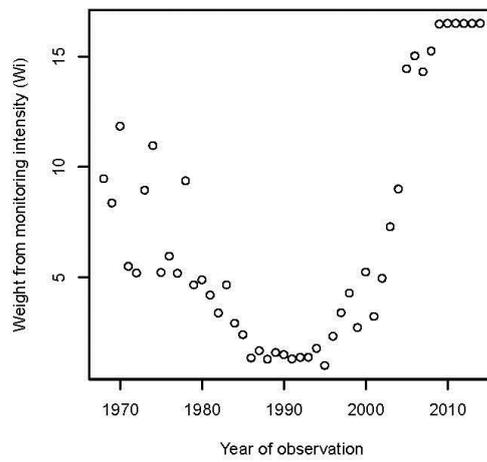
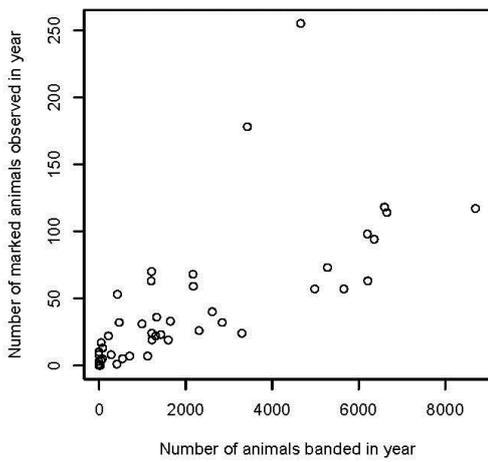
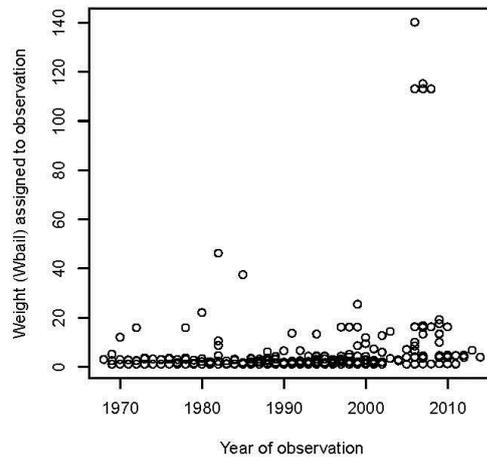
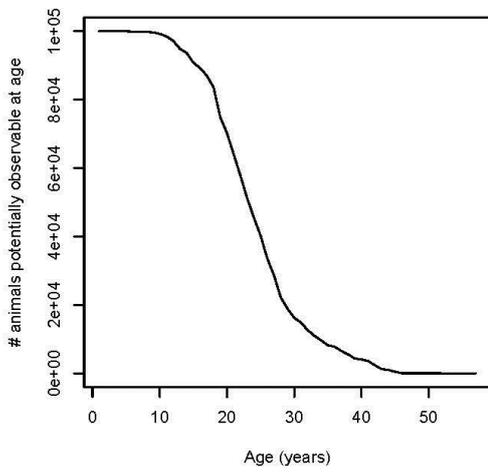
N = 2068

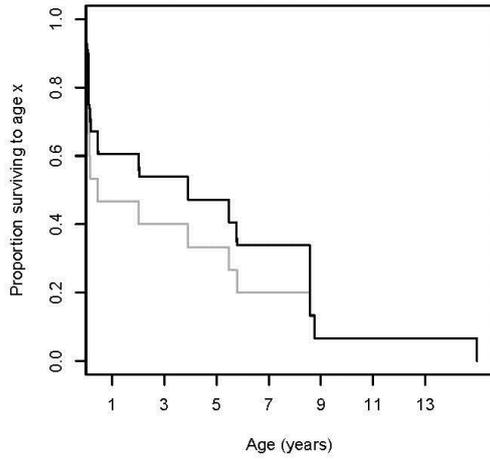
N locations = 66

MRA / MPA = 0.397

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Brown Falcon**

*Falco berigora*

Ann. adult surv.  $\sim 0.853$  (SE = NA)

Ann. Y1 surv.  $\sim 0.612$  (SE = NA)

Surv. senesc.  $\sim -0.037$  (SE = 0.096)

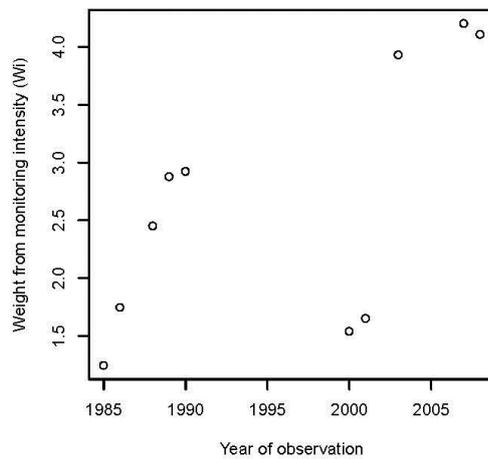
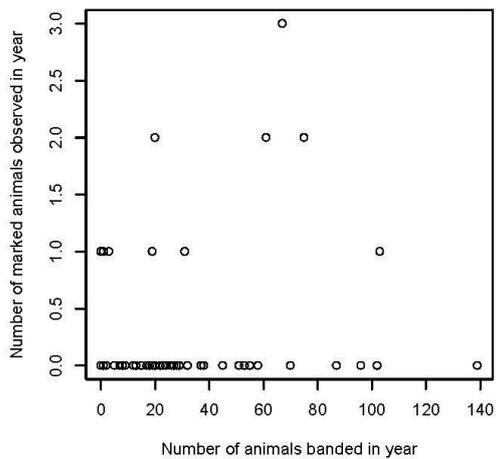
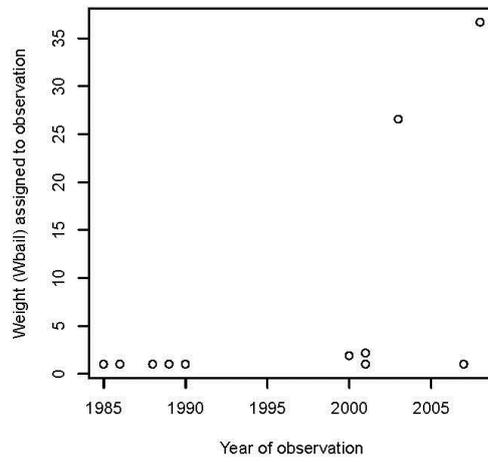
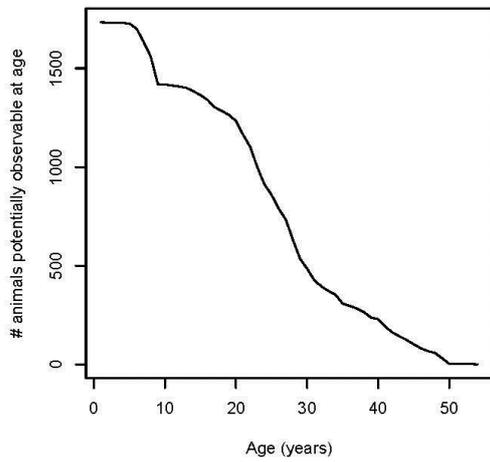
N = 15

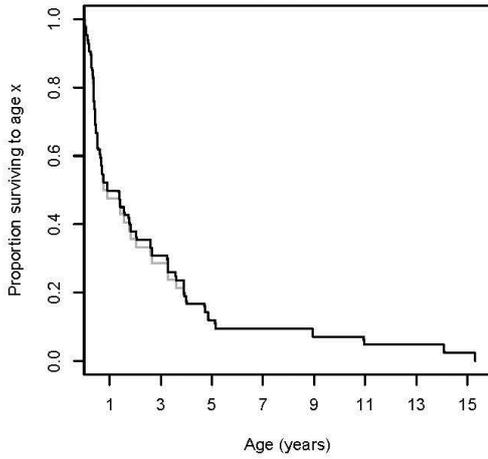
N locations = 8

MRA / MPA = 0.255

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Peregrine Falcon**

*Falco peregrinus*

Ann. adult surv.  $\sim 0.776$  (SE = NA)

Ann. Y1 surv.  $\sim 0.498$  (SE = NA)

Surv. senesc.  $\sim -0.169$  (SE = 0.071)

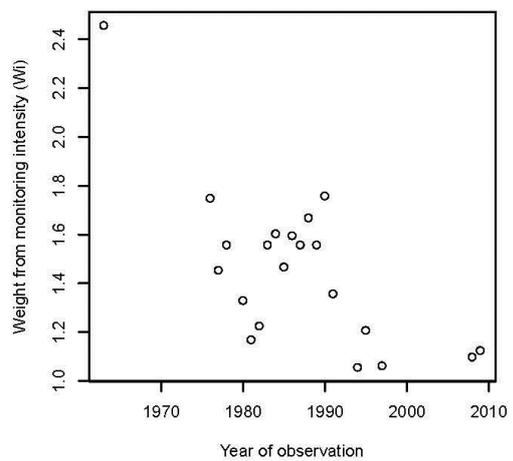
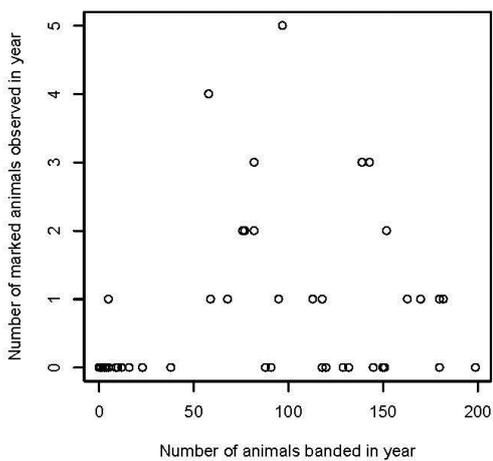
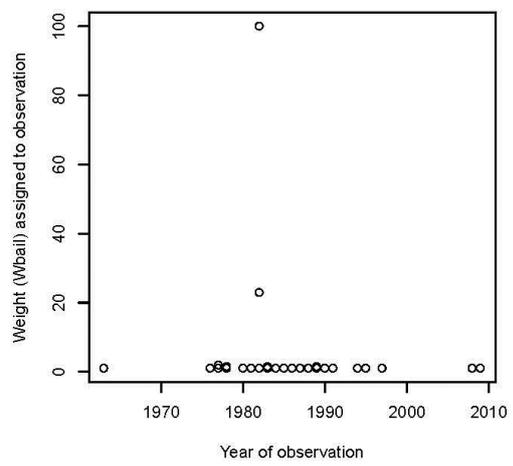
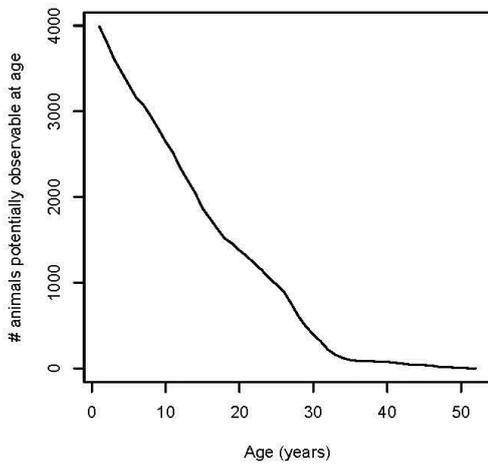
N = 42

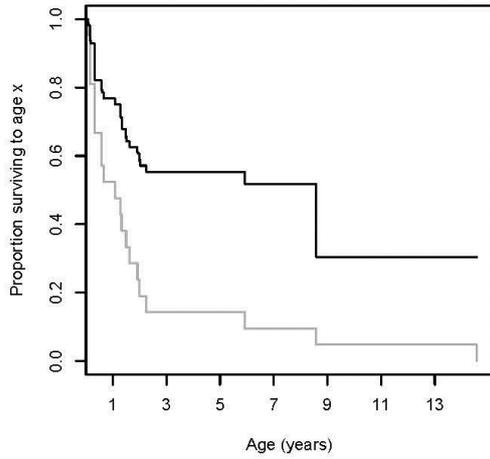
N locations = 36

MRA / MPA = 0.283

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Lord Howe Woodhen**

*Gallirallus sylvestris*

Ann. adult surv.  $\sim 0.933$  (SE = NA)

Ann. Y1 surv.  $\sim 0.768$  (SE = NA)

Surv. senesc.  $\sim -0.133$  (SE = 0.084)

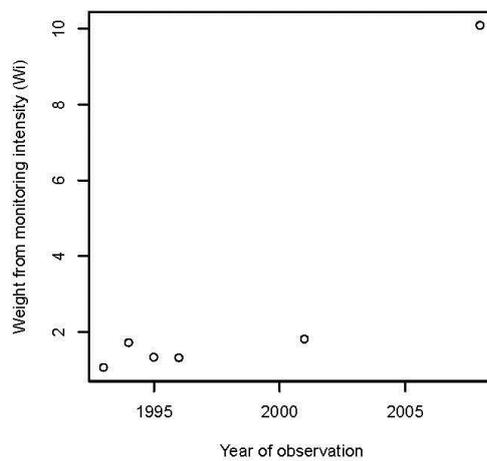
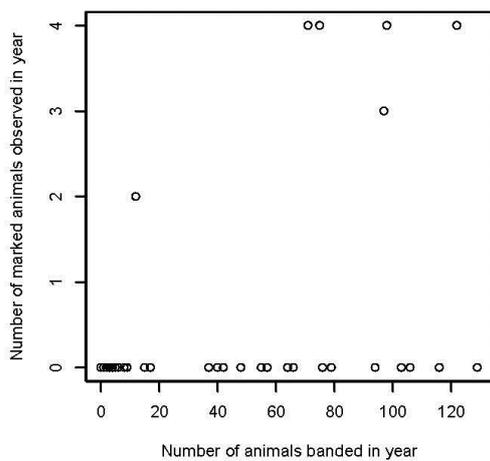
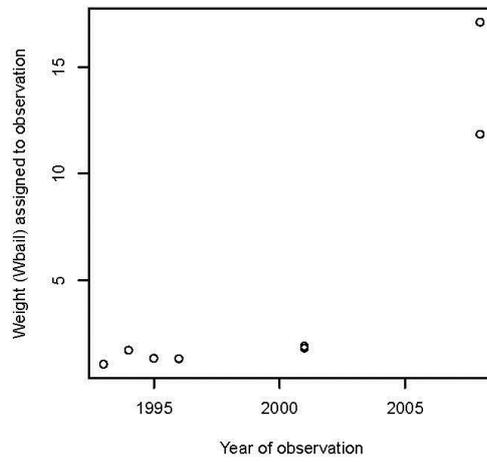
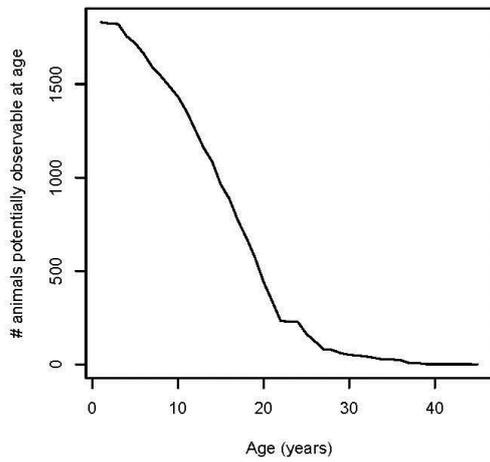
N = 21

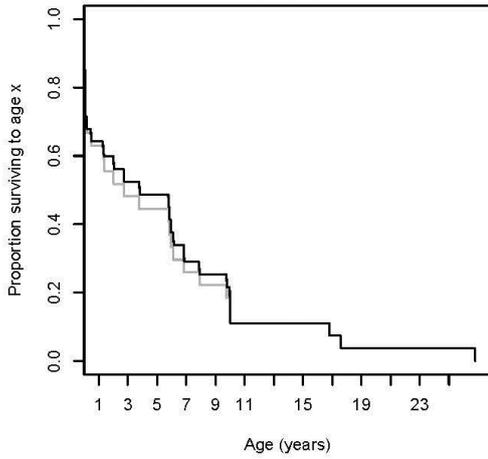
N locations = 1

MRA / MPA = 0.304

Prop. obs. dead = 1

Ann. wear-rate = 0.7 %





**Pied Oystercatcher**

*Haematopus longirostris*

Ann. adult surv.  $\sim 0.874$  (SE = NA)

Ann. Y1 surv.  $\sim 0.693$  (SE = NA)

Surv. senesc.  $\sim -0.046$  (SE = 0.045)

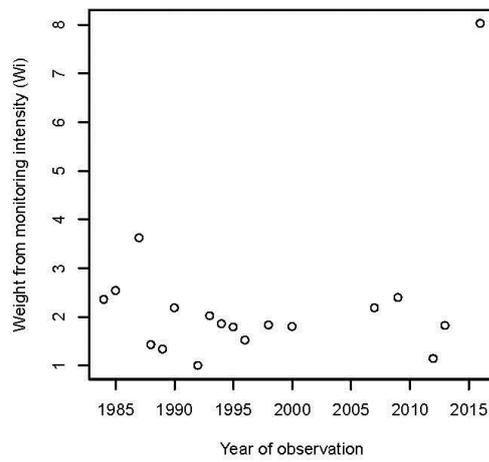
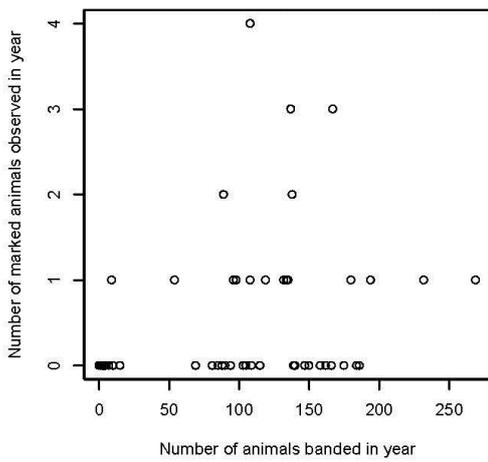
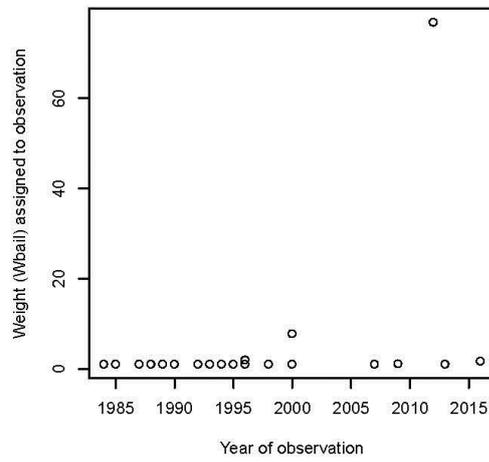
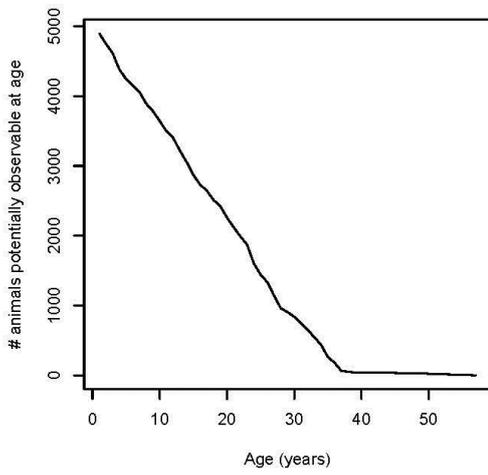
N = 27

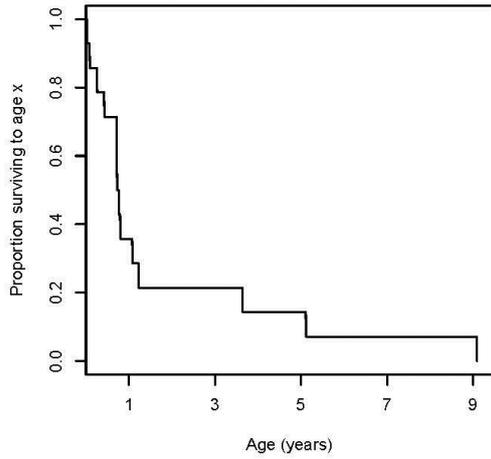
N locations = 19

MRA / MPA = 0.448

Prop. obs. dead = 1

Ann. wear-rate = 0.6 %





**Whistling Kite**

*Haliastur sphenurus*

Ann. adult surv.  $\sim 0.737$  (SE = NA)

Ann. Y1 surv.  $\sim 0.357$  (SE = NA)

Surv. senesc.  $\sim -0.489$  (SE = 0.248)

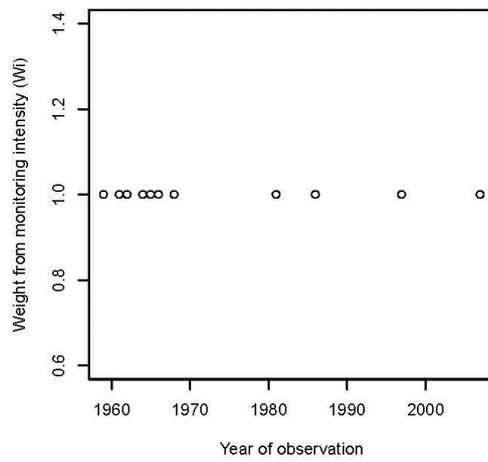
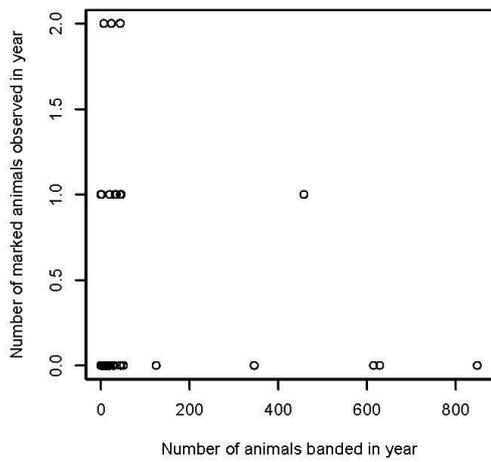
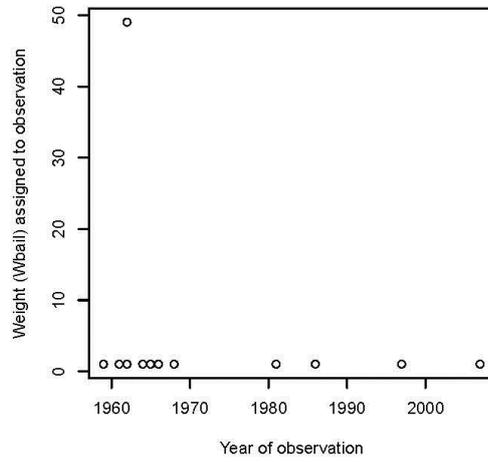
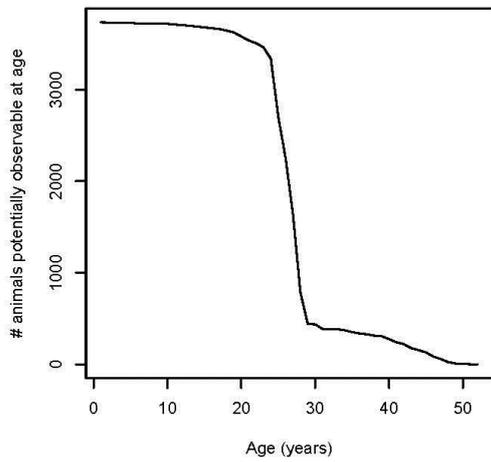
N = 14

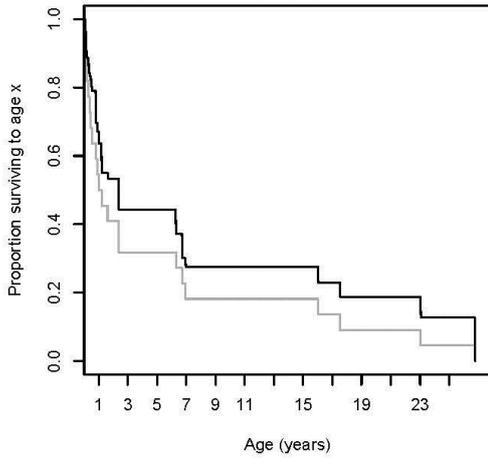
N locations = 14

MRA / MPA = 0.17

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





### Caspian Tern

*Hydroprogne caspia*

Ann. adult surv.  $\sim 0.914$  (SE = NA)

Ann. Y1 surv.  $\sim 0.671$  (SE = NA)

Surv. senesc.  $\sim -0.109$  (SE = 0.046)

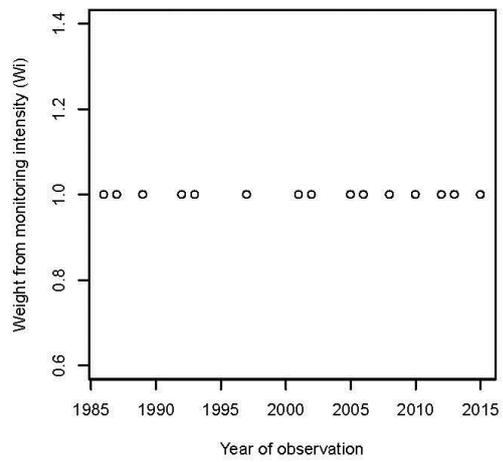
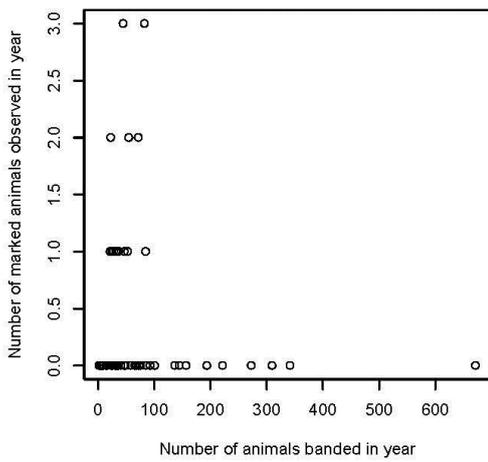
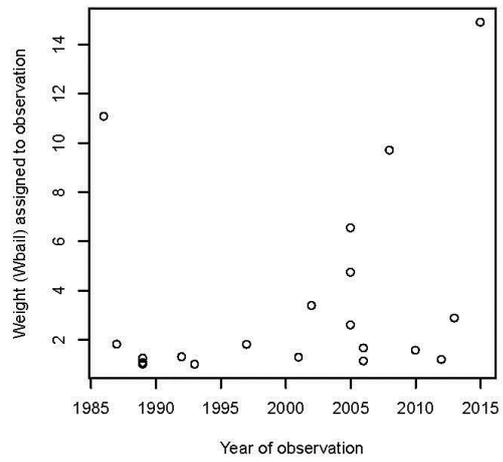
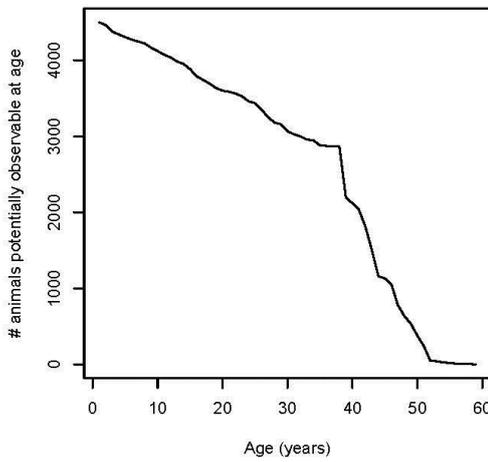
N = 22

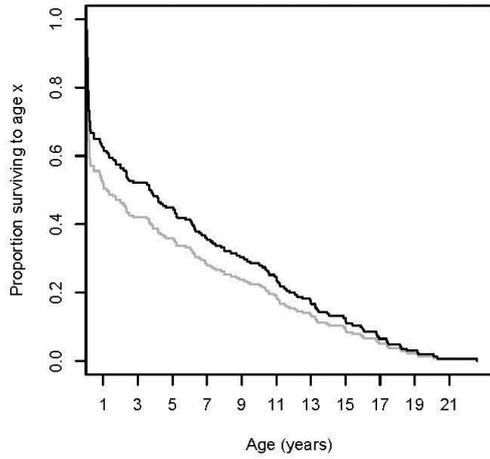
N locations = 4

MRA / MPA = 0.433

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Kelp Gull**

*Larus dominicanus*

Ann. adult surv.  $\sim 0.894$  (SE = NA)

Ann. Y1 surv.  $\sim 0.633$  (SE = NA)

Surv. senesc.  $\sim -0.013$  (SE = 0.016)

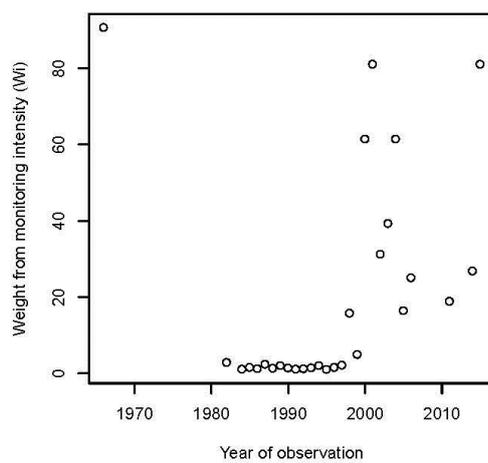
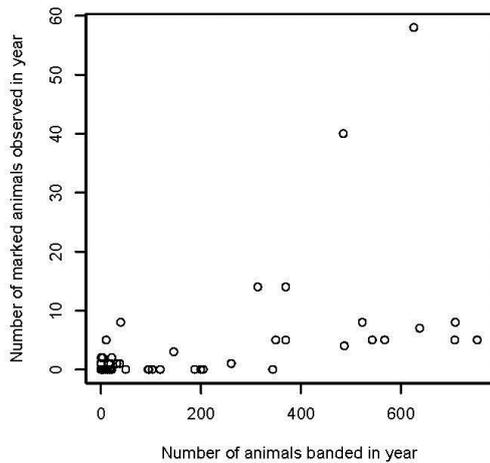
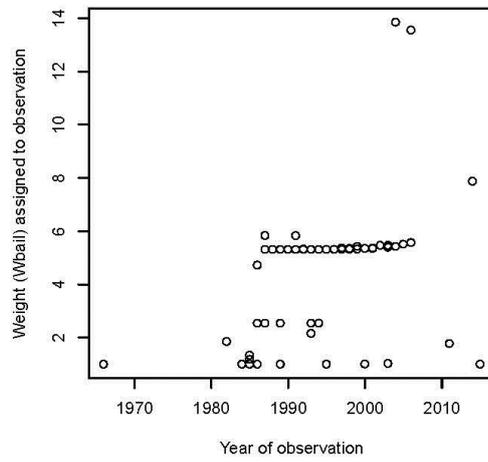
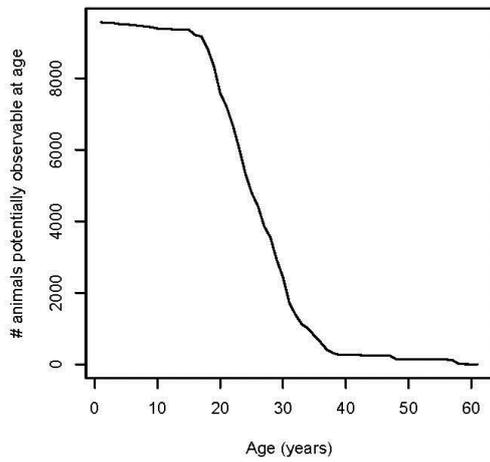
N = 214

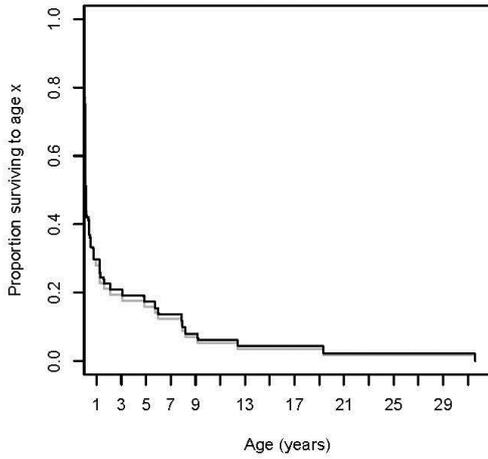
N locations = 8

MRA / MPA = 0.355

Prop. obs. dead = 1

Ann. wear-rate = 1.5 %





**Pacific Gull**

*Larus pacificus*

Ann. adult surv.  $\sim 0.88$  (SE = NA)

Ann. Y1 surv.  $\sim 0.345$  (SE = NA)

Surv. senesc.  $\sim -0.205$  (SE = 0.052)

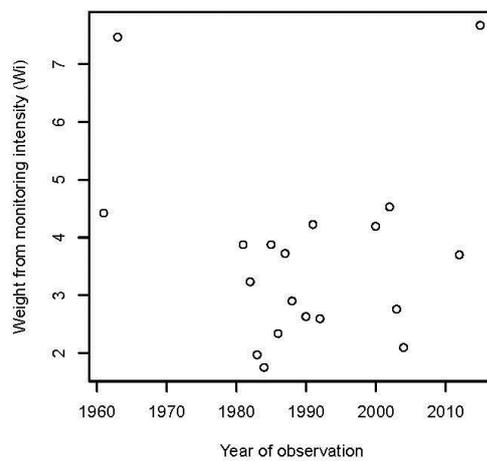
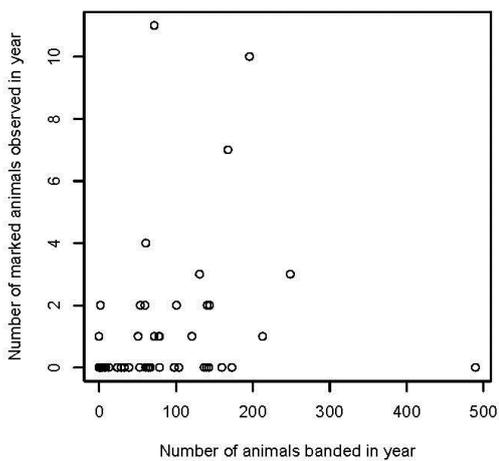
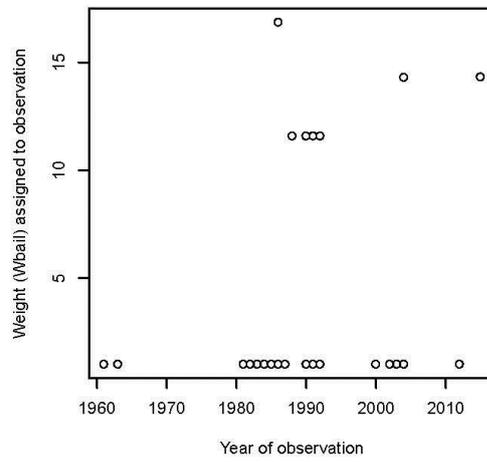
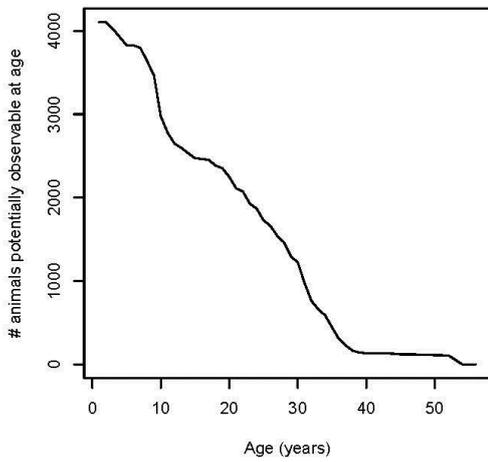
N = 57

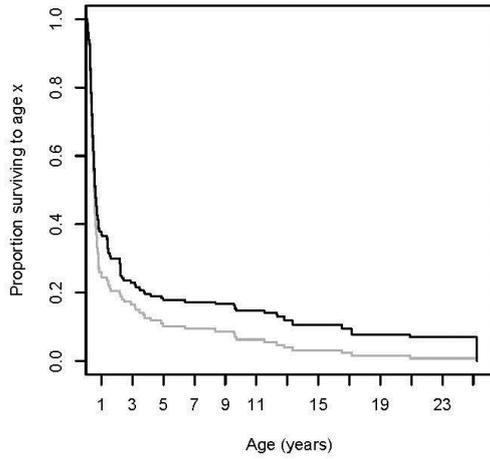
N locations = 10

MRA / MPA = 0.544

Prop. obs. dead = 1

Ann. wear-rate = 0.6 %





**Southern Giant-Petrel**

*Macronectes giganteus*

Ann. adult surv.  $\sim 0.894$  (SE = NA)

Ann. Y1 surv.  $\sim 0.379$  (SE = NA)

Surv. senesc.  $\sim -0.259$  (SE = 0.034)

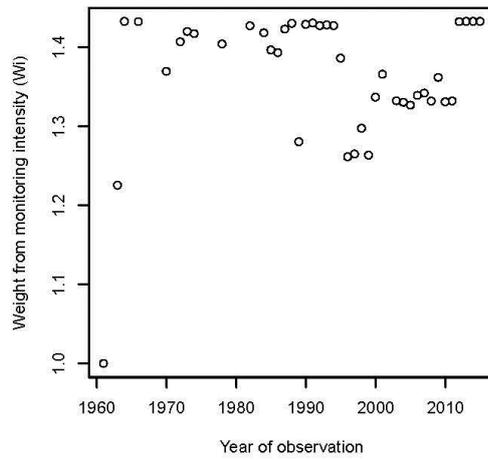
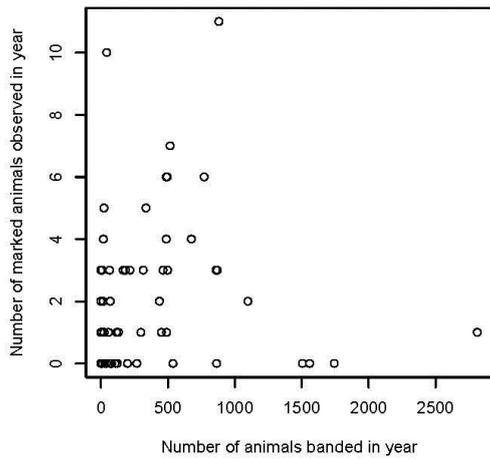
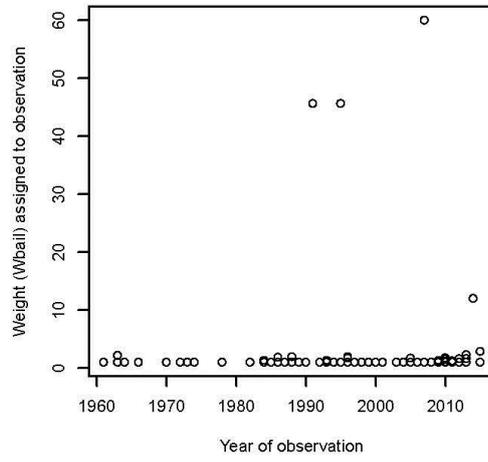
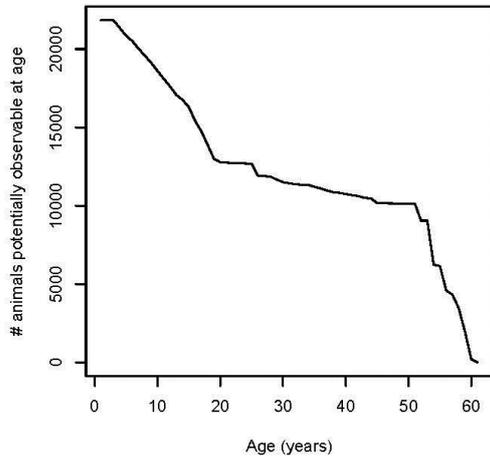
N = 127

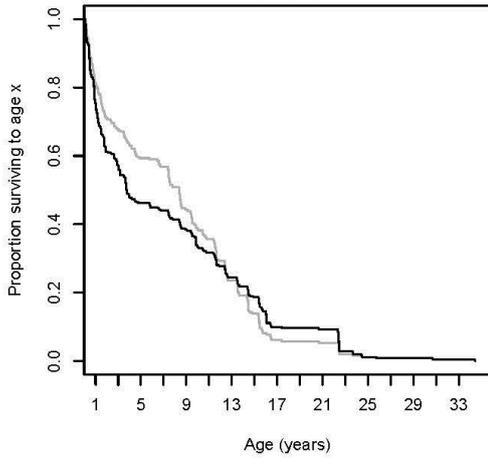
N locations = 36

MRA / MPA = 0.403

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Northern Giant-Petrel**

*Macronectes halli*

Ann. adult surv.  $\sim 0.894$  (SE = NA)

Ann. Y1 surv.  $\sim 0.755$  (SE = NA)

Surv. senesc.  $\sim -0.003$  (SE = 0.011)

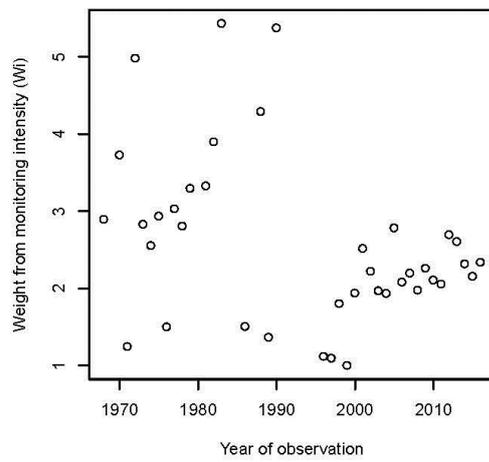
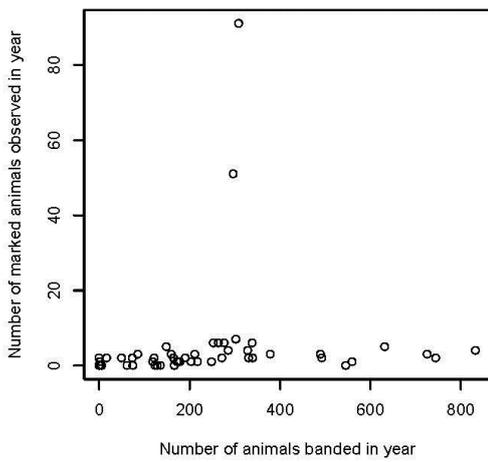
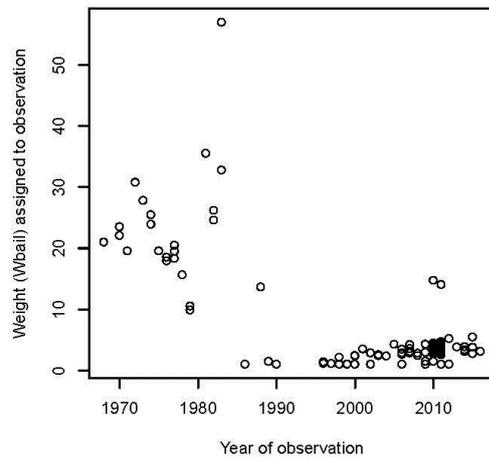
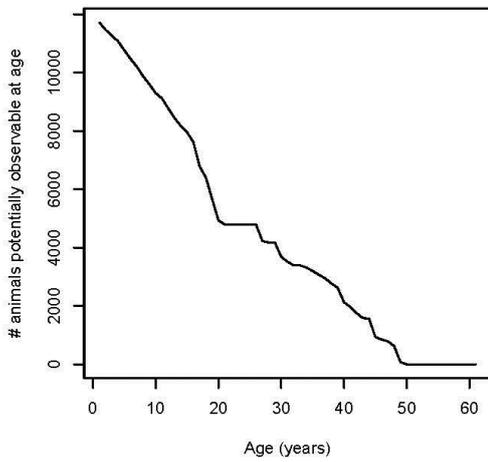
N = 246

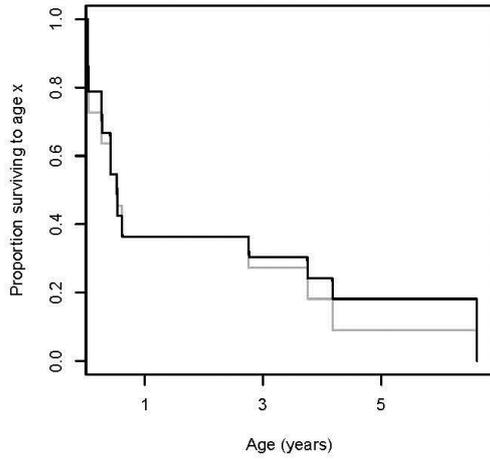
N locations = 10

MRA / MPA = 0.548

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Superb Lyrebird**

*Menura novaehollandiae*

Ann. adult surv.  $\sim 0.778$  (SE = NA)

Ann. Y1 surv.  $\sim 0.364$  (SE = NA)

Surv. senesc.  $\sim -0.452$  (SE = 0.289)

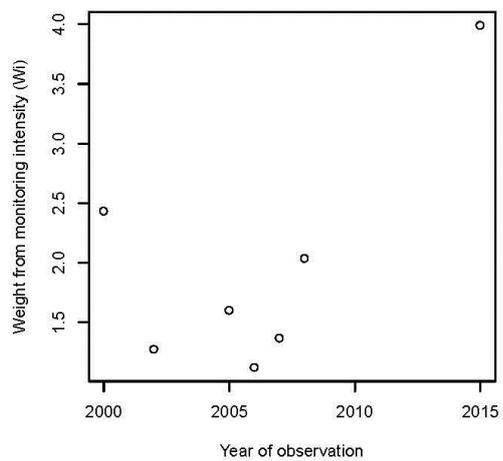
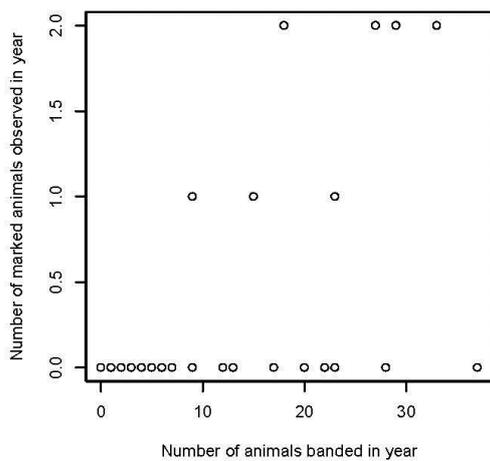
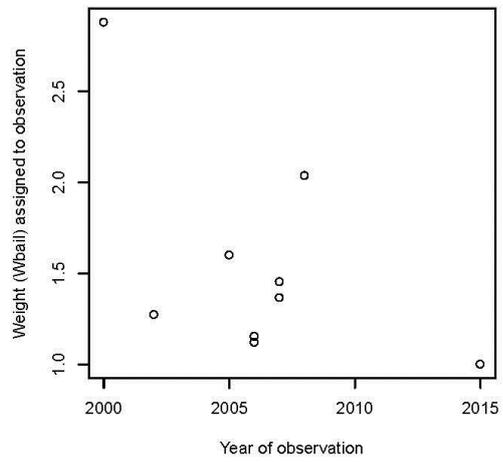
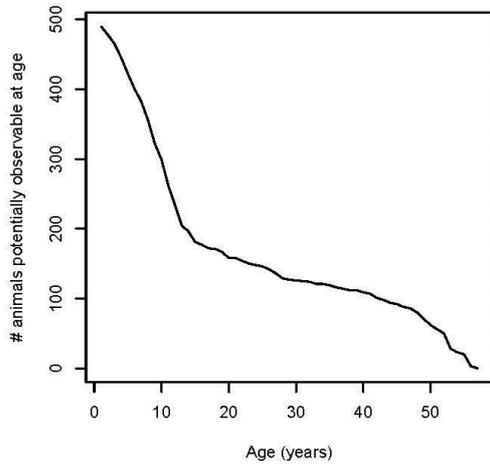
N = 11

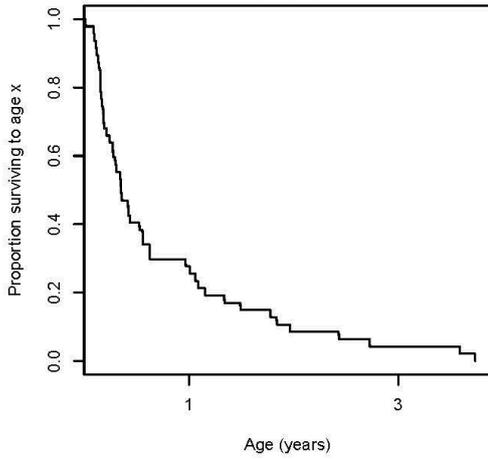
N locations = 2

MRA / MPA = 0.103

Prop. obs. dead = 1

Ann. wear-rate = 1.5 %





**Little Pied Cormorant**

*Microcarbo melanoleucos*

Ann. adult surv.  $\sim 0.316$  (SE = NA)

Ann. Y1 surv.  $\sim 0.277$  (SE = NA)

Surv. senesc.  $\sim -0.362$  (SE = 0.445)

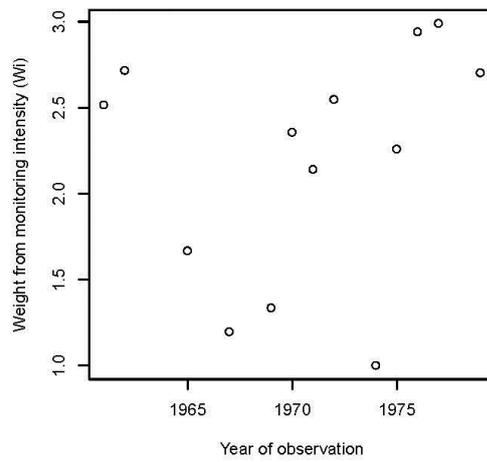
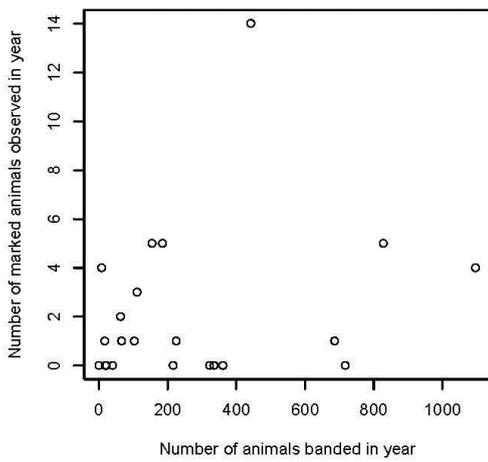
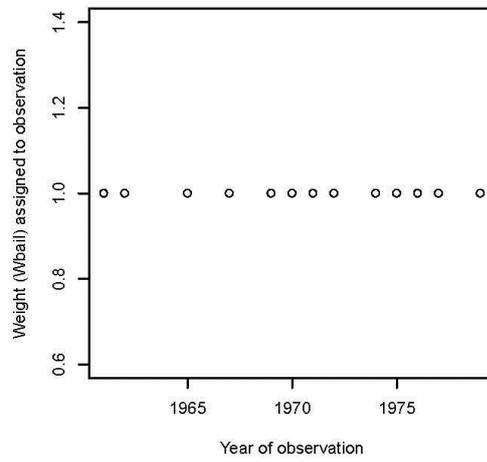
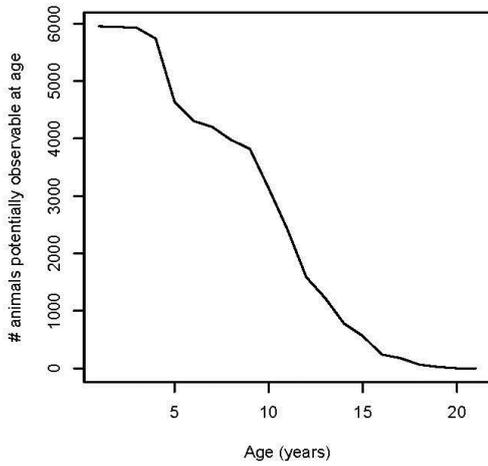
N = 47

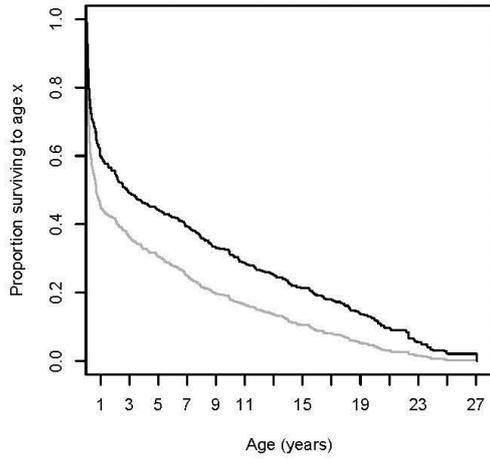
N locations = 16

MRA / MPA = 0.136

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Australasian Gannet**

*Morus serrator*

Ann. adult surv.  $\sim 0.913$  (SE = NA)

Ann. Y1 surv.  $\sim 0.614$  (SE = NA)

Surv. senesc.  $\sim -0.035$  (SE = 0.007)

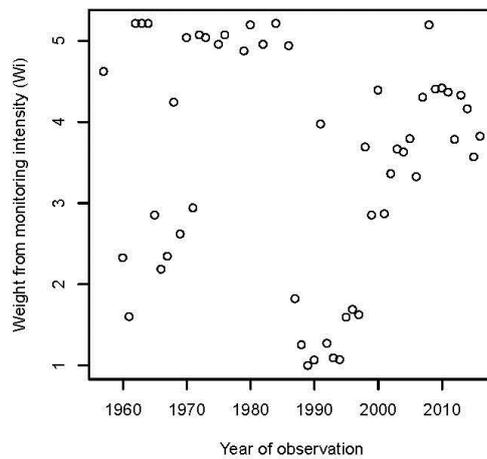
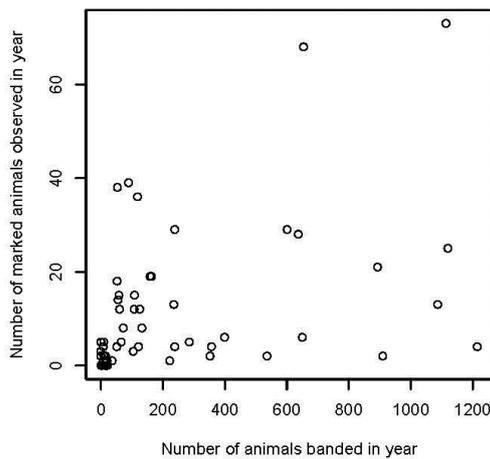
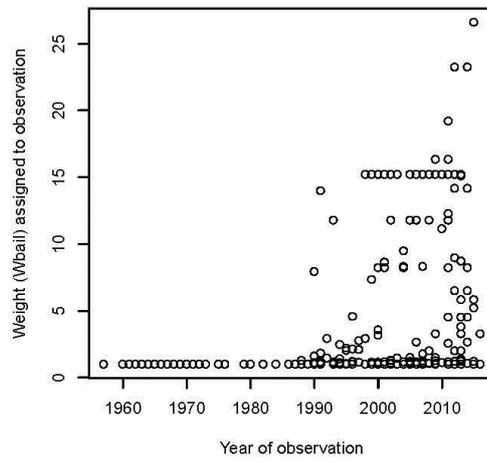
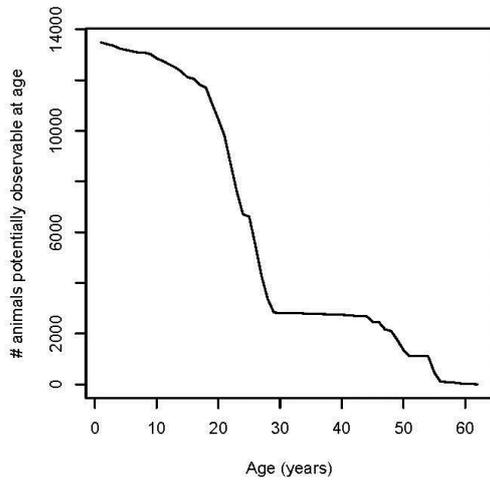
N = 654

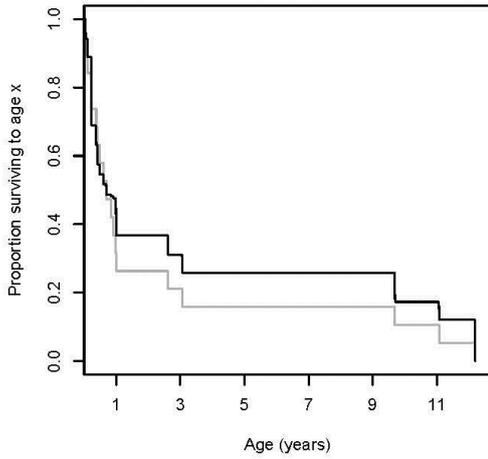
N locations = 17

MRA / MPA = 0.429

Prop. obs. dead = 1

Ann. wear-rate = 0 %





**Eastern Osprey**

*Pandion cristatus*

Ann. adult surv.  $\sim 0.88$  (SE = NA)

Ann. Y1 surv.  $\sim 0.477$  (SE = NA)

Surv. senesc.  $\sim -0.202$  (SE = 0.101)

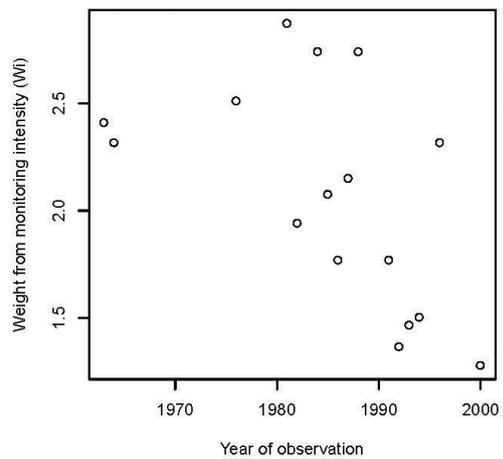
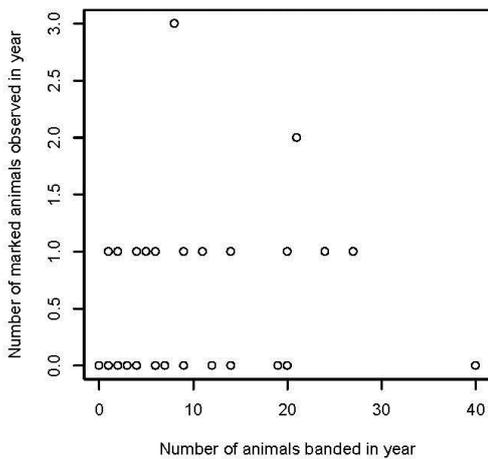
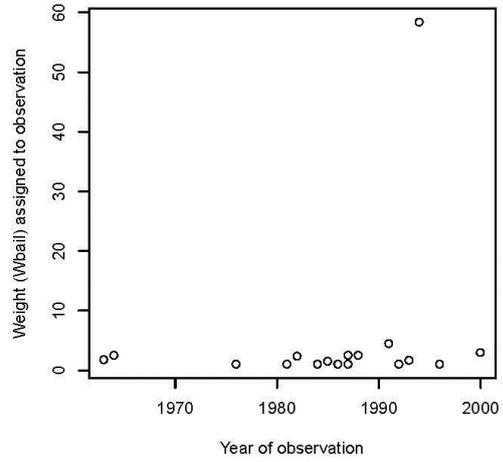
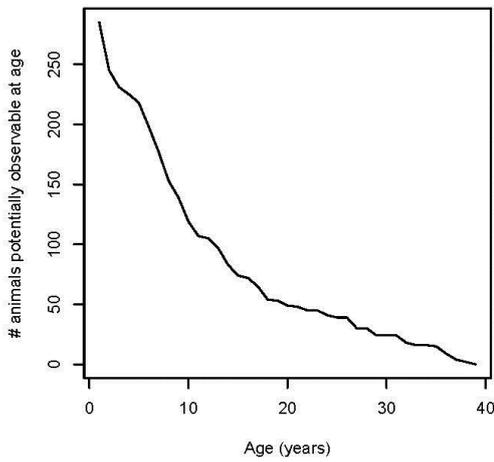
N = 19

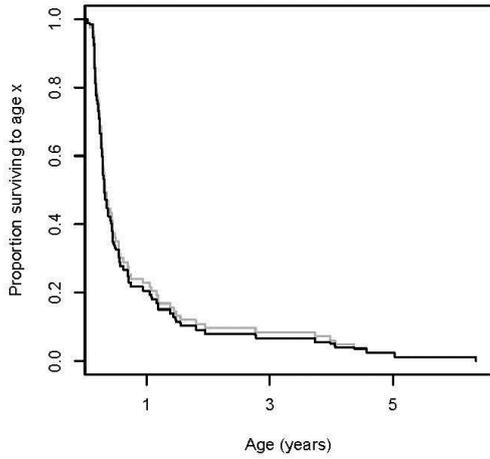
N locations = 8

MRA / MPA = 0.3

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Australian Pelican**

*Pelecanus conspicillatus*

Ann. adult surv.  $\sim 0.532$  (SE = NA )

Ann. Y1 surv.  $\sim 0.205$  (SE = NA )

Surv. senesc.  $\sim -0.637$  (SE = 0.187 )

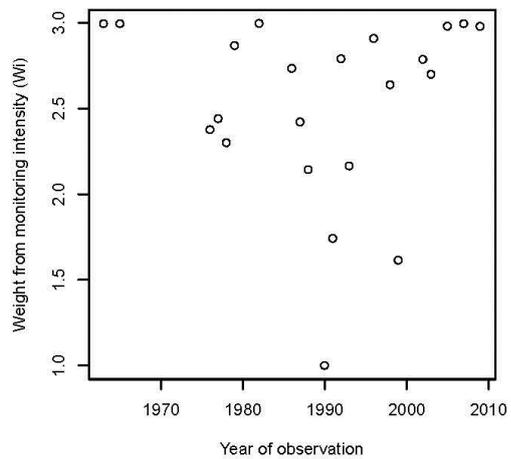
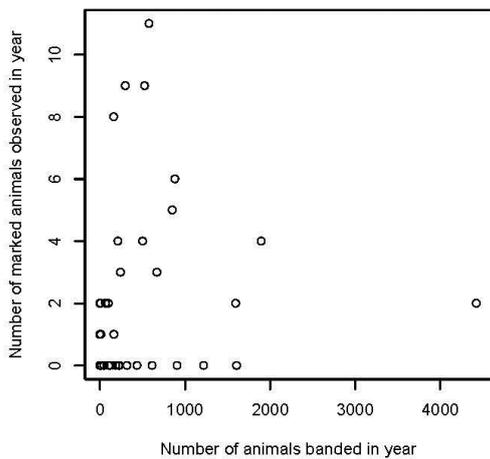
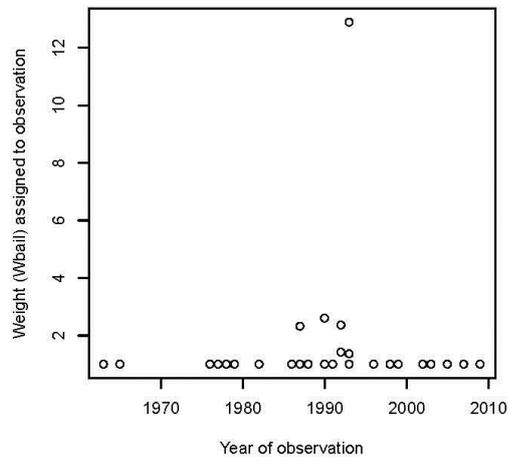
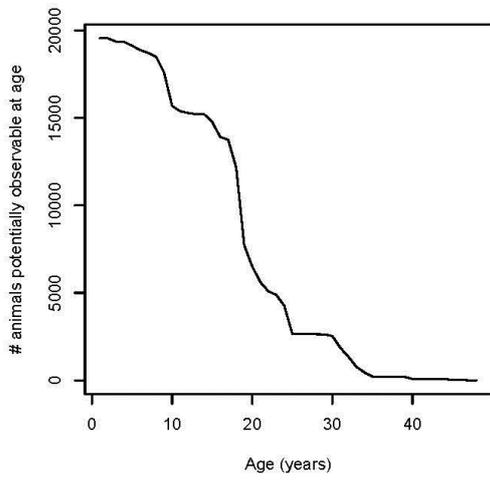
N = 83

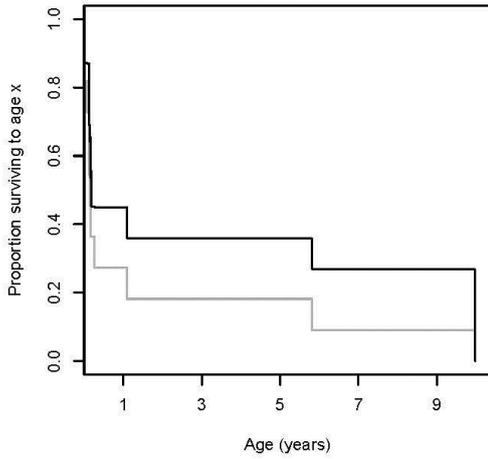
N locations = 17

MRA / MPA = 0.122

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Red-tailed Tropicbird**

*Phaethon rubricauda*

Ann. adult surv.  $\sim 0.848$  (SE = NA)

Ann. Y1 surv.  $\sim 0.516$  (SE = NA)

Surv. senesc.  $\sim -0.621$  (SE = 0.301)

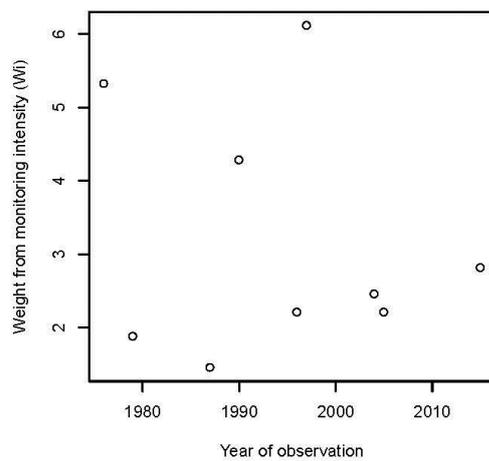
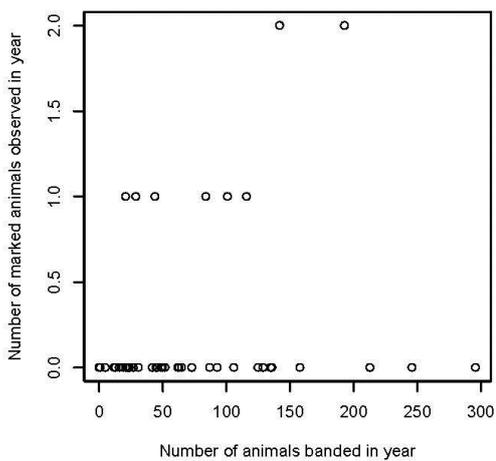
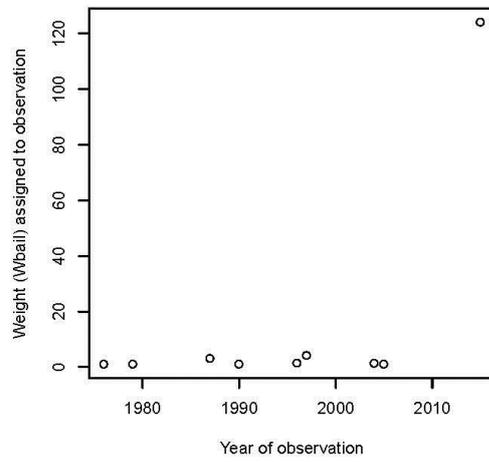
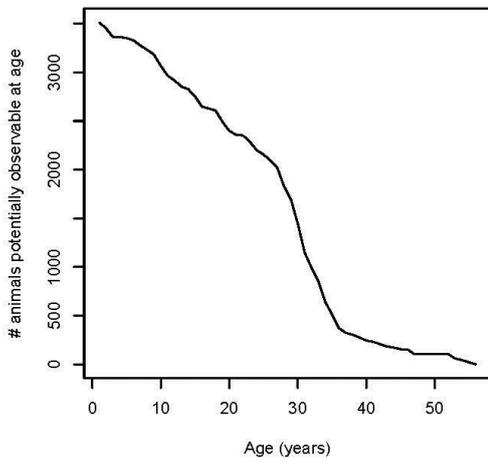
N = 11

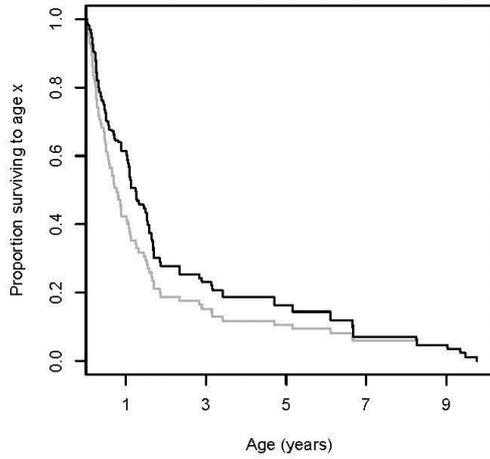
N locations = 7

MRA / MPA = 0.158

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Great Cormorant**

*Phalacrocorax carbo*

Ann. adult surv.  $\sim 0.66$  (SE = NA)

Ann. Y1 surv.  $\sim 0.614$  (SE = NA)

Surv. senesc.  $\sim -0.164$  (SE = 0.069)

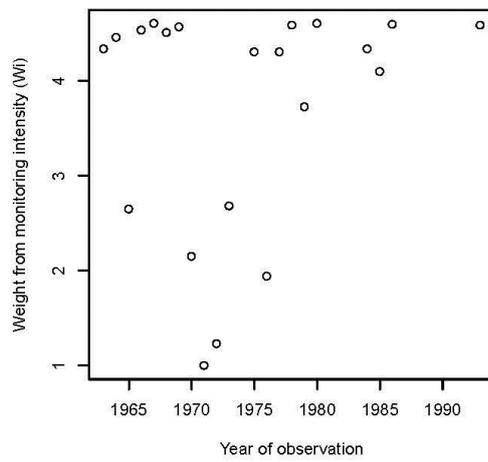
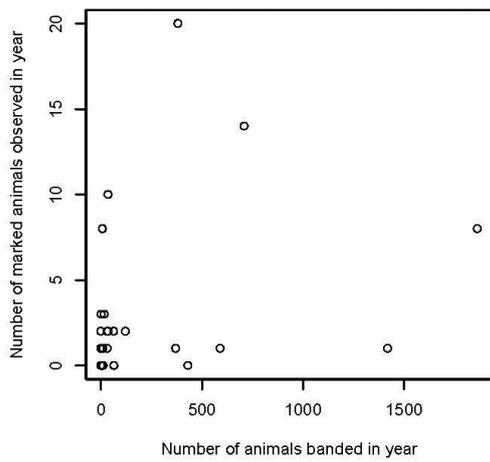
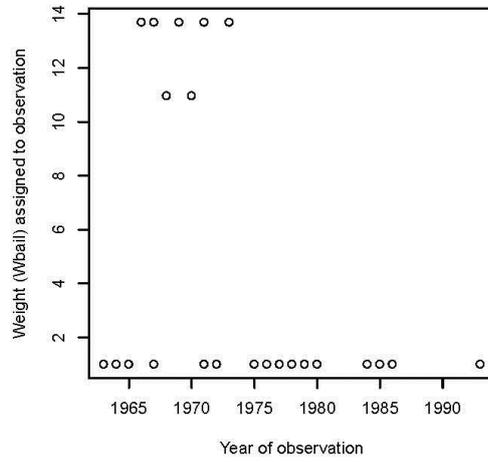
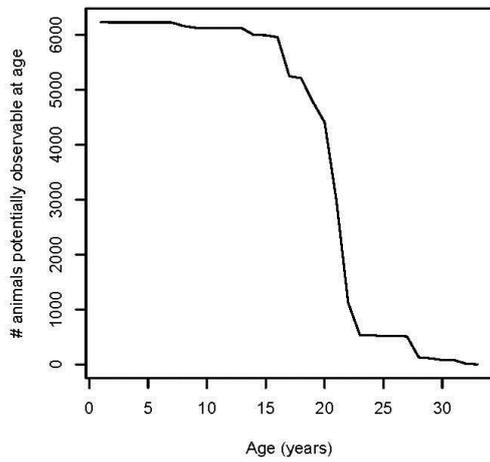
N = 85

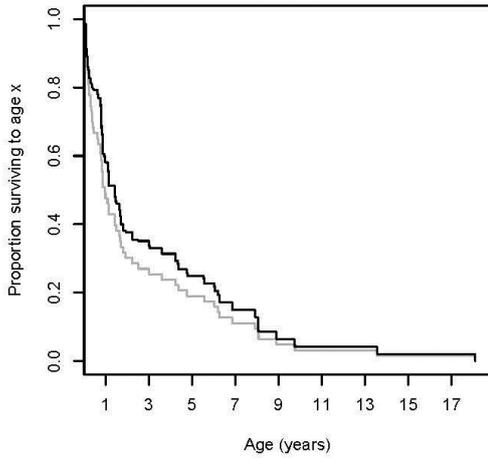
N locations = 15

MRA / MPA = 0.265

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Black-faced Cormorant**

*Phalacrocorax fuscescens*

Ann. adult surv.  $\sim 0.786$  (SE = NA)

Ann. Y1 surv.  $\sim 0.588$  (SE = NA)

Surv. senesc.  $\sim -0.105$  (SE = 0.05)

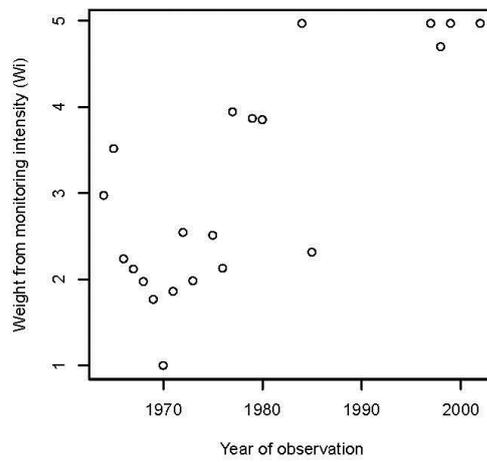
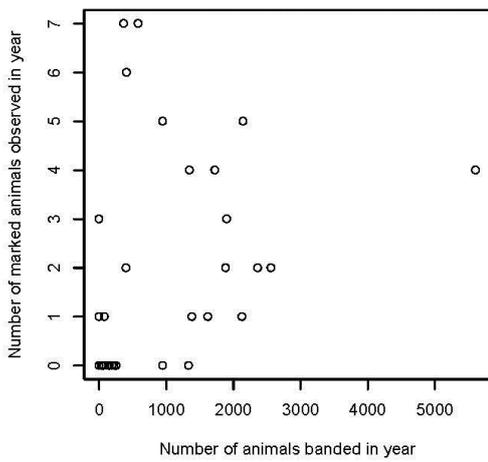
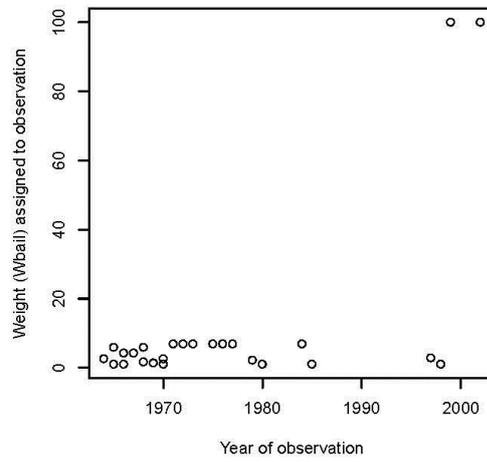
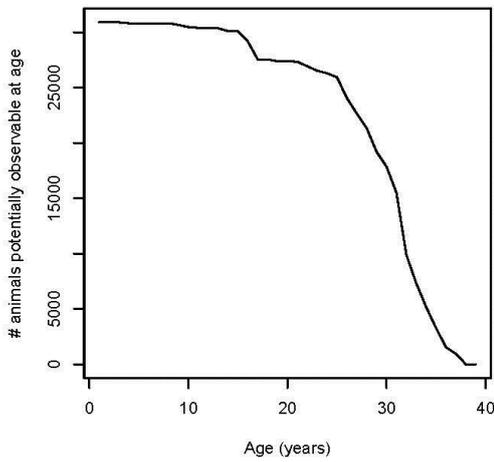
N = 63

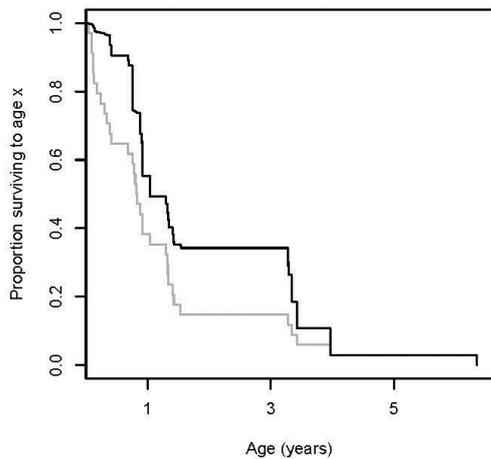
N locations = 7

MRA / MPA = 0.45

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





### Little Black Cormorant

*Phalacrocorax sulcirostris*

Ann. adult surv.  $\sim 0.583$  (SE = NA )

Ann. Y1 surv.  $\sim 0.553$  (SE = NA )

Surv. senesc.  $\sim 0.112$  (SE = 0.186 )

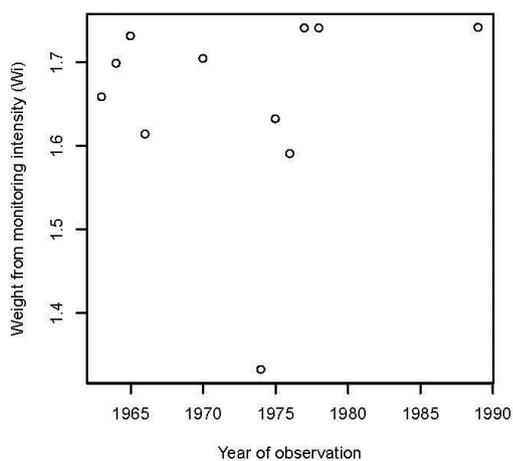
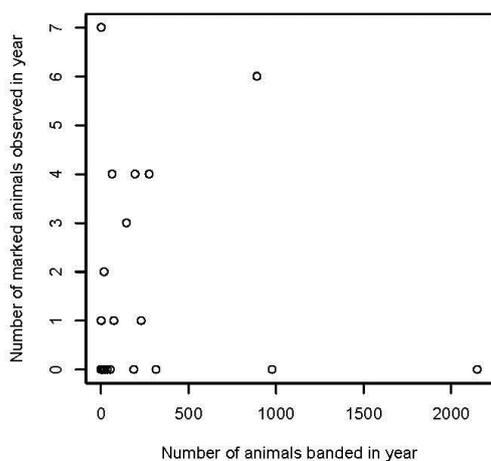
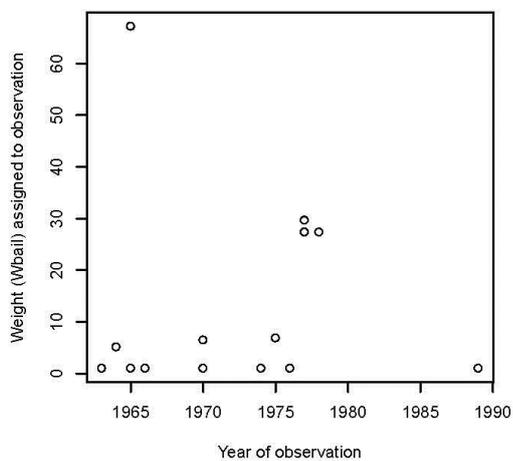
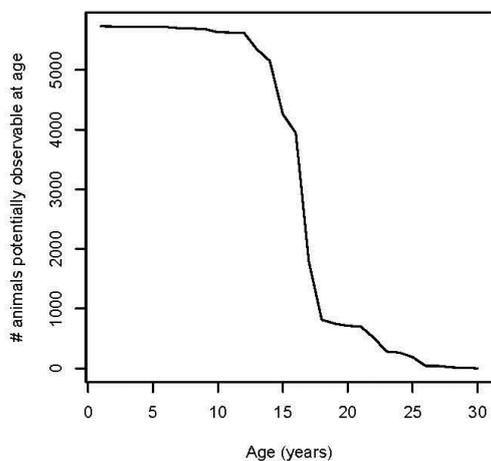
N = 34

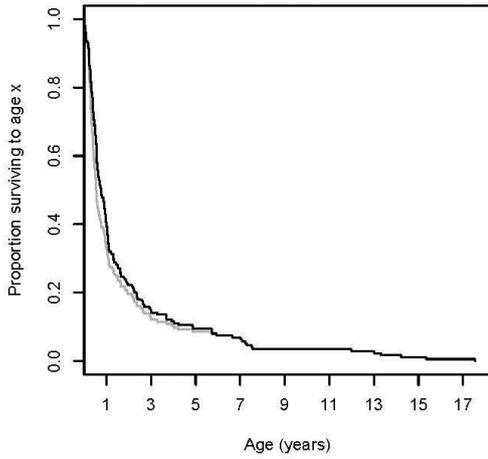
N locations = 7

MRA / MPA = 0.194

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Pied Cormorant**

*Phalacrocorax varius*

Ann. adult surv.  $\sim 0.717$  (SE = NA)

Ann. Y1 surv.  $\sim 0.415$  (SE = NA)

Surv. senesc.  $\sim -0.231$  (SE = 0.044)

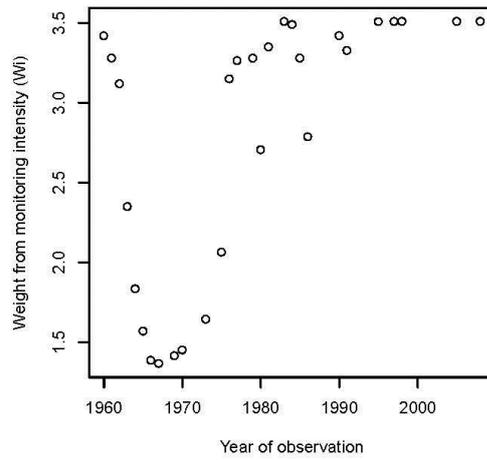
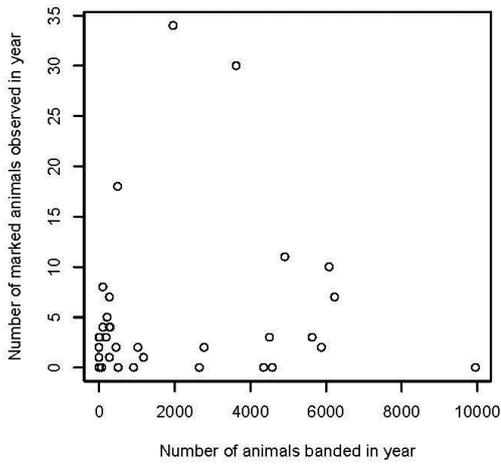
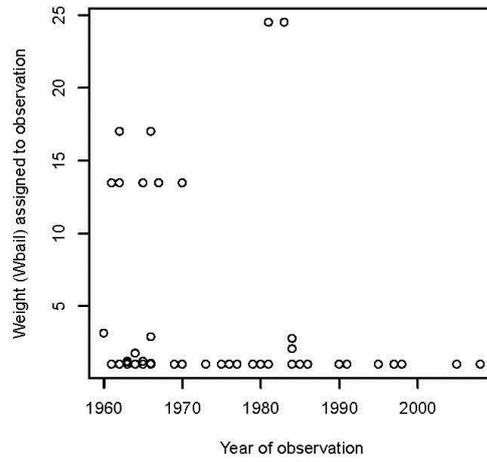
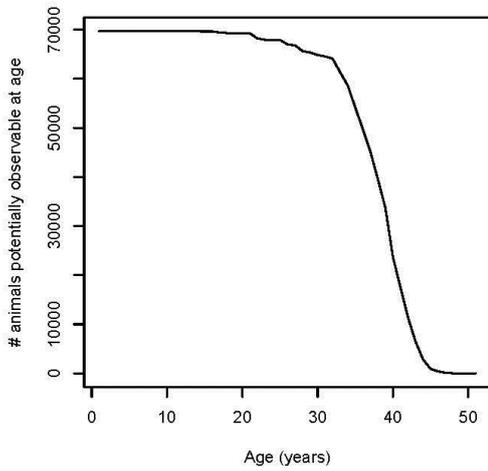
N = 174

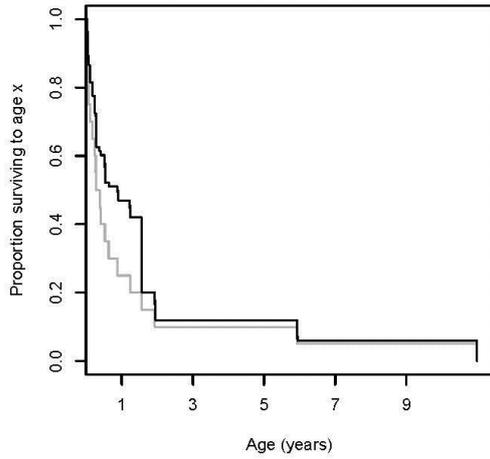
N locations = 16

MRA / MPA = 0.327

Prop. obs. dead = 1

Ann. wear-rate = 0 %





**Crimson Rosella**

*Platycercus elegans*

Ann. adult surv.  $\sim 0.624$  (SE = NA)

Ann. Y1 surv.  $\sim 0.47$  (SE = NA)

Surv. senesc.  $\sim -0.471$  (SE = 0.222)

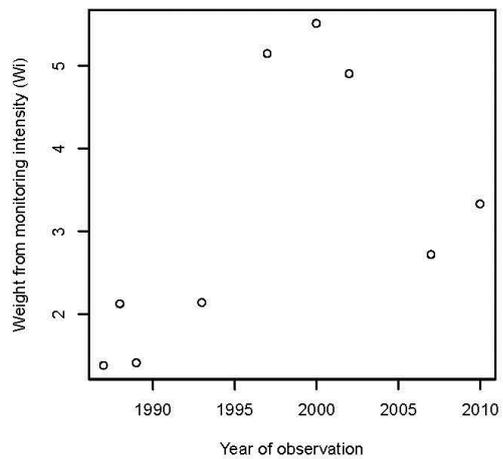
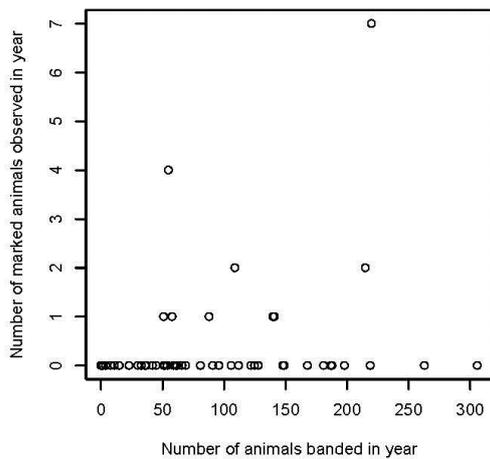
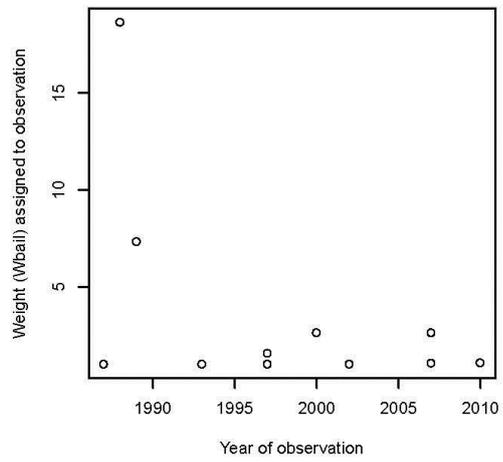
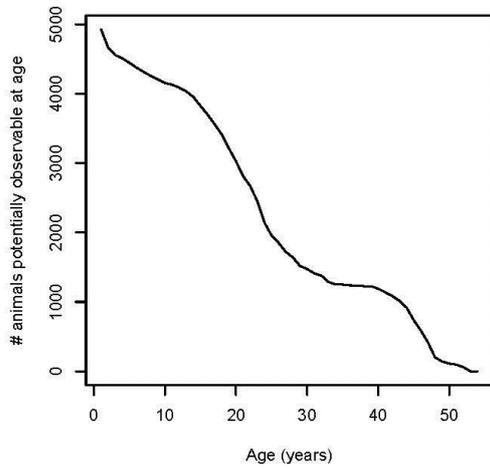
N = 20

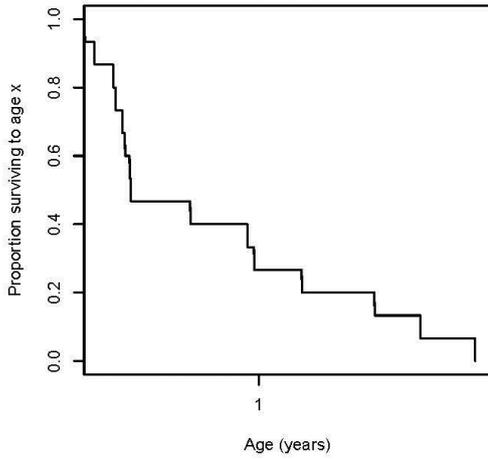
N locations = 7

MRA / MPA = 0.182

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Pied Currawong**

*Strepera graculina*

Ann. adult surv.  $\sim 0.2$  (SE = NA)

Ann. Y1 surv.  $\sim 0.267$  (SE = NA)

Surv. senesc.  $\sim 0.087$  (SE = 1.294)

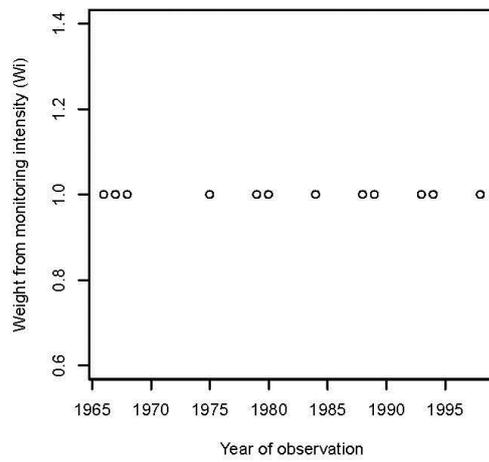
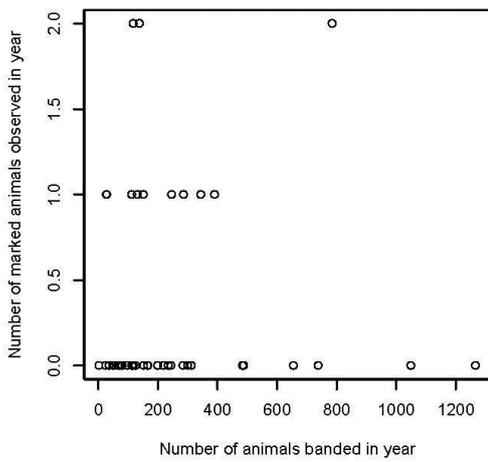
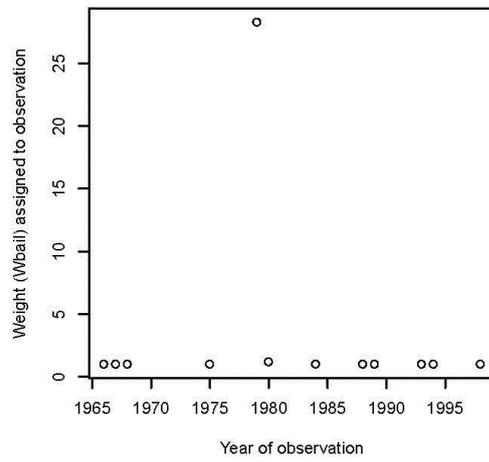
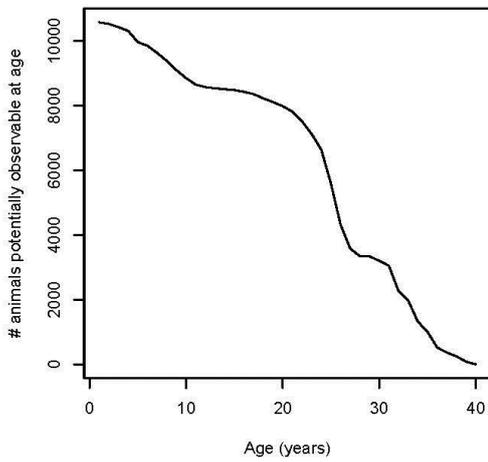
N = 15

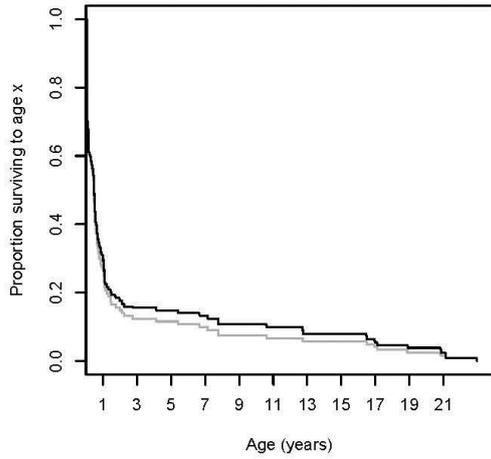
N locations = 13

MRA / MPA = 0.049

Prop. obs. dead = 1

Ann. wear-rate = 0.9 %





**Masked Booby**

*Sula dactylatra*

Ann. adult surv.  $\sim 0.863$  (SE = NA)

Ann. Y1 surv.  $\sim 0.31$  (SE = NA)

Surv. senesc.  $\sim -0.206$  (SE = 0.031)

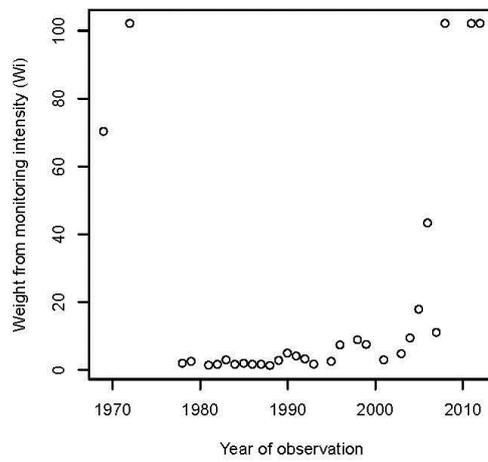
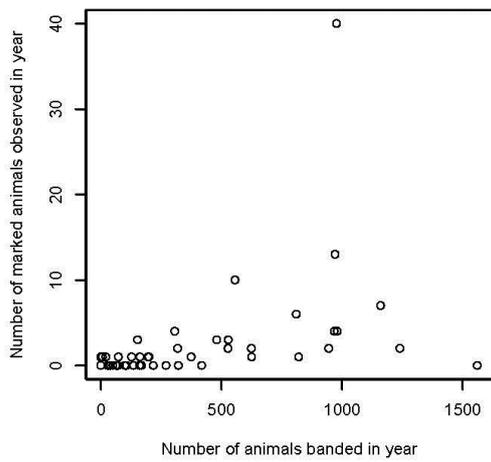
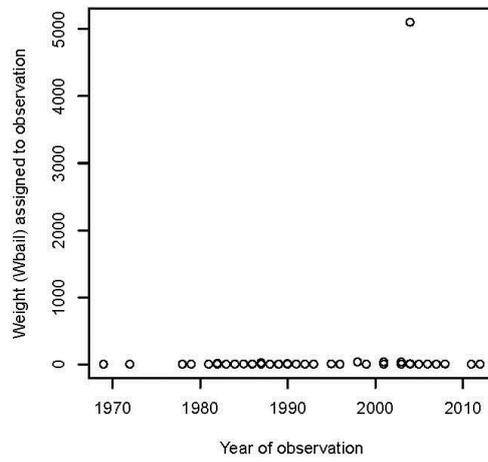
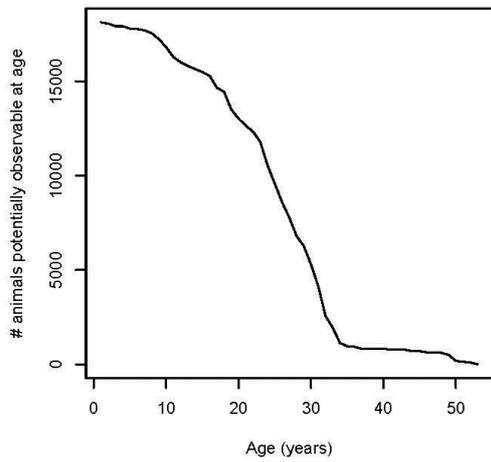
N = 121

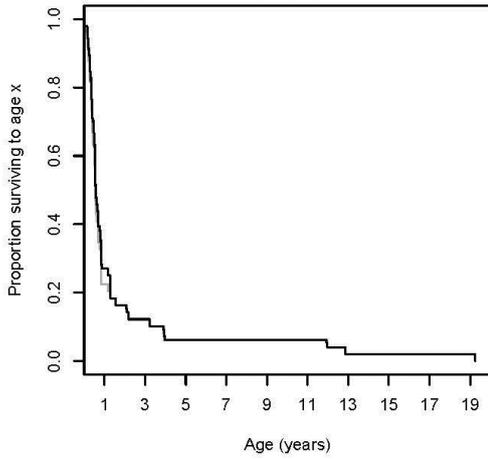
N locations = 17

MRA / MPA = 0.407

Prop. obs. dead = 1

Ann. wear-rate = 0.2 %





**Brown Booby**

*Sula leucogaster*

Ann. adult surv.  $\sim 0.779$  (SE = NA)

Ann. Y1 surv.  $\sim 0.277$  (SE = NA)

Surv. senesc.  $\sim -0.365$  (SE = 0.097)

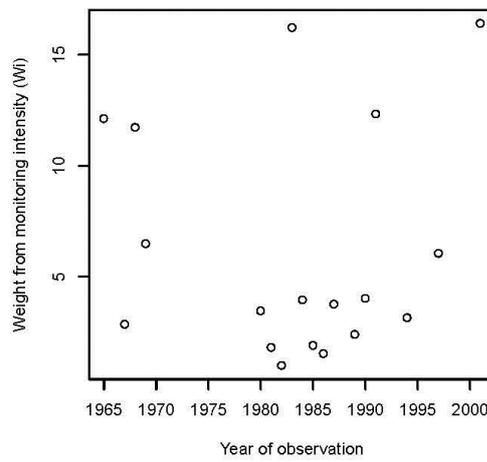
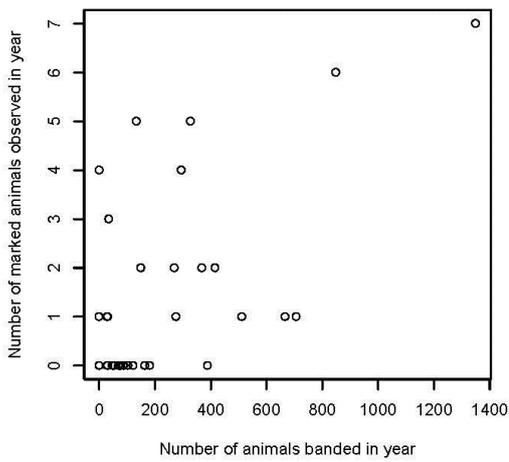
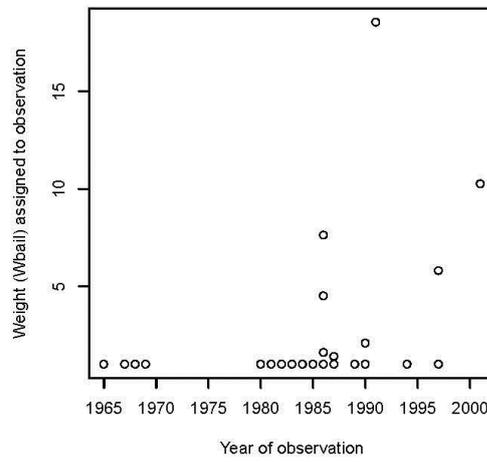
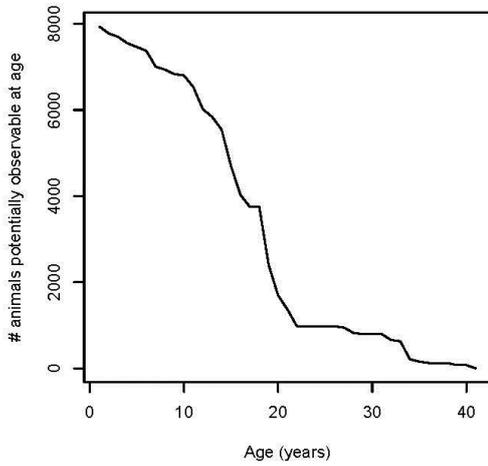
N = 49

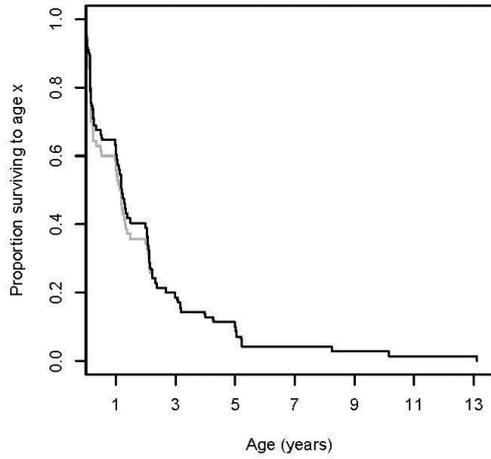
N locations = 14

MRA / MPA = 0.452

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Australian Shelduck**

*Tadorna tadornoides*

Ann. adult surv.  $\sim 0.631$  (SE = NA)

Ann. Y1 surv.  $\sim 0.636$  (SE = NA)

Surv. senesc.  $\sim -0.085$  (SE = 0.069)

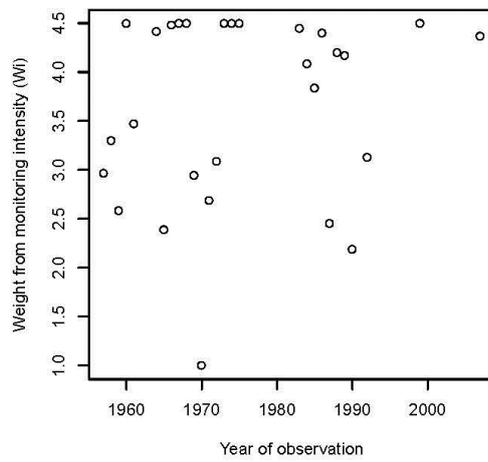
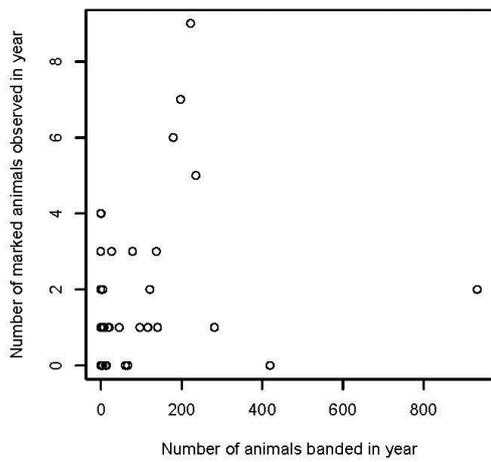
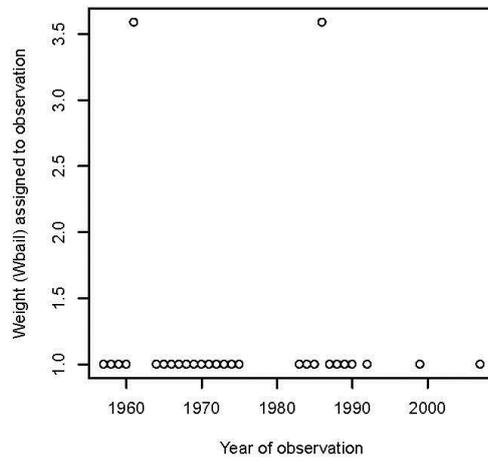
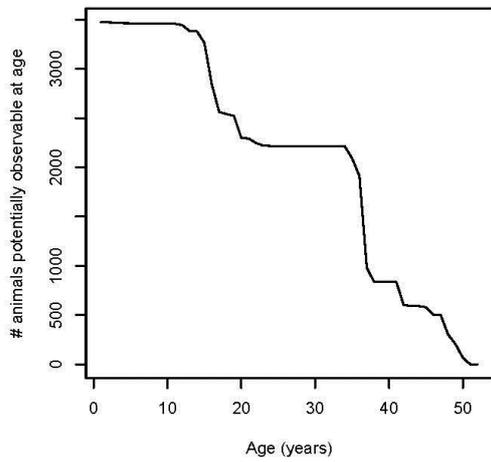
N = 70

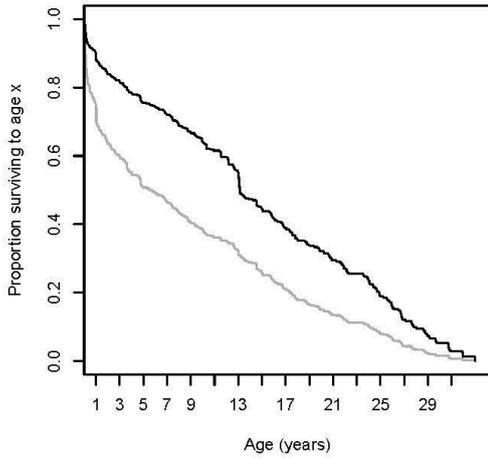
N locations = 12

MRA / MPA = 0.245

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





### Shy Albatross

*Thalassarche cauta*

Ann. adult surv.  $\sim 0.939$  (SE = NA)

Ann. Y1 surv.  $\sim 0.901$  (SE = NA)

Surv. senesc.  $\sim 0.065$  (SE = 0.006)

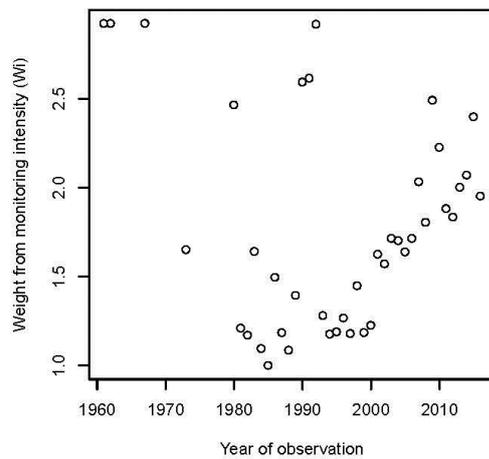
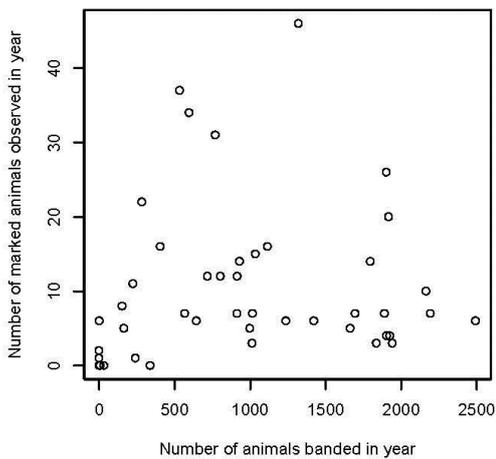
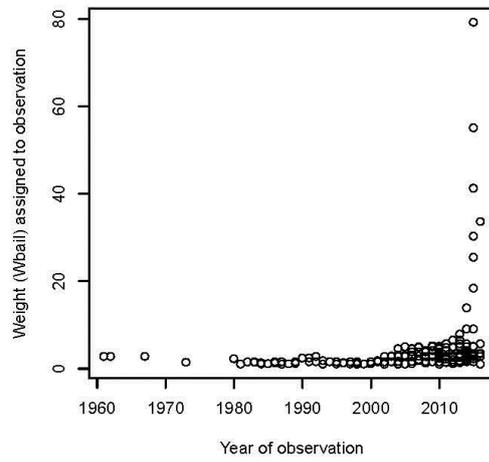
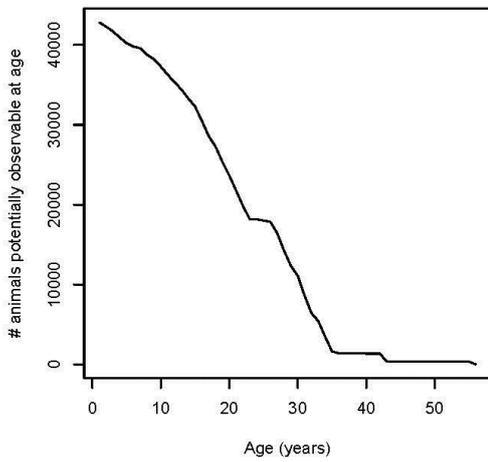
N = 465

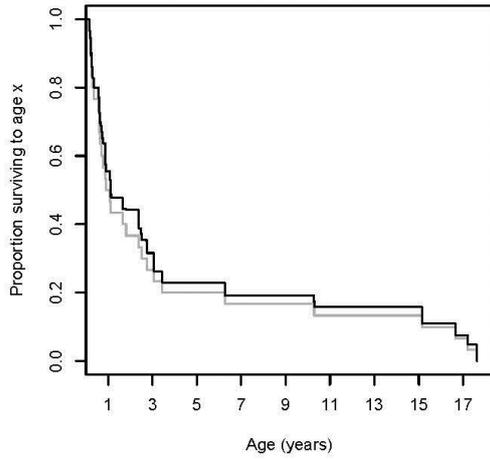
N locations = 6

MRA / MPA = 0.579

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Black-browed Albatross**

*Thalassarche melanophris*

Ann. adult surv.  $\sim 0.852$  (SE = NA)

Ann. Y1 surv.  $\sim 0.555$  (SE = NA)

Surv. senesc.  $\sim -0.147$  (SE = 0.056)

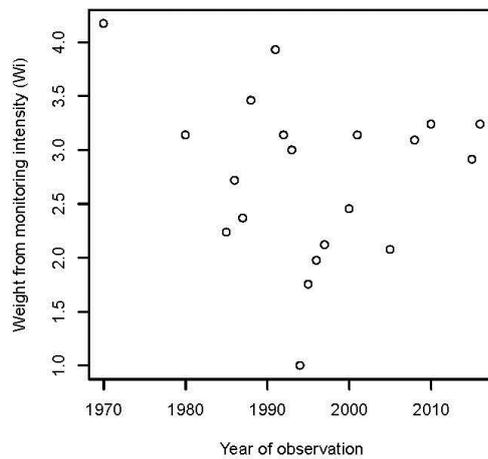
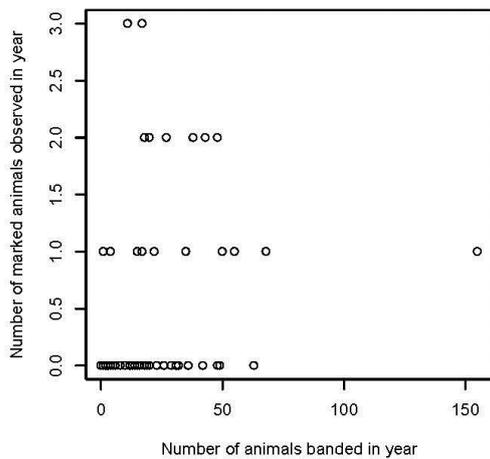
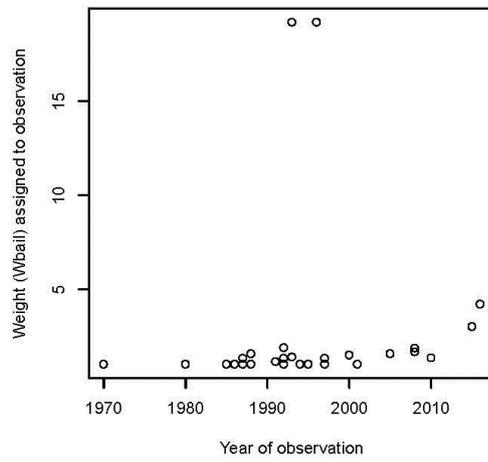
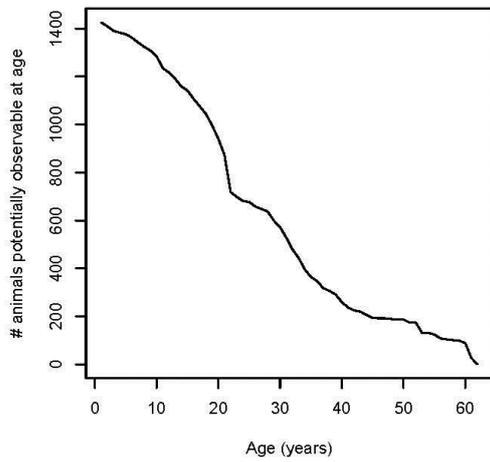
N = 30

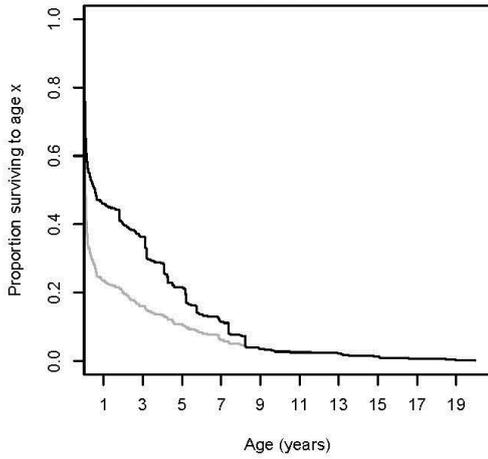
N locations = 11

MRA / MPA = 0.27

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %





**Australian White Ibis**

*Threskiornis molucca*

Ann. adult surv.  $\sim 0.796$  (SE = NA)

Ann. Y1 surv.  $\sim 0.542$  (SE = NA)

Surv. senesc.  $\sim -0.044$  (SE = 0.019)

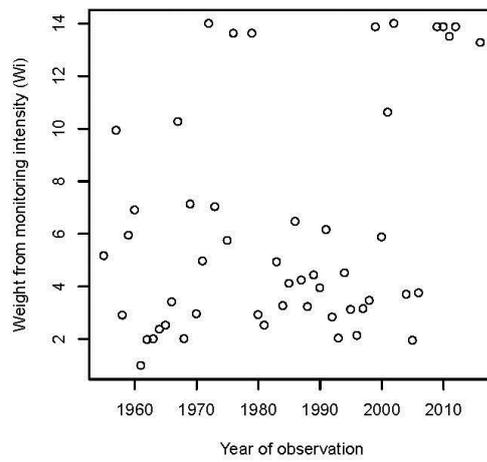
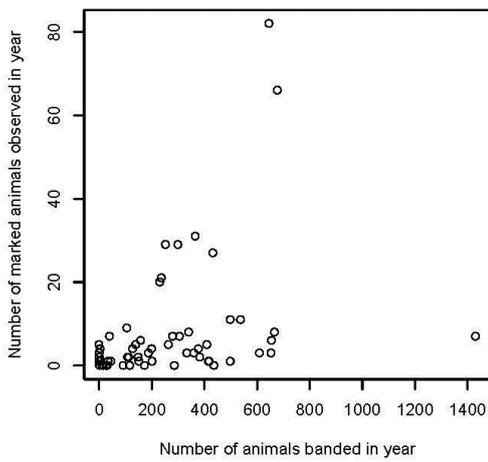
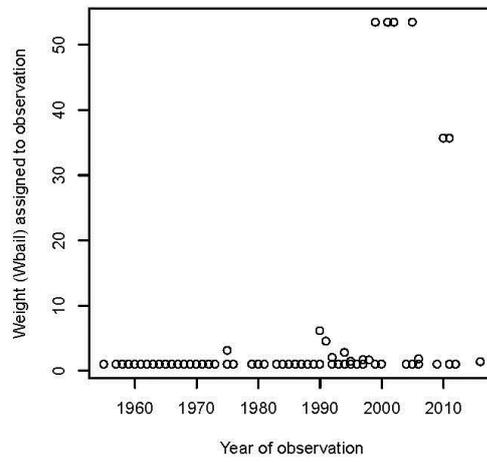
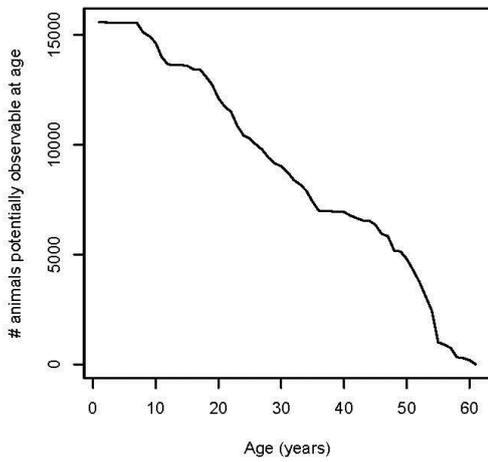
N = 469

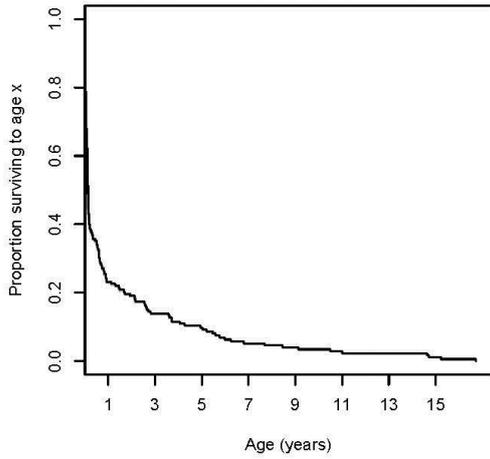
N locations = 29

MRA / MPA = 0.306

Prop. obs. dead = 1

Ann. wear-rate = 1 %





**Straw-necked Ibis**

*Threskiornis spinicollis*

Ann. adult surv. ~ 0.798 (SE = NA )

Ann. Y1 surv. ~ 0.263 (SE = NA )

Surv. senesc. ~ -0.301 (SE = 0.05 )

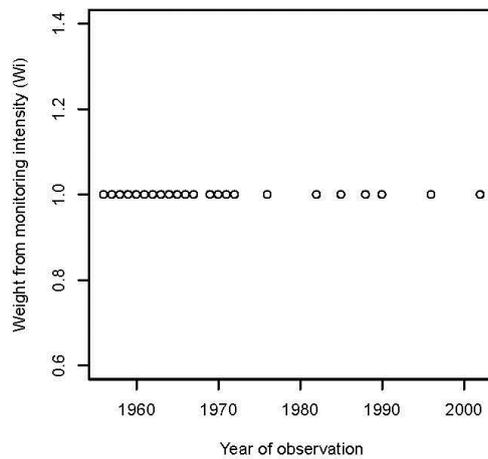
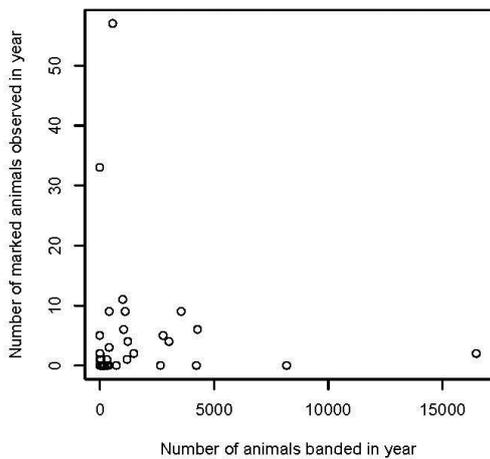
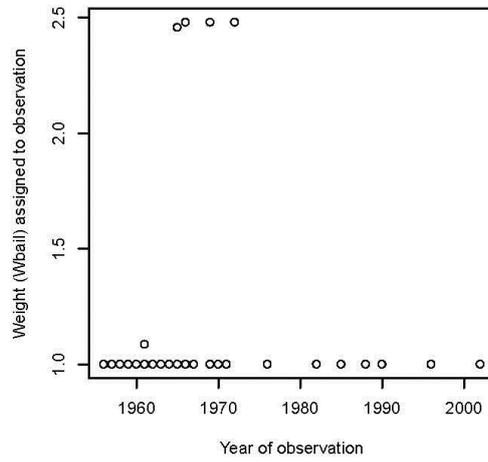
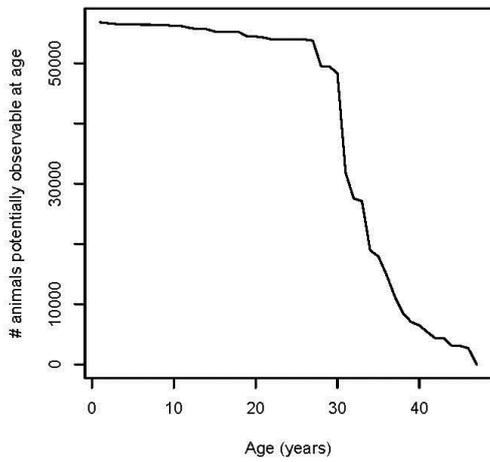
N = 175

N locations = 26

MRA / MPA = 0.333

Prop. obs. dead = 1

Ann. wear-rate = 0.1 %



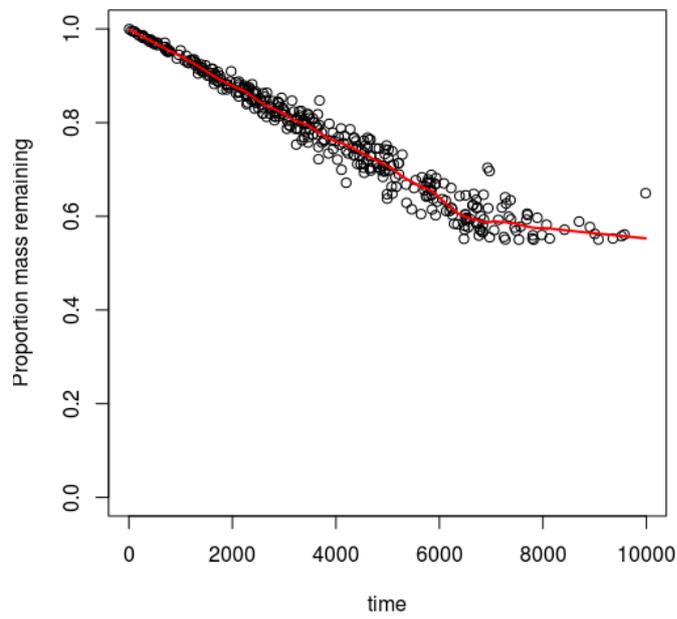
## Appendix 4

### *Supplementary materials to Chapter 4 – Estimates of wear rates in metal bird bands from the archives of a national banding scheme*

**Appendix 4.1:** Detection of under-estimates of wear-rates arising from under-sampling of rapidly-wearing bands

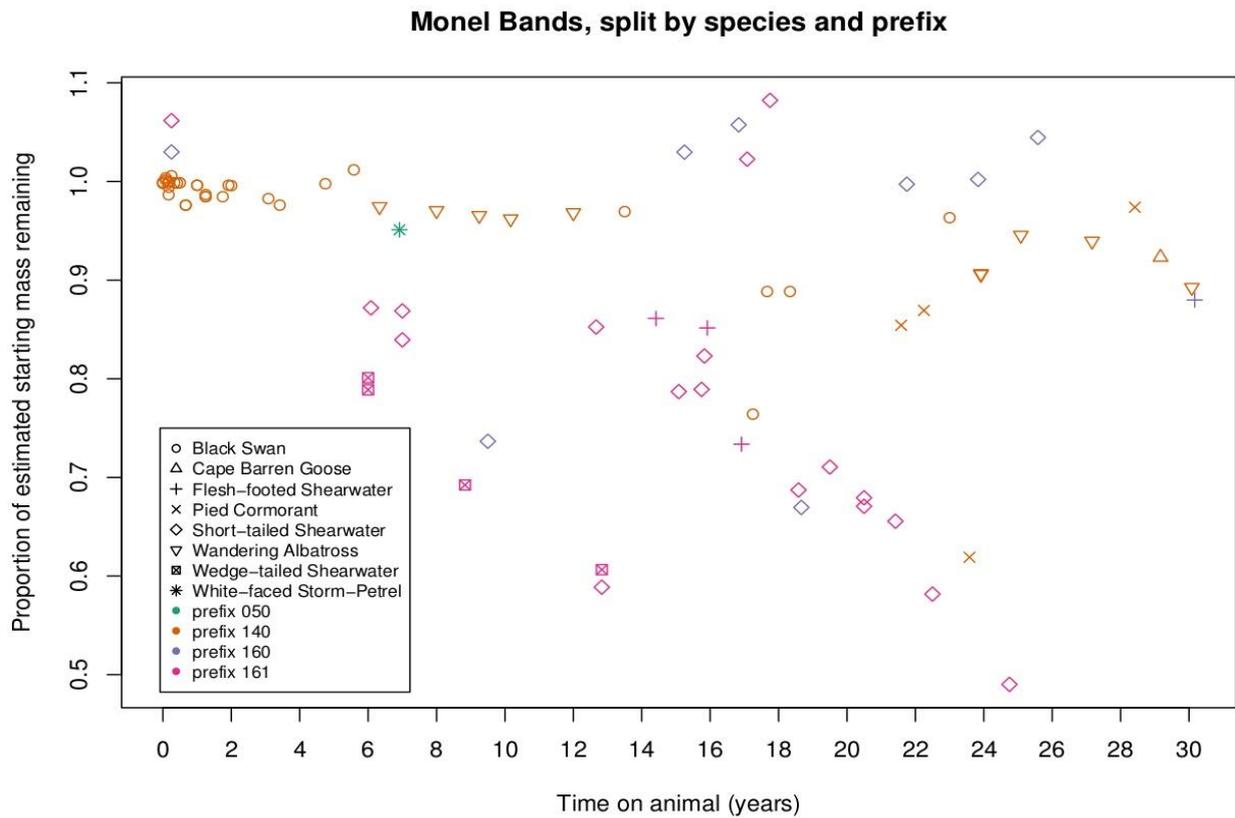
Wear-rates estimated by linear modelling can potentially be biased by under-sampling of rapidly-wearing bands as rapidly-wearing bands are more likely to have worn out and fallen off the bird, and therefore less likely to enter our sample. In principle, this bias is detectable via Lowess smoothing: if wear-rates of individual bands are Normally distributed and bands are lost to wear at a certain proportion of their starting mass, a Lowess smoothed-line fitted to proportional mass remaining through time will be linear until bands begin being lost, and will then change to a shallower slope (see Appendix figure 4.1.1).

**Appendix figure 4.1.1:** a demonstration of the expected bias resulting from under-sampling of rapidly-wearing bands. Here, bands are drawn from a population with a Normally-distributed wear-rate, but are not observed if less than 55 % of the band's starting mass remains. Note the change in slope of the Lowess line at the point where bands start being lost to wear.



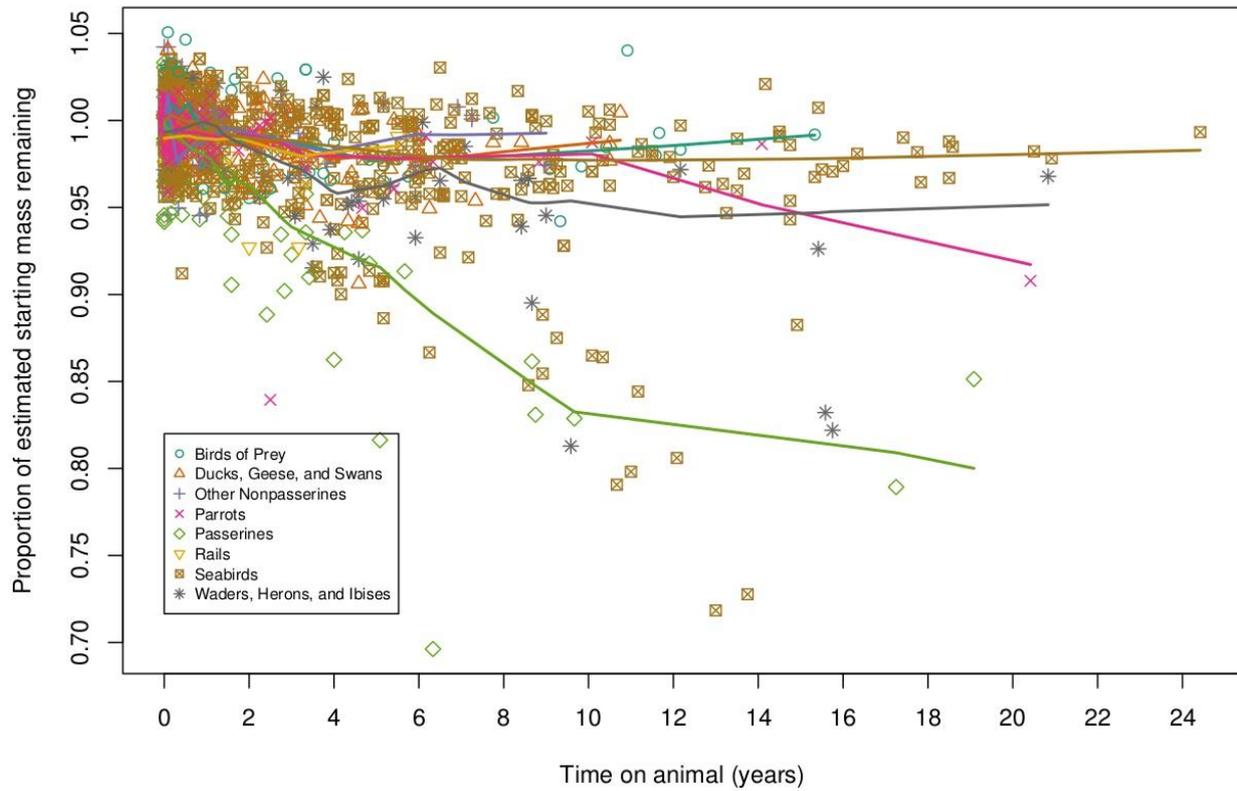
## Appendix 4.2: Estimates of wear-rates by metal and functional group

**Appendix figure 4.2.1:** Monel bands can show differing apparent wear-rates within species, apparently driven by differences in the bands: note the wear-rates within Short-tailed Shearwater *Ardenna tenuirostris*, which clearly cluster into a 'rapid-wearing', 'medium-wearing', and 'non-wearing' group. The 'rapid-wearing' and 'medium-wearing' bands are nearly all prefix 161, whereas the 'non-wearing' bands are nearly all prefix 160. Band prefixes correspond roughly to manufacturing batches, where bands are manufactured sequentially within the same prefix, then within the next prefix.



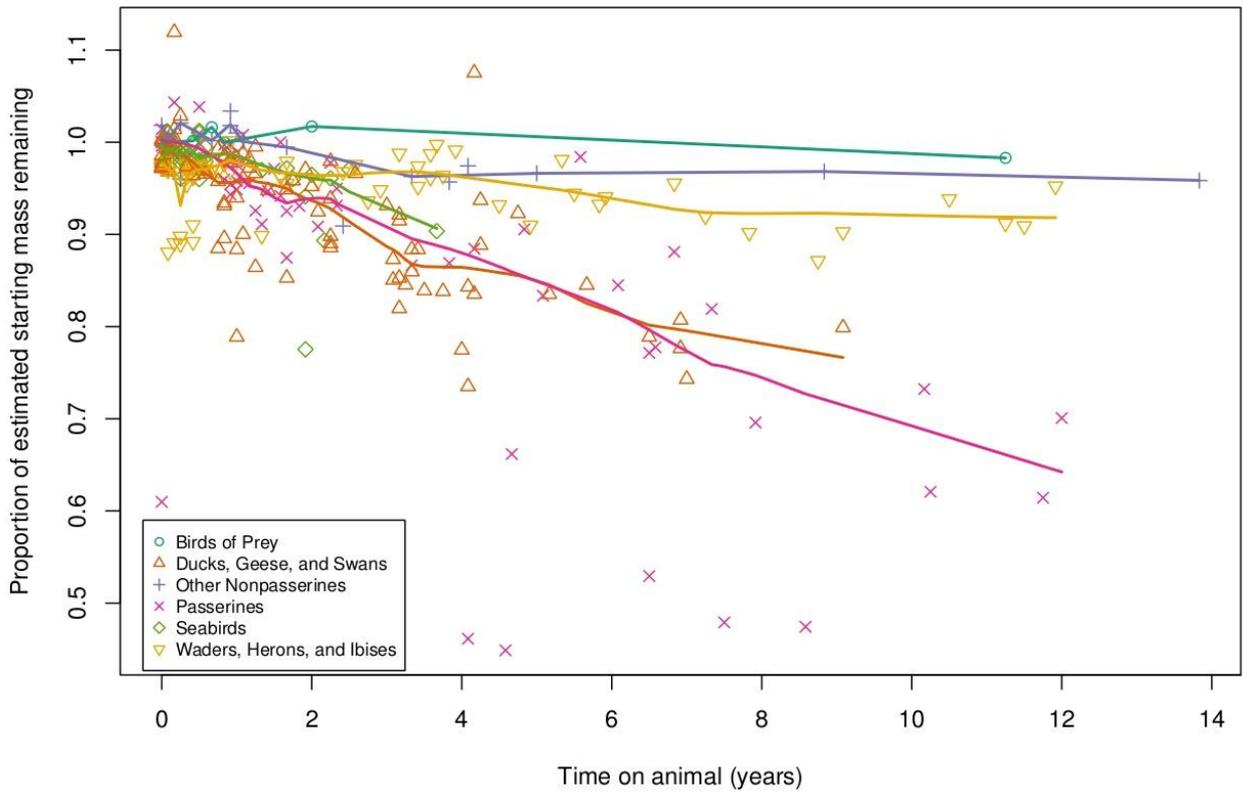
**Appendix figure 4.2.2:** Stainless bands appear to show heterogeneous wear-rates by functional group, with bands worn by Passerines losing a greater proportion of their mass per unit time than bands worn by other groups. Some seabirds, and possibly some parrots and some waders, herons, and ibises, also show elevated wear relative to the rest of their functional group.

### Stainless Bands, split by functional group



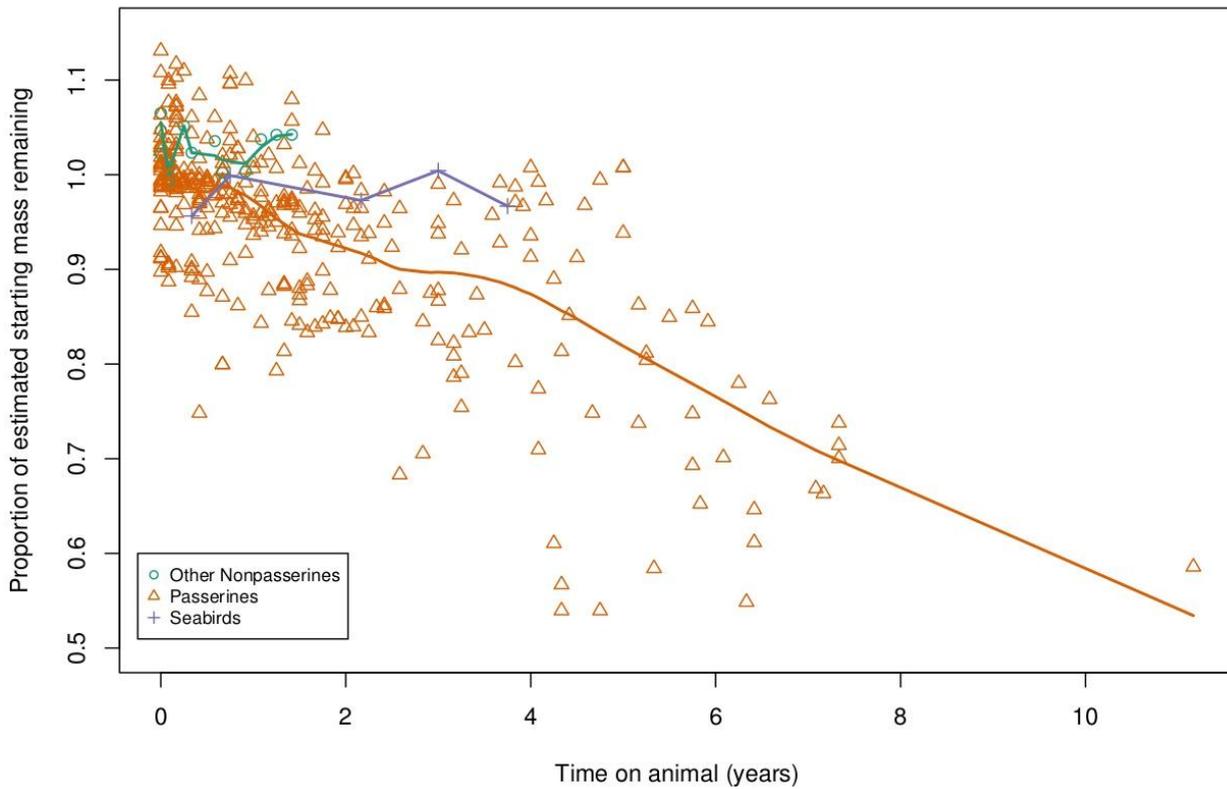
**Appendix figure 4.2.3:** Aluminium bands appear to wear in two clusters of rates, by functional group. Aluminium bands on seabirds, passerines, and ducks, geese, and swans wear at a fairly rapid rate (approximately 3 % / year), whereas bands on birds of prey, waders, herons, and ibises, and other non-passerines wear at a considerably slower rate (approximately 0.5 % /year). It is likely that the wear-rate given here for Passerines is an under-estimate: worn bands are observed down to 50 % of their starting mass from the fourth year on an animal, and 50 % of starting mass may represent the point by which bands are generally lost. If this is the case, then the bands remaining after 4 years represent a slower-wearing subset from the population of bands.

**Aluminium Bands, split by functional group**



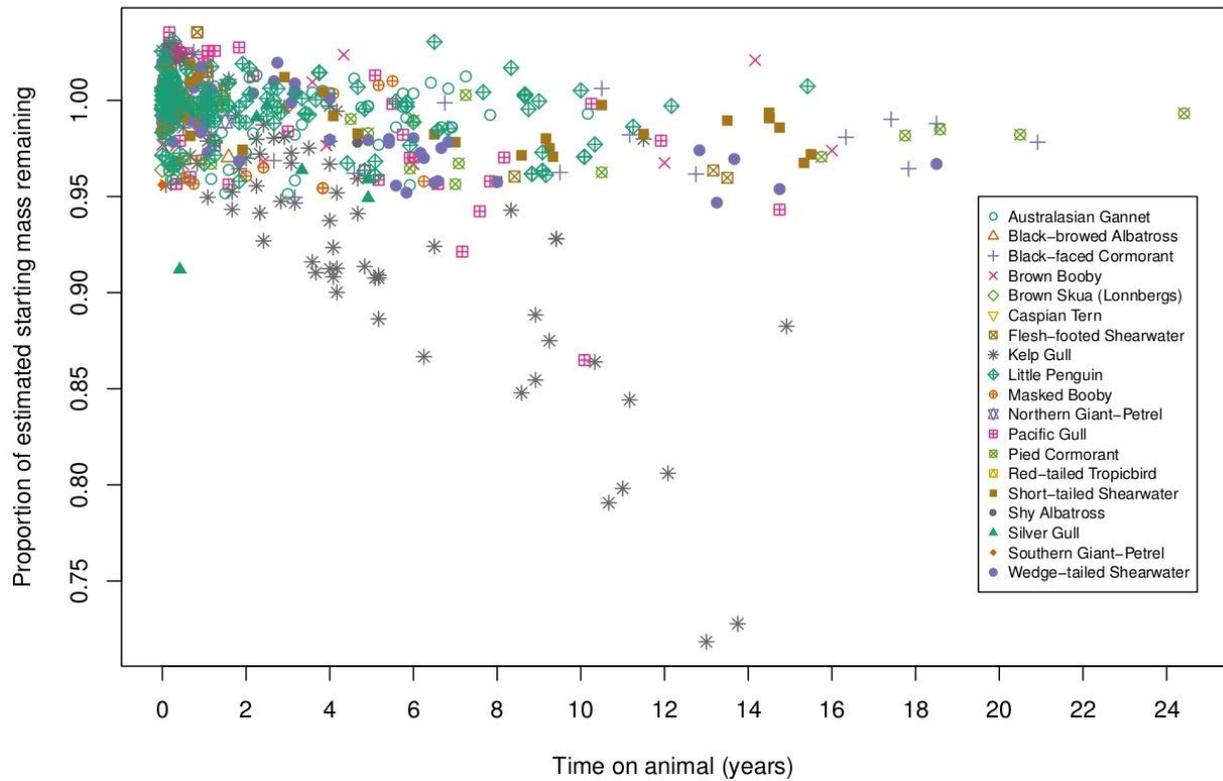
**Appendix figure 4.2.4:** Alloy bands on passerines appear to wear at a fairly rapid rate (approximately 4 % / year). This may be an under-estimate – worn bands are observed down to 50 % of their starting mass from the fourth year on an animal, and 50 % of starting mass may represent the point by which bands are generally lost. If this is the case, then the bands remaining after 4 years represent a slower-wearing subset from the population of bands. Comparatively few alloy bands have been worn on seabirds and other non-passerines, but alloy bands on these groups appear to wear more slowly than alloy bands on passerines in the limited sample that exists.

**Alloy Bands, split by functional group**



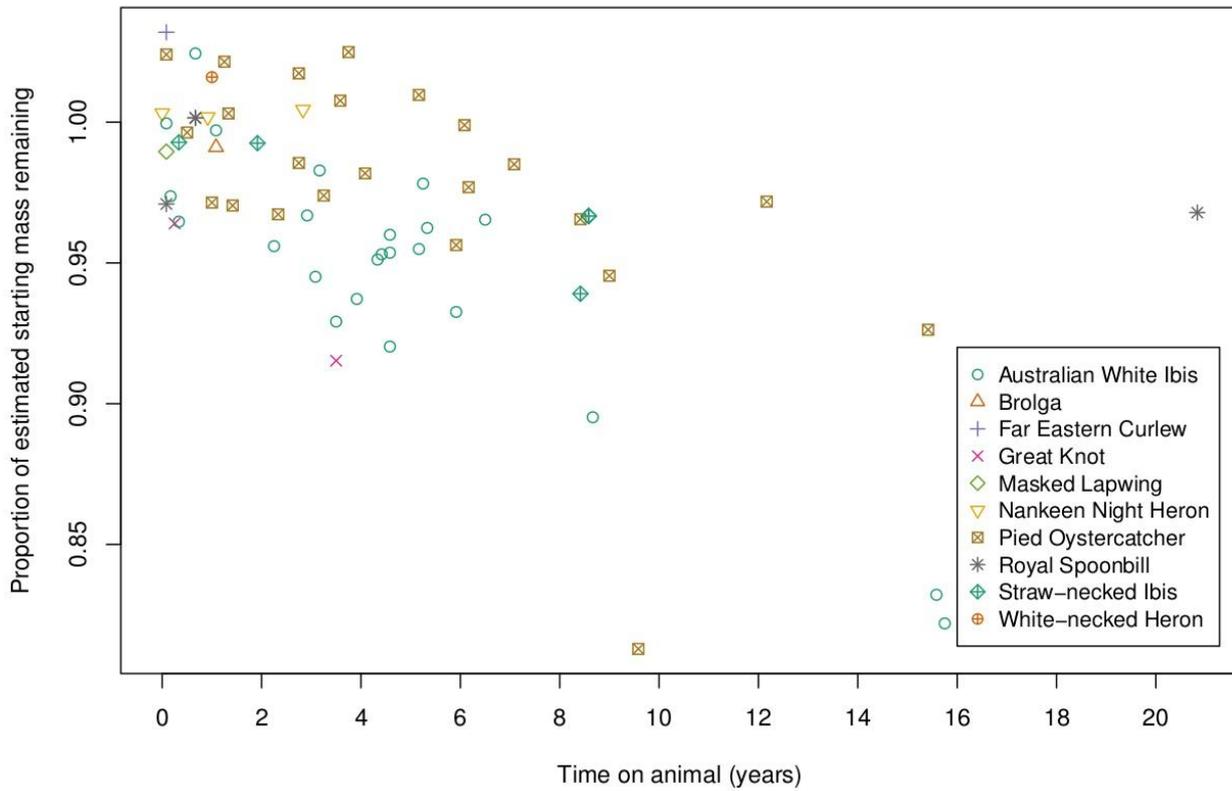
**Appendix figure 4.2.5:** Stainless Steel bands on seabirds uniformly show very little wear unless they are worn by Kelp Gulls *Larus dominicanus* or, possibly to a lesser extent, Pacific Gulls *L. pacificus*.

### Stainless Bands, split by Species within Seabirds



**Appendix figure 4.2.6:** Stainless Steel bands on waders, herons, and ibises show a split between the wear-rate for Australian White Ibis *Threskiornis molucca* and Pied Oystercatcher *Haematopus longirostris*; other species are data-poor in comparison, but Royal Spoonbill *Platalea regia* appears to have a particularly low wear-rate.

**Stainless Bands, split by Species within Waders, Herons, and Ibises**



**Appendix figure 4.2.7:** Stainless Steel bands on parrots show highly variable apparent wear in Galah *Eolophus roseicapillus*; other species have small sample sizes or limited durations on animals.

