Male reproductive strategies and parental investment in the wheatear, *Oenanthe oenanthe*.

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by

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For mum and dad

.......why study the wheatear ?
> *Anon*., E.G.I. student conference, January 1992.

Answer a fool according to his folly.
> The Proverbs, 26: 5, Old Testament.

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Abstract

Male reproductive strategies and parental investment in the wheatear,
Oenanthe oenanthe.
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1. This study investigated factors affecting individual reproductive success in the wheatear *Oenanthe oenanthe*, a migrant passerine species, on Bardsey Island, North Wales, 1991-93.

2. Behavioural and paternity data, obtained using DNA fingerprinting, indicated that males pursued a mixed reproductive strategy, i.e. they ensured their paternity during the fertile period of the pair female and pursued extra-pair copulations outwith this time. Behavioural observations were consistent with males using mate guarding to ensure their paternity. Males adjusted their intensity of guarding in response to the threat to their paternity. Males mainly pursued extra-pair copulations once their female had begun incubating. Intrusions by extra-pair males peaked in the fertile period, and later breeding territories were intruded upon more than early breeding pairs.

3. Natural levels of extra-pair paternity were relatively low: 11% of 71 offspring, occurring in 29% of 17 broods. Extra-pair fertilisations contributed little to a male's reproductive success. Not all extra-pair fathers were identified, but at two nests males within a three-territory radius were excluded as extra-pair fathers. There was no evidence that females increased their reproductive success by laying eggs in the nests of other females (intra-specific brood parasitism). Females were never observed off territory soliciting extra-pair males and rarely seen soliciting extra-pair males on territory. The majority of EPCs were resisted by the female and their co-operation appeared to be essential for males to obtain successful copulations. The presence of extra-pair young within broods indicates that females must have also pursued a mixed reproductive strategy by participating in EPCs.

4. Experimental removals of males for 24 hours during the fertile period were used to investigate the effect of the absence of the pair male on: (i) female behaviour; (ii) the behaviour of extra-pair males; and (iii) levels of extra-pair paternity. The number of intrusions and extra-pair copulations increased in the absence of the pair male. Females rejected the majority of extra-pair copulations, and there was no significant increase in extra-pair paternity resulting from these experiments: 10% of 78 offspring occurring in 38% of 16 broods. Female behaviour appeared to be the determining factor affecting the level of extra-pair paternity, although male guarding behaviours may have limited the opportunities for females to participate in extra-pair copulations by deterring intrusions.

5. Males contributed on average 50% of chick feeds, and did not adjust their investment in proportion to their paternity in the brood. There was no effect of the temporary male removals, used to simulate a male's uncertainty of paternity, on their subsequent investment. However, males which adopted broods provided 29% of chick feeds on average, but this was not in proportion to the paternity they had in the brood. This reduction in the number of chick feeds was partially compensated for by females increasing their frequency of chick feeds.

6. Territories remained relatively constant between years. There was evidence that territories varied in quality, as indicated by their consistent order of settlement between years, individuals moving to preferred areas when possible, and individuals being more faithful to preferred areas. Older males returned to the breeding ground earlier than first-year males, and were more likely to be paired than individuals breeding for the first time. This was probably due to the older males having settled on preferred territories. Territory quality had a significant effect on individual reproductive success. There were few correlates with individual quality and measures of breeding success. A male's mating status was dependent on arrival time, territory quality, breeding density and the operational sex ratio. Males which settled on preferred territories were more likely to be paired. Pairs which bred on preferred territories tended to have increased fledging success, and nestlings which fledged from preferred territories were more likely to return to the study area to breed. Female reluctance to copulate outwith the pair bond may be a result of individual reproductive success being determined more by territory quality rather than male quality.

Acknowledgements

Adriaensen, and others. On a personal note, a special thanks also go to Julia, Amanda and especially Nicky. Last and not least I'd like to thank my family who have supported me throughout my trials and tribulations, and 'kicked my arse' when it was needed.

Without the help and support of the persons named above, this thesis would not have been possible, and I am indebted to them. My apologies go to anyone I may have inadvertently forgotten to mention. At last the nightmare ends.

Dave Currie, Leicester, December, 1995.

Chapter 1. General introduction

1.1. Introduction

1.1. Introduction

There is now a considerable literature on the breeding biology of birds, not least on reproductive strategies. However, it is only during the last decade that the most significant advances have been made in quantifying the selective forces influencing reproductive success of individuals and their offspring. The aim of this section is to provide a brief overview of the background and current theory concerning reproductive strategies relevant to this study.

1.1.1. Natural selection and the 'selfish' gene

Reproduction is a costly part of an animal's existence, and can be considered to be a trade-off between current reproductive success (RS) and future survival. Natural selection is the process resulting in the preferential survival of individuals that are best adapted to the prevailing environmental conditions, with survivors producing more offspring than those less well adapted individuals. The traditional evolutionary view, expanded by Wynne-Edwards (1962), was that animals acted for the good of the species. However, this approach failed to explain apparently 'maladaptive' behaviour such as infanticide. The neo-

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darwinian view is that animals behave selfishly to maximise their fitness, i.e. the number of offspring they produce in their lifetime, at the expense of conspecifics, as natural selection will favour a genotype which confers a reproductive advantage to an individual over others of the same species (sensu Darwin 1871, Dawkins 1979, Dawkins 1982). Individuals are therefore expected to adopt behavioural strategies which maximise their own lifetime reproductive success.

Reproduction can be considered to involve a 'conflict' between the sexes due to the different selection pressures each experiences (discussed below). At its simplest, males try to maximise their number of matings with females while attempting to ensure their paternity. Females, on the other hand, choose between different males to breed with, and attempt to obtain maximum levels of paternal care during the raising of their offspring. Co-operation between two individuals which decide to breed together should therefore be considered as an uneasy alliance rather than an 'amicable' association, as individuals may make decisions which benefit themselves, but are at the expense of their partner.

1.1.2. Costs of reproduction

Reproductive effort is the amount of time and energy put into reproduction and is a trade-off between resource availability and allocation between other aspects of an organism's requirements. Reproductive effort can be divided into mating effort and parental effort (Low 1978). During reproduction, females generally put most of their energy into PE, investing more resources in offspring, while males usually invest more time and energy searching for females to inseminate (mating effort) (Krebs and Davies 1987). This is a consequence of females producing a limited number of large, immobile, energetically expensive gametes (eggs) and males producing a large number of small, mobile, energetically cheap gametes (sperm). Female reproductive success (RS) is limited primarily by the number of eggs they can produce while male RS is limited by the number of eggs they can fertilise. This is slightly over-simplified, as males usually deliver sperm in batches which may consist of millions of gametes (Dewsbury 1982), and will be limited in the number of these batches they can produce (but not to the same extent as females). As a consequence of these fundamental differences in the patterns of initial investment in reproduction, the optimal strategies for maximising RS are different for each sex.

1.1.3. Sexual selection

Selection for traits which are principally concerned with increasing mating success is termed 'sexual selection' (Halliday 1978). Males typically have conspicuous phenotypic characteristics (which may run counter to natural selection) or visual or vocal displays, termed secondary sexual characteristics. Such characteristics may be costly to produce (and wear), and the bearer is therefore expected to accrue compensating benefits from

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expressing such traits. Females are usually a limiting resource to male reproductive success, and males are expected to compete among themselves to maximise their number of matings or mates (intra-sexual selection). This is presumed to have led to the evolution of characteristics which provide a direct competitive advantage to males in the competitive process. Females on the other hand, due to their greater initial investment in reproduction, are expected to be selective in their choice of mate (inter-sexual selection). This may lead to the evolution of characters which reflect viability in the competing sex and act as an advertisement for attracting mates. Three main theoretical models of inter-sexual selection have been advanced to explain the evolution of these secondary sexual characteristics: (i) mate attractiveness: females prefer males with more ornate ornaments (Fisher 1930); (ii) good genes models: females are able to assess individual quality on the basis of the expression of the secondary characteristics (e.g. Zahavi 1977, Andersson 1982, Hamilton and Zuk 1982, Møller 1989a, 1991a, 1991b, Höglund *et al.* 1992); (iii) direct fitness benefits: the expression of male trait reflects aspects of male condition which correlate positively with female fitness e.g. male provisioning ability (e.g. Searcy 1982, Heywood 1989, Grafen 1990). Females may also select males on the basis of the quality of defended resources e.g. food and nest site quality (e.g. Alatalo *et al.* 1986). In species where sex roles are reversed, females tend to have secondary sexually characteristics, and males are the choosy sex (Petrie 1983). However, it is important to stress at the outset that sexual dimorphism or dichromatism is not necessarily a consequence of sexual selection, and can be attributed to natural selection (Selander 1972).

1.1.4. Mating sytems

Avian mating systems can be generally classed as monogamous or polygamous. The majority of bird species are monogamous (90%; Lack 1968), i.e. one male is paired to one female, with both parents helping to raise the offspring and the sexes typically contributing equal amounts to parental care. Individuals are considered to maximise their RS by pairing monogamously, as shown by male removal experiments during the provisioning of nestlings, which typically result in a reduction in fledgling success (see review in Bart and Tornes 1989). However, a better option for a male to increase his reproductive success is to pair with more than one female (Alatalo *et al.* 1981, Catchpole *et al.* 1985, Davies and Houston 1986, Pinxten *et al.* 1989). Polygyny, one male paired with several females, can arise by males controlling a limited resource which affects female settlement (e.g. Askenmo 1984, Bench and Hasselquist 1991, 1992), and secondly by males having the opportunity of deserting their partner. Mate desertion is expected because of the constraints that pairing monogamously places on male reproductive success and is possible because female investment earlier in the nesting cycle is relatively higher than that of their partners, thus committing them to continuing the breeding attempt if the male

deserts i.e. the 'cruel bind' (Trivers 1972). As well as experiencing a reduction in breeding success from pairing polygynously (by fledging fewer offspring, or offspring of lower quality; Dycrz 1988, Bart and Tornes 1989, Webster 1991), females may also suffer a reduction in body condition and survival (e.g. Dhondt 1987a). However, polygyny is relatively rare (occasionally observed in 39% of 122 well studied species, Møller 1986), and opportunities for males of mating polygynously may be limited by the conditions for the polygamy threshold model (Orians 1969) not being reached (Bjorklund and Westman 1986, Dhondt 1987b), through the pair female detering the settlement of additional females by inter-female aggression (Yasukawa and Searcy 1981, Slagsvold 1986, Viega 1992), or male-male competition for females.

1.1.5. Ensuring paternity and the pursuit of extra-pair copulations

Sexual association between individuals of the opposite sex does not necessarily reflect an exclusive mating relationship. Trivers (1972) argued that due to the potential variance in mating success between the sexes, males should attempt to pursue a mixed reproductive strategy (MRS), i.e. while ensuring his paternity of one brood and possibly providing care to the brood female he should opportunistically fertilise the eggs of other females. Extra-pair copulations (EPCs) are copulations with individuals other than the social mate (Westneat *et al.* 1990) and have been described in many bird species (see reviews in Westneat *et al.* 1990, Birkhead and Møller 1992). Males will gain an advantage if these copulations result in the fertilisation of one or more eggs, since they father more offspring and another male will provide parental care for these offspring.

In species where males invest in their putative offspring, and the cost of cuckoldry is high through losing paternity and investing care in unrelated offspring, behavioural adaptations have evolved to maximise the certainty of paternity. In birds these have taken two principal but not exclusive forms: (i) mate guarding, typified by close following of the pair female by the male (Beecher and Beecher 1979, Birkhead 1979); and (ii) a high copulation rate (Birkhead *et al.* 1987, Birkhead and Lessells 1988, Hunter *et al.* 1992). Female fertility peaks immediately prior to and during early laying (the fertile period), and paternity guards usually peak in their intensity during this time (see Birkhead and Møller 1992). The fertile period can therefore be considered to be a time of potential conflict between the sexes, with the pair male attempting to ensure paternity, extra-pair males attempting to gain extra-pair paternity, and the female 'choosing' which of the two are going to father her offspring.

Whether or not a female participates in EPCs depends on a trade-off between the potential costs and benefits. The main benefits females may receive by participating in an EPC are: (i) insuring against the pair male being infertile or having sperm of low viability (McKinney *et al.* 1984, Drummond 1984); (ii) receiving material benefits e.g. ejaculate

nutrients (which occurs principally in insects, e.g. Thornhill 1976), food and courtship feeding or parental care; and (iii) receiving genetic benefits either by her offspring inheriting 'good' genes or increasing their genetic diversity (see reviews in Westneat *et al.* 1990, Birkhead and Møller 1992). In birds, there is most support for the females receiving genetic benefis for their offspring by participating in EPCs, albeit in only a few studies (e.g. Smith *et al.* 1991, Kempenaers *et al.* 1992, Graves *et al.* 1993). Costs to females which participate in EPCs are the risk of: (i) producing poor quality offspring; (ii) physical injury and harassment by both the extra-pair males (whilst these males are pursuing EPCs) and the pair male (as a result of the female participating in EPCs); and (iii) reduced parental care by the pair male due to the possibility of being cuckolded (see reviews in Westneat *et al.* 1990, Birkhead and Moller 1992).

In birds, females may control paternity by a variety of pre-copulatory, copulatory and post-copulatory mechanisms (Birkhead and Møller 1993). By controlling which males they copulate with during the fertile period, females will be able to determine the paternity of their offspring (Lifjeld and Robertson 1992). Although speculative, females may exert control of paternity during copulations by controlling the extent of sperm transfer. Sperm ejection immediately following copulation has been recorded in several bird species (Davies 1983, 1992, Birkhead and Møller 1992) and may also be a post-copulatory mechanisim by which females also control paternity.

1.1.6. Sperm competition and storage

Not all copulations result in sperm transfer (Birkhead *et al.* 1988). However, even successful sperm transfer does not necessarily result in fertilisation due to sperm competition. Sperm competition is defined as "the competition between sperm from two or more males to fertilise the egg(s) of a single female" (Parker 1970) and in its broadest sense can refer to both the physiological (occurring in the female reproductive tract) and behavioural mechanisms involved in this process. The two important factors in determining the outcome of successful EPCs in the female reproductive tract are: (i) the degree of last male sperm precedence and (ii) the ability of females to store sperm (see Birkhead and Møller 1992). In most bird studies to date, the last male to copulate gains the majority of paternity in the brood, if inseminations by different males are more than four hours apart (Birkhead *et al.* 1988, but see Oring *et al.* 1992). If the time period between copulations is less than four hours, paternity is determined by the proportion of sperm inseminated by each male (Birkhead *et al.* 1988). The mechanism by which last male sperm precedence occurs is not clearly understood as there is conflicting evidence for sperm stratification (Birkhead *et al.* 1988, Birkhead *et al.* 1990) and sperm displacement (Lessells and Birkhead 1990) in accounting for this phenonomen. Sperm are stored in specialised storage tubules located in the utero-vaginal junction of the female reproductive tract and can remain

viable for up to several weeks (Howarth 1974, Birkhead 1988, Birkhead and Møller 1992). Sperm storage tubules (SSTs) have been found in all bird species studied to date and are probably ubiquitous in most avian taxa (Shugart 1988, Birkhead and Møller 1992, Briskie and Montgomerie 1993). The intensity of sperm competition depends on the frequency of extra-pair matings and the length of time that sperm remain viable in the storage tubules. Mate guarding and territoriality are considered to be behavioural adaptations to limit sperm competition, while a high copulation rate is thought to be a counter adaptation to high levels of sperm competition in the female reproductive tract (Birkhead and Lessells 1988, Møller and Birkhead 1992, Hunter *et al.* 1992).

1.1.7. Parental care

Males can either pursue additional matings or provide parental care. Since they are two exclusive behaviours which cannot be performed simultaneously, one expects a trade-off to occur between the two, depending on the circumstances that an individual male experiences (Westneat *et al.* 1990). The degree of paternal investment may therefore depend on the opportunities for additional matings and the ability of the female to compensate for a reduction in male investment (Trivers 1972, Westneat 1990, Whittingham and Robertson 1994). Females are expected to contribute more to the raising of the offspring due to their initially higher investment and, secondly, as a result of internal fertilisation they will be more sure of maternity than males will be of their paternity (Trivers 1972, Clutton-Brock 1991). Although controversial, under some circumstances males may also adjust their levels of parental care in relation to their certainty of paternity (Whittingham *et al.* 1992, Westneat and Sherman 1993, Dixon *et al.* 1994).

1.1.8. Measuring individual reproductive success

An accurate measure of individual reproductive success is needed in behavioural and evolutionary studies. In birds, it is not enough to assume that the number of chicks fledged is a sufficient measure of RS due to the behaviours which result in adults raising offspring other than their own, as known from e.g. behavioural evidence - EPCs by both sexes and egg dumping (intra-specific brood parasitism) by females - and genetic evidence of alternative reproductive strategies e.g. vasectomised male experiments (Bray *et al.* 1975), genetic plumage markers (Burns *et al.* 1980, Birkhead *et al.* 1989), differences between the parents in the heritabilities of morphological traits in the offspring (Alatalo *et al.* 1984c, Norris and Blakey 1989, for serious criticism of this approach see Dhondt 1991, Hasselquist *et al.* 1995), and allozyme analysis (Mumme *et al.* 1985, Westneat 1989). However, it was not until the advent of DNA fingerprinting (Jefferys *et al.* 1985a, b) that it was possible to accurately assign paternity and maternity to obtain a reliable measure of individual reproductive success (e.g. Burke and Bruford 1987, Wetton *et al.* 1987,

Birkhead *et al.* 1990, Gibbs *et al.* 1990, Morton *et al.* 1990, Westneat 1990, Kempenaers *et al.* 1992, Hartley *et al.* 1994, Dixon *et al.* 1994, Sheldon and Burke 1994). As a result, it is now possible to test models of sexual selection, parental investment and sperm competition.

1.1.9. Aims of study

This thesis uses behavioural observations and DNA fingerprinting to investigate the reproductive biology of the wheatear, and factors affecting this. It quantifies: (i) the success of paternity guards and alternative reproductive strategies in contributing to individual reproductive success; (ii) the effect the pair male has on female behaviour and the behaviour of extra-pair males during the fertile period, and levels of EPCs and extra-pair paternity (EPP); (iii) factors affecting levels of parental care of nestlings; and (iv) the effect of male and territory quality on reproductive success. This study seeks to integrate behavioural, molecular and ecological research to provide a comprehensive understanding of reproductive biology in the wheatear, focusing particularly on parental care and individual adult reproductive success.

1.2. The wheatear

The wheatear (*Oenanthe oenanthe L.*) is a medium sized, insectivorous, monogamous, sexually dimorphic passerine, the male being both brighter and larger than the female (Carlson and Moreno 1983, Svensson 1984). Both sexes have a conspicuous white rump and white tail with a black 'T' which is the basis of their name derived from Anglo Saxon, *wheat* meaning white and *ear* meaning arse or rump (Conder 1989). It is a migrant overwintering in north and central Africa and arrives at its breeding sites in Britain in early March, returning to its wintering grounds in early August (Cramp 1988, Conder 1989). Males usually arrive earlier at the site of breeding than do the females, and set up all purpose territories on which breeding occurs and the majority of food for nestlings and adults is collected (Brooke 1979, Conder 1989, Tye 1992). In Britain, wheatears are characteristically found on open upland and western coasts where there is short turf, either as a result of grazing or through extreme climatic conditions at higher altitudes. Their typical mode of feeding is termed 'dash and grab' and is best adapted to short vegetation, preying mainly on terrestrial inveterbrates. It is typified by individuals running several metres, picking up a food item and then running on and feeding again (Brooke 1981, Conder 1989, Tye 1992). Territories and their pattern of settlement are remarkably consistent between years (Brooke 1979, Conder 1989). Prey densities are usually higher on short vegetation, and individuals may use vegetation characteristics as an indirect measure of territory quality, preferentially settling on areas with short vegetation (Tye 1992).

The wheatear is a hole nesting species, laying 3-8 small blue eggs. The nest can be located in crevices in walls, or burrows or holes in the ground. Breeding commences about three weeks after the females return from their wintering grounds (Brooke 1979, Moreno 1989, Conder 1989). The monogamous pair bond lasts for the duration of the breeding season, but can be renewed annually through a strong bond to the territory. Males appear to employ the mate guarding strategy to ensure paternity, i.e. following and remaining in close proximity to the pair female during the fertile period (90% of male flights initiated by the female during the fertile period), and pursue additional matings during incubation (Carlson *et al.* 1985). Incubation lasts about 13 days and is done solely by the female (Conder 1989, Moreno 1989). After hatching, the female exclusively broods the chicks for the first 5-6 days (Moreno 1987a). Both sexes provision the nestlings, with males contributing up to 50% of chick feeds (Moreno 1987a), although their amount of investment during this time can vary (Cramp 1988). The chicks fledge after about two weeks, and then there is a period of post-fledgling care during which care of the juvenile wheatears is divided between the parents (brood division), for up to 10 days (Moreno 1984). In Britain, 15% to 47% pairs may have second broods (Cramp 1988, Conder 1989), though these are rare at the northern limits of their distribution (Moreno 1989). For a more comprehensive review of the wheatear see Cramp (1988) and Conder (1989).

1.3. Duration of study and study site

The field study was carried out from early March to the end of July in 1991 and mid-March to mid-June in 1992-93 on Bardsey Island, off the north-west coast of Wales (52° 46'N, 4° 47' W). The island is 2.8 km long, a maximum of 1 km wide and comprises 178 hectares. It is irregularly shaped, consisting of a northern rectangular 'slab' being joined to an inverted pear shaped southern part by a slender neck (see Fig 1.1). The east of the island is dominated by 'the mountain', and from the summit ridge (167m) slopes very steeply into the sea on its east side. The western aspect is less severe, and at its base levels out into an extensive and relatively flat plain, west of the mountain wall, comprising approximately 100 hectares (Jones 1988, see Fig 1.1).

The island is given over almost entirely to the grazing of sheep and consequently the plain is primarily pasture interspersed occasionally by gorse (*Ulex europaeus*) and bracken (*Pteridium aquilinum*). The southern tip, coastal margins of the plain, and eastern side of the mountain are mainly maritime grassland. The area west of the summit ridge to the beginning of the plain consists mainly of gorse and bracken. The study was carried out on the 20-27 territorial males (about 20 pairs) which bred west of the mountain wall. Pairs on the east side of the island were not studied due to the adverse nature of the slope. For a more detailed review of the natural history of Bardsey see Jones (1988).

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1.4. General methods

1.4.1. Catching and processing adults

All birds were trapped under licence from the Countryside Council for Wales (CCW) and British Trust for Ornithology (BTO). Adults were caught using Potter traps and spring traps (Davis 1981). In several instances adults were also caught at the nest while provisioning chicks more than 3 days old. Birds were ringed with a BTO numbered ring and three colour rings in combination (two rings per leg). They were measured, according to Svensson (1984), for wing length to the nearest mm (maximum chord, flattened) and weighed to the nearest 0.1g. Tarsus was measured to the nearest 0.1mm using vernier calipers, from the posterior notch at the inter-tarsal joint to the front of the tarsal bone with the toes bent down. All birds were blood sampled from the brachial vein under CCW and Home Office licence. Males were aged as first-year or second year or older according to plumage characteristics (Svensson 1984) and more precisely if their ringing history was known. Females could not be reliably aged unless their previous history was known.

1.4.2. Monitoring of nests and processing chicks

For study pairs the date when nest building commenced was noted and nests were checked daily to obtain the first egg date (FED). In the few instances in 1991 when the nest was found after FED but before clutch completion, I have assumed that eggs were laid on successive days (pers. obs., Conder 1989) and have back-calculated the FED accordingly. In 1991 six FEDs were estimated by back-calculating from chick age by assuming a 13-day incubation period (Conder 1989, Moreno 1989). In 1992-93 all nests were checked daily to obtain the FED. Nests were only revisited twice during incubation to obtain clutch sizes and hatching dates. Nests were numbered consecutively according to their FEDs and pairs were termed early or late depending on whether their FEDs were among the first or last half of the nests to be initiated, respectively.

Chicks were ringed and blood sampled as for the adults. Blood samples were taken 6 and 9 days after hatching. Tarsus and weight were also measured on day 9. Chick weight on day 9 was used as an estimate of fledging weight. After this time chicks became mobile and exhibited escape behaviour in response to disturbances at the nest by moving to the back of the burrow (see Conder 1989). Chick weights reach a plateau from about day 9 onwards (Moreno 1987, Conder 1989) and are probably a reliable indicator of fledging weights. Two measure of individual fledging success (F) were used in this study: (i) using the formula:

$$F = \frac{f}{e} \qquad\qquad 1.1$$

(Dhondt *et al.* 1990, Riddington and Gosler 1995), where f is the number of fledglings and e is the clutch size; and (ii) the number of fledglings produced per nest. The number of

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fledglings was calculated from the number of chicks weighed on day 9, taking into account any subsequently found dead in the burrow after their siblings had left the nest.

1.4.3. Defining the fertile period

There is a tendency in the literature to generalise on the duration of the avian fertile period which, however may be species-specific because it is impossible to accurately determine without invasive procedures and complex experimental regeimes (Birkhead *et al.* 1989, Birkhead 1992). To calculate the length of the fertile period (L) Birkhead and Møller (1992) use the formula:

$$L = (d + i + [c - i])\qquad\qquad 1.2$$

where d is the length of time (days) that viable sperm can be stored in the female tract, i is the inclusive number of days between fertilisation and oviposition of a particular egg, and c is the inclusive number of days between the first and last egg of the clutch. Without knowing the variable d, I have defined the fertile period on the basis of behaviours associated with reproduction: nest building, female solicitations, and copulations and associated displays (based on 220 hours of behavioural observations on 12 focal pairs from the 1991 field season).

(i) Nest building

In those days just prior to nest building, females were observed 'playing' with nest material and taking it into holes, which in many cases were far too big to nest in. This type of behaviour was an accurate cue in anticipating the start of building. In the main, nest building was carried out by the female although paired males were occasionally seen taking nesting material into the nest hole. The completed nest of a wheatear is usually in three parts: the foundation, the cradle, and the cup. Whether all three parts are present depends upon the shape and size of the burrow (see Conder 1989). The lining of the cup, with wool, hair and small feathers occurs in the three or four days just prior to and during early laying. Conder (1989) states that first clutch nests took between two and three weeks to build. Nest building was monitored due to the nature of experiments in 1992-93 (as discussed later in Chapter 5), and concerted building commenced on average 5.7 ± 0.4 (standard error, se) days prior to the FED (n = 26 pairs, 1992-93), which was similar to that observed by Moreno (1989).

(ii) Female solicitations, copulations and associated displays

The "greeting" display is well documented in the wheatear. It is similar to female copulatory solicitations in other avian species; ".. the breast is lowered so the body is almost horizontal but the head and neck stretched up. The tail is lifted slightly but not

fanned and the wings are outstretched, slightly drooped and shivered sideways very rapidly" (Conder 1989). It is exclusively a sexual display used by both sexes, typically when they meet, and is usually initiated by the female. Although Conder (1989) noted that this behaviour was most frequent during provisioning of the chicks at the nest, in this study a peak was observed prior to and during laying, all being directed at the male by the female (Kruskal-Wallis df = 2, H = 10.6, p < 0.001; Fig.1.2). "Greeting" displays were rarely observed during provisioning of the nestlings, however this is biased towards the time when the pair met at the nest hole (see section 6.3.1). In 230.5 hours (half-hour nest watches 1991-93), female-male greetings were only observed at a rate of 0.07 h-^{1} (n = 17) and male-female displays at 0.04 h-^{1} (n = 8). "Greetings" prior to and during laying have been observed to precede copulations (see also Conder 1989), and although not occurring exclusively during this time, appear to reliably indicate a female's readiness to mate. In 1991, all copulations (n = 10) and copulatory attempts (n = 5) occurred between days -5 and the penultimate egg date (Fig 1.3).

The dancing display is one of the better known wheatear displays (Cramp 1988, Conder 1989). When members of the pair display the male typically dances over the female. During this frenetic intra-pair display, females were often observed to crouch or become prostrate at the base of a wall, or in a small depression (see also Conder 1989). The male was observed to flutter across rapidly, in front of and behind the female, while seeming to flick and bounce over and around her using his wings. The male's tail is fanned during the display which can last up to about 8 seconds. At least 60% (6/10) of copulations and 100% of EPCs (n = 7) in 1991 were accompanied by this display, as were all attempted copulations. An approximate percentage is given for the number of copulations preceded by the dancing display, as some copulations were observed outwith watches. One third (3/9) of these displays terminated without the pair male copulating with the female. All displays occurred between days -5 and the penultimate egg date.

(iii) Definition of the fertile period

Based on the above observations I have defined the fertile period in the wheatear as from day -5 until the day the penultimate egg was laid (eggs being fertilised 24 hours prior to laying). This contrasts with that used by Carlson *et al*. (1985): -3 to +2, day 0 = first egg date.

1.4.4. Individual condition

Individual condition has been calculated using a mass/wing chord ratio (Mather and Robertson 1992) or (mass/[wing]^3) x 100 (Møller 1988). However, in the wheatear old males have longer wings than first-year males, creating a bias in either of these measures of condition (mean wing length [mm] ± se: young males = 96.58 ± 0.42, older males = 98.68

± 0.31, Mann-Whitney U-test, z = -3.78, p < 0.0001). First-year males returning to breed the following year also had longer wings (Wilcoxon paired-sign rank, n = 9, z = -2.42, p < 0.02).

The body condition index (BCI) was used as an alternative measure of individual condition, calculated as the residuals derived from the regression of log(weight) on log(tarsus) (Packard and Boardman 1987). The regression equation was calculated separately for each sex using all resident individuals sampled during 1991-93 (number of individuals used to calculate the regression: males, n = 62, representing 46 individuals; [equation of regression for males: $y = 1.03x - 0.06$]; females, n = 45, representing 35 individuals [equation of regression for females: $y = 0.50x + 0.70$]). The replication of some individuals between years had very little effect on the calculation of the BCI (BCI calculated from regression for all years together vs. yearly calculation of BCI: males, n = 62, $R^2 = 0.94$; females, n = 45, $R^2 = 0.99$). Individuals were not weighed on a standard date, but there was no suggestion that there was an effect of time in season on individual weight in either sex, which may otherwise have caused a bias in the calculation in the BCI (Spearman rank [1991-93 data combined]: male weight vs. weighing date, $R_{62} = 0.10$, ns; female weight vs. weighing date, $R_{42} = 0.09$, ns).

1.4.5. Calculation of the operational sex ratio (OSR)

The operational sex ratio (OSR) is the ratio of fertile females to non-guarding males (Emlen and Oring 1977, Birkhead and Møller 1992). I have made specific assumptions in the calculation of the OSR used in the following chapters (based on 220 hours of behavioural observations on 12 focal pairs from the 1991 field season): (i) males could only intrude on neighbours prior to and during the fertile period but were able to wander over the whole study area after clutch completion; and (ii) when males were provisioning chicks they were also only able to intrude on neighbours. Males were therefore assumed to be able to intrude at all times on neighbours during the breeding season. Unpaired males were assumed to be able to visit any territory on the island at any time. As a result, the OSR was slightly different on equivalent days for each male. A low value for the OSR indicates a male-skewed sex ratio, while a high value indicates a female skewed OSR.

The OSR may result in an under-estimate of the threat to a male's paternity because the absolute number of males as opposed to the ratio of available males to fertile females may be important. However, male availability is likely to be affected by the number of fertile females, at least to some degree, as accounted for by the use of the OSR.

1.4.6. Statistical tests

Unless otherwise stated statistical tests follow Sokal and Rohlf (1981) and Siegel and Castellan (1988) and the Statview 512+™ (Abucus Concepts Inc.), Statexact (Cytel

Software, Cambridge, US, 1991) and SAS (version 6.07) packages. All tests are two-tailed and corrected for continuity or tied ranks as appropiate.

1.5. Outline of chapters

This study examines male reproductive strategies and factors affecting paternal care and individual RS in the wheatear. Chapters 2 to 4 test for evidence of a male mixed reproductive strategy and the consequences for individual male reproductive success using a combination of behavioural and paternity data: Chapter 2 uses behavioural observations to examine mate guarding and factors affecting its initiation, intensity and termination; Chapter 3 uses behavioural observations to examine the pursuit of EPCs by males and females; Chapter 4 measures individual reproductive success using DNA multilocus fingerprinting. Chapter 5 examines the effect of temporarily removing the pair male during the fertile period on the behaviour of the pair female and extra-pair males and the consequences on levels of extra-pair paternity. Chapter 6 uses a combination of natural observations and temporary male removal experiments (as used in Chapter 5) to also simulate a male's uncertainty of paternity to examine factors affecting levels of parental and paternal care of nestlings. Chapter 7 examines the effect of territory quality on male mating success and individual reproductive success. Finally, Chapter 8 brings together the results from the data chapters in a brief resumé and discussion.
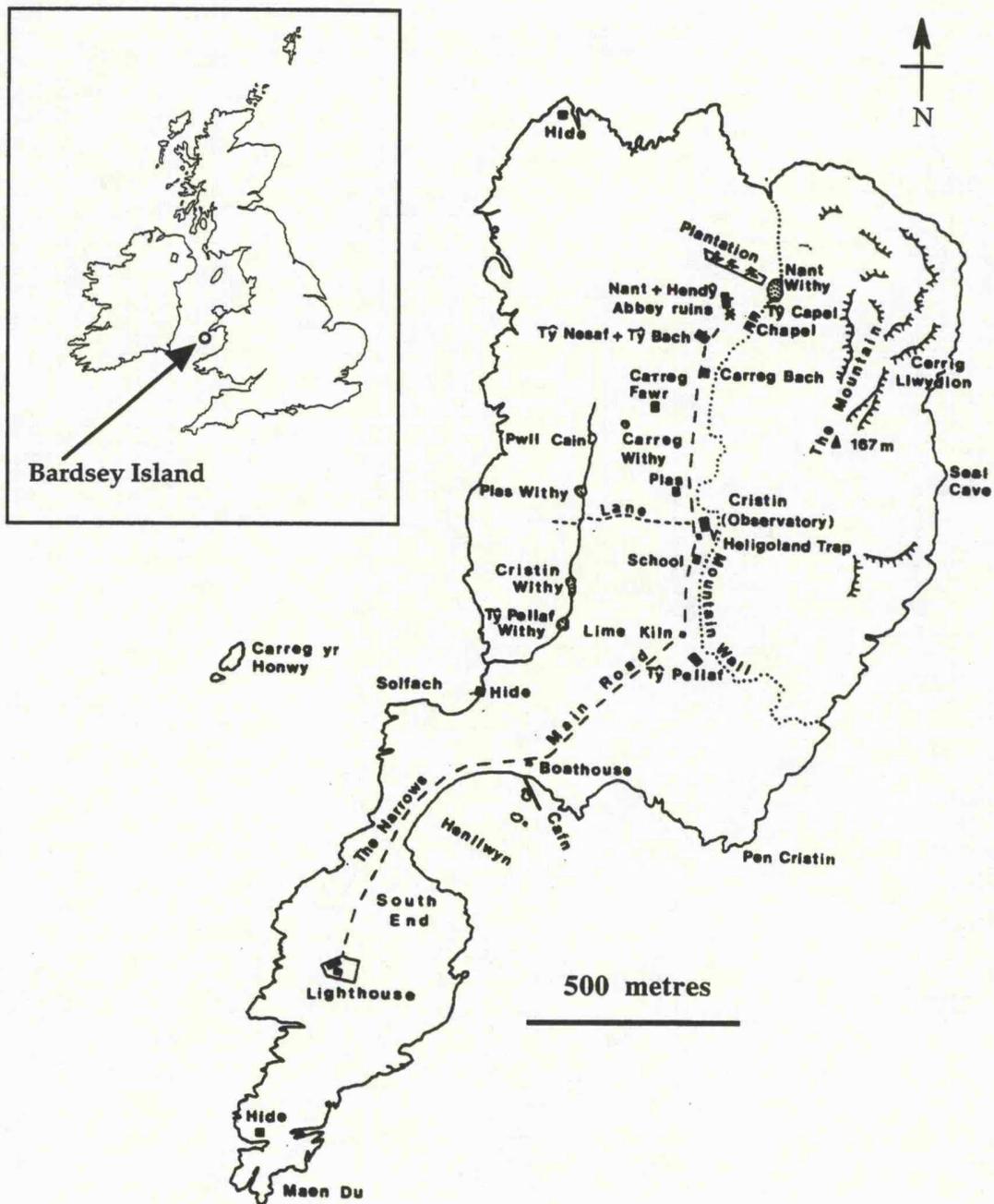
Fig 1.1. Map of Bardsey Island. Used courtesy of Peter Roberts and taken from his book *The Birds of Bardsey* (Bardsey Field and Bird Observatory, Wales 1985). Study pairs bred on the area west of the mountain wall, referred to in the text as the plain. Pairs east of mountain wall were not considered in the study.

(i)

(ii)
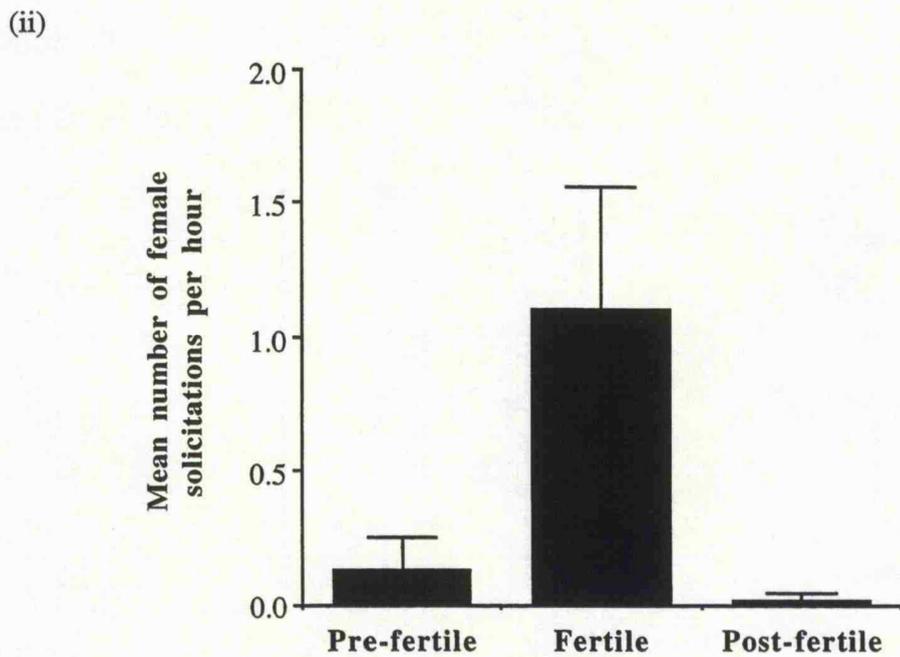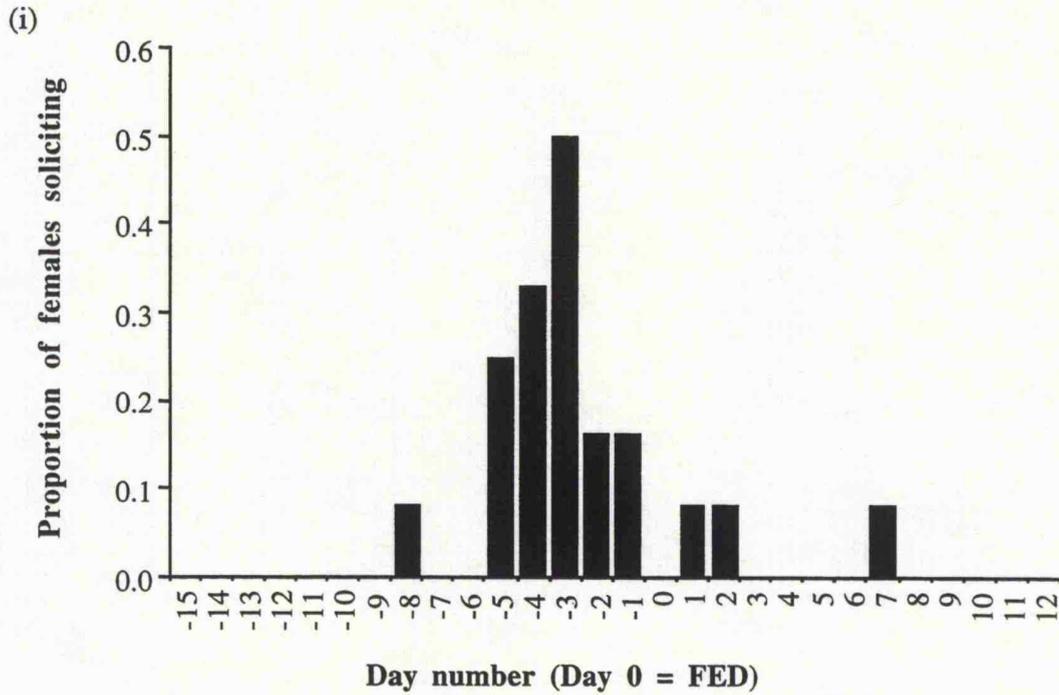
Fig. 1.2. Female solicitation displays: (i) shows the proportion of focal females (n = 12) that were observed performing solicitations relative to the first egg date (FED = day 0), and (ii) shows the mean number of female solicitations per hour (± se) in each time period relative to female fertility.

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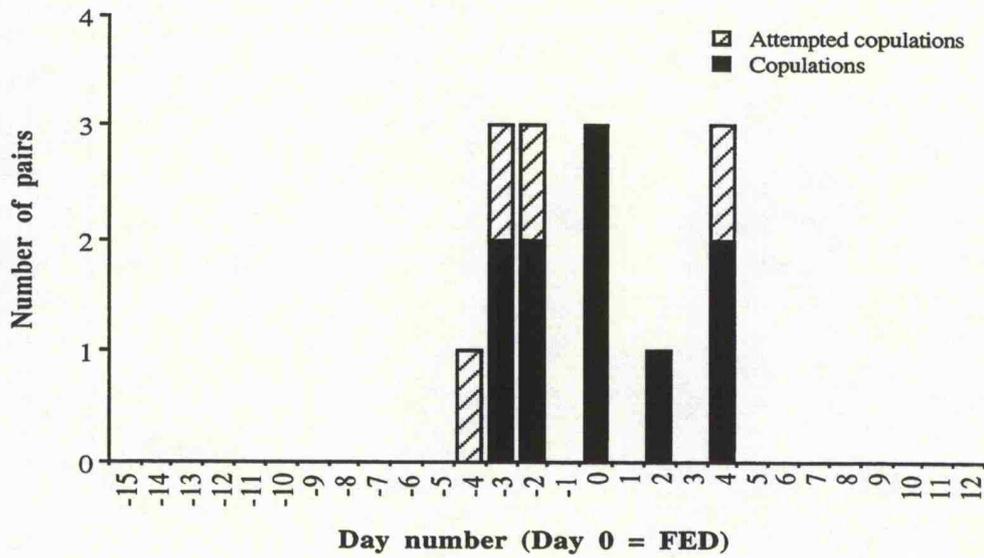
Fig 1.3. Number of pairs observed copulating or attempting to copulate relative to the first egg date (FED = Day 0). Data based on observations of 12 focal pairs.

Chapter 2. The pursuit of a mixed reproductive strategy
Part I: Paternity assurance behaviours

2.1. Introduction

In bird species where there is considerable male investment, for example in the provisioning of chicks and fledglings, the cost of being cuckolded is potentially high, and a male should attempt to ensure the paternity of any offspring he helps to raise. In many species, pair males are observed to follow and remain in close proximity to their female prior to and during egg laying. This close association between the sexes is assumed to be a means through which the pair male ensures his paternity, by limiting the access of extra-pair males to his female (Beecher and Beecher 1979, Birkhead 1979). This mate guarding behaviour has been documented in at least 53 species, including both solitary and colonial breeders (Birkhead *et al.* 1987). Short-term male removal experiments conducted prior to and during egg laying have shown an increase in the number of EPCs experienced by the pair female (Møller 1987a, Bjorklund and Westman 1983, Birkhead *et al.* 1989, Westneat

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1994). The risk of EPCs has also been shown to be proportional to intra-pair distance (Davies 1985, Alatalo *et al.* 1987, Møller 1987b). Therefore, by following and remaining close to his female, a male can reduce the access of extra-pair males and, ultimately, the risk of cuckoldry.

Mate guarding is potentially costly to a male in terms of time, energy and lost opportunities to pursue EPCs. Its intensity can be considered to be the result of a trade-off between ensuring paternity and these other requirements. Weight loss by males during the fertile period supports the idea that guarding can be energetically costly (Ridley and Hill 1987, Lambrechts 1989, Møller unpublished in Birkhead and Møller 1992). If such costs are incurred, mate guarding should coincide precisely with the pair female's fertile period, i.e. that time when an insemination can result in fertilisation of an egg or clutch (Lake 1975), and also should vary in intensity depending on the threat to paternity (Davies 1985, Møller 1987b).

The risk of being cuckolded can be influenced by several environmental factors. The synchrony of breeding in a population, and ultimately its effect on the operational sex ratio (OSR), i.e. the ratio of fertile females to non-guarding males (Emlen and Oring 1977, Birkhead and Møller 1992), may increase the opportunity for EPCs. In dense populations, such as colonial breeding species, there is greater scope for the pursuit of additional matings which can result in an increase in EPC intensity and a prolonged period of mate guarding (Møller 1987c). Additionally, although speculative, the vegetation and topography of the breeding environment may also affect opportunities for EPCs, with guarding being less intense in open habitats (Sundberg 1992, but see Bjorklund and Westman 1986). Differences between individual males in their guarding intensity or ability to guard have also been noted, and though in the main untested, factors potentially affecting interspecific variability are male age and experience, as well as male or female quality (Birkhead and Møller 1992).

The initiation of mate guarding has been shown in some species to be influenced by females beginning to solicit copulations and the onset of nest building and egg laying (Lumpkin 1981, Pinxten *et al.* 1987, Møller 1985, Birkhead and Møller 1992). A reduction in the chances of an EPC being successful as laying proceeds (potentially detectable by the male through the female spending more time on the nest) and a corresponding increase in the cost:benefit ratio of mate guarding, may herald its decline towards the end of clutch completion and a trend towards males pursuing EPCs instead (Birkhead 1982, Møller 1987b, Pinxten *et al.* 1987, Birkhead and Møller 1992).

In most species the frequency of copulation decreases after the first egg is laid. Once egg laying has started, subsequent copulations may be inefficient in transferring sperm, resulting in a decrease in their frequency during laying (Brillard and Bakst 1990). The general pattern of mate guarding reflects this apparent pattern of female fertility,

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peaking prior to and during early laying (Birkhead *et al.* 1987). Indeed sperm may be flushed out of storage tubules (located in the utero-vaginal area of the female reproductive tract) during laying. This response is possibly amplified for sperm inseminated during laying, and it may be more important for males to guard more intensively prior to laying as sperm from successful copulations during this time may be stored and have a greater chance of fertilising eggs (Birkhead and Møller 1992). Female fertility is also thought to vary within the fertile period, peaking about 24 hours before the laying of each egg, during the "insemination window" (Cheng *et al.* 1983). One therefore expects mate guarding to also be more intense and copulations to be more frequent in the morning and evening, as well as before and during early laying.

Mate guarding is not the only mechanism by which males attempt to ensure their paternity. In those species where mate guarding is not feasible, primarily in raptors and semi-colonial or colonial seabirds, it is compensated for by a high copulation rate (Birkhead *et al.* 1987). Territoriality is also considered to act as a paternity guard. As well as containing resources essential for breeding, territories can also be considered to act as a "buffer" between the pair female and extra-pair males. In some species males have been shown to maximise the size of their territory during their female's fertile period i.e. that time when an EPC poses the greatest threat to their paternity (Møller 1990b, 1992 but see Dunn 1992).

Accurate data on the duration of the avian fertile period are scarce and probably species- or genus-specific, ranging from two weeks prior to laying until 24 hours before clutch completion (Birkhead and Møller 1992 and references therein). Conclusions on the duration of the fertile period are further complicated by the fact that females can store sperm from more than one male (so inducing sperm competition, Parker 1970). Mate guarding and territoriality can be considered to be behavioural means of limiting sperm competition (and may explain why mate guarding begins in the days prior to laying) while a high rate of copulation is presumably an adaptation to counter sperm competition in the female reproductive tract.

Mate guarding can be considered to be the evolutionary corollary of the pursuit of additional matings outside the pair bond. Males are able to adjust the intensity and duration of mate guarding in relation to the threat of cuckoldry and costs of mate guarding (Møller 1987c). The duration, ability or intensity of a male's guarding (as well as his sperm viability) may reflect his quality and affect his overall reproductive success.

The wheatear exhibits a low rate of copulation and males appear to employ the mate guarding strategy to ensure paternity. As well as closely following the female (90% of male flights initiated by the female), and remaining close to her (less than two metres) during the fertile period, males also perched higher than the female during this time (Carlson *et al.* 1985). This chapter examines the extent of mate guarding in the northern wheatear and

identifies factors influencing its initiation, intensity and cessation.

2.2. Methods

2.2.1. Data collection

Twelve study pairs on territory were observed in 1991, from pairing until near hatching. Thirty minutes of behavioural observations were taken when both members of the pair could be observed. A maximum of one hour was spent on each territory, the watch beginning one minute after both members of the pair were found. Any watch with less than 15 minutes data was not used. The following specific behaviours and interactions between the pair were noted:

1. Intra-pair distance on the minute every minute, which was estimated to the nearest metre on the basis of "bird lengths" and known distances between local topographical features.

2. Which sex was perched above the other (an individual was considered to be perched higher if it was greater than one bird height (approximately 11 cm) above its partner, on the minute every minute.

3. Total number of male flights.

4. Total number of female flights.

5. Number of female and male flights which were followed by the other partner within 5 seconds.

6. Number of song bouts and other vocal displays per time spent on territory.

7. Number of territorial and sexual displays.

8. Amount of time spent off territory by each sex.

9. Number of intrusions and identity of intruding males. Boundary incidents were not considered to be intrusions. In the analysis the total male intrusion rate per hour was used as there was no reason to believe that residents treated migrant males differently from other residents during intrusions: 63% (24/38) and 65% (39/60) of intrusions by migrants and colour-ringed males respectively, were chased by the pair male. There was a weak correlation for the 12 focal territories between the total number of intrusions and intrusions by residents (Spearman rank, $R_{12} = 0.54$, $p < 0.1$).

Time and general weather conditions were also noted during each watch.

2.2.2. Data analysis

A total of 220 hours of behavioural observations was collected for the 12 study pairs, but only 150 hours were used in this analysis due to predation of three females before egg laying, since in this analysis behaviours are related to first egg dates (FED = day 0). The mean number of hours of observation per territory ± standard error (se) = 12.0 ± 1.1. The following analyses refer to three time categories based on the reproductive status of the female: pre-fertile (days prior to -5), fertile (-5 to penultimate egg date) and post-

fertile (day after last egg was laid to near hatching). For details of the definition of the fertile period see section 1.4.3.

The nests of the 12 study pairs were located whilst they were being built, and checked daily during the period of nest lining to obtain the FED. The FEDs of an additional seven nests in 1991 were back-calculated using the method previously described (see section 1.4.2). Nests were numbered consecutively according to their FED. Pairs were termed early or late depending on whether their FEDs were among the first or last half of the nests to be initiated respectively. The body condition index (BCI) (Packard and Boardman 1987) was used as a measure of individual condition. The BCI and OSR were calculated as in sections 1.4.4 and 1.4.5, respectively.

2.2.3. Multivariate analysis

The influence of a series of independent factors on male and female behaviour (dependent variables) over the whole breeding season was examined initially using stepwise multiple regression (termed step 1). There were two categories of independent variables: "control" variables and "selection" variables. Control variables were environmental factors which might have affected behaviour and selection variables were biological factors examined in the regression. The independent control variables were time, wind speed, percentage cloud cover, general weather conditions (i.e. separate variables for dull, sunny, bright or raining, entered categorically as 1 or 0), and daily temperature. Independent selection variables were operational sex ratio (OSR), extra-pair male intrusion rate, and the time relative to female fertility (pre-fertile, fertile, and post-fertile). Separate variables were entered for each of these time periods categorically as 1 or 0. Independent control variables were entered into the model before the independent selection variables (see Table 2.1). The effects of specific independent selection variables on dependent behavioural variables were also examined within the fertile period alone (see Table 2.2). There was a degree of pseudo-replication in these two analyses as individual territories were considered on successive days from days -20 to +12 and were not independent of each other. The purpose of these step 1 analyses was to identify any effect of temporary environmental factors on the behavioural variables and so allow these variables to be controlled for in subsequent analyses.

A second series of multivariate analyses was performed using the mean residuals for the 12 focal males for each behaviour from Table 2.1 as the dependent variables (termed step 2). Phenotypic, demographic and additional data were entered as independent variables in this second set of analyses, in which pseudo-replication was avoided by entering the mean value for each male only once. The independent variables were territory size, male age, FED expressed as days after first egg was laid on the study area (day 0 = 5th May, 1991), male settlement date, and male and female body condition. Among the independent

variables there was a correlation between (i) FED and OSR (the OSR was male-skewed for later breeding pairs), and (ii) male age and settlement date (old males returned earlier than first-year breeders) (Spearman rank, FED vs. mean OSR in the fertile period, R_{17} = -0.885, p < 0.001; Mann-Whitney U-test, male age vs. male settlement date, z = -3.84, p < 0.005). Step 2 analyses were performed for the whole breeding season and the fertile period (see Tables 2.3 and 2.4 respectively). Due to their non-independence, male age and settlement date were entered both separately and simultaneously in this set of analyses.

In both steps 1 and 2, the residual values resulting from the stepwise regressions between each dependent behavioural variable and the independent variable were often significantly skewed. Dependent variables were therefore transformed when appropriate (using log, rank or arcsine transformations). Stepwise multiple regression analyses were performed with F-to-enter values equivalent to p < 0.1 in linear regression (Sokal and Rohlf 1981). Degrees of freedom for F-to-enter values are expressed as $F_{V1,V2}$, where V1 = number of independent variables introduced into the final model and V1 + V2 + 1 = total number of observations. F-to-enter values prefixed with a minus sign represents a negative association. The robustness of the regression results was tested by "jack-knifing" the variables, i.e. omitting each variable in turn from the analysis to see if the significant variables remained in the regression model.

Many of the tests involved the use of multiple dependent variables. However, these variables were not always independent of one another and no global correction of statistical probabilities was therefore conducted. This must be kept in mind when interpreting the results (see Rice 1989).

2.2.4. Decline in mate guarding behaviours

Linear regressions were performed for the daily residuals of mate guarding behaviours, calculated from Table 2.1 after entering the significant independent control variables as indicated, for each of the 12 focal males from day -1 to the penultimate egg date. Regression slopes were compared among males to examine the effect on the rates of decline in mate guarding behaviours of: (i) the OSR in fertile period, (ii) male BCI, (iii) male settlement date, and (iv) male age. Later laying females laid smaller clutches, and rates of decline were also compared from days -1 to +2 in an attempt to control for the possible increased costs in mate guarding to early breeding males in experiencing a longer fertile period (see Table 2.5).

2.3. Results

2.3.1. Multivariate analysis: step 1, whole breeding season (see Table 2.1)

(i) Intra-pair distance and proportion of time spent near female

There was no significant reduction in intra-pair distance during the fertile period.

Males remained relatively close to their female from pairing until near clutch completion although the average intra-pair distance was minimal for 12 pairs on day -1. The intra-pair distance increased in the post-fertile phase (when the female was not incubating) ($F_{1,248}$ = 18.4, $p < 0.001$; see also Fig. 2.1).

Males spent less time within five, ten and 15 metres of their female in the post-fertile phase (% < 5m, $F_{1,248}$ = -28.8, $p < 0.001$; % < 10m, $F_{2,247}$ = -54.2, $p < 0.001$; % < 15m, $F_{2,247}$ = -33.2, $p < 0.001$). As the OSR decreased (i.e. the number of free males increased) males spent more time within 15 metres of their partner (% < 15m, $F_{2,247}$ = -7.1, $p < 0.01$).

(ii) Intra-pair following

Males followed their pair female more in the fertile period peaking for the 12 pairs on day -1, and less in the post-fertile periods (Fertile, $F_{2,247}$ = 9.2, $p < 0.01$; Post-fertile, $F_{2,247}$ = -3.9, $p < 0.05$; see also Fig. 2.1). This increase in male following during the fertile period was not due to an increase in the number of female flights during this time. There was no difference in the number of female flights per hour in the pre-fertile and fertile periods but there was a reduction during the post-fertile period, due to incubation which is done solely by the female (mean number of female flights per hour ± se: pre-fertile = 12.2 ± 1.19, fertile 9.21 ± 0.89, post-fertile = 3.32 ± 0.79; Wilcoxon paired-sign rank, mean number of female flights per hour; pre-fertile vs. fertile, n = 10, T+ = 42 p = 0.16; post vs. pre-fertile, n = 10, T+ = 55, p = 0.002; post-fertile vs. fertile, n = 12, T+ = 77, p = 0.001).

Females followed their partner more during the fertile period ($F_{2,247}$ = 3.78, $p < 0.05$).

(iii) Proportion of time male spent perched above female

Males spent more time perched above their female than vice versa throughout the breeding season (Wilcoxon paired-sign rank, proportion of time male perched above female vs. proportion of time female perched above male: prefertile, n = 11, T+ = 63, p = 0.004, fertile, n = 12, T+ = 78, p = 0.0004; post-fertile, n = 12, T+ = 78, p = 0.0004). This indicates that the male perch height was higher than their female's. Males also spent more time perched higher than their partner in the fertile period ($F_{1,246}$ = 8.7, $p < 0.01$; see also Fig. 2.1).

(iv) Tail flashing

This is a territorial display typically performed by the male and directed at

conspecifics (though females were occasionally seen displaying in the male's absence). It involves the individual adopting an upright posture and fanning its conspicuous white tail feathers at intruders or at neighbours during the establishment of a territory. It was often accompanied by a warbling sub-song (see also Conder 1989). Increased bouts of tail flashing were made by males during the fertile period ($F_{1,287} = 17.0$, p < 0.001). There was less tail-flashing during windy conditions ($F_{1,287} = -4.39$, p < 0.05).

(v) Song

Males sang more in the morning than later in the day ($F_{3,285} = -5.16$, p < 0.01), and less so when it was windy ($F_{3,285} = -10.5$, p < 0.001). There was no correlation with any of the selection variables. There was no difference among males in their respective song rates (Kruskal-Wallis, $H = 15.8$, df = 11, p > 0.1).

(vi) Aerial displays: song flights and non-vocal displays

Song flights are a conspicuous aerial display which involved the male flying upwards in a jerky flight with his tail fanned while uttering short clicks and calls. Just prior to and on reaching its zenith (5-18 metres above the ground), a male would sing one or more refrains and then dive back with his tail still fanned to a new or previous perch (Conder 1979, pers. obs.). Males also preformed these displays without singing. (The display total is the sum of vocal and non-vocal aerial displays).

There was no correlation with any of the control variables. Males song flighted when their pair female was incubating ($F_{2,286} = 11.3$, p < 0.001), and when the OSR was female-skewed ($F_{2,286} = 4.0$, p < 0.025). Similar results were obtained for total display rates (see Table 2.1.).

2.3.2. Multivariate analysis: step 1, fertile period

(i) Diurnal effects

The behavioural variables associated with the mate guarding hypotheses (intra-pair distance, % < 5m - % < 15m, %YF, %P+) were examined to test whether or not there was a diurnal pattern in their respective intensities during the fertile period. Males spent more time within five metres of their female later in the day ($F_{1,107} = 4.0$, p < 0.05). There was no effect of time on any of the other dependent variables.

(ii) OSR and intrusion rates (see Table 2.2)

The pattern of the male remaining in close proximity to the pair female in response to a male-skewed OSR throughout the whole season was also found to apply to the fertile period (see Table 2.2). Males remained closer to, and tended to spend more time perched

above and following their female when the OSR was male skewed (Mean intra-pair distance, $F_{1,107} = 6.6$, $p < 0.05$; $\% < 5m$, $F_{1,107} = -4.6$, $p < 0.05$; $\% < 10m$, $F_{1,107} = -13.0$, $p < 0.01$; $\% < 15m$, $F_{1,107} = -14.8$, $p < 0.01$; $\% P+$, $F_{1,107} = -3.1$, $p < 0.1$, $\%YF$, $F_{1,107}$, $F = -2.4$, $p < 0.1$) .

2.3.3. Summary: step 1, whole breeding season and fertile period

There was no reduction in intra-pair distance during the fertile period, but it increased during the post-fertile phase. Consequently, males spent less time within five, ten and 15 metres of their partner during this time. A male-skewed OSR resulted in males spending more time within 15 metres of their partner. Males spent more time perched above their females during the fertile period and in response to intrusions by extra-pair males and a male biased OSR. Males followed their females more during the fertile and less during the post-fertile period. Males sang less later in the day and during windy conditions. Males tail flashed more during the fertile period and performed more aerial displays when their pair female was incubating and when there was a female skewed OSR. There was no diurnal pattern to the behaviours traditionally associated with mate guarding. Males remained close to their female in response to a male-skewed OSR during the fertile period.

2.3.4. Multivariate analysis: step 2, whole breeding season (see Table 2.3)

Results varied when male age and settlement date were entered separately and together, but settlement date was the main factor in explaining variance in the data when both variables were entered together. There were never any cases when age explained variance in a dependent variable and male settlement date did not.

Whether entered separately or together with male age, later settling males consistently remained closer to and followed their females throughout the whole season than early settling males (Mean, $F_{2,9} = -22.9$, $p < 0.002$; $\% < 5m$, $F_{2,9} = 7.1$, $p < 0.05$; $\% < 10m$, $F_{2,9} = 9.2$, $p < 0.01$; $\% < 15m$, $F_{2,9} = 15.6$, $p < 0.002$; $\%YF$, $F_{2,9} = 52.9$, $p < 0.001$).

For those variables when additional variance was explained by age after entering male settlement date, old males spent more time within ten and 15 metres of, and more time perched above, their female ($\% < 10m$, $F_{2,9} = 4.29$, $p < 0.05$; $\% < 15m$, $F_{2,9} = 8.63$, $p < 0.001$; $\%P+$, $F_{1,10} = 6.52$, $p < 0.05$)

Males with a low BCI remained closer to and followed their female more than individuals of better condition and performed fewer tail flashing displays ($\%YF$, $F_{1,10} = -7.62$, $p < 0.025$; TF, $F_{1,10} = 10.41$, $p < 0.01$).

Table 2.1. Stepwise multiple regression of independent variables vs. dependent behavioural variables for the whole breeding season (step 1).

Independent variables

Independent variables		Dependent behavioural variables										
Control variables	Mean	%<5m	%<10m	%<15m	%P+	%YF	%YM	Song	TF	% off	SY	Dis Tot
Time	0.02	0.35	0.97	0.20	-0.10	-2.34	-3.35†	-5.16*	-1.97	-5.26*	-0.99	-1.35
Wind speed	0.03	0.00	0.05	0.14	0.15	0.25	0.15	-10.54***	-4.39*	-0.25	-1.82	-1.02
% cloud cover	-0.28	-0.43	-0.40	0.73	-0.06	0.20	-0.02	-0.21	0.76	-5.06*	0.00	0.01
Dull	2.50	-0.56	-1.77	-0.16	-1.07	3.25†	-3.78*	-0.06	0.93	-0.20	-0.52	-1.44
Bright	-0.59	-1.18	0.00	0.53	0.01	-0.72	-0.96	-0.41	0.08	-0.11	0.71	0.73
Sunny	-0.02	1.73	1.64	-0.02	0.89	0.48	0.84	0.68	-0.25	-0.01	0.16	0.43
Rain	-2.06	0.47	2.73†	2.14	-0.01	0.05	0.00	-0.02	-1.70	2.12	-0.95	-0.36
Daily temperature	-0.04	-1.06	-0.75	-0.80	-0.24	-1.17	-0.32	0.40	0.01	-0.12	0.16	0.29
Selection variables												
Intrusions h-1	-0.06	0.00	0.00	0.00	3.07	0.00	1.20	0.52	-0.06	-0.16	0.65	1.00
OSR	1.21	-0.08	-3.56†	-7.07**	-3.38†	-2.16	-2.53	-0.66	-1.99	0.06	4.03*	3.78*
Pre-fertile	0.66	0.20	-0.52	-2.11	0.99	-0.02	-0.01	-0.23	-0.44	0.28	-0.24	-0.32
Fertile	-0.95	0.07	1.64	2.32†	8.67**	9.22**	3.78*	-0.05	16.99***	-0.78	0.00	0.31
Post-fertile	18.42***	-28.76***	-54.20***	-33.24***	-0.79	-3.85*	-3.25†	0.01	-0.17	22.93***	11.33***	10.19***
Total R^2	0.07	0.10	0.18	0.12	0.04	0.08	0.06	0.05	0.06	0.10	0.04	0.03

Columns show F values resulting from stepwise multiple regressions between each dependent behavioural variable and the independent behavioural variable. Independent variables indicated with *, **, or *** were introduced into the final regression model and explained a significant amount of variation in the dependent variable († $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). F-to-remove values are given for those variables which entered the final model and F-to-enter values are given for other variables. Independant control variables were entered into the model before the independent selection variables. R^2 refers to the amount of variation in the data which is explained by the model.

Independent control variables are weather conditions and self explanatory (for more details see text). Independent selection variables are: intrusions h-1, male intrusion rate per hour; OSR, operational sex ratio; pre-fertile, fertile, and post-fertile, are periods of time relative to female fertility. Dependent behavioural variables are: Mean, mean intra-pair distance; %<5m, %<10m, and %<15m, proportion of time males was within five, ten, and 15 metres of the pair female respectively; %P+, proportion of time male perched above the pair female; %YF, proportion of female flights which the male followed; %YM, proportion of male flights which the female followed; TF, no. of tail flashes per hour; song, numbers of songs per hour; % off, proportion of time male spent off territory; SY, number of song flights per hour; Dis Tot, total number of aerial displays.

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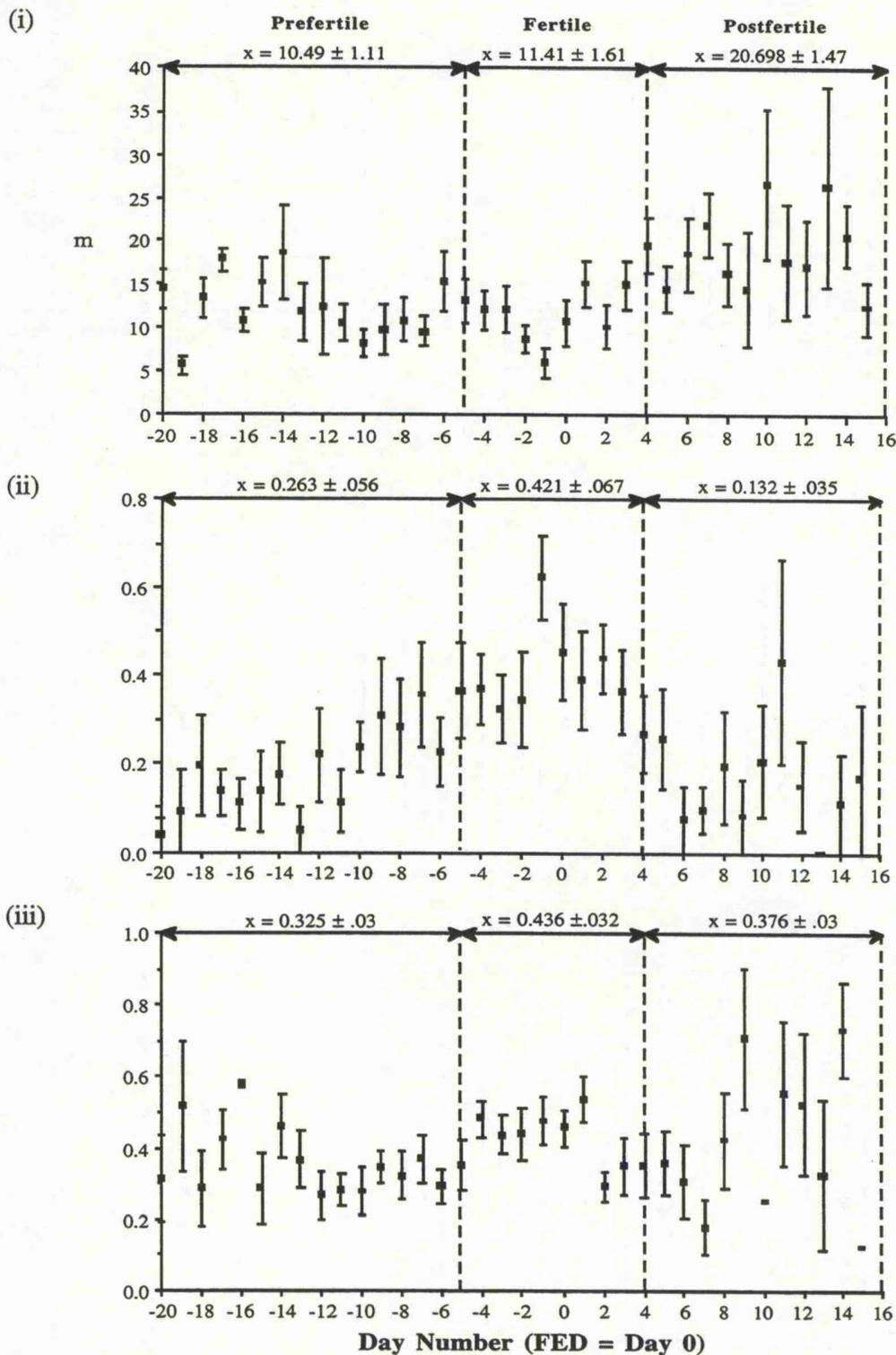
Fig. 2.1. (i) Mean intra-pair distance, (ii) mean proportion of female flights followed by the male, and (iii) mean proportion of time male spent perched above female, per day for the 12 focal pairs relative to their respective FEDs (day 0). The three time periods, pre-fertile, fertile, and post-fertile are marked with broken lines. A mean value (x) ± se is shown for each period.

Table 2.2. Stepwise regression of dependent behavioural variables in fertile period vs. independent selection variables (step 1).

Independent variables	Dependent behavioural variables					
	Mean	%<5	%<10	%<15	%P+	%YF
Intrusions h-1	0.01	0.05	0.08	0.18	2.08	0.03
OSR	6.63**	-4.55*	-13.02**	-14.77**	-3.06*	-2.44
R^2	0.05	0.03	0.10	0.11	0.02	-

Columns show F values resulting from stepwise multiple regressions between each dependent variable and the independent variables. Independent variables indicated with * or ** were introduced into the final regression model and explained a significant amount of variation in the dependent variable (* $p < 0.05$, ** $p < 0.01$). F-to-remove values are given for those variables which entered the final model and F-to-enter values are given for other variables. R^2 refers to the amount of variation in the data explained by the model.

Independent variables are: intrusions h-1, male intrusion rate per hour; OSR, operational sex ratio. Dependent behavioural variables are: Mean, mean intra-pair distance; %<5m, %<10m, and %<15m, proportion of time males was within five, ten, and 15 metres of the pair female respectively; %P+, proportion of time male perched above the pair female; %YF, proportion of female flights which the male followed.

Table 2.3. Stepwise multiple regression of independent variables vs. dependent behavioural variables for whole breeding season (step 2).

Dependent behavioural variables

Independent variables	Mean (m)			%<5m			%<10m			%<15m			%YF			%YM		
FED	-7.14*	-6.85*	-6.85*	2.17	0.93	0.93	1.99	4.13†	1.80	1.98	3.69†	1.36	32.40**	26.23**	26.23**	0.44	2.51	1.17
Male age	13.79**	-	-0.42	-5.38*	-	0.09	-3.98†	-	4.29*	-2.93	-	8.63†	-41.22**	-	-0.03	-1.94	-	5.32*
Ter size	-0.40	-0.17	-0.17	0.45	0.10	0.10	0.91	0.83	0.79	1.21	3.10	0.89	-0.56	-3.06	-3.05	1.62	2.18	0.27
Male BCI	-0.34	0.70	0.70	-8.96*	-8.72*	-8.72*	-0.06	-3.35†	0.00	-0.24	-1.14	-0.01	-12.67**	-7.62	-7.62*	-1.43	-2.75	0.14
Fem BCI	0.00	-0.29	-0.29	-0.77	-0.26	-0.26	-0.07	0.52	0.33	-0.06	0.07	0.56	-0.66	0.03	0.03	0.17	0.58	0.02
Set Date	-	-22.87**	-22.87**	-	7.06*	7.05*	-	12.06*	9.20**	-	7.89*	15.56***	-	52.86**	52.86**	-	5.32*	9.39*
R^2	0.63	0.74	0.74	0.49	0.54	0.54	0.59	0.59	0.59	0.41	0.68	0.68	0.85	0.88	0.88	-	0.32	0.56

Independent variables	%P+			TF			Song			% off territory			Song flights			Display total		
FED	-0.01	0.06	0.00	0.03	0.03	0.02	0.01	0.01	0.01	1.78	1.78	1.78	0.51	0.51	0.51	0.30	0.30	0.30
Male age	6.52*	-	6.52*	0.08	-	0.08	2.33	-	2.33	3.14	-	3.14	2.29	-	2.29	1.73	-	1.73
Ter size	0.02	0.17	0.02	-3.07	-3.07	-3.07	2.79	-	2.78	1.57	1.57	1.57	1.05	1.05	1.05	0.90	0.90	0.90
Male BCI	-0.02	-0.18	0.02	10.41**	10.41**	10.41**	0.00	0.00	-0.06	0.83	0.83	0.83	-3.14	-3.14	-3.14	-2.89	-2.89	-2.89
Fem BCI	0.00	-0.01	0.01	0.24	0.24	0.24	-0.27	-0.27	0.39	-0.02	-0.02	0.02	2.13	2.13	2.13	2.78	2.78	0.01
Set Date	-	-5.44*	0.01	-	-0.25	-0.24	-	-1.66	-1.67	-	-3.69†	-3.68†	-	-1.35	-1.35	-	-1.06	-1.07
R^2	0.59	0.56	0.59	0.49	0.49	0.49	0.59	-	-	-	-	-	-	-	-	-	-	-

Columns show F values resulting from stepwise multiple regressions between each dependent behavioural variable and the independent behavioural variable. Independent variables indicated with *, ** or *** were introduced into the final regression model and explained a significant amount of variation in the dependent variable († $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). F-to-remove values are given for those variables which entered the final model and F-to-enter values are given for other variables. Male settlement date and age were significantly correlated. The three columns for each dependent behavioural variable show F values (from left to right) when (i) male settlement date was excluded from the independent variables, (ii) male age was excluded and (iii) when both variables were entered into the model. R^2 refers to the amount of variation in the data which is explained by the model.

Independent variables are: FED, nest first egg date; male age (old or first-year breeder); Ter size, territory size; male BCI, male body condition index; Fem BCI, female body condition index; set date, male settlement date. Dependent behavioural variables are: Mean, mean intra-pair distance; %<5m, %<10m, and %<15m, proportion of time males was within five, ten, and 15 metres of the pair female; %P+, proportion of time male perched above the pair female; %YF, proportion of female flights which the male followed; %YM, proportion of male flights which the female followed; TF, number of tail flashes per hour; Song, numbers of songs per hour; % off territory, proportion of time male spent off territory; Song flights, number of song flights per hour; Display total, total number of aerial displays.

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Table 2.4. Stepwise multiple regression of independent variables vs. dependent behavioural variables in the fertile period (step 2).

Dependent behavioural variables

Independent variables	Mean (m)			% < 5m			% < 10m			%< 15m		
FED	-2.52	-2.52	-2.52	1.06	1.06	1.06	2.19	2.19	2.19	2.36	2.36	2.36
Male age	1.46	-	1.46	-1.31	-	-1.31	-0.91	-	-0.91	-0.93	-	-0.93
Terr size	-1.28	-1.28	-1.28	0.58	0.58	0.58	1.8	1.28	1.28	1.09	1.09	1.09
Male BCI	0.07	0.07	0.07	-0.17	-0.17	-0.17	-0.18	-0.18	-0.18	-0.27	-0.27	-0.27
Fem BCI	0.09	0.09	0.09	-0.01	-0.01	-0.01	0.00	0.00	0.00	0.00	0.00	0.00
Set Date	-	-3.88†	-3.88†	-	3.39†	3.39†	-	2.68	2.68	-	2.82	2.82
R^2	-	-	-	-	-	-	-	-	-	-	-	-

Independent variables	%YF			%YM			%P+			TF		
FED	3.34†	5.69*	5.69*	-0.38	-0.38	-0.38	1.65	1.65	1.65	1.84	1.84	1.84
Male age	-2.69	-	0.57	0.13	-	0.13	1.21	-	1.21	-0.04	-	-0.04
Terr size	1.17	0.63	0.63	0.56	0.56	0.56	1.76	1.76	1.76	0.00	0.00	0.00
Male BCI	0.13	-0.36	-0.36	-0.04	-0.04	-0.04	-1.59	-1.59	-1.59	3.82†	3.82†	3.82†
Fem BCI	-0.54	-0.54	-0.54	5.69*	5.69*	5.69*	0.60	0.60	0.60	-0.51	-0.51	-0.51
Set Date	-	8.12*	8.12*	-	-0.17	-0.17	-	-0.36	-0.36	-	0.00	0.00
R^2	-	0.55	0.55	0.22	0.22	0.22	-	-	-	-	-	-

Columns show F values resulting from stepwise multiple regressions between each dependent behavioural variable and the independant behavioural variable. Independent variables indicated with *, ** or *** were introduced into the final regression model and explained a significant amount of variation in the dependent variable († $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). F-to-remove values are given for those variables which entered the final model and F-to-enter values are given for other variables. Male settlement date and age were significantly correlated. The three columns for each dependent behavioural variable show F values (from left to right) when (i) male settlement date was excluded from the independent variables, (ii) male age was excluded and (iii) when both variables were entered in the model. R^2 refers to the amount of variation in the data which is explained by the model.

Independent variables are: FED, nest first egg date; male age (old or first-year breeder); Terr size, territory size; Male BCI, male body condition index; Fem BCI, female body condition index; set date, male settlement date. Dependent behavioural variables are: Mean, mean intra-pair distance; %<5,m %<10m and %<15m, proportion of time males was within five, ten, and 15 metres of the pair female respectively; %P+, proportion of time male perched above the pair female; %YF, proportion of female flights which the male followed; %YM, proportion of male flights which the female followed; TF, number of tail flashes per hour.

Table 2.5. Rates of decline in mate guarding behaviours from day -1 to +2 and, -1 to the penultimate egg date (day 0 = first egg date) in relation to: (i) operational sex ratio (OSR), (ii) male body condition (BCI), (iii) male settlement date, and (iv) male age.

Mate guarding behaviours

	Mean	%<5	%<10	%<15	%P+	%YF
(i) OSR						
-1 to +2	-0.04	-0.18	-0.12	-0.05	-0.05	-0.23†
-1 to pen.egg date	-0.04	-0.32*	-0.10	-0.38*	-0.05	-0.08
(ii) Male BCI						
-1 to +2	-0.07	-0.04	-0.09	-0.11	0.12	-0.11
-1 to pen. egg date	-0.07	-0.10	-0.09	-0.11	-0.02	-0.04
(iii) Male settlement date						
-1 to +2	-0.06	-0.03	-0.10	-0.10	-0.09	-0.02
-1 to pen. egg date	-0.11	-0.13	0.01	-0.01	-0.06	-0.25†
(iv) Male age						
-1 to +2	-1.07	1.66	1.00	0.51	-0.89	0.99
-1 to pen. egg date	-1.99	2.17†	1.5	1.76	-0.51	1.98

Mate guarding behaviours are; Mean, mean intra-pair distance; %<5m, %<10m, and %<15m, proportion of time males was within five, ten, and 15 metres of the pair female respectively; %P+, proportion of time male perched above the pair female; %YF, proportion of female flights which the male followed.

For OSR, male BCI and male settlement data the table shows R^2 values for regression (from slopes of mate guarding behaviours for days -1 to +2, and +1 to penultimate egg date [pen.egg date] for each of the 12 focal males) vs. continuous dependent variable. Sign donates nature of correlation. For male age table shows t-statistic for unpaired t-tests comparing regression slopes of mate guarding behaviours, as described for (i) to (iii), between old males (n = 6) and young males (n = 6). Levels of significance: † $p < 0.1$, * $p < 0.05$, ** $p < 0.01$.
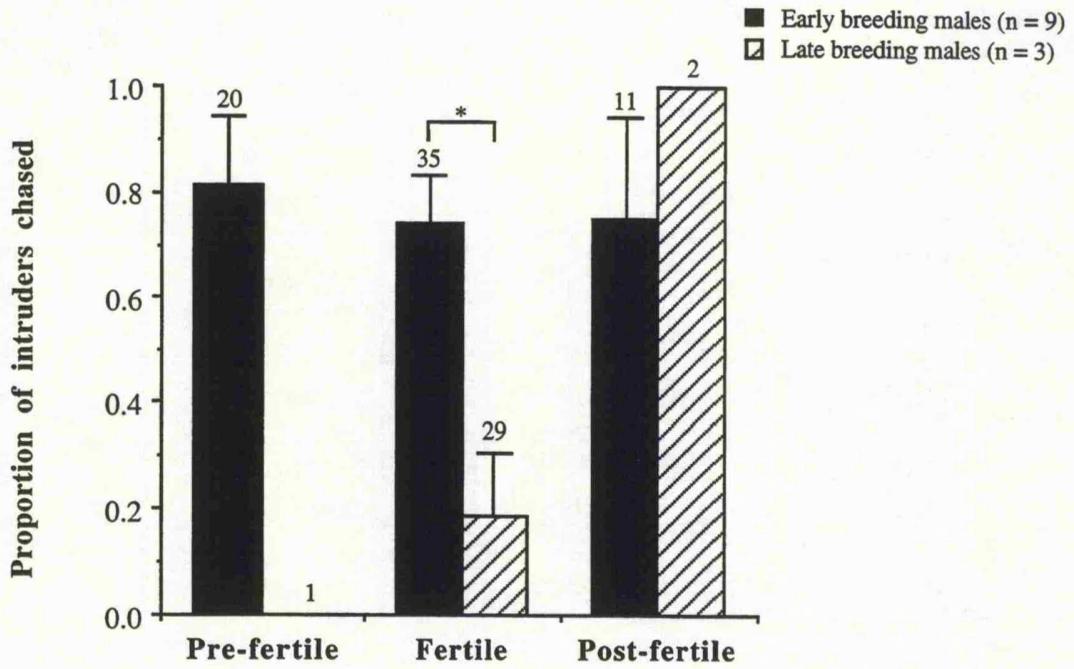
Fig. 2.2. Proportion of intruders chased by early and late breeding males in relation to female fertility. Actual values show the number of intrusions in each period. Late breeding males chased proportionately fewer intrusions in the fertile period (Mann-Whitney U-test, U = 2, * p < 0.05).

Table 2.6. Comparison of mate guarding behaviours in the fertile period between this study and Carlson *et al.*'s (1985) study.

	This study (12 pairs)	Carlson *et al.* (1985) (6 pairs)	z statistic
Intra-pair distance (m)	11.41 ± 1.60	6.65 ± 1.10	1.78†
	10.66 ± 1.10		1.59†
Proportion of female flights	0.42 ± 0.07	0.92 ± 0.03	-3.23**
followed by male	*0.39 ± 0.05*		-3.02**

The definition of the fertile period was days -5 to +3 in this study and -3 to +2 in Carlson *et al*'s (1985) study. Data in italics are from this study for a -3 to +2 fertile period. Mean values for intra-pair distance and proportion of female flights followed male calculated from Carlson's tables 5 and 6 respectively. The table shows z statistics for Mann-Whitney U-tests, this study (n = 12 pairs) vs. Carlson's study (n = 6 pairs). Level of significance, † p < 0.1, ** p < 0.01.

Table 2.7. Breeding synchrony in the study population between 1991-93, calculated using equation 2.1 (see page 40).

Year	Synchrony Index
1991	32.9%
1992	50.1%
1993	50.7% (40.9%*)

* Includes two relays

2.3.5. Multivariate analysis: step 2, fertile period (see Table 2.4)

Later settling males followed their female more than early settling males (%YF, $F_{2,9}$ = 8.12, p < 0.025). Males in late breeding pairs also followed their females more than in early pairs ($F_{2,9}$ = 5.69, p < 0.05).

2.3.6. Decline in mate guarding behaviours

There was no effect of OSR, male BCI, male settlement date or male age on rates of decline in mate guarding behaviours from days -1 to the penultimate egg date. Similar results were obtained from days -1 to +2, although rates of decline in the amount of time spent within five and ten metres were higher in response to a female skewed sex ratio (Table 2.6).

2.3.7. Frequency and pattern of copulations

A low number of copulations (n = 10) was observed all of which occurred in the fertile period (see section 1.4.3). There were 0.83 ± 0.29 (se) copulations per clutch (1.16 ± 0.37 including copulation attempts). There was no indication of a pattern in their timing with respect to the fertile period, or time of day. Four occurred prior to laying and six during laying, while six occurred in the morning and four in the afternoon.

2.3.8. Inter-male aggression: response to intruders

60% (59/98) of male intrusions were repelled by the pair male. 54% of these intrusions were by colour ringed males. Overall 47% of intruders were chased during the fertile period, however late breeding males chased only 21% of intruders (6/29) compared to 68.5% (24/35) by early breeding males. 93% (27/29) of the intrusions in the fertile period experienced by late breeding pairs were by colour ringed males. The reduction in chasing intruders was therefore not due to these males discriminating between migrants and residents (Mann-Whitney U-test, proportion of intruders chased in the fertile period, early breeders (n = 9) vs. late breeders (n = 3), U = 2, p < 0.05, see Fig. 2.2).

2.4. Discussion

2.4.1. Mate guarding

In general, males of species with a low rate of copulation employ a mate guarding strategy to ensure paternity (Birkhead *et al.* 1987) although guarding need not be an exclusive strategy and may also be accompanied by a high copulation rate (Sheldon 1994). Wheatears exhibited a low rate of copulation in this and in all other studies (Conder 1989, Carlson *et al.* 1985), although during the fertile period pairs were occasionally observed entering burrows and crevices other than the nest hole and copulations may have occurred during this time (pers. obs.).

The mate guarding hypothesis predicts that males should remain close to their mate, following them more during the fertile period and, where appropriate, should perch higher than them during this time, in an attempt to limit the access of extra-pair males and ensure paternity. Generally, males did not reduce intra-pair distance in the fertile period but increased their following of (range 2 - 64% of female flights followed during the fertile period), and the amount of time perched above their female.

Six hypotheses have been proposed to explain the close proximity of the pair male to his partner (see Birkhead and Møller 1992). These are discussed briefly with reference to this study.

1. The copulation access hypothesis: males should follow their female when copulations are likely to occur, and the intensity of mate following should remain constant even when the risk of EPCs increases (Gowaty and Plissner 1987).

Males followed their mates more during the fertile period, when all copulations observed occurred, however they appeared to adjust their behaviour in response to a potential threat of cuckoldry. Males remained in closer proximity to and perched above their female more in response to a male skewed OSR which occurred later in the season. Later breeding pairs experience higher intrusion rates during the fertile period (see section 3.3.4). These late breeding males also followed their female more than early breeding males during this time.

2. The pair bond hypothesis: the association between males and females should intensify as the breeding cycle progresses (Lumpkin *et al.* 1982).

There was no evidence that the pair bond intensified during the breeding season. Intra-pair distance remained comparatively constant from pairing until near clutch completion, and increased during the post-fertile period. Males followed their partner more during the fertile period than before or after it. It should also be noted that females also increased the following of their partner during the fertile period. However, this was at a much lower intensity than the following exhibited by the male (mean proportion of female flights followed by male in fertile period = 0.42 ± 0.07 [se], mean proportion of male flights followed by female in fertile period = 0.02 ± 0.01 [se]).

3. The predation hypothesis: males should follow females during the fertile and post-fertile period, probably more so during incubation (and the nestling period) when females are more vulnerable to predation and their loss would be costly to the male, especially if they are scarce (Martin 1984, Gowaty and Plissner 1987).

Males followed their partner during the fertile period, but negligibly during incubation when the female was off the nest. Additionally, during this time although males

were occasionally seen calling their female off the nest they spent a considerable proportion of their time off territory (see section 3.3.3). As a result, females were often unaccompanied by their mate during bouts of feeding between periods of incubation. There was no evidence of the male following the female during the nestling period as adults typically foraged separately while provisioning the chicks.

4. The passive presence hypothesis: the distance between pair members parallels changes in territory use, and the initiation of moves and following behaviour shows no sex bias (Bjorklund and Westman 1986).

No data were collected on habitat use and the initiation of moves by the sexes, but there was a sex bias in following. Males followed their partner more throughout the whole breeding season, with this behaviour peaking in the fertile period.

5. The female advantage hypothesis: benefits from avoiding harassment by other males should vary in relation to pair proximity, and that proximity should be maintained by both sexes (Lumpkin 1981, 1983, Lumpkin *et al.* 1982).

Proximity is not maintained by both sexes during the breeding season. The male followed the female more during the fertile period. The following of the male by the female also peaked during the fertile period.

6. The courtship feeding hypothesis: females should follow their mates to obtain food, and the following behaviour should coincide with the period of courtship feeding (Birkhead and Møller 1992).

Courtship feeding was not observed in this study (Conder 1989, but see Brooke 1979).

Behavioural observations presented here support the mate guarding hypothesis. In the absence of data determining which of the sexes maintained the proximity to the other, the strongest evidence of mate guarding was the increased following by the male of the pair female during the fertile period. Later breeding males increased their intensity of following, and proximity to, their female during this time, possibly in response to an increase in the threat to paternity. Females may also try to avoid harassment from extra-pair males by keeping in closer proximity to their partner during the fertile period (see also Kempenaers *et al.* 1995)

2.4.2. Factors affecting the intensity of mate guarding

In this study there appeared to be three principal factors which affected the intensity of mate guarding: OSR, FED and male age/settlement date.

Males spent less time in close proximity to their pair female when there was a

female-skewed sex ratio, as occurred early in the season. Consequently, when there was a male-skewed OSR, later in the season, pair males remained closer to their partner during the fertile period (see Table 2.2). A male-skewed sex ratio is a potential source of intrusions, however there was no significant correlation with OSR and intrusion rates (over the whole season or within the fertile period). Intrusions by extra-pair males peaked in the fertile period, suggesting males could identify fertile females and alter their behaviour accordingly (Birkhead and Møller 1992).

OSR is an indicator of breeding synchrony, with a female-skewed OSR indicating a high degree of synchrony. A low intensity of mate guarding in response to a female-skewed-OSR could be due to either the low threat to paternity, with the majority of males being involved in guarding duties (as indicated by a low intrusion rate), or to a more acute trade-off between mate guarding and the pursuit of EPCs. The mechanism by which pair males assess the OSR is not clear but may involve monitoring the behaviour of surrounding males or females.

Although there was a correlation between OSR and FED, there was an underlying effect of the time of laying on the pair male's behaviour. There was no significant effect of the OSR on the intensity of male following over the whole breeding season or within the fertile period. Later breeding males followed their females more than early breeders. As mentioned above, later breeding territories experienced higher intrusion rates and it may be in a response to these that later breeding males showed an increased intensity of mate guarding (although there was no direct correlation between following of the female and mean intrusion rates in the fertile period). Due to the correlation between OSR and FED there may also be an effect of the latter on intra-pair distance (and related factors) which is obscured.

In this analysis all late settling males were first year breeders, and it is difficult to determine whether age or settlement date was the predominant factor causing the differences between the two groups of males. Settlement date appeared to strongly influence male behaviour but there was also an underlying effect of age when considering the whole breeding season (see Table 2.3). However, in general, prior to and during the fertile period, later settling males followed and remained in closer proximity to their partner than did earlier settling individuals (see Tables 2.3 and 2.4). There was no evidence that later settling males were prone to losing their partners to older, earlier established individuals. The only three cases of mate switching soon after pairing all involved old males. Additionally, there was only one case of polygamy in three years (n = 54 pairs) and this was a result of a solitary female defending a territory which was subsequently taken over by a neighbouring paired male. It may be that later settling males, being less experienced, are less sure when their female is fertile and as a consequence remain in closer proximity to, and follow their female more, prior to and during the fertile period. This close

proximity may also be maintained by the females paired to these males following their partners.

There was no correlation between settlement date and FED and therefore late settling males were not at a direct disadvantage in the threat to their paternity. There was no correlation between male settlement date and mean intrusion rate in the fertile period (Spearman rank, $R_{12} = 0.07$, ns). Age differences may arise if individuals learn to behave optimally as mate guarders with increased breeding experience (Sundberg 1992). Morton *et al.* (1990) showed that young purple martins were cuckolded more than old males. In the wheatear, older males can be visually identified in the field due to plumage characteristics. Females might be less likely to copulate outwith the pair bond if paired to an older male, on the basis that they have survived between years and are of potentially higher quality.

Female settlement data were limited for 1991, but there was typically a longer period between female arrival and FED for females paired to older, early returning males. Although speculative, older males may remain close to and follow their female immediately after pairing, with these behaviours becoming less intense over time prior to the fertile period. Young males would therefore appear to follow their partner more than old males due to a shorter time between pairing and laying and not due to any 'experience' factor. A post-pairing period prior to laying of about three weeks may allow each sex to evaluate the 'quality' of their partner. Individuals could then behave according to their own and their partner's 'quality' e.g. in the blue tit 'preferred' males guarded their females less and had fewer extra-pair offspring in their broods, than less 'preferred' individuals (Kempenaers *et al.* 1992). If the BCI accurately reflects quality, males of lower quality followed and remained in closer proximity to their female throughout the breeding season. There was no indication that males altered their intensity of mate guarding with respect to the 'quality' of their female, though females with a high BCI followed their partners more during the fertile period.

2.4.3. Pattern of mate guarding

In the majority of bird species for which mate guarding has been documented, the intensity of behaviours associated with it typically peaks prior to and during early laying and then declines (see Table 7.2 in Birkhead and Møller 1992). It has been argued that there may be a diurnal pattern of mate guarding which reflects that of female fertility, with guarding being more intense in the morning immediately after laying and also in the evening just before laying (Briskie 1992). Additionally, the majority of bird species copulate most frequently in the morning (54% of 28 genera copulated most frequently during this time (Birkhead *et al.* 1987).

In this study, mate guarding peaked on or around day -1 and declined thereafter. There was no obvious diurnal pattern in mate guarding or in the timing of copulations in

this study (see also Sheldon 1994 and references therein). Intense mate guarding started soon after concerted nest building, from about day -6. By day -3 the female was using feathers and wool to line the nest which could provide a reliable indication that she was preparing to lay. These cues were reliably used as clues to fertility in experiments (see Chapter 5). The frequency of nest visits declined after the nest had been lined, though females continued to line their nests after the onset of laying (Conder 1989, pers. obs). Males could use the collection of lining material (followed by the decrease in visits to the nest), the decrease in female-male aggression in response to male approaches (in particular the female's response to the dancing display (see section 1.4.3), an increase in female solicitations, and the initial occurrence of copulations to more accurately assess female fertility.

Reasons for the decline in the intensity of mate guarding principally reflect the presumed decline in female fertility during the laying sequence, energetic costs of guarding to the male, and lost opportunities to participate in EPCs (see Birkhead and Møller 1992). Møller (1987) showed that in the swallow, males terminated their mate guarding earlier in response to a female-skewed OSR. Behaviours associated with mate guarding in this study were observed to decline in their respective intensities from day -1 (see Fig 2.1), however, there was no evidence that males terminated mate guarding earlier in response to a female skewed OSR. Male body condition, age or settlement date also had no effect on the rates of decline in mate guarding (Table 2.5, but see Møller 1987b). In an open environment energetic costs to guarding may be less limiting than they would be in a forest or colonial situation, with males being able to forage and simultaneously monitor their territory and their female as well as potential extra-pair males.

Males were observed to enter the nest hole during laying and incubation. Incubation occurs towards the end of clutch completion but precisely what cues might be used by the male to indicate a decline in female fertility, accounting for the decrease in the intensity of mate guarding, are unclear. Since in many studies the decline in mate guarding occurs soon after laying begins (Birkhead *et al.* 1989), males may use the laying of the first egg as a cue to alter their behaviour. Males are probably unclear about the exact clutch size their female is going to lay. By regularly checking the contents of the nest during early incubation, males would be able to determine their final clutch size and further adjust their behaviour e.g. the dunnock (Davies *et al.* 1992).

2.4.4. Comparable studies

Little work has been done to compare mate guarding between different populations of the same species. Probably the best example are studies of the pied flycatcher in Norway and Sweden (see also Møller's [1987c] study on mate guarding in solitary and colonially breeding barn swallows). Mate guarding has been documented in the Swedish population

(Bjorklund and Westman 1983) but not in the Norwegian one (Lifjeld *et al.* 1991). Male wheatears in this population appeared to mate guard less intensely than previously documented for this species (Carlson *et al.* 1985). The definition of the fertile period was longer in this study but, controlling for this, mate guarding was still less intense than previously documented (Table 2.6).

(i) Breeding synchrony

Females may breed synchronously to impose monogamy on males and avoid EPCs (Emlen and Oring 1977, Maynard Smith 1977) or prevent intra-specific brood parasitisim (IBP) (Yom-Tov 1980). Alternatively, synchrony may arise due to environmental factors, such as day length, temperature, and food supply.

The opportunities for EPCs are expected to be higher in an asynchronously breeding population due to its effects on the OSR. Males have been shown to adjust their intensity of mate guarding in relation to the threat of cuckoldry in this and other studies (e.g. Møller 1987b, c).

The breeding synchrony index (SI) was calculated using the formula:

$$SI = \frac{1}{F} \sum_{p=1}^{F} \left[\frac{\sum_{i=1}^{tp} fi.p}{tp(F-1)} \right] \times 100\% \qquad 2.1$$

where F = total number of breeding females in the population, fi.p = number of fertile females excluding fertile female p in the population on day i, tp = number of fertile days for female p (Bjorklund and Westman 1986, Kempenaers 1993). This index ranges from 0% when there is no overlap in fertile periods of the breeding female to 100% in a fully synchronous population. Bjorklund and Westman (1986) calculated that the breeding SI for Carlson *et al*'s (1985) study was 25% (calculated from their Table 1, though this is potentially misleading as this SI is based on a sub-sample of the population). Table 2.7 shows the SI for the three years of this study. There was a lower degree of breeding synchrony in 1991 than in the subsequent two years due to three females being predated prior to laying during nest building. The predicted FEDs for these nests were in the first half of the breeding season. Their males subsequently paired again later in the season. The lower SI in 1991 is possibly misleading as the eventually widowed males had been occupied with their pair female until early/late laying and had not been posing a threat to other males. Had these males bred, the SI would have been similar to that in 1992-93.

In a less synchronous population there will be less overlap in the fertile period of breeding females and, consequently at any one time, more males with non-fertile females than in a synchronous population. These males will be able to seek EPCs without risking a

loss in their paternity, while those with fertile females would be expected to guard their females more intensely due to the threat posed by the 'free' individuals (Birkhead and Biggins 1987). A higher degree of breeding synchrony could account for the lower intensity of mate guarding observed in this study than in Carlson *et al.*'s (1985).

(ii) Population Density

At high densities there is a greater probability of encountering fertile females, and the opportunity for males to obtain EPCs increases. One would therefore expect mate guarding to be more intense in dense populations. The density of Carlson *et al.*'s (1985) population (18 pairs in 0.7km^2) was higher than that in this study (15.2 territorial males, 11.7 pairs, in 0.7km^2 on the study area in 1991). The reduced opportunities for males to pursue EPCs at lower breeding densities and consequently the reduced risk of their losing paternity may further account for the reduced levels of mate guarding observed in the Bardsey population. Densities were higher at the north and south end of the study area (see Fig.7.1-7.3) and localised variations in density may affect the intensity of mate guarding exhibited by individual males.

(iii) Habitat

It has been argued that mate guarding should be less intense for territorial forest species due to the low detectability of females (Bjorklund and Westman 1986). However, it would seem to be more logical to expect reduced intensities of mate guarding for species which live in open habitats. In such an environment, males may not need to remain in close proximity to their partner to mate guard effectively. The behaviour and position of the female could be easily monitored and intruding males are likely to be conspicuous, not being obscured by dense vegetation (Davies 1985, Hobson and Sealy 1989, Sundberg 1992, Shepherd *et al.* in prep.).

In this study, males spent more time perched above their female in the fertile period than before or after it. Intrusions by resident males peaked during this time. Utilising a prominent perch may be a strategy to spot intruding males when the threat to their paternity is highest but also to monitor the behaviour of intruders and of the pair and neighbouring females. Additionally, males perched higher than the female over the whole breeding cycle, which suggests that they are the more vigilant of the pair. Qualitative behavioural observations indicated that males alarmed more than their partner, resulting in the female flying to them, with both then observing the potential threat (pers. obs.). Although difficult to quantify, males in this population seemed to try to keep their partner in sight by using the earthen walls and fences (approximately 1 metre high) which dissected the study site as prominent perches. The propensity of a male to keep his partner in sight was very noticeable when the pair female disappeared from his view, usually by dropping or flying

down on the opposite side of a wall. A male would typically respond by flying to the point where the female had dropped off. This was particularly conspicuous during the fertile period, and is reflected in the increased following seen during this time. When higher perches were available males used them for perching and displaying.

One would expect that increased following by the male observed during the fertile period would result in a reduction in intra-pair distance. This did not occur on early territories and it is unclear whether the increased following on later territories directly results in reduced intra-pair distance. The increase in intensity of mate guarding observed by later breeding males did not result in an increase in the amount of time spent perched above the female.

The risk of EPCs has been shown to be proportional to intra-pair distance and monitoring the female and extra-pair males from a distance using prominent perches has been interpreted to be comparatively ineffective, especially when intrusion rates are high. The species for which this argument has been made inhabit visually occluded habitats or breed colonially e.g. dunnock, pied flycather, barn swallow (Davies 1985, Alatalo *et al.* 1987, Møller 1987c). The extreme open nature of the wheatear's habitat may permit an overall lower intensity of mate guarding (see also Sundberg 1992, Shepherd *et al.* in prep.).

2.4.5. Additional paternity guards
(i) Song

Remaining close to and following the female during her fertile period could be used by neighbouring males as a cue to time intrusions to coincide with peak female fertility. If there is little cost to curtailing paternity guards then males may reduce their intensity of mate guarding, or alternatively, males might directly announce their female's fertility, e.g. by song (Møller 1991b). Male announcement is a potentially reliable indicator of male quality if the degree of male fertility announcement depends on male phenotypic quality and the quality of his resources and if the costs of announcement are relatively higher for low than high quality males. Under this hypothesis, intruding males should preferentially intrude on sites where there is a lower level of announcement and females should prefer males with a high announcement rate. Song may therefore be used as a means of ensuring paternity.

In this study, there was no evidence that song was used in mate guarding or for advertising female fertility. There was no discrete peak in song output during the fertile period. Additionally it seems unlikely that song flights were used in ensuring paternity or advertising fertility as their output peaked during the pair female's post-fertile period.

(ii) Tail flashing

Tail flashing peaked in the fertile period but also occurred during territorial disputes at other times, especially during territory establishment and boundary reinforcement early in the season. Males were occasionally observed displaying in the apparent absence of intruders, often in the vicinity of the nest hole. Individual males with a high BCI tail flashed more than individuals of lower condition. This display could be a means to deter intruders, with males directly advertising their quality to neighbours as has also been suggested for song (Møller 1991b, see above). In an exposed environment visual signals may be a better form of communication than vocal displays. However, this did not appear to be the case. Later breeding territories were intruded on more than earlier breeding pairs and later breeding males tail flashed more in response to increased intrusion rates (Spearman rank; mean intrusion rate per hour in fertile period vs. mean male Tf residuals [calculated from Table 2.1], $R_{12} = 0.63$, $p < 0.05$). The tail-flashing display would appear to be a response to intrusions (and perhaps other behaviours of extra-pair males) and not a mechanism that is directly involved in deterring them.

(iii) Territoriality

Territoriality has been proposed as an additional (supplementary) paternity guard in birds (Møller 1990b, Møller 1992, but see Dunn 1992). Wheatears are a highly territorial species and defend the territory from conspecifics and other species such as whinchats, meadow pipits and rock pipits (Conder 1989, Zamora 1990, pers. obs).

Males remained territorial and were aggressive to intruding males throughout the season, including during the provisioning of chicks. The integrity of the territory remained from pairing until at least fledging. If sperm competition influences territory size the territory should be largest prior to and/or during the female's fertile period (Møller 1990b). In 1991, nest location and territory boundaries were plotted on scale maps but no temporal variations were measured. Qualitative observations indicated that in the main territory boundaries remained constant and were strictly enforced throughout the breeding season once all the males had settled. These tended to break down after fledging following brood division (Conder 1989, pers. obs.). Early arriving males 'dominated' large ranges until the arrival of females and later arriving males (see also Conder 1989, Tye 1992). The density of wheatear territories was high at the north and south ends of the study area (see Fig. 7.1-7.3). In these situations, once the full complement of returning males had returned and set up their territories, extension of territory boundaries could only occur in the absence of close neighbours. Temporal territory maps were obtained in 1992-93 but due to the nature of the experiments (see Chapter 5), it was considered inappropriate to use them in such an analysis. In four instances between 1991-93, territory boundaries were seen to alter with nest site location, increasing the distance between the nest and the boundary of a

neighbour. Three of these were due to the initial female being predated and the replacement female selecting a different nest hole. There were also instances of nests being built on or near territory boundaries. Females were territorial to other females when they settled in the absence of males. This suggests that additional factors and not just sperm competition are involved in territory acquisition and maintenance.

Later breeding territories experienced higher intrusion rates. In extreme situations, when a territory was overrun by intruding males (on some days at least seven males were observed on later breeding territories), an alternative strategy to chasing intruders would be to tolerate the intrusions at the risk of potentially losing paternity. As a consequence of differences in the intrusion rate, early breeding males may tend to defend the territory while later breeding individuals tend to guard their mate directly.

2.6. Summary

1. There was no evidence to show that males used a high rate of copulation to ensure their paternity (on average pairs were seen to copulate less than once per clutch). Instead, behavioural data supported the hypothesis that male wheatears used the mate guarding strategy to ensure paternity.

2. Mate guarding peaked immediately prior to laying and consisted primarily of the close following of, but also by an increase in the amount of time spent perched above, the female during the fertile period. There was no reduction in intra-pair distance during this time although this has been documented for mate guarding in other species.

3. Males increased their intensity of mate guarding in response to a male-skewed operational sex ratio and also at later nesting attempts which experienced higher intrusion rates, possibly in response to an increase in the threat to their paternity. There was a significant correlation between male age and arrival times, with older males returning earlier. It proved difficult to distinguish between these two factors in determining which was the more important in affecting male behaviour, but later settling males followed their females more than earlier settling males during the fertile period.

4. Mate guarding was less intense in this study than previously documented for the wheatear. Increased breeding synchrony, a lower breeding density, and an extremely open habitat may have accounted for this.

5. The intensity of mate guarding declined during the laying sequence. Rates of decline were unaffected by the operational sex ratio, male condition or 'experience'.

6. There was no evidence that males used song or aerial displays to advertise female fertility directly, but territorial defence cannot be ruled out as an additional paternity guard. Later breeding males appeared to guard their female, whilst early breeding males defended their territory.

Chapter 3. The pursuit of a mixed reproductive strategy
Part II: Extra-pair copulations

3.1. Introduction

In numerous bird species both males and females have been observed copulating outwith the pair bond (59% of 70 studies, Birkhead and Møller 1992). The obvious benefit to the male of a successful extra-pair copulation (EPC) is increased reproductive success, but whether a female should participate in an EPC depends on a variety of potential costs and benefits (Westneat *et al.* 1990, see also Birkhead and Møller 1992). Females may benefit by: (i) gaining future parental help from the extra pair male (though there is little evidence to support this); (ii) her offspring inheriting "good" genes; (iii) increasing the genetic diversity of her offspring; or (iv) insuring against the pair male being infertile or having sperm of low viability (Westneat *et al.* 1990, Wetton and Parkin 1991). Costs to females that accept EPCs may include physical injury and harassment by both the pair and non pair male, or reduced parental care by the pair male due to the possibility of being cuckolded.

The opportunity for males to obtain additional matings depends on several factors: the operational sex ratio (OSR), population density, possible conflicting behaviours (e.g.

mate guarding), and female responses to EPCs (Birkhead and Møller 1992). In an asynchronous breeding population the OSR is more male-skewed, i.e. at any one time there is a larger number of 'free' males than fertile females, and therefore outwith their female's fertile period males have a greater chance of encountering fertile females to copulate with. At high densities, in particular, colonial species, there is also an increased probability of encountering fertile females which further increases the opportunities for both sexes to participate in EPCs (Birkhead 1979). Conflicting behaviours such as mate guarding and parental care will also affect a male's ability to seek additional matings and individuals may be limited to pursuing them outwith their own female's fertile period and the nestling/post-fledgling period. There are three possible outcomes of males attempting EPCs. They may be: (i) rejected by the female; (ii) forced out by the male (McKinney *et al.* 1983); or (iii) accepted and/or solicited (both on and off the breeding territory) by the female (Birkhead *et al.* 1989, Kempenaers *et al.* 1992, Sheldon 1994). Female co-operation is probably important but not essential for males to obtain EPCs (Fitch and Shugart 1984, Westneat *et al.* 1990, Wagner 1991a). Forced copulations can occur in species with or without intromittent organs, but it is more likely that their possession facilitates sperm transfer. The extent of female participation will have a significant effect on the overall opportunities for males to pursue EPCs, as they appear to have ultimate control of the pattern of copulations during their fertile period (Lifjeld and Robertson 1992). If female co-operation is essential then EPCs can only occur if a mixed reproductive strategy exists for both sexes (Fitch and Shugart 1984).

For EPCs to be successful, males should ideally time their intrusions to coincide with a female's fertile period, and in the majority of studies this is what has been observed (Birkhead and Møller 1992). It is unclear how extra-pair males accurately time their intrusions to coincide with a female's fertile period, but they might cue in on the behaviour of one or both members of the pair. In many species it has been shown that intruding males during the fertile period are more likely to be neighbours (Birkhead *et al.* 1987), the assumption being that due to their closer proximity they are more accurate in assessing the fertility of surrounding females. Female fertility is thought to vary within the fertile period, peaking about 24 hours prior to the laying of the first egg, and during the laying sequence just after laying(the insemination window; Cheng *et al.* 1983), and decline during the laying sequence. Extra-pair males are expected to preferentially target EPCs during this period in an attempt to limit the potency of copulations by the pair male and enhance their own probability of success.

Males seeking EPCs often approach fertile females secretively using vegetation and topographical features as cover, but they may also advertise for additional matings by conspicuous visual or vocal displays, which may be used during initial pairing and are the basis of female choice, e.g. song and other vocal and/or visual displays (see Birkhead and

Møller 1992). In the wheatear, Carlson *et al.* (1985) proposed that males adopted two strategies in the pursuit of EPCs: intruding on neighbouring territories during a female's fertile period and increasing their visual displays outwith their pair female's fertile period (in an attempt to either attract a second female or advertise for EPCs).

This chapter examines behavioural evidence for the pursuit of EPCs in the wheatear, in particular, the timing of EPCs relative to the fertile period of both the pair and extra-pair females and the extent of the trade-off between mate guarding and the pursuit of additional matings.

3.2. Methods

3.2.1. Data collection

The data were collected as described in chapter 2.

3.2.2. Data analysis

Nests were numbered consecutively according to their FED. Pairs were termed early or late depending on whether their FEDs were among the first or last half of the nests to be initiated respectively. For details on definition of fertile period, and calculation of the operational sex ratio (OSR) and body condition index (BCI) see sections 1.4.3, 1.4.4 and 1.4.5, respectively.

3.2.3. Multivariate analysis

The influence of a series of independent factors on male and female behaviour (dependent variables) over the whole breeding season were examined using stepwise multiple regressions (termed step 1). There were two categories of independent variables: "control" variables and "selection" variables. Control variables were environmental factors which might have affected behaviour and selection variables were biological factors examined in the regression. The independent control variables were time, wind speed, percentage cloud cover, general weather conditions (i.e. separate variables for dull, sunny, bright or raining, entered categorically as 1 or 0), and daily temperature. Independent selection variables were operational sex ratio (OSR), extra-pair male intrusion rate, and the time relative to female fertility (pre-fertile, fertile, and post-fertile). Separate variables were entered for each of these time periods categorically as 1 or 0. Independent control variables were entered into the model before the independent selection variables (see Table 2.1). The effects of specific independent selection variables on dependent behavioural variables were also examined within the fertile period alone (see Table 2.2). There was a degree of pseudo-replication in these two analyses as individual territories were considered on successive days from days -20 to +12 and were not independent of each other. The purpose of these step 1 analyses was to identify any effect of temporary environmental

factors on the behavioural variables and so allow these variables to be controlled for in subsequent analyses.

A second series of multivariate analyses was performed using the mean residuals for the 12 focal males for each behaviour from Table 2.1 as the dependent variables (termed step 2). Phenotypic, demographic and additional data were entered as independent variables in this second set of analyses, in which pseudo-replication was avoided by entering the mean value for each male only once. The independent variables were territory size, male age, FED expressed as days after first egg was laid on the study area (day 0 = 5th May, 1991), male settlement date, and male and female body condition. Among the independent variables there was a correlation between (i) FED and OSR (the OSR was male-skewed for later breeding pairs), and (ii) male age and settlement date (old male returned earlier than first-year breeders) (Spearman rank, FED vs. mean OSR in the fertile period, R_{17} = - 0.885, p < 0.001; Mann-Whitney U-test, male age vs. male settlement date, z = -3.84, p < 0.005). Step 2 analyses were performed for the whole breeding season and the fertile period (see Tables 2.3 and 2.4 respectively). Due to their non-independence, male age and settlement date were entered both separately and simultaneously in this set of analyses.

A third multivariate analysis (step 3) was performed which examined song, the frequency of aerial displays and proportion of time spent off territory in the three time periods: pre-fertile, fertile, and post-fertile. A mean residual for each male in each period was calculated from Table 2.1 after entering the control variables. The independent variables in this regression analysis were: male BCI; FED; male settlement date; male age; and territory size.

In steps 1, 2 and 3, the residual values resulting from the stepwise regressions between each dependent behavioural variable and the independent variable were often significantly skewed. Dependent variables were therefore transformed when appropriate (using log, rank or arcsine transformations). Stepwise multiple regression analysis was performed with F-to-enter values equivalent to p < 0.1 in linear regression (Sokal and Rohlf 1981). Degrees of freedom for F-to-enter values are expressed as $F_{V1,V2}$, where V1 = number of independent variables introduced into the final model and V1 + V2 + 1 = total number of observations. F-to-enter values prefixed with a minus sign represents a negative association. The robustness of the regression results was tested by "jack-knifing" the variables, i.e. omitting each variable in turn from the analysis to see if the significant variables remained in the regression model.

Many of the tests involved the use of multiple dependent variables. However, these variables were not always independent of one another and no global correction of statistical probabilities was therefore conducted. This must be kept in mind when interpreting the results (see Rice 1989).

3.2.4. Factors affecting frequency of EPCs

Male behavioural and phenotypic characteristics, and breeding data were analysed to determine whether some individuals were more prone to their partners experiencing EPCs. Behavioural comparisons utilised the mean residuals (calculated from Table 2.1 after entering the control variables) of mate guarding behaviours (intra-pair distance, %<5m, %,10m, %<15m and %YF) for the fertile period for each of the 12 focal males and were analysed using multiple t-tests. The effect of male phenotypic characteristics (male age and BCI) and breeding biology (FED, territory size, intrusions rate during the fertile period, OSR, clutch size and male settlement date) on whether females paired to certain males experienced EPCs was analysed using multiple Mann-Whitney U-tests (see Table 3.1).

3.3. Results

3.3.1. Song

Males sang more in the morning than later in the day ($F_{3,285} = -5.16$, p < 0.01), and less so when it was windy ($F_{3,285} = -10.54$, p < 0.001). There was no correlation with any of the selection variables (see Table 2.1).

3.3.2. Aerial displays

There was no correlation with any of the control variables. Males song flighted when their pair female was incubating ($F_{2,286} = 11.33$, p < 0.001; see also Fig. 3.1), and when the OSR was more female biased ($F_{2,286} = 4.03$, p < 0.01). Similar results were obtained for total display rates (see Table 2.1).

Later settling males performed fewer song flights (and total aerial displays) than earlier arriving individuals in the post-fertile phase (song flight, $F_{1,84} = -10.4$, p < 0.01; display total, $F_{1,84} = -5.2$, p < 0.025).

Limited data were collected on the duration of song flights (to the nearest second counted orally). For the 12 focal males, song flights were shorter during the fertile period (Kruskal-Wallis, df = 11, H = 26.91, p < 0.01). There was no correlation between mean song flight duration and male BCI (Spearman rank, $R_{12} = 0.15$, p > 0.5).

3.3.3. Time spent off territory

Males spent more time off territory in the morning than later in the day and when the temperature was higher (time, $F_{2,286} = -5.26$, p < 0.01; temperature, $F_{2,286} = 6.23$, p < 0.01; see Table 2.1). Males were rarely seen leaving their territory prior to clutch completion. With the onset of incubation, the frequency and duration of these absences increased, and consequently males spent more time off territory ($F_{1,287} = 22.93$, p < 0.001: range 5 - 24% of time spent off territory; see Table 2.1 and Fig. 3.2). As males had

to be observed leaving their territory, this may be an underestimate of the time they spent off territory.

In the fertile period males with larger territories spent less time off territory than did males with a small territory ($F_{1,111} = -12.89$, $p < 0.001$). Later breeding and later settling males spent more time off territory in the post-fertile phase (time of breeding, $F_{1,86} = 7.62$, $p < 0.01$; time of male settlement, $F_{1,84} = -7.08$, $p < 0.01$).

3.3.4. Intrusions

A total of 98 intrusions were observed during the behavioural observations, 60 of which were by colour-ringed males and the remainder by migrants. 68% (41/60) of the colour-ringed males were identified. Daily intrusion rates by colour-ringed males, over both the breeding season and during the fertile period alone, did not correlate with a male-skewed OSR (Spearman rank; intrusions in the breeding season, $n = 288$, $z = 0.92$, $p = 0.32$; intrusions in fertile period, $n = 109$, $z = 0.85$, $p = 0.39$). For the 12 focal territories, mean intrusion rate did not correlate with mean OSR during the fertile period (Spearman rank, $R_{12} = -0.435$, $p < 0.2$).

Intrusions peaked in the pair female's fertile period (Kruskal-Wallis, $H = 17.04$, df $= 2$, $p < 0.001$; Wilcoxon paired-sign rank: pre-fertile vs. fertile, $n = 12$, $T+ = 75$, $p = 0.0024$; fertile vs. post-fertile, $n = 12$, $T+ = 77$, $p = 0.001$; pre-fertile vs. post-fertile, $n = 11$, $T+ = 49$, $p = 0.16$; see Fig. 3.3.). 61% (39/64) of colour ringed intruders were identified during this time. Later breeding pairs were intruded upon more than earlier breeding pairs during the fertile period (Mann-Whitney U-test, early breeding pairs ($n = 9$) vs. late breeding pairs ($n = 3$), $U = 0$, $p < 0.05$; see Fig. 3.2). Intrusions tended to occur earlier in the day (Spearman rank, intrusion rate per hour vs. time in day, $n = 109$, $z = -1.81$, $p = 0.07$).

Males tended to intrude on more distant territories when their female was incubating (Kruskal-Wallis, df $= 2$, $H = 5.09$, $p < 0.08$; see Fig. 3.4). During the fertile period neighbouring males intruded more during focal watches on early breeding territories, however for later breeding pairs males came from territories further away (Chi-squared test, early breeding pairs ($n = 9$) vs. late breeding pairs ($n = 3$), $X^2 = 15.72$, df $= 3$, $p < 0.01$; see Fig. 3.5).

3.3.5. Extra-pair copulations

Of the 64 intrusions observed during the fertile period, only seven resulted in EPCs (10.9%), observed on six territories. All these occurred in the predicted fertile period of the pair female, but in the post-fertile period of the extra-pair male's mate. EPCs were rapid events and only three of the males which performed them were identified. There were no
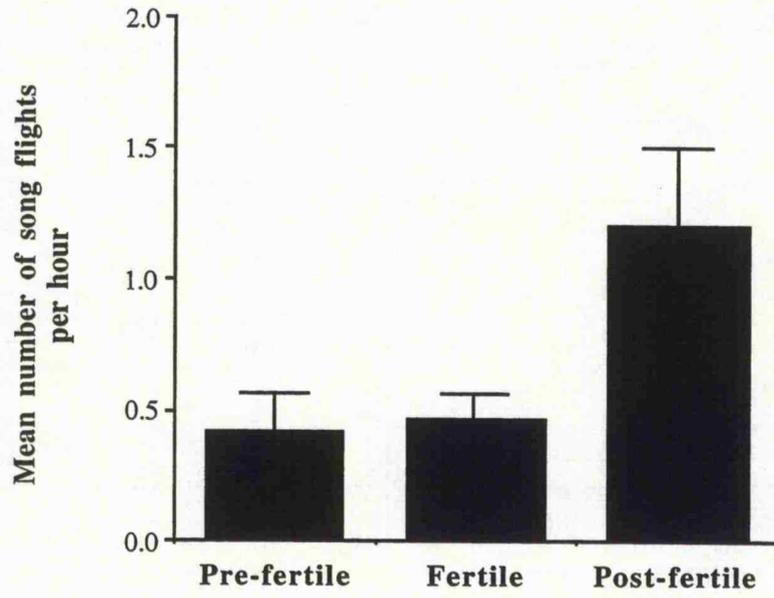
Fig. 3.1. Mean number of song flights per hour relative to the fertility of the pair female. Mean for 12 focal males ± se.

(i)
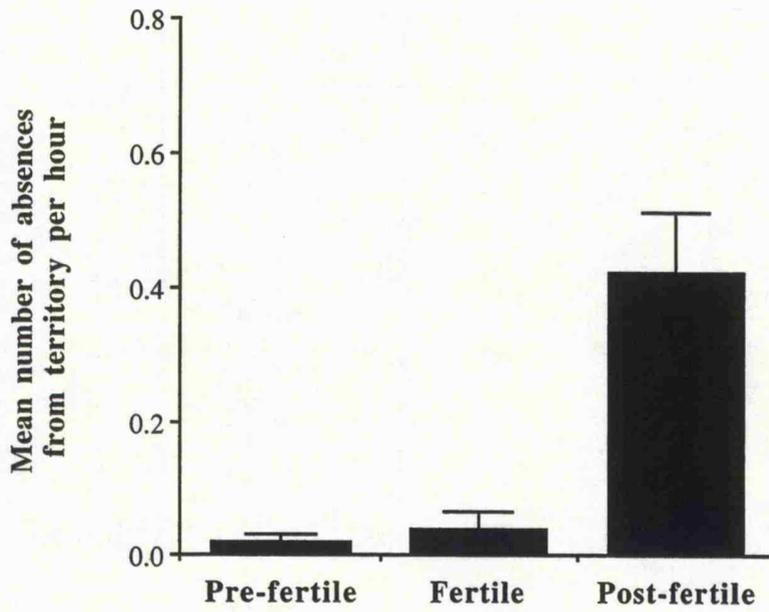
(ii)
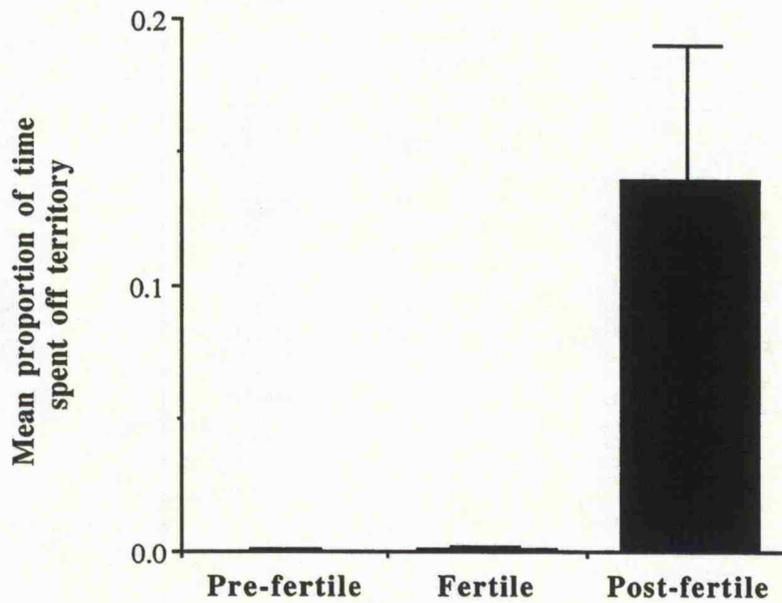
Fig. 3.2. Time spent off territory in relation to female reproductive period: (i) mean number of absences from territory per hour, and (ii) mean proportion of time spent off territory, by the pair male relative to the fertility of the pair female. Mean for 12 focal males ± se.

(i)
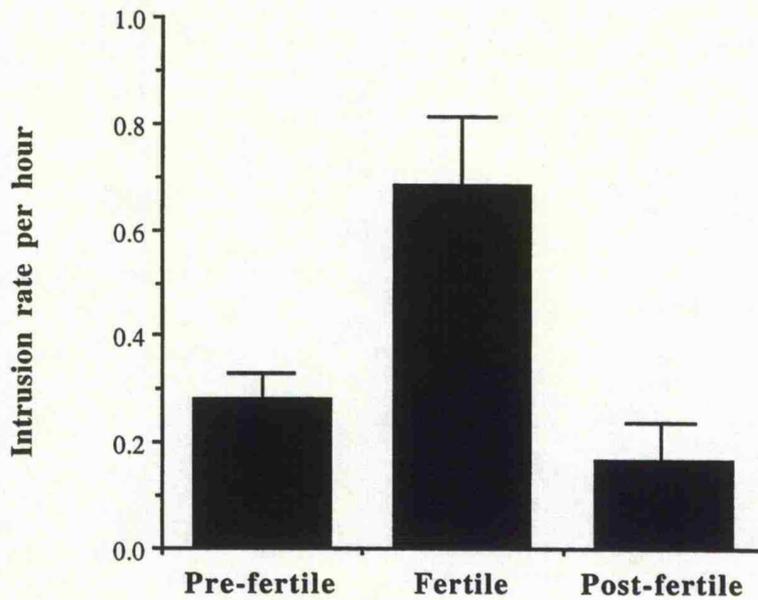
(ii)
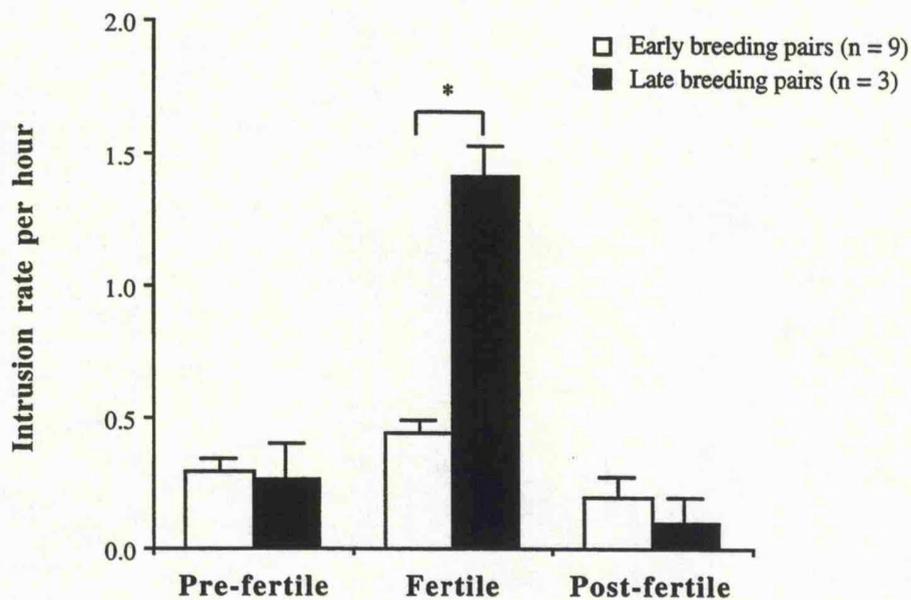
Fig. 3.3. Mean intrusion rate per hour by extra-pair males on the territories of (i) all pairs and (ii) early and late breeding pairs separated, relative to the fertility of the pair female. Mean for 12 focal males ± se. Intrusions by extra-pair males peaked in the fertile period (Kruskal-wallis, df = 2, H = 17.47, p < 0.01). Late breeding territories were intruded upon more in the fertile period than early breeding pairs (Mann-Whitney U-test, U = 0, * p < 0.05).
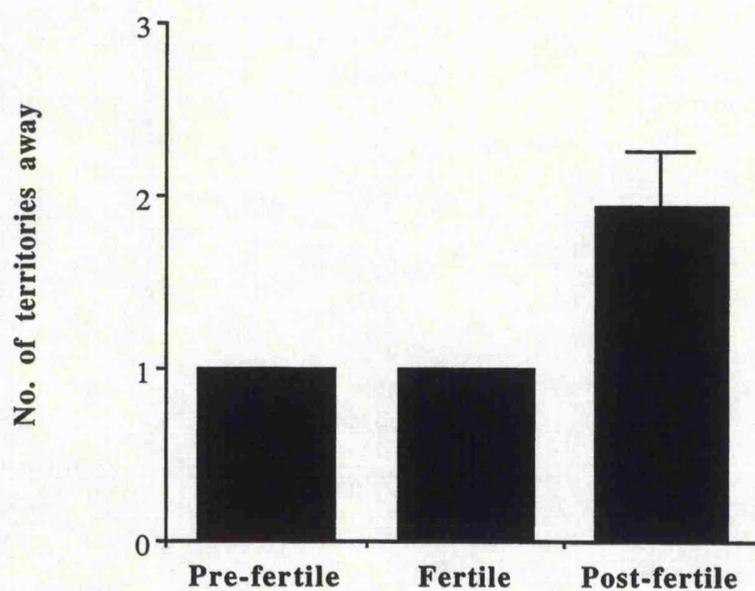
Fig. 3.4. Mean number of territories over which extra-pair males crossed during intrusions relative to the fertility of the pair female. Mean ± se for 12 focal males. Extra-pair males tended to intrude on more distant territories when their pair female was incubating during the post-fertile period (Kruskal-Wallis, df = 2, H = 5.09, p < 0.08). Note in pre-fertile and fertile periods males were only ever observed to intrude on neighbours.
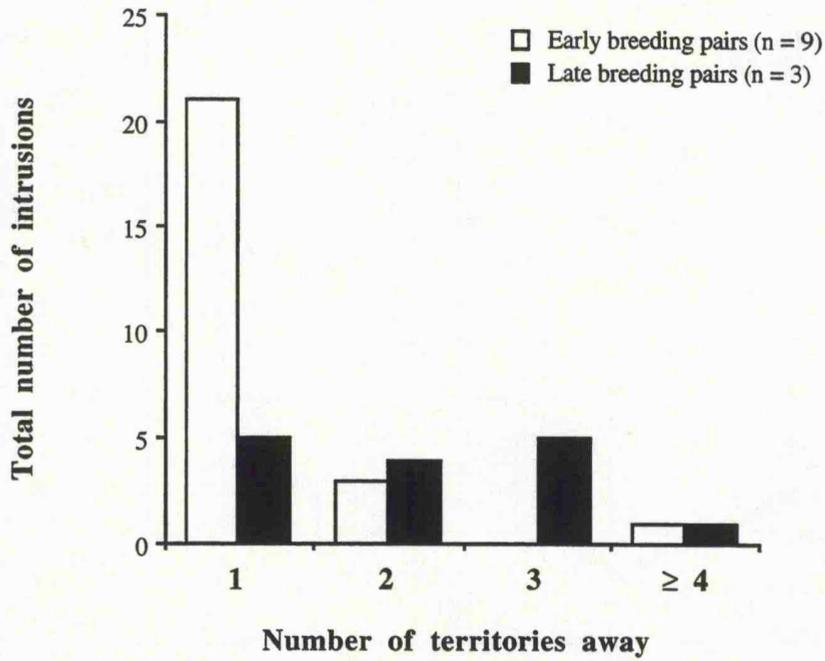
Fig. 3.5. Number of intrusions in relation to the distance to the intruder's territory, measured as the number of separating territories, for early and late breeding pairs. 1 denotes a neighbouring territory. Intruders came from more distant territories for later breeding pairs (Chi-squared test, $X^2 = 15.72$, df = 3, p < 0.01). The number of identified intruders was 41.

Table 3.1. Comparison of behavioural, phenotypic and breeding data for males whose female experienced extra-pair copulation attempts vs. males whose partner did not experience extra-pair copulation attempts during the fertile period.

(i) Mate guarding behaviours (in fertile period)	t-statistic
Mean	-0.75
%<5m	0.44
%<10m	1.10
%<15m	0.98
%P+	-1.13
%YF	-0.84

(ii) Male characteristics	z value
Male BCI	-0.84
Male age	-0.50
Male settlement date	-0.24

(iii) Breeding data	z value
FED	0.33
Territory size (ha)	0.44
Intrusions in fertile period (h-1)	0.98
OSR	-1.31
Clutch size	-0.05

Mate guarding behaviours are: Mean, mean intra-pair distance; %<5m, %<10m and %<15m, proportion of time males was within five, ten, and 15 metres of the pair female respectively; %P+, proportion of time male perched above the pair female; %YF, proportion of female flights which the male followed. Male characteristics are: Male BCI, male body condition index; Male age, first-year breeder or older male; Male settlement date, date of arrival on study area. Breeding data are: FED, first egg date; Territory size (in hectares); Intrusions in fertile period (h-1), intrusion rate by extra-pair males per hour during the fertile period; OSR, operational sex ratio; Clutch size.

t-statistics are for unpaired t-tests and z values are for Mann-Whitney U-tests. None of the values was statistically significant.

behavioural, phenotypic or chronological differences which explained why females paired to some males experienced EPCs (see Table 3.1).

The pattern of EPCs did not reflect that of female fertility with the majority occurring during mid to late laying (5/7), and between 1300 - 1700 hours BST (5/7). Most EPCs were carried out with neighbours. In the majority of cases, intruding males appeared discretely on focal territories but did not interfere with the pair female and often perched on walls overlooking the pair. All seven of the EPC attempts were preceded by the intruding male flying directly to and dancing over the female (for details of dancing display see Chapter 1). In all instances the pair male was at least 15 metres from the female. The female acted aggressively to 85% (6/7) of these EPCs, and the intruder was subsequently chased off territory by the pair male. On the one occasion that the female did not act aggressively, the pair male was distracted by other intruders. The female dropped off a wall and was danced over by the extra-pair male. The female subsequently solicited and participated in an EPC out of sight of her partner. Another of the EPC attempts occurred when a pair copulation was interrupted by the intruding male who subsequently attempted to copulate with the female. On two occasions extra-pair males (one neighbouring male, the other from three territories away) were also observed entering nest holes during early laying. The respective females were not on the nest at the time (see also Carlson *et al.* 1985).

During early spring migratory females also intruded upon territories while feeding. If the resident male was already paired and the intrusion took place prior to his female incubating he usually chased the intruding female away, though this was typically initiated by the pair female. The male's attitude to intruding females changed once his own had commenced incubating. On the rare occasions that solitary females appeared on territories males typically displayed to them. In 1991 there was one instance of a male performing the dancing display and attempting to copulate with a 'migratory' female twice in quick succession. There was no evidence of migrant males attempting to copulate with resident females, though some set up small, short term feeding territories (see also Conder 1989).

3.4. Discussion
3.4.1. Intrusions

The timing of intrusions and EPCs by resident extra-pair males peaked in the pair female's fertile period (Ford 1983, Møller 1987d), tending to be more frequent in the morning (Møller 1987d). Intrusions by residents over the whole season and in the fertile period, did not correlate with a male-skewed OSR. The precise timing of intrusions and EPCs and the absence of a correlation between intrusions and a male-skewed OSR suggests that extra-pair males can identify fertile females and alter their behaviour accordingly (see Birkhead and Møller 1992). This could be due to them cueing in on the reproductive status of the pair female. Although there was no evidence that females directly

advertised their fertility to neighbouring males, as in the case of the blue tit and chaffinch where females make conspicuous calls when copulating (Kempenaers *et al.* 1992, Sheldon 1994, see also Montgomerie and Thornhill 1989), female solicitations peaked during the fertile period (see section 1.4.3). These could be performed either discretely e.g. behind walls, or more conspicuously e.g. on top of walls, however female solictations (as well as copulations and accompanying dancing displays) were infrequent, and in the wheatear it is more likely to be the male which advertises female fertility via mate guarding behaviours (see Birkhead and Møller 1992).

3.4.2. Time spent off territory

Although remaining territorial towards conspecifics and interspecifics throughout the breeding season, males did not remain permanently on their territory. There were occasional short absences during the pre-fertile and fertile periods, all involving intrusions onto neighbouring territories. Their duration and frequency increased markedly in the post-fertile period (incubation), and males were observed to roam the study area, tending to congregate on territories where there was a fertile female. There was a significant decrease in the amount of time spent near the female when she was off the nest feeding during incubation (see section 2.3.1), and in many of these instances the female was unaccompanied by the male. Most foraging was performed on territory, and males were rarely seen feeding off territory (though were occasionally seen provisioning for nestlings off territory). Later in the breeding season more males were released from guarding duties and congregated on the few territories where there was a fertile female, resulting in higher intrusion rates than experienced by earlier breeding males. There were a few extreme instances of males being identified more than 1.6 kilometres from their territory during this time. If intrusions were primarily due to males feeding off territory, it does not explain why intruders travelled longer distances after the onset of incubation and later in the season. Later in the season there were fewer fertile females. This is reflected in the reduction in the proportion of neighbouring paired males that had a fertile female (Mann-Whitney U-test, proportion of paired neighbouring males with fertile females, early territories [n = 13] vs. late territories [n = 7], z = -2.90, p < 0.01). Males had to travel greater distances in search of females and as a result spent more time off territory during incubation. Once hatching had occurred these long distance roamings declined, but males provisioning nestlings were occasionally caught on neighbouring territories (see assumptions for calculating OSR in section 1.4.5).

Breeding passerine males develop a specialised structure for storing sperm, the cloacal protrusion (CP) (Wolfson 1954, Birkhead *et al.* 1993). In 1991 the majority of males were caught soon after their arrival and before any behavioural observations. CPs developed about two weeks after the males had returned to the island and were not noted

until about 16 days after arrival for normally arriving individuals. Later arriving residents caught in subsequent years had fully developed CPs (n = 2). None of the 16 migrant males caught over three years had developed CPs. Males caught after their pair female's fertile period had prominent CPs until at least 13 days after their respective FEDs. Unpaired males had CPs late into the breeding season. Males therefore had the capability to participate in EPCs throughout the majority of the breeding season. (Mean dimension of CPs from 11 males (caught in 1993) : width, 6.19 ± 0.18 mm; length, 5.78 ± 0.25 mm; height, 6.28 ± 0.16 mm).

Males were rarely seen off territory in the pre-fertile period. The mean difference between male settlement date and FED (± se) in 1991 was 42.67 ± 1.85 days. (1992: 37.83 ± 2.37; 1993: 33.41 ± 2.46). These data exclude relays due to nest failure or mate predation. If CPs develop about two weeks after arrival on territory then lack of male cloacal development cannot explain the few absences from territory prior to laying as males appeared to be capable of copulating 3-4 weeks before their pair female's fertile period. For the earliest breeding males the lack of fertile females could account for the lack of absences from territory but not for those individuals breeding later in the season. There may be a risk of territory loss and/or female desertion with prolonged and/or frequent absences prior to laying. However, there was no evidence that males had to re-establish territorial boundaries or evict extra-pair males during any of the temporary or more prolonged absences from their territory. It is unlikely that participating in few and short absences prior to the fertile period is a means by which males limit their females experiencing/participating in EPCs (as females were not observed copulating with their partners until their fertile period and were aggressive to their mate's approaches prior to this time). The lack of fertile females for early breeding males could explain the few extrusions (if leaving the territory is costly) prior to laying, however some females were fertile during the pre-laying period of later breeding males, and these too were rarely observed off territory during this time. Later breeding males therefore appear to lose out on possibly additional matings which suggests there are important reasons why there are few extrusions prior to laying. It was argued in section 2.4.4(iii) that the male is typically the more vigilant of the pair, and a continuing male presence may be required to 'watch over' the female to reduce the predation risk (Martin 1984) and allow her to forage efficiently without being harassed by extra-pair males (e.g. Aschcroft 1976). Although speculative, limited extrusions prior to laying may also maintain and/or reinforce the pair bond.

3.4.3. Vocal and aerial displays

There was no evidence in this study that song was used to gain additional matings or females because there was no discrete peak in output during the breeding season. However, there were distinct temporal variations in the rate of aerial displays, indicating

that they may be associated with the pursuit of additional matings.

On arrival at the study area males were often observed displaying to neighbours while setting up territories and during boundary interactions. Males were also observed singing and song flighting frequently in the presence of females, many of which were migrants. Intense bouts of displaying occasionally culminated in the males collecting nest material and entering potential nest sites. This was observed on five occasions during the three-year study. Four of these nest holes were used for breeding in at least one of the study years. Once a male had paired up, his frequency of song flights declined. In 1991, three males were widowed during early nest building. Limited data were obtained on singing and song flighting prior to pairing and for these widowed males, but there was a noticeable increase in the number of song flights performed by these males while they were unpaired in comparison to paired males at that time (pers. obs.). Once they had repaired there was a noticeable decline in the frequency of aerial displays. Males were also observed to congregate on territory boundaries and song flight when there was a fertile female on neighbouring territories. This was especially conspicuous on territories of later breeding pairs.

Males increased their song flight output while their female was incubating. There were few male intrusions during this time and no immediate threat to paternity, suggesting that these displays have an additional function other than territoriality. Males also displayed more when there was a female-biased OSR but did not perform many aerial display during their pair female's fertile period. Males 'advertised' their presence when they were not mate guarding and also when there were fertile females available (as indicated by a female skewed OSR). This supports the idea that they may be used in the pursuit of additional matings, as suggested by Carlson *et al.* (1985). Males also spent more time off territory during the post-fertile period and song flights could also be used to signal a male's continuing presence to neighbours and the pair female. Later settling males performed fewer song flights and overall displays in the post-fertile period. These males also spent less time off territory during this time although there was no direct correlation between song flights and the proportion of time spent off territory).

Aerial displays may impose considerable energetic costs. Flying birds consume energy at a rate of approximately 10 to 15 times their resting rate (Pennycuick 1975). Singing may also be energetically costly (Greig-Smith 1982, Read 1987). Song flights may therefore be costly to male wheatears and may therefore function as an honest signal of male quality and lead to the expectation that higher quality individuals will display more (Mather and Robertson 1992). However, there was no evidence in this study that male body condition affected the frequency and duration of aerial displays.

There seems to be some evidence to support the idea that song flights are used in attracting females and the pursuit of additional matings but they did not appear to reflect

quality as measured in this analysis. Anecdotal evidence from the beginning of the breeding season, during male settlement prior to the females returning to the study area, and displaying after absences from their territory during the post-fertile period, indicate that there may also be a territorial component in their function.

3.4.4. Mate guarding and the pursuit of EPCs

The pursuit of EPCs were limited primarily to the pair female's post-fertile period, suggesting that mate guarding takes precedence over trying to obtain additional matings (Westneat *et al.* 1990). There was some evidence to suggest a trade-off exists between territoriality, mate guarding and the pursuit of EPCs. Little time was spent off territory during the fertile period, but males with larger territories spent less time off territory during this time than did individuals with small territories. Territoriality has been suggested as an additional paternity guard (Møller 1990), and a larger territory is likely to provide a larger 'buffer' zone between extra-pair males and the pair female, but may require more time to defend effectively than smaller territories.

The risk of EPCs has been shown to be proportional to intra-pair distance (Davies 1985, Alatalo *et al.* 1987, Møller 1987b). However, there was no indication that males which exhibited a low level of mate guarding were more succeptible to EPCs, although they were only observed to occur when males were at least 15 metres from their partner.

Unlike the pattern of intrusions, EPCs did not reflect the predicted pattern of diurnal and daily female fertility, with most occurring mid afternoon and during the period of declining mate guarding. A low proportion of intrusions resulted in EPCs, yet these and the majority of intrusions coincided with the pair female's fertile period. The open nature of the island may limit the opportunities for EPCs as the pair male may also be able to more easily monitor the behaviour of his female and intruders (e.g. Sundberg 1992). During intrusions, extra-pair males typically viewed the behaviour of the pair from a prominent perch which would explain how they were able to locate and subsequently visit nest holes. Such vigilance may enable intruding males to assess female fertility and, like the pair male, assess the status of the pair female from the stage of nest building as well as interactions between the members of the pair, or through the behaviour of other extra-pair males. The lack of phenotypic and breeding correlates in a male's succeptibility to EPCs strongly suggests that extra-pair males are opportunistic in pursuing additional matings.

3.4.5. Female behaviour

In recent years, females have been considered to exert a large degree of control over EPCs and subsequently paternity (Lifjeld and Robertson 1992, Birkhead and Møller 1993) and have been observed to visit and, solicit EPCs from, neighbouring males as well as seeming to advertise their fertility (Kempenaers *et al.* 1992, Sheldon 1994). In this study,

females were never observed leaving their territory (extra-pair males always approached the females on their breeding territory, not vice versa). They were also never observed to solicit extra-pair males directly, and resisted the majority of the EPCs (see also Beecher and Beecher 1979, McKinney 1983, Westneat 1987). Female resistance to extra-pair copulations may be a method of testing male quality (see Birkhead and Møller 1992). However in practice it is difficult to distinguish between females resistance and male assessment.

3.5. Summary

1. Males pursued extra-pair copulations outwith their pair female's fertile period. This was typified by an increase in the proportion of time spent off territory during incubation and the timing of their intrusions on surrounding territories to coincide with the fertile periods of extra-pair females.

2. Mate guarding appeared to limit the pursuit of EPCs by males during their pair female's fertile period, and males were rarely observed off territory during this time. The few occasions that paired males were observed off territory in the fertile period were only on neighbouring territories. Males also infrequently left their territories during the pre-fertile period.

3. There was some circumstantial evidence to suggest that conspicuous aerial displays were used to advertise for additional females or EPCs. Males frequently displayed prior to pairing and after losing their female. Males also increased their rate of aerial displays when their pair female was incubating and when there was a female-skewed sex ratio.

4. Territories with later nests were intruded upon more than those with early nests. The majority of intruders at early nests came from neighbouring territories but at later breeding nests intruders came from more distant territories.

5. Extra-pair copulations were infrequent, and in the majority of intrusions during the fertile period extra-pair males did not interfere with the female. Only 7.8% (7/64) of intrusions resulted in attempted extra-pair copulations, the majority of which (6/7) were resisted by the female. There were no behavioural or phenotypic indicators as to whether or not a male's female experienced an extra-pair copulation attempt. Extra-pair males appeared to be opportunistic in their pursuit of additional matings, rather than targeting certain pair females. Females, on the other hand, appeared to be more 'selective' in their pursuit of extra-pair copulations, and were never observed soliciting males off territory, and rarely on territory.

Chapter 4. Extra-pair paternity in the wheatear

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4.5. Summary

4.1. Introduction

Trivers (1972) suggested that individuals should pursue a mixed reproductive strategy (MRS) to maximise their own reproductive success, that is by pursuing additional mating attempts while raising some offspring themselves. In birds, these take two general sex-based strategies. First, males can pursue additional matings outwith the pair bond (EPCs) (Birkhead *et al.* 1987). Second, females can 'dump' eggs in the nests of conspecifics (intra-specific brood parasitism: IBP) (Yom-Tov 1980, MacWhirter 1989). As well as seeking these additional opportunities for increasing their own reproductive success, individuals should also attempt to limit their exploitation by conspecifics. Males ensure their certainty of paternity by two distinct but not necessarily mutually exclusive strategies: mate guarding and frequent copulation (Birkhead *et al.* 1987), while females may increase their certainty of maternity by own-egg recognition and discrimination against foreign eggs (Petrie and Møller 1991).

The frequency of EPCs may not be a reliable indication to levels of EPP because copulations do not always result in sperm transfer and, of the possible confounding effects of sperm competition in the female reproductive tract. Although other techniques exist which have provided evidence of alternative reproductive strategies (see section 1.1), it was not until the recent advent of DNA fingerprinting (Jeffreys *et al.* 1985a, b) that it was possible to assign the genetic parentage of offspring accurately to specific individuals and so obtain a true measure of the success of these alternative mating strategies. As a

consequence, there has been a rapidly developing body of literature looking at the success of these alternative mating strategies through the use of DNA fingerprinting. Reported extra-pair paternity rates vary widely between species, for example 0% for wood warblers and willow warblers (Gyllensten *et al.* 1990) to 55% in the reed bunting (Dixon *et al.* 1994, see Table 4.1).

EPCs resulting in EPP have been suggested to be important in contributing to the variance in reproductive success among males and therefore to be an important component of the sexual selection operating in many often otherwise monogamous species. In monogamy, the predominant mating system in birds (Lack 1968) there are numerous species which show characteristics which have evolved under or are maintained by sexual selection (Darwin 1871, Møller 1986, Kirkpatrick *et al.* 1990). EPCs have been suggested to be a major factor responsible for the evolution and maintenance of bright plumage in these species (Birkhead and Møller 1994). Females may only be able to choose to pair with available males but can participate in EPCs with any of the males in a population. Female choice of EPCs may therefore be a major component of sexual selection in monogamous species.

To date, few studies have examined variation among males in obtaining EPP and tested for correlates with fitness (Smith *et al.* 1991, Kempenaers *et al.* 1992, Sundberg and Dixon in press, Wetton *et al.* 1995). This chapter describes the use DNA fingerprinting to obtain an accurate measure of the contribution of EPCs in increasing male reproductive success in the wheatear.

4.2. Methods

4.2.1. Data analysis

Nests were numbered consecutively according to their first egg date (FED). Pairs were termed early or late depending on whether or not their FEDs were amongst the first or last half of the nests to be initiated, respectively. The definition of the fertile period and calculation of body condition (BCI) and operational sex ratio (OSR) was as in sections 1.4.3, 1.4.4 and 1.4.5 respectively.

Male behavioural and phenotypic characteristics, and breeding data were analysed to determine their effect on the presence of extra-pair offspring in the nest. Behavioural comparisons utilised the mean residuals (calculated from Table 2.1 after entering the independent control variables, see section 2.3.1) of mate guarding behaviours (intra-pair distance, %<5m, %<10m, %<15m and %YF) and behaviours associated with the pursuit of EPCs (song flights and the proportion of time spent off territory) for each of the 12 focal males and analysed using multiple t-tests. The effect of phenotypic characteristics (male age and BCI) and breeding biology (FED, territory size, intrusions rate during the fertile period, OSR, clutch size and male settlement date) were based on 17 pairs and

analysed using multiple Mann-Whitney U-tests (see Table 4.2).

4.2.2. DNA fingerprinting

The techniques used for DNA fingerprinting in birds have been well described elsewhere (Burke and Bruford 1987, Burke *et al.* 1989, Bruford *et al.* 1992) and only a brief summary is given here.

(i) Blood collection

Approximately 40 - 150 μl of blood was taken by brachial venipuncture and immediately placed in at least 500μl of 1 x SSC, 10mM EDTA blood buffer (0.15 M NaCl, 15mM trisodium citrate, 10mM EDTA, pH 7.0, autoclaved) in labelled, screw-cap, 1.5ml tubes. Samples were stored at 4°C for up to four months on Bardsey Island, then they were transferred to a -70°C freezer in Leicester.

(ii) DNA extraction from blood

30-50 μl of blood was added to 400μl 0.1 M Tris - Cl, pH 8.0, 0.1 M NaCl, 1mM EDTA, 0.5% SDS and incubated overnight at 37°C with 1μl of proteinase K (3-5 units ml^{-1}, Sigma). This was followed by two phenol/chloroform and one iso-amyl alcohol/chloroform extractions and precipitations of the DNA in 100% ethanol. The DNA was then allowed to completely dry overnight at room temperature and dissolved in 0.5ml 1x TE (10mM Tris, 1mM EDTA, pH 7.6).

(iii) DNA digestion and electrophoresis

Approximately 5μg of DNA was digested with 15 units of Mbo I restriction enzyme, used as instructed by the manufacturer, then extracted with phenol/chloroform, followed by precipitation in 100% ethanol and air drying at room temperature. Digested DNA was dissolved in double distiled water.

Electrophoresis was carried out in 1% agarose (Sigma, Type 1) in a TBE buffer (0.089 M Tris, 0.089 M Borate, 2mM EDTA, 0.5μ/ml ethidium bromide, pH 8.8) at 50 - 80V for 50 - 60 hours until fragments of 2kb had migrated 28cm. Samples were balanced for equal amounts of DNA, prior to loading on the gel, using a fluorometer (Hoeffer).

After electrophoresis, gels were washed in 0.25 M HCl twice for 7.5 minutes, 0.5 M NaOH, 1.0 M NaCl twice for 15 minutes and finally 1 M Tris, 3 M NaCl, pH 7.4, twice for 15 minutes. Gels were then Southern blotted using 20 x SSC onto Hybond - Nfp (Amersham) nylon membranes, for three hours. After blotting, membranes were briefly washed in 2 x SSC, allowed to air dry and then fixed by exposure to 254 nm ultra-violet light on a transilluminator.

(iv) Probing filters

Jeffreys 33.15 probe was used, labelled with ^{32}P by primer extension from single stranded M13 vectors (Jeffreys et al 1985 a, b). Filters were prehybridised at 65°C for three hours in 0.5 M Na phosphate, 1mM EDTA, 7% SDS and 1% bovine serum / albumin, pH 7.2. Hybridization was carried out in the same solution for 16 hours at 65°C, then the filters were washed once in 0.5 M Na phosphate, 1% SDS, once in 2 x SSC, 0.1% SDS then several times in 1 x SSC, 0.1%SDS at 65 °C until background levels of radiation were negligible. Filters were then exposed against X-ray film (Fuji RX) for 3 -14 days at -70°C, either with one, two or no intensifying screens, depending on the intensity of the radiation on the filters.

(v) Fingerprint analysis

Offspring were run on the same gels as their putative parents, which avoided the problem of trying to compare fingerprints between gels. Bands between 23 and 2.5 kb were scored as these had the clearest resolution and highest diversity on the fingerprints. Bands were scored as being the same when their centres were within 0.5 mm of each other and did not differ in intensity by more than two-fold. Band sharing coefficients were calculated as described in Wetton *et al.* (1987), using the equation:

$$X_{ab} = \frac{2n_{ab}}{na + nb} \qquad\qquad 4.1$$

where X_{ab} is the band sharing coefficient between two individuals (a and b), n_{ab} is the number of shared bands and na and nb are the number of scored bands in individuals a and b, respectively. Background band sharing was calculated from 56 pairwise comparisons of unrelated individuals over the three-year study (36 pairs and 20 from unrelated males run on the same gel). Band sharing coefficients were calculated for all pair-wise comparisons between all offspring and both parents (Jeffreys *et al.* 1985a, b, Burke and Bruford 1987, Birkhead *et al.* 1990). Some bands were apparently shared by the parents, and some parental bands were also homozygous, so that the band sharing coefficients for first order relationships (parent-offspring and sibling-sibling) were expected to be significantly greater than 0.5. Unrelated individuals on average should show the background level of band sharing, and the distribution of all pair-wise band sharing coefficients should therefore show a bimodal distribution of unrelated individuals and first order relatives.

When both putative parents were available, the number of mismatched bands was calculated for each offspring i.e. the number of bands in the offspring which could not be accounted for in either of the parents. Random mutation can account for occasional mismatches, which in previous studies have been detected at a rate of 1 in every 100-300

bands (Jeffreys *et al.* 1985a, b, Burke and Bruford 1987, Westneat 1990). Mismatches occurring more frequently than this are more likely to be due to individuals not being directly related to the putative parents, rather than to multiple mutations.

In the fingerprint analysis the observed and expected degrees of band sharing are compared under the assumption that bands are inherited independently of one another and are not linked. This assumption can be tested by a segregation analysis of a large family of 10 or more offspring (Jeffreys *et al.* 1985a b, Burke *et al.* 1989, Birkhead *et al.* 1990). I used the alternative approach which involves comparing the distribution of band sharing values between individuals of known or deduced relationship. DNA fingerprint analysis using band sharing coefficients in this way has been successfully applied in several studies (Wetton *et al.* 1987, Westneat 1990, Lifjeld *et al.* 1991, Hunter *et al.* 1992). For potential problems associated with determining paternity on band sharing coefficients see Hartley *et al.* (1993).

4.3. Results

4.3.1. Actual reproductive success

The paternity of 17 families was examined using multilocus DNA fingerprinting. Ninety-four scorable fingerprints were obtained for 60 offspring from 14 families where both the male and female were available, and for 11 offspring from three families where no fingerprint was obtained for the female. Fig. 4.1 shows an example of a wheatear multilocus DNA fingerprint.

The mean number of scorable bands were 28.14 ± 0.78 (standard deviation; sd). Single mismatching bands occurred in six offspring, giving a band mutation rate of 1 in 436, comparable to that found in other studies (Jeffreys *at al.* 1985a, b, Burke and Bruford 1987, Westneat 1990). The mean band sharing coefficient for nestlings which could be compared with both putative parents, and which could therefore be included or excluded on the basis of multiple band mismatches, was 0.57 ± 0.104 (sd) for male:offspring and 0.55 ± 0.12 (sd) for female:offspring. Fig. 4.2 shows the frequency distribution of band sharing between nestlings and their putative fathers, mothers and siblings. The mean band sharing coefficients for 56 apparently unrelated birds was calculated as 0.20 ± 0.11 (sd) including a high band sharing coefficient of 0.61, which most likely represents two related individuals. Both sexes are philopatric to their natal area (see section 7.3.3, see also Brooke 1979, Conder 1989), and with a relatively small population on the study site, the inclusion of a pair of related individuals in the sample is not unexpected (see also Hartley *et al.* 1993). Eight offspring from five broods had 5 mismatched bands or more (see Fig. 4.3). The parent-offspring band sharing coefficients fell outwith the 95% confidence limits (t x sd) of male:true offspring band sharing coefficients in each case but within that of the female:offspring. EPP accounted for 11.2% of offspring in 29.4% of broods. There was

no evidence of intra-specific brood parasitism, as there were no mismatched bands between offspring and putative mothers. Low band sharing coefficients with the female were primarily due to poor quality fingerprints (and consequently a low number of scorable bands) for a few individuals.

4.3.2. Identification of fathers.

Three of the extra-pair offspring were sired by one male (two in a neighbour's nest and one in another two territories away from his own). This male had his female predated during late nest building and was temporarily single during the fertile period of the extra-pair females with which he mated. Unfortunately, the fathers of the other five offspring could not be identified (three in one brood and single individuals in another two nests). For the two broods which held single EPY, these offspring were run against all immediate neighbouring males (up to three territories away) all of which were excluded. This indicates that in some cases extra-pair fathers were not nearest neighbours.

There was no evidence of multiple extra-pair paternity in broods. Out of the five offspring for which extra-pair fathers could not be found, the three EPY in one nest were probably sired by the same male, given their sib-sib band sharing coefficients which were within the 95% confidence limits for known sib-sib comparisons (see Fig. 4.2). The band sharing coefficient between the two EPY in separate nests was 0.15 and they were therefore likely to have been fathered by two different males.

4.3.3. Characteristics of cuckolded males

(i) Behaviour

For the 12 focal males there were no correlates of mate guarding behaviours, and time spent off territory or display rates, with the presence of extra-pair young (EPY) in the nest (see Table 4.2). Female solicitations peaked during the fertile period (see Chapter 1), and EPY were found in broods where female solicitation rates were highest (Mann-Whitney U-test, mean female solicitation rate per hour in fertile period, nests with EPY vs. nest with no EPY, $z = -1.96$, $p = 0.05$).

(ii) Phenotypic characteristics

There was no apparent age bias among the males which were cuckolded. Out of the 17 families fingerprinted, seven of the putative fathers were first year breeders and 10 were older males. Out of five of the cuckolded fathers, two were young males and three were older individuals. There was also no effect of settlement date or body condition on whether a male was cuckolded (see Table 4.2).

Table 4.1. Frequencies of extra-pair paternity (EPP) and intra-specific brood parasitism (IBP) found in some field studies using DNA fingerprinting. The mating system of the DNA fingerprinted population is indicated.

	n offspring tested	%EPP	%IBP	Mating system	Reference
Willow warbler	120	0	0	m	Gyllensten *et al.* 1990
Wood warbler	56	0	0	m	Gyllensten *et al.* 1990
Black vulture	36	0	0	m	Decker *et al.* 1993
Fulmar	91	0	0	m,c	Hunter *et al.* 1994
Wood warbler	56	0	0	pt	Gyllensten *et al.* 1990
Corn bunting	56	0	0	pm	Hartley *et al.* 1993
Dunnock	133	< 1	0	pa	Burke *et al.* 1989
European bee-eater	100	1	0	m,c	Jones *et al.* 1991
Zebra finch	92	2.4	11	m,c	Birkhead *et al.* 1990
Pied flycatcher	135	4	0	pt	Lifjeld *et al.* 1991
House finch	119	8.3	0	m	Hill *et al.* 1994
Blue tit	314	11	0	m	Kempenaers *et al.* 1992
Wheatear	71	11.2	0	m	Currie *et al.* unpublished
Crested tit	121	12.4	0	m	Lens 1994
House sparrow	536	13.6	0	m,c	Wetton and Parkin 1991
Chaffinch	47	17	0	m	Sheldon and Burke 1994
Purple martin	52	18	17	m,c	Morton *et al.* 1990
Red-winged blackbird	232	24	0	pm	Westneat 1992
Red-winged blackbird	616	25.6	0	pm	Weatherhead and Boag 1995
Red-winged blackbird	111	28	0	pm	Gibbs *et al.* 1990
Hooded warbler	78	29	0	m	Stutchbury *et al.* 1994
Indigo bunting	63	35	0	m	Westneat 1990
Yellowhammer	123	37	0	m	Sunberg and Dixon in press
Tree swallow	205	44	0	m,c	Dunn *et al.* 1994
Reed bunting	38	55	0	m	Dixon *et al.* 1994

m = monogamous, pa = polyandrous, pt = polyterritorially polygynous, pm = monoterritorial polygynous, c = colonial.
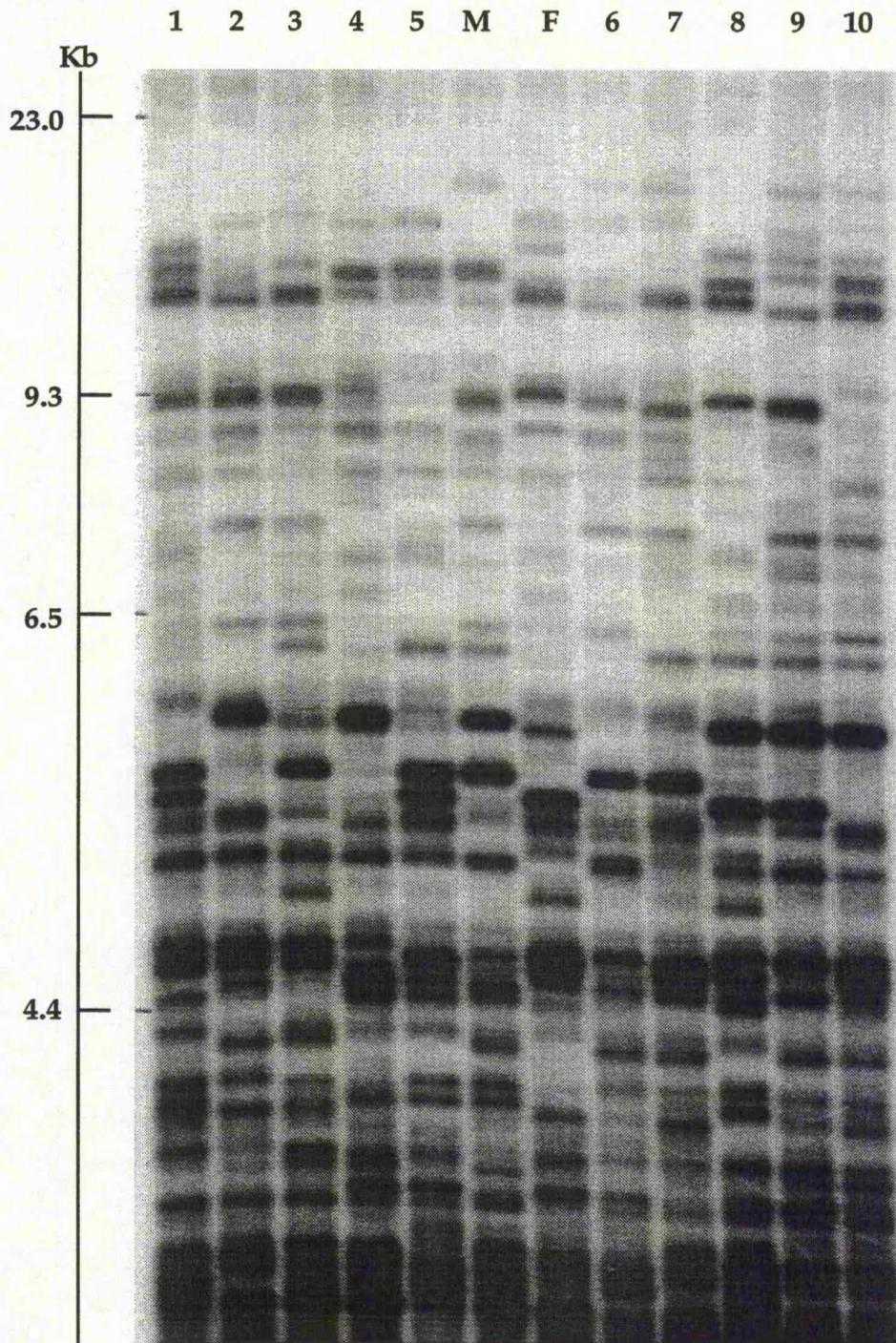
Fig. 4.1. An example of a multilocus DNA fingerprint for two families raised in successive years by the same parents (M and F). Chicks 1-5 were raised in 1991 and chicks 6-10 were raised in 1992. All offspring were assigned as the true, genetic offspring of both the male (M) and female (F) because all bands present in any offspring were also present in one or both parents.
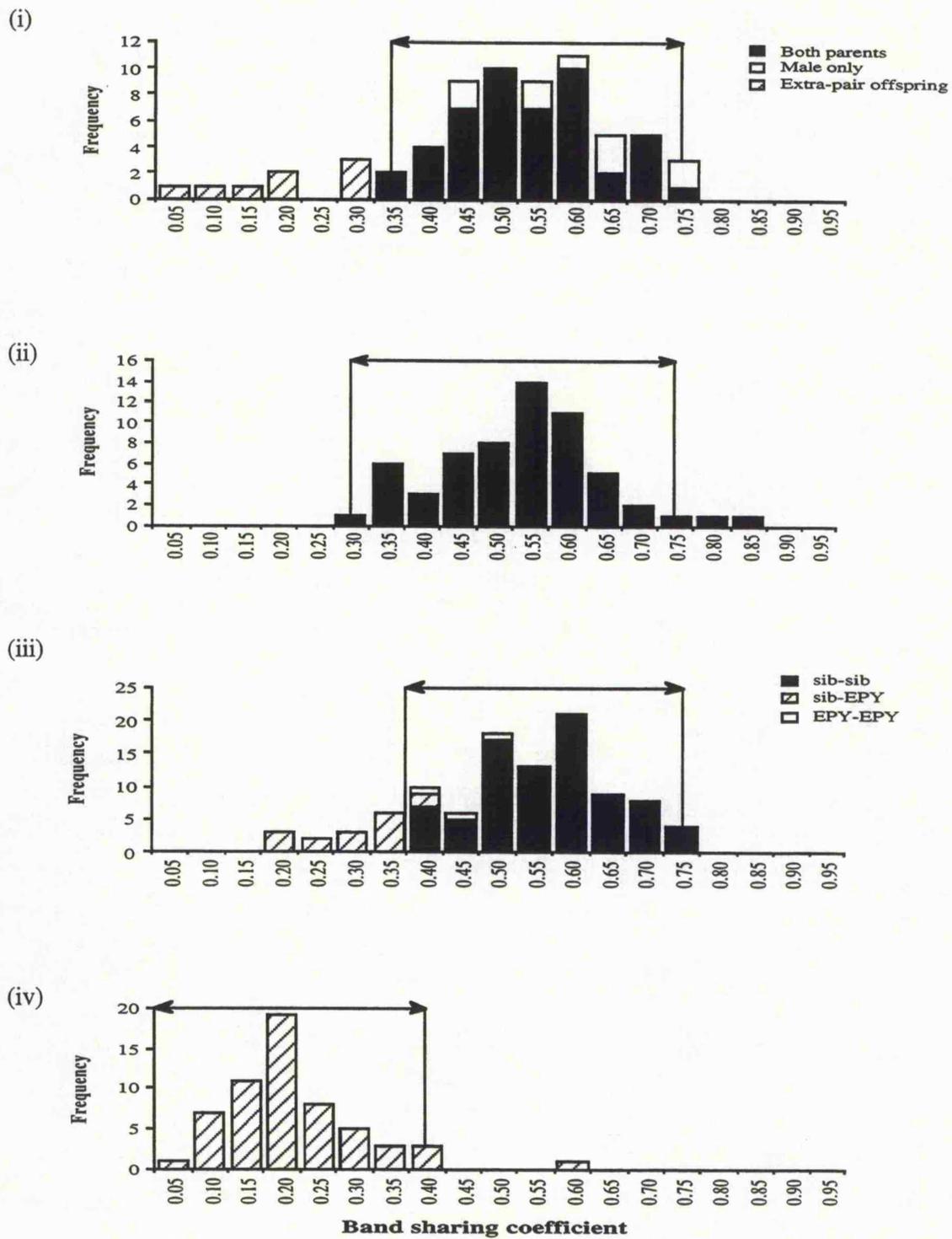
Fig. 4.2. Frequency distribution of band sharing coefficients for 1991 paternity data between (i) males and their offspring, (ii) females and their offspring, (iii) siblings within broods (sib = sibling, EPY = extra-pair young) and (iv) unrelated individuals. Arrows show 95% confidence limits of band sharing ranges.
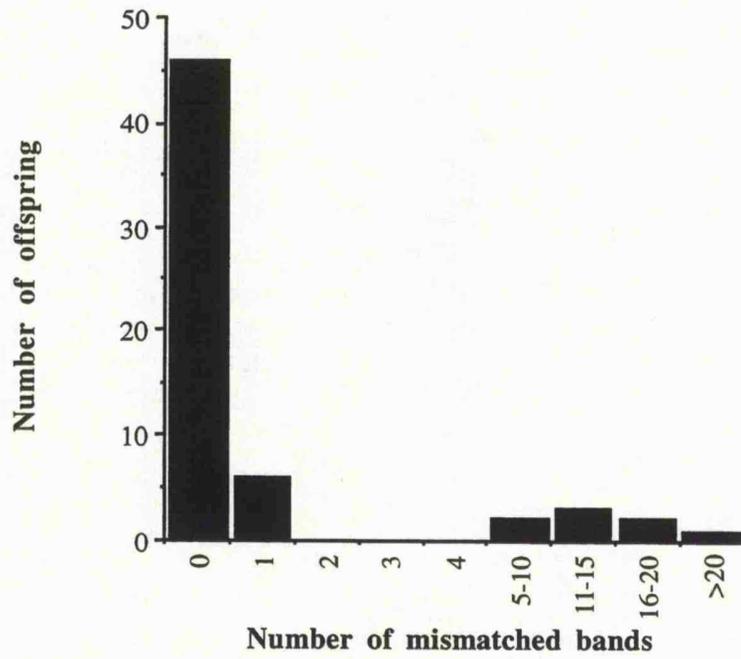
Fig 4.3. Number of offspring with mismatched bands. Offspring with more than five mismatched bands were considered to be extra-pair young.

Table 4.2. Comparison of behavioural, phenotypic and breeding data for males which had extra-pair paternity in their nests vs. males which did not have EPP in their nests.

(i) Mate guarding behaviours (in fertile period)	t-statistic
Mean	-1.39
%<5	0.78
%<10	0.96
%<15	0.93
%P+	0.25
%YF	0.77

(ii) Displays	t-statistic
% off territory	0.62
Song flight	0.74
Display total	0.98

(iii) Male characteristics	z value
Male BCI	-1.48
Male age	-0.64
Male settlement date	-0.37

(iv) Breeding data	z value
FED	-0.09
Territory size (ha)	0.44
Intrusions in fertile period (h^{-1})	0.74
OSR	-1.79†
Clutch size	-2.08*

Mate guarding behaviours are: Mean, mean intra-pair distance; %<5,m %<10m and %<15m, proportion of time males was within five, ten, and 15 metres of the pair female respectively; %P+, proportion of time male perched above the pair female; %YF, proportion of female flights which the male followed. Displays are: % off territory, proportion of time spent off territory; Song flight, number of song flights per hour; Display total, total number of aerial displays per hour. Male characteristics are: Male BCI, male body condition index; Male age, first-year breeder or older male; Male settlement date, date of arrival on study area. Breeding data are: FED, first egg date,; Territory size (in hectares); Intrusions in fertile period (h^{-1}), intrusion rate by extra-pair males per hour; OSR, operational sex ratio; Clutch size.

Analyses of behavioural data are based on 12 focal pairs, while analyses considering male characteristics and breeding data are based on 17 pairs. t-statistics are for unpaired t-tests and z values are for Mann-Whitney U-tests. Levels of significance: † $p < 0.1$, * $p < 0.05$, ** $p < 0.01$.

(iii) Breeding data

Four out of the five broods with EPY were in the first half of the breeding season, on days 4, 5, 6 and 9 (day 0 = first FED on study site; mean FED of nests with EPY [n = 5] = 8.4 ± 3.5 [se], mean FED of broods with no EPY [n = 12] = 15.67 ± 3.93 [se]; Mann-Whitney U-test, z = -0.89, ns). EPY tended to be found in nests for which there was a female-skewed OSR in the fertile period. The mean OSR in the fertile period for broods with EPY was 0.42 ± 0.08 (se), while the mean OSR for broods without EPY was 0.25 ± 0.06 (se) (Mann-Whitney U-test, OSR in the fertile period, broods with EPY [n = 5] vs. broods without EPY [n = 7], z = -1.79, p < 0.07, see Table 4.1). There was a male-skewed sex ratio in the fertile period at later nests (Spearman rank, R_{17} = -0.89, p < 0.002).

EPY occurred in broods with larger clutch sizes (mean clutch size with EPY = 6.4 ± 0.25, mean clutch size without EPY = 5.4 ± 0.28; Mann-Whitney U-test, z = -2.10, p < 0.05, see Table 4.2). Later laying females laid smaller clutches (R_{17} = 0.31, p = 0.01). There was no difference in the residuals from the regression of laying date vs. clutch size between broods which contained EPY and broods without (T-test, t = -1.79, df = 16, p = 0.09), suggesting that the presence of EPY in larger broods was a consequence of clutch size and not laying date.

4.4. Discussion

4.4.1. Extra-pair paternity

Extra-pair paternity (EPP) was comparatively infrequent (see Table 4.1) and accounted for 11.2% of offspring in 29.4% of broods. In general, observed male reproductive success reflected genetic parentage (Spearman rank, number of fledglings raised vs. number of fledglings fathered, R_{17} = 0.72, p < 0.01). EPP can occur as a result of three behaviours: (i) forced EPCs; (ii) rapid mate switching; or (iii) unforced EPCs (Birkhead *et al.* 1990). In the wheatear, female co-operation seemed to be essential for males in gaining successful EPCs. Only one of the observed EPCs was accepted, all others were forced by the male and rejected aggressively by the female. No rapid mate switching (McKinney *et al.* 1984, Birkhead *et al.* 1990) was observed and EPP can therefore be assumed to be a result of female accepted or solicited EPCs (Smith 1988, Kempenaers *et al.* 1992).

There is variation among studies in the correlation between observed EPC rates and the frequency of EPP as detected by DNA fingerprinting. Some studies show a good correlation between the two (Birkhead *et al.* 1990, Hunter *et al.* 1992, Kempenaers *et al.* 1992) while others show little agreement (Westneat 1987a, b 1992, Lifjeld *et al.* 1993, Dixon *et al.* 1994). 32% (7/17) of all copulation attempts observed in this study were EPCs, however 10% (1/10) of successful copulations were EPCs, which is close to the

11.2% rate of EPP.

The paternity data suggest that not all extra-pair fathers were immediate neighbours (see Gibbs *et al.* 1990, Sundberg and Dixon in press, but see Westneat 1990, Sheldon and Burke 1994). The majority of identified intrusions in the fertile period, 25 (60.9%), were by paired males while the remainder were by unpaired individuals. There were six permanently unpaired males, but early in the season there was a maximum of 12 unpaired males due to predation and delays in pairing. There was limited evidence to suggest that a few of the unpaired males who were unable to attract a female became floaters, i.e. individuals which ceased to defend a territory and roam the study area. There was one example when an unpaired male 'disappeared' early in the season, and was trapped on a territory 50 days later without having being seen in the meantime. Although speculative, roaming unpaired males and floaters possibly pose the greatest threat to paternity early in the season due to their lack of guarding duties and are able to capitalise on the reduced male-male competition for fertile females. Their possible impact on paternity later in the season is likely to be reduced due to more intense sexual selection as more males are freed from guarding duties. The only extra-pair father identified was a temporarily unpaired male and although Westneat (1990) found that unpaired males did not play a significant role in pursuing EPCs (see also Hartley *et al.* 1993), their possible role cannot be ruled out in this study. EPP was relatively infrequent and the roaming male strategy, should EPP be attributed to such individuals, would appear to make "the best of a bad job". This contrasts with the behavioural observations as the majority of intruders (early in the season) were by neighbouring males.

4.4.2. Intra-specific brood parasitism

There were no cases of intra-specific brood parasitism (IBP) and female reproductive success can therefore be accurately estimated by the number of young she fledged. IBP often occurs in hole nesting species, e.g. starlings (Pinxten *et al.* 1991), colonial species e.g. swallow species (Møller 1989b, Morton *et al.* 1990), and in populations where there are unpaired floating females, e.g. ducks (see Yom-Tov 1980). In hole-nesting species IBP is likely to be detected prior to laying by the pair female due the presence of an "alien" egg. However, parasitic eggs are likely to be tolerated during the laying sequence due to the risk of removing the wrong egg, visual recognition proving difficult at low light intensities. Under these conditions behavioural adaptations are expected to have evolved. The lack of IBP in the wheatear was not unexpected due to female-female territoriality, which may serve as a behavioural mechanism to prevent IBP (Møller 1989b), and the absence of unmated females in the population.

4.4.3. Breeding synchrony and extra-pair paternity

From behavioural observations one would expect EPY to be more likely to occur in the broods of late breeding pairs since they experienced higher intrusion rates by extra-pair males during the fertile period. Surprisingly, EPY tended to occur in the nests of early breeding males, when there was a female-skewed sex ratio i.e. a greater number of fertile females to non-guarding males, and intrusion rates were low. This was similar to the seasonal pattern of EPCs, with five of the seven observed attempts (two by a non-paired male and three by paired males) also being early in the season. Male-male competition per fertile female early in the season is likely to be less intense than later in the season, when there are fewer fertile females, due to pair males being occupied with guarding duties. Intense mate guarding and intra-sexual competition may reduce the opportunities of males to successfully pursue EPCs on later breeding territories. The chances of gaining EPP may therefore be greater from a successful EPC on early nesting territories.

Male wheatears have been shown to mate guard during their pair female's fertile period and to pursue additional matings outwith it, primarily in the post-fertile period (Carlson *et al.* 1985, Chapters 2 and 3 respectively). These are two mutually exclusive and potentially conflicting behaviours, but mate guarding is assumed to take precedence (Westneat *et al.* 1990). However, the trade-off between the two may be more acute for early breeding males, with them attempting to capitalise on a female-biased OSR. Early breeding males were occasionally observed to intrude on neighbouring territories during their pair female's fertile period (0.06 extrusions per hour, 0.01% of time spent off territory), while later breeding males were never seen off territory during their partner' fertile period. This may be due to increased mate guarding exhibited by later breeding individuals (see section 2.3.5), possibly in response to higher intrusion rates, as well as the lack of fertile females in surrounding territories (Mann-Whitney U-test, mean proportion of paired neighbours with fertile females, early nests = 0.92 ± 0.04 [n = 13], late nests = 0.36 ± 0.17 [n = 7], z = -2.90, p < 0.01).

4.4.4. Clutch size and extra-pair paternity

Broods with EPY tended to have about one more egg in their clutches than broods without. In birds, females have been shown to be able to store sperm in specialist tubules located in the utero-vaginal region of the reproductive tract (Shugart 1988, Birkhead and Hunter 1990, Birkhead *et al.* 1990, Birkhead 1992). Although the general rule appears to be last male sperm precedence (Birkhead *et al.* 1988, 1989, Lessells and Birkhead 1990, but see Oring *et al.* 1992), females laying a larger clutch are likely to utilise more sperm reserves than those laying a smaller one. This may increase the probability of a female using more than one male's sperm should she have experienced a successful EPC. Although speculative, this effect may be acute in species exhibiting a low rate of copulation

which rely on mate guarding to ensure paternity.

Although there is an increased likelihood of detecting EPY in larger clutches, there was a significant correlation between the proportion of EPY within a brood and clutch size (Spearman rank, $R_{17} = 0.66$, p < 0.01). This suggests that the presence of EPY in larger clutches was not just a result of the increased opportunity for successful EPCs which larger clutches provide, but possibly a deliberate strategy by the females concerned. Females have been shown to control fertilisation of eggs through active selection and rejection of partners (Lifjeld and Robertson 1992), resulting in males attempting to mate guard around the behaviour of their partner. In most species, the intensity of mate guarding decreases during laying (Birkhead *et al.* 1989) even though removal experiments have shown that EPCs during this time can affect paternity (Davies *et al.* 1992). Males are possibly unsure about the exact clutch size their female is going to lay. A low intensity of mate guarding towards the end of clutch completion combined with the male's uncertainty about the clutch size could enable females to participate in EPCs, especially in larger clutches. Although based on a small sample size, the majority of observed EPCs occurred during the mid-late period of laying, during the period of declining mate guarding (5/7 from day 2 onwards). Extrapolation from the behavioural observations and paternity data indicate that EPCs during the laying sequence resulted in fertilisation of eggs. Due to nest site inaccessibility, no data on the position of the EPP in the laying sequence are available, but in the reed bunting EPP occur equally throughout the clutch (Dixon *et al.* in prep.). These results run contrary to the expectation that copulations during laying may be devalued due to sperm being flushed out of, or prevented from entering, the storage tubules (see also Davies *et al.* 1992).

4.4.5. Female control of extra-pair paternity

The ability of a female to determine paternity via the frequency and timing of copulations is likely to depend on the: (i) the presence of a guarding partner; (ii) the costs and benefits to the female of participating in EPCs; (iii) the availability of relatively good quality males; and (iv) the degree of 'last male' sperm precedence (Birkhead *et al.* 1990).

The reduced intensity of mate guarding early in the season may be due to a lower perceived threat to paternity (as indicated by a lower intrusion rate) but also in response to a more acute trade-off between mate guarding and the pursuit of EPCs due to a female-skewed OSR. A combination of these two factors could allow females to have more control over the paternity of early broods.

Westneat *et al.* (1990) reviewed the costs and benefits for females of participating in EPCs. Potential costs include poor quality offspring, retaliation by the pair male (either a reduction in paternal care or physical abuse), or harassment or the risk of injury by extra-pair males (see also Birkhead and Møller 1992). In monogamous birds, benefits to the

female in accepting EPCs are more likely to be genetic as opposed to material, either by increasing the diversity of the brood, or by allowing a 'better quality' male to father some or all of her offspring (Smith *et al.* 1991, Kempenaers *et al.* 1992, Graves *et al.* 1993,Wetton *et al.* 1995, Sundberg and Dixon in press). The genetic diversity hypothesis predicts that EPP in nests should be infrequent but common among broods, while the good genes hypothesis predicts the opposite (Westneat *et al.* 1990). The paternity data from this study are inconclusive, but if anything the distribution of extra-pair offspring among broods supports the good genes hypothesis. All extra-pair offspring in each of the respective nests were fathered by on male, as would be expected if females were seeking 'good' genes (more than one extra-pair father might be expected if females were seeking to produce genetically diverse offspring). However, there were no obvious phenotypic or behavioural differences between cuckolded and non-cuckolded individuals (see also Dunn *et al.* 1994), and females were never observed to visit extra-pair males on their territories (which would have suggested they were specifically seeking EPCs).

Several studies have shown that males successful in gaining EPP were also most successful in ensuring the paternity of their own brood(s) (Gibbs *et al.* 1990, Kempenaers *et al.* 1992, but see Dixon *et al.* 1994, Wetton *et al.* 1995). However, not all extra-pair fathers were identified in this study and it was not possible to test this hypothesis, and circumstantial evidence even suggests that some extra-pair fathers may have been unpaired. EPP occurred in broods where the pair female exhibited a high solicitation rate. Lens (1994) showed a negative correlation between copulating in response to female solicitations and male body condition in the crested tit, and argued that females may assess male quality depending on their response to repeated solicitations (the male assessment hypothesis).

Crested tits copulated frequently during the fertile period (2.1 ± 0.7 h-^{1}) while copulations were rarely observed in the wheatear (see also Conder 1989). Wheatears were estimated to copulate approximately once per clutch, and so females are unlikely to assess male quality in the same way as has been suggested in the crested tit. Although running counter to the suggestion that the distribution of EPY supports the good genes hypothesis, if pair males do not copulate in response to repeated solicitations females may also accept EPCs in an attempt to ensure her eggs are fertilised (Walker 1980, Drummond 1984, Wetton and Parkin 1991). Insurance copulations may promote sperm competition with only the most viable sperm fertilising the eggs. As well as insuring fertilisation of their eggs, this may also benefit the female, because any males produced in her offspring will also have viable sperm (Devine 1984). However, there was no indication in this study that EPY occurred in broods which contained infertile eggs (Spearman rank, % EPP in brood vs. % eggs which failed to hatch, $R_{17} = 0.12$, ns).

Male wheatears can be aged on the basis of plumage characteristics (Svensson 1984), and one would have expected females to accept, or even solicit, EPCs from older

males, especially when paired to first year males, as they have returned between years (an additional measure of male quality). There was no age bias in males whose females experienced EPCs or had EPP in their broods. There is some suggestion from other studies that younger males are more likely to be cuckolded (e.g. Westneat 1987, Morton *et al.* 1990, Gowaty and Bridges 1991) but this is not the case for all species (e.g. Morton and Sherman 1988, Westneat 1990). The data in this study are inconclusive on whether older males gained EPP as the majority of fathers were not identified. One of the most convincing studies to show an effect of age on gaining extra-pair fertilisations (EPFs) is that by Weatherhead and Boag (1995) (see also Wetton *et al.* 1995), in which older and longer lived males sired more EPY, with male success in a given year being significantly correlated with success the previous year. Large data sets are needed for such analyses (Weatherhead and Boag's was based on six years' data for 341 nests). Other than obtaining levels of extra-pair paternity, a study such as the current one, on 17 pairs, is limited in the conclusions that can be drawn from it regarding models of sexual selection and factors accounting for levels of EPP, unless there are very clear cut patterns in the data.

In the cliff swallow, two distinct female reproductive strategies have been identified: promiscuity and faithfulness (Lifjeld and Robertson 1992). The low rate of EPP and the seeming reluctance of females to participate in EPCs suggests that such female strategies are not so clear-cut in the wheatear. The lack of behavioural and phenotypic correlates with EPP suggests a more opportunistic nature to females participating in EPCs, though this does not preclude the possibility that females choose extra-pair males to enhance the genotypic quality of their offspring (see also Dunn *et al.* 1994). If last male sperm precedence applies, the low rate of EPP indicates that pair males generally got the last copulation before each fertilisation. In the wheatear, female co-operation appears to be essential for males to obtain a successful EPC. This is also the case for other species e.g. the tree swallow, where female solicted copulations were more likely to result in cloacal contact than male initiated copulations (Venier *et al.* 1993, see also review in Hunter *et al.* 1993). This suggests that in the wheatear, females choose to participate in EPCs and control paternity by both soliciting (or accepting) and rejecting copulations from different males (Lifjeld and Robertson 1992, Birkhead and Møller 1993, Dunn *et al.* 1994).

4.5. Summary

1. Recent work using DNA fingerprinting has focused particular attention on extra-pair paternity as a potential source of variation in male reproductive success, especially in monogamous species (see review in Birkhead and Møller 1992). In this study, extra-pair paternity was infrequent and there was little difference between observed male reproductive success and actual genetic parentage.

2. Since female co-operation was essential for males to achieve successful

copulations, some females as well as males must have pursued a mixed reproductive strategy via extra-pair copulations. There was no evidence that females pursued a mixed reproductive strategy by dumping eggs in the nests of other females (intra-specific brood parasitism).

3. The extent of extra-pair paternity in a population depends on the ability of the pair male to pursue extra-pair copulations, the inability of males to avoid being cuckolded, and the degree of female participation in seeking extra-pair copulations (Briskie 1992). Mate guarding, in conjunction with the female's apparent reluctance or selectivity in participating in extra-pair copulations, apparently resulted in low levels of extra-pair paternity in the wheatear. Not all extra-pair fathers were identified but in two broods, neighbouring males (up to three territories away) were excluded as being extra-pair fathers.

5. There were no behavioural correlates between male mate guarding behaviours or phenotypic characteristics and the presence of extra-pair young in the nest. Extra-pair paternity tended to occur when there was a female-skewed sex ratio in the fertile period of early breeding females and in larger clutches. The shorter fertile period associated with the smaller clutches, increased mate guarding and inter-male competition (as a result of a male-skewed sex ratio) may limit the opportunity for extra-pair males to gain EPP at later nests.

Chapter 5: The effect of male removal experiments on extra-pair paternity.

5.1. Introduction

5.2. Methods

    5.2.1. Male removals

    5.2.2. Paternity analysis

5.3. Results

    5.3.1. Removals prior to laying

    5.3.2. Removals during early laying

    5.3.3. Summary: removals during the fertile period

    5.3.4. Removals during incubation

    5.3.5. Paternity analysis

    5.3.6. Effect of experiments on extra-pair paternity

    5.3.7. Identification of fathers

5.4. Discussion

    5.4.1. Behaviour of extra-pair males

    5.4.2. Extra-pair paternity and female behaviour

    5.4.3. Sperm competition

5.5. Summary

5.1. Introduction

    In birds, it is assumed that the close proximity frequently observed between pair individuals during the fertile period is one mechanism through which males ensure their paternity of a brood, i.e. by mate guarding (Beecher and Beecher 1979, Birkhead 1979). Short-term male removal experiments have shown that the presence of the pair male reduces territorial intrusions and courtship by extra-pair males, and can prevent females from engaging in EPCs (see Table 5.1). However, few studies have examined whether or not the absence of the pair male actually results in an increase in extra-pair paternity.

    Numerous studies have shown varying levels of extra-pair paternity (EPP) in natural populations (e.g. Burke and Bruford 1987, Wetton *et al.* 1987, Burke *et al.* 1989, Westneat 1990, Birkhead *et al.* 1990, Gibbs *et al.* 1990, Sheldon and Burke 1994, see Table 4.1) but few have been able to determine the effect of the presence of the pair male on the copulation behaviour of his female. A few exceptional studies have shown that females alter their behaviour according to the quality of their partner/extra-pair males (e.g. Smith 1988, Kempenaers *et al.* 1992) but it is still unclear to what extent the presence of the pair male constrains the behaviour of the female. There is some evidence that males may have limited control over the behaviour of their female. To date the data are equivocal on the

significance of the presence of the male during the fertile period in ensuring paternity, although the majority of behavioural observations are consistent with the mate guarding hypothesis (Birkhead and Møller 1992).

Birkhead *et al.* (1989) showed that EPCs occurring during short-term absences of the pair male can result in extra-pair young (EPY), though Westneat (1994) was unable to show any differences in levels of EPP between removal and control broods. In a series of permanent removal experiments, Lifjeld and Robertson (1992) showed that in the cliff swallow females had two distinct reproductive strategies: faithfulness or promiscuity, irrespective of whether the pair male was present. Such studies indicate that fertilisation patterns are determined by the female through active selection and rejection of copulation partners, and the outcome of any sperm competition which this invokes, with males attempting to mate guard around this. Longer term removals (Lifjeld and Robertson 1992, Davies *et al.* 1992) have shown that copulations during the laying sequence can result in fertilisation i.e. the results were consistent last male sperm precedence (Birkhead 1988, Birkhead *et al.* 1989).

This chapter examines the effects of a series of 24-hour removal experiments carried out during the fertile period in the wheatear *Oenanthe oenanthe*, to further examine male and female reproductive strategies, sperm competition and the importance of the presence of the pair male in ensuring paternity.

5.2. Methods

5.2.1. Male removals

In 1992 ten males were caught using Potter traps during early laying, eight on the first egg date (FED, day 0) and two on day +1. The latter two males were removed on the day +1 to avoid removing neighbours on the same day. In 1993 nine males were trapped using Potter and spring traps between days -5 and -1 when nest building was near completion. The date of the removal was back-calculated from the day the first egg was laid. Males were removed on average on day -3 ± 0.56 (standard error; se). Three males in 1992 and four males in 1993 were removed during their pair female's incubation period to act as controls for the removals during the fertile period. The mean time required for the capture of the males removed (i) during early laying was 0.64 ± 0.24 hours, (ii) prior to laying was 1.69 ± 0.38 hours, and (iii) during incubation was 3.21 ± 0.89 hours. The mean capture time for controls did not reflect the additional hours put in on other territories where it proved impossible to catch the pair male.

Territories were observed for 60 minutes, before, one hour after, and 24 hours (but prior to the return of the pair male) after the removals. Since it was not possible to capture males at specific times, behavioural watches prior to the experiment were conducted for an hour on the day the removal was performed. The number and identity of male intruders,

and the behaviour of these males and of the pair females were noted. Additionally in 1993 male and female interactions were noted prior to the experiments. Due to the small sample size for males removed during incubation, as a result of mate predation and difficulty in capture, the data for 1992 and 1993 were combined. All males in the study area were colour-ringed prior to the experiments and unringed individuals were presumed to be migrants and not considered as intruders in this analysis. Removed males were kept in isolation for 24 hours in a cage (1m x 0.5m x 0.5m) located in a shed with a window experiencing a normal light/dark cycle. They were provided with food (meal worms) and fresh water. Mean male weight loss during the 24-hour removals (n = 13) was 1.2 g $\pm$ 0.18 (se) (mean percentage weight loss = 4.6 $\pm$ 0.7(se)). The nest was checked prior to the male's return to determine whether the female continued laying in the male's absence. Males were released on territory.

Two males removed in 1993 during the fertile period were unable to regain their territories. Males who took over these respective territories are treated as intruders in the following analysis. A third territory takeover occurred as a result of predation of the pair male during laying at a nest at which he had been removed on the FED (exact date of takeover unknown, about day +2). Due to the philopatric nature of the study species four males removed during the fertile periods in 1992 and 1993 were the same.

Nests were termed early and late depending on their time of initiation in relation to the first nest in the study area. Due to difficulties in gaining access to nests there were limited data from this study on the times eggs were laid but data from four non-experimental nests (1991-93) indicated that first eggs were laid between 0700 and 0800 BST (British Summer Time), although there seemed to be one exceptional case when one egg was laid between 0915 and 0930. Conder (1989) estimated that most eggs were laid before 0730. As a result males were not removed during the fertile period prior to 0830, and only then after the contents of the nest had been checked. Males were removed prior to laying between 0915 and 1515 and during early laying between 0830 and 1445. Control males were removed between 1000 and 1805.

5.2.2. Paternity analysis

The paternity of broods was analysed using multilocus DNA fingerprinting (Jeffreys *et al.* 1985a, b, Burke and Bruford 1987; for summary of methods see section 4.2.2). These two years of experiments were affected by bad weather, prolonged rain and winds during hatching and early provisioning. This sometimes resulted in hatching failure and chick mortality before blood samples could be obtained. Five out of the 19 nests subject to removals in the fertile period suffered some kind of brood reduction due to the adverse weather. Additionally, three nests used for removals in 1993 were flooded and failed completely. Therefore, in 1993 only paternity data were only obtained for six

experimental broods (see Table 5.2). Although only seven behavioural controls were carried out over the two years, four broods from non-removal pairs (1992-93) were considered as additional controls for the paternity analysis since the pair males were not removed during laying. There was no difference in FED between controls and removal nests (Mann-Whitney U-test, experimental nests, controls (n = 7) vs. removals (n = 19), z = -0.64, p = 0.52; nests with genetic data, controls (n = 11) vs. removals (n = 19), z = -1.27, p = 0.20). Due to the small sample size for controls, paternity data from 17 pairs in 1991 were used as a further indicator of the background level of EPP. In the territory takeover where the female subsequently associated with the incoming male, he was assumed to be the putative father. Due to a lack of any observed association between the sexes in the other takeovers, the original territory holder was regarded as the putative father.

5.3. Results

5.3.1. Removals prior to laying

(i) Behaviour of extra-pair males

There was a total of 37 male intrusions during these experiments, in 100% of which the intruder was identified. There was no initial increase in intrusions by extra-pair males. There was a non-significant increase in the number of these intrusions during the following 24 hours. (Kruskal-Wallis, H = 5.56, df = 2, p < 0.07; Wilcoxon paired-sign rank; prior vs. 1-hour, T+ = 10, n = 4, p = 0.12; prior vs. 24-hour, T+ = 36, n = 8, p = 0.008; 1-hour vs. 24-hour, T+ = 15, n = 5, p = 0.06). In three of these experiments one hour after the pair male was removed neighbours were seen to noticeably increase their boundaries at the expense of the removed male. Two of these extensions were maintained for the duration of the experiments but returned to their status prior to the removal on the male's return. These extensions were not considered to be intrusions. The third extension resulted in a permanent territory takeover by the extra-pair male. Neighbours were often observed concentrating their activities on the territory boundaries of the removed male, in particular song flighting and singing. A total of 13 EPC attempts were observed in 59% of experiments.

(ii) Behaviour of females

Only two of the observed EPC attempts (by the same male) were accepted by one female. Just one EPC attempt which was rejected, was preceded by a 'greeting display' by the intruding male. Females were never seen to leave their territories as a response to the removals and all EPC attempts occurred on the removal territory. Females were not seen to chase intruding males, but in several instances when a migrant female temporarily appeared on territory the pair female reacted aggressively and chased her from it. All females

continued nest building in the absence of the pair male.

Females were less likely to greet extra-pair males after the removal than they were their pair male before the removal (mean rates of female solicitations prior to removal = 1.11 h^{-1} ± 0.35, 1-hour after removal = 0.0, and 24-hours after removal = 0.23 h^{-1} ± 0.17; Wilcoxon paired-sign rank; prior vs. 1-hour, T^{+} = 21, n = 6, p < 0.05; prior vs. 24-hour, T^{+} = 13, n = 4, p < 0.05; 1-hour vs. 24-hour, T^{+} = 3, n = 2, p > 0.5). Two of the females each consorted with one specific extra-pair male respectively. One of these females was observed to perform the greeting display to the replacement male after 24 hours. One of these intrusions resulted in a permanent territory takeover by the extra-pair male. No interactions were observed between the pair female and intruding male during the other permanent territory takeover. The female continued nest building and the male appeared to ignore her completely.

(iii) Behaviour of removed males

On release, eight out of the nine removed males immediately performed a song flight. Intruding extra-pair males were subsequently chased from their territories and territory boundaries were re-established. Three of the returned males fought 'permanent' intruders, but two were unable to regain their territory. In two experiments, on the release of the removed male the pair female performed the greeting/solicitation display and one of these displays resulted in an immediate pair copulation. This female had previously been consorting with a neighbouring male and had accepted two EPCs.

5.3.2. Removals during early laying

(i) Behaviour of extra-pair males

There was a total of 42 male intrusions during these experiments, 83.3 % (35/42) of which were by identified males. As a result of these removals there was an initial increase in intrusions by extra-pair males, but there was no further increase over the following 24 hours in these intrusions (Kruskal-Wallis, H = 5.56, df = 2, p < 0.07: Wilcoxon paired-sign rank, prior vs. 1-hour T^{+} = 15, n = 5, p = 0.06; prior vs. 24-hour T^{+} = 42.5, n = 9, p = 0.02; 1-hour vs. 24-hour T^{+} = 15, n = 7, p > 0.5). Six of these intrusions, five of which were by neighbours, were preceded by a song flight performed by the extra-pair male.

In two removals a neighbouring male took over the territory after 24 hours but was ejected on the pair male's return. One of these males was unpaired (1st year breeder) and the other was a paired male whose female's FED was exactly the same as that of the removed male's female. This paired male performed a prolonged greeting display to the removal female which has been observed to precede on many other occasions pair and

extra-pair copulations.

In three of these experiments, one hour after the pair male was removed neighbours were seen to increase their boundaries at the expense of the removed male. These extensions were maintained for the duration of the experiments but returned to their status prior to the removal on the return of the male. These extensions were not considered to be intrusions. Neighbours were often observed concentrating their activities on the territory boundaries of the removed male, in particular song flighting and singing. EPC attempts were observed on eight occasions in 40% of experiments. Four of these EPC attempts involved the intruding male chasing the female.

(ii) Behaviour of pair females

Three of these EPC attempts were accepted by the pair female. Two of these were performed by one intruding male to one female. Females were never seen to leave their territories as a response to the removals and all EPC attempts occurred on the experimental territory. Females were not seen to chase intruding males, but in two instances when migrant females appeared on their territories the pair female reacted aggressively and chased or attempted to chase them from it. In the instance where there was a temporary male takeover by a paired male, the two neighbouring females concerned were never observed on each other's territory. Females were never seen to perform the greeting/solicitation display to the intruding males. Eight out of the nine females continued laying in the absence of the pair male. The other female laid about 15 minutes after the male was returned.

(iii) Response of removed males

When the males were released on their territories eight out of the nine males immediately performed a song flight. All observed intruding extra-pair males were subsequently chased from their territories and territory boundaries were rapidly re-established.

5.3.3. Summary: removals during the fertile period

There was no significant difference in the pattern and number of intrusions and EPC attempts for removals carried out during the fertile period in 1992 and 1993 in each period of observation i.e. before removal, one hour after removal and 24 hours after the removal, and the data for each time period for both years were therefore grouped (repeated measures ANOVA: (a) intrusions, Wilk's Lambda [Johnson and Wichern 1992]: year, df = 1, F = 0.06, ns; time/year effect, df = 2, F = 0.74, p = ns; (b) EPCs, Wilk's Lambda: year, df = 1, F = 0.08, ns; time/year effect, df = 2, F = 0.76, ns).

(i) Behaviour of extra-pair males

There was an immediate increase in intrusions by extra-pair males one hour after the removal and a subsequent increase in the following 24-hours (Kruskal-Wallis, H = 11.18, df = 2, p < 0.01; Wilcoxon paired-sign rank: prior vs. 1-hour z = -3.21, p < 0.01; prior vs. 24-hour, z = -3.56, n = 16, p < 0.001; 1-hour vs. 24-hour, z = -2.23, n = 15, p < 0.05; see Fig. 5.1). Later breeding pairs experienced higher intrusion rates prior to and one hour after the pair male was removed, but this was less obvious after 24-hours (Mann-Whitney U-test, early vs. late; prior, z = -1.74, p = 0.08; 1-hour, z = -2.39, p = 0.016; 24-hours, z = -1.32, p = 0.18; see Fig. 5.1).

Of the 65 intrusions which were observed during these experiments, 35% resulted in the male approaching the female (contact visit). The remaining 65% involved the male arriving on the focal territory but not approaching the female (non-contact visit). Twenty-six percent of removals during the fertile period resulted in a territory takeover. The duration of 55.4% (36/65) of intrusions was noted. There was a tendency of intrusions to increase in their duration with time during the experiment (mean duration of intrusions in minutes ± se; prior to removal (n = 3) = 1.3 ± 0.33, 1 hour after removal = 3.8 ± 1.52 (n =15), and 24 hours after removal = 9.78 ± 2.68 (n = 18); Kruskal-Wallis, H = 6.69, df =, 2, p < 0.1). Fifty-three of the 65 intrusions were by pair males, 9 were by unpaired individuals.

There were two types of intrusions during the fertile period: those announced by song flight (13%) and those where the male sneaked onto the focal territory (87%). Those announced by song flights were typically by neighbours (8/9). The distance covered by intruding males depended on the fertility of their female. Males ventured further from their territories when their female was not fertile. The mean number of territories traversed in pair female's prefertile period = 1.75 ± 0.48 (n = 4); in fertile period = 1.33 ± 0.19 (n = 18); in post-fertile period = 1.81 ± 0.15 (n = 31) (Kruskal-Wallis, H = 5.92, df = 2, p < 0.06). Unlike in 1991 there was no suggestion that males intruding on to later breeding territories came from more distant territories (Chi-square test [using a 3 x 2 contingency table as intruding males came from up to three territories away], early vs. late; prior to removal, X^2 = 0, df = 2, ns; 1-hour, X^2 = 1.55, df = 2, ns; 24-hours, X^2 = 3.46, df = 4, ns). There was also no indication that intruding males came from further away after 24-hours (Chi-squared test, prior to removal vs. 24-hours after removal [3 x 2 contingency table], X^2 = 3.17, df = 2, ns).

(ii) Extra-pair copulations

A total of 21 EPC attempts was observed, occurring in 53% of the removals (10/19). There was an increase in the number of EPCs in the absence of the pair male one and 24 hours after the removal (Wilcoxon paired-sign rank; prior vs. 1-hour, n = 8, T^+ =

36, p = 0.009; prior vs. 24-hours, n = 5, T+ = 15, p = 0.06). More EPCs occurred after the removal (1- and 24-hour data grouped) than before it (Wilcoxon paired-sign rank, before removal vs. after removal (1-hour and 24-hour combined) T+ = 45, n = 9, p < 0.05, see also Fig. 5.2). There was no increase in the frequency of EPCs experienced between one hour and 24 hours (Wilcoxon paired-sign rank, n = 9, T+ = 26.5, ns). More EPCs occurred 24 hours after the removal than prior to it. Later breeding territories experienced a higher number of EPCs one hour after the removal but there was no significant difference prior to and 24-hours after the removal. (Mann-Whitney U-test; prior, z = 0, p > 0.8; 1-hour, z = -1.89, p = 0.06; 24-hour, z = -1.27, ns).

(iii) Behaviour of pair females

Only 16% EPCs were accepted by the female (including subsequent copulations by the same male as a single copulation event). In all but one case where the female rejected the EPC, the female responded aggressively to the male. Forty percent of EPC attempts involved the female being chased by extra-pair males. Females were also observed to actively avoid contact with extra-pair males, especially after such encounters. Females were never seen to solicit EPCs directly (though in two instances they were seen to perform the greeting/solicitation display to extra-pair males which during the fertile period have often been observed to precede copulations), or leave their territories and visit neighbouring males.

5.3.4. Controls: removals during incubation

Males spent on average 55.1% ± 18.76 (se) of their time off territory during incubation (males were rarely observed off territory in their female's fertile period) and as a result it was more difficult to catch them during this time.

(i) Behaviour of extra-pair males

There was no initial increase in the number of intrusions by extra-pair males but there was an overall increase over 24 hours in the number of male intruders due to these removals (Kruskal-Wallis, H = 9.44, df = 2, p < 0.01: Wilcoxon paired-sign rank; prior vs. 1-hour, T+ = -1, n = 1, ns; 1-hour vs. 24-hours, T+ = 15, n = 5, p = 0.06, prior vs. 24-hour, T+ = 15, n = 5, p = 0.06). All intruders were identified with the majority being neighbours (7/8). Five (71%) of these removals resulted in temporary territory take-overs by neighbours. In four of the controls one hour after the pair male was removed, neighbours were also observed to increase their boundaries at the expense of the removed male. These extensions were maintained for the duration of the experiments but returned to their status prior to the removal on the male's return.

Intrusions by extra-pair males tended to be less frequent when the pair male was removed during incubation than during the fertile period. There were significantly more intrusions during the fertile period one hour and 24 hours after the removal (if territory takeovers are excluded from the analysis) (Mann-Whitney U-test, removals (n = 19) vs. controls (n = 7) ; prior, z = -1.47, p = 0.14 ; 1-hour, z = -2.06, p = 0.039; 24-hours, z = - 1.38, p = 0.16 [z = -3.07, p = 0.02 excluding territory takeovers]; see Fig. 5.1).

The nature of intrusions in the fertile period and incubation was different, the emphasis being on territory takeover during incubation. Seventy-one percent of controls resulted in a territory takeover (all by neighbours) as opposed to 26% of removals during the fertile period (Mann-Whitney U-test, z = -2.06, p < 0.05).

(ii) Behaviour of pair females

During the controls females spent the majority of the time incubating. However, during the periods when the female was off the nest feeding, no EPCs or any other interactions between the female and intruding extra-pair males were observed during the control removals (Mann-Whitney U-test, number of EPCs after removal of the pair male in controls [1-and 24-hours grouped, n = 7] vs. number of EPCs after removal of the pair male in experiments [1-and 24-hours grouped, n = 19], z = -2.32, p = 0.02, see Fig. 5.3). In several instances migrant females were chased off territory on successive occasions when the pair females were off the nest feeding between bouts of incubation.

5.3.5. Paternity analysis

In the 1992-93 field seasons a total of 149 scorable fingerprints were obtained for 100 offspring from 19 families where both the male and female were available, 32 from five families (containing 27 offspring) where no fingerprint was obtained for the female, and 15 from two families (13 offspring) where no fingerprint was obtained for the male. The mean number of scorable bands was 28.53 ± 0.53 (se). For broods where both parents were available, single mismatch bands occurred in 11 offspring, giving a band mutation rate of 1 in 411, a comparable rate to that expected by mutation (Jeffreys *et al.* 1985a, b, Burke and Bruford 1987, Westneat 1990). Band sharing coefficients for nestlings which could be compared to both putative parents, and which could therefore be included or excluded on the basis of multiple band mismatches, were 0.54 ± 0.09 for male:offspring and 0.54 ± 0.11 for female:offspring. Fig. 5.2 shows the frequency distribution of band sharing between nestlings and their putative fathers, mothers and siblings. Band sharing coefficients for unrelated birds were calculated as 0.20 ± 0.11 including a band sharing coefficient of 0.61 which most likely represents two related individuals (see 4.3.1). Seven offspring from five broods had 5 mismatched bands or more (see Fig. 5.3). The band sharing values for all these offspring fell outwith the 95%

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confidence limits of male:true offspring (Fig 5.3 (i)) but within that of the female:offspring (Fig 5.3 (ii)), and are therefore considered to be extra-pair young (EPY).

In the two families where no fingerprint was available for the male parent high band sharing confirmed the maternity of the assigned females and high sib-sib band sharing was consistent with single paternity. In the five families where no fingerprint was available for the female parent, high sib-sib band sharing indicated single maternity and 17 of the 22 male:offspring band sharing coefficients were within the 95% confidence limits for first order relatives calculated from the 19 complete families. The other five offspring from two broods (one and four chicks respectively) were outwith the male:offspring 95% confidence limits and are therefore considered to be EPY. Table 5.3 shows the levels of extra-pair paternity (EPP) for removals prior to laying, removals during early laying (considered separately and grouped as removals in the fertile period), non-removals and controls in 1992-93, and non-removal pairs from 1991. There was no evidence of intra-specific brood parasitism, due to the absence of mismatched bands between offspring and putative mothers in families where both parents were fingerprinted, and high sib-sib banding sharing when no fingerprint was available for the female.

5.3.6. Effect of experiments on extra-pair paternity

There were no differences in the number of EPY or nests containing EPY between the non-removals from 1991 and the controls and non-removals from 1992-93 (Fisher exact test, number of EPY, $p = 0.11$; number of broods with EPY, $p = 0.22$). There tended to be more EPY in experimental nests than control and non-removals in 1992-93 (Fisher exact test, $p = 0.06$). When the paternity data from 1991 were included in the this analysis (combined with control and non-removals 1992-93), there was no effect of the removal experiments on the number of EPY (Fisher exact test, $p = 0.24$). There was no significant difference in the proportion of broods containing EPY between experimental and control nests including or excluding paternity data from 1991 (Fisher exact test; including 1991 paternity data, $p = 0.30$; excluding 1991 paternity data, $p = 0.18$)

There were no differences in the number of EPY or the number of broods containing them between removals carried out prior to and during early laying (Fisher exact test, number of EPY, $p = 0.72$; number of broods with EPY, $p = 1.0$). Removals prior to laying were performed between days -5 and -1 (day 0 = first egg date). Experimental nests were grouped arbitrarily as removals which took place immediately prior to laying (days -2 to -1) and those which took place earlier in the fertile period (days -5 to -3). More EPY occurred in removals that were performed immediately prior to laying (from days -2 to -1) than those performed earlier (days -5 to -3) (mean proportion of chicks which were EPY; removals (-5 to -3) (18 chicks from 3 broods) = 0; removals (-2 to -1) (17 chicks from 3 broods) = 0.32 ± 0.24 (in 2/3 broods); Fisher exact test, $p = 0.02$).

Table 5.1. Effect of temporary male removal experiments in fertile period on frequency of intrusions by extra-pair males and extra-pair copulations.

	Intrusions by extra-pair males	Rate of EPCs	
Pied flycatcher	+	+	Bjorklund and Westman 1983
Swallow	+	+	Møller 1987a
Great tit	+	0	Bjorklund *et al.* 1991
Zebra finch #	+	+	Birkhead *et al.* 1989
Yellowhammer	+	+	Sundberg 1994
Red-winged blackbird #	+	+	Westneat 1994
House martin #	+	?	Riley *et al.* 1995

(+ indicates an increase, 0 indicates no increase, ? no data available, # studies examining effect on paternity as a result of male removals).

Table 5.2. Mean clutch size and percentage of clutch that paternity analysis was based on.

	No. nests	Mean clutch size ($\pm$ se)	% clutch sampled ($\pm$ se)
Removals 1992	10	6.00 $\pm$ 0.17	0.79 $\pm$ 0.08
Removals 1993	6	5.70 $\pm$ 0.26	0.65 $\pm$ 0.16
Removals 1992-93	16	5.84 $\pm$ 0.16	0.72 $\pm$ 0.09
Controls and non-removals (1992-93)	11	5.85 $\pm$ 0.27	0.99 $\pm$ 0.02
Non-removals 1991	17	5.75 $\pm$ 0.23	0.81 $\pm$ 0.06
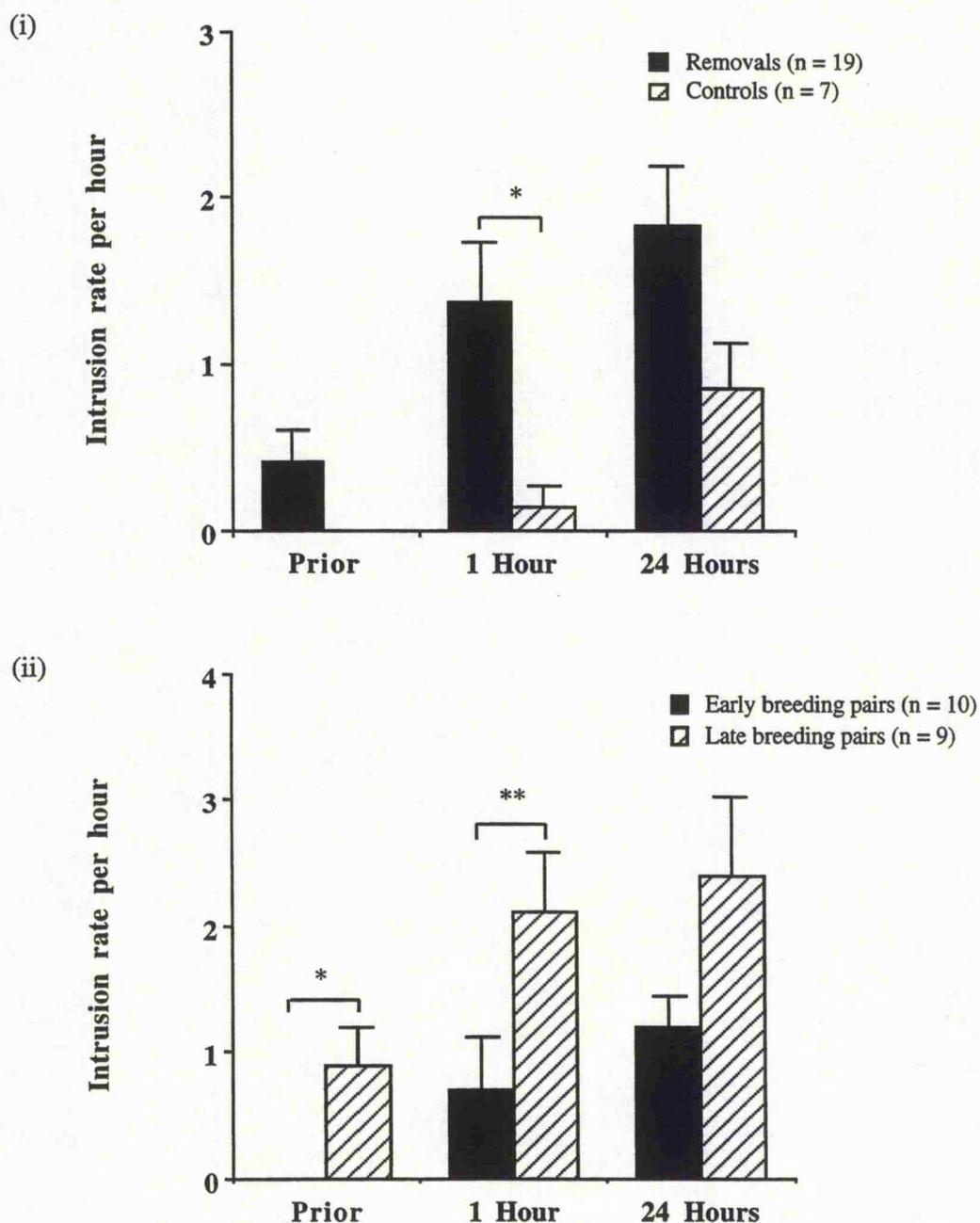
Fig 5.1. Mean male intrusion rate per hour (± se) for (i) experimental and control nests, and (ii) early and late (experimental) nests, prior to, 1 hour after and 24 hours after the removal of the pair male during the fertile period. Intrusion rates increased during the duration of the removal for both experimental and control pairs (Kruskal-Wallis: removals. df = 2, H = 11.18, p < 0.01; controls, df = 2, H = 9.44, p < 0.01). Intrusion rates were generally higher for: (i) removals than controls, and (ii) late breeding nests than early ones, in each time period. Mann-Whitney U-tests, * p < 0.05, ** p < 0.01.
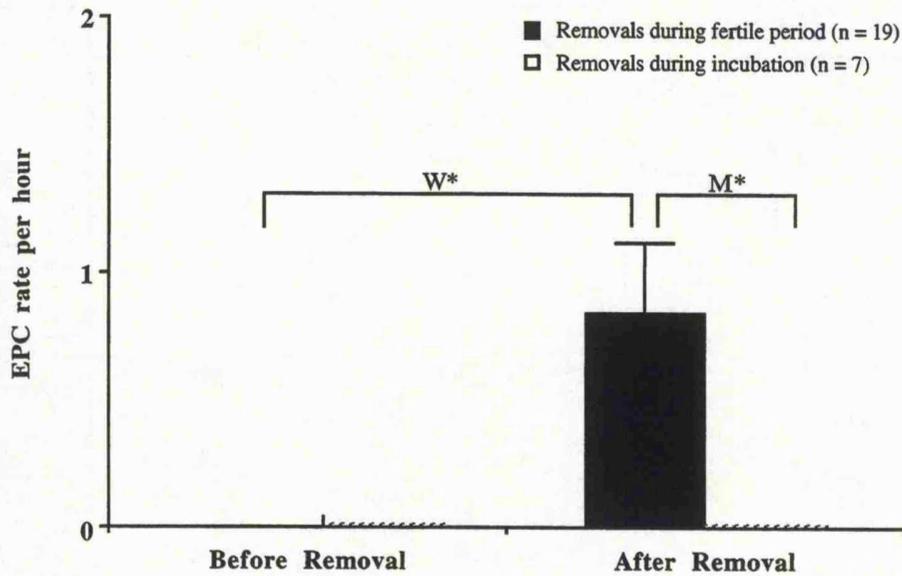
Fig 5.2. Mean number of extra-pair copulations per hour (± se) prior to and after removal (data for 1-hour and 24-hours combined) for experimental and control nests. More EPCs occurred after the removal of the pair male during: (i) the fertile period than prior to the experiment (W), and (ii) the fertile period than after the removal in the control experiments (M). W refers to a Wilcoxon paired-sign rank test, and M refers to a Mann-Whitney U-test. Levels of significance: * $p < 0.05$.

(i)

(ii)

(iii)

(iv)
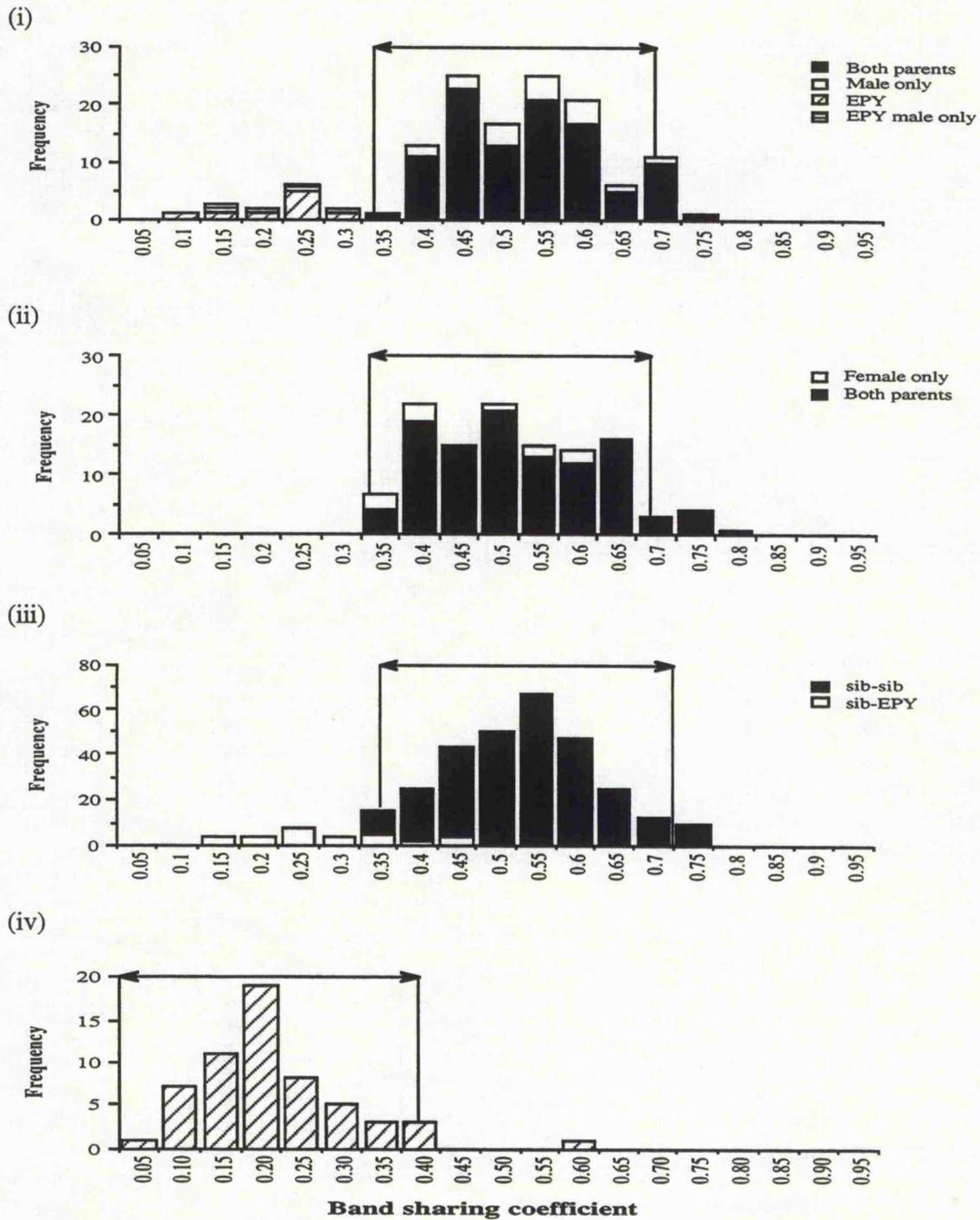
Fig. 5.3. Frequency distribution of band sharing coefficients for 1992-93 paternity data between (i) males and their offspring (EPY = extra-pair young), (ii) females and their offspring, (iii) siblings within broods (sib = sibling), and (iv) unrelated individuals (from Chapter 3). Arrows indicate 95% confidence limits of band sharing ranges. Legend indicates whether either or both parents were compared with the offspring.
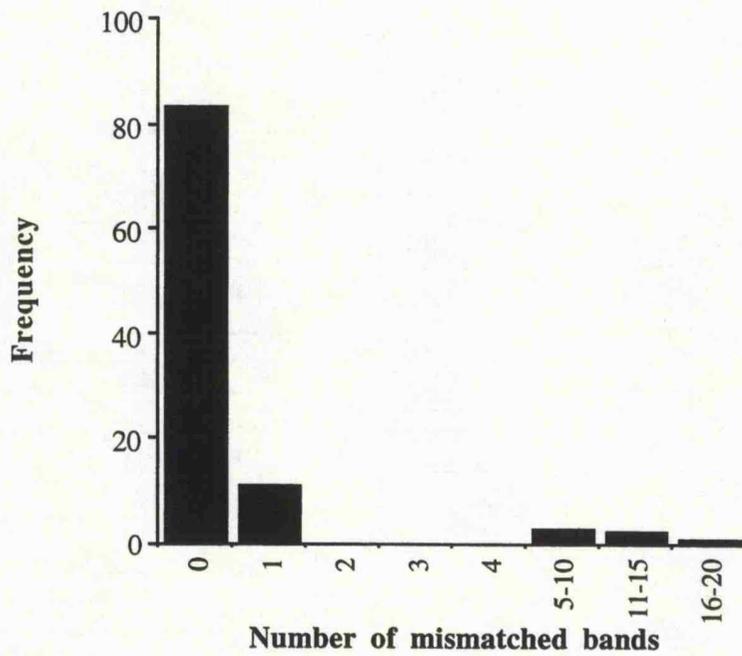
Fig 5.4. Number of offspring with mismatched bands. Individuals with five or more mismatched bands were considered to be extra-pair young.

Table 5.3. Percentage of extra-pair young (EPY) and percentage of broods with extra-pair paternity (EPP) for experimental, control and non-removal nests. Data in parentheses for % EPY are number of EPY/number of chicks, and % nests with EPP is the number of broods with EPY/ total number of broods.

	No. nests	% EPY	% nests with EPP
Removals 1992	10	10.8 (5/43)	40.0 (4/10)
Removals 1993	6	14.3 (5/35)	33.3 (2/6)
Removals 1992-93	16	9.9 (10/78)	37.5 (6/16)
Controls and non-removals (1992-93)	10	3.2 (2/62)	10.0 (1/10)
Non-removals 1991	17	11.2 (8/94)	29.4 (5/17)

5.3.7. Identification of fathers

Only two of the extra-pair fathers, which fathered two offspring respectively, were identified. Extra-pair male band sharing coefficients with these four extra-pair offspring (two from experimental nests and two from one control nest) were 0.53, 0.55, 0.50, and 0.41, and accounted for all mismatched bands. The identified extra-pair males were immediate neighbours, one of which had been removed prior to laying. None of the fathers was observed copulating with the focal female.

Three broods had more than one EPY. A sib-sib band sharing coefficient of 0.22 suggests that there may have been multiple extra-pair fathers for one of these broods. A mean band sharing value of 0.47 ± 0.03 (between 4 chicks, range 0.39 - 0.6), and a band sharing of 0.48 (between two chicks) in the other two broods suggests that these broods each had only one extra-pair father. In the territory takeover where the female associated with the replacement male, that male fathered all the offspring. In the other territory takeovers where no associations were observed between the sexes, the original pair male fathered all the offspring.

Among the males removed in the fertile period, those which were cuckolded had a significantly lower body condition index (BCI) than those individuals which were not cuckolded (Mann-Whitney U-test, BCI cuckolded males (n = 9) vs. non-cuckolded males, U = 9.5, p < 0.05). There was no effect of male age, first egg date (FED), clutch size, or mean operational sex ratio (OSR) in the fertile period on levels of EPP in experimental and control and non-removal nests (Mann-Whitney U-test or Spearman rank test, ns). There was no effect of male BCI on levels of EPP, including experimental and control broods.

5.4. Discussion

5.4.1. Behaviour of extra-pair males

The presence of the pair male during the fertile period deterred intrusions, EPCs, and general harassment of the female by intruding males. Intrusion rates were higher during the fertile period, more so on late breeding territories. Those during the fertile period were targeted more towards the female while those during incubation were aimed at territory acquisition: during the control watches there were no interactions between extra-pair males and the pair female, but territorial takeovers were more frequent. These observations suggest that males were able to identify fertile females and alter their behaviour accordingly.

Only 35% of intrusions in the fertile period resulted in the extra-pair male approaching the female (7% in 1991). This contrasts with the great tit, where 74.2% of intrusions during male removals in the fertile period resulted in the male approaching the female (Bjorklund *et al.* 1991). Since few intrusions during the experiments resulted in contact with the female or territorial takeovers, and males were not observed to feed

intensively during these incursions, their main objective would appear to have been monitoring either the female or the territory. It may be that males require a series of visits and perhaps the presence of other males, as well as the behaviour of the female in order to more precisely assess her fertility.

As was observed in Chapter 3, males were limited in their pursuit of additional matings during their own female's fertile period, with intrusions being confined (but not as strictly limited as was observed in 1991) to neighbours during this time. The pursuit of EPCs was concentrated to their pair female's post fertile period. This was reflected in the greater amount of time needed to catch control removals, as males spent at least 50% of their time off territory during this time. Several males could not be caught as controls due to the large amount of time they were absent from their territory.

5.4.2. Extra-pair paternity and female behaviour

The increase in the rate and duration of intrusions and in the frequency of EPC attempts in response to the absence of the pair male over the 24 hours provided opportunities for an increase in EPP, especially on later breeding territories. However, there was only limited evidence from these experiments that the presence of the pair male ensured his paternity (i.e. mate guarding), and no suggestion that later breeding territories had higher levels of EPP.

The paternity data reflected the apparent reluctance of females to participate in EPCs. The majority of attempted EPCs resulting from the removal experiments, were rejected by the female; only 15.7% were accepted, a comparable rate to that observed in 1991 (14%) (see also Bjorklund *et al.* 1991). Additionally, females were never observed to leave their territory during any of the removal experiments, were rarely observed to associate with intruders, and were rarely observed to solicit extra-pair males (only observed in 2/19 experiments, see section 3.3.5). Females seemed to be either reluctant or else selective in copulating with extra-pair males in both the presence and absence of the pair male. Additional anecdotal evidence from the observations of mate replacements further supports the idea of females being selective in copulating with extra-pair males. In 1992, a male was predated during the laying sequence (about day +2, exact date unknown; day 0 = first egg date) and was replaced by a neighbouring unmated male. The original male fathered all the chicks although the replacement male fed them. The other three mate replacements occurred in 1993, on days -1, -4, and the morning after the final egg had been laid. It was impossible for this latter male to fertilise any of the eggs during the takeover. In the removal on day -1, the female was not observed to associate with the replacement male and all the chicks were fathered by the original male. In the removal on day -4, the female associated with the replacement male and was seen to solicit him on several occasions. This male fathered all the chicks in the nest. These observations also suggest that in the wheatear

female co-operation was important for males to obtain successful copulations (Fitch and Shugart 1984, but see Westneat *et al.* 1990, Wagner 1991, Birkhead and Møller 1992). Although rejecting the majority of EPCs, females were never aggressive territorially to intruding extra-pair males, but were very territorial to intruding females (all of which were migrants, identified by their lacking colour rings). This may be a behavioural adaptation to avoid intra-specific brood parasitism (Møller 1989) or to prevent polygny which could result in a sharing of any male help (Emlen and Oring 1977).

Female reluctance or resistance to participating in EPCs may be a means to test male quality or, alternatively, if the resistance is genuine, it may occur because there are costs to participating in EPCs (Birkhead and Møller 1992). Potential costs to females participating in EPCs include: poor quality offspring, retaliation by the pair male (either a reduction in paternal care or physical abuse), or harassment or the risk of injury by extra-pair males (Westneat *et al.* 1990, Birkhead and Møller 1992). Retaliation by the pair male is unlikely to apply due to the simulated mate predation. Most EPCs were aggressively resisted by females who were frequently chased by extra-pair males during these interactions, especially on later breeding territories. Resistance would therefore seem at least as likely to result in injury as would participation in EPCs. Females may avoid harassment by accepting EPCs (Westneat *et al.* 1990), however, females which were chased did not appear to be more likely to accept EPCs. Possible retaliation by the pair male, risk of injury, or avoiding harassment do not provide satisfactory reasons in these experiments to explain females' reluctance to participate in EPCs.

Potential benefits to females of participating in EPCs include: (i) fertility insurance (females mate with more than one male as an insurance against their mate being sterile); (ii) material benefits (nutritional benefits from ejaculate, courtship feeding and parental care); (iii) genetic benefits (increased genetic diversity or quality of offspring); (iv) avoidance of infanticide and (v) avoidance of rejection costs (see review in Birkhead and Møller 1992).

The laying/hatching sequence of eggs and their resulting paternity was not known, and as a result it is not possible to determine whether EPP was due to the behaviour of the female, regardless of the experiments or was a direct consequence of the removals. Under 'normal' conditions it has been shown that benefits to females in participating in EPCs are most likely to be genetic, either by increasing the diversity of the brood, or by allowing a 'better quality' male to father some or all of her offspring (Westneat *et al.* 1990, Smith 1988, Kempenaers *et al.* 1992, Sundberg and Dixon in press, see review in Birkhead and Møller 1992). However, benefits may differ in these experiments, as to all intents and purposes they simulated mate predation (males were absent for 24-hours, which was far longer than the normal territorial excursions during this time, see section 3.3.3). There was no evidence that removal experiments induced females to participate in EPCs to be sure of fertilising their complete clutch (although individual female responses might differ

depending on the frequency of copulations prior to removal of the pair male). Females typically do not gain either nutritional benefits or parental care from participating in EPCs, but polygamous males may feed secondary broods (Cramp 1988, pers. obs.). A possible strategy for these 'widowed' females could be to induce extra-pair males to help provision their offspring by soliciting copulations, however this did not seem to be the case.

The genetic diversity hypothesis predicts that the frequency of EPP in nests should be low but common among broods, while the good genes hypothesis predictions are opposite to these (Westneat et *al*. 1990). As in Chapter 4, the paternity data are inconclusive, but if anything the distribution of EPY in these experiments was more consistent with the good genes hypothesis. EPY were found in few broods and in all but one within a clutch were sired by the same extra-pair father. If body condition accurately reflects quality there is a suggestion that male quality may have affected female behaviour during the experiments. Males cuckolded during removals were of lower quality, though paradoxically this was not the case when non-removals, controls and removal experiments are considered. This suggests that even poor quality males are able to ensure their paternity by mate guarding, but in their absence females are able to copulate with better quality males (although not enough extra-pair fathers were identified to test this). Although males may have only limited control over their partner's copulation behaviour, their presence appeared to reduce the opportunities and choices for their female to participate in EPCs by them deterring intrusions. However, if females are seeking good genes by copulating outside the pair bond then one would expect them to mate with the best males regardless of whether their mate was present (e.g. Kempenaers et *al*. 1992). If, as argued, females are seeking good genes by participating in EPCs, female reluctance to participate in EPCs may be a mechanism to avoid producing offspring of poor genetic quality.

The presence of the pair male did not seem to be a prerequisite for females to breed. Ninety percent (9/10) of females continued laying during the 1992 removals, and all females continued building in the 1993 experiments, although it is impossible to tell whether females delayed the onset of laying in response to the removal of the pair male. Although males contribute on average 50% of chick feeds, females were capable of successfully raising a brood by themselves, although fledging weights were reduced (see section 6.4.4).

Higher intrusion rates at later breeding experimental nests did not result in an increase in EPP, although there was a weak suggestion that later breeding territories experienced higher EPC rates. Intruders on these territories were frequently observed to fight among themselves, and intense male intra-sexual competition, as well as female reluctance to participate in EPCs, may account for the absence of the expected increase in the leves of EPP in the nests of later breeding pairs (see also section 4.3.3(iii)).

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5.4.4. Sperm competition

In birds, fertilisation occurs about 24-hours before an egg is laid, with there being only a short period of time, about 15-30 minutes after ovulation, termed the fertilisation or insemination window (Cheng *et al.* 1983), in which the egg can be fertilised (Howarth 1971, see also Birkhead and Møller 1992). After this time, successive layers of albumen, which sperm are unable to penetrate, are laid down around the ovum.

The removals during early laying in 1992 ensured that the pair male was absent during the insemination window of the 3rd/4th egg. Copulations during the laying sequence can fertilise later laid eggs (Davies *et al.* 1992),and therefore, if copulations occurred then one would predict the occurrence of one EPY in each of these experimental nests. However, this was not the case in this study (see also Riley *et al.* 1995). Although wheatears are known to copulate throughout the laying sequence (see section 1.4.3), they exhibit a relatively low rate of copulation (see also Conder 1989), which may lead to a lower probability of eggs being fertilised during this time than observed in dunnocks (Davies *et al.* 1992).

The removals during 1993 attempted to promote sperm competition in the female reproductive tract prior to laying (Parker 1970). Because last male sperm precedence generally appears to be the rule (e.g. Birkhead *et al.* 1988, but see Oring *et al.* 1992), in species exhibiting a low rate of copulation, such as the wheatear, a successful EPC could have an effect on paternity. Surprisingly, there were very few successful EPCs, and consequently one would expect low levels of sperm competition in the female reproductive tract. There were no differences in the level of EPP in the nests of males removed before and during laying. However, the timing of removals prior to laying appeared to have an impact on the degree of EPP. Removals performed immediately prior to laying had higher levels of EPP than those performed earlier (see also Westneat 1994). This peak in fertility/susceptibility to EPCs corresponds to the timing of maximum mate guarding documented in this and most other studies (see Chapter 2, Birkhead *et al.* 1987, Birkhead and Møller 1992). This short period of time is possibly that of most conflict between the sexes. Last male sperm precedence probably enables the female to control the paternity of her offspring, and it is therefore crucial for the pair male to limit the access of extra-pair males to his female during this time, either by controlling her behaviour directly or by deterring intrusions in an attempt to ensure paternity.

In the two cases of mate replacement where the females were not observed to associate with the replacement male, the former territory holder accounted for all the paternity in the broods. In the other example of mate replacement, where the female was observed to associate with the male, he fathered all the chicks in the brood. Two apparently successful EPCs occurred during laying and one prior to laying. One would expect that the EPCs which occurred during laying would have resulted in EPP, however the respective

extra-pair males did not obtain any paternity as a result of these copulations. These observations suggest that either copulations during the laying sequence are unlikely to result in the fertilisation of eggs in wheatears or (sufficient) sperm transfer did not occur during these copulations. In the removal prior to laying which resulted in a successful EPC, the pair male immediately copulated with his female (female solicited) on his return on day -3 and sired all the chicks in the brood. The above anecdotal observations are again consistent with the hypothesis of last male sperm precedence and female control of copulations in the wheatear.

5.5. Summary

1. Behavioural observations and paternity data from 1991 indicated that the males adjusted their intensity of mate guarding according to the threat to their paternity. Furthermore, females were reluctant to participate in EPCs and their co-operation seemed essential in achieving successful copulations. Mate guarding and female reluctance to participate in EPCs were reflected in the low frequency of EPP. Both the paternity and behavioural data from male removal experiments indicated that females were no more willing to copulate outside the pair bond in the absence of the pair male than in his presence. Lifjeld and Robertson (1992) showed that there were two female reproductive strategies in the tree swallow: faithfulness and promiscuity. In this study female wheatears appeared to adopt a predominantly faithful strategy.

2. These removal experiments highlight that males have more to gain from pursuing EPCs, due to the few costs entailed. In contrast, there is a dilemma for females: either to participate in, or reject EPCs. In these experiments, females were reluctant to copulate outwith the pair bond. The presence of the male had a limited effect on female copulation behaviour, but it significantly affected the behaviour of extra-pair males (by deterring intrusions and EPCs) and therefore indirectly influenced female choice and options.

3. Conclusions based on behavioural observations of previous short-term male removal experiments have frequently suggested that EPCs induced by such experiments may result in fertilisation of at least some of the eggs (e.g. Bjorklund and Westman 1983). Although the absence of the pair male did not appear to result necessarily in an increase in EPP, the presence of the pair male seemed particularly important in ensuring paternity in those days immediately prior to laying. Although speculative, paternity data may not reflect the pattern of observed EPCs and male-female associations due to female copulation patterns, the confounding effect of sperm competition and last male sperm precedence.

4. The presence of the pair male during the fertile period would appear to be beneficial to the female in avoiding physical harassment from extra-pair males, possibly allowing her to forage efficiently during the important period of egg development and to expend less energy on avoidance behaviour.

Chapter 6. Parental and paternal care of nestlings.

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6.5. Summary

6.1. Introduction

Parental care is an energetically costly part of reproduction, and individuals providing it are expected to incur a survival cost (Low 1978, Nur 1984). Parental effort is therefore considered to be a compromise between the benefits of enhanced reproductive success and the costs of reduced survival probability which care entails. Chick feeding frequencies are an expression of a trade-off between offspring needs and parental condition, and parents should therefore optimise their level of effort in order to maximise the difference between benefits (to their offspring) and costs (to themselves) (Charnov and Krebs 1974).

Biparental care is common in many bird species (Lack 1968, Silver *et al.* 1985). The levels of investment by each partner may be influenced by numerous factors e.g. number of chicks, condition of parent and chicks and time in season (e.g. Gibb 1955, Royama 1966, van Balen 1973, Nur 1984). The optimal level of investment may differ for each sex and individuals may alter their investment according to their partner's bargaining for their individual optimum, or they may have a fixed investment strategy according to the situation in which they find themselves (Houston and Davies 1985). It is generally assumed that in response to a reduction in investment by one parent, the other should increase its effort in an attempt to compensate for its partner's shortfall. However, male removal experiments during this time have shown females are usually unable to fully

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compensate for the loss of paternal care and these breeding attempts are typically associated with a reduction in the number of chicks fledged (see review in Bart and Tornes 1989). It is this premise that has been used to explain why 90% of birds are monogamous (Lack 1968, Lefelaar and Robertson 1986, Lyon *et al.* 1987). Females may also suffer additional costs in the form of reduced survivorship in attempting to compensate for reduced or absent male care.

For males, reproductive effort (RE) is a trade-off between investing in offspring (parental effort, PE) and the pursuit of additional matings (mating effort, ME) (Low 1978). Male birds can invest in their offspring by defending a territory, defending the female, incubating the eggs and feeding and protecting the nestlings or fledglings (Trivers 1972). Male investment varies among mating systems, with males in polyandrous and monogamous species investing more than in other systems (Birkhead and Møller 1992). Male investment also varies among different stages during the breeding season. Males tend to invest less than the female early in the breeding cycle, during nest building and incubation and increase their investment during provisioning of the nestlings (Collias and Collias 1984). The opportunity for extra-pair copulations (EPCs) may account for the reduced paternal investment prior to hatching, with males concentrating on maximising their mating effort (Westneat 1990). Additionally, potential aspects of male parental effort such as nest building could interfere with paternity guards, also resulting in a reduction in investment during this time (Birkhead and Møller 1992). The value of offspring to parents increases with time, so potentially less benefit is derived for males from pursuing EPCs later in the breeding cycle and obtain greater benefit through paternal care.

In birds, as a consequence of internal fertilisation females are more likely to be certain of maternity than their partners are of paternity (Trivers 1972, Clutton-Brock 1991). Due to the energetic costs of parental care natural selection will favour males that avoid caring for unrelated offspring. Trivers (1972) was the first to suggest that males could reduce their parental investment with uncertainty of paternity. There is no evidence that males can recognise their own offspring (Burke *et al.* 1989, Dixon *et al.* 1994) and by reducing paternal care males risk the survival of their own chicks. Whether males alter their investment may depend on the costs of paternal care in terms of their own survival prospects and their perception of the likelihood of extra-pair paternity.

There are several ways in which a male can reduce investment: through mate desertion (Trivers [1972] original suggestion but for which there is no evidence in birds), through delayed breeding or abandonment of the current breeding attempt (Zenone 1976, Wittenberger 1982), and through a reduction in the parental care of chicks (and fledglings). Most models concerning male investment have concentrated on the latter, with the majority indicating that paternal care will evolve when confidence of paternity is high (e.g. Whittingham *et al.* 1992, Westneat and Sherman 1993). It has been argued that uncertainty

of paternity is not enough on its own to cause a reduction in male parental care (e.g. Maynard Smith 1977) but more recent theoretical studies indicate that males should reduce their paternal care under certain conditions (Werren *et al.* 1980, Xia 1991, Whittingham *et al.* 1992, Westneat and Sherman 1993). Many of these models are based on the benefits of non-parental care activities and the relationship between offspring recruitment and parental care. The effect of parentage on parental care is expected to depend on the response of the parents, the ability to recognise kin, and variation in paternity in successive nesting attempts (Westneat and Sherman 1992).

There is equivocal evidence from behavioural studies as to whether males alter investment with uncertainty of paternity. Some have found no correlates with paternity (e.g. Gavin and Bollinger 1985, Westneat 1988, 1995) while others have shown degrees of reduction in paternal effort with uncertainty of paternity (Møller 1988a, Morton *et al.* 1990) but the results from these latter studies are confounded by other factors e.g. see Wright (1992) and Birkhead and Møller (1992). The best evidence of males altering paternal care in proportion to the amount of paternity comes from studies of polyandrous trios in the dunnock (Davies *et al.* 1992) and of the socially monogamous or polygynous reed bunting (Dixon *et al.* 1994). The share of paternity by males has been shown to correlate with his share of the matings during the fertile period (Burke *et al.* 1989, Davies *et al.* 1992, Møller 1988a, 1991). Møller and Birkhead (1994) have also found a negative correlation between the frequency of EPP and paternal investment in a comparative study among species.

Since male parental care and multiple paternity within a brood are widespread among avian species it is important to determine how male parental care relates to paternity. This chapter investigates the natural variations in parental care and the effect of 24-hour experimental removals of males during the early part of the fertile period (as a means of simulating uncertainty of paternity) on paternal care in the wheatear.

6.2. Methods

6.2.1. General methods

Individual nest holes were observed for daily half-hour periods alternately in the morning and afternoon from the day after hatching (day 1) until at least day 12. Chicks fledge after about 14 days (pers. obs., Conder 1989) after which they are fed by both parents for up to two weeks (Moreno 1984). A total of 40 nests was observed between 1991-93 (12 in 1991, 14 in 1992, and 14 in 1993), giving 240.5 hours of observations (mean number of hours per nest $\pm$ se $= 5.87 \pm 0.19$).

Twenty-six male removals were carried out as described in section 5.2.1 between 1992-93, 19 in the fertile period and seven during incubation as controls to those when the female was assumed to be fertile. Twelve nests in 1991 and two in 1992-93 were non-

experimental and are used in the subsequent analysis as an additional comparison for the effect of male presence on subsequent parental care. Four territory take-overs were observed between 1991-93. Three were a consequence of the removal experiments (complicated by a case of polygny), and one resulted following predation of a male. A male removed on day -5 was unable to regain his territory on release as a neighbouring polygnous male had taken it over (during the removal this male had become temporarily trigamous, with the territories bounding each other). Instead the removed male took over the neighbouring territory of the secondary female of this male on day +4 (clutch size of secondary female = 6). The polygnous male was never subsequently observed on this territory. The other experimentally induced take-over which occurred on day -1 was by an unmated neighbouring male. The mate replacement which occurred as a result of predation resulted in a neighbouring unpaired male taking over the territory in the middle of the laying sequence (clutch size = 6, exact date not known). Since all mate replacements occurred during the fertile period of the females concerned these males are considered as a separate and additional experimental group.

At each nest visit the following were recorded: start time of watch, time of entry to nest, sex and identification of provisioning adult, prey size, wind speed, and general weather details (sunny, bright, overcast or rainy). Load size was estimated by comparison to the bill length and categorised as small, medium, and large. Watches commenced one minute after one parent had visited the nest. Nests were observed from about 40-80 metres using a 20-45x60 telescope and 10x40 binoculars (except six which were observed from 10 metres using a hide).

Nests were numbered consecutively according to their FED. Pairs were termed early or late depending on whether their FEDs were among the first or last half of the nests to be initiated, respectively. The operational sex ratio (OSR) and body condition index (BCI) were calculated as described in sections 1.4.4 and 1.4.5, respectively. Chicks were weighed on day 9 to get an estimate of fledging weight. Fledging success was calculated using the equation 1.1, and the number of chicks which left the nest (see section 1.4.2). Not all adults were caught between years and some had been ringed as pulli and were not subsequently retrapped and measured. As a result, there was an incomplete data set of male and particularly female body condition indices. Female wheatears cannot be aged on the basis of plumage characteristics and could only be reliably aged if their previous history is known. Therefore, female age and BCI were not included in the following analyses due to an incomplete data set.

6.2.2. Multivariate analysis

The influence of a series of independent factors on chick feeding frequencies (dependent variables) were examined using a stepwise multiple regression (termed step 1).

There were two categories of independent variables: 'control' variables and 'selection' variables. Control variables were environmental factors which might have affected behaviour and selection variables were biological factors examined in the regression. Independent control variables were time, wind speed, percentage cloud cover, weather conditions (i.e. separate variables for dull, sunny, bright or raining, entered categorically as 1 or 0), and daily temperature. Dependent selection variables were chick age expressed as days after hatching (day 0), brood size and whether there was a fertile female in the neighbouring territory during the period of observation of the focal nest. Independent control variables were entered into the model before the independent selection variables (see Table 6.1). There were three instances of females raising broods on their own. Provisioning data were only available for two of these nests and not entered into this analysis. There was a degree of pseudo-replication in these two analyses as chick feeding frequencies were considered from days 1 to 13 for each of the 38 observed territories and were not independent of each other. The purpose of these step 1 analyses was to identify any effect of temporary environmental factors on the behavioural variables and so allow these variables to be controlled for in subsequent analyses.

A second set of stepwise regressions was performed to examine the effect of a series of independent variables- chick age, brood size, and number of total feeds- on prey load sizes during the provisioning of nestlings. The data on load sizes from 1992-93 were incomplete due to the position of certain nest holes and consequently adults flying straight into them without first perching nearby where their prey could be observed. This analysis was based on 97 hours of data from 32 territories (see Table 6.2).

A third series of multivariate analyses were performed using the mean residuals per male (per year) for each regression in Table 6.1 as the dependent variable (termed step 2). Phenotypic, demographic and additional data were entered as independent variables in this set of analyses to avoid their replication in step 1. Two different analyses were performed:
(a) An examination of natural variation in provisioning rates using data from the 12 non-experimental territories observed in 1991. The dependent variables were male age, male body condition, female body condition, first egg date, mean intrusion rate of extra-pair males during the fertile period, and the presence of extra-pair young (EPY) in the brood (see Table 6.3).
(b) An examination of the effect of the experiments on male and female provisioning rates. The independent variables were experimental status of the nest (non-removals [1991-93], male replacements, removals during early laying, removals prior to laying, and removals in the fertile period [removals prior to and during laying combined], controls). Removals during the fertile period were considered individually in the separate analyses and were not entered simultaneously (see Table 6.4).

Due to philopatry, 12 returning males were considered more than once in the above

analyses (9 males twice and two males three times; see 6.3.4). The residual values resulting from the previous stepwise regressions between each dependent behavioural variable and the independent variable were often significantly skewed. Dependent variables were therefore transformed when appropriate (using log, rank or arcsine transformations). Stepwise multiple regression analysis was performed with F-to-enter values equivalent to p < 0.1 in linear regression (Sokal and Rohlf 1981). Degrees of freedom for F-to-enter values are expressed as $F_{V1,V2}$, where V1 = number of independent variables introduced into the final model and V1 + V2 + 1 = total number of observations. F-to-enter values prefixed with a minus represents a negative association. The robustness of the regression results was tested by "jack-knifing" the variables, i.e. omitting each variable in turn from the analysis to see if the significant variables remained in the regression model.

Many of the tests involved the use of multiple dependent variables. However, these variables were not always independent of one another and no global correction of statistical probabilities was therefore conducted. This must be kept in mind when interpreting the results (see Rice 1989).

6.3. Results

6.3.1 Provisioning of nestlings (see Table 6.1)

(i) Male provisioning rates

The number of male feeds per brood increased with temperature, chick age, and brood size ($F_{1,472}$ = 5.30, p < 0.05; $F_{2,471}$= 27.62, p < 0.001; $F_{2,471}$ = 50.95, p < 0.001, respectively). The proportion of male feeds declined with chick age and number of chicks ($F_{2,471}$ = -42.26, p < 0.001; $F_{2,471}$ = -8.21, p < 0.01, respectively). The number of male feeds per chick increased with chick age ($F_{2,471}$ = 27.42, p < 0.001) but decreased with brood size ($F_{2,471}$ = -9.12, p < 0.01).

(ii) Female provisioning rates

The number of female feeds per brood increased with temperature, chick age, and brood size ($F_{2,471}$ = 6.14, p < 0.01; $F_{3,470}$ = 168.07, p < 0.001; $F_{3,470}$ = 96.02, p < 0.001, respectively). The female's feeding rate was negatively correlated with rain occurring during the watch and the presence of a fertile female in a neighbouring territory ($F_{2,471}$ = -11.75, p < 0.001; $F_{3,470}$ = -3.86, p < 0.05, respectively). The proportion of female feeds increased with chick age and brood size ($F_{2,471}$ = 43.04, p < 0.001; $F_{2,471}$ = 8.87, p < 0.01). The number of female feeds per chick increased with temperature and chick age ($F_{2,471}$ = 4.47, p < 0.05; $F_{2,471}$ = 163.05, p < 0.001) and decreased during rain and with the presence of a fertile female in a neighbouring territory ($F_{2,471}$ = -11.23, p <

0.0001; $F_{2,471}$ = -3.47, p < 0.05).

(iii) Total provisioning of nestlings

The total feeds delivered to the nest increased with daily temperature, chick age, and brood size ($F_{2,471}$ = 8.94, p < 0.01; $F_{2,471}$ = 161.23, p < 0.001; $F_{2,471}$ = 111.77, p < 0.001, respectively). There were fewer total feeds when it rained ($F_{2,471}$ = -8.69, p < 0.01). The total feeds per chick increased with temperature and chick age ($F_{2,471}$ = 6.30, p < 0.05; $F_{2,471}$ = 136.26, p < 0.001) and decreased when it rained and with brood size ($F_{2,471}$ = -5.58, p < 0.05; $F_{2,471}$ = -16.38, p < 0.001). As with male and female feeds per chick, total feeding rate increased linearly with time, reaching a peak on day 12 (see Fig. 6.1).

6.3.2. Factors affecting prey load sizes (see Table 6.2)

The proportion of small feeds decreased and the number of large feeds increased with chick age (small feeds: $F_{2,305}$ = -195.80, p < 0.001; large feeds, $F_{2,322}$ = 345.43, p < 0.001; see Table 6.2). There was some indication that fewer small feeds and more large feeds were delivered to larger broods (small feeds: $F_{2,305}$ = -4.82, p < 0.05; large feeds, $F_{2,322}$ = 8.46, p < 0.05; see Table 6.2). Males delivered more large feeds than females (Wilcoxon paired sign rank, proportion of large feeds, male vs. female, n = 184 (from 32 territories), z = -7.37, p < 0.001).

6.3.3. Factors affecting rates of provisioning in non-experimental nests (see Table 6.3)

None of the independent variables entered into the regression significantly affected provisioning rates in either sex. There was also no effect of the proportion of the brood which were EPY on the number or proportion of male feeds. EPCs were rare events and there were insufficient variability in the data to enter into the multiple regression, however using univariate analysis there was no suggestion that the frequency of EPC attempts by extra-pair males affected investment by the pair male (Spearman rank, mean residual of male feeds [from Table 6.1] vs. number of EPCs, R_{12} = -0.32, ns).

6.3.4. Effect of experiments on provisioning of nestlings

There was variation in the pattern of feeds by the replacement males (see Table 6.5). There was no evidence of replacement males destroying the clutch or killing the young of the previous males (Møller 1988b, Robertson and Stutchbury 1988). In three of the four instances the replacement male 'adopted' the young (see also Alatalo *et al.* 1983) and in the other example was indifferent to the nestlings (see also Power 1975, East 1981). The polygynous male fed the chicks of his tertiary female from hatching onwards, as did

the male whose territory take-over was induced by predation. The male who took over the polygamous male's secondary female did not feed the chicks in this nest until 4 days after hatching. The male who took over the territory on day -1 was not observed to feed the chicks, though he made a few very infrequent visits to the nest. The polygynous male was observed to simultaneously feed the fledglings from the nest of his primary female and the chicks of the tertiary female. In a further complication the original territory holder started to feed the chicks of the tertiary female from day 9 onwards, and provided the majority of male feeds by day 11 (the chicks from the nest that he had taken over had fledged).

There was no correlation between male investment and the removal experiments conducted in the fertile period (removals on first egg date, $F = 0.02$, ns; removals prior to laying, $F = -0.39$, ns; removals in the fertile period, $F = -0.51$, ns; see Table 6.4). Variance in male feeding frequency was explained both by non-removals and territory takeovers. Males who took over a territory made fewer nest visits (number of nest visits, $F_{2,36} = -23.29$, $p < 0.001$; proportion of male feeds, $F_{1,37} = -7.60$, $p < 0.01$; see Table 6.4). Females which had experienced territorial take-overs made proportionately more feeds but did not significantly increase their number of feeds (proportion of female feeds, $F_{1,37} = 7.63$, $p < 0.01$; number of female feeds, $F = 0.27$, ns; see Table 6.4). This resulted in fewer total feeds being delivered at nests which had experienced a takeover ($F_{2,36} = -4.75$, $p < 0.05$; see Table 6.4). There were also fewer total feeds at non-removal nests ($F_{2,36} = -8.75$, $p < 0.01$), probably a consequence of fewer male feeds ($F_{2,36} = -6.19$, $p < 0.01$; see Table 6.4). If territory takeovers were excluded from the above analyses, there were fewer male feeds and total feeds at non-removal nests, the majority of which were performed in 1991.

The above data were analysed in more detail to determine the extent to which male and female feeding frequencies differed between the experimental groups. There was no difference in the number of male feeds between males removed prior to laying and during early laying and the data were grouped as one experimental group; experimental males (unpaired t-test on mean residuals of number of male feeds; removals prior to laying (n = 6) vs. removals during early laying (n = 10), df = 16, t = 0.43, ns). A one-way ANOVA was performed to compare the mean residuals (used in the above regression) for number of male and female feeds, proportion of male and female feeds, and total feeds between non-removal, removal, control and territorial takeover nests. There was a significant difference in residual male feeding frequencies between the four experimental groups ($F_{3,34} = 8.54$, $p < 0.005$). Replacement males made fewer nest visits than removal or control males and also made proportionately less visits than experimental, control or non-removal males (number of nests visits; Scheffe F-test [Sokal and Rolf 1981]; replacement male vs. control males, $F = 5.90$, $p < 0.01$; replacement males vs. experimental males, $F = 5.85$, $p < 0.01$:

proportion of nest visits; $F_{3,34} = 5.61$, $p < 0.005$; Scheffe F-test; replacement males vs. control males, $F = 5.59$, $p < 0.01$; replacement males vs. experimental males, $F = 4.54$, $p < 0.01$; replacement males vs. non-removals, $F = 4.12$, $p < 0.05$; see Fig. 6.2(i)). There was no difference in female feeding frequencies between the experimental groups ($F = 1.88$, $p = 0.15$; see Fig 6.2). However, females which had experienced territorial take-overs made proportionately more feeds than at non-removal, control or experimental nests ($F_{3,34} = 5.72$, $p < 0.005$: Scheffe F-test; territorial takeover vs. non-removal nests, $F = 4.26$, $p < 0.05$; territorial takeover vs. control nests, $F = 5.19$, $p < 0.01$; territorial takeover vs. experimental nests, $F = 4.19$, $p < 0.05$; see Fig 6.2(ii)). There was a significant difference in the number of total feeds delivered to the four experimental groups ($F_{3,34}$, $F = 4.03$, $p = 0.02$). Significantly fewer feeds were made at non-removal nests than at experimental nests (Scheffe F-test, non-removal nests vs. experimental nests, $F = 2.94$, $p < 0.05$; see Fig 6.3). Fewer total feeds were made at mate replacement nests, but not significantly so. There was no significant increase in the number of female feeds in response to a reduction in the number of male feeds at the latter nests. This suggests some degree of female compensation in their feeding frequencies in response to a reduction in male feeds. There was no indication that either sex fed larger prey to nestlings in an attempt to compensate for reduced feeding frequencies (one-way ANOVA, experimental condition [non-experimental, removal prior to laying, removal during laying, controls, adoptions], vs. mean residuals per territory for proportion of large prey items [calculated from the stepwise-regression in 6.3.2, see Table 6.2]; female feeds, $F = 1.22$, ns; male feeds, $F = 2.66$, $p < 0.1$).

Using a larger data set based on the mean residuals calculated from Table 6.4, there was no still effect of male age or body condition (BCI) on rates of male provisioning (number of male feeds; male age, first-year vs. older, unpaired t-test, $t = 0.014$, $df = 36$, ns; BCI, $df = 36$, $R = 0.04$, ns). There was also no effect of first egg date on the total number of feeds (first egg date vs. mean residual of total feeds, $R_{38} = -0.04$, ns).

Wheatears are philopatric, returning to the same breeding area in successive years (e.g. Conder 1989, Tye 1992). Some adults were used in the above analysis more than once. Seven males observed in 1991 were removed in 1992, three of which were also removed in 1993. One male was observed in 1992 and 1993. Provisioning rates of five of the same females were compared in successive years, and two females were compared in seasons two years apart (five 1991-92 and two from 1992-93).Wilcoxon paired-sign rank tests were used to compare mean male residuals calculated from Table 6.1 for the number of male and female feeds, proportion of male and female feeds, and total feed for eight males (seven from 1991-92, and one for 1992-93) and seven females between years. There was no effect of either the experiments or individual age on feeding rates or patterns of

Table 6.1. Stepwise multiple regression to test for the influence of independent environmental and brood variables on male and female parental care (38 nests, 1991-93) (step 1).

Dependent behavioural variables

Independent varaibles	No. male feeds	No. female feeds	% Male feeds	% Female feeds	Total feeds	Male feeds per chick	Female feeds per chick	Total feeds per chick
Control variables								
Rain	-0.80	-11.75***	-1.17	-2.79†	-8.69**	-8.63**	-11.23***	-5.58**
Temperature	5.30*	6.14*	-0.79	0.90	8.94**	0.78	4.47*	6.30**
Cloud	-0.55	-0.23	0.51	-0.97	-0.23	-0.15	-0.55	-0.16
Time	0.01	1.12	-1.08	0.63	0.43	0.12	1.23	0.61
Wind speed	-0.91	0.03	-0.21	0.40	-0.12	0.04	1.34	1.25
Selection variables								
Chick age	27.62***	168.00***	-42.26***	43.04***	161.23***	27.42***	163.05***	136.26***
Brood size	50.95***	96.02***	-8.21**	8.87**	111.77***	-9.12*	-1.59	-16.38***
Fert Female	0.03	-3.86*	1.85	-1.71	-1.96	-0.11	-3.47*	-1.96
Total R^2	0.15	0.40	0.10	0.09	0.40	0.09	0.29	0.27

Columns show F values resulting from stepwise multiple regressions between each dependent variable and the indpendent variables. Independent variables indicated with *, ** or *** were introduced into the final regression model and explained a significant amount of variation in the dependent variable († $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). F-to-remove values are given for those varaibles which entered the final model and F-to-enter values are given for other variables. Independant control variables were entered into the model before the independent selection variables. R^2 refers to the amount of variation in the data which is explained by the model. R^2 refers to the amount of variation in the data which is explained by the model.

Independent control variables are: rain, whether it rained during the period of observation; temperature, daily ambient temperature; cloud, the amount of cloud cover (expressed on a scale of 1 to 8); time, time of observation; wind speed (expressed on a scale of 1 to 6). Independent selection variables are: chick age, age in days (day 0 = hatching date); brood size, number of chicks in nest; fert female, presence of a fertile female in a neighbouring territory. Dependent variables are: No. male feeds, number of male feeds; No. female feeds, number of female feeds; % male feeds, proportion of total feeds delivered by the male; % female feeds, proportion of total feeds delivered by the female; total feeds, total number of feeds delivered to nestlings; male feeds per chick, number of male feeds/brood size; female feeds per chick, number of female feeds/brood size; total feeds per chick, total number of feeds/brood size.
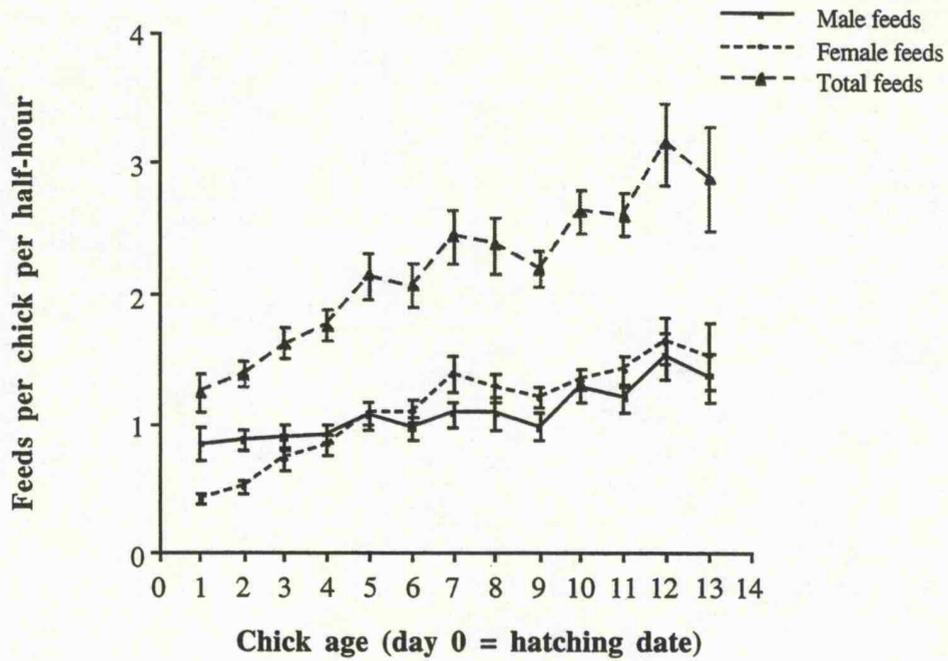
Fig. 6.1. Graph showing mean number of feeds per chick per half-hour (± se). Data are for 12 non-experimental pairs from 1991.

Table 6.2. Stepwise multiple regression to test for factors affecting the proportion of small and large prey items in chick diet.

Independent variables	Dependent variables					
	% male s	% fem s	% total s	% male l	% fem l	% total
Chick age	-218.17***	-266.67***	-195.80***	359.62***	227.23***	345.43***
Clutch size	-4.22*	-1.17	-4.82*	0.52	-0.50	8.46*
Total feeds	0.47	-3.60†	-0.50	0.04	-4.82*	-0.12
R^2	0.39	0.46	0.49	0.51	0.42	0.53

Columns show F values resulting from stepwise multiple regressions between each dependent variable and the independent variables. Independent variables indicated with *, ** or *** were introduced into the final regression model and explained a significant amount of variation in the dependent variable († $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). F-to-remove values are given for those variables which entered the final model and F-to-enter values are given for other variables. R^2 refers to the amount of variation in the data which is explained by the model.

Independent variables are: chick age, age in days (day 0 = hatching date); brood size, number of chicks in nest; total feeds, number of feeds delivered by the male, female or in total (number of male feeds + number of female feeds), depending on whether dependent variable refers to the male, female or total feeds respectively. Dependent variables are: % male s, proportion of items fed by male which were small; % fem s, proportion of items fed by female which were small; % total small, proportion of items fed by both parents which were small; % male l, proportion of items fed by male which were large; % fem l, proportion of items fed by female which were large; % total large, proportion of items fed by both parents which were large.

Table 6.3. Stepwise multiple regression to test for the influence of phenotypic and breeding data on male and female parental care (step 2(a)).

Dependent variables

Independent variables	No. Male Feeds	No. Female Feeds	% Male Feeds	% Female Feeds	Total feeds
Male BCI	0.74	-0.87	0.09	0.01	0.02
Female BCI	-0.13	-2.46	2.31	-2.91	-1.28
Male age	-1.39	0.22	-1.24	0.27	-1.43
FED	0.57	-0.42	0.17	-0.19	-0.15
Intrusions	1.32	-2.11	0.55	-1.61	-0.05
EPP	-0.24	-0.11	-0.29	0.01	-0.29
R^2	0.00	0.00	0.00	0.00	0.00

Columns show F values resulting from stepwise multiple regressions between each dependent variable and the independent variables. R^2 refers to the amount of variation in the data which is explained by the model. No variables were entered into the final model ($p > 0.05$ in all cases).

Independent variables are: male BCI, male body condition index; female BCI, female body condition index; male age (old or first-year breeder); FED, first egg date; intrusions, mean intrusion rate per hour in fertile period; EPP, presence of extra-pair young in the nest. Dependent variables are: No. male feeds, mean residual of number of male feeds; No. female feeds, mean residual of number of female feeds; % male feeds, mean residual of proportion of total feeds delivered by the male; % female feeds, mean residual of proportion of total feeds delivered by the female; total feeds, mean residual of total number of feeds delivered to nestlings.

Table 6.4. Stepwise multiple regression to test for the influence of temporary male removal experiments on male and female parental care (step 2(b)).

Independent variables	Dependent variables				
	No. Male Feeds	No. Female Feeds	% Male Feeds	% Female Feeds	Total feeds
MR	-23.29***	0.27	-7.60**	7.63**	--7.09*
NR	-8.24**	-2.53	-0.57	0.18	-8.75**
Control	0.51	0.40	1.08	-0.78	0.02
Rem FED	0.02	1.22	-1.00	1.28	0.03
Rem FER	-0.39	-0.01	0.13	-0.07	0.13
Rem FERTOT	-0.51	0.09	-0.45	0.72	0.18
R^2	0.41	0.00	0.53	0.16	0.20

Columns show F values resulting from stepwise multiple regressions between each dependent variable and the independent variables. Independent variables indicated with *, ** or *** were introduced into the final regression model and explained a significant amount of variation in the dependent variable († $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). F-to-remove values are given for those variables which entered the final model and F-to-enter values are given for other variables. R^2 refers to the amount of variation in the data which was explained by the model.

Independent variables are: MR, territory takeovers (n = 4); NR, non-removals (n = 14); Control, males removed during incubation (n = 7); Rem FED, males removed on first egg date (n = 10), Rem FER, males removed in fertile period prior to laying (n = 6), Rem FERTOT, males removed during the fertile period (n = 16). Dependent variables are: No male feeds, mean residual of number of male feeds; No female feeds, mean residual of number of female feeds; % male feeds, mean residual of proportion of total feeds delivered by the male; % female feeds, mean residual of proportion of total feeds delivered by the female; total feeds, mean residual of total number of feeds delivered to nestlings.
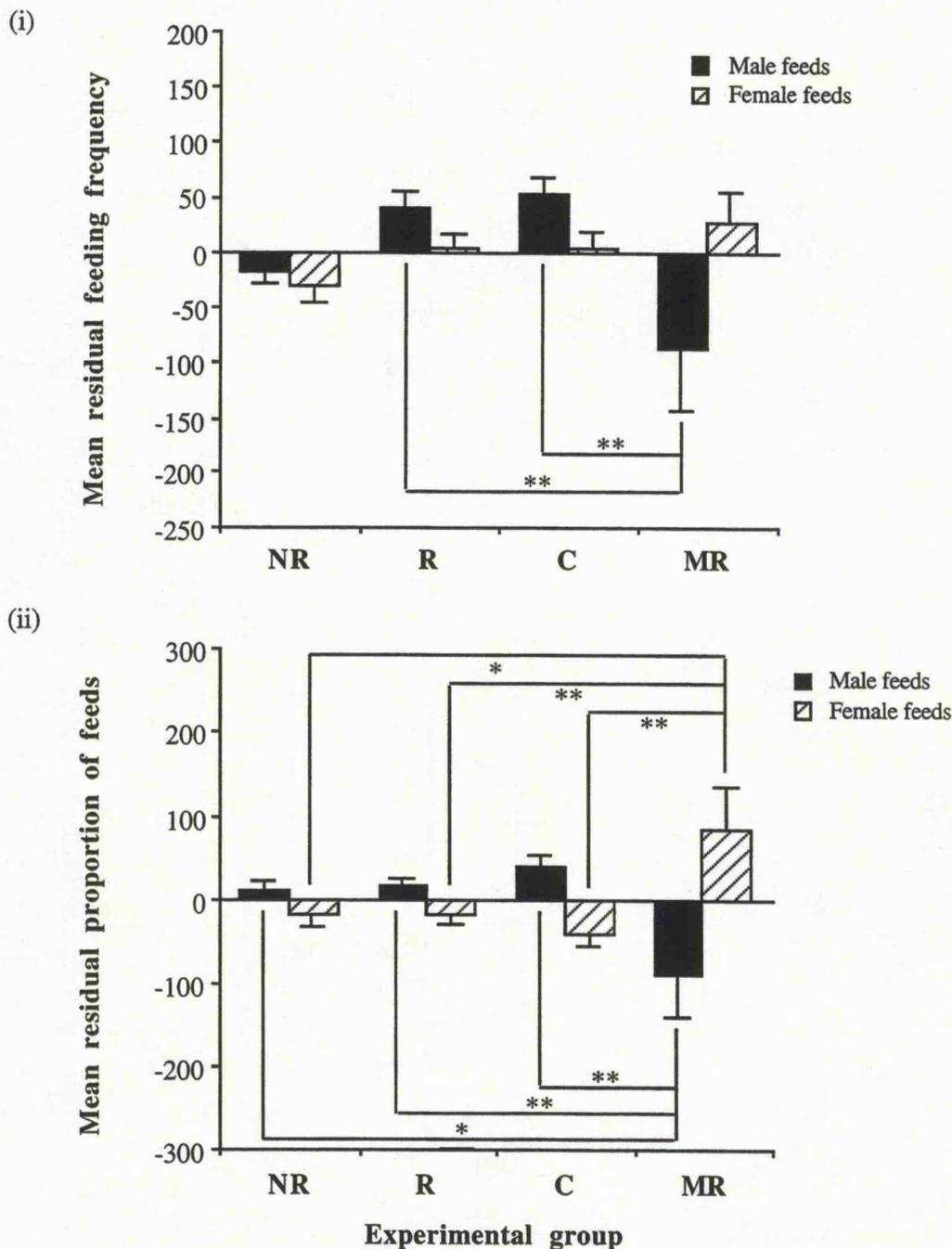
Fig. 6.2. Mean residuals (± se) (from regression model in Table 6.1) for (i) male and female feeding frequencies, and (ii) proportion of male and female feeds, for experimental and control groups. Experimental groups: **NR**, non-removals; **R**, removals in fertile period; **C**, controls; **MR**, territory takeovers. Residual of number of male feeds, proportion of male feeds, and proportion of female feeds differed between experimental groups (ANOVA: male feeds, $F_{3,34}$ = 8.54, p < 0.005; proportion male feeds, $F_{3,34}$ = 5.61, p < 0.005; proportion female feeds, $F_{3,34}$ = 5.72, p < 0.005). Scheffe F-tests were used to compare between groups, * p < 0.05, ** p < 0.01.

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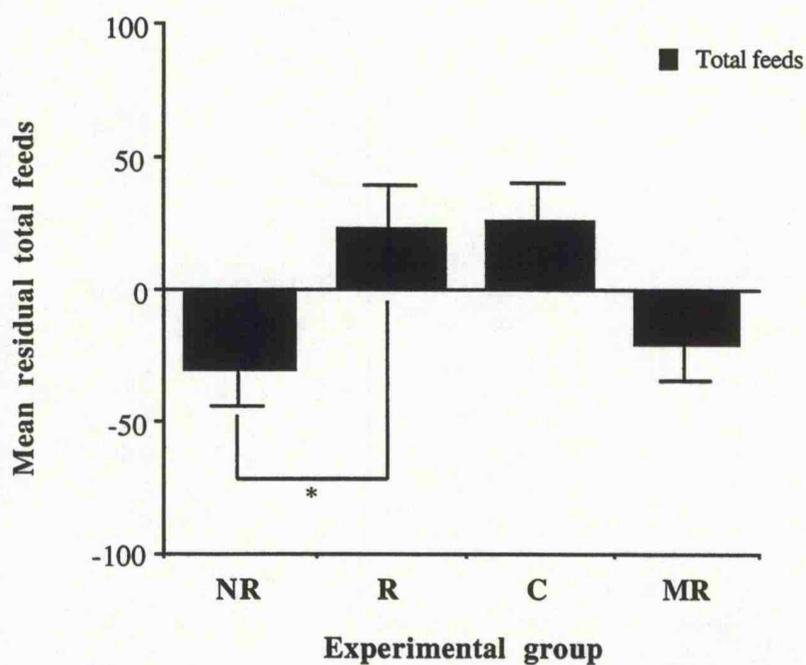
Fig. 6.3. Mean residuals (± se) (from regression model in Table 6.1) for total feeds, for experimental and control experiments. Experimental groups: **NR**, non-removals; **R**, removals in fertile period; **C**, controls; **MR**, territory takeovers. Residual of total feeds differed between experimental groups (ANOVA, $F_{3,34}$ = 4.13, p = 0.02). Scheffe F-tests were used to compare between groups, * p < 0.05.

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Table 6.5. Mean percentage of male feeds provided at nests which had experienced a territorial takeover. Paternity data are for replacement males.

Male	Day of takeover	Mean % feeds	No. Chicks	% Paternity
1	+2 *	56	5	0
2	-1	0	6	0
3	+4	36	6	0
4	-4	41	5	100

(Day 0 = first egg date, * exact date unknown)

Table 6.6. Mean chick weights and fledging success (± se).

	Number of nests	Mean chick weight (g)	Fledgling success (f/e)	Mean number of fledglings
Non-removals	14	23.76 ± 0.97	0.61 ± 0.10	3.71 ± 0.57
Experimental removals	16	24.33 ± 0.82	0.64 ± 0.11	3.85 ± 0.64
Control removals	7	25.14 ± 0.29	0.98 ± 0.02	5.43 ± 0.30
Mate replacements	4	24.86 ± 1.57	0.92 ± 0.05	5.25 ± 0.25
Female only	3	22.23 ± 0.61	0.77 ± 0.06	4.67 ± 0.33

Table 6.7. Mean proportion of females (± se) which were fertile during provisioning of nestlings for all, early and late breeding males.

Year	No. breeding females	All males	Early males	Late males
1991	23	0.11 ± 0.01	0.13 ± 0.01	0.05 ± 0.02
1992	17	0.01 ± 0.01	0.01 ± 0.01	0.00 ± 0.00
1993	19	0.06 ± 0.01	0.07 ± 0.01	0.00 ± 0.00

feeding (number of male feeds, n = 7, T^+ = 15, ns; proportion of male feeds, n = 7, T^+ = 11, ns; number of female feeds, n = 7, T^+ = 13, ns; proportion of female feeds, n = 7, T^+ = 13, ns; total feeds, n = 6, T^+ = 14, ns).

6.3.5. Chick weight and fledging success.

There was no difference in chick weights or fledging success (f/e or number of fledglings produced) between experimental procedures (Kruskal-Wallis; chick weights, df = 3, H = 1.48, ns; f/e, df = 3, H = 7.16, p < 0.1; number of fledglings, df = 3, H = 5.19, p > 0.1; see Table 6.6). Chicks in nests fed only by the female were lighter though there was no reduction in fledging success (Kruskal-Wallis; chick weights, df = 4, H = 14.71, p < 0.01; f/e, df = 4, H = 7.88, p < 0.1; number of fledglings, df = 4, H = 5.74, p > 0.2; see Table 6.6). Nest failure was due primarily to bad weather, principally wind and rain which resulted in a reduction in feeding rates and starvation of the chicks (see also Conder 1989).

Discussion

6.4.1. Factors affecting parental care

Provisioning rates observed during these half-hour observations are comparable to those observed for longer periods of time (see Table 12.2 in Conder 1989, and Fig. 2(a), 2(b) in Moreno 1987a), and can therefore be assumed to give an accurate measure of parental investment.

Both sexes increased their rate of provisioning in response to chick age and brood size, reaching a maximum around day 12 (see also Moreno 1987a). Prey size increased with chick age and brood size. Although the number of feeds per chick declined with brood size (see also Gibb 1955, Royama 1966, Bryant and Gardiner 1979, Westerterp *et al.* 1982, Nur 1984), this was possibly compensated for by each chick being fed larger prey, which suggests a possible switch in the prey selection or foraging behaviour of the adults in response to increased brood size. There was little evidence of provisioning adults adjusting their feeding frequencies inversely with load size (but see also Kluijver 1950, Royama 1966, van Balen 1973).

In this study, males provided about 50% of chick feeds. They provided proportionately more feeds than the female when the chicks were between one and five days old. This is probably because she exclusively broods the chicks during this time and consequently made fewer nest visits (Moreno 1987, Conder 1989, see Fig. 6.1). As chick age increased, the amount of time spent brooding decreased, resulting in an increase in the proportion of feeds the female delivered to the nestlings and a corresponding decrease by the male (see also Moreno 1987a).

Males provided proportionately more large prey items than the female. In the·

wheatear, sexual dimorphism is most marked with respect to plumage dichromatism, bill and wing lengths. As a consequence of having larger bills, males are able to handle larger prey items (Carlson and Moreno 1983). The resulting differences in loading capabilities between the sexes may also have consequences for prey selection and other aspects of the foraging ecology of this species.

Feeding frequencies were affected by two main weather variables: ambient temperature and whether or not it rained during the period of observation. Temperature has been shown to effect the mobility of prey (e.g. Avery and Krebs 1984). Increased mobility associated with higher temperatures may result in an increase in the ability to find food and result in higher rates of provisioning. Parents fed less when it was raining and this may reflect a reduction in foraging success and/or adults sheltering from the rain. Prolonged periods of rain are associated with reduced growth rates and starvation of the chicks (see also Conder 1989).

The synchronous nature of this breeding population over the three-year study meant there were few opportunities for males to participate in additional matings (see Table 2.8). It was consequently rare to have a fertile female in a neighbouring territory during the provisioning of nestlings (Table 6.7) and not surprising that this variable has no effect on male investment. There was only one instance in three years when a male provisioning nestlings was observed intruding on a neighbouring territory which contained a fertile female. Westneat (1990) argues that in such circumstances males should provide parental care as there are no other options open to them. However, in the majority of studies the absence of paternal care results in a reduction in reproductive success (Bart and Tornes 1989), and Birkhead and Møller (1992) argue that due to the costs of parental care, the lack of opportunities for EPCs are not enough to account for paternal care. A high degree of synchrony may not fully explain paternal care but could account for the high degree of male investment in this study. Although the ratio of feeds between the sexes was similar to that observed by Moreno (1987a), females have been documented as feeding proportionately more in other studies (Cramp 1988), e.g. 70.5% of total feeds being provided by the female (Conder 1989). One might predict that in a more asynchronous population there would be reduced levels of paternal care.

Mate guarding has been documented in the wheatear (Carlson *et al.* 1985, Chapter 2). Van Rhijn (1991) proposes that in guarding species, males are predisposed to paternal care because they are present at laying i.e. remaining with the female until the onset of incubation in an attempt to ensure paternity can be considered to be the beginning of the monogamous pair bond and a basis for the evolution of paternal care. There was a weak suggestion that the presence of a fertile female correlated with a reduction in the number of female feeds. Provisioning rates have been shown to be a consequence of brood size, and begging intensity. A reduction in the number of feeds by the female, as observed in this

study, could be a strategy to maintain male help. By reducing her investment and possibly increasing the begging intensity of chicks she may prevent him from pursuing additional matings and investing in another female at her expense. However, there was no effect of the presence of a fertile female on the proportion of feeds that the pair female contributed as would be expected if this were a deliberate strategy on her part.

6.4.2. Paternity and paternal care

As in the majority of field studies (e.g. Frederick 1987, Westneat 1988, 1995 Wagner 1992, Whittingham and Lifjeld 1995, but see Dixon *et al.* 1994), there were no indications that under natural conditions male wheatears reduced their parental care in response to either being cuckolded or to indicators which may have reflected the threat of cuckoldry (such as intrusion rates or EPCs).

The effects of paternity on parental care have been proposed to depend on a hierarchy of factors, including the ability of males to assess paternity, the predictability of cuckoldry and the costs and benefits of male parental care (Whittingham *et al.* 1992, Westneat and Sherman 1993). Costs to males of parental care are lost opportunities to pursue additional matings and energetic costs, as well as the possible additive detrimental effects on future survival. If parents are unable to assess paternity, patterns of parental care are likely to have evolved in response to the pattern of parentage in subsequent broods. If however parents can assess paternity, the extent of parental care will depend on the costs and benefits of parental behaviour. Slight reductions in paternity are likely to have little effect on male parental behaviour because they will probably have a relatively small effect on the net benefits of care. Large reductions in paternity are more likely to result in the benefits of care being low, with the male altering his investment accordingly. Evidence to date indicates that males are unable to recognise EPY in the nest (Burke *et al.* 1989, Dixon *et al.* 1994) and any reduction in parental care is probably based on other cues indicating the likelihood of lost paternity in the brood.

There were low levels of extra-pair paternity in un-manipulated nests, 11% of offspring in 29% of broods (see section 4.3.1). Females also did not appear to pursue EPCs to a great degree (see sections 3.3.4 and 5.3.4(iii), Westneat 1992b, but see also Kempenaers *et al.* 1992, Dixon *et al.* 1994). It is unclear whether or not males can perceive they have been cuckolded. However, since there were low levels of EPP, a strong association between behavioural correlates of paternity and actual paternity, and a lack of consistent patterns of paternity in time of season or with male age (see section 4.3.3), one should not expect reduced levels of paternal care (Westneat 1995). The most unambiguous example of a reduction in parental care in response to reduced paternity in a monogamous species has been documented in the reed bunting, in which the level of EPP is very high; 55% of young in 86% of nests (Dixon *et al.* 1994). High levels of EPP and unpredictable

variation in paternity between nesting attempts (as observed in this species) will favour a reduction in paternal care (Westneat and Sherman 1993).

6.4.3. Removal experiments, adoption and paternal care

The removal experiments were designed specifically to examine the effects of the absence of the pair male on brood paternity (see section 5.3.6) and their effects on patterns of paternal care were a secondary area of study. Within the constraints of the experimental design there was no reduction in parental care, as measured by the provisioning of the nestlings, in response to removing the male during the fertile period and attempting to simulate uncertainty of paternity.

Manipulations of certainty of paternity have predominantly been carried out by isolating males using temporary removals (Møller 1988a, 1991, Davies *et al.* 1992, Whittingham *et al.* 1993) or permanent removals followed by male replacements (Meek and Robertson 1991) during the female's fertile period. Such experiments have the potential to increase extra-pair paternity but are accompanied by a degree of artificiality as a male's perception of his partner's fidelity may not necessarily follow from being captured and excluded from social interactions. To date, in socially monogamous species there are no unambiguous studies showing a reduction in paternal care with simulated uncertainty of paternity using this experimental approach. Only temporary male removal experiments performed in co-operative breeders have led to a reduction in paternal care (Koenig 1990, Davies *et al.* 1992). Wright and Cotton (1994) argue that a more appropriate approach to manipulating a male's certainty of paternity is to simulate a change in the female's behaviour. Utilising this approach, they were able to show a reduction in paternal care in the starling.

In birds, potential male responses to offspring after a territorial take-over are: (i) infanticide (Møller 1988b, Robertson and Stutchbury 1988); (ii) indifference (Power 1975); or (iii) adoption (Meek and Robertson 1991). The timing of the territorial take-over may affect it's outcome, with those occurring after clutch completion often resulting in infanticide. All take-overs in this study took place during the fertile period, and in general, replacement males fed less at their adopted broods. Although there was not a significant increase in the number of female feeds, this did not result in a significant reduction in the number of total feeds, suggesting some degree of compensation by the female in response to a reduction in male feeds (see also Kluijver 1950, Alatalo *et al.* 1982, 1988, Lefelaar and Robertson 1986).

Replacement males did not alter their investment proportionately to their paternity in the brood (see Table 6.5), but did tend to reduce their overall investment, providing on average 29% of total feeds (although responses by individual males differed) as opposed to non-replacement males providing about 50%. A reduction in male investment may be a

consequence of differential male ability, a more acute trade-off between mating effort and parental effort, or uncertainty of paternity. Two of these replacement males provided about 50% of chick feeds in previous nesting attempts and male body condition had no significant effect on provisioning rates so it seems unlikely that the quality of the replacement male affected the amount of paternal care that they provided. Adoption of a brood by a male after a territorial take-over can be considered a trade-off between the costs and benefits of staying with a female. The extent of his investment in the offspring will depend on whether the take-over is to acquire a female for a subsequent mating (typically associated with low male investment) or whether there is a perception of having paternity in the brood (associated with higher levels of male care) (Meek and Robertson 1991). Additional factors that may influence the level of adoption include the behaviour of the female and opportunities to pursue EPCs.

Females have been observed to prolong sexual receptivity in the presence of replacement males, possibly in an attempt to 'fool' them into adopting the brood (Robertson 1990), e.g. by soliciting copulations (East 1981, Gjershaug *et al.* 1984), and copulating with these males even after clutch completion (Bowman and Bird 1987, Robertson 1990). In the three adoptions where the male fed the nestlings the female was observed to associate with him, either by soliciting for copulations or remaining in close proximity prior to the onset of incubation, while no such interactions were observed between the sexes in the take-over when the male was not observed to feed the nestlings. There was no suggestion that the adopting males pursued EPCs to any greater extent than other males, but Male 2 (see Table 6.5), who did not feed, was observed participating in EPCs and frequently displaying throughout the experiments conducted in 1993. As a result of a takeover males, can either concentrate on their mating effort, parental effort, or achieve a trade-off between both, the outcome of which will depend on specific factors at that time.

In the dunnock, males have been observed to alter their parental care with respect to their association with the female and their presence during egg laying (Davies *et al.* 1992, Hatchwell and Davies 1992). There is some limited anecdotal evidence in this study which suggests that males may also use similar but fallible clues as a rough guide to paternity. Male 3 (see Table 6.5), who could not have fertilised any of the eggs during the take-over as it occurred after the laying of the penultimate egg, still fed the nestlings. The female was observed in close association with this male prior to the onset of, and during, the initial days of incubation. Male 3 returned to feed his previous partner's chicks after the nestlings had fledged on the territory he had been forced to take over. This male had been observed to associate closely and perform sexual displays with his previous partner prior to the removal. There was no evidence that replacement males mated with these females in subsequent years. Examination of the paternity data in Table 6.5 shows that two out of four males were possibly deceived into feeding unrelated offspring.

Surprisingly, there were also fewer total feeds at non-removal nests. There was a high correlation between experiment and year, with 12 of the 14 non-removals being from 1991. It is unclear whether removing the pair males during both the fertile period and incubation resulted in both sexes increasing their feeding rates but it seems more likely that the reduction in the number of feeds was a year effect. Temperature significantly affected provisioning rates of both sexes (see Table 6.1). The mean temperature was lower during the period of provisioning in 1991 than in 1992 or 1993 (Kruskal-Wallis, df = 2, H = 13.14, p < 0.01) which may account for lower rates of chick feeding at non-removal nests (see above).

6.4.4. Chick weights and fledging success

Lower rates of feeding were not associated with lower chick weights in either the non-removal or mate replacement nests. Feeding frequencies are not necessarily a reliable indicator of the amount of food delivered due to variations in load sizes (e.g. Gibb and Betts 1963, Royama 1966, van Balen 1973). However, there was no suggestion that either sex at non-removal nests, females which had experienced territory takeovers, or the adopting male increased their proportion of larger prey items fed to nestlings to make up for the shortfall in provisioning rates. The size grouping of prey items in this analysis was based on length (a linear measurement) and may not be accurate in providing an indication of mass given to the nestlings (a cubic measurement). Diet composition, which was not examined, has also been shown to influence mass gain and condition of chicks (Tinbergen 1981, Krebs and Avery 1984). Both these considerations could help to explain the discrepancy between feeding frequencies and chick weights. Fledging weights were measured on day 9, but the nestlings remained in the burrow until at least day 14. Consequently the effects of reduced feeding rates on chick weights may be more pronounced nearer fledging. However, chick weights reach a plateau from about day 9 onwards (Moreno 1987b, Conder 1989) and there was no suggestion that nestlings associated with reduced feeding frequencies took longer to fledge.

As in the majority of studies, male investment was only examined during the nestling period. There was no measure of the post-fledgling survival of the offspring, though young fledglings are prone to predation (Brooke 1981). On fledging, care of the juvenile wheatears is divided between the parents (Moreno 1984) and any detrimental effects of reduced parental care are possibly more accentuated during this time.

6.5. Summary

1. Chick feeding frequencies increased with chick age, brood size and temperature, and declined when it rained. The number of feeds per chick increased with chick age but decreased with brood size. Prey load sizes increased with chick age, with males feeding

larger prey to nestlings than females.

2. In this study, male investment in the offspring was primarily through provisioning and defence of the chicks and nestlings, and territorial defence. Males provided on average 50% of chick feeds, more when the female was brooding young chicks. There was no reduction in male investment in response to losing paternity in non-experimental pairs, or as a result simulating uncertainity of paternity using male removal experiments during the fertile period. However, adopting males did reduce their number of feeds, although not in proportion to their paternity within broods.

3. Females appeared to be able to compensate, at least in part, for the reduction in male help during the provisioning of chicks observed in the cases of adoption. Furthermore, females seemed to be capable of raising a brood on their own or with reduced male help. However, the absence of male help resulted in reduced fledging weights.

Chapter 7. The effect of territory and individual quality on breeding success in the wheatear.

7.1. Introduction

7.2. Methods

7.3. Results

7.4. Discussion

7.5. Summary

7.1. Introduction

The majority of land birds breed in pairs on territories: 84% of passerines and 81% of non-passerines (Lack 1968). Territory ownership and quality, especially for species which occupy an all-purpose territory, are likely to be major contributors to an individual's fitness and reproductive success. Competition for good territories is therefore likely to be intense as well as costly in terms of both time and energy (Goodburn 1991).

Within species there is considerable variation in individual breeding performance which has been attributed to differences in territory quality (Hogstedt 1980, Møller 1982), parent quality (Newton and Marquis 1982, Goodburn 1991), experience of parents (e.g. Thompson *et al.* 1986 and in the timing of breeding, which typically shows a seasonal decline (Perrins 1970, Brooke 1978, Møller 1990). If territories vary in quality in a consistent way, individuals are expected to develop behaviours that allow them to maximise territory quality, e.g. settling preferentially on good territories (Brooke 1979, Møller

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1983), and shifting to better sites whenever possible (Beletsky and Orians 1987).

Individuals can use their experience of previous breeding seasons to assess the value of an area, although conditions on site may differ between years as a result of short or long term local changes in habitat or prey populations (see O'Connor 1984). Birds resident throughout the year are more likely to be able to monitor such changes and modify their territory boundaries accordingly, but migrants who are absent for part of the year and individuals breeding for the first time may need to assess a potential territory solely on information gained at the time of their settlement. It will therefore be important for individuals to make the correct choice during this time as modification of boundaries at a later date may be difficult (Tye 1992).

In migrant species, the main benefits of arriving early are being able to settle on the best territories and having the opportunity to breed earlier, both possibly enhancing reproductive success (Møller 1994). The major cost of arriving early is the risk of mortality due to unsuitable environmental conditions (Møller 1994). Variations in arrival times can therefore be considered to be phenotype-dependent and to have costs and benefits, and as such are likely to be a reliable indicator of an individual's quality (Møller 1994). As a consequence, territory and individual quality are likely to be correlated: early arriving birds will also have the opportunity to pair with good quality mates.

Fidelity to a breeding area is common among many bird species (Greenwood 1980, Greenwood and Harvey 1982). The degree of site fidelity exhibited by a species is likely to depend on whether it is a resident or migrant, local population density, and the degree of variation in territory quality (Bensch and Hasselquist 1991). Resident species typically exhibit high site fidelity, possibly due to the limited options of finding a better territory, but fidelity in migrants will in part be a consequence of differences in arrival times. Early arriving individuals preferentially choosing good territories will force later arrivals to settle elsewhere (Harvey *et al.* 1984, Beletsky and Orians 1987). Secondly, at higher breeding densities an individual is more likely to lose its territory whilst seeking another. Individuals may benefit by being more site faithful under such conditions (e.g. Searcy 1979, Weatherhead and Boak 1987). If there is large variation in territory quality individuals may exhibit less fidelity to those of poor quality (e.g. Newton and Marquis 1982, Beletsky and Orians 1987, Thompson *et al.* 1988, Bollinger and Gavin 1989).

In the wheatear, males defend an all-purpose territory from which the majority of food for the pair and dependent young is collected (Conder 1989, Cramp 1988, Tye 1992). Brooke (1979) showed a consistent preference between years for certain territories which were associated with earlier breeding attempts and higher fledging success. In a separate study prey densities were shown to be highest on short vegetation. Individuals may use vegetation characteristics as an indirect measure of territory quality, preferentially settling on areas with short vegetation (Tye 1992).

This chapter examines territory settlement and the basis of territory choice in the wheatear. Since both sexes exhibit varying degrees of site/mate fidelity (Brooke 1979, Conder 1989) this chapter also investigates the effect of territory quality on site/mate fidelity and breeding success.

7.2. Methods

7.2.1. Territory settlement

The study site was monitored three times daily between 0600-0800, 1200-1400, 1600-1800 (BST) from the middle of March until late April, to obtain the arrival, settlement and pairing dates of resident individuals. The study was started in 1991 and few birds were colour-ringed initially. Resident males were identified by their territorial behaviour (see Conder 1989, Cramp 1988) and were trapped and colour-ringed shortly after they arrived. The settlement dates of seven males (out of 26) in 1991 were not obtained. Female settlement and pairing data were incomplete for 1991 and are not included in the following analysis. Individuals returned to breed in subsequent years and in 1992/93 the majority of adults were colour ringed. 82.3% (14/17) of females and 92% (21/24) of males in 1992, and 70.5% (12/17) of females and 72.2% (13/18) of males in 1993 were ringed when they arrived. Unringed adults in 1992-93 were initially individually identified by their behaviour and plumage characteristics. Complete settlement and pairing data were obtained for all individuals in 1992-93. Territories were also ranked in relation to settlement of the first individual of each sex to compensate for differences in arrival and settlement dates between years. Lower ranked territories were settled on earlier than higher ranked ones.

An individual was considered to have settled only when it stayed in an area where it subsequently bred or, if unpaired, remained for the majority of the breeding season. Any short term settlements and subsequent movements by colour ringed individuals were noted. Territory boundaries were plotted during the breeding season on a scale map by observing boundary disputes, territorial behaviour and by "driving" (see Tye 1992 and references therein). Territories were assumed to be unchanged between years if the same nest site was used or if the defended area contained the nest site from previous or subsequent years. If territories were consistently not bred upon then there had to be an overlap of at least 50% in the defended area between years for them to be regarded as the same. Thirty such territories were identified, 28 of which were used at least twice in the three-year study. Although boundaries altered between years, territories remained remarkably constant (see Figures 7.1-7.3). Territories numbered the same in Figures 7.1-7.3 are assumed to occupy the same area. Given this consistency between years, a mean male and female settlement rank was calculated for a total of 28 territories (two territories were used only once in 1991 for which no rank was obtained). Territories were also categorised as preferred or non-preferred (see also Bensch and Hasselquist 1991). Mean male territory ranks were used as

the basis for categorising preferred and non-preferred territories as these correlated significantly with mean female territory ranks (Spearman rank correlation, mean male territory rank vs. mean female territory rank, $R_{21} = 0.75$, $p < 0.002$). The range in mean rank of preferred territories was 1-7, non-preferred territories ranked 8-14. There were six instances where a male occupied a territory which had contained two territories in previous years (two territories used in both 1992 and 1993, and two others in 1993). In these situations the locality of the previous territory in which the later breeding attempt actually occurred was considered to be the one utilised again.

Mating success of male wheatears was defined according to the presence or absence of a female during the breeding season. There was only one unpaired male in 1993 and due to the small sample size he was excluded from the following analyses. There were never any unpaired females, although there was one case of polygyny in 1993 when a male defended two neighbouring territories. There was no overlap in the territories of the two females. Territories were monitored to obtain the first egg date (FED) and clutch size. Nests were numbered consecutively according to their FED. Pairs were termed early or late depending on whether their FEDs were among the first or last half of the nests to be initiated respectively (see section 1.4.2). Chicks were weighed on day 9 (day 0 = hatching date) to give an indication of fledging weight. Fledging success was expressed as the number of fledglings per egg (f/e), and number of fledglings per nest (see section 1.4.2).

7.2.2. Territory characteristics
(i) Vegetation

Vegetation maps of each territory were plotted using a vegetation map commissioned by the Countryside Commission for Wales. Vegetation was categorised as permanent pasture (including wet pasture), halophytic (including halophytes, and coastal heath), or gorse/bracken. The total area of each vegetation type in each territory was calculated by counting squares on a grid overlay and converting the counts using a measured scale factor into hectares. No direct measure of vegetation height was made but in the following analyses pasture and halophytes are considered as short vegetation whilst gorse/bracken are considered as tall vegetation.

(ii) Food availability

Attempts to estimate invertebrate densities on territories using vacuum sampling proved unsuccessful. Since in a previous study of the wheatear, prey densities at the beginning of the season correlated with those during feeding of the nestlings (Tye 1992), provisioning rates were used as an alternative measure of prey density (the potential confounding effects of parent condition seem to have little effect on chick feeding rates, see sections 6.3.4 and 6.3.5). Mean residuals of total feeds per territory (1991-93) (calculated

from Table 6.1) were used to estimate food availability. An additional stepwise regression was also performed to examine the effect of territory characteristics on provisioning rates. Mean residual per territory of total feeds were entered against territory size, total area of each vegetation type, and male territory settlement rank. The actual areas of vegetation cover were used in this analysis as they are likely to be more important in affecting feeding rates than the proportion of each vegetation type.

The residual values resulting from the stepwise regressions between each dependent behavioural variable and the independent variable were often significantly skewed. Dependent variables were therefore transformed when appropriate (using log transformations). Stepwise multiple regression analyses were performed with F-to-enter values equivalent to p < 0.1 in linear regression (Sokal and Rohlf 1981). Degrees of freedom for F-to-enter values are expressed as $F_{V1,V2}$, where V1 = number of independent variables introduced into the final model and V1 + V2 + 1 = total number of observations. F-to-enter values prefixed with a minus represents a negative association. The robustness of the regression results was tested by "jack-knifing" the variables, i.e. omitting each variable in turn from the analysis to see if the significant variables remained in the regression model.

7.2.3. Territory quality

Three methods have been used to show variation in territory quality in bird populations: (i) non-random variance in either occupancy frequency (Weatherhead and Boag 1986) or reproductive success among territories (Hogstedt 1980, Blancher and Robertson 1985), (ii) a correlation of habitat characteristics with presumed indicators of quality such as occupation frequency (Møller 1982), site shifts (Peterson and Best 1987), and reproductive success (Catchpole *et al.* 1985), and (iii) a correlation of several independent indicators of territory quality related both to preference for and performance in territories (Brooke 1979, Tye 1992). I used (iii) to examine territory quality in this study (see Mathyssen 1990). Due to the inter-correlations between mate, territory, and site fidelity much of the analysis was performed on a yearly basis to avoid pseudo-replication and the complexities of non-independence of data.

7.2.4. Individual condition

As a measure of individual condition, the body condition index (BCI) was calculated for both sexes derived from the regression of log(weight) vs. log(tarsus) (Packard and Boardman 1987, see section 1.4.4). Not all individuals were caught between years and there was an incomplete data base for male BCI in 1993, and female BCI in all years. Due to the limited data set, analyses considering female BCI used data pooled over three years. As an additional measure of male 'quality' in 1991, paternity data were used

(see section 4.3.1), the hypothesis being that levels of extra-pair paternity in broods would correlate negatively with male quality. Paternity data from 1992-93 were excluded due to the nature of experiments carried out in these years (see section 5.2.1).

Males were aged on the basis of plumage characteristics as either first-year breeders or older individuals (Svensson 1984). Females cannot be aged on the basis of plumage and so were aged on the basis of their ringing history. Consequently, the majority of females in 1991 and unringed individuals who returned to the study in subsequent years could not be aged and are excluded from the following analyses.

7.3. Results

7.3.1. Male territory settlement

Males returned and settled earlier than females (Mann-Whitney U-test, return date expressed as days after the 20th March, males vs. females; 1992, z = -4.92, p < 0.001; 1993, z = -3.01, p < 0.002; see Table 7.1). Males settled on a territory soon after arriving on the study area, resulting in a strong correlation between arrival and settlement dates (Spearman rank, male arrival date vs. settlement date; 1991, R_{19} = 0.90, p < 0.001; 1992, R_{23} = 0.92, p < 0.001; 1993, R_{19} = 0.90, p < 0.001).

Early settling unpaired males typically defended large areas on their arrival, in excess of the equivalent of four breeding territories (see also Tye 1992). These males were also frequently found off territory feeding in "communal" areas, often in the presence of migrants (unringed individuals) and other resident males. Territories decreased in size when individuals paired and when other males arrived and as a result there was no effect of settlement date on final territory size (Spearman rank, territory size vs. settlement date; 1991, R_{19} = 0.27, ns; 1992, R_{20} = -0.14, ns; 1993, R_{19} = -0.13, ns). There was also no correlation between male BCI and territory size (Spearman rank; 1991, R_{19} = 0.19, ns; 1992, R_{14} = 0.14, ns; 1993, R_{10} = -0.29, ns). Mean territory size (± se) was 2.13 ± 0.12 hectares.

There was less variation in the rank occupation of territories between years than within years indicating that the pattern of male settlement was consistent during the period of study, (Kruskal-Wallis, H = 48.33, df = 30, p < 0.02; Spearman rank of male territory ranks; 1991 vs. 1992; R_{20} = 0.48, p < 0.05; 1991 vs. 1993, R_{19} = 0.37, p < 0.20; 1992 vs. 1993, R_{19} = 0.55, p < 0.02). There were seven instances between 1992 and 1993 when a returning male could have occupied his territory from the previous year but moved to another. Examining territory changes by males between 1991-92, the settlement ranks from 1991 were used. Territory changes between 1992-93, used mean settlement ranks from 1991-92 thus avoiding the effect of an individuals settlement within that year. Males who changed territories between years usually moved to a territory of a lower rank

(Wilcoxon paired-sign rank, n = 7, T+ = 28, p = 0.014). Two males who moved to territories of a higher rank were unable to settle on their territories from the previous year due to their prior occupation and so settled in unoccupied areas. There were eight instances where a male was seen to temporarily settle in one or two areas before settling permanently. Two males in 1992 were seen to initially settle on territories for which no rank was obtained in 1991. For the remaining six males there was no obvious movement to territories of a lower rank during these samplings (Wilcoxon paired-sign rank, n = 5, T+ = 10.5, p = 0.62). Two moved to nearby areas where a female had recently turned up and four were unable to settle due to the aggression by unpaired neighbouring males. Two of these males had tried to settle in the same area and both failed, however once the neighbouring territorial males had paired up, a third later arriving male was able to settle on this area.

7.3.2. Female territory settlement

There were never any unpaired females during the period of study. Typically on their return they would pair up with an unmated male that occupied their territory from the previous year, or one nearby. Females were rarely observed 'visiting' males on the study area prior to pairing and usually bred in the vicinity of the area in which they had settled initially. Neighbouring unpaired males typically altered their boundaries to accommodate the female. Females were never seen to defend a territory from males but were territorial towards other females.

As with males, female arrival and settlement dates were highly correlated (Spearman rank, arrival date vs. settlement date; 1992, R_{18} = 0.95, p < 0.001; 1993, R_{17} = 0.96, p < 0.001). There was no effect of female settlement date on territory size (Spearman rank, female settlement date vs. territory size; 1992, R_{17} = -0.38, p > 0.2; 1993, R_{17} = 0.24, p > 0.2). Sample sizes were small but there was no indication that BCI affected female arrival time (Spearman rank, R_{13} = 0.04, ns).

The pattern of female settlement was less predictable between years than it was for the males (Kruskal-Wallis, df = 16, H = 20.42, p > 0.1; Spearman rank of female territory ranks 1992 vs. 1993, R_{16} = -0.02, p > 0.1). Female settlement correlated with male settlement in 1993 but not in 1992 (Spearman rank; male settlement rank vs. female settlement rank; 1992, R_{17} = 0.33, p > 0.1; 1993, R_{17} = 0.74, p < 0.002). Four females that could have settled on the same territory as in the previous year settled on one with a lower mean rank. All other switches were to higher ranked territories and were a result of a pair already occupying their territory from the previous year. There were two instances of resident females settling on a territory but then changing and settling on that of a neighbouring male whom they had bred with previously, but who had arrived after the

female. There were also instances of females temporarily associating with resident males but leaving the study area after a few days.

7.3.3. Territory and site fidelity

Fifty-six percent of males from both 1991 and 1992 (14/25 and 10/18, respectively) returned to breed from the previous year. Fifty-seven percent (8) of these returning males in 1992 and 40% (4) in 1993 bred on the same territory, and 79% in both 1992 and 1993 bred within two territories distance of the one they had used previously. The mean distance moved by males between years was 242m. There was no difference in the distance moved between years for males that were paired or unpaired. Males who were paired in previous years (n = 13) moved on average 210m while previously unpaired individuals (n = 4) moved 346m (Mann-Whitney U-test, z = -1.02, ns).

Thirty-six percent (8/22) of females in 1992 and 44% (7/16) in 1993 had also bred in the previous year. Sixty-three percent (5) in 1992 and 44% (3) in 1993 bred on the same territory, and 88% (7) and 71% (5) bred within two territories of the one they had used previously. The mean distance moved between years was 304m. There was no difference in the distance moved by the sexes between years (Mann-Whitney U-test, z = -1.25, p > 0.20). Significantly more males than females returned to the island between 1991-92 and 1992-93 (Chi-squared test, male site fidelity vs. female site fidelity; 1991-92, $X^2 = 14.74$, df = 1, p < 0.001; 1992-93, $X^2 = 4.0$, df = 1, p < 0.05).

Both sexes were more faithful to apparently preferred, lower ranked territories (Mann-Whitney U-test; mean female territory rank, faithful [n = 8] vs. non-faithful [n = 7], z = -1.84, p = 0.06; mean male territory rank, faithful [n = 12] vs. non-faithful [n = 12], z = -2.26, p < 0.03; male and female data combined, faithful [n = 20] vs. non-faithful [n = 19], z = -2.68, p < 0.01). There was no suggestion that territory fidelity was influenced by mate fidelity. Four of the eight site faithful females (50%), and seven of the 12 site faithful males (58%) were paired with different mates. There was no difference in the degree of territory fidelity between the sexes in either 1991-92 or 1992-93 (1992, $X^2 = 0.36$, df = 1, p > 0.5; 1993, $X^2 = 0.07$, df = 1, p > 0.5). Excluding territories that were only used once, there was a turnover of about two males and two females per territory during the three-year study (mean number of males per territory ± se [1991-93] = 2.15 ± 0.19, mean number of females per territory ± se [1991-93] = 2.46 ± 0.18).

Inter-year territory movements had no effect on female reproductive success (f/e or number of fledglings produced) (Wilcoxon paired-sign rank; f/e prior to change vs. f/e after change, n = 7, T+ = 16, ns; number of fledglings prior to change vs. number of fledglings after change, n = 5, T+ = 14, ns). However, inter-year movements had a significant effect on male RS (Wilcoxon paired-sign rank; f/e prior to change vs. f/e after change, n = 9, T+

= 39.5, p < 0.05; number of fledglings prior to change vs. number of fledglings after change, n = 11, T+ = 55.5, p < 0.05). This was due to unpaired males returning the following breeding season, to settle on lower ranked, preferred territories. Males which settled on low ranking territories were more likely to be paired (see section 7.3.5). If unpaired males (n = 4) are excluded from this analysis there was no affect of inter-year movements on either measure of male RS. There was no difference in RS between individuals which were faithful to the territory they bred in previously and individuals which moved between years (Mann-Whitney U-test; f/e (faithful) vs. f/e (non-faithful); male, [n = 11] v [n = 8], U = 23.5, ns; female, [n = 6] vs. [n = 7], U = 13, ns; number of fledglings produced (faithful) vs. number of fledglings produced (non-faithful); male, [n = 11] v [n = 8], U = 41.5, ns; female RS, [n = 6] vs. [n = 7], U = 23.5, ns). Territory infidelity seemed to be a consequence of arrival times, with later arriving individuals being unable to settle on their territory from the previous year.

7.3.4. Mate fidelity

There were seven instances where individuals which had paired previously returned in subsequent years but bred with another (three in 1991-92 and four in 1992-93). Four pairs remained faithful in successive years (three in 1991-92 and one 1992-93). In six cases where an individual returned (five female and one male) their previous partner was already paired nearby. Sample sizes were small but there was no suggestion that either sex improved their RS as a result of the divorce (Wilcoxon paired-sign rank; male RS, n = 3, T+ = 4, ns; female RS, n = 4, T+ = 4, ns). There was no difference in either measure of RS between faithful and divorced pairs (Mann-Whitney U-test: f/e divorced individuals [n = 7] vs. f/e faithful individuals [n = 4], male RS, U = 5, ns; female RS, U = 5.5, ns: number of fledglings produced by divorced individuals [n = 7] vs. number of fledglings produced by faithful individuals [n = 4], male RS, U = 7, ns; female RS, U = 8.5, ns). Divorce seemed to be a consequence of differences in time of settlement and not a result of breeding failure in the previous year.

7.3.5. Male mating status

There were never any unpaired females but between 10-27% of males were unpaired (see Table 7.2). A male's breeding status did not depend on his BCI (Mann-Whitney U-test, paired vs. non-paired; 1991, z = -0.96, ns; 1992, z = -0.17, ns) but on his time of arrival at the study area. Males which arrived early and consequently settled on lower ranked territories were more likely to be paired (Mann-Whitney U-test; 1991, z = -2.20, p < 0.03; 1992, z = -2.28, p < 0.003). There was no difference in territory size between paired and unpaired males (Mann-Whitney U-test, territory size, paired males [n = 52] vs. unpaired males [n = 14], z = -0.55, ns).

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There was an age component in arrival times, with older males returning earlier than younger males (Mann-Whitney U-test; 1991, $z = -2.82$, $p < 0.005$; 1992, $z = -2.82$, $p < 0.005$; 1993, $z = -1.64$, $p < 0.1$; 1991-93, $z = -3.98$, $p < 0.0001$). Old males tended to have larger territories than young males (Mann-Whitney U-test, territory size, old males [n = 39] vs. young males [n = 28], $z = -1.79$, $p = 0.07$) even though there was no correlation between settlement date and territory size (see above). Unpaired males tended to be individuals returning to breed in their first year (Mann-Whitney U-test, male age vs. pairing status [paired or non-paired]; 1991, $z = -2.55$, $p < 0.02$; 1992, $z = -3.07$, $p < 0.03$). Ten of the 11 unpaired males (excluding a male who was unpaired in successive years) were first-year individuals and occurred on just six territories. The fact that these males were unpaired was not a consequence of them returning after the females. In 1992 the majority of arriving females were free to choose because on average only 11% (range 0-50%) had returned by the time these males had acquired a territory (data from 1991 are not considered due to an incomplete data set on female settlement). There was a weak suggestion that unpaired first year males arrived later than paired first year males (mean settlement rank of paired first- year males = 8.87 ± 0.80, mean settlement rank of unpaired first-year males = 11.25 ± 1.25; Mann-Whitney U-test, settlement date of unpaired [n = 15] vs. paired [n = 8], $z = -1.56$, $p < 0.10$).

Anecdotal evidence also suggests that arrival time influences a male's mating status. There were three examples of unpaired males which returned relatively earlier the following year and bred on other territories. A male who arrived late in 1993 occupied a high ranking territory and remained unpaired, although having previously bred in both 1991 and 1992.
If male and territory quality are correlated one would expect early arriving males to have low levels of EPP in their own broods and possibly to gain EPP in the nests of other males if females are seeking good genes. Sample sizes were small and not all fathers were identified so the latter possibility cannot be tested (see section 4.3.2). However, in 1991 there was no effect of male arrival time on brood paternity (Mann-Whitney U-test, rank of male arrival vs. broods with or without extra-pair young [EPY], $z = -0.28$, ns; n = 5 and 12 respectively for broods with or without EPY).

Although one unpaired male occupied the same territory in two successive years, in all other cases the territories associated with unpaired males were either not used or were occupied by different individuals in subsequent years. There were proportionately more unpaired males at higher densities and when the sex ratio was more male biased (see Table 7.2). Apparently less preferred, higher ranked territories were occupied less often by males during the study (Spearman rank, number of years occupied vs. mean male rank, $R_{27} = -0.55$, $p < 0.005$) and experienced proportionately fewer actual breeding attempts (Spearman rank, breeding score (number of years bred upon/number of years occupied) vs. mean male rank, $R_{27} = -0.65$, $p < 0.001$) (see Table 7.3).

7.3.6. Adult survivorship

There was no indication that individuals were more likely to survive between years if they had previously settled on a low ranking territory (Mann-Whitney U-test, rank of territory individuals returned vs. rank of territory individuals did not return; male survival 1991-92, n =13 vs. n =7, z = -0.26, ns; 1992-93, n =13 vs. n =10, z = -0.34, ns. Female survival, 1991-92, n = 7 vs. n = 10, z = -0.74, ns; 1992-93, n = 10 vs. n = 7, z = -0.44, ns). There was no age component in male survivorship between years. Old individuals were just as likely to return to breed in subsequent years as were young males (Mann-Whitney U-test, survival between years vs. male age (young vs. old), 1991-92, n = 11 vs. n = 14, z = -1.37, ns; 1992-93, n = 13 vs. n = 11, z = -1.10, ns).

Male condition as measured using the BCI varied between years. There was no correlation in male BCI between years (Spearman rank, $R_{10} = 0.17$, ns), or in male arrival times between years (Spearman rank, $R_{17} = 0.18$, ns [taking into account the tendency of first-year breeders to return earlier in subsequent years]). As a result there was no age component in male condition (Mann-Whitney U-test, male age vs. BCI; 1991, z = -0.17, ns; 1992, z = -1.44, ns; 1993, z = -0.94, ns). There was also no indication that BCI determined future survival (Mann-Whitney U-test, returned males vs. non-returned; 1991 [n = 15] vs. 1992 [n = 7], z = -1.13, ns; 1992 [n = 7] vs. 1993 [n = 8], z = -0.81, ns), or settlement date (Spearman rank; 1991, $R_{18} = -0.04$, ns; 1992, $R_{14} = -0.29$, ns; 1993, $R_{10} = -0.52$, p > 0.1).

7.3.7. Reproductive success
(i) Clutch size

There was no indication that female BCI influenced clutch size or laying date (Spearman rank; female BCI vs. clutch size, $R_{28} = -0.12$, ns; female BCI v FED rank, $R_{28} = -0.08$, ns).

There was about a three-week delay between female settlement and laying (n = 34, mean = 25.24 ± 1.49 days, range 14 to 46 days) with there being a shorter delay for later settling females (Spearman rank, [FED - female settlement date] vs. female return date; 1992, $R_{17} = -0.49$, p < 0.05; 1993, $R_{17} = -0.50$, p < 0.05). Later laying females laid smaller clutches (Spearman rank, clutch size vs. FED; 1991, $R_{19} = -0.61$, p < 0.01; 1992, $R_{17} = -0.62$, p < 0.02; 1993, $R_{17} = -0.45$, p < 0.1; 1991-93 data combined, $R_{54} = -0.53$, p < 0.001; see Table 7.4). Lower female ranked territories tended to have earlier FEDs (Spearman rank, FED vs. female territory rank; 1992, $R_{17} = 0.65$ p < 0.01; 1993, $R_{17} = 0.44$, p < 0.10) but there was no consistent indication that lower ranked territories had larger clutch sizes (Spearman rank; clutch size vs. male territory rank; 1991, $R_{16} = -0.12$, ns; 1992, $R_{17} = -0.62$, p < 0.02; 1993, $R_{17} = -0.04$, ns; clutch size vs. female territory

rank; 1992, R_{17} = -0.61, p < 0.02; 1993, R_{17} = -0.05, ns), although the mean clutch size tended to be smaller on less preferred territories (see Table 7.3). Females cannot be aged on the basis of plumage characteristics but the pattern of female settlement was similar to that of the males. Old females showed some tendency to return earlier than young females (Mann-Whitney U-test, return date vs. female age [old, n = 14 vs. young, n = 9], z = -1.87, p = 0.06). Smaller clutch sizes on higher ranked territories may therefore be influenced by the individual's age. The mean clutch size (± se) of first year breeders was 5.44 ± 0.24 (n = 9), old females = 6.07 ± 0.14 (n =14) (Mann-Whitney U-test, clutch size vs. female age, z = -2.09, p < 0.05), although all seven females which bred in successive years and which were known to be one-year old in the first year laid identical clutch sizes.

(ii) Fledging success

There was no significant seasonal decline in either measure of fledging success (number of fledglings per nest or f/e) which has been observed in other avian studies e.g. tits and wheatears (Perrins 1971, Brooke 1979), if data for the three years were considered separately (Spearman rank: number of fledglings vs. FED; 1991, R_{20} = -0.38, p < 0.1; 1992, R_{17} = -0.35 p > 0.1; 1993, R_{17} = -0.36, p > 0.1: f/e vs. FED; 1991, R_{20} = -0.08, ns; 1992, R_{17} = 0.21, ns; 1993, R_{17} = -0.02, ns). However, if the data were combined for all years there was a seasonal decline in the number of fledglings produced per nest, but not in chick survival to fledging (Spearman rank; number of fledglings vs. FED, n = 53, z = -3.85, p < 0.0001; f/e vs. FED, n = 53, z = -0.98, p > 0.3; see Table 7.4).

There was no correlation between fledging success and male territory rank or in the number of fledglings produced per territory (Spearman rank, fledging success vs. male territory rank; 1991, R_{16} = -0.12, ns; 1992, R_{16} = -0.05, ns; 1993, R_{16} = 0.06, ns; number of fledglings vs. male territory rank; 1991, R_{16} = -0.31, p > 0.1; 1992, R_{16} = -28, p > 0.1; 1993, R_{16} = -0.07, ns). On average, more offspring were fledged and fledging success was higher on preferred territories, but not significantly so (Table 7.3).

There was no effect of male BCI on RS (Spearman rank, male RS vs. BCI, R_{41} = 0.03. ns). Old males tended to fledge more offspring than first-year breeders (Mann-Whitney U-test vs. RS young male (n = 17) vs. RS old male (n = 36), z = -1.70, p = 0.09), and this was not an artifact of old males breeding earlier (Mann-Whitney U-test, FED young male (n = 17) vs. FED old male (n = 36), z = -1.0, ns).

(iii) Fledgling recruitment

Recruitment data were available for two years, 1991-92 and 1992-93. 17 fledglings (nine females, eight males) from 11 different territories (14 putative fathers) were either recruited to the population or observed to visit the study area temporarily, nine from 1991

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(11.1% of chicks ringed) and eight from 1992 (7.6% of chicks ringed). Accurate breeding data were available for 12 of these nests.

There was no correlation between fledgling recruitment and male age or BCI (Mann-Whitney U-test; male age, recruits [n = 12] vs. no recruits [n = 36], z = -0.37, ns; male BCI, recruits [n = 12] vs. no recruits [n = 36], z = -1.56, ns). There was also no effect of FED (Mann-Whitney U-test, FED of nests with recruits [n = 10] vs. FED of nests with no recruits [n = 27], z = -0.24, ns; see Table 7.4) or chick weight (Mann-Whitney U-test, mean weight of recruits [n = 12] vs. mean weight non-recruits [n = 109], mean chick weight of recruits = 24.23 ± 0.78g, mean chick weight of non-recruits = 23.73 ± 0.31g, z = -0.52, ns) on subsequent fledgling recruitment. More recruits fledged from territories with a lower mean rank (excluding territories associated with unpaired males) (Mean rank of territory with recruits = 4.40 ± 0.61, Mean territory rank no recruits = 8.41 ± 0.82; Mann-Whitney U-test, z = -2.99, p < 0.003; Table 7.3). This was possibly a consequence of low ranked territories being used in more years of the study. However, when the number of years a territory was used for breeding was controlled for (number of recruits per territory/number of years used for breeding), preferred territories still fledged more recruits (Mann-Whitney U-test, z = -2.34, p < 0.02; Table 7.3).

7.3.8. Territory characteristics

Territory size was not influenced by male characteristics or breeding chronology (see above). Larger territories had a greater area of short vegetation, principally due to the larger territories containing more pasture (Table 7.5). Male and female settlement patterns did not consistently correlate with either total area or percentage cover of any vegetation type (Table 7.6).

(i) Food availability

There was no effect of territory size, male territory rank or area of gorse/bracken (tall vegetation) on provisioning rates (unpublished data), but there was a weak suggestion that provisioning rates were higher on territories containing a larger area of short vegetation ($F_{1,41} = 3.67$, p < 0.10). Further analysis revealed the area of halophytes and not the area of pasture accounted for this correlation (area of halophytes, $F_{1,41} = 7.25$, p < 0.01; area of pasture $F_{1,41} = 0.12$, ns).

There was no indication that lower ranked territories were associated with higher provisioning rates. There was no difference in the mean residuals for total feeds (calculated from chapter 6) between preferred (n = 13) and non-preferred territories (n = 4) (Mann-Whitney U-test, z = -0.11, ns). As an additional measure of food availability mean chick weights were also compared between preferred and non-preferred territories (mean chick weight ± se: preferred territories = 24.64 ± 0.48g (n = 39 broods), non-preferred territories
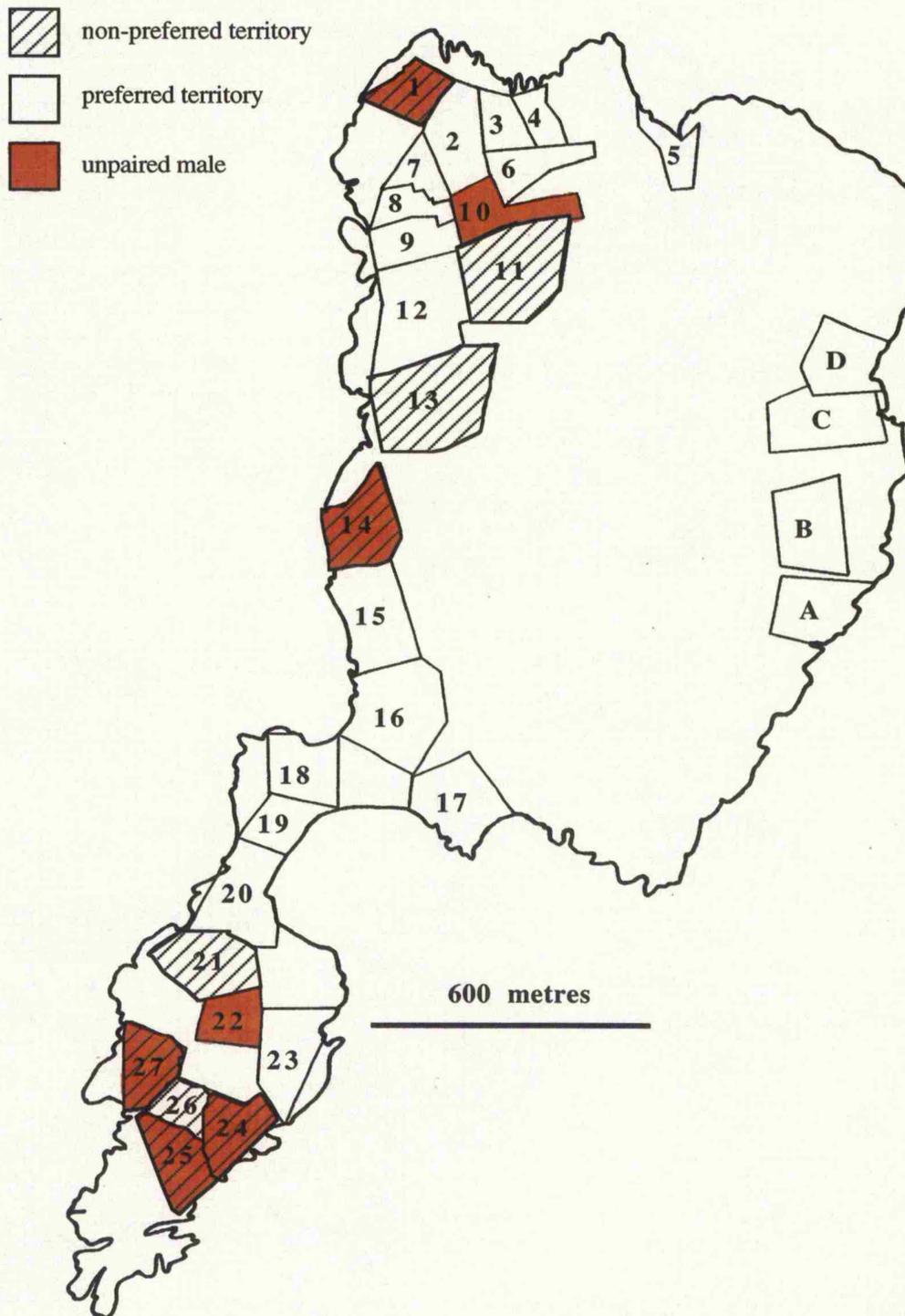
Fig. 7.1. Territory map for the 1991 breeding season. The map highlights preferred territories, non-preferred territories, and those occupied by unpaired males. Territories A - D were not considered in the study.
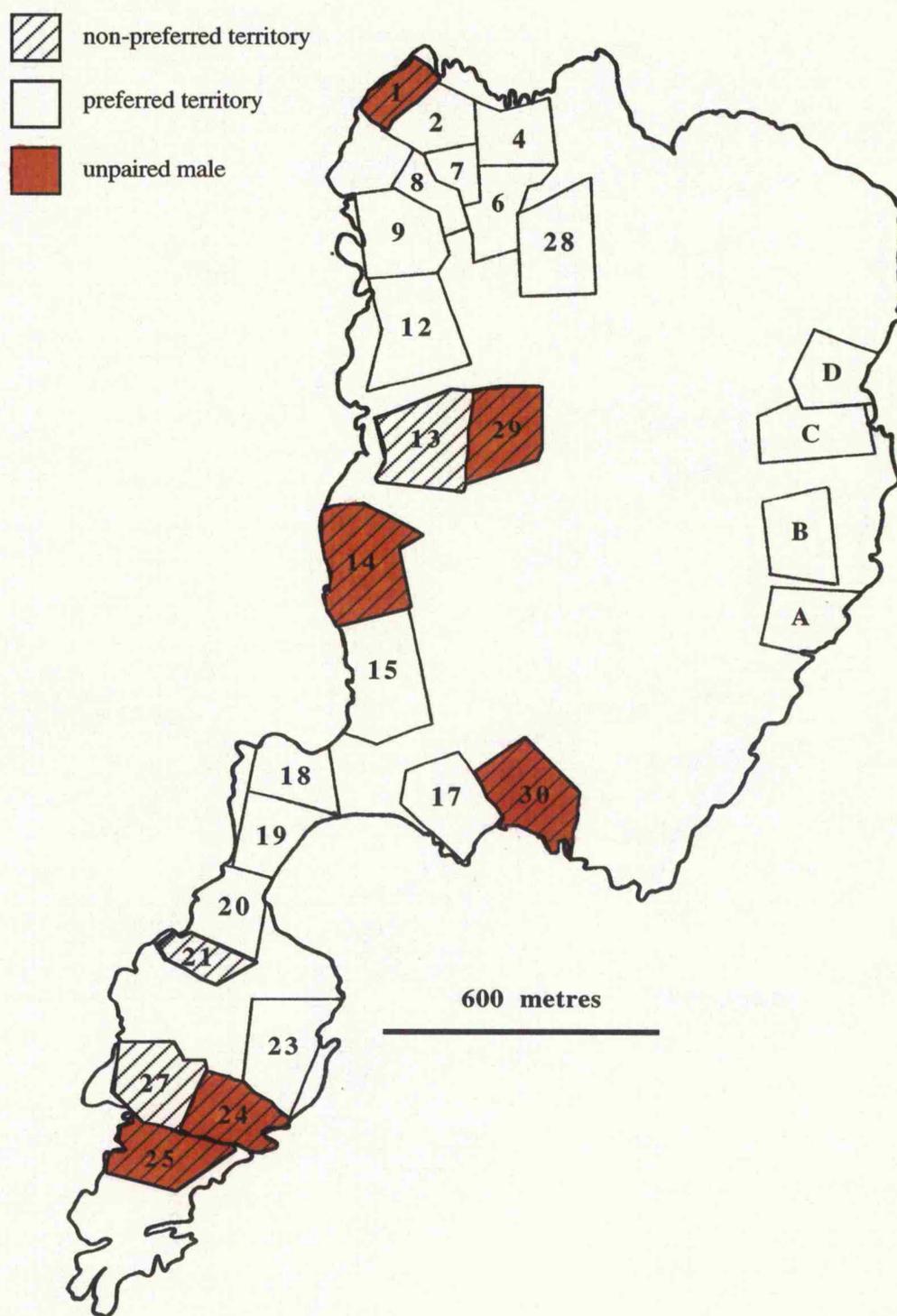
Fig. 7.2. Territory map for the 1992 breeding season. The map highlights preferred territories, non-preferred territories, and those occupied by unpaired males. Territories A - D were not considered in the study.
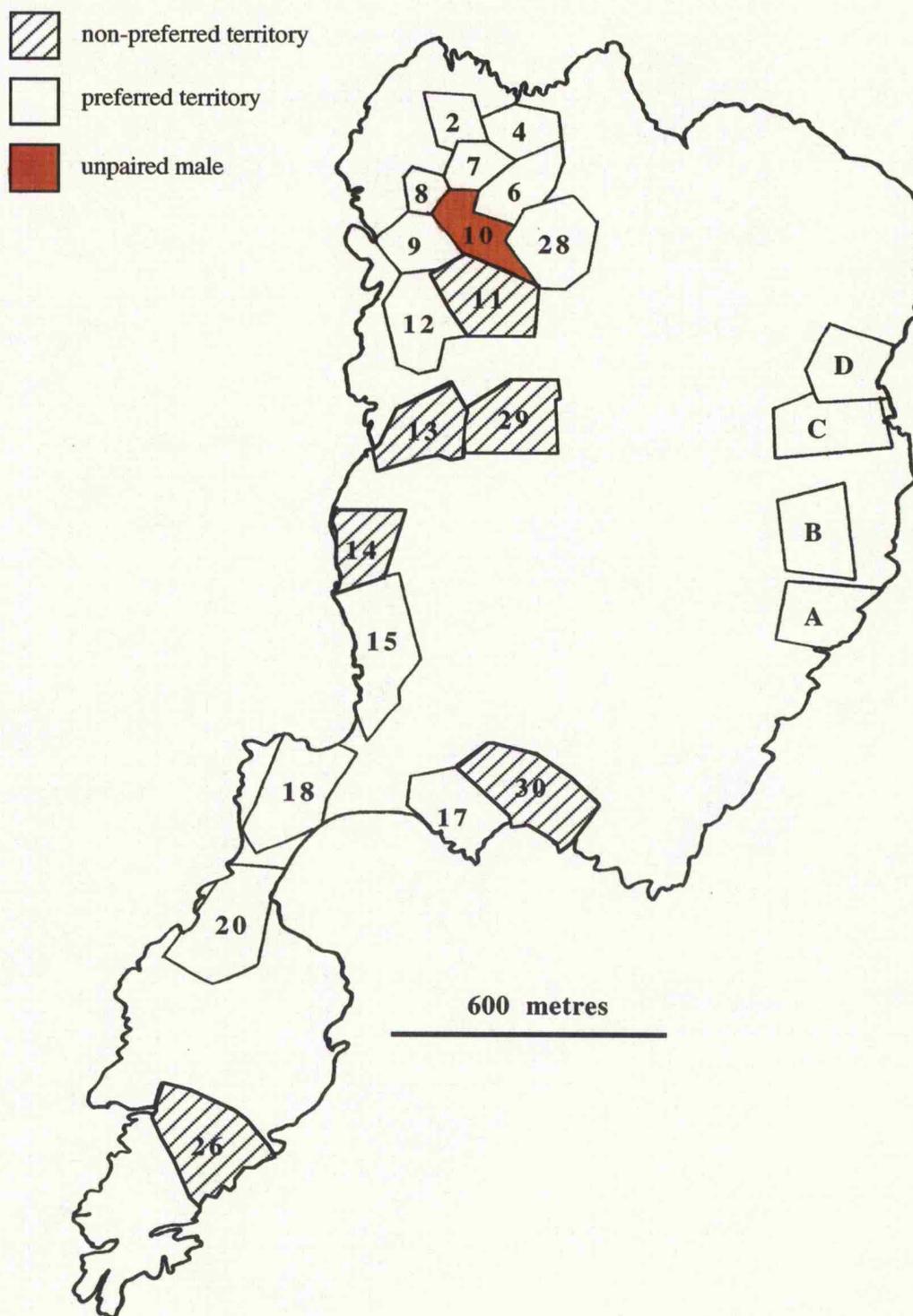
Fig. 7.3. Territory map for the 1993 breeding season. The map highlights preferred territories, non-preferred territories, and those occupied by unpaired males. Territories A - D were not considered in the study.

Table 7.1. Mean arrival dates (± se) (expressed as days after 20th March) for all males, paired males, unpaired males and females.

Year	All males	Paired males	Unpaired males	Females
1991	10.00 ± 1.64	8.65 ± 1.50	21.50 ± 2.45	-
1992	14.52 ± 1.76	11.69 ± 1.93	21.00 ± 2.45	26.29 ± 3.32
1993	13.11 ± 2.00	12.71 ± 2.08	20*	19.72 ± 2.22

*n = 1

Table 7.2. The number of resident females and males, sex ratio (females:males), number of first-year and older males (1 year +), and percentage of males unpaired (%NP) in each of the study years. Numbers of unpaired males in each age class are in parentheses.

	No. females	No. males	Sex ratio	1st year males	Old males	%NP
1991	20	26	0.77	13 (7)	13 (0)	27
1992	17	23	0.74	9 (5)	15 (1)	23
1993	17	19	0.90	7 (0)	12 (1)	5

Table 7.3. Breeding data for preferred and non-preferred wheatear territories (1991-93). Table shows mean values ± se

	Preferred	Non-preferred	
Mean no. years used[1]	2.60 ± 0.24	1.18 ± 0.35	**
Breeding score[2]	0.93 ± 0.70	0.51 ± 0.11	**
Mean FED rank	5.95 ± 0.75	7.92 ± 0.47	*
Mean clutch size	6.07 ± 0.10	5.54 ± 0.32	†
Fledging success (f/e)	0.80 ± 0.07	0.70 ± 0.15	ns
Mean no. fledglings	4.83 ± 0.37	4.04 ± 0.50	ns
Mean no. recruits	0.80 ± 0.19	0.18 ± 0.15	**
Mean no recruits/no. years bred[3]	0.29 ± 0.05	0.09 ± 0.09	*

Mann-Whitney U-test; ns $p > 0.10$, † $p < 0.1$, * $p < 0.05$, ** $p < 0.01$.

[1] Sample sizes for mean number of years used; preferred territories (n = 13), non-preferred (n = 15). Samples sizes for other breeding data; preferred territories (n = 13) and non-preferred territories (n = 4).

[2] Number of years bred upon/ number of years occupied.

[3] Study was for three years but only two years of recruitment data were available.

Table 7.4. Breeding data for early (n = 32) and late (n = 21) breeding wheatear territories (1991-93). Table shows mean values ± se.

	Early	Late	
Mean clutch size	6.17 ± 0.11	5.13 ± 0.15	**
Fledging success (f/e)	0.82 ± 0.06	0.67 ± 0.09	ns
Mean no. fledglings	5.00 ± 0.36	3.50 ± 0.49	*
Mean no. recruits	0.35 ± 0.10	0.19 ± 0.08	ns

Mann-Whitney U-test; ns $p > 0.1$, † $p < 0.1$; * $p < 0.05$; ** $p < 0.01$.

Table 7.5. Spearman rank coefficients for relationship between territory size and vegetation characteristics of the territory.

Territory size vs.	1991 (R_{20})	1992 (R_{23})	1993 (R_{19})
Total area of short vegetation	0.75*	0.63*	0.50*
Total area of tall vegetation	-0.10	0.12	-0.29
Area of pasture	0.56*	0.57*	0.45†
Area of halophytes	0.14	-0.06	0.06
% short vegetation	0.20	0.51*	0.55*
% tall vegetation	0.11	0.16	-0.23
% pasture	0.22	-0.03	0.06
% halophytes	0.10	-0.23	0.06

Levels of significance: † $p < 0.1$, * $p < 0.05$

Table 7.6. Spearman rank coefficients for relationship between male and female settlement rank and total area and percentage cover of vegetation types.

	1991	1992		1993	
Settlement rank vs.	male(R_{20})	male (R_{23})	female (R_{17})	male (R_{19})	female (R_{17})
Area of short vegetation	0.01	-0.05	0.35	-0.08	-0.06
Area of tall vegetation	0.14	-0.18	-0.36	-0.14	-0.28
Area of pasture	0.02	-0.38†	0.16	-0.27	-0.36
Area of halophytes	-0.11	0.42†	0.13	-0.11	0.29
% short vegetation	0.58*	0.02	0.21	-0.33	0.15
% tall vegetation	-0.45†	0.06	-0.13	0.14	-0.15
% pasture	0.72**	-0.04	0.22	-0.13	-0.31
% halophyte	-0.40	-0.02	-0.07	0.17	0.35

Levels of significance: † $p < 0.1$, * $p < 0.05$, ** $p < 0.01$

Table 7.7. Nest hole characteristics: aspect and wind direction (1st April to 31st May, 1991-93), percentages in parentheses.

Direction hole faces	No. Nests	Days of wind
N	7 (12.7)	31 (17.3)
NW	14 (25.5)	21 (11.7)
NE	12 (21.8)	25 (14.0)
E	8 (14.6)	12 (6.7)
SE	2 (3.6)	15 (8.4)
S	4 (7.3)	34 (19.0)
SW	3 (5.5)	39 (21.8)
W	5 (9.1)	2 (1.1)

= 24.18 ± 0.91g (n = 9 broods); Mann-Whitney U-test, z = -0.38, ns).

(ii) Nest holes

The number of suitable nest holes was partly limited by the activities of rabbits and Manx shearwaters. Although wheatears typically selected holes with entrances too small for larger vertebrates to gain access, there were three definite instances of shearwaters gaining access to and destroying nests and possibly contributing to the desertion of another two. There was an extreme case when a Manx shearwater was found sitting on a brood of 10-day old wheatear chicks. Starlings were also observed attempting to gain access to the nest hole and in one instance an individual was observed removing the chicks and destroying the nest on three occasions.

The majority of nests in the study area were in stone walls (45/50). A greater number of potential nest holes are provided on territories with longer walls, however there was no suggestion that wall length correlated with either male or female settlement patterns (Spearman rank, male settlement vs. wall length: 1991, R_{20} = -0.21, ns; 1992, R_{14} = -0.10, ns; 1993, R_{10} = -0.05, p < 0.2; female settlement; 1992, R_{17} = -0.29, ns; 1993, R_{17} = -0.13, ns). There was some evidence for nest sites being traditional in the 18 territories that were bred upon more than once during the duration of the study, the same nest hole being used on average 56% of the time. On six of these territories (33%), the same hole was used in each of the three successive breeding seasons, even if the pair changed. Although males frequently advertised potential nest holes during the pre-pairing period via a grass carrying display (in four instances males were observed to advertise nest holes and although not used that year they were used in subsequent years), there was no suggestion that the nest hole was a basis of male or female choice (Mann-Whitney U-test, [number of years hole used/ number years breeding attempt occurred] vs. preferred or non-preferred territories, z = -0.77, ns; n = 13 and 5 for preferred and non-preferred territories, respectively).

The wind direction between the 1st April and 31st May (1991-93) mainly came from the south, while the majority of nest holes tended to face in the opposite direction (see Table 7.7). There was no effect of nest hole direction on male settlement date (Kruskal-Wallis, df = 6, H = 10.69, ns), female settlement date (Kruskal-Wallis, df = 6, H = 4.28, ns) or reproductive success (Kruskal-Wallis, df = 6, H = 7.19, ns).

7.4. Discussion

7.4.1. Distribution of territories

Although the wheatear is a migrant species territories remained remarkably constant between years (see also Brooke 1979). Recorded annual adult mortality in this study (44.0% in males, 59.9% in females) was similar to the 45% for both sexes recorded by

Brooke (1979). Of the returning individuals in this study, a high proportion, about 50% (48.5% of males, 52.7% of females), bred on the same territory as in the previous year. However, fidelity is unlikely to fully explain the constancy of territories between years as there was a turnover of about two males/females per territory during the three-year study. Additionally, although not part of an intensive study, maps showing nest sites were available from previous years (1984-85) (P. Jenks, pers. comm.). There was considerable overlap in the location of nests and territories mapped out in this study, suggesting that territories remained constant for even longer periods of time.

Males typically appear at the site of breeding earlier than females in order to compete for access to the resources essential for reproduction or mate acquisition (Lack 1954). Wheatears conform to this pattern and males set up and defended territories on their arrival from which the majority of food for the pair and dependent young was collected (see also Brooke 1979, Conder 1989, Tye 1992). Since territories were originally selected by the males, and females rarely settled in the absence of a male (see also Tye 1992), the constancy of territories is likely to be a consequence of male settlement behaviour and the availability of suitable habitat (Brooke 1979).

7.4.2. Territory settlement

There was good evidence that some territories were preferred by both sexes irrespective of fidelity by individuals in successive breeding seasons. There was a consistent male settlement pattern on territories between years (less so in females) and a significant correlation between mean male and female territory ranks. This predictable settlement on territories between years indicates that either individuals recognise variations in quality and adjust their pattern of settlement accordingly (Brooke 1979, Møller 1983), or that there are traditional settlement patterns (Warner 1988). Given the opportunity, both sexes moved to preferred, lower ranking territories between years. All movements to higher ranked territories were due entirely to more preferred areas being occupied when individuals returned from their wintering grounds. Both sexes were more faithful to lower ranking territories between years, irrespective of the presence of their previous partner, and higher ranking territories were less frequently occupied and experienced fewer breeding attempts (see also Brooke 1979, Mathyssen 1990). Higher rates of occupancy, territory shifts and higher fidelity to lower ranked areas indicate that some aspect of territory quality influenced the order of settlement. Male territory acquisition early in the breeding season was also affected, to a lesser degree, by whether or not already resident territorial males were paired, because paired males were less aggressive towards neighbours. In this study, female settlement patterns were less consistent than those of the males (but see Tye 1992, cf. Alatalo *et al.* 1986). This may have been a result of only having two years' data, but may also have been a consequence of confounding variables, in particular mate choice and

mate fidelity.

Arrival time determined the pattern of territory settlement, with later arriving individuals settling on low quality territories. This has two potentially opposite consequences for territory size. Later arriving males may find most of the suitable habitat occupied and be forced to take a smaller territory or they may be forced into poorer habitat and require a larger territory (Tye 1992). There was no effect of arrival date on territory size in this study. Arrival times (and territory quality) also influenced a male's mating status, with early arriving individuals being more likely to be paired (see also Alatalo *et al.* 1984, Arvidsson and Neergaard 1991). All unpaired males were late arrivals (usually first-year breeders, although late arriving old males also remained unpaired) and were concentrated on six high ranking territories. These males did not remain unpaired because they returned to the study area after the females. If arrival times reflect an individual's quality, then females may be choosing good quality males as well as good territories (Møller 1994). The additive effect of arrival times and territory quality on a male's mating status was more acute in years with a high population density and a male-skewed sex ratio. The range of habitats occupied by a bird species has been shown to be influenced by population density, with optimal habitats being occupied at low densities and sub-optimal ones at high densities (Møller 1982 and references therein). In this study, high ranking territories occupied in high density years were either not utilised or incorporated into other territories in years with a smaller breeding population, indicating that lower quality areas were only used in higher density years. Furthermore, as sub-optimal territories were also occupied at high densities, female mate choice may also be more acute as a result of having a greater number of males to choose from.

Male quality has been measured in a variety of different ways, e.g. (i) display rates and song repertoire size (e.g. Catchpole *et al.* 1985, Catchpole 1986, McGregor *et al.* 1981, Lambrecht and Dhondt 1986); (ii) age (e.g. Best 1977, Weatherhead 1984), (iii) plumage characteristics (e.g. Jarvi *et al.* 1987, Norris 1990, Møller 1991a, b) and (iv) measures of body condition (e.g. Møller 1988, Mather and Robertson 1992, Lens 1994). There has been much discussion in the literature as to the relationship between such measures of male quality and territory quality, with some studies showing a correlation between these two factors (e.g. Best 1977, Catchpole *et al.* 1985, Askenmo 1984), but others show it to be lacking (e.g. Searcy 1979, Davies and Lundberg 1985, Lambrechts and Dhondt 1988, Norris 1990). Møller (1994) observed that in the barn swallow, a species in which most food is collected off territory, there was no consistency in territory quality between years, and male quality accounted for female settlement patterns. One would expect territory quality to be a more important factor affecting male and female settlement patterns in those species such as the wheatear which utilise an all-purpose territory. Both Slagsvold (1986) and Alatalo *et al.* (1986) showed convincingly, in their

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respective studies of the pied flycatcher, that territory quality was more important than male quality in accounting for female settlement patterns. However, they still could not exclude the hypothesis that female settlement patterns were also influenced by male quality.

Three alternative measures of male quality were used in my study: (i) the body condition index (BCI); (ii) levels of extra-pair paternity (EPP); and (iii) male age. There was no correlation between settlement dates and BCI or levels of EPP in broods, as might have been expected if male and territory qualities were linked. Also, females were never observed sampling males or territories prior to settling, so implying that this was a rapid event happening soon after their arrival. The ability to defend a large area of suitable habitat may be used by a female as a measure of male quality (Brooke 1979, Hamilton and Zuk 1982, Kodric-Brown and Brown 1984), but there was no effect of female settlement date or male BCI on territory size, supporting the idea that territory quality was more important than male quality (as measured using the BCI or levels of EPP) in influencing female territory settlement. However, female settlement patterns could be explained in part by their preferentially pairing with older males (possibly last year's partner), the majority of unpaired males being first-year individuals. Age can be considered to be another measure of male quality, because older males have proved their ability to survive (see Brooke 1979, Askenmo 1984, Weatherhead 1984). Old and young males can be differentiated in the field on the basis of conspicuous plumage characteristics (Svensson 1984). This could be a reliable indicator to females of individuals who had returned between years, which one might expect to be an important factor in female mate choice, especially in a migrant species.

There was a strong effect of age on arrival times in both sexes, with older individuals arriving earlier than those returning to breed in their first year (see also Conder 1989). As a result of arriving earlier, older males are able to acquire better quality territories than young males (see also Dhondt and Huble 1968, Brooke 1979, Yasukawa 1980, Jarvi 1983), which could explain the lack of unpaired older males observed in this study. There were insufficient first-year males among early arriving individuals to make it possible to distinguish whether female settlement patterns were influenced by male age or territory quality (female settlement data were only available for 1992-93). However, females paired to the few early arriving first-year males were never observed to repair with single later arriving older males, and there was also no effect of male age on the frequency of EPP within broods (see section 4.3.3). This further supports the idea of territory quality as opposed to male quality being important in influencing female settlement patterns.

Arrival times may also be influenced by stochastic factors, such as weather conditions (Møller 1989), potentially confounding any correlation between arrival dates, male and territory qualities, and accounting for differences in the order of settlement between the sexes due to females choosing males rather than territories. Another potential

confounding variable, mate fidelity, was unlikely to affect female settlement patterns due to its low frequency between years. Mate fidelity was probably a consequence of territory fidelity as there were never any instances of fidelity between individuals other than on territories bred on together from the previous year. There were only four instances of mate switching after initial pairing (two by females and two by males, three of which involved individuals separating to pair with their partner from the previous year).

A male wheatear's mating status appeared to be dependent upon territory quality, his arrival time, and the operational sex ratio. There was no evidence that female settlement patterns were influenced by male quality, as measured using the BCI and levels of EPP in broods in relation to arrival times. The BCI has been shown in the crested tit to be a good measure of male quality, where males with a low BCI responded less to female solicitations and were more likely to have EPP in their nest (Lens 1994). It is perhaps not surprising that male condition varied between years in a migrant species, probably being dependent on conditions experienced during migration and at their winter quarters (Møller 1989c). Conclusions regarding the effect of male age on female settlement patterns are more ambiguous due to the unresolved correlation between age, arrival times and territory quality. In the pied flycatcher, there is some suggestion that male quality may be more important than territory quality in determining female settlement patterns in a homogeneous environment (Lifjeld and Slagsvold 1988). In this study, there was good evidence that there was variation in territory quality (as indicated by predictable settlement patterns, territory fidelity and individuals moving to preferred territories between years whenever possible, see section 7.4.1) This suggests that the study area can be considered to be a heterogeneous habitat, and therefore territory quality is likely to be more important than male quality in affecting female settlement patterns.

7.4.3. Benefits of settling on preferred territories

Given the predictable pattern of settlement between years, one would expect benefits for individuals which settled on preferred territories. There was no suggestion that individuals which occupied low ranking territories survived any better between years than those which occupied high ranking territories. Benefits to individuals of settling on low ranking territories were associated with mating and reproductive success.

Male mating status depended upon arrival times and their settling on preferred territories. Individuals which settled on high ranking territories were less likely to be paired. Female mating status was unaffected by territory quality as there was a male skewed sex ratio in each of the of study years and females were unable to settle on the same territory as another female due to inter-female aggression (pers. obs).

There was about a three-week delay (14-46 days) between females arriving and laying. (18-40 days, Brooke 1979: 13-61 days, Tye 1992: 18-40 days, Conder 1989).

Brooke (1979) suggested that this delay was required for ovarian development, but due to the variable period between female arrival and first egg dates (FEDs), Tye (1992) argued that the time needed to build up sufficient energy reserves for egg laying made the length of the delay dependent on the availability of food on a territory (the delay being shorter on preferred territories). In this study this delay was shorter for later returning females, which tended to lay smaller clutches. Birds time their breeding to coincide with maximum food availability (e.g. Lack 1954, Perrins 1971, Conder 1989). Food abundance is not necessarily a major determinant of clutch sizes (Davies and Lundberg 1985, Conner *et al.* 1986) and the shorter delay on less preferred territories may be a trade-off between building up energy reserves and breeding early, rather than due to aspects of territory quality limiting clutch sizes. Later arriving females may have to breed more quickly to coincide with this peak. Smaller clutch sizes on higher ranking territories could also be due to younger, later arriving females laying smaller clutches (e.g. Perrins and McCleery 1985).

Although pairs which bred on preferred territories had earlier FEDs, individuals did not accrue the benefits normally associated with this, as in this study there was no seasonal decline in reproductive success during the breeding season (but see Perrins 1971, Brooke 1979). More fledglings were produced at early nests but measuring reproductive success as the number of fledglings per egg (f/e), the seasonal effect observed in fledging success observed in some studies (e.g. Brooke 1979) may be a consequence of later laying females laying smaller clutches.

Differential breeding success may reflect differences in parental quality (Goodburn 1991), although in some circumstances such differences are outweighed by the effects of habitat quality (Hogstedt 1980). There was no effect of male BCI or age on reproductive success, and reduced fledging success in this study was usually the result of a failure of the eggs to hatch (7.1% eggs in 20.8% of broods), or starvation of chicks as a result of reduced provisioning rates during prolonged periods of bad weather (5.5% chicks in 16.9% of broods). Female predation, nest desertion and flooding accounted for the other nest failures. Reproductive success was higher on preferred territories though not significantly so. Food availability has been shown to influence the production of nestlings (Conner *et al.* 1986) and less preferred territories may be associated with less food.

The recruitment probability of fledgling birds has been shown in the great tit, blackbird and barn swallow, to be determined by nestling body mass and time of breeding (fledglings from later nests are less likely to be recruited to the population) (e.g. Perrins 1965, 1979, Magrath 1991, Møller 1994, 1995). In this study, recruits were more likely to fledge from low ranking territories, irrespective of chick weight, time of breeding, male age and body condition.

7.4.4. Choice of territories

Tye (1992) convincingly showed that vegetation structure and its effect on prey densities influenced the pattern of territory settlement in the wheatear. Prey densities were highest on short vegetation, and he argued that individuals of both sexes (although his analysis only concerned male settlement) used the latter as a measure of territory quality at the time of arrival. In contrast to this, individuals in this study did not appear to use vegetation as a measure of territory quality, since there was no correlation between either male or female settlement and vegetation type.

The feeding technique of the wheatear has been termed as "dash and grab" and is best suited to short vegetation (Tye 1992 and references therein). No measure was made of adult feeding frequencies and foraging success on different vegetation types, but higher provisioning rates were observed on territories containing more short vegetation, in particular halophytes. Territory size is expected to vary with the quantity and quality of food resources required for egg formation and the successful rearing of offspring (Hinde 1956). In Tye's (1992) study, territory size correlated with the amount of long vegetation, possibly as a means to compensate for low prey densities. In this study, territory size correlated with the area of pasture (assumed to be short vegetation). There was no indication that this was a means to compensate for less halophyte vegetation (Spearman rank, area of pasture vs. area of halophyte, $R_{42} = -1.01$, ns). The reasons for the apparent discrepancy between the two studies are not resolved.

There were no differences in either provisioning rates or chick weights between preferred and non-preferred territories. This suggests that there was little difference in food availability between territories, however provisioning rates may not necessarily give an accurate indication of food availability in this analysis since the observations were biased towards lower ranking, preferred territories. These territories experienced more breeding attempts and any differences in food availability between preferred and non-preferred territories might therefore not have been detected. Six high ranking territories were never used for breeding. Tye's (1992) extensive study provides convincing evidence that individuals assessed the quality of an area from its vegetation structure. The findings from this study run contrary to the majority of his findings. Possible reasons for these differences are the uniformity in Bardsey territories in vegetation structure (due to uniform grazing by herbivores, primarily sheep, horses and rabbits), a less detailed analysis, and fewer territories being considered (Tye 1992, n = 53 (six areas); this study n = 23).

It is likely that in a hole nesting species that the choice of nest hole is important. Nest holes may be important because of variation in quality (Alatalo *et al.* 1986, Lundberg and Alatalo 1992) or because their numbers are limited. No direct measure was made of nest hole quality but in this study wheatears generally selected nest holes with small entrances just large enough for individuals to gain access, typically cracks in stone walls.

Those nests which were destroyed or deserted by the activities of other animals were in burrows with larger entrances. Wheatears generally preferred nest holes facing in the opposite direction to the prevailing winds (see also Conder 1989), although this did not affect male and female settlement dates nor reproductive success. Due to the potential for disturbance by other animals suitable nest holes may be more limited than previously supposed (but see Tye 1992). There was some evidence to suggest that there were traditional nest sites on about one-third of territories, which suggests that on some territories the number of suitable nest holes was limiting (Conder 1989 and references therein). However, there was no relationship between settlement patterns and the presence of traditional nest sites. The reduced occupancy and breeding attempts on high ranking territories may have been due to a lack of suitable nest sites but this seems unlikely as these territories were used successfully for breeding in previous years (P. Jenks pers. comm.). Nest site availability may also influence territory size (Hinde 1956, Conner *et al.* 1986). As previously mentioned, there was a suggestion that nest sites may have been limited on some territories, however in the absence of quantitative data no comment can be made on this.

The lack of correlation between settlement patterns and territory characteristics in this study suggests that males may choose territories that are simply attractive to female (Davies 1978). However, the benefits accrued by individuals suggests a more functional explanation.

7.5. Summary

1. Territory boundaries were relatively constant between years. Territories were ranked according to their pattern of settlement by both sexes within years. There was a predictable order territory settlement by males between years, less so for females.

2. Settlement patterns could be explained by variation in territory quality. Individuals moved to preferred territories when possible, preferred territories were more frequently used, and both sexes were more faithful to lower ranked preferred areas.

3. Male mating status was dependent on arrival time, territory quality, breeding density and the operational sex ratio. Early arriving, usually older males were able to settle on preferred territories, and were more likely to be paired. Individuals which settled on less prefered territories usually remained unmated.

4. Both sexes benefited by breeding on "good" territories through enhanced fledging success and an increased probability that their offspring would be recruited to the population in subsequent years. There were few correlates between measures of breeding success and individual quality.

5. There were no obvious vegetational or topographical differences between preferred and less-preferred territories. I could not completely differentiate between male

and territory quality, and patterns of female settlement may also be influenced by male quality.

Chapter 8. Resumé

8.1. Male and female reproductive strategies
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      8.3.2. Lifetime reproductive success
8.4. Conclusion

8.1. Male and female reproductive strategies

8.1.1. Ensuring paternity and the pursuit of EPCs

Behavioural observations and paternity data presented in Chapters 2 and 3, and 4, were consistent with the hypothesis that male wheatears pursue a mixed reproductive strategy (MRS), i.e. they ensure their paternity during their fertile period, and pursue EPCs outwith this time. There was no evidence that females pursued a MRS by laying eggs in the nests of other females (intra-specific brood parasitism), but some females must also have pursued a MRS through EPCs, as female co-operation was essential for males to obtain successful copulations.

In birds, there are two principal ways by which males can ensure their paternity: through mate guarding or through a high copulation rate (Birkhead *et al.* 1987, Birkhead and Møller 1993). Wheatears exhibited a low rate of copulation (see also Carlson *et al.* 1985, Conder 1989), on average once per clutch, which is likely to be ineffectual as a paternity guard. Behavioural observations were consistent with the hypothesis that male wheatears mate guard their females to ensure paternity. Mate guarding was typified by close following of the pair female during the fertile period, but was less intense than previously documented in the wheatear (Carlson *et al.* 1985). I have suggested that this was due to increased breeding synchrony, and a less dense breeding population. A combination of these factors would reduce the opportunities for males to pursue EPCs (Birkhead and Biggins 1987), and lessen the need for intense mate guarding. I have also argued that, due to the open nature of the study area, males need not remain close to their female to monitor her behaviour and that of extra-pair males (Hobson and Sealy 1989, Sundberg 1992).

Paternity data from male removal experiments (section 5.3.6) indicated that EPCs immediately prior to laying (on days -2 and -1: day 0 = first egg date), in the absence of the

pair male, were more likely to result in EPFs (see also Westneat 1995). Males maximised their intensity of mate guarding to coincide with this peak in female fertility (on day -1; see Fig 2.1). The intensity of mate guarding declined during the laying sequence, possibly in response to an increase in the cost:benefit ratio of mate guarding due to a reduction in female fertility (as indicated by female incubation behaviour) (see Birkhead and Møller 1992). There was no indication in this study that males ceased to mate guard earlier in response to potentially lost opportunities to pursue EPCs, indicated by a female-skewed sex ratio, as has been observed in other studies (e.g. Møller 1987a).

There were individual differences in levels of mate guarding, and males increased their intensity of guarding under conditions that might be expected to pose a threat to their paternity. Increased levels of guarding were observed in response to a male-skewed sex ratio, and at later breeding nests which experienced higher intrusion rates (on average three times higher than early territories, see Fig 3.3[ii]). Early and late breeding males exhibited two distinct forms of mate guarding. That exhibited by early breeding males concentrated more on territory defence with the majority of intruders being chased from the territory. Later breeding males, on the other hand, guarded their female more directly and tolerated intrusions. These distinct strategies appeared to be adaptations to the differences in intrusion rates experienced by early and late breeders. If late breeding males were to adopt an 'early male' strategy, i.e. chase intruders, individuals would be unable to monitor the pair female, being continually involved in chasing intruders, which would prove potentially ineffectual as a paternity guard. Later arriving males, usually first-year breeders, guarded their females more intensely than early arriving, older males. It was suggested that this may be because first-year males were lacking in breeding experience, and unsure of when their female was fertile. However there was no effect of male age, or settlement date, on rates of decline in guarding observed during the laying sequence.

Although the paternity data indicated that some females pursued a MRS, females were never observed off territory soliciting extra-pair males, and rarely seen soliciting extra-pair males on territory. This was in contrast to males, which were more conspicuous in their pursuit of EPCs. Males mainly pursued EPCs once their female had started incubating. Intruding males timed their intrusions to coincide with the fertile period of extra-pair females (see Fig.3.3[i]). This suggests that males could identify fertile females, and timed their intrusions to maximise the chances of an EPC being successful. However, surprisingly few intrusions at non-experimental nests (7/64) resulted in EPCs, and even fewer (1/7) were successful. In the vast majority of intrusions, extra-pair males did not 'interfere' with the female, but just observed the pair. Frequent copulations drain a male's sperm reserves (Birkhead 1991b, Birkhead and Møller 1992 and references therein). Males should therefore time their EPCs to coincide with female fertility. This could be by either monitoring intra-pair behaviours, or finding the nest hole and checking the stage of nest

development and clutch sizes, as were observed in this study. Males could also use their observation stints of the pair to wait for an opportunity to attempt an EPC. There was some suggestion that males also 'advertised' for EPCs or additional females using song flights. These were performed frequently prior to pairing, after males became 'widowed', and when the pair female was incubating.

8.1.2. Low levels of extra-pair paternity: mate guarding or female choice ?

There were relatively low levels of EPP in non-experimental broods (see Table 4.1). This may have been due in part to mate guarding, and the open nature of the habitat which potentially limited the opportunities for males and females to pursue EPCs without 'interference' from their partners. However, the male removal experiments during the fertile period did not result in a significant increase in EPP (10% of offspring in 38% of broods, see section 5.3.6), as might have been expected from the increase in intrusions by extra-pair males, and attempted EPCs (observed in the absence of the pair male; see Figs. 5.1 and 5.2 respectively). Low levels of EPP, in both non-experimental and experimental broods, appeared to be a result of female reluctance to participate in EPCs, with the majority being rejected by the female. In light of these observations, how important was 'mate guarding' in ensuring a male's paternity?

Due to the method of collecting data, it was not possible to determine whether females co-operated with males during mate guarding but, in general, males seemed to have had little effect on female behaviour directly. There were no correlates between the intensity of guarding and levels of EPP at non-experimental nests, and females controlled the success of copulations (both within-pair and extra-pair), and therefore ultimately the paternity of the brood. However, the presence of the pair male did deter intrusions and EPC attempts by extra-pair males, and 'guarding' may have limited the opportunities for females to participate in EPCs. Behavioural observations, particularly from the male removal experiments, also suggest that the presence of the pair male during the fertile period may have been beneficial to females under certain conditions, by reducing harassment from extra-pair males (e.g. Aschroft 1976, Kempenaers *et al.* 1995). This hypothesis is further supported by the fact that females also increased their following of the pair male during the fertile period.

Why were females reluctant to participate in EPCs? Possible costs to females of participating in EPCs are: (i) producing offspring of poor genetic quality; (ii) retaliation by the pair male, either actual physical retaliation, or in reducing levels of paternal care; (iii) the risk of injury and harassment by extra-pair males; (iv) the transmission of diseases and parasites; and (v) increased predation risks, some of which have been discussed in sections 4.4, 5.4 and 6.4 (see also reviews in Westneat *et al.* 1990, Birkhead and Møller 1992). Several of these reasons were excluded in accounting for female reluctance to participate in

EPCs in this study. First, copulations in the wheatear (both within-pair and extra-pair) are rapid and covert events, occurring infrequently, and although they are usually accompanied by the conspicuous dancing display, are unlikely to increase vulnerability to predation. Second, females did not risk any form of retaliation by the pair male during the removal experiments, which to all intents and purposes simulated mate predation, but were still reluctant to participate in EPCs despite the increased opportunities for them. Third, risk of injury is normally associated with forced copulations. Unwanted copulations (both within- and extra-pair) were rapidly rejected by the female and never forced out by the male. I cannot exclude the hypotheses that females rejected EPCs either to avoid producing poor quality offspring, or to avoid diseases or parasites. Female resistance to participate in EPCs has also been suggested as a means of assessing male quality. However, in practice it is difficult to distinguish between male assessment and actual resistance, although extra-pair males whose EPC attempts were rejected by the respective females did not gain any EPP. Extra-pair fathers were never observed copulating with the respective females.

There may be additional reasons, specific to this study, to explain female reluctance to participate in EPCs. First, there may be little variance in male quality. In a migrant species, individuals which return are presumably higher quality than those which do not. If only 'good' quality individuals return then there may be less need for females to copulate outwith the pair bond. Female arrival dates will determine which male a female can pair with. This has potential consequences for female reproductive strategies, as later arriving individuals will be limited in the number of males they can pair with due to female-female aggression (see section 8.2[i]), but would be able to modify their initial choice by participating in EPCs. Female settlement data were only available for 1992-93, but there was no suggestion that later settling females were more likely to have EPY in their nests, as might be expected if they were paired to poorer quality males (Mann-Whitney U-test, female settlement date vs. presence of EPY in brood [paternity data from 1992-93 combined], $z = -0.62$, ns). Secondly, territory quality as opposed to male quality appeared to be more important in affecting female reproductive success, influencing both the number of fledglings produced, and their subsequent survival as measured by recruitment to the population (see section 7.3.7 and Table 7.3). It may be less important for female wheatears to pursue EPCs to enhance their RS, as this was determined primarily by the quality of the resources defended by males.

Since females controlled the success of copulations, the presence of EPY within broods can be considered to be a deliberate strategy by the females concerned. There was no evidence that females gained material benefits from extra-pair males by participating in EPCs or having EPY in their broods. Although the data are not particularly conclusive, I have argued in Chapters 4 and 5 that the distribution of EPY within broods, if anything, was consistent with females seeking good genes as opposed to enhancing the genetic

diversity of their offspring. The reasons for this were two-fold: (i) EPY were not found in many broods (as would be expected if only females paired to poor quality males participated in EPCs), and (ii) except in one case all EPY within a brood were fathered by one male. The low proportion of broods containing EPY and the lack of multiple extra-pair paternity within broods are not consistent with the hypothesis that females attempted to increase the genetic diversity of their offspring by participating in EPCs (Westneat *et al.* 1990).

Two measures of male quality were used in this study: (i) male age, which could be determined in the field as either first-year breeder or older on the basis of plumage characteristics (Svensson 1984); and (ii) the body condition index (BCI, see section 1.4.4). Unfortunately, too few extra-pair fathers were identified (3/8) to test statistically for differences in 'quality' between extra-pair fathers and cuckolded males. However, all extra-pair fathers which were identified (considering the paternity data 1991-93, non-experimental and experimental broods combined) were old males, although there was no obvious trend in the BCI data. EPCs which were accepted by females under 'natural' conditions or during the removal experiments were also all by older males. There was no difference in either age or BCI between cuckolded and non-cuckolded males in non-experimental pairs, although there was some evidence to suggest that males which were cuckolded during the removal experiments were of low quality. This indicates that poor quality males may be able to limit female options to participate in EPCs by remaining in close proximity to their partner in the fertile period. However, one would expect females to copulate with high quality extra-pair males regardless of whether or not the pair male was present (e.g. Kempenaers *et al.* 1992). There was an *a priori* expectation that old males were likely to be extra-pair fathers, if females were seeking good genes from participating in EPCs, as they have proved their ability to survive, which may be especially important in a migrant species. Although I am limited in the conclusions I can make due to the low level of EPP and the small numbers of extra-pair fathers identified, the available data suggests that if females participated in EPCs it was with older males (see also Weatherhead and Boag 1995, Wetton *et al.* 1995).

The distrubution of EPY between cuckolded males and extra-fathers for non-experimental and experimental broods is also similar to that recently observed in an unmanipulated population of house sparrows (Wetton *et al.* 1995). In their study, there was no age bias in which males were cuckolded, but older males gained almost all extra-pair fertilisations. However, males which sired EPY were just as likely to be cuckolded. Wetton *et al.* (1995) argue that these results run counter to the good genes hypothesis, in that females paired to older males should remain faithful to their partners and suggest that females may participate in EPCs to ensure their eggs were fertilised. Although insufficient extra-pair males were identified to test Wetton *et al's* hypothesis in this study of the

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wheatear, males which fathered extra-pair offspring did not have EPY within their own broods in any of the years of study, and there was also no direct evidence that females participated in EPCs to ensure their clutch was fertilised (although in the male removal experiments during the fertile period, females may have participated in EPCs to ensure that their eggs were fertilised). There was no correlation in non-experimental nests between the presence of EPY and infertile eggs (Wetton and Parkin 1991), or any indication that the same males were cuckolded in successive years, as might be expected if females were participating in EPCs due to mate infertility.

As a result of experiencing higher intrusion rates, there was an expectation that broods raised later in the season would have higher levels of EPP than early nests. However, there was no effect of time in the season on levels of EPP. A combination of more intense mate guarding, and increased male-male competition (behaviourally in the form of 'interference' by other extra-pair males, or through increased sperm competition) later in season may have resulted in reduced opportunities to obtain successful EPCs. In non-experimental nests, EPY were more likely to be found in larger clutches. Smaller clutches were laid later in the season, which may also account for the low levels of EPP in later broods. There was circumstantial evidence that EPY resulted from successful EPCs during the laying sequence. Males are unlikely to know the exact clutch size a female is going to lay until the last egg has been laid. Larger clutch sizes and a decline in the intensity of mate guarding during the laying sequence, combined with a males uncertainty about clutch size, could provide opportunities for females to participate in EPCs during the laying sequence.

Models of sperm precedence are best tested in the laboratory, under controlled conditions, or using invasive techniques (e.g. Birkhead *et al.* 1988, 1989, Birkhead 1992). Although lacking such conditions, the behavioural data and low levels of EPP in the removal experiments were consistent with a last male sperm precedence hypothesis, with the pair male generally obtaining the last copulation. In the removals prior to laying, extra-pair males were observed to obtain successful copulations, yet these males did not gain any EPP. In one of these experiments, the pair male was observed to copulate with his female immediately on release and subsequently had all the paternity in the brood.

8.2. Parental care

8.2.1. Monogamy and the importance of paternal care

Monogamy was the predominant mating system in the wheatear in this study (see also Cramp 1988, Moreno 1989, Conder 1989), with both sexes typically providing about 50% of chick feeds during the nestling period (Moreno 1987a). However, although considering small sample sizes, females appeared capable of successfully raising a brood on their own, or with reduced male help (see also Gowaty 1983, 1987, Bart and Tornes

and references therein). There was no reduction in either of the measures of fledging success used when only one parent fed the nestlings, although fledging weights were significantly less (see Table 6.6). Lighter fledging weights have been correlated with a reduced probability of recruitment to the population (Perrins 1965, 1979, Magrath 1991, Møller 1994, 1995). In fact, a fledgling from a nest raised by one parent in 1992 returned to breed the following year. In this study, recruitment was mainly influenced by the quality of territory from which individuals fledged, rather than fledging weight (see section 7.3.7 and Table 7.3).

Females were visibly aggressive to other females which appeared on the territory regardless of the time in the season, or whether or not the 'intruders' were residents or migrants. This female-female aggression appeared to limit the settlement of additional females. The only natural case of polygny which occurred during the period of study was as a result of a male defending two neighbouring territories, which had originally been set up by the respective females. In the case of polygny described in sections 6.2.1 and 6.4.3, the male fed the fledglings of one nest and the nestlings of the other, which resulted in a reduction in paternal care at both broods. I suggest that monogamy in the wheatear was primarily due to female-female aggression (see also Yasukawa and Searcy 1981, Slagsvold 1988, Veiga 1992), possibly to prevent the sharing of male help and the costs this might entail for the female in terms of reduced survivorship brought on by trying to compensate for the lack of paternal care (see section 6.3.4), rather than necessarily being a means of maximising RS for both sexes. The ability of males to mate polygynously was further limited, in this population, by a male-skewed sex ratio in each of the years of study (see Table 7.2). However, if females can successfully raise offspring on their own, why do males contribute a high proportion of chick feeds?

One of the major costs to males of providing paternal care is lost opportunities to pursue EPCs. Westneat *et al.* (1990) argue that males may contribute to parental care if there are no other options open to them. This population bred relatively synchronously (see Table 2.7), and consequently there was a low number of fertile females 'available' for males during provisioning (see Table 6.7). This lack of fertile females would limit the opportunities to pursue EPCs. However, there was no reduction in levels of paternal care at early nests when there were some fertile females in the population (see Table 6.7), or when there was a fertile female in a neighbouring territory. Parental care is energetically costly, and by providing care individuals are trading off current RS against future survival. Although not detected when considering single parent and adopted nests, one has to assume that due to the high levels of male investment during the nestling period, paternal care is important in contributing to fledging success in the wheatear.

8.2.2. Paternal care and certainty of paternity

One of the more contentious issues in behavioural ecology is whether males should reduce paternal care with uncertainty of paternity. This is based on the premise that females are more likely to be certain of their maternity than males are of their paternity due to internal fertilisation (Trivers 1972, Clutton-Brock 1991). Paternal care should evolve only when males have reasonable confidence in the paternity of their offspring (Knowlton and Greenwell 1984). Recent models of parental care indicate that males may reduce their investment with uncertainty of paternity under certain conditions (e.g. Whittingham *et al.* 1992, Westneat and Sherman 1993). However, to date there are only two studies that have provided conclusive field data to support the theory: (i) polyandrously paired dunnocks, in which males alter their investment according to the proportion of paternity they have in the brood (Burke *et al.* 1989), and (ii) monogamous reed buntings, a species which has high levels of EPP (see Table 4.1), in which males adjusted their paternal care in proportion to the amount of paternity they had within a brood (Dixon *et al.* 1994). With the low levels of EPP observed in this study, it was not unsurprising that under 'natural' conditions males did not reduce paternal care in relation to the presence of EPY in the nest. The male removal experiments were designed specifically to test the effect of the presence of the pair male on (i) the behaviour of the female and extra-pair males, and (ii) brood paternity. I have discussed in section 6.4.3 the inappropriate nature of using temporary male removal experiments to simulate uncertainty of paternity (see also Wright and Cotton 1994), and it was therefore not surprising that males did not reduce their investment as a result of the experiments. Males did reduce their investment in broods which they adopted (n = 4), providing on average 29% of chick feeds, although individual responses differed (see Table 6.5). Males which did contribute parental care had been observed in close association with the pair female. However, there was no correlation between levels of paternal care and proportion of nestlings these adopting males fathered, and in fact in three of the four cases the adopting male did not gain any paternity in the brood. This sugggests that the 'rules of thumb' males may use to apportion their investment under such conditions were not very precise, and females were able to 'fool' them into feeding the offspring.

8.3. Factors affecting reproductive success

8.3.1. Reproductive success: an effect of territory or individual quality ?

Males returned earlier than females and set up territories from which the majority of food for adults and nestlings was collected. Territories were remarkably consistent between years (see Fig. 7.1-7.3). There was good evidence that some territories were preferred over others: (i) there were consistent patterns of settlement between years, particularly for males; (ii) individuals moved to preferred territories when possible; (iii) individuals were more faithful to preferred areas; (iv) preferred territories were used more frequently between

years; and (v) males which settled on preferred territories were more likely to be paired.

In migrant species, a correlation is expected between individual quality and arrival times at the breeding grounds, with high quality individuals returning earlier (e.g. Møller 1995). In this study, there was no effect of BCI on individual arrival times, but male arrival times were age dependent, with older males returning earlier than first-year males. It is unclear whether a similar pattern exsists in females due to the difficulty in ageing unringed individuals. I suggest that differences in wing length, as well as 'experience', account for this result in males, rather than differences in quality (see section 7.4.2). As a consequence of arriving earlier older males had the opportunity to settle on the better territories, and were more likely to be paired than first-year males. The fact that older males were more likely to be paired appeared to be a consequence of territory quality (Hogstedt 1980, Møller 1982), as there was little effect of individual quality, either age or BCI, in either sex on measures of breeding success. Fledging success tended to be higher on preferred than non-preferred territories, and nestlings which fledged from preferred territories were more likely to be recruited to the population. Tye's (1992) extensive study on territory quality and individual settlement patterns convincingly showed that preferred territories contained short vegetation, and were correlated with higher prey densities than less preferred areas. In this study I was unable to detect any differences between preferred and non-preferred territories with respect to vegetation or food availability.

8.3.2. Lifetime reproductive success

Lifetime reproductive success (LRS) is the total number of young raised by an individual during its life. LRS values are considered useful because they combine two key measures of performance (annual survival and annual breeding success) and provide a close approximation to Darwinian fitness (see review in Newton 1995). However, in short field studies such as the current one, it is not possible to obtain LRS values as individuals frequently live longer than the period of study, and typically only annual reproductive success is considered.

Since male mating success was influenced, at least in part, by territory quality (see section 7.3.7), there was considerable variation in annual male reproductive success. This was particularly the case in years with a male-skewed sex ratio (e.g. 1991 and 1992) when individuals which settled on less preferred territories were less likely to be paired. Seventy per cent of all males which failed to fledge any offspring in 1991-93 were unpaired (see Fig 8.1). EPFs contributed little to annual male reproductive success, and although there was circumstantial evidence that some unpaired males may have gained EPP via successful EPCs (in 1991, suggested by the fact that in some broods extra-pair fathers were not found in surrounding territories), this probably occurred at a low frequency.

Individual longevity has potentially significant consequences for individual RS.

Wheatears can live up to seven years (Cramp 1988), and several individuals in this study were at least four years old (being at least two years old at the beginning of this study, or their actual age was known having been ringed as part of an earlier study; P. Jenks pers. comm.). Fig. 8.2 shows the number of fledglings produced by individuals of both sexes over the duration of the three-year study. This under-estimates the number of fledglings produced by successful individuals, as some males and females may have bred successfully in years prior to and after the study, but gives an indication of the effect of individual longevity on the variance in RS between individuals. In general, longer lived individuals produced more fledglings than individuals which bred in only one season. The majority of first year males failed to produce any offspring as they settled on poor quality territories and remained unpaired. Previously unpaired males which returned in subsequent years returned earlier, settled on better territories and usually bred successfully.

8.4. Conclusion

A major determinant of reproductive success in the wheatear was determined by their social mating situation, with alternative reproductive strategies contributing very little to an individual male's reproductive success. This is in contrast with other species such as the house sparrow and reed bunting, in which alternative reproductive strategies contributed significantly to an individual male's reproductive success: there was an average contribution to the annual reproductive success of those males obtaining extra-pair paternity of 36% in house sparrows (Wetton *et al.* 1995) and ca. 60% in the reed bunting (Andrew Dixon pers. comm.) (see also Kempenaers et al. 1992, Weatherhead and Boag 1995). Environmental factors are likely to be important in determining the contribution of alternative reproductive tactics to an individual's success. Few studies have compared reproductive strategies between different populations of the same species, but probably the best examples are the Swedish and Norwegian studies on pied flycatchers. In the Swedish population alternative reproductive strategies contributed significantly to some male's RS (25% of offspring were sired by extra-pair males, Gelter and Tegelstrom 1992), while in Norway observed RS and genetic RS were closely correlated (only 4% of offspring were sired by extra-pair males, Lifjeld *et al.* 1991). Further studies need to be made at both the inter-specific and intra-specific levels, to discover what factors determine the observed wide variation in the contribution of alternative reproductive strategies to individual reproductive success, between populations and species.

Future research needs also to concentrate on the rigorous experimental testing of current theory. For example, behaviours associated with mate guarding are assumed to be a means by which a male ensures his paternity. However, in this and other experimental studies there is little direct evidence that male guarding behaviours actually ensure paternity, with the paternity of the brood apparently being controlled to a large extent by the female.

In light of these observations, future research should take full account of the likelihood that females control male reproductive success as implied by the results from this and other studies (e.g. Lifjeld and Robertson 1992, Kempenaers *et al.* 1992, Birkhead and Møller 1993, Hunter *et. al.* 1993, Sheldon 1994).
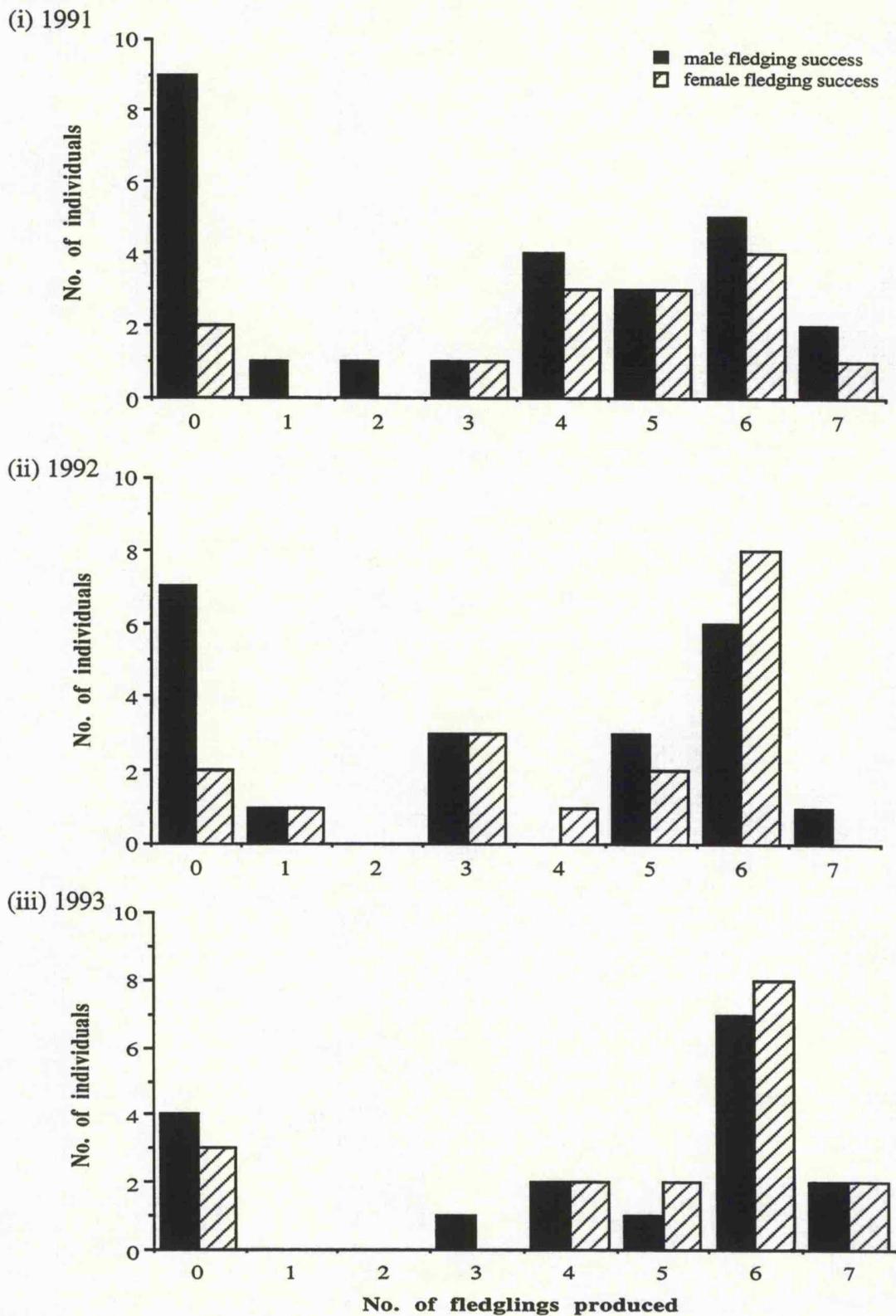
Fig 8.1. Annual male and female fledging success, expressed as number of fledgings produced. 70% of males which failed to produce any fledglings in 1991-93 were unpaired. Nest failures accounted for all incidences of females failing to produce fledglings.

(i)

(ii)
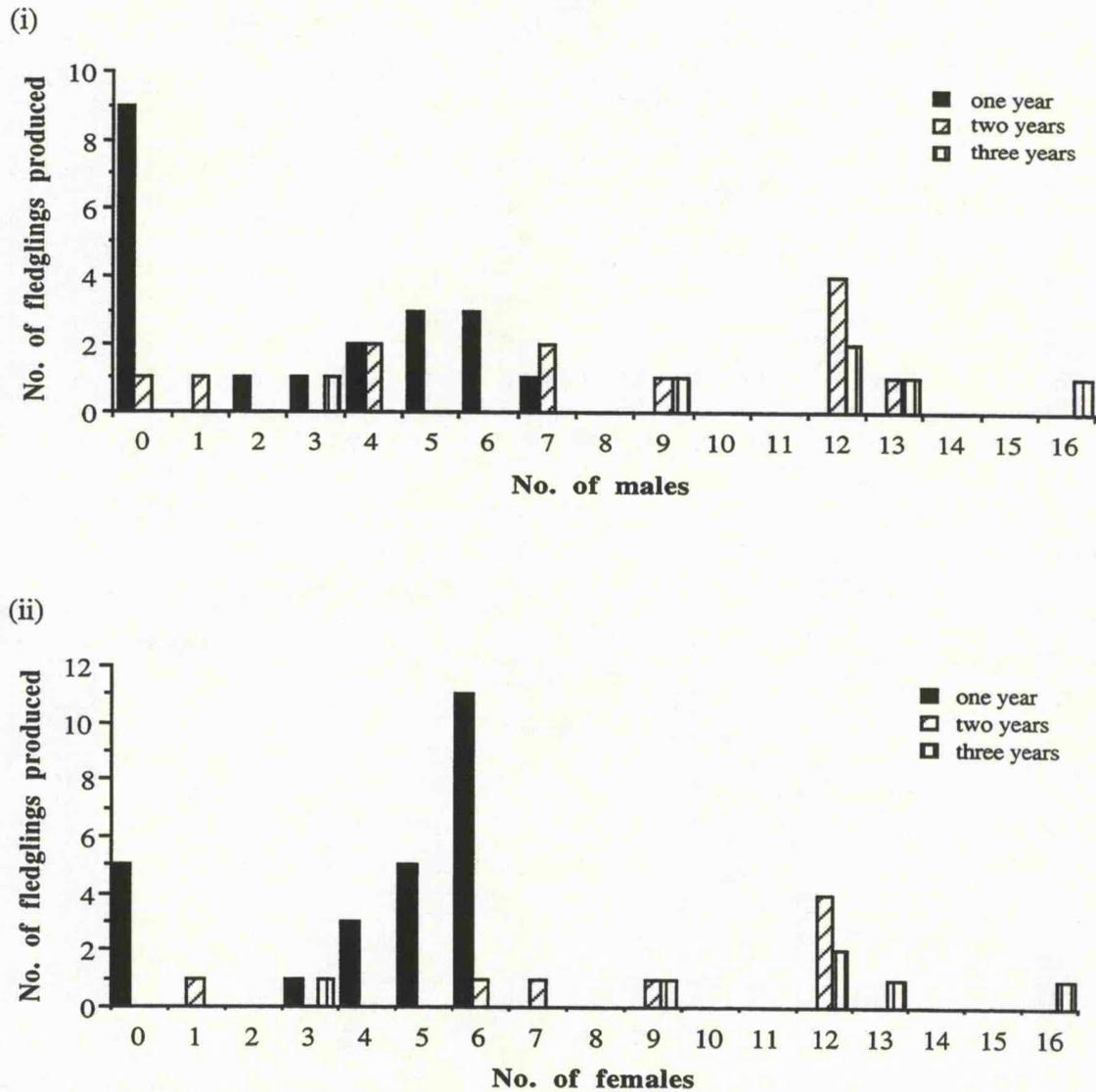
Fig 8.2. The effect of individual longevity on total fledging success. The graphs show the number of fledglings produced by (i) males and (ii) females in relation to the number of years individuals bred on the study area. Older individuals generally produced more fledglings (Kruskal-Wallis, number of years bred vs. number of fledglings produced: males, df = 2, H = 15.15, p < 0.001; females, df = 2, H = 9.24, p < 0.01). The majority of males that failed to produce any fledglings did so because they were unpaired. Nest failures accounted for all incidences of females failing to produce fledglings. The graphs understimate individual lifetime reproductive success, as some individuals may have bred before the start and after the end of the study.

Appendix 1. Scientific names of birds mentioned in the text.

barn swallow	*Hirundo rustica*
black vulture	*Aegypius monachus*
blue tit	*Parus caeruleus*
chaffinch	*Fringilla coelebs*
cliff swallow	*Petrochelidon pyrrhonota*
corn bunting	*Milaria calandra*
crested tit	*Parus cristatus*
dunnock	*Prunella modularis*
european bee-eater	*Merops apiaster*
fulmar	*Fulmaris glacialis*
great tit	*Parus major*
hooded warbler	*Wilsonia citrina*
house finch	*Carpodacus mexicanus*
house sparrow	*Passer domesticus*
indigo bunting	*Passerina cyanea*
meadow pipit	*Anthus pratensis*
purple martin	*Progne subis*
pied flycatcher	*Ficedula hypoleuca*
red-winged blackbird	*Agelaius phoeniceus*
reed bunting	*Emberiza schoeniclus*
rock pipit	*Anthus spinoletta*
starling	*Sturnus vulgaris*
tree swallow	*Iridoprocne bicolor*
willow warbler	*Phylloscopus trochilus*
wood warbler	*Phylloscopus sibilatrix*
whinchat	*Saxicola rubetra*
yellowhammer	*Emberiza citrinella*
zebra finch	*Taeniopygia guttata*

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