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Sexual selection and reproductive strategies in songbirds

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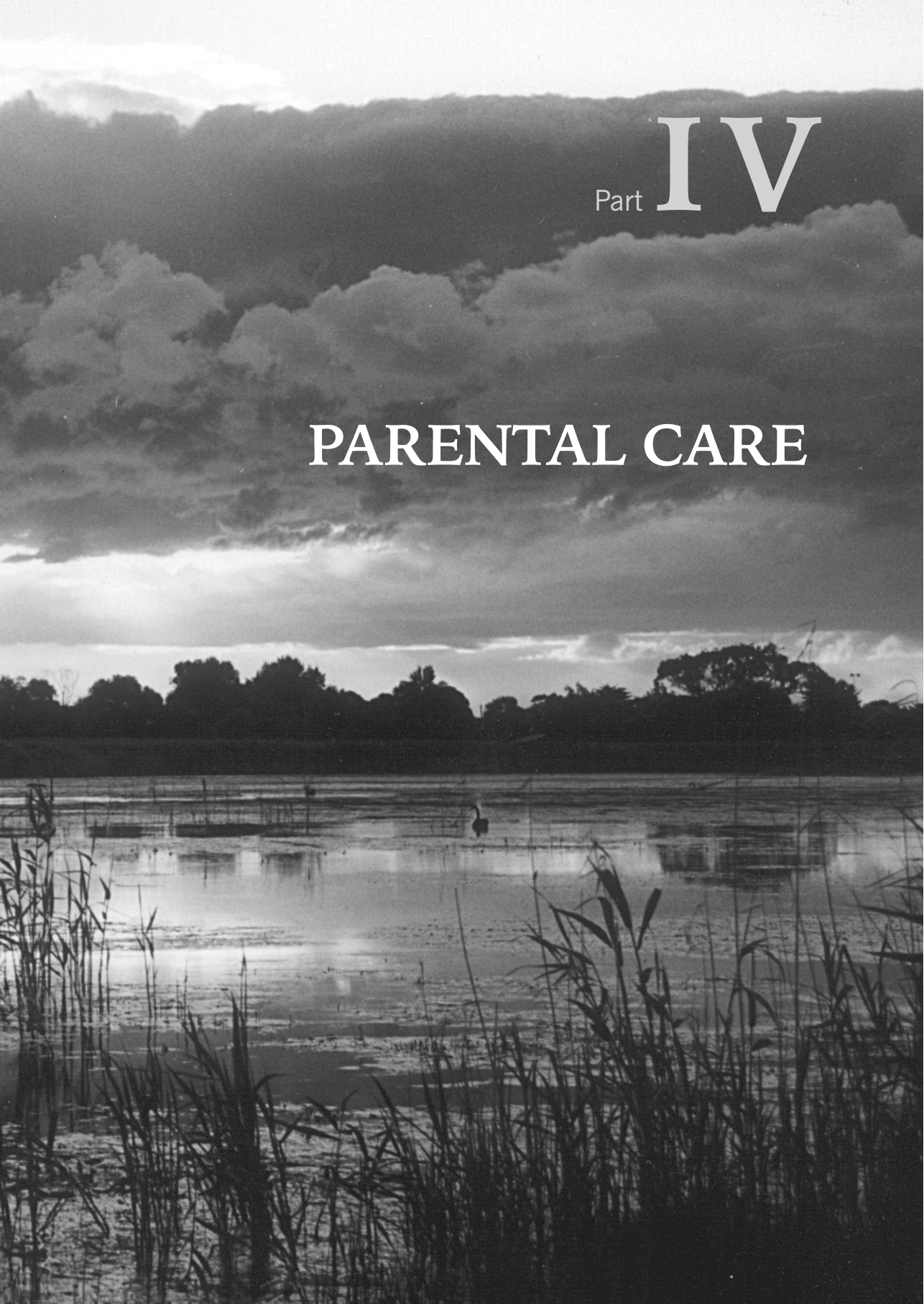
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Part **IV**

PARENTAL CARE



**Trade-offs between paternal care,
mate attraction and territory defence in the
Australian reed warbler**

Mathew L. Berg & Jan Komdeur

ABSTRACT

Offspring care, mating effort and somatic effort are major components of reproductive effort in many species. Trade-offs between these activities can be expected when time and energy are limited, and this conflict will usually be greater for males. The possible trade-offs between paternal care, extra-pair mating effort and territory defence are expected to vary with the spatial and temporal incidence of mating opportunities or territorial competitors. We investigated whether male Australian reed warblers (*Acrocephalus australis*) vary their food provisioning effort to nestlings in response to the availability of extra-pair mating opportunities and territorial intrusions by conspecific males. Male investment in offspring care was negatively related to the number of neighbouring territories, while female care remained unchanged. This suggests that behavioural trade-offs lead to a reduction in male care when the chance of encountering conspecifics is greater. To investigate whether extra-pair mating or territorial activities may lead to this pattern, we presented reed warbler parents with caged conspecifics during the nestling period. Male feeding rates were lower in the presence of either a female or a male conspecific, while female behaviour was not affected. The reduction in paternal feeding rate was similar to either sex of intruder. Neither parental sex reduced feeding in response to a caged heterospecific. This study thus demonstrates that male Australian reed warblers reduce their food provisioning effort to nestlings in response to increased opportunities for extra-pair mating and increased territory intrusions from other males. We discuss the outcomes of this behaviour for offspring growth and parental fitness.

INTRODUCTION

Parental effort (PE), mating effort (ME) and territorial effort (TE) are major components of reproductive behaviour (Williams 1966; Maynard Smith 1977). In many animals, males contribute substantially to parental care (Clutton-Brock 1991; Ketterson & Nolan 1994) but can also enhance their reproductive success by attracting additional mates (Webster 1991) or by gaining extra-pair copulations (EPCs) which result in extra-pair fertilizations (EPFs; Westneat *et al.* 1990; Birkhead & Møller 1992a). A conflict between male PE and ME is thus likely to occur when the periods of PE and ME occur simultaneously (Westneat *et al.* 1990; Whittingham 1993; Magrath & Komdeur 2003). In addition, periods of ME and TE are often likely to covary, because the main periods for territory establishment and mate attraction will often coincide early in the breeding season, or with changes in breeding density or synchrony. The potential trade-off facing males between investing in PE or ME is well accepted in the theory of mating systems (Oring 1982; Westneat *et al.* 1990; Westneat & Sherman 1993), although empirical data is scant (Magrath & Komdeur 2003).

When a conflict between PE, ME and TE arises males are expected to adjust their investment in these behaviours in a way that maximizes their fitness (Trivers 1972; Maynard Smith 1977; Beecher & Beecher 1979; Fitch & Shugart 1984). The benefits of caring for the offspring, such as improved quality or survival of offspring, should be balanced against the need to engage in territory defence and the opportunities for attracting additional mates (Trivers 1972; Emlen & Oring 1977; Patterson *et al.* 1980; Magrath & Komdeur 2003), such as the temporal (e.g. Westneat 1988; Magrath & Elgar 1997) or spatial (Westneat & Sherman 1997) availability of intruding males or fertile females. These factors have a potentially important and often overlooked influence on parental behaviour (Magrath & Komdeur 2003). A number of studies have shown that the amount of time a male spends off-territory increased with the number of neighbouring females that were fertile, although no corresponding reduction in male care was observed (Westneat 1988; Green *et al.* 2000; Pitcher & Stutchbury 2000; Chuang-Dobbs *et al.* 2001). In the fairy martin (*Cecropis ariel*), the contribution to incubation of individual males has been shown to decline with the proportion of fertile females present in the colony (Magrath & Elgar 1997). Furthermore, the incubation period was longer at nests where males contributed less to incubation. Similarly, a higher breeding density may lead to a greater spatial availability of potential mates for males seeking extra-pair copulations. Several lines of evidence indicate that the frequency of EPFs within species can increase with female density (reviewed in Westneat & Sherman 1997; Møller & Ninni 1998; Griffith *et al.* 2002). Owens (2002) has shown a strong link across avian families between nesting density (considered an index of remating opportunities) and the presence of uni-parental male or female care. However, to our knowledge no previous studies have reported on male PE or ME in relation to density within a species.

In order to demonstrate that a trade-off between PE and either ME or TE exists it is necessary to show a causal and inverse relationship between PE and ME or TE. For example high level of ME or TE might not necessarily result in a low level of PE, because high-

quality or experienced males might be able to invest relatively more in both activities because they can afford to invest less in somatic effort (activities to increase survival; Lessells 1991; Whittingham 1993). In addition, for a trade-off to be necessary positive relationships between male fitness and PE, ME and TE would generally be anticipated (Magrath & Komdeur 2003).

We examined variation in male and female PE (frequency of food provisioning to nestlings) in the Australian reed warbler (*Acrocephalus australis*) in relation to (a) natural spatial variation in breeding pairs (number of neighbouring territories), and (b) experimental variation in the presence of males or females. In our study population, Australian reed warblers are typically socially monogamous and produce several broods from September to January in dense beds of Australian reed (*Phragmites australis*; chapter 6). Only the female incubates the eggs (chapter 9), but males contribute substantially to the feeding of nestlings. This species maintains strict breeding territories in which nest sites are unlikely to be limited (chapter 6). Genetic parentage analyses have revealed that extra-pair paternity is extremely common (affecting *ca.* 50% broods) and, due to re-nesting following depredation, occurs throughout the season (Berg 1998; M. Bleeker & M. Berg unpubl. data). Thus, both parental effort and mating effort occur simultaneously. These features make this a good system in which to study the trade-off between PE and ME.

This study was designed to answer three questions: (i) is there a decline in male PE with increasing spatial availability of conspecifics of either sex, (ii) what are the benefits of male PE in terms of offspring growth and relieving the female partner, and (iii) do males adjust their PE directly in relation to the presence of male or female conspecifics. The last question was addressed experimentally by presenting live Australian reed warblers in a cage to parents during the nestling feeding period.

METHODS

Study population

This study was conducted during the main breeding season of the Australian reed warbler in 1997 (23 October to 13 January), 1999 (20 November to 25 November) and 2000 (1 November to 13 December). Two nearby field sites in south-eastern Australia were used: Cherry Lake, Altona North (6 ha, 37°53' S, 144°48' E) and Edithvale Wetlands (10 ha, 38°02' S, 145°07' E). Both sites consisted of homogenous beds of Australian reed surrounding a lake or watercourse. Birds were caught using mist-nets, and each individual was banded with a numbered aluminium band (Australian Bird and Bat Banding Scheme) and with a unique combination of three colour bands. Approximately 50 μ l of blood was collected from each bird by puncturing the brachial vein and stored in 99% ethanol. DNA was extracted from blood samples using a salt extraction method following Richardson *et al.* (2001) and birds were sexed using the molecular method described by Griffiths *et al.* (1998). All individuals sexed by this method and validated by behavioural observations, morphology and presence or absence of a brood patch were correctly assigned ($n = 55$). Territory borders were estimated based on catching and resighting, nest locations, the

location of singing males and noting territorial interactions on a regular basis (see chapters 5 & 6). Locations were plotted to the nearest 5 m using a 10 m grid system throughout the study area.

Nests were found by searching systematically through the reeds every 1-2 weeks on 5 m transects, parting the vegetation carefully to minimise disturbances. Nests were marked with a small piece of green or yellow plastic tape on a nest support stem (to match the surrounding vegetation and allow exact relocation of the nest even if it disappeared) and located with a handheld satellite global positioning system (Garmin GPS 12®) to a precision of <5 m. All nests were monitored every second day for changes in their contents. The nestlings in each nest were measured regularly (in most cases every second day) from soon after hatching (day 0) or after the nest was located, until fledging (day 10-11) or depredation. In this way, each nest was measured on a mean of 3.5 days \pm 1.7 SD. Nestlings were weighed to the nearest 0.1 g with a spring balance (Pesola) and tarsus length (mean of right and left tarsus) and bill (exposed culmen) length measured to the nearest 0.1 mm with vernier callipers.

Throughout this study, we used the rate of food provisioning to nestlings (number of feeding visits to the nest) as the measure of parental effort (PE). Nestling feeding is likely to be the most energetically and time consuming form of parental care in most bird species (Moreno & Hillström 1992). Food provisioning observations (2.8 hours \pm 1.5 SD) were performed at nests on day 5-8 after hatching (one nest per territory). During each observation, the number of feeding visits to the nest by both the male and female parent was recorded. In order to reduce disturbance to the breeding birds, observations were made with Sony Handycam® 8 mm video cameras (Sony Corporation, Japan) setup on tripods 1-3 m from the nests and covered with hessian.

In order to investigate how the local spatial availability of conspecifics influences parental care, we classified territories ($n = 29$ breeding pairs) into two categories according to the number of adjoining territories. 'Low neighbour number' (LN) territories ($n = 8$) had 1-2 neighbouring breeding territories, while 'high neighbour number' (HN) territories ($n = 21$) had 3-4 neighbouring breeding territories. The number of neighbouring territories was determined by the spatial arrangement of the territories. LN territories occurred in a linear strip one territory wide, while HN territories occurred in a clumped arrangement. The narrow linear arrangement of LN territories was created artificially by mowing reeds around property boundaries and to create open access areas and fire-breaks, which was done regularly as part of the Melbourne Water management program. This meant that we could analyse the effect of neighbour number through the spatial arrangement of territories largely independently of variation in the actual territory density (territory size) and territory quality. Both classes of territory occurred on the borders of a series of lakes on the study site. There were no indications of differences in habitat quality between LN and HN nests (other than the variation in paternal food provisioning presented in this paper), as breeding dates, clutch size and fledging success were the same (see Results). Furthermore, we did not detect any differences in vegetation structure between LN and HN territories (M. Berg & J. Welbergen, unpubl. data). Only one nest or breeding attempt per territory was observed.

Intruder experiments

In order to test how changes in male and female PE may arise from the presence of either a male or female conspecific on the breeding territory, we conducted experimental intrusions in reed warbler breeding territories during 1999 and 2000. Male Australian reed warblers defend their territories vigorously against intruding males. The presence of females on the territory may be interpreted by males as an extra-pair mating opportunity, as females in this and several other species (Double & Cockburn 2000 and references therein) frequently undertake extra-territorial forays. We presented the 'focal' birds (male and female parent) at each experimental nest with caged 'trial' birds approximately halfway through the nestling period (day 5-7 after hatching). Cages were made of blackened wire-mesh (to eliminate glare), measured approximately 0.4 m cubed and were mounted on a pole approximately 1.2 m above the ground. Each cage had two horizontal reed stems for perches. Cages were placed approximately 5 m from the nest to ensure they were within the breeding territory of the focal pair (chapter 6), and left in the same position for each trial. An empty cage was put into place at each focal nest at least one day before the trials, and remained there throughout the experimental period on that nest (2-3 days), so the focal birds would become accustomed to its presence. In a random order, each focal nest underwent a empty cage control trial to test the reaction of the focal birds to the cage treatment, and one of the following three experimental trials chosen randomly: 1) female Australian reed warbler, 2) male Australian reed warbler to control for intra-specific aggression, and 3) a greenfinch (*Carduelis chloris*) as a neutral (non-warbler) control. This design allowed us to make paired comparisons of experimental and control trials on each nest, thereby avoiding potentially confounding effects of clutch size, density or territory quality (although focal nests were chosen randomly with respect to these variables). Trial reed warblers were adults caught in the study population but at least 100 m (approximately five territories; cf. chapter 6) away from the focal birds to reduce the chance of familiarity between focal and trial individuals affecting the experimental results. A different trial reed warbler was used for each trial. All trial female reed warblers had brood patches, indicating that they were approaching or engaging in incubation, but were not necessarily fertile, at the time of the experiments (Rogers *et al.* 1986); in only two cases were trial females known to be fertile (egg laying) at the time of the experiment. The greenfinch is an introduced passerine approximately the same size as the Australian reed warbler that is well established throughout the breeding range of the Australian reed warbler in south-eastern Australia (e.g. Slater *et al.* 1989) and is abundant on the study site. This species was chosen to be a familiar, non-predatory or brood parasitic species but to minimise the possibility of any sort of innate reaction (e.g. nest defence), thus testing only the reaction of the focal birds to the cage with a bird treatment. We randomly selected one of six adult greenfinches of unknown sex for each trial. These greenfinches had been recently captured from sites elsewhere in Melbourne and kept in flight cages with *ad libitum* food and water. Trials lasted for one hour and were performed on consecutive days at each focal nest or on the same day but separated by at least two hours. To quantify parental effort during each trial, feeding observations (one hour) were made as described above. All experimental nests had biparental care (i.e. both the

male and female parent were observed contributing substantially to feeding the nestlings during control observations).

Data analyses

All statistical tests were performed using SPSS 11 for Windows (SPSS Inc., USA) and followed Quinn & Keough (2002). Feeding rate data were often not homoscedastic or normally distributed, so we used non-parametric statistical tests. Growth rates were analysed using the linear mixed model (MIXED) procedure with restricted maximum likelihood (REML) estimation, and included class of territory (LN or HN) and nestling age as fixed effects, and nest, nestling identity and brood age as random effects. We tested the effects of number of neighbours (LN or HN) and brood age with Type III tests of fixed effects. Means are given \pm SEM unless otherwise stated, *P*-values are two-tailed and corrected for ties, and the null hypothesis is rejected at $P < 0.05$.

RESULTS

Parental care and spatial availability of conspecifics

We detected significant differences in the food delivery rate to nestlings between LN and HN territories. Male reed warblers fed at a significantly lower rate in HN territories than LN territories (Mann-Whitney test, $Z = 2.302$, $n = 29$, $P = 0.021$; Fig. 8.1), with a mean difference of 3.2 ± 1.3 more feeds per hour at LN nests (52%). In contrast, maternal feeding rates did not differ between these same LN and HN territories ($Z = 0.196$, $n = 29$, $P = 0.867$; Fig. 8.1), with a mean difference of 0.5 ± 1.2 more feeds per hour at LN nests (9%). As a result of the lower paternal feeding rate, the total feeding rate (male parent + female parent) was significantly lower to HN nests than to LN nests ($Z = 2.028$, $n = 29$, $P = 0.041$; Fig. 8.1), with a mean difference of 3.6 ± 1.7 feeds per hour (32%). The conclusions of these analyses were qualitatively similar when controlling for brood size (food delivery rate per nestling), and we found no significant associations between any measure of feeding rate and observation date ($r < 0.111$, $n = 29$, $P > 0.572$).

Brood size may affect nestling growth rates or feeding rates due to the greater nutritional needs of larger broods. In addition, brood size may change the value of parental care and thus the trade-off between PE and ME, with larger broods resulting in a shift from ME to PE (Westneat 1988). Brood size in our study varied from 2 ($n = 7$) to 3 ($n = 16$), but we found no significant difference in brood sizes between LN and HN nests ($\chi^2_1 = 0.163$, $P = 0.686$). Furthermore, the larger (three nestling) broods were slightly over-represented in HN nests (75%) compared to LN nests (67%).

To further examine the possibility that females compensated for the lower feeding rates of their mates at HN nests, we tested the correlation between male and female feeding rate at each nest. A negative correlation could indicate that females were compensating for lower male feeding rates (or vice versa). Instead, we found a non-significant positive correlation between male and female feeding rates (Spearman's rank correlation, $r_s = 0.280$, $n = 29$, $P = 0.142$; Fig. 8.2). Both paternal and maternal feeding rates were strongly

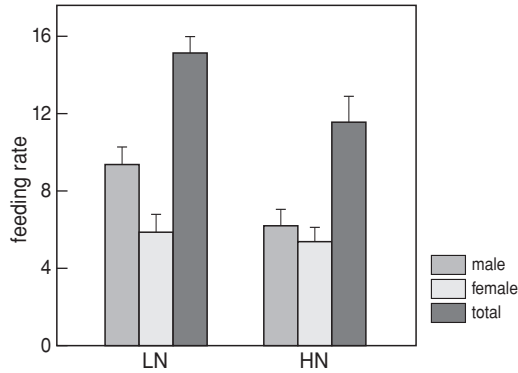


Figure 8.1. Mean \pm SEM male (white bars), female and total feeding rates (feeds per hour) breeding in territories with a low number (LN, $n = 8$) or high number (HN, $n = 21$) of neighbours. Male and consequently total feeding rate to HN nests was significantly lower, while female feeding rate did not change (see text).

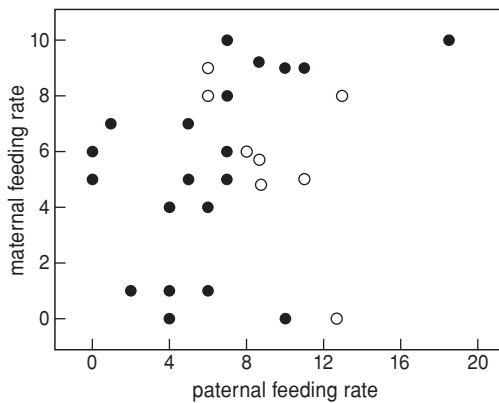


Figure 8.2. Correlation between male and female feeding rates (feeds per hour). There was no significant correlation between male and female feed rates (see text). Open circles represent low neighbour number (LN, $n = 8$) nests, and closed circles represent high neighbour number (HN, $n = 21$) nests.

correlated with total feeding rate at the nest ($r_s = 0.819$ and 0.753 respectively, $n = 29$, $P < 0.001$).

To investigate whether the differences in feeding rates between LN and HN nests were reflected in offspring growth, we compared growth rates of body mass, tarsus length and bill length between the nestlings in LN and HN nests (Fig. 8.3). Nestlings in LN nests grew significantly faster than nestlings in HN nests as measured by mass ($F_{1, 48.787} = 7.779$, $P = 0.008$, age: $F_{1, 36.419} = 1615.915$, $P < 0.001$), tarsus length ($F_{1, 41.481} = 9.811$, $P = 0.003$, age: $F_{1, 36.597} = 1673.946$, $P < 0.001$) and bill length ($F_{1, 54.770} = 7.521$, $P = 0.008$, age: $F_{1, 37.355} = 858.209$, $P < 0.001$). Despite these differences in growth rates, nestling mortality was not observed in any of the 29 nests included in this analysis.

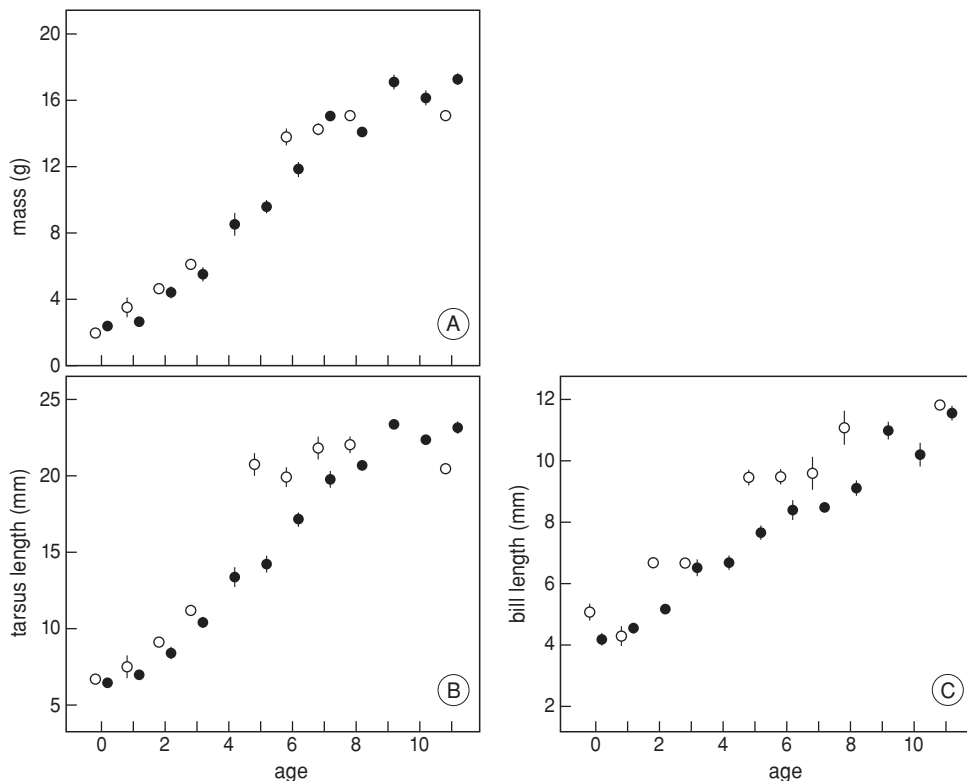


Figure 8.3. Nestling growth measured by (A) body mass (g), (B) tarsus length (mm), and (C) bill length (mm). Open circles represent low neighbour number (LN) nests, and closed circles represent high neighbour number (HN) nests. Values show mean \pm SEM. Hatching is day 0. Nestlings grew significantly faster in LN nests than HN nests according to all three morphometric variables.

Intruder experiments

When compared to a control empty cage, male parents dramatically reduced their feeding rate in the presence of both a male (65% decline in mean feeding rate; $Z = 2.462$, $n = 12$, $P = 0.012$; Fig. 8.4) and a female (63% decline; $Z = 2.847$, $n = 12$, $P = 0.003$; Fig. 8.4) conspecific territorial intruder. There was no significant difference in male feeding rate in the presence of a greenfinch intruder (27% decline; $Z = 1.705$, $n = 12$, $P = 0.109$; Fig. 8.4). In contrast, female parents did not change feeding rate significantly to conspecific intruders of either sex compared to the control empty cage (male intruder: $Z = 0.572$, $n = 12$, $P = 0.648$, <1% increase; female intruder: $Z = 0.893$, $n = 12$, $P = 0.432$; 22% decline) or to a greenfinch intruder ($Z = 0.380$, $n = 12$, $P = 0.788$, 35% increase). As a result, total feeding rates (Fig. 8.4) declined significantly compared to control empty cage trials in the presence of a conspecific intruder of either sex (male conspecific: $Z = 2.457$, $n = 12$, $P = 0.012$, 42% decline; female conspecific: $Z = 2.192$, $n = 12$, $P = 0.030$; 48% decline), but not in the presence of a greenfinch intruder ($Z = 0.567$, $n = 12$, $P = 0.648$, 5% decline).

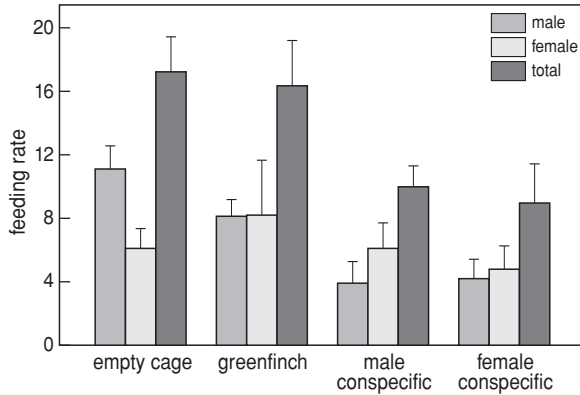


Figure 8.4. Mean \pm SEM male, female and total feeding rates (feeds per hour) in response to the experimental presence on the breeding territory of an unknown male or female conspecific, or a greenfinch. Male feeding rate was significantly lower in the presence of a male or female conspecific but not a greenfinch, while female feeding rate did not change in response to any intruder.

DISCUSSION

Parental effort and the spatial availability of conspecifics

We examined how the local spatial availability of conspecifics of both sexes affects the PE of Australian reed warblers, by comparing the feeding rates of both parents in nests with few (1-2; LN nests) and many (3-4, HN nests) territorial neighbours. Our study design was such that we could isolate the effect of number of neighbours independently of territory density, but such variation in the number of neighbours can be expected to covary with territory density in most territorial arrangements along with nearest neighbour distances. Our results show that male reed warblers reduced their feeding rate when breeding with more neighbours. In contrast, there was no difference in female feeding rate between LN and HN territories. This decline in the male share of food provisioning with the number of neighbouring territories suggests that males face a trade-off between PE and activities directed at conspecifics. As breeding territories in Australian reed warblers typically consist of socially monogamous breeding pairs, such activities could include (extra-pair) ME (directed towards neighbouring females) and TE (directed towards neighbouring males). There was no evidence that this variation was related to seasonal factors. Larger (3-nestling) broods were slightly over-represented in HN territories (75%) compared to LN territories (67%), which means that the food demands of larger broods was not responsible for the higher feeding rate in LN nests.

Unfortunately, due to the dense habitat and cryptic habits of reed warblers, the activity of individuals could not be monitored away from the nest sufficiently to assess the relative importance of ME and TE in the trade-off with PE. Similarly, we could not collect adequate data on natural intrusion rates by males or females. However, both male and female Australian reed warblers frequently make extra-territorial forays of up to several

hundred metres during the breeding season (pers. obs.). The specie-level rates of extra-pair paternity and territorial intrusions have been previously shown to increase with breeding density in a number of avian taxa (reviewed in Birkhead & Møller 1992a; Westneat & Sherman 1997; Møller & Ninni 1998; Griffith *et al.* 2002; Charmantier & Perret 2004; Mougeot 2004).

In addition, a number of alternative explanations exist for the pattern of PE described above. Undetermined differences in habitat quality between LN and HN territories may lead to differences in feeding rates, although this is unlikely to explain our results since only male care and not female care was affected. Furthermore, a decline in male care with increasing spatial availability of conspecific males may also be related to the male's actual or perceived paternity in his own nest (Westneat & Sherman 1993; Wright 1998; Whittingham & Dunn 2001; Neff & Sherman 2002; Sheldon 2002). For these reasons, experimental investigation of these trade-offs in direct response to the presence of conspecifics of both sexes is required.

Our results from experimentally increasing the presence of conspecifics indicate that trade-offs with both ME and TE may have significant effects on the level of male PE. Paternal feeding rates were lower in the presence of either a male or a female conspecific, while maternal feeding rates were not affected. As when comparing LN and HN territories, the reduced share of male food provisioning led to lower total food provisioning rates were lower when another reed warbler was present on the territory. The reductions in paternal feeding rates were similar regardless of the sex of the caged bird. Neither parent reduced feeding in response to a caged European greenfinch, a common introduced species on the field site. Thus our experimental results suggest that males trade-off PE against both ME and TE, in the form of intrusions from female and male conspecifics, respectively.

A notable shortcoming of the present experiment is that we did not directly address the issue of whether males distinguished between sexes of intruders. Furthermore, the fertility status of the females presented during experiments was in most cases not known, so it is unknown whether males would distinguish between fertile and non-fertile females as potential mates and adjust their ME accordingly. Nevertheless, our experimental results demonstrate that male, but not female, PE is affected by the availability of conspecifics of either sex. We believe this is likely to involve both TE towards male conspecifics and ME towards female conspecifics. The presence of a female on the territory is likely to be interpreted by males as an extra-pair mating opportunity, as females in this and several other species (Double & Cockburn 2000 and references therein) frequently undertake extra-territorial forays. Furthermore, extra-pair copulations occur throughout the breeding season (M. Berg & M. Bleeker, unpubl. data). We have not observed males reacting aggressively to extra-pair females in this species (pers. obs.). However, male Australian reed warblers defend their territories vigorously against intruding males throughout the breeding season (chapter 5). Future experiments could tease apart the basis of male responses to intruding males, and fertile and non-fertile females.

Trade-offs between PE and ME

Despite the robust predictions there has been little empirical support for a trade-off

between male parental care and the opportunity for extra-pair copulations, and few studies have simultaneously considered corresponding female behaviour (Magrath & Komdeur 2003). The extent to which males should invest in PE or ME may depend on several factors (reviewed in Magrath & Komdeur 2003). These include: (i) variation in female competence to provision a brood without male help (e.g. Whittingham 1989; Beletsky & Orians 1990; Dunn & Robertson 1992), (ii) the value of the brood (e.g. Westneat *et al.* 1990; Magrath & Elgar 1997; Komdeur *et al.* 2002), (iii) stochastic factors that may affect the chance of successful reproduction, such as nest predation (e.g. Komdeur & Kats 1999; Veiga *et al.* 2002), and (iv) the opportunity for males to gain additional matings (e.g. Smith 1995), such as the experience or quality of the male (e.g. Morton & Derrickson 1990), the social organisation of the population (e.g. Mulder *et al.* 1994), or the temporal (e.g. Westneat 1988; Magrath & Elgar 1997) or spatial availability of potential mates (Westneat & Sherman 1997). Of these factors, we expect that the spatial availability of potential mates is likely to be the most important difference between the LN and HN nests used in our analyses because the spatial arrangement of territories was largely controlled artificially and should have been independent of territory quality (see Methods).

Among birds, trade-offs between PE and ME have more commonly been observed during the incubation rather than the nestling feeding period. This may be because in synchronously breeding populations fertile females are more abundant in the population during incubation than later during nestling feeding (Magrath & Elgar 1997; Magrath & Komdeur 2003). Furthermore, incubating birds are usually confined to the nest for extended periods whereas nestling feeding involves regular trips away from the nest, which might enable greater interaction with fertile neighbours without a large impact on the level of PE (Magrath & Komdeur 2003). In European starlings (*Sturnus vulgaris*), Komdeur *et al.* (2002) have found a trade-off between ME and PE in relation to early incubation but not nestling feeding, while Smith (1995) has reported a trade-off between ME and PE during the early, but not late, incubation period. Males with an additional easily defended nest-box spent less time incubating, more time singing and had a greater chance of attracting a secondary female. There was no relationship with male incubation during the late incubation period or male feeding of nestlings, presumably because breeding is highly synchronous in starling populations and males attract most females during the early incubation period (Komdeur *et al.* 2002).

If the spatial availability of additional mates mediates a trade-off between PE and ME, with higher breeding densities generating a shift towards ME, one would also expect a positive association between breeding density and mating success. In line with this, previous studies have supported such a relationship between breeding density and extra-pair paternity (EPP) within species (e.g. Møller & Birkhead 1993; Westneat & Sherman 1997; Møller & Ninni 1998; Charmantier & Perret 2004; Mougeot 2004). Two studies considering the rate of EPP following experimental manipulation of nest density found a positive effect of breeding density on the rate of EPP in eastern bluebirds (*Sialia sialis*; Gowaty & Bridges 1991) and blue tits (*Parus caeruleus*; Charmantier & Perret 2004) although a further study using this approach found no such effect in pied flycatchers (*Ficedula hypoleuca*; Rätti *et al.* 2001).

Trade-offs between PE and TE

Few studies considering the trade-off between PE and ME have adequately taken into account concurrent trade-offs involving TE and somatic activities. This is a particular shortcoming in the absence of direct information about changes in mating effort (Magrath & Komdeur 2003). Our results suggest that trade-offs between PE and TE could be of similar importance to those trade-offs involving PE and ME. Male Australian reed warblers maintain small breeding territories vigorously throughout the breeding season (chapter 5), which may be important to secure ongoing access to food resources and future breeding opportunities. Our results suggest that the necessity of being aggressive to maintain breeding resources throughout a breeding season may constrain male PE. The high cost of losing a minimum breeding site may select for the maintenance of aggressive behaviour and low paternal investment, even when paternal care improves short-term reproductive success.

Costs of reduced male care

We found no evidence that females compensated for reductions in male PE. There was a weakly positive correlation between the feeding rates of the male and female parents at each nest ($r_s = 0.280$; Fig. 8.2), and no evidence that females responded to the reduced male feeding during experiments by increasing their own feeding rate. Thus, lower male feeding rates led to lower total feeding rates at both observational and experimental nests. Although females could have been expected to compensate for reduced male feeding to some extent, complete compensation is unlikely because that would lead to selection favouring males that provide less care (Houston & Davies 1985; Winkler 1987; Wright & Cuthill 1989).

Variation in the level of male feeding is likely to have an important influence on the success of a reproductive attempt in many species with biparental care (e.g. Nur 1984a; Whittingham *et al.* 1994; Møller 2000). Nestling growth rates were significantly lower in HN nests than in LN nests, reflecting the variation in male and total feeding rates to these groups of nests. Although starvation was rare in this population (pers. obs.), and was not observed in any of the 29 nests used in this study, there are likely to be significant costs to reduced male feeding in terms of post-fledging survival and recruitment among these nests (e.g. Garnett 1981; Gustafsson & Sutherland 1988; van Noordwijk *et al.* 1988; Tinbergen & Boerlijst 1990; Lindén *et al.* 1992; Verboven & Visser 1998; Merilä *et al.* 1999).

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