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The illusion of monogamy

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**No effect of breeding density,
synchrony or predation on levels
of extra-pair paternity in the reed bunting**

Karen M. Bouwman & Jan Komdeur

Abstract

Part of the large variation found in extra-pair paternity (EPP) within and between species may be explained by breeding density and synchrony, since these may affect the costs and benefits of extra-pair mating behaviour by influencing the number of potential mates. Brood predation may influence breeding synchrony, and is therefore also likely to affect costs and benefits of EPP. Furthermore, brood predation may also induce a male bet-hedging strategy: to avoid complete loss of reproductive success males may increase their attempts to fertilise offspring in different broods. We investigated the effect of local breeding density, local breeding synchrony and predation on the levels of EPP in reed buntings. The reed bunting (*Emberiza schoeniclus*) is a socially monogamous passerine, with extremely high levels of EPP (50% of offspring in 80% of broods). We found no effect of local breeding density or two measures of local synchrony (breeding synchrony index and number of fertile females) during the peak fertile period of the female on the proportion of EPP in broods. Neither did we find an effect of predation of the first brood (both natural and experimental) on the proportion of EPP in the subsequent brood, or on the number of extra-pair fertilisations gained by the social male in other broods. We conclude that extra-pair mating behaviour in our population of reed buntings was not constrained by the number of potential mates and that male nor female extra-pair mating behaviour appeared to be altered by predation of their brood.

Introduction

Molecular techniques have revealed that extra-pair paternity (EPP) is common in many socially monogamous birds (Griffith *et al.* 2002), but large variations in levels of EPP have been found between species, between populations of the same species and between years within the same population (Petrie & Kempenaers 1998). Breeding density and synchrony affect the temporal and spatial distribution of potential extra-pair mates. Since the availability of extra-pair mates is likely to affect the costs and benefits of EPP, and thus the chance that individuals engage in extra-pair copulations (EPCs; Birkhead & Møller 1992), breeding density and synchrony have been suggested to contribute to the variation in levels of EPP (Westneat & Sherman 1997; Møller & Ninni 1998).

At higher breeding densities, searching costs for extra-pair mates may be reduced (Westneat 1990; Birkhead & Møller 1992). However, greater densities may also impose costs, as the number of territorial intrusions by potential extra-pair males increase (Komdeur *et al.* 1999), thereby increasing the chance of losing paternity in a male's own nest (Birkhead & Møller 1992). In addition, females may experience more harassment by extra-pair males (Morton *et al.* 1990). In an inter-species comparison, Møller and Ninni (1998) reported higher levels of EPP with increasing densities, while Westneat and Sherman (1997) found no relation between density and levels of EPP. In an intra-species comparison, a positive relationship was found in several studies (Hoi & HoiLeitner 1997; Langefors *et al.* 1998; Richardson & Burke 2001), while others failed to find a relationship (Dunn *et al.* 1994; Sundberg & Dixon 1996; Tarof *et al.* 1998; Veiga & Boto 2000; Conrad *et al.* 2001). We are only aware of one study reporting high levels of EPP at low breeding densities, but this was only the case when breeding synchrony was also low (Thusius *et al.* 2001).

Studies on the effect of breeding synchrony on the level of EPP have generated two main hypotheses. If EPCs are mainly male driven, a trade-off between mateguarding and extra-pair mating behaviour may be expected, leading to a negative relationship between breeding synchrony and EPP (Birkhead & Biggins 1987; Westneat & Sherman 1997; Weatherhead & Yezerinac 1998). If on the other hand EPCs are mainly female driven, females may be expected to make a better judgment of relative male quality since more male-male competition is occurring at the same time, leading to a positive relationship between breeding synchrony and EPP (Stutchbury & Morton 1995; Stutchbury 1998a; Stutchbury 1998b). Support has been found for both hypotheses, as a negative (Strohbach *et al.* 1998; Dunn *et al.* 1999; Saino *et al.* 1999; Thusius *et al.* 2001) and positive (Stutchbury *et al.* 1997; Stutchbury 1998b; Chuang *et al.* 1999) relationship between breeding synchrony and levels of EPP have been reported. However, also no relationship between breeding synchrony and levels of EPP has been found in a

number of studies (Dunn *et al.* 1994; Perreault *et al.* 1997; Weatherhead 1997; Yezerinac & Weatherhead 1997).

Brood predation is likely to affect breeding synchrony, since renesting attempts following predation will occur later in the season than first attempts. Furthermore, brood predation may also influence male and female extra-pair mating strategies. If failure of the nest reflects the low quality of her social male, females may increase their extra-pair mating effort (Gissing *et al.* 1998). Alternatively, males may invest in a 'bet-hedging strategy'. Males that gain fertilisations in different broods may salvage some reproductive success when brood predation rate is high (Perreault *et al.* 1997). Following predation of the first brood, males may increase their investment in gaining extra-pair fertilisations (EPFs) in other broods. As a trade-off between mate guarding and seeking EPCs has been found to exist in several species (Chuang-Dobbs *et al.* 2001; Johnsen *et al.* 2003; Eikenaar *et al.* 2004), an increased investment in EPCs may result in higher levels of EPP in the male's own replacement brood. To our knowledge, only one study has presented results on the effect of clutch or brood predation on subsequent levels of EPP. In American goldfinches (*Carduelis tristis*), a positive association between nest failure and proportion of EPP in the replacement brood was found (Gissing *et al.* 1998). However, the mechanism behind this increase in EPP remained unclear (Gissing *et al.* 1998).

We investigated the effects of breeding density, synchrony and predation on levels of EPP in a population of reed buntings (*Emberiza schoeniclus*) in The Netherlands. The reed bunting is a socially monogamous passerine, but with extremely high levels of EPP (50% of offspring in 80% of nests; Bouwman *et al.* 2005). This species is capable of raising two broods in a single season. Extra-pair mating behaviour seems to be male-driven in this species, since males, but not females, were often observed intruding in other territories (Marthinsen *et al.* 2005; pers.obs). We therefore expected a negative relation between breeding synchrony and levels of EPP. Furthermore, we expected breeding density to be positively related to frequency of EPP, as higher densities lead to increased extra-pair mating opportunities. Finally, we predicted that, following both experimental and natural nest predation, males increase their investment in seeking EPCs. This was expected to result in more EPFs gained in other broods, and in higher cuckoldry rates in their own broods.

Methods

Study area and data collection

From 2002 to 2003 we studied a population of reed buntings in a 13 ha study site, on the island of Noorderplaat (45 ha) in 'De Biesbosch' National Park in the Netherlands (51°45'N, 4°45'E). In 2002 and 2003 respectively 44 and 35 pairs were breeding within our study site. On average, 96% of adult reed buntings were caught using mist nets and ringed with a numbered aluminium ring and a specific combination of three colour rings for individual recognition. A blood sample was taken from the brachial vein for DNA analysis, and stored in 96% ethanol at room temperature.

Nests are built on or just above the ground and were located through systematic searches that flushed females off the nest, or by observing territorial birds for nest-related activities. The identities of the social pair of a nest were determined by direct or video observations of colour-ringed birds protecting the nest, incubating and feeding nestlings (for a description of the method using video recordings see chapter 4). Nestlings were bloodsampled two days after hatching by taking a small blood sample from the leg vein. Unhatched eggs were inspected for embryonic development, which, if present, was used as a source of DNA. We located 97% of all nests that fledged young ($n = 78$) in 2002 and 2003; only in two cases fledglings were seen without having located the nest.

Predation and nest protection

Predation rates of both eggs and nestlings of unprotected nests was high (67%, $n = 46$ nests). The main predators were stoats (*Mustela erminea*) and polecats (*Mustela putorius*); no avian predators were seen in the study area. Due to these high levels of predation, we were unable to locate all nests before they were predated. However, as there was no obvious gradient in risk of predation across the site, we believe we obtained a random sample of individual reproductive success for all males in our site.

In the breeding seasons of 2002 and 2003, we protected nests against ground predators. After clutch completion, nests were protected using small enclosures (30 cm high and approximately 1 metre wide), made of bamboo sticks and wire netting that was pinned down with tent pegs (see chapter 2 for a detailed description of the procedure). Nest protection was removed when the nestlings were approximately 5 days old. In 2002 the nest protection was very effective, as 93% of protected nests were not predated ($n = 42$). However, apparently predators learned to circumvent the nest protection, as the three nests that were predated were among the last nests of the season. In 2003 broods were already occasionally predated early in the season; after 37% of protected nests ($n = 27$) were predated, we stopped protecting the nests in the second half of the breeding season.

Breeding density and synchrony

Because more than 90% of all extra-pair sires were resident within two territories of the focal female (chapter 2), we determined breeding density and synchrony at a local scale. Local breeding density was defined as the number of territories that were at least partly located within a 100-meter radius (i.e. approximate equivalent of including two territories) around the focal nest.

An index for local breeding synchrony (Synchrony Index (SI); Kempnaers 1993) was calculated for each nest by determining the proportion of females that were fertile on territories at least partly located within a 100-meter radius around the focal nest during the fertile period of the focal female. The local SI for a nest equals the sum of the number of other fertile females on each day within a 100-meter radius divided by the product of the number of days the focal female is fertile and the number of other females within a 100-meter radius (Stutchbury *et al.* 1998).

As an alternative measure for breeding synchrony, we calculated the number of females within a 100-meter radius around the focal nest that had at least one day overlap in fertile period with the focal female (Johnsen & Lifjeld 2003). This 'number of fertile females' is an absolute measure for extra-pair mating opportunities, while SI is a relative measure. As there is a very strong correlation between these two measures of breeding synchrony ($r_s = 0.89$, $n = 121$, $p < 0.001$), we only included one of these two variables at the same time in the analyses.

In general, females are expected to be fertile for the duration of sperm storage before the first egg is laid, until the day the penultimate egg is laid (Birkhead & Møller 1992). However, mate guarding behaviour of male reed buntings peaks three days before the female lays the first egg, and dramatically drops after the first egg has been laid (O'Malley 1993), indicating that this is likely to be the peak fertile period. A similar peak fertile period has been shown in other passerines (Krokene *et al.* 1996; Lifjeld *et al.* 1997; Sheldon & Ellegren 1998; Komdeur *et al.* 1999). We therefore defined the peak fertile period of a female as three days before the first egg is laid until the day the first egg is laid.

Experimental predation

To experimentally test the effect of predation on levels of EPP, we induced re-nesting by removing the first clutches of seventeen pairs after six to eleven days of incubation (2002: 6 pairs, 2003: 11 pairs; total incubation period: twelve to fourteen days; under licence of the Dutch ethical committee). The embryos of first clutches were used as a source of DNA, while replacement clutches were blood-sampled after hatching.

Following successful first nests, the first egg of second nests was laid with a median of 19 days after the fledglings leave the nests (range 4–32 days, $n = 19$;

figure 6.1). As fledglings may be predated soon after leaving the nest, the number of successful broods may be overestimated. The distribution of the number of days between fledging or predation of the first nest and laying the first egg of the second nest is shown in figure 6.1. A replacement clutch is usually laid around 5 days after failure (range 3-29; figure 6.1). If females start egg-laying soon after fledging the first brood, it is likely that they have lost their offspring. We used the gap in the distribution of the number of days between nests following fledging (i.e. 11 to 14 days; figure 6.1) to distinguish between successful fledging and non-successful fledging. We assumed that females that initiated their second nest within 10 days of fledging their first nest had lost their offspring ($n = 5$) and these broods were included in the group of predated first broods.

Paternity analysis

DNA was extracted from blood samples using salt extraction (Richardson *et al.* 2001). Individuals were genotyped using six fluorescently labelled microsatellite markers: *Escu1*, *Escu4*, *Escu6* (Hanotte *et al.* 1994), *Pdou5* (Griffith *et al.* 1999), *Mcyu4* (Double *et al.* 1997) and *Ppi2* (Martinez *et al.* 1999). Parentage was determined by using a likelihood-based approach in CERVUS (version 2.0; Marshall *et al.* 1998). This program assesses the confidence of paternity assignment using criteria generated through a simulation taking into account allele frequencies in the population, the number of possible candidate parents, the proportion of candidate parents sampled, and the percentage of missing genetic data and genotyping errors. The criteria (delta criteria) estimate the critical difference between the LOD scores -the natural logarithm of the likelihood ratio-

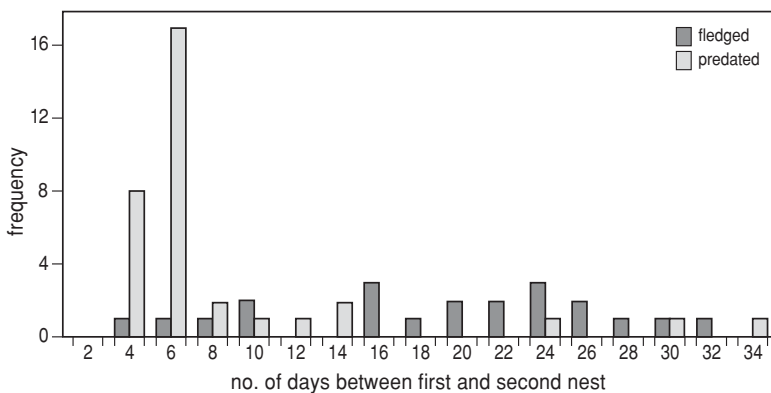


Figure 6.1. Frequency distribution of the number of days between the end of the first brood and the laying of the first egg of the subsequent brood by the same pair in reed buntings for the years 2002 and 2003. The first brood may end either through fledging of the nestlings, or through predation (either naturally, during the egg or nestling stage, or experimentally).

of the first and second most likely candidate at a level of >95% confidence and >80% confidence. For a detailed description of the methods see chapter 2. In 2002 and 2003 combined, 501 offspring were genotyped from 129 nests and paternity was assigned to 90% of offspring with 80% confidence. Extra-pair males sired 54.6% of offspring in 2002 ($n = 262$) and 46.4% of offspring in 2003 ($n = 211$).

Data analyses

We used multilevel generalised linear models to analyse the effect of breeding density, synchrony and the time of season the clutch was initiated ('first egg date') on the proportion of EPP in a brood, assuming a binomial error distribution with logit-link function and using the number of offspring in the brood as the denominator. The two-level hierarchical structure of the proportional response data (i.e. proportion of EPP in a brood) was built up with the identity of the pair as the highest level and the broods belonging to each pair as the lowest level. This approach allowed us to make full use of all available data, while at the same time accounting for (i) having included pairs more than once, as often a pair produced more than one brood in a season or in different years, and (ii) the number of offspring in a brood, which varied between two and five offspring. The model was implemented using reweighted iterative generalised least squares (RIGLS) and 2nd order penalised quasi-likelihood approximation (PQL; Rasbash *et al.* 2004). The significance of variables was tested using the Wald statistic, which follows a χ^2 -distribution. Variables with $p > 0.1$ were backwards eliminated, starting with interaction terms. We presented the Wald statistic values of the variables in the final model and of the eliminated variables prior to elimination. We tested the effect of variables on the proportion of EPP in a brood including all broods. As female may actively choose not to engage in EPCs (Birkhead & Møller 1992), we also performed the multivariate analysis only using broods with at least one extra-pair offspring.

To test if predation of the first nest affected the proportion of EPP in the subsequent nest, we used a multilevel generalised linear model, as described above. Next we tested whether males of which the first nest was predated gained more EPFs than males that fledged their first brood. To allow a proper comparison, all males need to be in a similar stage of their reproductive cycle. We therefore compared the proportion of males in each group (i.e. first nest predated or fledged) that gained EPP in another brood during the second peak fertile period of their own female.

Statistical analyses were performed using SPSS 11.0.1 (2001) and MLwiN 2.0. Means are expressed with standard errors, probability values are two-tailed and we assumed significance if $p < 0.05$.

Results

Breeding density and synchrony within and between years

The average local breeding density and local SI differed significantly between 2002 and 2003 (mean local breeding density: 9.6 ± 0.4 ($n = 66$) vs. 7.0 ± 0.3 ($n = 55$); $t = 4.67$, $df = 119$, $p < 0.001$; mean local SI: 0.12 ± 0.01 ($n = 66$) vs. 0.26 ± 0.03 ($n = 55$); $t = -4.77$, $df = 119$, $p < 0.001$). The average number of fertile females was not significantly different between the years (no. of fertile females: $U = 1533.0$, $n_{2002} = 66$, $n_{2003} = 55$, $p = 0.13$). Furthermore, there was a significant negative relationship between the first egg date and both local SI ($r = -0.41$, $n = 121$, $p < 0.001$; figure 6.2) and the number of fertile females ($r_s = -0.33$, $n = 121$, $p < 0.001$), but not between the first egg date and local breeding density ($r = -0.06$, $n = 121$, $p = 0.55$).

Influence of breeding density and synchrony on EPP

We found no significant interactions between year and any of the variables (all: $p > 0.14$), nor between local breeding density and local SI ($p = 0.55$). Furthermore, no significant effect was found of first egg date, local breeding density, local SI or number of fertile females (after exchanging with breeding synchrony) on the proportion of EPP, either when including all broods, or when including only broods with EPP (table 6.1).

Influence of predation on EPP

There was no difference in the probability of a female laying a replacement clutch between naturally predated clutches (75%; $n = 12$) and experimentally predated

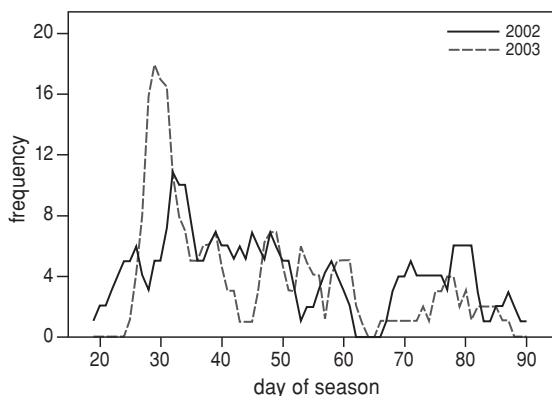


Figure 6.2. Frequency distribution of the number of reed bunting females in their peak fertile period on a given day during the breeding season (1 April = day 1) for the years 2002 and 2003.

Table 6.1. Multilevel generalised linear model of the relation between time of season and local socio-ecological factors during the peak fertile period of the female, and the proportion of EPP in reed bunting nests for the years 2002 and 2003. The effect of variables are tested in a multivariate analysis; (i) all broods are included ($n = 121$), (ii) only broods containing EPP are included ($n = 88$). The direction of the parameter estimates, values of the Wald test statistics and their significance are shown.

Variable	All broods		Broods containing EPP	
	Wald	p	Wald	p
Year	- 5.12	0.024	- 0.01	0.92
First egg date	- 0.05	0.82	- 1.49	0.22
Breeding density	+ 1.59	0.21	+ 0.92	0.34
Synchrony index (SI)	+ 1.22	0.28	+ 0.35	0.55
No. fertile females (exchanged with SI)	- 0.01	0.92	- 0.54	0.46

clutches (76%, $n = 17$; $\chi^2 = 0.01$, $df = 1$, $p = 0.93$). Replacement rates were not different between nests that were predated in the egg (75%, $n = 12$) or nestling stage (62%, $n = 13$; $\chi^2 = 0.52$, $df = 1$, $p = 0.47$). Furthermore, there was no difference in the number of days before a replacement clutch was laid by the same female for naturally predated clutches (median = 5 days, range = 3-29 days, $n = 7$) or broods (median = 5 days, range = 4-23 days, $n = 9$), and experimentally predated clutches (median = 5 days, range = 3-14 days, $n = 15$). We therefore made no distinction between natural and experimental predation or between predated clutches and predated broods in subsequent analyses. Pairs that produced a second clutch (either after predation or fledging), always initiated their first clutch before 55 April days (i.e. 25 May). Of all pairs that successfully fledged a brood, which was initiated before this date, 57% ($n = 37$) laid a second clutch (compared with predated first broods: $\chi^2 = 1.85$, $df = 1$, $p = 0.17$).

There was no difference between the two groups (i.e. with first nest fledged or predated) in the clutch size of first or second nests, nor in the difference in clutch size between first and second nests (table 6.3). Furthermore, there was no difference between the fledged or predated group in the proportion of EPP in the first or second nests, nor in the difference in proportion of EPP between first and second nests (table 6.3).

Second broods after fledging were produced significantly later in the season than second broods after predation (median (range) day of first egg for fledged vs. predated group: 2002: 81 (70-90), $n = 12$ vs. 52 (43-81), $n = 12$; $t = 6.61$, $df = 22$, $p < 0.001$; 2003: 85 (73-98), $n = 7$ vs. 58 (49-83), $n = 16$; $t = 5.00$, $df = 21$, $p < 0.001$). However, we found no difference between the peak fertile period of second broods following either fledging or predation in breeding SI

(respectively 0.12 ± 0.02 ($n = 12$) and 0.14 ± 0.02 ($n = 31$); $t = -0.61$, $df = 41$, $p = 0.55$) or mean number of fertile females available (1.6 ± 0.3 ($n = 12$) and 1.5 ± 0.3 ($n = 31$); $U = 175.0$, $p = 0.76$). We found no effect of predation of the first nest on the proportion of EPP in the subsequent brood in a multivariate analysis, after correcting for the effect of year, first egg date and proportion of EPP in the first brood (table 6.2).

Since there was no difference in the number of fertile females available during the peak fertile period of second broods following either fledging or predation, no correction for EPC opportunities was necessary. Males that had their first nest predated were not more likely to gain EPFs during the peak fertile period of their second nest than males that fledged their first brood (respectively 6% ($n = 31$) and 8% ($n = 12$); $\chi^2 = 0.05$, $df = 1$, $p = 0.83$).

Table 6.2. Multilevel generalised linear model of the relation between fledging ($n = 12$) or predation ($n = 31$) of the first brood and the proportion of EPP in the subsequent brood in reed buntings for the years 2002 and 2003. Other ecological factors are also included in the initial model. The direction of the parameter estimates, values of the Wald test statistics and their significance are shown.

	Wald	p
Year	- 5.22	0.022
First egg date	+ 1.55	0.21
EPP first brood	+ 0.19	0.76
Predated 0/1	+ 0.62	0.43

Table 6.3. The difference in clutch size and proportion of EPP between two groups of reed bunting pairs for which the first brood either fledged ($n = 12$) or was predated ($n = 27$). Presented are mean values \pm se, Mann-Whitney U test statistics and their significance, for first and second nests and the difference between them.

	Fledged	Predated	U	p
Clutch size				
First nest	4.1 ± 0.4	4.3 ± 0.2	156.5	0.86
Second nest	3.3 ± 0.1	3.7 ± 0.2	112.5	0.11
Difference	0.8 ± 0.4	0.6 ± 0.3	143.0	0.55
Proportion of EPP				
First nest	0.43 ± 0.11	0.56 ± 0.07	126.0	0.27
Second nest	0.41 ± 0.10	0.43 ± 0.06	152.0	0.76
Difference	0.02 ± 0.12	0.14 ± 0.08	137.5	0.46

Discussion

Influence of breeding density and synchrony on EPP

Local breeding density and synchrony did not significantly affect the proportion of EPP found in reed buntings broods. Neither did we find an interaction between breeding density and breeding synchrony, as was reported in the common yellowthroat (*Geothlypis trichas*; Thusius *et al.* 2001). Possibly the breeding density in our population exceeded a certain threshold level, resulting in sufficient extra-pair mating partners available at all densities throughout the study site (Dunn *et al.* 1994; Tarof *et al.* 1998). Alternatively, mate guarding behaviour may increase as a response to a higher cuckoldry risk with increasing density (Dickinson & Leonard 1996; Komdeur 2001; but see Vaclav & Hoi 2002), resulting in similar levels of EPP in nests at low and high densities. Unfortunately, we do not know whether mate guarding in the reed bunting is affected by breeding densities.

Despite a large variation in breeding synchrony, we found no effect of local synchrony index or the number of fertile females on the proportion of EPP, which is in agreement with several other studies (Perreault *et al.* 1997; Weatherhead 1997; Yezerinac & Weatherhead 1997; Johnsen & Lifjeld 2003). Since synchrony varied with time of season, an effect of synchrony could be underlying an association between the time of season a clutch was initiated and the proportion of EPP (Stutchbury *et al.* 1994; Thusius *et al.* 2001). However, we neither found an effect of the time of season on EPP. This suggests that males were not constrained in their extra-pair mating behaviour through mate guarding, which is in agreement with the finding that Norwegian male reed buntings gain extra-pair fertilisations during the fertile period of their female (Marthinsen *et al.* 2005).

In the tree swallow (*Tachycineta bicolor*), also high levels of EPP but no effect of breeding density or synchrony was found (Dunn *et al.* 1994). The absence of these relationships is suggested to be a result of the capability of female tree swallows to both solicit and reject EPCs (Lifjeld & Robertson 1992; Dunn *et al.* 1994). Density is not expected to hinder females seeking EPCs, providing it is above a certain threshold level, since female tree swallows have been seen to fly long distances to forage (Dunn *et al.* 1994). Possibly females are able to judge the quality of a male, without the necessity of simultaneous male display as a consequence of breeding synchrony (Stutchbury 1998b). In addition, the absence of an effect of breeding synchrony may be explained by the considerable number of EPCs that is gained by floaters, which have no nest of their own (Kempnaers *et al.* 2001). In reed buntings, floating is not a recognised strategy, since the paternity of almost all offspring could be assigned to territorial males. Whether the absence of a relationship between breeding density, synchrony and level of EPP may be a result of female control of EPCs, remains unclear. More behavioural observations

are needed to determine whether in addition to at least some male control of EPCs through intrusions into female territories, female reed buntings have an active role in soliciting and rejecting EPCs.

Influence of predation on EPP

Studying the influence of predation on levels of EPP is hampered by the incomplete knowledge of the fate of fledglings and nests. We were unable to determine offspring survival to independence, as reed bunting young and their parents leave their territory after fledging (pers.obs.). We have therefore adopted an indirect measure to determine the survival of fledged offspring using the number of days between nests. Furthermore, second nests may have been predated, resulting in third nests being classified as second and thus a false inclusion in the group of fledged first nests. Unfortunately, we were not possible to distinguish between delayed reneesting by the female, and nest predation prior to us locating the nest.

We did not find any indication that predation of the first brood had an effect on the proportion of EPP in the replacement brood. Although the fertile period of the second nest is later in the breeding season for the fledged group than for the predated group, this did not have an effect on the number of fertile females locally available. Since predation did not increase asynchronous breeding, and we found no effect of breeding synchrony on the proportion of EPP when including all broods (see above), we cannot expect an effect of predation on levels of EPP from a constrained male point of view. In reed buntings, females may not change their extra-pair mating strategy following predation, if nest predation does not reflect male quality. Females mainly build the nest (Cramp & Perrins 1994; pers.obs.) and probably decide on its location, and nest defence against mammalian predators is unlikely to be successful. In red-winged blackbirds, nests with higher proportions of EPP were more often predated, due to reduced nest-defence by the social male (Weatherhead *et al.* 1994). We did not find any difference in proportion of EPP between first nests that fledged (0.49 ± 0.10 , $n = 15$) and that were naturally predated (0.50 ± 0.11 , $n = 11$; $t = -0.07$, $df = 24$, $p = 0.95$).

Female bet-hedging strategies in response to predation, such as through brood parasitism (Rubenstein 1982; Petrie & Moller 1991; Poysa 2003), have received more attention than male bet-hedging strategies, for instance through extra-pair paternity (Perreault *et al.* 1997). Perreault *et al.* (1997) showed that as a result of high levels of predation, male variance in reproductive success did not increase through EPP, but males with EPP were able to salvage at least some reproductive success. In reed buntings, EPP did increase male variance in reproductive success, since actual reproductive success was 2.4 times larger than apparent reproductive success (unpubl.data). This may have been influenced by the use of nest protection, causing more broods to fledge than under natural predation conditions. We did

not find any evidence that following predation of their nest, males invest more in a bet-hedging strategy than following a successful nest. Males that fledged their first brood are likely to have spent much energy on parental care, as both males and females provide care to fledglings (Cramp & Perrins 1994; pers.obs.). Males of which the first nest was predated are thus expected to have more reserves that they could invest in seeking EPCs. Despite this potential difference in reproductive effort between the two groups, no difference was found in the number of EPFs gained.

To conclude, we did not find any evidence that males or females adjust their extra-pair mating behaviour following predation of their nest. However, since EPP may allow males to salvage some reproductive success when suffering from high predation rates, this may potentially be an adaptive strategy in response to high levels of predation. A comparative analysis between species or populations with regard to the effect of nest predation rate and levels of EPP may reveal interesting patterns.

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