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The illusion of monogamy

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Weather conditions constrain extra-pair mating behaviour in the reed bunting

Karen M. Bouwman & Jan Komdeur

Abstract

Extra-pair paternity (EPP) is common in many socially monogamous birds, but large variations in frequency of EPP are found both between and within species. Local ecological factors can affect the costs and benefits of extra-pair mating behaviour, and may therefore influence the chance that individuals engage in extra-pair copulations (EPCs). We investigated the effect of weather conditions during the peak fertile period of the female on the levels of EPP in reed buntings. The reed bunting is a socially monogamous passerine, with extremely high levels of EPP (50% of offspring in 80% of broods). We found that higher daily minimum temperatures and longer periods of rain during the peak fertile period were associated with lower proportions of EPP. As during adverse weather conditions individuals have to invest more in self maintenance, we suggest that during long periods of rain the extra-pair mating behaviour of all individuals will be restricted, leading to lower proportions of EPP. During cold mornings, time-consuming activities such as mate guarding are likely to be more strongly affected than less time-consuming activities such as EPCs, leading to higher proportions of EPP.

Introduction

Extra-pair paternity (EPP) is common in many socially monogamous birds (Griffith *et al.* 2002), but large variations in frequency of EPP are found both between and within species (Petrie & Kempenaers 1998). Interspecies comparisons have found the occurrence of EPP to correlate with severable types of variables, such as adult mortality, level of paternal care, morphological characteristics and genetic variability (reviewed by Westneat & Stewart 2003). However, as levels of EPP can be highly variable not only between species, but also between populations of the same species (Gyllensten *et al.* 1990; Bjornstad & Lifjeld 1997; Griffith *et al.* 1999) or even within a population between years (Lanfjors *et al.* 1998; Johnsen & Lifjeld 2003), it is essential to get a better understanding of factors influencing extra-pair mating behaviour on the individual level (Westneat & Stewart 2003). Local ecological factors can affect the costs and benefits of extra-pair mating behaviour (Birkhead & Møller 1992), and may therefore influence the chance that individuals engage in extra-pair copulations (EPCs).

Adverse weather conditions may act as constraints on extra-pair mating behaviour through influencing energy expenditure or food availability and thus time budgets (Westneat 1994; Dawson & O'Connor 1996; Redpath *et al.* 2002; Vaclav *et al.* 2003). Up to date only one study investigated the effect of weather conditions (i.e. morning temperature and precipitation) on frequencies of EPP. In bluethroats (*Luscinia s. svecica*), lower morning temperatures during the peak fertile period lead to lower levels of EPP in the brood, whereas the amount of precipitation had no effect (Johnsen & Lifjeld 2003). We investigated the effects daily minimum temperature and daily precipitation on levels of EPP in a population of reed buntings (*Emberiza schoeniclus*) in The Netherlands. The reed bunting is a socially monogamous passerine, with extremely high levels of EPP (50% of offspring in 80% of nests; Bouwman *et al.* 2005). When adverse weather conditions (i.e. low minimum temperatures and high rainfall) were prevailing during the fertile period of the female, we expected a lower frequency of EPP in broods, because both males and females will have to invest more in self maintenance.

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 were fledglings seen without locating the nest.

Fertile period

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.

Weather variables

The following weather data were retrieved from the Royal Netherlands Meteorological Institute (KNMI) in De Bilt (The Netherlands), approximately 50 kilometers from our studysite: daily minimum and maximum temperature (°C), daily amount of precipitation (mm) and daily precipitation duration (hours). There were significant correlations between these variables among themselves and with the time of season (i.e. day the first egg of a clutch was laid (1 April = day 1; table 7.1). Although the timing of EPCs in reed buntings is unknown, in many species both within- and extra-pair copulations occur mainly in the morning (Birkhead & Møller 1992; Double & Cockburn 2000; Johnsen & Lifjeld 2003). We expected low temperatures to have a larger impact on behaviour than high temperatures, and therefore used daily minimum temperature ('Tmin') in the analyses. As we expected the duration of precipitation ('rain duration') to impose larger constraints on behaviour than the amount of precipitation ('rainfall'; i.e. longlasting lighter rain vs. short heavy rain shower), we initially included the

duration of precipitation in the analyses. However, to allow a comparison with the study on bluethroats (Johnsen & Lifjeld 2003), we also analysed the effect of the amount of precipitation on EPP by replacing rain duration with rainfall in the analysis. The daily minimum temperature (°C) and daily precipitation duration (hours) were averaged over the days of peak fertility of the focal female.

Paternity analysis

DNA was extracted from blood samples using salt extraction (Richardson *et al.* 2001). Individuals were genotyped using six fluorescently labelled microsatellite markers: *Escμ1*, *Escμ4*, *Escμ6* (Hanotte *et al.* 1994), *Pdμ5* (Griffith *et al.* 1999), *Mcyμ4* (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- 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. Extra-pair males sired 54.6% of offspring in 2002 ($n = 262$) and 46.4% of offspring in 2003 ($n = 211$).

Table 7.1. Correlations between weather variables and the first egg date of reed buntings nests ($n = 121$) for the years 2002 and 2003 combined. The correlation coefficients are shown for daily minimum (Tmin) and maximum temperature (Tmax) in °C, daily amount of rainfall in mm and daily duration of rain in hours. The statistical significance is indicated by §: $p < 0.1$, *: $p < 0.05$, **: $p < 0.01$ and ***: $p < 0.001$.

	First egg date	Tmin	Tmax	Rainfall
Tmin (°C)	0.75***	-		
Tmax (°C)	0.64***	0.75***	-	
Rainfall (mm)	0.05	0.03	-0.23*	-
Rain duration (hours)	-0.16§	-0.21*	-0.57***	0.78***

Data analyses

We used multilevel generalised linear models to analyse the effect of weather conditions 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. As females may actively chose not to engage in extra-pair copulations (Birkhead & Møller 1992), we also performed the multivariate analysis only using broods with at least one extra-pair offspring (following Johnsen & Lifjeld 2003).

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

The average daily minimum temperature, rainfall and rain duration during peak fertile periods were not significantly different between the years (all $p > 0.36$). After correcting for the effect of year and time of season, we found a significant negative effect of rain duration and a near significant negative effect of minimum temperature on the proportion of EPP (table 7.2). In contrast to rain duration, rainfall did not significantly predict the proportion of EPP (Wald = + 2.61, $p = 0.11$) after exchanging these two variables in the model. When excluding broods that did not contain any extra-pair offspring from the analysis, both minimum temperature and rain duration during the fertile period of a female negatively predicted the proportion of EPP in her brood (table 7.2, figure 7.1). Again, after exchange with rain duration, rainfall did not significantly predict the proportion of EPP (Wald = 1.34, $p = 0.25$).

Table 7.2. Multilevel generalised linear model of the relation between minimum temperature ‘Tmin’ and rain duration (hours) 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, and corrected for the effect of year and time of season (‘first egg date’); (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. The values of variables included in the final model are highlighted.

Variable	All broods		Broods containing EPP	
	Wald	p	Wald	p
Year	- 4.09	0.043	- 0.02	0.88
First egg date	+ 1.00	0.32	+ 0.53	0.47
Tmin	- 3.25	0.071	- 5.69	0.017
Rain duration	- 5.70	0.017	- 3.90	0.048

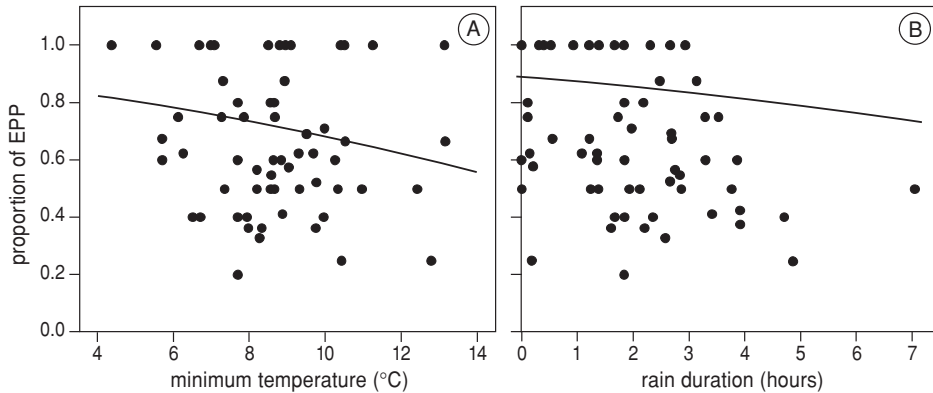


Figure 7.1. Relationship between the proportion of EPP in a brood and (A) the average minimum temperature ($^{\circ}\text{C}$), and (B) the average duration of rainfall (hours) during the peak fertile period of the female in reed buntings for the years 2002 and 2003. Only broods containing at least one extra-pair offspring are included ($n = 88$). As the data were analysed using a multilevel GLM with pair identity on the highest level, the data in the figure are presented as the average proportion of EPP per pair ($n = 62$). The line represents the predicted values of the final model. For additional information see table 7.3.

Discussion

Daily minimum temperature and duration of rainfall during the peak fertile period of the female both had a negative effect on the proportion of EPP in her brood. Although there is a positive correlation between minimum temperature and first egg date, the association between minimum temperature and EPP could not be explained by the time of season at which the clutch was produced. Minimum temperatures are likely to affect the amount of time that individuals have to invest in self maintenance (Dawson & O'Connor 1996). In addition, insect abundance will decrease with lower temperatures (Pollard *et al.* 1996), making foraging more difficult. In contrast to the results found in bluethroats (Johnsen & Lifjeld 2003), lower minimum temperatures during the fertile period lead to higher proportions of EPP. For bluethroats in Norway, weather conditions encountered especially early in the breeding season will be much harsher (e.g. reports of snow; Johnsen & Lifjeld 2003) than for reed buntings in the Netherlands. Therefore the trade-off between self maintenance and extra-pair mating behaviour is expected to be stronger in Norway, leading to the negative relationship between morning temperature and EPP (Johnsen & Lifjeld 2003). Possibly energy demands during low temperatures in the Netherlands are such that time-consuming activities, such as mate guarding, are limited, but less time-consuming activities, such as EPCs (Dickinson 1997), are not. Reed buntings forage mainly off their territory on communal breeding grounds (Cramp & Perrins 1994; pers.obs.), which is likely to conflict with other behaviours such as mate guarding (Westneat 1994; Komdeur 2001). Although mate guarding behaviour has not been studied in our population, in Norwegian reed buntings mate guarding has been found to be effective in protecting paternity (Marthinsen *et al.* 2005). We therefore suggest that at low temperatures, mate guarding is traded against self maintenance, e.g. foraging, thereby increasing the opportunity for females and extra-pair males to gain EPCs. At higher minimum temperatures, mate guarding behaviour may be less constrained, resulting in lower levels of EPP.

In serins (*Serinus serinus*), levels of EPP were higher in territories with high food availability (Hoi-Leitner *et al.* 1999). The authors suggest that this relation is a result of females in good quality habitat being less dependent on male assistance in caring for offspring and therefore being more likely to seek EPCs (Hoi-Leitner *et al.* 1999). However, Johnsen *et al.* (2003) prefer the interpretation that in serins, as in bluethroats, extra-pair behaviour is constrained by energy demands. In contrast to the study on serins, but in agreement with our study, lower levels of EPP were found in broods of food-supplemented red-winged blackbirds (*Agelaius phoeniceus*; Westneat 1994). The time budget of especially the male red-winged blackbird was affected by the availability of additional food: with extra food, males spent more time on their territories. As EPCs only occurred on the female's territory, the increased presence of the social male on the territory allowed him to

prevent more EPCs (Westneat 1994). Similarly, in house sparrow broods (*Passer domesticus*) levels of EPP were lower when the social parents were food-supplemented (Vaclav *et al.* 2003). However, in this species, females, but not males, spent more time at the nest when extra food was available. This resulted in partners being together for a longer period of time and consequently lower levels of EPP in the brood (Vaclav *et al.* 2003).

Longer periods of rain during the peak fertile period of reed buntings lead to a lower proportion of EPP in the brood, which is in agreement with our expectation. During rain, individuals probably seek cover to avoid getting wet, and thus avoid an increase in energy expenditure (Nye 1964; McCafferty *et al.* 1997). Furthermore, foraging is likely to be more difficult, as insects are less active and thus less easy to find during rain (Poulsen 1996; Pollard *et al.* 1996). Therefore, rain is likely to restrict movements of all individuals who are involved in extra-pair mating, not only of the social male. The effect of the amount of rainfall was not as strong as the effect of the duration of rainfall; longer periods of rain are more restrictive to the behaviour of individuals than brief but heavy showers which may fall in a relatively short period of time. Although not affected by the amount of rain (Johnsen & Lifjeld 2003), possibly the extra-pair mating behaviour of bluethroats is affected by the duration of rain.

Concluding remarks

Our data show that weather conditions during the peak fertile period of female reed buntings affect levels of EPP. This is in agreement with the results found in bluethroats (Johnsen & Lifjeld 2003), although mechanisms seem to differ between these species. As weather conditions may explain part of the variation found in EPP within and between species, they deserve more attention from researchers studying EPP. Our next step would be to determine the specific role played by male and female reed buntings in extra-pair mating, and which aspects are affected by ecological factors. Detailed behavioural observations are required to answer these questions.

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