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Ecological constraints on extra-pair paternity in the bluethroat

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Abstract The mating system of the bluethroat (*Luscinia s. svecica*) involves a high level of sperm competition, and consequently a high frequency of extra-pair paternity (EPP). There is considerable variation in the frequency of EPP. Over the course of ten study years in a population in Norway, the frequency has fluctuated between 7% and 33% of young, and 8% and 76% of broods. In this paper, we address the issue of whether ecological factors can explain some of the variation in EPP between years and broods. Factors include breeding density, breeding synchrony and two meteorological variables (ambient temperature and precipitation) during the period of peak female fertility. There were no significant relationships between annual averages of the four variables and the annual level of EPP, but the statistical power of these tests was low, due to a restricted sample ($n=10$ years). Focussing on individual broods, none of the factors had significant effects when including all broods in the analyses (including those with zero EPP). When limiting the analyses to broods with one or more extra-pair offspring, morning temperature had a significant effect on the frequency of EPP. When the temperature was low during the peak of the fertile period, EPP occurred less frequently. Male extra-pair behaviour was not generally constrained by synchrony between the fertile periods of the social mate and the extra-pair mate, but for a subgroup of males ("unattractive males") there appeared to be a trade-off between mate guarding and pursuing extra-pair copulations. Our results indicate that ecological conditions have no influence on whether or not a brood will contain extra-pair offspring, but when EPP does occur, its

frequency is influenced by air temperature. Possibly, there is a causal relationship between weather conditions and the frequency of extra-pair encounters in this species. The breeding season is initiated at a phenologically early stage, when large parts of the territories are still covered with snow, and cold weather conditions may force the birds to devote most of their time to maintenance and thereby constrain sexual activities.

Keywords Breeding density · Breeding synchrony · *Luscinia s. svecica* · Sperm competition · Weather conditions

Introduction

Extra-pair paternity (EPP) is common in many birds, but the frequency varies considerably between species, populations, years and individuals (Petrie and Kempenaers 1998; Hasselquist and Sherman 2001; Griffith et al. 2002). In order to understand why this variation exists, it is important to identify factors that influence the likelihood that individuals engage in EPP. In other words, we need to know what affects the costs and benefits of performing extra-pair copulations (EPCs) at the individual level, in order to explain variation at the population level and beyond (Petrie and Kempenaers 1998).

A number of factors have been suggested to influence the costs and benefits of EPC behaviour (Birkhead and Møller 1992). These include factors that relate directly to the costs and benefits of EPCs for females, for example the degree to which females have knowledge of male quality (Slagsvold and Lifjeld 1997), the importance of paternal care (Gowaty 1996), and the degree of genetic variation in the population (Petrie and Kempenaers 1998). However, for both sexes, EPC behaviour may also be influenced by extrinsic ecological factors. Socio-ecological factors, like breeding synchrony (Stutchbury 1998) and breeding density (Westneat and Sherman 1997), may constrain individual ability to engage in EPCs by influencing the availability of potential mates. The

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weather conditions during the fertile period have so far been largely ignored, but may in fact play an important role in the variation of EPP at the temporal and individual level. Weather conditions may act as a constraint on EPC behaviour by influencing the availability of food resources and thus the birds' need to prioritise maintenance, or more indirectly by affecting other factors like breeding synchrony or breeding density that in turn may influence EPC activity.

We present analyses of paternity data collected from a single bluethroat (*Luscinia s. svecica*) population over 10 years. With these data, we are able to investigate both the annual and the between-brood variation in EPP frequency. Variation at the individual level has been extensively studied in the present bluethroat population, and some of the variation has been shown to be related to male phenotypic appearance (e.g. Johnsen et al. 1998a, 1998b, 2001). In other words, when females are mated to relatively unattractive males, they are more likely to have offspring sired by other males. Here, we investigate whether the frequency of EPP is influenced by aspects of the social environment (local synchrony, local density) and weather conditions (morning temperature, daily precipitation) during the period of peak female fertility, i.e. the few days around the start of egg laying. We predict that broods from females that had experienced relatively bad weather conditions (low temperature, high amount of precipitation) during the period of peak fertility would contain proportionately fewer offspring sired through extra-pair copulations than broods from females that experienced more benign conditions. The predictions concerning breeding synchrony can go in either direction depending on the underlying mechanism of EPCs. If EPCs are predominantly male driven, a trade-off between mate guarding and EPC behaviour could result in a negative relationship between synchrony and frequency of EPP (Birkhead and Biggins 1987). On the other hand, if EPCs are predominantly female driven, it may be beneficial for females that many males are displaying at the same time to allow for more precise judgement of male relative quality (Stutchbury and Morton 1995; Stutchbury 1998; but see Weatherhead and Yezerinac 1998). In this case, a positive relationship would be predicted between synchrony and level of EPP. Finally, since EPCs are often performed by close neighbours in the bluethroat (Johnsen et al. 2001), we predict that a high density would increase the likelihood of extra-pair encounters, which should result in a positive relationship between breeding density and frequency of EPP (Westneat and Sherman 1997).

Materials and methods

The study population is breeding in Øvre Heimdalen, Norway (61°25'N, 8°52'E), at an altitude of about 1,100 m. Data on parentage have been gathered from this population since 1991, for the purpose of several other studies (Krokene et al. 1996; Johnsen et al. 1998a, 1998b, 2000b, 2001). The present study is based on data from 10 years (1991–2000).

Details about general field methods and parentage analyses can be found in the above-mentioned papers. In total, 305 broods containing 1,568 chicks were analysed by means of multilocus DNA fingerprinting (1991–1993) and microsatellite typing (1994–2000).

Breeding synchrony was estimated in two ways. First, population synchrony was estimated for all 10 years, using the synchrony index proposed by Kempnaers (1993). Second, from five of the years (1995–1999) we had more or less complete knowledge about the position of territories and nests within a core study area. Based on field maps with all territories indicated, we calculated local synchrony, defined as the number of females within a radius of 200 m whose peak fertile periods partly or completely overlapped that of the focal female. The period of peak fertility was defined as a 4-day period lasting from 3 days before the start of laying (day 3) until the day of the first egg (day 0). This relatively short peak fertile period was chosen because male mate guarding peaks during this time in the bluethroat (Krokene et al. 1996), indicating that this is a period of high fertilisation likelihood. Also, studies of other small passerines have shown that the peak period of fertilisations is confined to a few days just around start of egg laying (Lifjeld et al. 1997; Sheldon and Ellegren 1998). Local density was defined as the number of territories within a radius of 200 m of the focal territory.

Data on morning temperature (0800 hours) and daily amount of precipitation was retrieved from Bygdin weather station, which is situated about 12 km from the study site, at a similar altitude (1,055 m asl). We chose to use the morning temperature because most copulatory activity seems to take place in the morning hours (J.T. Lifjeld and A. Johnsen, personal observation). The weather data were not detailed enough to look at precipitation during the morning hours only. We therefore used the daily amount of precipitation in the analyses. For the analyses of annual variation, we calculated the annual averages in temperature and precipitation during the period 15 May to 5 June, a period that covers the pre-fertile and the fertile period in this bluethroat population. For the analyses of individual variation, we calculated the average morning temperature and the average amount of precipitation during the peak of female fertility (day 3 to day 0).

During five of the breeding seasons (1993–1997), males were subject to one of three different phenotypic manipulations. In the first experiment (1993 and 1996; half the study area), we blackened the throat patch of one group of males and used another group as controls. In the second experiment (1994 and 1995), we fitted ornament-matching blue and orange colour bands on one group of males and bands with colours not present in the male ornament on a control group. In the third experiment (half the study area in 1996 and 1997), we reduced the UV component of the throat patch of one group of males and used another group as controls. In each of these experiments, we attempted to create one group of relatively unattractive males (blackened males, males with non-ornamental colour bands, UV-reduced males, respectively) and one group of relatively attractive males (control males, males with ornament-matching colour bands, control males, respectively). The experiments had effects on male behaviour during the fertile period of their mates (all three experiments), and some effects on paternity (the blackening experiment only) and extra-pair fertilisation success (the UV-reduction experiment only) (see Johnsen et al. 1997, 1998a, 1998b, 2000b, Johnsen and Lifjeld 1995). There was no significant difference in rate of EPP between years in which male phenotype was manipulated (1993–1997; brood means \pm SE: 0.25 ± 0.028 , $n=138$) and years without manipulation (1991, 1992, 1998–2000; 0.28 ± 0.27 , $n=163$; Mann-Whitney test: $Z=-0.67$, $P=0.51$), suggesting that the experiments did not affect the overall level of EPP. Due to the random assignment of males to experimental groups, there were no systematic differences in the socio-ecological conditions experienced by the different groups (A. Johnsen and J.T. Lifjeld, unpublished data). Furthermore, there was no significant difference in the timing of breeding between females mated to "attractive" and "unattractive" experimental males in the present sample (relative laying date (adjusted according to the median each year) for "attractive" group: -0.08 , unattractive group: 0.42 , $n_1=71$, $n_2=59$, $Z=-1.1$, $P=0.27$). We therefore included data

from the manipulated years to increase the power of the analyses. However, it should be noted that the results were qualitatively similar (i.e. similar effect sizes) when restricting the analyses to years without manipulations (data not shown).

Statistical procedures

We used logistic regression (performed in StatView 5.0) to test whether the occurrence of EPP was influenced by the four ecological factors, and generalised linear models (GLM) when testing for relationships between the proportion of extra-pair offspring (EPO) and the ecological factors. In the latter tests, we defined a binomial error distribution, and used number of EPO as the dependent variable and brood size as the binomial denominator. The scale was estimated by Pearson Chi-square, due to overdispersion of the data. All GLMs were performed in GLMStat 5.2.1.

Some birds bred in more than one year. However, since pairs were never the same (with the exception of one pair that stayed together for three consecutive years), we used all parentage-determined broods in the analyses. Only the first breeding of the exceptional pair was included. Seven re-nestings were excluded from the analyses.

Results

Variation in extra-pair paternity between years

Overall, 49.5% (151/305) nests contained one or more EPO and 26.3% (412/1,568) of the young were EPO. There was significant variation between the years, both in frequency of nests with EPP ($\chi^2=27.3$, $df=9$, $P=0.0013$; Table 1), and in the proportion of EPP within nests (Kruskal Wallis test: $H=19.6$, $df=9$, $P=0.020$; Table 1).

Figure 1 shows the annual proportion of nests with one or more EPO, and the annual averages of the four ecological variables, for each of the ten study years. There were no significant correlations between the level of EPP and: (1) average morning temperature during the pre-fertile and fertile period (Spearman rank correlation: $n=10$, $r_s=0.47$, $P=0.16$; Fig. 1a), (2) average amount of precipitation during the pre-fertile and fertile period ($n=10$, $r_s=-0.18$, $P=0.58$; Fig. 1b), (3) population synchrony ($n=10$, $r_s=0.16$, $P=0.62$; Fig. 1c), or (4) average local density ($n=10$, $r_s=0.49$, $P=0.14$; Fig. 1d). Visual inspection of correlation scatter plots suggested that some of the relationships might be better explained by curvilinear models. A polynomial regression model made a better fit to the relationship between temperature and proportion of nests with EPO ($R^2=0.45$, $P=0.13$; linear term $P=0.058$, quadratic term $P=0.086$), but this was not the case for the remaining three relationships (all $R^2<0.16$, all $P>0.54$). Qualitatively similar results were obtained when using the annual proportion of EPO in the analyses. It should be noted that the power of these tests is low, due to the low sample size ($n=10$ years).

Table 1 Percentage of extra-pair offspring and broods with at least one extra-pair offspring in bluethroat (*Luscinia s. svecica*) nests, for each of 10 study years

Year	% offspring	% nests	% unmanipulated nests ^a
1991	19 (13/67)	27 (4/15)	27 (4/15)
1992	25 (36/143)	45 (13/29)	45 (13/29)
1993	33 (36/110)	76 (16/21)	70 (7/10)
1994	7 (4/61)	8 (1/12)	0 (0/5)
1995	11 (14/127)	30 (8/27)	35 (6/17)
1996	29 (50/173)	52 (17/33)	40 (8/20)
1997	30 (73/243)	54 (26/48)	45 (13/29)
1998	32 (95/297)	64 (35/55)	64 (35/55)
1999	28 (78/280)	50 (26/52)	50 (26/52)
2000	19 (13/67)	39 (5/13)	39 (5/13)

^a includes control nests from years with manipulation (1993–1997)

Table 2 Generalised linear model tests of the relationship between four ecological factors and frequency of EPP, controlling for year effects. All broods included

Variable	Deviance	df	F-ratio	P	Slope±SE
Temperature ^a	4.71	1	1.60	0.21	0.11±0.09
Year	40.95	9	1.54	0.13	
Precipitation ^a	1.49	1	0.50	0.48	-0.01±0.02
Year	37.51	9	1.40	0.19	
Local synchrony ^b	7.86	1	2.74	0.10	-0.16±0.10
Year	29.01	4	2.53	0.042	
Local density ^b	1.66	1	0.56	0.45	-0.07±0.09
Year	25.28	4	2.15	0.076	

^a Data from 1991–2000 ($n=286$ nests)

^b Data from 1995–1999 ($n=190$ and $n=195$ nests for local synchrony and local density, respectively)

Variation in extra-pair paternity between broods

The data were analysed in three different ways. First, we performed GLM analyses separately for each ecological factor with the number of EPO as dependent variable. Year was entered in each model to control for between-year differences. None of the factors were significantly related to the frequency of EPP (Table 2). Similar results were obtained when testing whether the likelihood that a brood would contain EPP was influenced by the ecological factors, using logistic regressions (all $\chi^2<0.32$, all $P>0.57$).

Second, we included only the broods with EPP in the analyses and otherwise kept conditions as in the previous tests. The morning temperature during the period of peak fertility was significantly and positively related to the proportion of EPP (Table 3), and there was a tendency for a negative relationship between local synchrony and the proportion of EPP (Table 3). Removing year from the model, and thus including the variation between years, strengthened the relationship between temperature and EPP (deviance=11.0, $df=1$, F -ratio=6.52, $P=0.012$, estimate±SE=0.11±0.04) and weakened the relationship between synchrony and EPP (deviance=2.76, $df=1$, F -ratio=1.51, $P=0.22$, estimate±SE=-0.10±0.08).

The morning temperature increased with laying date ($n=143$, $r_s=0.44$, $P<0.0001$), and there was a weak

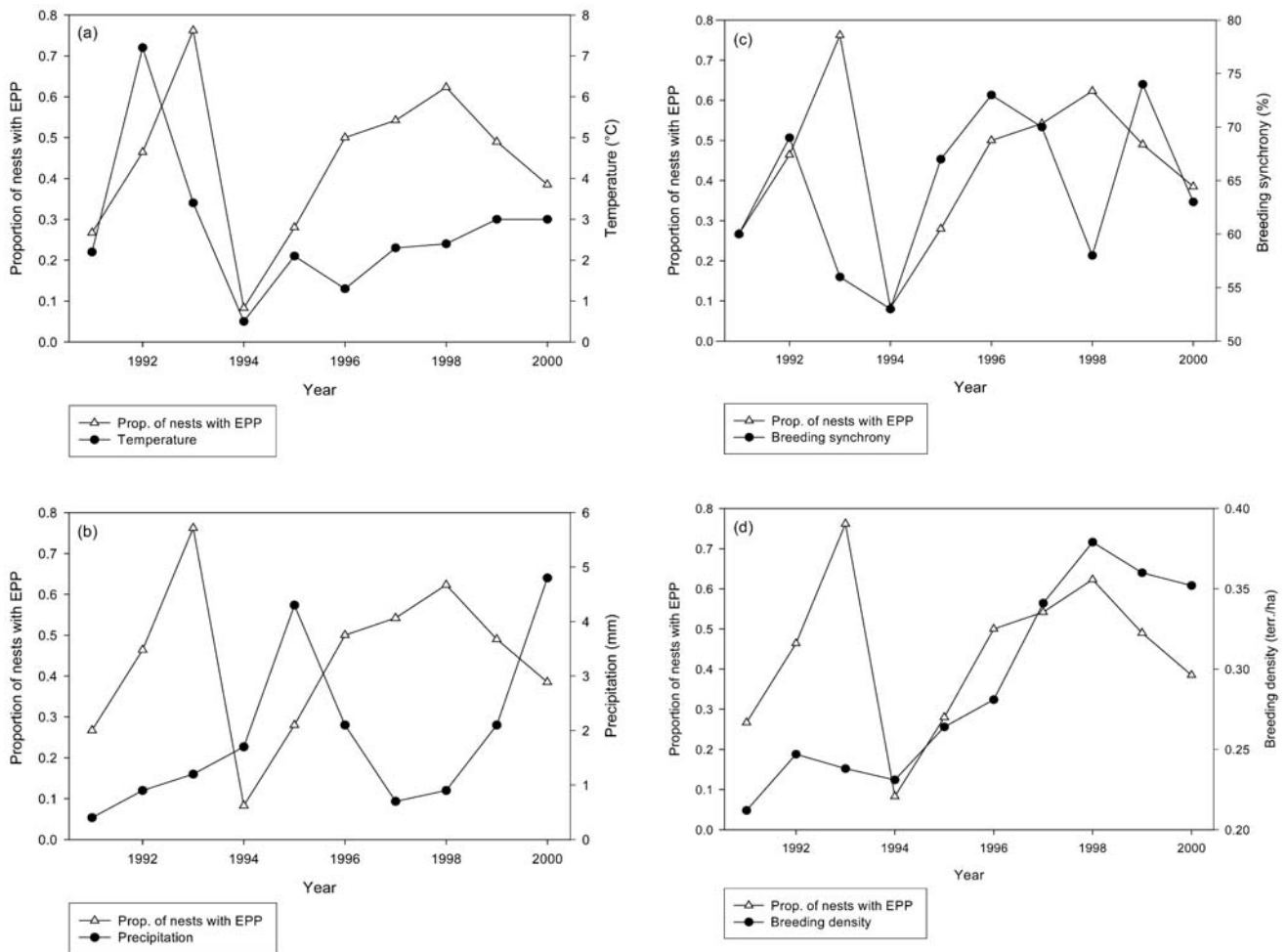


Fig. 1 Patterns of annual variation in the level of extra-pair paternity and **a** average morning temperature during the pre-fertile and fertile period (15 May to 5 June), **b** average precipitation

during pre-fertile and fertile period, **c** population synchrony, and **d** average local density, over a 10-year period (1991–2000)

Table 3 Generalised linear model tests of the relationship between four ecological factors and frequency of EPP, controlling for year effects. Only broods with EPP included

Variable	Deviance	df	F-ratio	P	Slope±SE
Temperature ^a	7.18	1	4.22	0.042	0.17±0.08
Year	19.19	9	1.25	0.27	
Precipitation ^a	2.03	1	1.18	0.28	-0.01±0.01
Year	22.11	9	1.43	0.18	
Local synchrony ^b	6.35	1	3.53	0.063	-0.17±0.09
Year	14.94	4	2.08	0.090	
Local density ^b	0.79	1	0.43	0.51	-0.06±0.09
Year	10.60	4	1.43	0.23	

^a Data from 1991–2000 ($n=143$ nests)

^b Data from 1995–1999 ($n=97$ nests)

tendency that late broods contained proportionately more EPO ($n=143$, $r_s=0.14$, $P=0.11$). Thus, to test whether the effect of temperature was confounded by laying date, we performed a GLM with laying date and morning temperature as factors. This test included nests with one or more EPO from all the study years. The overall model was

significant (deviance=11.72, $df=2$, F -ratio=3.45, $P=0.034$), and the effect tests showed that temperature had a significant effect when controlling for laying date (deviance=7.51, $df=1$, F -ratio=4.43, $P=0.037$), whereas laying date had no significant effect when controlling for temperature (deviance=0.72, $df=1$, F -ratio=0.43, $P=0.52$).

Finally, we performed multivariate GLM analyses on the restricted data set (only broods with EPP) including the four ecological variables, laying date and year as factors. Only data from the years 1995–1999 were included in these analyses (see Materials and methods). In the initial model (deviance=32.19, $df=9$, F -ratio=2.05, $P=0.043$), there was a significant effect of temperature and a tendency for a year effect (Table 4). None of the other factors contributed significantly to the model. Sequential removal of non-significant terms ($P>0.10$) from the model resulted in a final model with a significant effect of temperature only (Table 4).

Table 4 Generalised linear model with number of EPO as dependent variable

Variable	Deviance	df	F-ratio	P	Slope±SE
Initial model ^a					
Temperature	9.38	1	5.37	0.023	0.28±0.12
Precipitation	3.69	1	2.11	0.15	-0.03±0.02
Local synchrony	1.20	1	0.68	0.41	-0.09±0.10
Local density	0.03	1	0.02	0.89	0.01±0.10
Laying date	0.33	1	0.19	0.67	0.02±0.05
Year	16.96	4	2.43	0.05	
Final model ^b					
Temperature	8.95	1	5.03	0.027	0.14±0.06

^a $n=98$ nests (data from 1995–1999). Scale estimated at 1.75 using Pearson Chi-square

^b $n=105$ nests (data from 1995–1999). Scale estimated at 1.78 using Pearson Chi-square

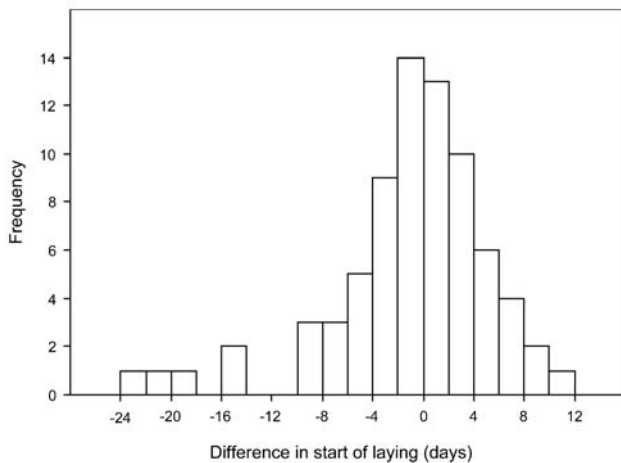


Fig. 2 Frequency distribution of the difference in start of laying between a male's social mate and his extra-pair mate. A negative value means that the social female started laying before the extra-pair female and vice versa

Timing of EPCs

If males were constrained in their EPC activities by the need to guard their mates, there should be little overlap in the fertile periods of the mates of extra-pair males and cuckolded males. From the distribution of the difference between the first-egg laying dates of the two females involved, it appears that quite a few males pursue EPCs when their own females are highly fertile, whereas others mainly copulate with other females outside of this time window (Fig. 2). The median difference between the first egg of the extra-pair male's female and the first egg of the extra-pair female was -0.5 days (mean=-1.68 days). There was no significant relationship between the likelihood that an extra-pair male would lose paternity and whether there was overlap in the fertile period between his own female and the extra-pair female, but if anything, there was a tendency that males with overlap ($n=37$) were less likely to lose paternity (37.8% lost paternity) than males with no overlap ($n=23$, 60.9% lost paternity,

Fisher's exact test: $P=0.11$). Furthermore, there was a significantly positive correlation between the absolute difference in start of egg laying between the fertile periods of the two females and the proportion of paternity loss in the extra-pair males brood ($n=60$, $r_s=0.31$, $P=0.019$). Thus, there is no indication that males that perform EPCs when their own females are fertile run a higher risk of losing paternity than males that perform EPCs outside this period, rather the opposite seems to be the case.

As stated in the method section, three different manipulations of male phenotype were carried out during five of the study years. In each experiment, "unattractive males" guarded their mates with higher intensity than "attractive males" (Johnsen et al. 1997, 1998a, 1998b). Pooling the data for males in each group, there was a marginally significant tendency that "unattractive males" ($n=65$) were more likely to lose paternity than "attractive males" ($n=74$, Fisher's exact test: $P=0.063$). There was no significant difference between the two male groups in the likelihood of getting EPP in other nests (Fisher's exact test, $P=0.10$), but for males that did, there was a significant difference in the degree of overlap between the two involved females' fertile periods. For "attractive males" ($n=21$), the mean±SE absolute difference in laying date between own mate and extra-pair mate was $2.2±0.5$ days, and for "unattractive males" ($n=11$) it was $7.5±2.2$ (Mann Whitney test: $U=51.5$, $P=0.01$).

Discussion

Annual variation in EPP

The present dataset comprises one of the longest time-series on paternity in any bird population studied so far. Yet, the power of the correlations between the annual level of EPP and annual averages of the four ecological variables is inevitably low ($n=10$), illustrating that it is difficult to obtain sufficient sample sizes to investigate the variation of the frequency of EPP at the temporal level. It is therefore not surprising that none of the correlations were statistically significant. The effect sizes, as measured by the correlation coefficients, were quite high in the tests between temperature and level of EPP ($r_s=0.47$) and between density and level of EPP ($r_s=0.49$), and might reflect biologically relevant associations. Our analyses of the variation at the individual level (see below) indicate that air temperature plays a role by influencing the frequency of extra-pair encounters whereas local breeding density is of no detectable importance within the present range.

Determinants of the occurrence of EPP

The absence of EPP was not significantly related to any of the meteorological or ecological factors. Hence, whether or not a female would obtain extra-pair fertilisations

could not be predicted from the weather conditions or the socio-ecological situation she experienced during the period of peak fertility. About half the broods in this study did not contain any EPO, a situation that may arise for at least three reasons. First, females might be truly faithful and only copulate with the males that they are pair-bonded to. Second, females might be constrained by male mate guarding or unavailability of potential extra-pair mates, and not succeed in getting extra-pair fertilisations. Third, most females might be copulating with several males, but the social male might in many cases father most or all offspring due to superiority in sperm competition (Birkhead 1998). Since females with no EPP did not experience a lower local breeding density and were not more or less synchronous with surrounding females than females with EPP, unavailability of potential extra-pair mates seems unlikely to explain the absence of EPP. Furthermore, we have previously shown that females are able to escape male mate guarding when their motivation to do so is strong (Johnsen et al. 1998b). Hence, even if some females might be constrained in their extra-pair activities, this is hardly a general explanation for the absence of EPP. We are left with two not mutually exclusive possibilities: many females are innately faithful (for unknown reasons) and/or pair males in many cases gain full paternity through advantages in sperm competition (see below).

A central question in discussions about the effects of breeding synchrony on levels of EPP is whether EPCs are male- or female-driven (Birkhead and Biggins 1987; Stutchbury and Morton 1995). Detailed information about EPC behaviour is lacking from the present bluethroat population, but there is evidence that females benefit from EPCs in terms of increased offspring immunocompetence (Johnsen et al. 2000a). On the other hand, most EPCs seem to occur by neighbouring male intrusions (Johnsen et al. 2001). Hence, it seems likely that both sexes play active roles in EPCs in this species. In such a species, the occurrence of EPP should be dependent on the particular interests of and constraints on all the potential participants (pair male, pair female, one or more extra-pair males; cf. Petrie and Kempenaers 1998), and our data suggest that the socio-ecological circumstances have little or no influence on this. A similar lack of relationship between social environment and the occurrence of EPP has been found in studies of several other bird species (e.g. Kempenaers 1997; Weatherhead 1997; Yezerinac and Weatherhead 1997; Krokene and Lifjeld 2000), but there are also some studies reporting significant associations (e.g. Chuang et al. 1999; Thusius et al. 2001).

Does synchrony constrain male EPC behaviour?

Our data suggest that the bulk of the EPCs are performed during a time when both the pair and extra-pair females are fertile. Furthermore, males are not more likely to lose paternity in their own nest when the two females involved are breeding synchronously. There is therefore little

evidence to suggest that male bluethroats are constrained in their EPC behaviour by synchrony, e.g. due to mate guarding (see also Kempenaers 1997). However, our earlier studies suggest that it is too simplistic to view males as being a uniform group, with similar threats to their own paternity and similar likelihood of success in EPCs. On the contrary, it seems that males fall into two distinctly different groups: one group invests little in mate guarding and more in advertisement during their own females' fertile period, and the other group invests quite heavily in mate guarding and little in advertisement (e.g. Johnsen et al. 1997, 1998b). These two different behavioural strategies (guarding versus advertising) were reflected in the data on timing of EPCs. The experimental males that belonged to the "attractive group" were able to secure fertilisations with other females during their own females' fertile period, whereas the males in the "unattractive group" probably faced a trade-off between guarding and EPCs (Brodsky 1988; Hasselquist and Bensch 1991) and were predominantly able to gain fertilisations with other females outside of their own mates' fertile period.

Do weather conditions constrain extra-pair behaviour?

About half the females in this study must have engaged in at least one EPC. As indicated above, there may be many reasons for why they did so. However, our data suggest that the degree to which these females engaged in EPCs was to some extent influenced by the weather conditions during the period of peak fertility. More specifically, when the morning temperature was low, the EPP broods tended to contain relatively fewer EPO than when the temperature was higher. The correlative nature of this study does not allow for strong conclusions about causality, but a causal effect seems likely. The investigated bluethroat population starts breeding at a time when the weather conditions are very unpredictable. In most years, there is still a large degree of snow cover when breeding starts, and the temperature may be well below 0°C during the fertile period. It therefore seems likely that there is a trade-off between investing in maintenance and extra-pair behaviour in this population. Bluethroats are ground foraging insect eaters. When the ambient temperature is low, the low activity level of insects probably makes them harder to find. Thus, after a cold night, the birds are faced with a strong need to restore body condition and a great difficulty in finding food to do so. It therefore makes intuitive sense that the birds give priority to foraging over sexual activity under such weather conditions. In a study of serins (*Serinus serinus*), Hoi-Leitner et al. (1999) found evidence that the frequency of EPP was higher in territories with high food availability. One interpretation of this finding (not the one favoured by the authors) is that extra-pair behaviour is constrained by energy demands also in that species. Since most EPCs occur by male intrusions in the bluethroat (Johnsen et al. 2001), it seems likely that male EPC behaviour is more

constrained by ambient temperature than female EPC behaviour.

Could the positive relationship between ambient temperature and proportion of EPP be confounded by seasonal effects? As expected, there is a gradual increase in ambient temperature as the season progresses. Hence, if late arriving females were more likely to engage in EPCs (e.g. because they have relatively unattractive mates), there might be a seasonal pattern of increasing frequencies of EPP that spuriously co-varied with temperature. However, there was no significant relationship between laying date and proportion of EPP, and when including both morning temperature and laying date in a multivariate test, only morning temperature was significant. Hence, there appears to be a direct effect of ambient temperature on the frequency of extra-pair encounters in this species.

We have recently shown that offspring resulting from EPCs have a better cellular immune response than both maternal and paternal half siblings, indicating that EPC mates are more genetically compatible than social mates (Johnsen et al. 2000a). How does this result relate to the present demonstration of an influence of temperature on the frequency of EPP? We propose the following model to unite the compatibility hypothesis with the weather constraint hypothesis. It is reasonable to assume that there is numerical asymmetry in the competition between sperm from the social mate and the EPC mate(s), i.e. there are usually many more sperm from the social mate present in the female's reproductive tract (Birkhead 1998). However, the present results suggest that the amount of sperm from extra-pair males is temperature dependent, so that more EPC sperm are inseminated when the weather is relatively warm. If the social mate is more compatible than the EPC mate(s), the EPC sperm will not succeed in any case, resulting in full paternity for the social mate. If the EPC mate is more compatible, the EPC sperm still have to win the race despite their numerical handicap in order to fertilise the egg. The likelihood of success in this competition should be positively related to the number of sperm, and should thus be higher under better weather conditions. This model would predict a relationship between the proportion of EPP and temperature in broods with EPP, but no relationship with the occurrence of EPP, as found in the present study.

Conclusions

This study shows that the frequency of extra-pair paternity is weakly, but significantly, influenced by properties of the physical environment and unrelated to the social environment in which the birds live. We suggest that future studies take weather conditions during the fertile period into account when investigating variation in the frequency of extra-pair paternity at the individual and the temporal level.

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