动物学报 52(Supplement): 232–234, 2006
Acta Zoologica Sinica

S13-2 Do weather conditions affect the frequency of extra-pair paternity in the bluethroat (*Luscinia svecica svecica*)?

Arild JOHNSEN[1], Jan T. LIFJELD[2]
1. Reproductive Biology and Behaviour Group, Research Centre for Ornithology of the Max Planck Society, Postfach 1564, D-82305 Starnberg (Seewiesen), Germany; johnsen@erl.ornithol.mpg.de
2. Zoological Museum, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway; j.t.lifjeld@nhm.uio.no

Abstract Ecological factors may affect levels of extra-pair paternity (EPP) by influencing the costs and benefits of extra-pair copulation. During a 10-year study of a Norwegian bluethroat population, the frequency of EPP has varied extensively (8%–76% nests with EPP, 7%–33% extra-pair offspring among years). Here, we investigate whether socio-ecological factors (breeding density, breeding synchrony) and weather conditions (ambient temperature, precipitation) during the peak fertile period explain some of the variation in the frequency of EPP. None of the factors assessed were related significantly to the likelihood that a nest would contain extra-pair offspring. Among broods that contained at least one extra-pair offspring, however, ambient temperature was related significantly to the frequency of EPP: broods contained more extra-pair offspring when the temperature was relatively high during the period of peak female fertility. We suggest that there is a direct link between weather conditions and the level of EPP in this population of bluethroats. Environmental conditions are often harsh when the birds start to breed, a large proportion of the ground being covered by snow and night temperatures falling well below zero. It therefore seems likely that there is a trade-off between investment in self-maintenance and extra-pair behavior, which shifts towards self-maintenance when the weather conditions are severe.

Key words Sperm competition, Breeding density, Breeding synchrony, Ambient temperature, Precipitation

1 Introduction

Ecological factors may influence the costs and benefits of extra-pair copulation (EPC) behavior by constraining individual ability to engage in it and / or influencing the availability of potential mates. Studies of the influence of socio-ecological factors on the frequency of extra-pair paternity (EPP), such as breeding synchrony (e.g., Stutchbury, 1998) and breeding density (e.g., Westneat and Sherman, 1997), have been several. However, the potential influence of weather conditions during the fertile period has not yet been explored. Weather conditions may constrain EPC behavior directly by affecting the need to prioritize maintenance, or indirectly by affecting other factors such as breeding synchrony or density that in turn may influence EPC-activity.

In this study, we explore the relationship between the frequency of EPP and breeding density, breeding synchrony and weather variables (temperature and precipitation) in a Norwegian population of the bluethroat (*Luscinia svecica*). EPP occurs frequently in this population, but with considerable annual variation, fluctuating over the course of 10 study years between 7 and 33% of young, and 8 and 76% of broods. Here, we investigate whether ecological factors explain some of the variation in EPP between years, and between broods within years.

2 Materials and methods

Fieldwork was conducted in Øvre Heimdalen, Norway (61°25'N, 8°52'E; 1 100 m a.s.l.), and analyses of paternity were carried out on data from 10 years (1991–2000). In total, 305 broods containing 1568 chicks were analyzed by means of multilocus DNA fingerprinting (1991–1993) and microsatellite typing (1994–2000).

We calculated population synchrony, using the synchrony index proposed by Kempenaers (1993), and local synchrony, defined as the number of females within a radius of 200 m whose peak fertile periods (day-3 to day-0 *day of first egg*) overlapped that of the focal female partly or completely. Local density was defined as the number of territories within a radius of 200 m of the focal territory. Local synchrony and density were calculated only from the year 1995, after we had gained sufficient knowledge of the breeding population.

Data on morning temperature (0800 hours) and daily precipitation was retrieved from Bygdin weather station, situated 12 km southwest of the study site at a similar altitude (1 055 m a.s.l.). For analyses of annual variation, we calculated the annual averages in morning temperature and daily precipitation from 15 May to 5 June, a period that covers the pre-fertile and fertile periods in the local bluethroat population. For analyses of individual variation, we calculated average morning temperature and average

precipitation during the peak of female fertility (day –3 to day 0).

3 Results

3.1 Annual variation

In total, about half (151/305) of the nests contained one or more extra-pair offspring, and 26.3% (412/1 568) of the young were sired by extra-pair males. There was significant variation between years, both in the frequency of nests with EPP (Fig. 1) and in the proportion of EPP within nests (Johnsen and Lifjeld, 2003).

We found no significant correlations between the annual proportion of nests with extra-pair offspring and (1) annual average morning temperature during the pre-fertile and fertile period, (2) annual average precipitation during the pre-fertile and fertile period, (3) annual population synchrony, and (4) annual average local density ($P > 0.14$ for all tests; Johnsen and Lifjeld, 2003). It should be noted that sample sizes were low in these tests ($n = 10$ years).

3.2 Variation between broods

Generalized linear model (GLM) analyses revealed no significant relationships between any of the ecological factors and the frequency of EPP when all broods were included in the analyses (Johnsen and Lifjeld, 2003). Similarly, neither factor was related significantly to the likelihood that a nest would contain EPP, as shown by logistic regressions (Table 1).

There may be several reasons why nests did not contain extra-pair young (see Discussion). Therefore, we repeated the above GLM analyses on the potentially more uniform and comparable fraction of the nests that contained one or more extra-pair offspring. Within this data set, the morning temperature during peak fertility was related significantly and positively to the proportion of EPP (Fig. 2; Johnsen and Lifjeld, 2003), and there was a tendency for a negative relationship between local synchrony and the proportion of EPP (Johnsen and Lifjeld, 2003).

Multivariate GLM analyses on the restricted data set (only broods with EPP), using the four ecological variables, laying date and year as factors, revealed a significant effect from temperature only (Johnsen and Lifjeld, 2003).

Table 1 Logistic regression analyses (controlling for year) of the effect of ecological factors on the occurrence of extra-pair paternity

	n	r^2	*P*
Temperature	286	0.06	0.68
Precipitation	286	0.06	0.91
Local Synchrony*	190	0.03	0.57
Local density*	195	0.03	0.81

*Data from 1995–1999 only.

4 Discussion

About half the broods in this study lacked EPP, a situation that may arise because (1) females are truly faithful, (2) females do not succeed in obtaining extra-pair fertilizations, and/or (3) the pair males are superior in sperm competition. Whatever the ultimate reason, we could not predict whether or not a female would obtain extra-pair fertilizations from the weather conditions, nor from the socio-ecological situation that she experienced during her period of peak fertility. Earlier studies have suggested that both sexes play active roles in EPCs in the bluethroat (Johnsen et al., 2000; Johnsen et al., 2001). In such species, the occurrence of EPP should depend on the particular interests of, and constraints on, all potential participants (pair male, pair female, one or more extra-pair males; cf. Petrie and Kempenaers, 1998). Our data suggest that socio-ecological circumstances have little or no influence on this.

About half the females in this study engaged in at least one EPC. As indicated above, there may be many rea-

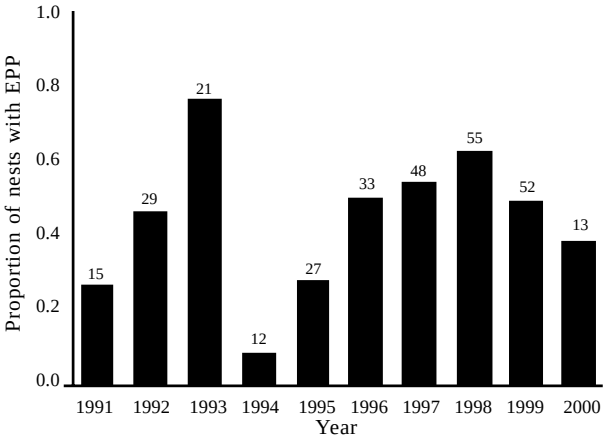

Fig. 1 Annual proportion of nests with extra-pair paternity (EPP) 1991–2000
Numbers above bars represent sample sizes (number of nests).

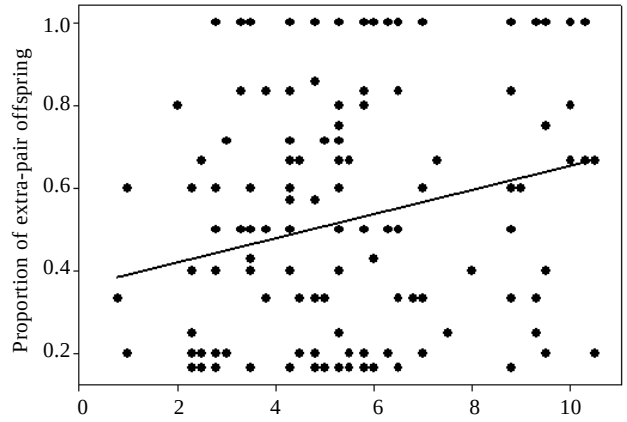

Fig. 2 Relationship between the proportion of extra-pair offspring in nests with mixed paternity and ambient temperature (horizontal axis) during the peak fertile period
The regression line is shown for illustrative purposes.

sons why they did so. Even so, our data suggest that the degree to which they engaged in it was influenced to some extent by weather conditions during the period of peak fertility. When morning temperatures were low, EPP-broods contained relatively fewer extra-pair offspring than when temperatures were higher. There may well be a causal relationship between weather conditions and the frequency of extra-pair encounters in Norwegian bluethroats. The breeding season is initiated very early in the phenological cycle, when large parts of territories are still covered with snow and poor weather conditions may force the birds to spend more time on self-maintenance than to sexual activity.

This study shows that properties of the physical environment may influence levels of EPP by affecting the trade-off between self-maintenance and sexual behavior. We urge investigators of extra-pair mating systems to take weather conditions into account when assessing the frequency of EPP at the individual and the temporal level.

References

Johnsen A, AndersenV, Sunding C, Lifjeld JT, 2000. Female bluethroats enhance offspring immunocompetence through extra-pair copulations. Nature 406: 296–299.

Johnsen A, Lifjeld JT, 2003. Ecological constraints on extra-pair paternity in the bluethroat. Oecologia 13: 476–483.

Johnsen A, Lifjeld JT, Andersson S, Örnborg J, Amundsen T, 2001. Male characteristics and fertilization success in bluethroats. Behaviour 138: 1 371–1 390.

Kempenaers B, 1993. The use of a breeding synchrony index. Ornis Scand. 24: 84.

Petrie M, Kempenaers B, 1998. Extra-pair paternity in birds: explaining variation between species and population. Trends Ecol. Evol. 13: 52–58.

Stutchbury BJM, 1998. Female mate choice of extra-pair males: breeding synchrony is important. Behav. Ecol. Sociobiol. 43: 213–215.

Westneat DF, Sherman PW, 1997. Density and extra-pair fertilizations in birds: a comparative analysis. Behav. Ecol. Sociobiol. 41: 205–215.