

## Age-Related Variation in Mate-Guarding Intensity in the Bluethroat (*Luscinia s. svecica*)

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### Abstract

Female extra-pair copulations (EPCs) have selected for male paternity guarding strategies in many bird species. In the bluethroat, *Luscinia s. svecica*, males guard their mates closely during the last 2 d before the start of egg laying, but there is great individual variation in the intensity of mate guarding. Here we show that some of this variation is related to male age. Old males guarded their mates with much lower intensity and sang more than young males, although the latter difference was not statistically significant. Controlling for male age, male and female coloration and size were not significantly related to the intensity of mate guarding. We have previously shown that young and old males had a similar paternity loss in their own broods. On the other hand, old males were far more successful than young males in achieving extra-pair fertilizations. These patterns suggest that young and old males have different trade-offs between preventing paternity loss in own nest and gaining paternity in others, because male skills in obtaining EPCs improve with experience and/or because of female preferences for old males as copulation partners. There were no significant relationships between paternity and male mate-guarding behaviour during the fertile period, indicating that mate guarding is not a very effective paternity-assurance strategy in the bluethroat.

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### Introduction

Mate guarding by close following is a common paternity-assurance strategy in many birds, particularly among territorial passerines (Birkhead & Møller 1992). It is often assumed (e.g. in comparative studies) that most or all males in a population of a 'mate guarding species' guard their mates with the same level of intensity. However, in several species the intensity of mate guarding varies

considerably between males (Morton 1987; Welling et al. 1995; Johnsen et al. 1998a). For males, there is a potential trade-off between guarding the already acquired mate and seeking additional mates and/or extra-pair copulations (EPCs) (Brodsky 1988; Hasselquist & Bensch 1991). Thus, to understand patterns of mate-guarding behaviour, it is important to identify factors that influence the costs and benefits of guarding vs. seeking additional matings for individual males. Potentially important factors include local socio-ecological conditions like breeding density and synchrony, which may affect encounter rates and intrusion pressure, and male characteristics (e.g. phenotypic quality and age), which may influence female willingness and male ability to perform EPCs.

Studies of the relationship between male characteristics and mate-guarding intensity have given two fundamentally different sets of results. On the one hand, high-quality males guard their mates more intensely than males of lower quality in the house sparrow *Passer domesticus* (Møller 1987) and the large cactus finch *Geospiza conirostris* (Grant & Grant 1989). The explanation for this might be that only high quality males (i.e. males in good condition) can afford spending energy on intense mate guarding. On the other hand, phenotypically unattractive males guard more intensely than relatively attractive males in the bluethroat *Luscinia s. svecica* (Johnsen & Lifjeld 1995; Johnsen et al. 1998a). Furthermore, in purple martins *Progne subis* and willow tits *Parus montanus*, young males guard more intensely than old ones (Welling et al. 1995; Wagner et al. 1996). A negative relationship between quality-indicating characteristics and guarding intensity may reflect differences in the perceived threat to paternity, mediated by female preferences for certain males or age/phenotype-related patterns of dominance. However, an age effect may also be related to age-specific differences in activity patterns caused by differences in ability to perform EPCs.

Male paternity guards have evolved in response to female involvement in EPCs (Birkhead & Møller 1992). Hence, mate guarding would seem likely to have effects on patterns of paternity. However, while experimental studies have indicated that the absence of male mate guarding results in more intrusions and EPCs (Björklund & Westman 1983; Dickinson 1997; Komdeur et al. 1999), the effects on actual paternity have been less clear cut (Westneat 1994; Riley et al. 1995; MacDougall-Shackleton et al. 1996; Currie et al. 1999; Chuang-Dobbs et al. 2001). Some correlational studies have indicated a reverse relationship, where males guarding more intensely lose more paternity (Gowaty & Bridges 1991; Kempnaers & Dhondt 1995, but see Burke et al. 1989).

Extra-pair paternity (EPP) is common in bluethroats (Krokene et al. 1996; Johnsen et al. 2001), and usually results from female EPCs with intruding neighbours (Johnsen et al. 1998a). Males guard their mates intensely during the period of peak female fertility (Krokene et al. 1996). There is extensive individual variation in the intensity of male mate guarding and some of this variation is related to male phenotypic appearance (Johnsen & Lifjeld 1995; Johnsen et al. 1997, 1998a). Experimental blackening of the throat patch of males resulted in lower pairing success and intensified mate guarding by blackened males compared with control males (Johnsen & Lifjeld 1995; Johnsen et al. 1998a), showing that in

an experimental setting, unattractive males guard their mates more closely in this species. The paternity guard seems to be rather inefficient, as evidenced by the fact that blackened males lost more paternity than controls despite having guarded more intensely (Johnsen et al. 1998a).

The aims of the present study of an unmanipulated population of bluethroats are twofold. First, we examine the relationships between mate-guarding intensity, and male and female characteristics. Secondly, we investigate how male and female behaviours during the fertile period relate to patterns of paternity. In a previous study based on data collected from the same bluethroat population in 1992, Krokene et al. (1996) found that males that did not lose paternity tended to follow a larger proportion of their females' movements and receive fewer intrusions than males that lost paternity. However, as these tests were performed on a rather restricted sample, we test whether the earlier found trends are supported when using a larger sample, including the data from 1992.

## Methods

### Field Procedures

Fieldwork was conducted in Øvre Heimdalen, Southern Norway (61°25'N, 8°52'E), during the breeding seasons of 1992, 1998 and 1999. Adult birds were caught in mist nets, measured (mass, wing length and tarsus length), aged (2 yr or older; Svensson 1992), and a 50 µl blood sample was taken by brachial venipuncture. Nestlings were blood sampled (maximum 25 µl) between days 2 and 10 post-hatch.

Two male plumage traits were measured. Similar to most other birds studied to date, bluethroats see in the ultraviolet (UV) parts of the light spectrum, and the blue feathers of the throat patch reflect significant amounts of UV light (Andersson & Amundsen 1997; Johnsen et al. 1998b). Previous studies have indicated that the UV-reflecting blue feathers have an intra-specific signalling function in this species (Andersson & Amundsen 1997; Johnsen et al. 1998b; Johnsen et al. 2001). Using a spectroradiometer, we measured the reflectance from the blue feathers in 1998. The methods for these reflectance measurements and the calculation of objective colour parameters (chroma, hue and brightness) can be found in Johnsen et al. (2001). Another plumage trait of potential importance is the lower chestnut breast band, the width of which has been shown to correlate with within-pair paternity success (Johnsen et al. 2001). We measured this trait with a slide calliper in 1992 and 1999. Both measured plumage traits show age-dependence, with old males having more chromatic blue feathers and wider chestnut bands (Andersson & Amundsen 1997; Johnsen et al. 2001). Female coloration was scored on a 10-point scale, as described in Amundsen et al. (1997).

When the birds had established in pairs and the females had almost finished building nests, we started recording 22-min time budgets on focal pairs by visual observations. We recorded time budgets from 32 pairs (1992: 8, 1998: 12, 1999: 12), all of which we had exact knowledge of first egg laying date for. Details of the

observational procedures can be found elsewhere (Johnsen & Lifjeld 1995; Krokene et al. 1996). Every second minute, we recorded the distance between mates (<1, 1–5, 6–10, 11–20, > 20 m), resulting in a maximum of 11 distance scores for each time budget. In addition, all movements (flights >2 m), intrusions and song activity were recorded continuously during each 2-min period. When the pair mates were not together, we focused on the males. A previous study has shown that there is a distinct peak in mate-guarding intensity during the last couple of days before start of egg laying in the present bluethroat population (Krokene et al. 1996). In fact, the majority of guarding males only guard intensively during the last 2 d before the start of egg laying (A. Johnsen & J. T. Lifjeld, pers. obs.). Thus, in order to get a comparable sample, we only used time budgets recorded on the days  $\pm 2$  and/or  $\pm 1$  (day 0 being the day of the first egg) in the analyses. Whenever we had data from both days on a given pair ( $n = 9$ ), we used the average of the measured variables, as we have previously shown that there is a significant correlation ( $r_s = 0.45$ ) in mate-guarding intensity between the 2 d (Johnsen et al. 1997). The time budgets were recorded throughout the day ( $\bar{x} = 12.16$  h, range: 05.40–20.20 h), and constituted 902 min in total ( $23 \times 22 + 9 \times 44$  min). The average number of minutes of actual observation of at least one pair member was  $22 \pm 11$  SD (range 6–44). Excluding four pairs with less than 10 min of observation from the analyses did not affect the results of this paper significantly. From the raw data, we calculated five behavioural parameters: (1) the proportion of time males were less than 1 m from their mates (a measure of mate-guarding intensity; Johnsen & Lifjeld 1995), (2) the proportion of female movements followed by the male, (3) song rate (proportion of 2-min periods with one or more song bouts), (4) intrusion rate (intrusions/min of observation of the territory), and (5) female movement rate (number of flights >2 m/min of observation of the female).

#### Parentage Analysis

The details about parentage determination for the broods included in this study have been published previously (Krokene et al. 1996; Johnsen et al. 2001). Briefly, extracted DNA was analysed by means of multilocus DNA fingerprinting (1992 samples; Krokene et al. 1996) or microsatellite typing (1998 and 1999 samples; Johnsen et al. 1998a, 2001). In the analysis of multilocus fingerprints, we used the band sharing coefficient (<0.40) and the number of novel bands ( $\geq 3$ ) as criteria for parentage exclusion (Krokene et al. 1996). The microsatellite analysis was based on six heterologous (i.e. isolated from other species) microsatellite markers, with a combined probability of exclusion (Jamieson 1994) of 0.995 (see Johnsen et al. 1998a for details about this microsatellite marker system).

#### Statistical Procedure

Each male contributed only one data point to each analysis. Non-parametric tests were used when testing whether male and female characteristics were related to mate-guarding intensity and song rate, because the response variables were not

normally distributed (tested with Shapiro–Wilk tests in JMP 3.1.1 (© 1989–1992, SAS Institute, Inc., Cary, NC, USA);  $n = 32$  and  $31$  respectively, both  $W < 0.87$ , both  $p < 0.0008$ ). We used logistic regressions to test whether the occurrence of EPP was associated with male and female behaviour during the peak fertile period. For the latter tests, we calculated power using G\*POWER (Buchner et al. 1997), assuming a medium effect size. All other tests were performed using STATVIEW 5.0 (© 1992–98, SAS Institute, Inc.). Sample sizes vary in the different tests due to missing data points. All p-values are two-tailed and parameter values are given as  $\bar{x} \pm SE$ .

## Results

### Behaviour vs. Male and Female Characteristics

We tested whether mate-guarding intensity and song rate were related to a suite of male characteristics. Young males guarded their mates with much higher intensity than old males (Table 1; Fig. 1) and they sang less, although the difference in song rate was not statistically significant (Table 1).

There was no significant difference between the age classes in the amount of time that they were observed (young males:  $24.4 \pm 3.6$  min, old males:  $21.0 \pm 2.2$  min,  $U = 90.0$ ,  $p = 0.41$ ), but young males were observed earlier in the day

Table 1: Relationships between behaviour during the peak fertile period, and male and female age. Values are given as average  $\pm$  SE. Sample sizes are shown in brackets

| Variable                             | Male age             |                      | Test statistic | p      |
|--------------------------------------|----------------------|----------------------|----------------|--------|
|                                      | Young                | Old                  |                |        |
| Mate-guarding intensity <sup>a</sup> | $0.77 \pm 0.10$ (10) | $0.26 \pm 0.06$ (22) | $U = 23.5$     | 0.0004 |
| Young females                        | $0.75 \pm 0.11$ (9)  | $0.30 \pm 0.16$ (5)  | $U = 6.0$      | 0.027  |
| Old females                          | –                    | $0.18 \pm 0.07$ (12) | –              | –      |
| Song rate <sup>b</sup>               | $0.20 \pm 0.10$ (10) | $0.40 \pm 0.08$ (21) | $U = 66.0$     | 0.095  |
| Intrusion rate <sup>c</sup>          | $0.03 \pm 0.02$ (10) | $0.04 \pm 0.01$ (22) | $U = 94.0$     | 0.47   |
| Female movements <sup>d</sup>        | $0.34 \pm 0.07$ (9)  | $0.23 \pm 0.03$ (16) | $U = 39.0$     | 0.06   |
|                                      | Female age           |                      |                |        |
|                                      | Young                | Old                  |                |        |
| Mate-guarding intensity <sup>a</sup> | $0.58 \pm 0.10$ (14) | $0.18 \pm 0.07$ (12) | $U = 34.0$     | 0.009  |
| Young males                          | $0.75 \pm 0.11$ (9)  | –                    | –              | –      |
| Old males                            | $0.30 \pm 0.16$ (5)  | $0.18 \pm 0.07$ (12) | $U = 23.0$     | 0.43   |
| Song rate <sup>b</sup>               | $0.24 \pm 0.09$ (14) | $0.45 \pm 0.12$ (12) | $U = 57.5$     | 0.16   |
| Intrusion rate <sup>c</sup>          | $0.03 \pm 0.01$ (14) | $0.03 \pm 0.01$ (12) | $U = 81.0$     | 0.87   |
| Female movement rate <sup>d</sup>    | $0.33 \pm 0.06$ (11) | $0.27 \pm 0.03$ (8)  | $U = 31.5$     | 0.30   |

<sup>a</sup> Proportion of time males spent <1 m from their mates.

<sup>b</sup> Proportion of 2-min periods with male song.

<sup>c</sup> Intrusions/minute.

<sup>d</sup> Flights (>2 m) per minute.

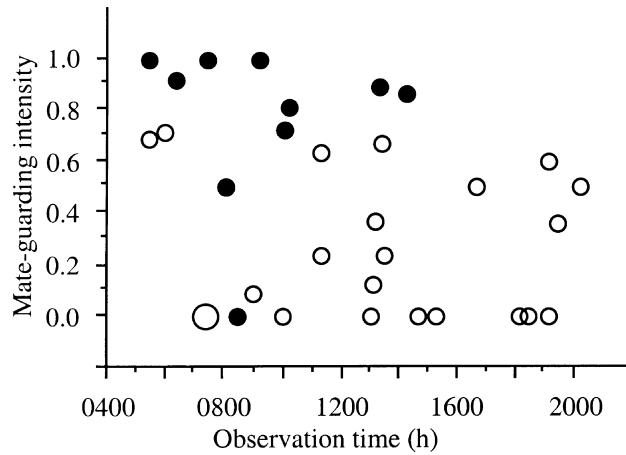


Fig. 1: Relationship between the timing of observation and male mate-guarding intensity (proportion of time males spent <1 m from their mates), for young males (black dots) and old males (white dots). The enlarged dot represents two data points

( $\bar{x}$  = 08.59 h, range: 05.45–14.18) than old males ( $\bar{x}$  = 13.30 h, range: 05.40–20.20;  $U = 56.0$ ,  $p = 0.028$ ). However, within each age class, observation time was not correlated with mate-guarding intensity (Spearman rank correlation, young males:  $n = 10$ ,  $r_s = -0.35$ ,  $p = 0.29$ , old males:  $n = 22$ ,  $r_s = -0.11$ ,  $p = 0.63$ ; Fig. 1), or song rate (young males:  $n = 10$ ,  $r_s = 0.11$ ,  $p = 0.75$ , old males:  $n = 21$ ,  $r_s = -0.22$ ,  $p = 0.33$ ). Hence, the large difference in mate-guarding intensity and tendency for a difference in song rate between the age classes cannot be explained by differences in the timing of observations.

The relationships between the remaining male characteristics and the two behavioural variables are summarized in Table 2. Intensely guarding males had

Table 2: Relationships between male traits and behaviour during the peak of their females' fertile period

| Male trait              | Mate-guarding intensity <sup>b</sup> |                |      | Song rate <sup>c</sup> |                |      |
|-------------------------|--------------------------------------|----------------|------|------------------------|----------------|------|
|                         | n                                    | Test-statistic | p    | n                      | Test-statistic | p    |
| Chroma <sup>a</sup>     | 11                                   | $r_s = -0.21$  | 0.51 | 11                     | $r_s = -0.02$  | 0.95 |
| Brightness <sup>a</sup> | 11                                   | $r_s = 0.04$   | 0.91 | 11                     | $r_s = 0.36$   | 0.26 |
| Hue <sup>a</sup>        | 11                                   | $r_s = 0.05$   | 0.89 | 11                     | $r_s = -0.11$  | 0.72 |
| Chestnut band width     | 16                                   | $r_s = -0.61$  | 0.02 | 15                     | $r_s = 0.47$   | 0.08 |
| Body mass               | 28                                   | $r_s = -0.22$  | 0.26 | 27                     | $r_s = 0.04$   | 0.85 |
| Wing length             | 28                                   | $r_s = -0.49$  | 0.01 | 27                     | $r_s = -0.02$  | 0.93 |
| Tarsus length           | 28                                   | $r_s = 0.20$   | 0.29 | 27                     | $r_s = -0.07$  | 0.72 |

<sup>a</sup> Objective measures of the colour reflectance from the blue feathers. See Johnsen et al. (2001) for explanations of the calculation of these parameters.

<sup>b</sup> Proportion of time males spent <1 m from their mates.

<sup>c</sup> Proportion of 2-min periods with song.

narrower chestnut bands and shorter wings. However, as both of these characteristics are positively correlated with male age (Johnsen et al. 2001; A. Johnsen & J. T. Lifjeld, unpubl. data), we also performed separate analyses within each age class. For old males, there was no significant correlation between mate-guarding intensity and chestnut band width ( $n = 12$ ,  $r_s = -0.30$ ,  $p = 0.32$ ), but short-winged males guarded marginally significantly more intensely than long-winged ones ( $n = 18$ ,  $r_s = -0.45$ ,  $p = 0.06$ ). For young males, neither of the traits were significantly related to mate-guarding intensity (chestnut band width:  $n = 4$ ,  $r_s = 0.06$ ,  $p = 0.92$ , wing length:  $n = 10$ ,  $r_s = -0.26$ ,  $p = 0.44$ ). Sample sizes are low in these tests, so the results should be interpreted with caution. Most likely, the relationship between mate guarding and chestnut-band width is mainly due to a co-variation with male age. As for a relationship with wing length the results remain inconclusive.

Young females were guarded significantly more intensely by their mates than old females, whereas there was no significant relationship between female age and male song rate (Table 1). None of the other female traits were significantly related to the mate-guarding intensity or song rate of their mates (Table 3). However, there was a non-random pattern of pairing with respect to age (Fisher's exact test,  $p = 0.0007$ ), with all young males being paired to young females ( $n = 9$ ), and old males being paired to both young ( $n = 5$ ) and old females ( $n = 12$ ). To determine whether the effect on mate-guarding behaviour was mediated by male or female age, we tested each sex within the age group that contained pairings with both young and old individuals (i.e. young females and old males). Within the group of males that were paired to young females, young males guarded their mates with a higher intensity than old males (Table 1). For females that were paired to old males, the guarding intensity of their mates did not differ significantly between young and old females (Table 1). Hence, the apparent effect of female age on the guarding intensity of their mates was probably a by-product of the fact that all young males were paired to young females.

Table 3: Relationships between female traits and the behaviour of their mates during the peak of the fertile period

| Female trait              | Mate-guarding intensity <sup>b</sup> |                |      | Song rate <sup>c</sup> |                |      |
|---------------------------|--------------------------------------|----------------|------|------------------------|----------------|------|
|                           | n                                    | Test-statistic | p    | n                      | Test-statistic | p    |
| Colour score <sup>a</sup> | 26                                   | $r_s = -0.15$  | 0.45 | 26                     | $r_s = 0.18$   | 0.37 |
| Body mass                 | 26                                   | $r_s = 0.13$   | 0.51 | 26                     | $r_s = -0.22$  | 0.28 |
| Wing length               | 26                                   | $r_s = 0.21$   | 0.30 | 26                     | $r_s = -0.27$  | 0.18 |
| Tarsus length             | 26                                   | $r_s = -0.008$ | 0.97 | 26                     | $r_s = -0.08$  | 0.70 |

<sup>a</sup> Female coloration scored on a 10-point scale. See Amundsen et al. (1997) for explanation of the scoring procedure.

<sup>b</sup> Proportion of time males spent <1 m from their mates.

<sup>c</sup> Proportion of 2-min periods with song.

To investigate possible proximate reasons for the age differences in mate-guarding behaviour, we compared the rate of intrusions into each focal male's territory and the rate of their females' movements, for young and old males, respectively. There was no significant difference in the intrusion pressure experienced by the two age groups (Table 1). Females paired with young males initiated flights (>2 m) at a higher rate than those paired with older males but the difference was not statistically significant (Table 1). The latter test included only those pairs in which the female was observed during the time-budget session, and thus excluded seven males that were not guarding at all (6 old, 1 young). However, within this more limited subset of the data, there was still a strong effect of male age on the intensity of guarding ( $U = 6.0$ ,  $p = 0.0002$ ). There were no significant differences between young and old females in movement rate or in the intrusion rate into their territories (Table 1). Contrary to expectation from the above results, there was no significant correlation between mate-guarding intensity and female movement rate ( $n = 25$ ,  $r_s = 0.076$ ,  $p = 0.71$ ). Splitting the data by male age, we found a significant negative correlation between mate-guarding intensity and female movement rate for young males ( $n = 9$ ,  $r_s = -0.77$ ,  $p = 0.03$ ), and a non-significant negative correlation for old males ( $n = 16$ ,  $r_s = -0.29$ ,  $p = 0.27$ ).

#### Relationships Between Behaviour and Paternity

Overall, 30.3% (44 of 145) of the offspring distributed in 55.6% (15 of 27) of the nests were sired by extra-pair males. The age of the parents did not influence the likelihood of EPP significantly (Table 4).

Krokene et al. (1996) analysed the relationship between behaviour and paternity by comparing nests containing EPP with nests without EPP. In order to be able to control for the potentially confounding effect of male age, we performed logistic regressions with the occurrence of EPP (yes/no) as dependent and five behavioural variables (mate-guarding intensity, proportion of female movements followed by the male, female movement rate, song rate and intrusion rate) and male age as independent variables. We found no significant associations between these behaviours and the occurrence of EPP when testing for each variable separately (Table 5). Furthermore, a multivariate logistic regression model including all five behavioural variables and male age revealed no significant relationships ( $n = 20$ , all  $\chi^2 < 2.1$ , all  $p > 0.14$ ). It should be noted, however, that the power of these tests was low, ranging between 0.27 and 0.34.

Table 4: Average ( $\pm$ SE) proportion of extra-pair offspring in broods of young and old males and females. Sample sizes are shown in brackets

|         | Young                | Old                  | Test-statistic | p    |
|---------|----------------------|----------------------|----------------|------|
| Males   | 0.30 $\pm$ 0.10 (9)  | 0.28 $\pm$ 0.08 (18) | U = 74.0       | 0.71 |
| Females | 0.26 $\pm$ 0.09 (14) | 0.34 $\pm$ 0.09 (12) | U = 70.5       | 0.47 |

Table 5: Relationships between estimates of male and female behaviour during the peak fertile period and the occurrence of extra-pair paternity in their subsequent broods

| Behavioural variable                       | n  | $\chi^{2f}$ | p    |
|--|----|-------------|------|
| Mate-guarding intensity <sup>a</sup>       | 27 | 0.04        | 0.84 |
| Proportion of male followings <sup>b</sup> | 27 | 0.23        | 0.64 |
| Song rate <sup>c</sup>                     | 27 | 0.53        | 0.47 |
| Intrusion rate <sup>d</sup>                | 27 | 0.03        | 0.85 |
| Female movement rate <sup>e</sup>          | 20 | 1.15        | 0.28 |

<sup>a</sup> Proportion of time males spent <1 m from their mates.

<sup>b</sup> Proportion of female movements followed by the male.

<sup>c</sup> Proportion of 2-min periods with male song.

<sup>d</sup> Intrusions/min.

<sup>e</sup> Flights (>2 m)/min.

<sup>f</sup> Logistic regression models, controlling for male age.

## Discussion

The main result of this study is that old males guarded their mates less intensely than young ones, whereas no other male or female characteristics were significantly related to male behaviour during the fertile period after controlling for male age. Male mate guarding behaviour was not significantly related to patterns of paternity.

The present pattern of age-related mate-guarding behaviour adds to our previously reported age effect on success in EPCs; old bluethroat males are far more successful than young ones in achieving extra-pair fertilizations (Johnsen et al. 2001). In several bird species, there appears to be a trade-off between guarding own paternity and seeking extra mating opportunities (Brody 1988; Hasselquist & Bensch 1991). Our results provide indirect evidence for such a trade-off, as old males as a group spend less time guarding their mates (this study) and have a higher success in achieving extra-pair fertilizations (Johnsen et al. 2001). We have previously shown that there is a trade-off between mate guarding and advertisement (song) in this species (Johnsen et al. 1997, 1998a). Furthermore, song during the fertile period is often performed close to territory borders (Johnsen & Lifjeld 1995). Thus the combined results of this and previous studies suggest a trade-off between mate guarding and EPC-behaviour. However, to conclusively demonstrate such a trade-off, one would have to show on an individual basis that males guarding intensely spend less time pursuing EPCs and at present we do not have the data to test this. If there is such a trade-off in the bluethroat, it seems that old males prioritize EPC-behaviour whereas young males largely remain in their territories and guard their mates.

The ability to successfully gain EPCs may improve with experience and therefore with age. This may be connected to improved skills in detecting fertile females and/or performing a successful intrusion (Johnsen et al. 2001). Hence, old males may be more successful in gaining EPCs than young males, and reduce their

investment in mate guarding accordingly. Young males, on the other hand, may invest more in mate guarding because they have lower prospects of achieving EPCs and/or because their paternity is more at risk because of frequent intrusions from neighbouring old males. Under the male-experience scenario, our finding that old males were more successful in EPCs than young ones (Johnsen et al. 2001) would simply reflect a higher investment in EPC-behaviour by old males.

A non-exclusive alternative to the male-experience hypothesis is that females prefer old males as copulation partners. Females may prefer to have their eggs fertilized by old males rather than young ones e.g. if there is an association between male age and genetic quality (Brooks & Kemp 2001). Such a preference could also result in old males investing more energy in EPC-behaviour and/or young males intensifying mate guarding, perhaps as a response to signs of female infidelity. In support of this, females paired to old males moved less than those paired with young males although this difference was only marginally significant. This may suggest that the females of young males were trying to escape male mate guarding to adjust paternity (Møller 1992; Johnsen et al. 1998a) but this needs to be confirmed with a larger data set. Contrary to expectations from a model of age-related female preferences, there was no difference between young and old males in within-pair paternity (see Johnsen et al. 2001 for a similar result in a larger sample). Nevertheless, we cannot exclude the possibility that young males would have experienced a higher loss if they had not guarded their mates intensely (Johnsen et al. 1998a). Temporary removal of males from each age category might distinguish the relative roles of mate guarding and female choice on the outcome in terms of paternity.

Long-winged old males guarded less intensely than short-winged ones, which may suggest that high quality males perceive a lower threat to paternity (Wagner et al. 1996). Again, this difference was only marginally significant, so this result should be confirmed with a larger data set. However, long-winged males did not have a higher paternity and were not more successful in EPCs than short-winged males (Johnsen et al. 2001). Hence, female choice based on wing length seems unlikely to account for the lower mate guarding intensity of long-winged males. At present, we cannot determine whether the non-significant tendency for long-winged old males to guard less intensely is biologically relevant or spurious.

Intuitively, male mate guarding should have an effect on the outcome of the sexual conflict over fertilizations. However, it has proved difficult to perform unequivocal tests of the relationship between guarding intensity and paternity (e.g. Westneat 1994; Currie et al. 1999). As different males probably experience different levels of threat to paternity, a correlation between paternity and mate-guarding intensity may not be an appropriate test of the effectiveness of mate guarding. This is because it is impossible to know what the degree of paternity loss would have been for a given male at lower mate guarding intensity. On the other hand, experimental removal of males may not be appropriate either, because females might then be responding to a perceived loss of mate. In the present study, mate-guarding behaviour was not significantly related to paternity. Hence, the previously reported tendency for an effect of mate guarding on paternity

(Krokene et al. 1996) was not supported. However, even if the present sample is more than three times larger than the previous one and also contains those previous nests, the power of the tests is still low. Accordingly, we can only conclude that mate guarding does not have a profound effect on paternity in the bluethroat, leaving the possibility that it does have an effect on the level of paternity for individual males open for further research.

In conclusion, there are obvious differences between young and old bluethroat males in behaviour during the fertile period, suggesting that there is a trade-off between preventing paternity loss in own nest and gaining paternity in other nests, which affects the two age-classes differently. The skew towards extra-pair behaviour at the expense of mate guarding for old males may be explained by improved experience and success with EPCs with age and/or female preferences for old males as EPC partners.

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### Literature Cited

- Amundsen, T., Forsgren, E. & Hansen, L. T. T. 1997: On the function of female ornaments: male bluethroats prefer colourful females. *Proc. R. Soc. Lond. B* **264**, 1579–1586.
- Andersson, S. & Amundsen, T. 1997: Ultraviolet colour vision and ornamentation in bluethroats. *Proc. R. Soc. Lond. B* **264**, 1587–1591.
- Birkhead, T. R. & Møller, A. P. 1992: *Sperm Competition in Birds: Evolutionary Causes and Consequences*. Academic Press, London.
- Björklund, M. & Westman, B. 1983: Extra-pair copulations in the pied flycatcher (*Ficedula hypoleuca*). A removal experiment. *Behav. Ecol. Sociobiol.* **13**, 271–275.
- Brodsky, L. M. 1988: Mating tactics of rock ptarmigan, *Lagopus mutus*: a conditional mating strategy. *Anim. Behav.* **36**, 335–342.
- Brooks, R. & Kemp, D. J. 2001: Can older males deliver the good genes? *Trends. Ecol. Evol.* **16**, 308–313.
- Buchner, A., Faul, F. & Erdfelder, E. 1997: G\*Power: a priori, post-hoc, and compromise power analyses for the Macintosh (Version 2.1.2) (Computer program). Univ. of Trier, Trier.
- Burke, T., Davies, N. B., Bruford, M. W. & Hatchwell, B. J. 1989: Parental care and mating behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature* **338**, 249–251.
- Chuang-Dobbs, H. C., Webster, M. S. & Holmes, R. T. 2001: The effectiveness of mate guarding by male black-throated blue warblers. *Behav. Ecol.* **12**, 541–546.
- Currie, D., Krupa, A. P., Burke, T. & Thompson, D. B. A. 1999: The effect of experimental male removals on extrapair paternity in the wheatear, *Oenanthe oenanthe*. *Anim. Behav.* **57**, 145–152.
- Dickinson, J. L. 1997: Male detention affects extra-pair copulation frequency and pair behaviour in western bluebirds. *Anim. Behav.* **53**, 561–571.
- Gowaty, P. A. & Bridges, W. C. 1991: Behavioral, demographic, and environmental correlates of extra-pair fertilizations in eastern bluebirds, *Sialia sialis*. *Behav. Ecol.* **2**, 339–350.

- Grant, R. B. & Grant, P. R. 1989: Evolutionary Dynamics of a Natural Population: The Large Cactus Finch of the Galápagos. Univ. of Chicago Press, Chicago and London.
- Hasselquist, D. & Bensch, S. 1991: Trade-off between mate guarding and mate attraction in the polygynous great reed warbler. *Behav. Ecol. Sociobiol.* **28**, 187–193.
- Jamieson, A. 1994: The effectiveness of using co-dominant polymorphic allelic series for (1) checking pedigrees and (2) distinguishing full-sib pair members. *Anim. Genet.* **25**, 37–44.
- Johnsen, A. & Lifjeld, J. T. 1995: Unattractive males guard their mates more closely: an experiment with bluethroats (Aves, Turdidae: *Luscinia s. svecica*). *Ethology* **101**, 200–212.
- Johnsen, A., Lifjeld, J. T. & Rohde, P. A. 1997: Coloured leg bands affect male mate-guarding behaviour in the bluethroat. *Anim. Behav.* **54**, 121–130.
- Johnsen, A., Lifjeld, J. T., Rohde, P. A., Primmer, C. R. & Ellegren, H. 1998a: Sexual conflict over fertilizations: female bluethroats escape male paternity guards. *Behav. Ecol. Sociobiol.* **43**, 401–408.
- Johnsen, A., Andersson, S., Örnborg, J. & Lifjeld, J. T. 1998b: Ultraviolet plumage ornamentation affects social mate choice and sperm competition in bluethroats (Aves: *Luscinia s. svecica*): a field experiment. *Proc. R. Soc. Lond. B* **265**, 1313–1318.
- Johnsen, A., Lifjeld, J. T., Andersson, S., Örnborg, J. & Amundsen, T. 2001: Male characteristics and fertilization success in bluethroats. *Behaviour* **138**, 1371–1390.
- Kempenaers, B. & Dhondt, A. A. 1995: Mate guarding and copulation behaviour in monogamous and polygynous blue tits: do males follow a best-of-a-bad-job strategy? *Behav. Ecol. Sociobiol.* **36**, 33–42.
- Komdeur, J., Kraaijeveld-Smit, F., Kraaijeveld, K. & Edelaar, P. 1999: Explicit experimental evidence for the role of mate guarding in minimizing loss of paternity in the Seychelles warbler. *Proc. R. Soc. Lond. B* **266**, 2075–2081.
- Krokene, C., Anthonisen, K., Lifjeld, J. T. & Amundsen, T. 1996: Paternity and paternity assurance behaviour in the bluethroat, *Luscinia s. svecica*. *Anim. Behav.* **52**, 405–417.
- MacDougall-Shackleton, E. A., Robertson, R. J. & Boag, P. T. 1996: Temporary male removal increases extra-pair paternity in eastern bluebirds. *Anim. Behav.* **52**, 1177–1183.
- Morton, E. S. 1987: Variation in mate guarding intensity by male purple martins. *Behaviour* **101**, 211–224.
- Møller, A. P. 1987: House sparrow, *Passer domesticus* communal displays. *Anim. Behav.* **35**, 203–210.
- Møller, A. P. 1992: Frequency of female copulations with multiple males and sexual selection. *Am. Nat.* **139**, 1089–1101.
- Riley, H. T., Bryant, D. M., Carter, R. E. & Parkin, D. T. 1995: Extra-pair fertilizations and paternity defence in house martins, *Delichon urbica*. *Anim. Behav.* **49**, 495–509.
- Svensson, L. 1992: Identification Guide to European Passerines. Lars Svensson, Stockholm.
- Wagner, R. W., Schug, M. D. & Morton, E. S. 1996: Condition-dependent control of paternity by purple martins: implications for coloniality. *Behav. Ecol. Sociobiol.* **38**, 379–389.
- Welling, P., Koivula, K. & Rytönen, S. 1995: Differences in mate guarding between age classes in the willow tit, *Parus montanus*. *Anim. Behav.* **49**, 852–854.
- Westneat, D. F. 1994: To guard or go forage: conflicting demands affect the paternity of male red-winged blackbirds. *Am. Nat.* **144**, 343–354.

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