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Female Bluethroats (*Luscinia s. svecica*) Regularly Visit Territories of Extrapair Males Before Egg Laying

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Recent evidence suggests that female birds play a more active role in sperm competition than traditionally recognized. Rather than passively awaiting male intruders, females may actively seek extrapair mates by moving outside their mate's territory (Kempenaers et al. 1992). Very little is known, however, on the movements of mated females before egg laying. We radio-tracked six female Bluethroats (*Luscinia s. svecica*) during the prelaying period to investigate whether they regularly move outside their mate's territory, a behavior that may allow assessment of and copulations with potential extrapair mates.

During the last decade, extrapair paternity has been demonstrated in an increasing number of bird species (Smith 1984, Birkhead and Møller 1992). Traditionally, multiple matings in birds have been interpreted as the result of male efforts to increase their own fitness by pursuing a mixed reproductive strategy of caring for their own offspring and seeking extrapair copulations (EPCs; Trivers 1972). According to this view, EPCs result from competition between males for fertilizable females, whereas females are considered almost passive. Recent studies, however, suggest that females may have a much more active role in extrapair mating and sperm competition (e.g. Smith 1988, Montgomerie and Thornhill 1989, Kempenaers et al. 1992, Lifjeld and Robertson 1992, Wagner 1992, Lifjeld et al. 1994, Mills 1994, Sheldon 1994). For in-

TABLE 1. Movements and observation dates for six female Bluethroats radio tracked during prelaying period.

Female no.	Observation date	Day relative to first egg	Observation period	Outside home territory?	Percent time outside home territory	Maximum-polygon distance (m)	Polygon area (ha)	No. foreign territories visited
1	8 June	−3	0640–1040	N	0	189	0.9	0
	11 June	0	0730–1130	Y	68	366	3.4	1
2	5 June	−10	0710–1110	Y	13	196	1.9	0
	9 June	−6	0640–1040	Y	54	571	7.1	1
3	28 May	−14	0620–0720	Y	60	[145][a]	[0.6][a]	1
4	7 June	?	0630–1030	Y	76	439	6.7	3
	10 June	?	0650–1050	Y	47	388	5.1	2
5	2 June	?	0600–0800	Y	48	[137][b]	[0.8][b]	1
	3 June	?	0540–0940	Y	2	165	1.0	1
6	12 June	−5	0720–1120	[N][c]	0	[90][c]	[0.3][c]	0

[a] Observed for 1 h only.
[b] Observed for 2 h only.
[c] Observed during nest building.

stance, females mated to low-quality males may seek EPCs to obtain good genes, while at the same time obtaining assistance from their mate in feeding the offspring (e.g. Buitron 1983, Møller 1988, Birkhead and Møller 1992, Houtman 1992, Kempenaers et al. 1992, Graves et al. 1993, Lifjeld et al. 1993). According to this hypothesis, females mated to high-quality males would gain nothing by seeking EPCs (Kempenaers et al. 1992, Graves et al. 1993, Mills 1994). At present, it is unknown for most species whether EPCs take place in the territory of the female or in the territories of males chosen as EPC partners. In Tree Swallows (*Tachycineta bicolor*), extrapair paternity occurs in 50 to 87% of the nests, but EPCs are rarely observed (Lifjeld et al. 1993, Venier et al. 1993, Dunn et al. 1994). This suggests that EPCs either occur cryptically (Birkhead and Møller 1992, Sheldon 1994), or take place outside the home territory (Kempenaers et al. 1992, Sheldon 1994).

The aim of our study was to investigate female spatial use in the prelaying period, in order to determine whether they visit males for EPCs. Very little is known about this aspect of female behavior. The Bluethroat is a sexually dichromatic passerine in which males have colorful throat patches (Peiponen 1960, Rangbru 1994). Bluethroats are usually socially monogamous, but 5 to 15% of males are polygynous (Peiponen 1960, Järvinen and Pietiäinen 1983, Johnsen 1994). Extrapair paternity has been found in around one-third of the broods examined in our study population (Krokene et al. in press). In previous observational studies, female Bluethroats remained out of sight of the observer for about 30 to 40% of the time (Evensen 1994). During these periods, they may have moved outside their mate's territories to visit other males.

Methods.—The study was carried out in Øvre Heimdalen (61°25′N, 8°52′E) at an elevation of 1,100 m in southern Norway during May and June 1994. Male and female Bluethroats were caught in mist nets placed in their territories and color banded to allow individual recognition. In order to follow individual females, we attached Holohil BD-2A radio transmitters to them. The transmitters, with a mass of about 0.8 g, were 3.9 to 5.4% of female body mass. We attached the transmitters to the back of the females, so that they would not interfere with flying, by shortening the feathers on a central area between their wings, and gluing the transmitter to the shortened feathers using cyanoacrylate glue (gel type). This procedure has been successfully adopted previously in studies of Great Reed Warblers (*Acrocephalus arundinaceus*; Bensch and Hasselquist 1992) and Bluethroats (H. Ellegren pers. comm.). The radio transmitters usually fell off after one or two weeks.

We searched for the radio-tagged females daily to identify their position using a Televilt RX 89 10HE directional antenna. Each day, we followed one focal female continuously for up to 4 h in the morning (Table 1). During the observation sessions, we marked the position of the female on a map every 2 min. At the same time, we recorded the position of the resident male, as well as the position and identity of intruding males, if such were seen. If the female was not seen, we noted whether the radio signal was clearly and steadily received, which we interpreted to mean that the female was close (i.e. <20 m) to a supposed position determined by triangulation with two bearings. We avoided approaching females closer than 10 m in order not to disturb them. We calculated the extent of female movements in two ways: (1) the maximum distance between two points in a polygon area of points where the females were positioned; and (2) the area covered by the same polygon, calculated using a planimeter. We determined whether each position of the female was within the territory defended by her mate from observations of the singing activities of males. We assumed territory borders to be halfway between the nearest singing posts used by separate males. Based on this, we calculated the amount of time each female spent within, and outside, her mate's territory. We recorded all social interactions between the female and males. We determined the date on which the first egg was laid either directly by searching for nests in the laying period, or by estimating the age of recently hatched nestlings. In estimating the date on which the first egg was laid, we assumed an incubation period of 14 days (the mean value for 1994; A. Johnsen pers. comm.) and a normal development of mass in the nestlings (Rangbru 1994).

We followed six females equipped with radio transmitters for a total of 35 h. All females were resident in a stable position and mated to a male of known identity. Most sampling sessions (8 of 10) lasted for 4 h (Table 1). Four females were observed during sampling sessions on two separate days. One female was observed during nest building. This female will be treated separately, since females may restrict their movements during this period (Järvinen and Pryl 1980). Her nest was not found, but the observation was assumed to have been made about five days prior to the first egg, based on observations of the duration of nest building and of the interval between nest completion and laying. One female was followed during a 1-h sampling session quite early in the prelaying period. Another female was followed for only 2 h during one of two sampling sessions. We were unable to find the nests of two additional females, and the dates the first eggs were laid, therefore, are unknown. We present our results as $\bar{x}$ ± SD.

Results.—Excluding those that were engaged in nest building, females were positioned during 92 ± 15% of the observation periods. They were sighted 20 ± 18% of the time and, for the remaining 72 ± 17% of the time, they were positioned by triangulation. Females were difficult to observe because they moved cryptically in dense vegetation on the ground. For the remaining 8 ± 15% of the time, the positions of the females were uncertain or unknown. All five females moved outside their home territory during at least one sampling session (Table 1). On average, females spent 41 ± 29% of the time outside their mate's territory and visited 1.1 ± 0.9 foreign territories (Table 1). All females visiting foreign territories were well within the area defended by the owner. Territories were contiguous within the breeding area. One female (Table 1, female 2) moved to an area outside the breeding area where no males had been observed singing. Females that were followed for 4 h moved across an average maximum distance of 331 ± 153 m, and within a polygon area of 3.7 ± 2.6 ha (Table 1). In comparison, the mean nearest-neighbor distance between nests in the study area was only 119 m in 1994, approximately one-third of the maximum distance covered by females. We believe that females spent most of their time foraging during the observation sessions because, when seen, they moved cryptically on the ground searching for food. When not seen, but positioned by triangulation, females appeared to behave in a similar way, since the radio signals changed at a steady rate, indicating that the birds were moving on the ground.

We observed no clear mate guarding in our study. Resident males were out of sight 84 ± 19% of the total time and, even when females were within their home territories, males were out of sight 80 ± 24% of the time. Males never were observed following females out of their territories. Males were seen singing at some distance (>20 m) from their mate 7 ± 9% of the time, and were seen not singing 9 ± 18% of the time. Males were seen less than 5 m from the females 1 ± 2% of the time. When close to a female, males were often observed displaying towards the female and/or copulating with her. These close associations never lasted more than 2 min. In only one observation session did we fail to observe the male in some sort of display towards his mate. In three cases, we observed copulations including cloacal contact. In addition, 19 possible copulations, in which the male and the female were hidden in the vegetation, were observed. In 14 cases of certain and possible copulations, the identity of the male was known, and all were resident males. Most displays and copulations occurred cryptically on the ground or in bushes and, therefore, some copulations and copulation attempts may have been overlooked. All observed copulation attempts took place within the home territory.

We observed 13 intrusions by other males. In four cases the intruder was chased away by the resident male; in contrast, the females never behaved aggressively towards male intruders. In nine cases the intruder was probably not detected by the resident male. We observed no copulations between intruding males and resident females, but EPCs may have been overlooked since these may occur cryptically as for example in Chaffinches (*Fringilla coelebs*; Sheldon 1994). In one particular case, an intruding male approached a female in her territory, whereupon the female followed the intruder out of the territory. The female was away for 2 min until she returned to her home territory. We were unable to follow the female during this event and, therefore, we do not know whether the female copulated with the male. The resident male was not observed during the event, nor was he observed immediately afterwards.

In contrast to the other females, the female that was followed during nest building spent all of her time less than 50 m from her nest, and never moved outside her mate's territory (Table 1, female 6). The female occasionally was seen carrying nest material in her beak. The male was not seen 86% of the time. He was observed singing more than 20 m away from the female 11% of the time, and was seen close to the female at the nest 3% of the time. We observed one intruding male, which was chased away by the resident male.

Discussion.—Our study demonstrates that female Bluethroats regularly move outside their mate's territory during the prelaying and fertile periods. Females, therefore, were in a position to encounter and potentially to assess and mate with other males. We observed no sexual interactions between the females and other males. However, assessment of potential extrapair mates may not be restricted to the fertile period. Rather, it may benefit a female to initiate such activities as soon as the social pair bond is established, although the eventual sexual interactions should not take place until the most fertile period (i.e. close to egg laying). Female Blue Tits (*Parus caeruleus*) also move outside their mate's territory during the fertile period (Kempenaers et al. 1992). In Blue Tits, most EPCs occur in the territory of the female's EPC partner and, in contrast to female Bluethroats, female Blue Tits never foraged during intrusions.

Female Bluethroats may combine foraging with assessing potential extrapair mates. They probably have sufficient food resources in their home territories, since the female that was observed during nest building never left her home territory to feed elsewhere. Studies of other populations of the species further suggest that food for nestlings normally is collected well within the territory boundaries (Schmidt 1970, Wartmann 1980). Thus, foraging alone probably cannot explain why female Bluethroats leave their territories. Female Bluethroats moved cryptically and, apparently, were not detected by males when outside the home territory. We suggest that this cryptic behavior may allow females to assess males without males being aware of their presence. Mate assessment may be seen as an information-gathering process (Sullivan 1994). Females may behave cryptically to allow prolonged mate assessment, since female exposure may elicit a sexual interaction that interrupts assessment before a precise estimate has been obtained.

Our finding that almost all females visited neighboring territories may seem surprising if our suggestion that visits are made to assess the quality of potential extrapair males is correct. According to the good-genes hypothesis for female-initiated EPCs, females mated to high-quality males should not seek EPCs, because extrapair males would probably be of lower genetic quality than their social mate (e.g. Birkhead and Møller 1992). We suggest that by visiting neighboring territories females improve their evaluation of the quality of their social mate relative to potential extrapair mates. Female knowledge of their social mate's relative quality may be incomplete, and subject to revision, if mate search is restricted, as for example in Pied Flycatchers (*Ficedula hypoleuca;* Dale et al. 1990, 1992) and Great Reed Warblers (Bensch and Hasselquist 1992).

Our study also provides information on the function of the territory in Bluethroats. Two hypotheses for the function of territoriality predict that females should spend most of their time foraging within their mate's territory in the prelaying and fertile periods: (1) territories function to secure nutritional resources that are required for egg formation and successful rearing of nestlings (Hinde 1956, Schoener 1969); and (2) territories function as a paternity guard in defending the fertile female (Møller 1987, 1990, see also Dunn 1992). These hypotheses are inconsistent with our observation that females regularly moved outside their mate's territory. Instead, male territories may function in attracting social and sexual partners (Price 1982, Dale and Slagsvold 1990). Two lines of evidence suggest that male Bluethroats give high priority to attracting mates. First, male singing seems to function in attracting mates, rather than in defending resources on territories (Merilä and Sorjonen 1994). Second, in our study, male Bluethroats never followed their mates outside their home territories, in contrast to male Chaffinches (Hanski 1992). Further studies are needed to test hypotheses for the function of territoriality in Bluethroats.

In conclusion, we suggest that female Bluethroats are able to assess potential extrapair mates while outside their mate's territory. With the exception of one female that was engaged in nest building, all females moved outside the territory of their mate. While outside their mate's territory, females came close to other males, although no extrapair sexual interactions were observed. Finally, the function of male territoriality in the Bluethroat apparently is not to defend exclusive feeding areas or the fertile female, but may be related to attraction of female mates.

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