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Timing of copulations and mate guarding in the Chaffinch *Fringilla coelebs*

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Copulation behaviour and mate guarding among radio-tagged male Chaffinches were studied in conifer-dominated forest in southern Finland in 1990–1991. Pair copulation rate was highest (one copulation hour^{-1}) about 1 to 3 days before egg laying and thereafter decreased. Neighbouring males attempted to obtain extra-pair copulations during the presumed fertile period of the female. Both intra-pair copulations and EPC-attempts were observed throughout all daylight hours. Males guarded their mates by close following and guarding was most intensive in the population of high breeding density. Mate guarding began several days before egg laying and continued until the start of incubation in high density population but not in the low density. As eggs are fertilized during a short insemination window after laying and sperm transferred just after laying most probably fertilizes the following egg, males would be expected to ensure paternity by copulating both with their own mates and other females during this time. However, male Chaffinches do not seem to recognise the insemination window, as there were no diurnal differences in intra-pair copulations or mate guarding intensity either prior to or during the days when eggs were fertilized. Another explanation is that they have to spread out their copulations to decrease the risk of cuckoldry. Intensive mate guarding until the start of incubation seems to be important due to continuous threat of EPC-seeking males especially in high breeding density. This may be most likely in coniferous habitat where extra-pair males are able to inconspicuously approach females and guarding males may easily lose contact with their mates.

1. Introduction

Males of monogamous species of birds are expected to try to maximize their reproductive success by ensuring the paternity of offspring in their own nests and copulating with other females to fertilize extra-pair young (mixed reproductive strategy, e.g. Trivers 1972, Birkhead & Møller 1992a). Males should ensure the paternity of young in their own nests by guarding their mates during the fertile period or by frequent copulations (see Birkhead et al. 1987, Birkhead & Møller 1992a). To pursue a mixed reproductive strategy a male should be capable of identifying the fertile period of both his own mate and other females. This could be accomplished in several ways: for example, by inspecting nest building activities (Pinxten et al. 1987) or eggs in the nest (Møller 1987), body mass and flying ability of the female (Beecher & Beecher 1979, Jones 1986), and dis-

play and copulation solicitations of the female (Lumpkin 1981, Møller 1985) or a combination of clues (Hatchwell & Davies 1992).

In all bird species examined to date females have been found to store sperm after insemination in special sperm storage tubules located at the utero-vaginal junction (see Birkhead & Møller 1992a and references therein). Therefore, sperm transferred in a single copulation several days before the start of laying may be capable of fertilizing an entire clutch. In the Zebra Finch *Taeniopygia guttata*, the fertile period of the female includes an average of 10 days before the laying of the first egg (i.e. the average time sperm can be stored) plus the number of laying days until the penultimate egg is laid (Birkhead et al. 1989). Based on the length of sperm storage tubules it has been estimated that the duration of sperm storage is 8.5 days in the Chaffinch (Birkhead & Møller 1992b, Sheldon 1994). However, not all inseminations during the fertile period are equally successful. If a female has been inseminated by sperm from two or more males, sperm transferred in the last copulation are more likely to fertilize subsequent eggs (last male sperm precedence; Birkhead et al. 1988). Furthermore, each egg is fertilized within ca. one hour of ovulation and ca. 24 hours before it is laid. At other times of the day the access of sperm to the fertilization site is blocked by the developing egg in the oviduct. This short time period when sperm are able to reach the ovum is called the insemination window (Cheng et al. 1983). In most species ovulation and laying (and hence the fertilization window) occur in the morning.

Males should adjust their copulations and mate-guarding activities to both the fertile period of the female (days before incubation) and to the insemination window during the morning hours. This gives rise to following predictions about male behaviour:

1) To secure the fertilization of eggs pairs should copulate most actively on days when ovulation takes place, especially during insemination windows. Due to last male sperm precedence a male should try to ensure that he is the last male to copulate before ovulation.
2) Similarly, males trying to fertilize eggs of strange females should concentrate their extra-pair copulation (EPC) attempts on days when eggs are fertilized and to morning hours in order to be the last copulating male before ovulation. The selective pressure on pair males to time their copulations right is likely to be stronger than on extra-pair males because of the subsequent investment of care by pair males.
3) To prevent cuckoldry a male should guard his mate several days before the start of laying but most intensively on days when the eggs are fertilized (one day before the first egg is laid until the day when the penultimate egg is laid). Further, the male should guard most intensively at the time of fertilization.

These predictions may not necessarily be compatible with theoretical and empirical studies implying female control of both intra- and extra-pair copulations in some species (Lumpkin 1981, Kempenaers et al. 1992, Birkhead & Møller 1993a, Sheldon 1994). Because successful forced copulations are probably lacking among Chaffinches (Sheldon 1994), the success of copulation is dependent on female co-operation. Therefore, the female may decide when and with whom she wants to copulate. However, this does not apply to predictions 2) and 3) because other males should attempt EPCs at any time to check if the female is willing to copulate, and to prevent cuckoldry the focal male should guard his mate continuously during her fertile period.

In this study I investigate the behaviour of radio-tagged male Chaffinches in relation to the presumed fertile period and fertilization window of the female. My objective was to determine how closely the observed male behaviour fits the predictions of males trying to ensure their paternity and maximize their reproductive success.

2. Materials and methods

The study was conducted in two study areas in southern Finland. The study area in Seitseminen National Park (61°N, 23°E) comprised conifer-dominated (spruce and pine) forests (for details of habitat, see Haila et al. 1987, 1989, Hanski & Haila 1988). Field work was done from 29 April until 18 June in 1990. The second study area was situated near Lammi biological station (61°N,

25°E) and comprised spruce-dominated forests with an admixture of deciduous trees (for details of habitat, see Tiainen et al. 1983, Hanski 1992). The field work was done from 22 April until 3 July and from 9 April until 10 July in 1990 and 1991, respectively. Breeding density of Chaffinches was high in Lammi study site (ca. 200 pairs km^{-2}) but low in Seitseminen (ca. 50 pairs km^{-2}).

The data were gathered by radio tracking. Radio tags (1.5 g) were attached on the back of male Chaffinches with a harness. Once located using the signal, birds were observed for up to one hour at a time. If the male was lost from sight, it was tracked again. The tag-attachment and tracking methods are described in more detail in Hanski & Haila 1988, Hanski 1992 and Hanski et al. 1992. I have no evidence that a radio tag would have affected males' behaviour. All males got mates and radio tags had no effect on their nesting success (Hanski & Laurila 1993a). However, I can not test the effect of radio tag on male's copulation behaviour, because similar data were impossible to gather without radio tracking in my coniferous study areas.

A total of 19 male Chaffinches were radio-tagged. Most of the data (13 males) and nearly all observed copulations (28 of 33) originate from Lammi study area. Males were observed throughout the day but more in the morning. Of the total tracking time (90 hours) when a pair was in visual contact 77% was done between 5.00 and 12.00 h and 23% between 12.00 and 17.00 h. When observing male behaviour I quantified the time that the male spent with his mate, intra-pair copulations and interactions with other males and females. The breeding cycle of each pair was divided into five main stages: pre-mating, pre-incubation, incubation, nestling and fledgling stage. Only observations during the last 10-day period of the pre-incubation stage were included in the analyses. In this study I relate all observations on copulation and mate guarding behaviour to the start of the incubation, not to the day when the first egg was laid. That is because some of the nests were situated high (range 3–23 m, mean 11 m, n = 50 nests) in sites that were not possible to reach, but it was possible to check the start of incubation by inspecting nests from a distance with binoculars. Females start incubation after laying the penultimate egg (pers. obs.), therefore I included the last laying day in the incubation stage. I defined guarding as occurring whenever a male spend time near his mate, mostly within 5 metres, and followed most of her movements closely (see Hanski 1992).

Behaviourally successful copulations, i.e. when the male mounted the female and apparent cloacal contact occurred, were included in the analyses. Sometimes a pair copulated in bouts up to four times within a few seconds, but I counted each bout as one behaviourally successful copulation. I did not observe any successful extra-pair copulations, but I interpret the behaviour of extra-pair males as EPC-attempts when the male of the focal pair was guarding her mate during her presumed fertile phase and an extra-pair male approached them. An extra-pair male often clearly approached the female and was on several occasions seen to court her. As a consequence, the guarding male fought and tried to chase the extra male away (see also Hanski et al. 1992). I observed both radio-tagged males and males without tags attempting EPCs. Either tagged male flew to another pair or an untagged male approached the female of the radio-tagged male. In the following, my results are presented in relation to observation time. Time during which the pair was out of sight, and could not be observed, was omitted from analyses.

3. Results

Mean clutch size in the Chaffinch in this study was 4.3 eggs which is smaller, but not significantly so, than in the Finnish nest-card data (mean 4.7, von Haartman 1969, Hanski, unpubl.). Hence, the first egg was laid on average three days before the start of incubation (on day –3, see Fig. 1). The time period when all eggs of the clutch are fertilized is on average four to five days starting on the day –5 (in a five-egg clutch) or –4 (in a four-egg clutch). The earliest intra-pair copulation was observed 10 days before the start of incubation, thus, the 10-day period before incubation was considered as the fertile period in this study.

I observed 33 intra-pair copulations in 90 hours during the 10-day period before incubation (Fig. 1A). The copulations peaked on the days –6

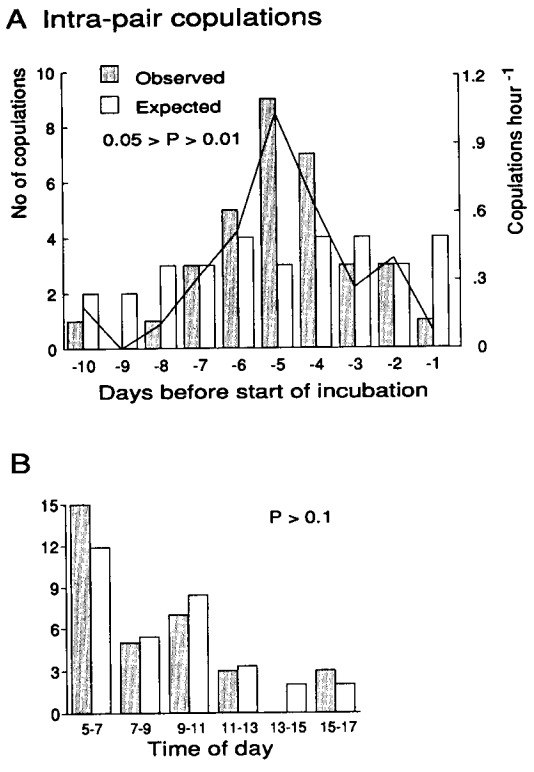

Fig. 1. A. Observed (hatched bars) and expected (open bars) numbers of intra-pair copulations (n = 33) in relation to the start of incubation and copulation rate (line). Day –1 is the laying day of the penultimate egg. B. Diurnal distribution of intra-pair copulations in two-hour intervals. Expected numbers have been calculated in relation to the observation time. 19 males were observed for 90 hours.

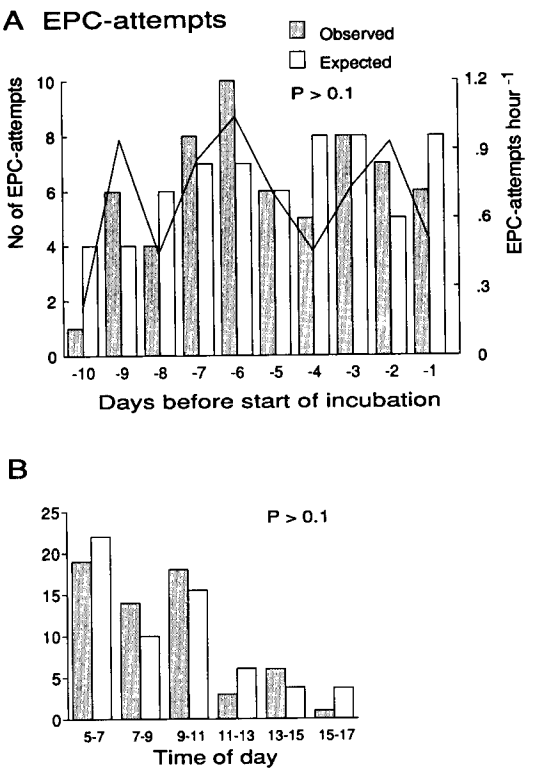

Fig. 2. A. Number of extra-pair copulation (EPC) attempts (bars, n = 61) and EPC-attempt rate (line) among Chaffinches during 10 days before the start of the incubation. B. Diurnal distribution of EPC-attempts. For legends, see Fig. 2.

to –4. The observed distribution differed significantly from the number expected on the basis of observation time (Goodness of fit, $G^2 = 21.2$, df = 9, $0.05 > P > 0.01$; Fig. 1A). This means that copulations peaked on average 1–3 days before the first egg. The highest observed copulation rate was 1.04 copulations hour^{-1} on day –5 (Fig. 1A). The mean copulation rate over the entire 10-day fertile period was 0.37 copulations hour^{-1}. In addition I saw three copulations during incubation: one on the first and two on the second day of incubation. Chaffinches copulated throughout the day. There was no difference between observed and expected copulation patterns with respect to time of day ($G^2 = 5.5$, df = 5, $P > 0.1$; Fig. 1B). From the mean diurnal copulation rate (assuming one day being 12 hours) I estimated that each pair copulated on average 44 times per clutch. However, this is only a rough estimate and should be considered with caution.

EPC-attempts followed a similar pattern to that expected during the entire 10-day period before incubation ($G^2 = 8.5$, df = 9, $P > 0.1$; Fig. 2A). EPC-attempts were observed on average 0.67 times hour^{-1}. The EPC-attempt rate varied during 10-day period, but there was no similar peak as in intra-pair copulation rate (Fig. 2A). As in the diurnal intra-pair copulation pattern, there was no difference between observed and expected patterns in EPC-attempts with respect to time of day ($G^2 = 7.8$, df = 5, $P > 0.1$; Fig. 2B). Three EPC-attempts were observed before the analysed 10-day period (on day –11).

Mate guarding intensity, measured as the proportion of time the male spent close to his mate,

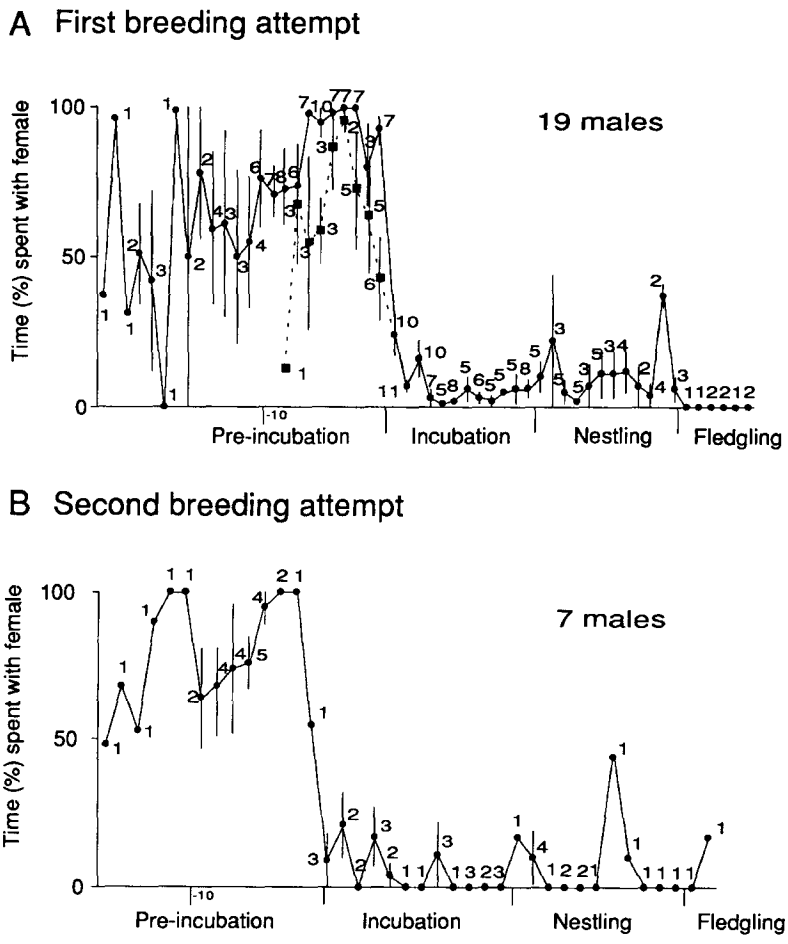

Fig. 3. The proportion of time (%) the males spent with their mates in different days during the breeding season. A. During the first breeding attempts in Lammi (line and dots) and in Seitseminen (dotted line and squares) and B. during further breeding attempts (Lammi only). Note that the data of both populations were combined from the incubation onwards (A). Each black dot indicates one day, vertical bars SE. Day –10 is shown as a comparison to Figs. 1A and 2A.

increased over the pre-incubation period and was at its peak from days –7 to –1 (Fig. 3A). The same pattern was seen during second breeding attempts which followed after nesting failure, although the number of males was not as large as in the first breeding attempts (Fig. 3B). Mate guarding activity was different in two study areas. Males spent on average larger proportion of time with their females in Lammi than in Seitseminen (t-test, two tailed, $t = 3.9$, $df = 17$, $P = 0.0012$). Percentage values were arcsin-transformed before tests. Males guarded their mates at a high rate until the start of incubation in Lammi but tended to reduce guarding activity in Seitseminen (Fig. 3A). There were no diurnal differences in the mate-guarding intensity when the proportions of time spent together were analysed in two-hour intervals, neither during days when fertilizations took place (days –5 to –1; one-way ANOVA, $F = 0.3$, $df = 5$, $P >> 0.1$) nor earlier in the pre-incubation stage (days –10 to –6; $F = 0.3$, $df = 5$, $P >> 0.1$).

In summary, Chaffinches copulated during the whole 10-day period before incubation, but most actively on the few days before the start of laying. Strange males attempted EPCs throughout this period. There was no diurnal activity peak either among intra-pair copulations or EPC-attempts. Males guarded their mates most actively during one week before the incubation and the same pattern was seen both in first and second breeding attempts. The average proportion of time spent in mate guarding was lower in Seitseminen than in Lammi. Males guarded actively during all day-light hours and continued to guard until the start of incubation in Lammi but seemed to reduce it in Seitseminen.

4. Discussion

The copulation rate among Chaffinches in a Finnish population was lower than in a population studied in England (Sheldon & Burke 1994). In England the copulations peaked three days before the onset of egg laying and was 4.4 copulation attempts hour^{-1}, of which 40% were successful. Copulation rate decreased during egg laying but pairs still copulated nearly every hour. In Finland the rate was lower, but still fairly high when compared with most other solitarily breeding birds (Birkhead et al. 1987, Birkhead et al. 1993). The estimated number of successful copulations per clutch was nearly a half of that in England (44 vs 83: Sheldon & Burke 1994). Sheldon & Burke (1994) argued that the high copulation rate in English Chaffinches may be due to an extremely high rate of female copulation solicitations. By soliciting frequently a female should advertise her fertility and increase a level of male-male competition between her mate and neighbouring males and furthermore, try to assess a quality of males (Sheldon 1994). I did not quantify the copulation solicitation rate of females and cannot make comparisons but there seems to be a real difference in the copulation rate between English and Finnish populations. The intra-pair copulation peak in the Chaffinch matched fairly well the general pattern in birds: copulations are usually most frequent 3 days before the first egg (see Birkhead & Møller 1992a, Birkhead & Møller 1993b).

Most passerines lay their eggs in early morning (Birkhead et al. 1987) and a copulation immediately after laying should have a high probability of fertilizing the following egg (Birkhead & Møller 1992a), although there is still competition for fertilization from previously inseminated sperm that have been stored in the sperm storage tubules. Although generally occurring in the morning, there does not seem to be any strictly determined egg-laying time among small passerine birds. Female Chaffinches laid (data of eight eggs) over a period of 2.5 hours from 5.30 a.m. onwards (Sheldon & Burke 1994) and Pied Flycatchers *Ficedula hypoleuca* laid their eggs over 3.5 hours from 5.00 a.m. onwards (Rosengren 1993). Laying was not strictly bound to a particular hour, and the same females often lay at different times on subsequent days (Rosengren 1993). Therefore, one would expect males to adjust their copulations within the morning hours. The expected pattern has been found among most bird species (e.g. Arvidsson 1992, Birkhead et al. 1987), but not in all (Birkhead et al. 1987). Copulations in the English Chaffinch population are more frequent in the morning, but were not concentrated during early morning hours (Sheldon & Burke 1994). In Finland copulations were fairly evenly distributed over all day-light hours. This may indicate that male Chaffinches are not capable of recognizing the insemination window of the female (see also Aguilera & Alvarez 1989, Venier & Robertson 1991). Another explanation is that for a male it is beneficial to inseminate a female often due to sperm precedence (see below).

One essential factor in the success of sperm competition is the timing of copulations in relation to other copulating males. If the female copulates several times and perhaps with more than one male, the sperm inseminated in the last copulation fertilize on an average 80% of subsequent eggs (Birkhead et al. 1988). Such sperm precedence has been experimentally confirmed by letting caged female Zebra Finches to copulate with several males and thereafter examining the paternity of offspring in relation to a single last-copulating male by using genetic polymorphism as a marker (Birkhead et al. 1988). However, if the copulation rate is high, i.e. pair copulations take place less than 4-hour intervals, last sperm precedence is not observed (Birkhead & Møller 1992a). The copulation rate in the Chaffinch was higher than in 4-hour intervals during egg laying, therefore the last sperm precedence is unlikely in the Chaffinch. However, a female Chaffinch may still be able to control paternity during laying through copulation solicitations. Closer to laying, female Chaffinches solicit EPCs significantly more often than they solicit intra-pair copulations (Sheldon 1994). This may hold true also among Finnish Chaffinches because strange males attempted EPCs till the end of egg laying but intra-pair copulation rate decreased after start of egg laying. Møller (1985) found that EPCs in the Barn Swallow *Hirundo rustica* occurred closer to the time of egg laying than intra-pair copulations. During egg laying the female can control paternity through EPCs, if for example there are males of

higher quality than her mate in the neighbourhood (Birkhead & Møller 1993a).

The fact that I did not see any successful extra-pair copulations may be partly due to their inconspicuousness. Males seeking EPCs behave very secretively (Ford 1983, pers. obs.) and most of the observed EPCs in the Chaffinch take place on the ground (Sheldon & Burke 1994). Their inconspicuousness is further supported by the finding that the proportion of extra-pair young is usually higher than would be expected according to observed EPCs (Westneat 1990, Sheldon & Burke 1994). However, the opposite pattern was found in the Willow and Wood Warblers (Gyllensten et al. 1990).

The male attempt to keep in close proximity with the female before and during egg laying is referred to as mate guarding (Beecher & Beecher 1979, Birkhead 1979). Mate guarding has been presented as a way that the male tries to prevent extra-pair copulations (see Birkhead & Møller 1992a and references therein) and this has been experimentally confirmed by male removal experiments (Björklund & Westman 1983, Møller 1987, Birkhead et al. 1989). EPCs have been frequently shown to fertilize eggs and yield extra-pair young (e.g. Gavin & Bollinger 1985, Sherman & Morton 1988, Birkhead et al. 1990, Westneat 1990, Gelter & Tegelström 1992, Kempenaers et al. 1992). Thus, for the male, mate guarding seems to be an efficient way to prevent cuckoldry. Because fertilization takes place after laying early in the morning, the risk of cuckoldry is also at its highest during this time. Therefore, the male should concentrate on active guarding in the morning and probably reduce guarding and allocate time for other activities later on the day. However, there was no diurnal pattern in the mate guarding activity. Male Chaffinches seemed to try to keep proximity with female even during periods eggs are not fertilized. This is may occur because of the risk of EPC-seeking males and cuckoldry throughout the day. The lack of differences in mate guarding in the Chaffinch during day-light hours is parallel to the behaviour of Barn Swallow males (Møller 1987).

Similarly, to secure the paternity of all offspring, a male should guard until the last egg of the clutch has been fertilized. In fact, this prediction was supported among Chaffinches in Lammi. Instead, in Seitseminen males seemed to reduce their guarding to the end of egg laying period. This is similar pattern than in the English Chaffinch population (Sheldon 1994). Several other studies have reported that mate guarding ceases before the clutch has been completed (e.g. Birkhead 1982, Mace 1988, Arvidsson 1992). As Chaffinches in Lammi, European Magpies *Pica pica* guarded until the female started to incubate (Birkhead et al. 1992). Birkhead & Møller (1992a) argued that males reduce guarding before the end of laying period, either because the risk of EPCs decreases, mate guarding is costly due to increased energy requirements and reduced opportunities to feed or because the male himself tries to obtain EPCs from other females. My results indicate that although the risk of lost paternity may decrease when there are fewer eggs left for fertilization, neighbouring males form a continuous threat due to their EPC-attempts. Furthermore, the males themselves do not begin to search for EPCs until their females have started to incubate and as breeding in the local Chaffinch population was asynchronous, males still have opportunities to find fertile females (Hanski 1992). I have no data on energetic costs of mate guarding, but male Chaffinches seem to be capable of continuing their guarding to the end of laying and again during subsequent breeding attempts.

5. Conclusions

One possible explanation for the observed difference in the mate-guarding pattern between English and Finnish Chaffinches might be the differences between breeding habitats and population densities. The English study was done in semi-open park containing mostly deciduous trees and having a Chaffinch density similar to Lammi (ca. 180 pairs km^{-2}, B. C. Sheldon, unpubl.). My study areas were in dense spruce-dominated forests where the visibility is limited throughout the year, beginning in the first part of the breeding cycle (Hanski 1992). Thus, guarding males may easily lose contact with their mates, particularly if the female is willing to seek EPCs with other males. In fact, males lose tract of their females

every now and then, especially when the male is involved in other activities, e.g. chasing intruders (Hanski & Laurila 1993b). On the other hand, males seeking EPCs may approach females in the cover without being seen by the focal male. High breeding density apparently increases the number of EPC-seeking males and the threat of cuckoldry forcing males to intensive mate guarding. Observed differences in guarding intensity between Lammi (high density) and in Seitseminen (low density) were parallel to the prediction.

Finnish Chaffinches seem to follow a different strategy from English Chaffinches: in parallel with mate guarding by following, males do not rely as much on additional paternity guards like frequent copulations. Birkhead & Møller (1992a) argued that if sperm competition is intense, it would pay for males to continue to copulate at a high rate throughout the egg-laying period as found in polyandrous species (e.g. Briskie 1992). However, this does not hold true in Finnish Chaffinches. Stored sperm in male's sperm storage organ available for copulations may be limited (Birkhead 1991) and frequent copulations as a principal paternity guard may not be possible in all species. In the situation of intense sperm competition one would expect males, as well as of frequent copulations, to continue their mate guarding throughout the egg-laying period. This was found among Chaffinches in high density are but not in low density area. High density together with dense conifer cover may create circumstances, where the risk of cuckoldry and the intensity of sperm competition are high and efficient mate guarding is inevitable to ensure paternity. However, more studies are still needed. It would be interesting to compare the degree of extra-pair paternity in English and Finnish Chaffinch populations, between populations with different behavioural patterns and habitats, but these data are not yet available in Finland.

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Selostus: **Peipon parittelujen ja puolisonvartioinnin ajoittuminen**

Radiolähettimillä varustettujen peippokoiraiden parittelu- ja puolisonvartiointikäyttäytymistä tutkittiin Lammilla ja Seitsemisen kansallispuistossa vuosina 1990–1991. Peipot parittelivat oman puolisonsa kanssa aktiivisimmin 5 päivää ennen haudonnan alkua (Kuva 1A). Koiraat yrittivat paritella vieraiden naaraiden kanssa 10 päivänä ennen haudontaa ja yritykset ajoittuivat odotetusti (Kuva 2A). Jakso vastaa naaraan fertiiliä vaihetta. Parin väliset ja parin ulkopuoliset paritteluyritykset ajoittuivat tasaisesti päivän ajalle (Kuvat 1B ja 2B). Koiraat vartioivat puolisoitaan seuraamalla niitä useita päiviä ennen haudontaa (Kuva 3). Vartiointi näytti olevan tehokkaampaa Lammin tiheässä populaatiossa. Peipon munasolu hedelmöityy aamulla heti munimisen jälkeen (hedelmöittymisikkuna). Koiraat eivät näytä tunnistavan munasolun tarkkaa hedelmöittymisaikaa sillä parittelut eivätkä vartiointi olleet aktiivisinta silloin. Vaihtoehtoisesti koiraat ajoittivat parittelut koko päivän ajalle, koska useat omat parittelut vähentävät parin ulkopuolisten hedelmöitysten todennäköisyyttä. Parin ulkopuoliset parittelut ovat mahdollisesti suuri uhka etenkin havumetsissä joissa vieraat koiraat voivat helposti lähestyä puuston suojassa.

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