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Mate guarding in forest-living, territorial Willow Tits

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A population of Willow Tits was studied during one breeding season in northern Finland, to find out whether copulations outside the pair bond (EPCs) occur in this basically monogamous species and whether mate guarding operates to prevent EPCs. Only two EPCs and two within-pair copulations were seen. The EPCs were not true ones; in both cases, a newly widowed female copulated with a paired male from a neighbouring territory. During the female's fertile period, average and maximum distances between the mates were shorter than during the non-fertile stage. During the fertile period, the pairs also spent more time in the same trees than during the non-fertile period. In the fertile, but not in the non-fertile period, males were the sex that kept near their mates by letting the females initiate most of the site changes. There was no clear difference in intensity of guarding between adult and juvenile males. Thus, male Willow Tits guard their mates during the fertile period and the most probable explanation is the avoidance of cuckoldry. Despite the rarity of witnessed extra-pair copulations, the existence of a mate defence strategy implies that a mixed reproductive strategy could exist in the Willow Tit.

1. Introduction

Extra-pair copulations (EPCs) are relatively common and result in fertilized eggs even in predominantly monogamous bird species (e.g. Bray et al. 1975, Alatalo et al. 1984, Gavin & Bollinger 1985, Møller 1987a, Quinn et al. 1987, Westneat 1987a, Sherman & Morton 1988, Brooker et al. 1990). Trivers (1972) suggested that at high levels of paternal care males stealing additional copulations, and thereby pursuing a mixed reproductive strategy, have a selective advantage over strictly faithful males. At the same time, however, natural selection should favour strategies to ensure the paternity of the young for which the males care. One such possible counter-tactic in birds is mate guarding behaviour, which in its most common form emerges as close following of the female during the period she is fertile. Since Beecher & Beecher (1979) first described the behaviour in the Sand Martin *Riparia riparia* and Birkhead (1979) in Magpies *Pica pica*, mate guarding has been found in dozens of bird species (see e.g. Birkhead et al. 1987 for a review).

In many species, especially in waterfowl, males can successfully obtain forced copulations (e.g. Mineau & Cooke 1979, McKinney et al. 1983, Birkhead et al. 1985).

However, because of the lack of an interomittent organ in most birds (e.g. passerines), it has been concluded that the willingness of the female is usually needed for EPC attempts to be successful (e.g. Lumpkin 1981, Fitch & Shugart 1984). One explanation for why females often do not resist is that they try to avoid the risk of injury, which struggling with a "rapist" might cause (McKinney et al. 1983). The fact that females can control or even actively seek EPCs, implies that other advantages might arise. Females could gain from EPCs in several ways, e.g. by obtaining additional paternal care for their offspring from males other than their mates (Trivers 1972), avoiding the consequences of possible sterility of their mate (Buitron 1983), increasing the genetic variability of the progeny (Gladstone 1979) or transmitting the EPC trait to male offspring (Møller 1985). One additional proposal is that EPCs could enable females to obtain genes for their progeny from superior-quality males (Gladstone 1979, Mineau & Cooke 1979). Smith (1988) found that in Black-capped Chickadees *Parus atricapillus* all the EPCs she observed occurred with males that were more dominant in winter flocks (and probably of better quality) than the ones with which the females were mated. A similar experimental result was reported by Møller (1988) for the Swallow *Hirundo rustica*, in which the quality was assessed in terms of tail ornament size.

Logically, the investment of males in the prevention of cuckoldry should increase with the readiness of their mates to accept EPCs and with the decreasing possibility of their obtaining additional copulations with other females. In the case of the Black-capped Chickadee, the low-ranking birds (juvenile males) would gain most by guarding their female, whereas the high-ranking birds should invest less in guarding.

We studied mate guarding in the Willow Tit *Parus montanus*, a forest-living territorial passerine with a monogamous mating system and biparental care, during one breeding season. To date, most studies of EPCs and mate guarding have concerned either species utilizing open habitats or colonial birds (Beecher & Beecher 1979, Birkhead 1979, 1982, Power et al. 1981, Goodburn 1984, Carlson et al. 1985, Birkhead et al. 1985, 1987, Møller 1985, Westneat 1987 a,b, Aguilera & Alvarez 1989, but see Björklund & Westman 1986, Alatalo et al. 1987, Hobson & Sealy 1989). Our intention was to find out, first whether EPCs and mate guarding occur in the Willow Tit, and secondly, if mate guarding exists, whether its intensity differs between different age (i.e. quality) classes.

2. Material and methods

The study area lies near Oulu in northern Finland and contains coniferous forests of all ages. Due to the habitat preferences of the Willow Tit, most observations were made in middle-aged spruce-dominated forests. All the birds were marked individually and their sex and age (adults/juveniles) were known (for details see Orell & Ojanen 1983).

A total of 48 pairs were observed between 17 April and 21 May 1990. To ensure statistical independence, we had only one observation period for each pair. The observation periods covered all times of the day, although most took place in the morning hours. After a pair had been detected, and the members identified, it was observed as long as possible. Pairs for which we had less than five distance records were excluded from the calculations involving distance variables. The distance between the mates and their position in the trees were recorded every 15 seconds. To randomize observations, the first records were not made until 15 seconds after the birds were sighted. All the observations were dictated to a tape-recorder and transcribed later.

Variables measured:

(1) Distance between the male and female: This was estimated to the nearest 0.5m. The mean and maximum distances were used in calculations. Maximum distance is sensitive to the total number of observations. However, even if the number of observations varied between pairs, no systematic variation should exist between the groups compared in the calculations. The distances were log10 - transformed to fulfill the requirements of parametric tests.

(2) Tree use: Were male and female utilizing the same or a different tree? The proportion of observations of birds in the same tree was used in the calculations. Again, sequences containing less than five observations were excluded. The proportions were $\arcsin\sqrt{x}$-transformed.

(3) Sex of the site-change initiator: Only movements to other trees with the mate following the initiator were taken into account. Site changes were not recorded when the birds were hoarding food. When doing this, the birds constantly flew between the food source (usually a tree top with cones) and hoarding sites. This made it difficult to decide who was initiating and who was following initiator or just flying to the hoarding site.

(4) Copulations: Both EPCs and pair copulations were recorded.

(5) Fertility stage: Four periods were separated: prefertile II, prefertile I, fertile and postfertile. Using the information provided by Birkhead (1982), the presumed fertile period was defined to last from day –3 (day 0 = date of laying first egg) to the day after which three last eggs were laid. Prefertile II and I covered the 10 day periods from –23 to –14 and from –13 to –4, respectively. The postfertile period covered the days during which the three last eggs were laid. For most pairs we could determine the exact laying date of the first egg. For some pairs whose nests were destroyed by predators or where one of the mates later disappeared, the female could be scored only as non-fertile, since all the pairs were followed in the beginning of the nest-excavating stage. Willow Tits excavate their nesting holes in rotten wood. Excavation and construction of the nest lining usually takes more than one week (Orell, Koivula and Rytkönen, unpublished). We therefore also grouped the pairs as fertile and non-fertile (including prefertile II and I and postfertile periods).

Whenever possible parametric tests were used. If not otherwise mentioned, the tests were one-tailed, because the prediction in comparing the fertility periods was a increase in intensity of guarding from pre-fertile periods to fertile and a subsequent decrease. Similarly, in comparing the age classes the prediction was that juveniles guard more intensively than adults. In paired comparisons after ANOVA we used Dunnett's t-test. When the sample sizes were unequal, it was used with the Kramer modification (e.g. Day & Quinn 1989).

3. Results

3.1. Copulations

We saw only four copulations, two within-pair copulations (WPCs) and two EPCs. One of the WPCs occurred four days after the initiation of egg-laying, the exact timing of the other remained unknown. In both EPCs a female that had lost her mate (most probably through death), just a few days before the initiation of egg-laying, copulated with a paired male. Both males were from neighbouring territories, but the copulations took place in the immediate vicinity of the nests of the single females. In both cases a clear "invitation" was given by the single female. This included a soft song, which apparently attracted the males. Typical precopulatory movements and vocalizations were also observed.

3.2. Distance between the mates and tree use

The average distance between mates tended to decrease towards the fertile period and seemed to increase again in the postfertile period. The differences between the fertility stages were significant (1-way ANOVA, Fig. 1a). However, in paired comparisons, when the fertile period was compared with others, no significant differences emerged (Dunnett's t-test, all $P > 0.05$). When we pooled the non-fertile periods and added all the pairs (see methods), the distances in the fertile period were significantly shorter than in the non-fertile period (t-test, $t = 4.32$, $df = 36$, $P < 0.001$).

The maximum distance might be a better measure of guarding intensity than the average distance since, even if the male spent most of the time near his female, a few long-distance "escapes" could give opportunities for successful EPCs. The variation of the maximum distance showed the same trend as the average distance and the differences between fertility stages were also significant (1-way ANOVA, Fig. 1b). Here too, the paired comparisons between fertile and other periods revealed no differences between the groups (Dunnett's t-test, all $P > 0.05$). When we compared two stages as above, the average maximum distance was significantly shorter in the fertile period than in the non-fertile period (t-test, $t = 3.54$, $df = 36$, $P < 0.001$).

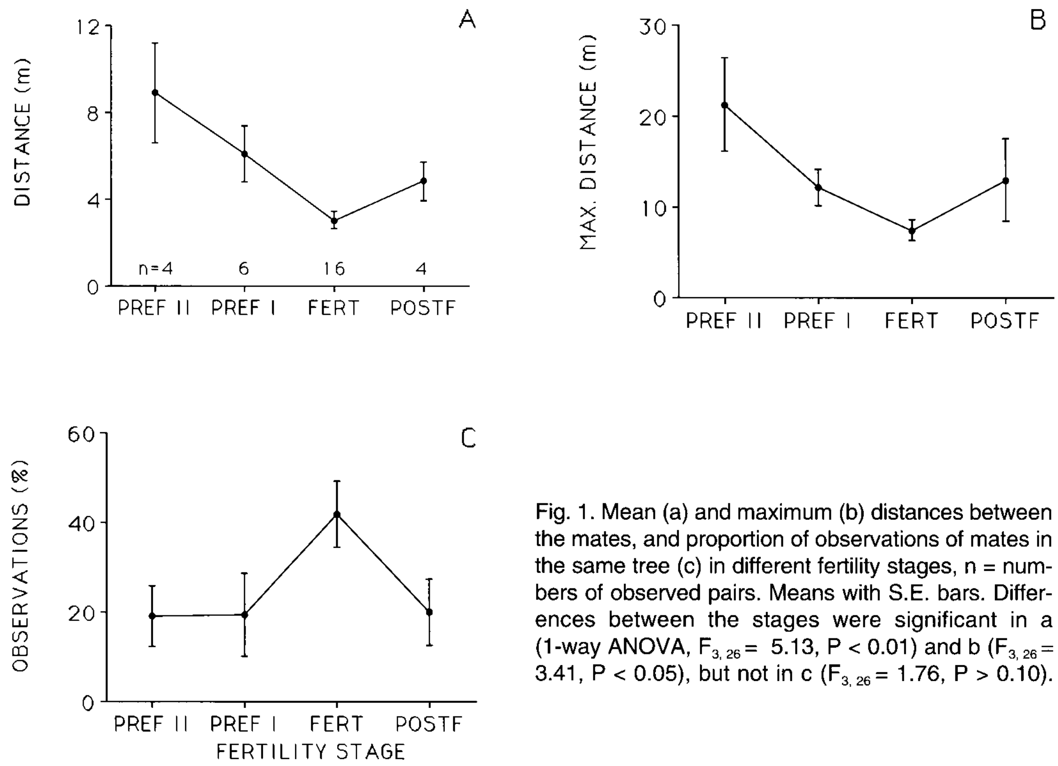

Fig. 1. Mean (a) and maximum (b) distances between the mates, and proportion of observations of mates in the same tree (c) in different fertility stages, n = numbers of observed pairs. Means with S.E. bars. Differences between the stages were significant in a (1-way ANOVA, $F_{3,26} = 5.13$, $P < 0.01$) and b ($F_{3,26} = 3.41$, $P < 0.05$), but not in c ($F_{3,26} = 1.76$, $P > 0.10$).

During the fertile period, birds were observed twice as often in the same tree as in other periods. However, no significant difference existed between the groups (1-way ANOVA, Fig. 1c) or in paired comparisons between the fertile period and the others (Dunnett's t-test, all $P > 0.05$). When we pooled the non-fertile periods and added all the pairs, the birds were seen more often in same trees in the fertile than in the non-fertile period (t-test, $t = 3.13$, $df = 36$, $P < 0.01$).

3.3. Site change initiation

We recorded a total of 111 site changes. As statistical unit, however, movements are certainly highly interdependent. Therefore, we picked only the first observation for each pair. In the non-fertile period males and females initiated movements equally often, but in the fertile period the female initiated movements more often than the male (Fig. 2). In addition, comparison between the fertility stages showed that females initiated a higher proportion of the movements in the fertile than in the non-fertile period (Fisher's exact probability test, $p = 0.04$).

3.4. Effect of male's age on intensity of guarding

With all three variables the overall trend was for the juvenile males to remain closer to their females than the adults, but none of the differences were significant (2-tailed t-tests, average distance: $t = 1.19$, $df = 36$, $P > 0.10$, maximum distance: $t = 0.64$, $df = 36$, $P > 0.10$, tree use: $t = 0.28$, $df = 36$, $P > 0.10$). When the two fertility stages were tested separately the same tendencies were visible in the fertile period and also in the non-fertile period for average and maximum distances (Fig. 3). However, except for a suggestive difference between average distances in the fertile period, the differences were not significant (Fig. 3).

4. Discussion

We did not observe any true extra-pair copulations. Therefore, we cannot prove that EPCs happen, but neither can we say that they are absent, because normal pair copulations also

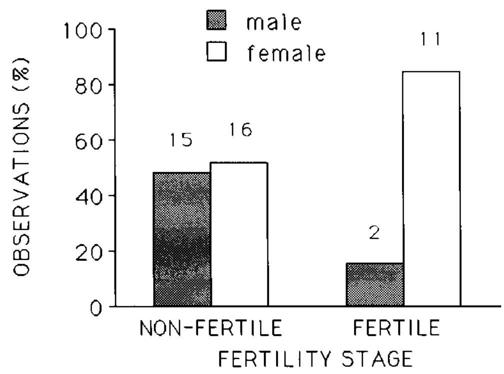

Fig. 2. Proportion of site change initiations by male and female in non-fertile and fertile periods. Numbers above the bars indicate the absolute number of observations. In the non-fertile period the sexes initiated movements equally often (binomial test, P = 0.50). In the fertile period females were the initiators more often than males (binomial test, P = 0.01)

seemed difficult to observe. It is likely that the copulation frequency is low, as in the Great Tit *Parus major* (Björklund & Westman 1986, see also Birkhead et al. 1987). This, combined with the short duration of the event, might explain why we failed to see more. One additional reason might be that copulations took place at a time of the day not covered by our observations: the early morning hours just after dawn. Willow Tits lay in the morning and, at least in domesticated species, ovulation and fertilization generally occur within 2.5 hours of laying of the previous egg, which might mean a copulation peak just after the laying (Birkhead et al. 1987).

At the moment, we can only suppose that EPCs occur in the Willow Tit. This assumption is partly justified by the fact that EPCs occurred in newly widowed and consequently unguarded females. Alternatively, the willingness of these females to copulate might simply mean that they tried to establish new pair bonds or to obtain additional care for their young. EPCs have also been observed in the closely related Black-capped Chickadee (Smith 1988).

Males remained closer to their mates during the fertile than the non-fertile period. Males also maintained close proximity between the mates, by following the movements of the female. This supports the idea that males were guarding their females. However, there are at least four different alternative, although not mutually exclusive, explanations for the pattern. (1) The short distances might be caused by courtship feeding, which occurs in Paridae (e.g. Krebs 1970), including the Willow Tit (Westneat 1987b). (2) The proximity of the mate might increase vigilance against predators (Birkhead 1979, Lumpkin 1981). This could be advantageous, for example, if a female's ability to produce a clutch requires increased time for feeding prior to the laying period. (3) Males might actually guard the females in order to avoid cuckoldry, but the females might encourage the males to do so before the start the fertile period, in order to protect themselves from time-consuming and otherwise harmful courtship from other males (Lumpkin 1981). The females might trigger mate guarding by their readiness to copulate. By doing this in the prefertile period, thereby disguising the real fertile period, they could obtain prolonged protection from the male. (4) A high copulation frequency could produce the short distances in species in which multiple copulations are needed, either to ensure fertilization or for other reasons (Birkhead et al. 1987, Westneat 1987b).

Male Willow Tits feed their females chiefly during incubation. Before and during the laying period this happens so rarely that it cannot explain the observed distance pattern. As already pointed out, the frequency of copulation is not high in this species. Nor the ideas of vigilance against the predators and female manipulation fit the present case. The latter implies extremely frequent contacts with other males, which in territorial species like the Willow Tit do not occur. Neither of these ideas can properly explain the differences in guarding intensity between the fertile and non-fertile periods. Furthermore, the predator vigilance hypothesis does not explain why it is the male that maintains the proximity between the mates.

Many studies describing frequent EPCs and strong mate guarding concern species that are colonial or nest in open habitats (see introduction). This might reflect the importance of ecological and behavioural factors connected with nesting dispersion and habitat in the evolution of mixed reproductive strategy. On the other hand,

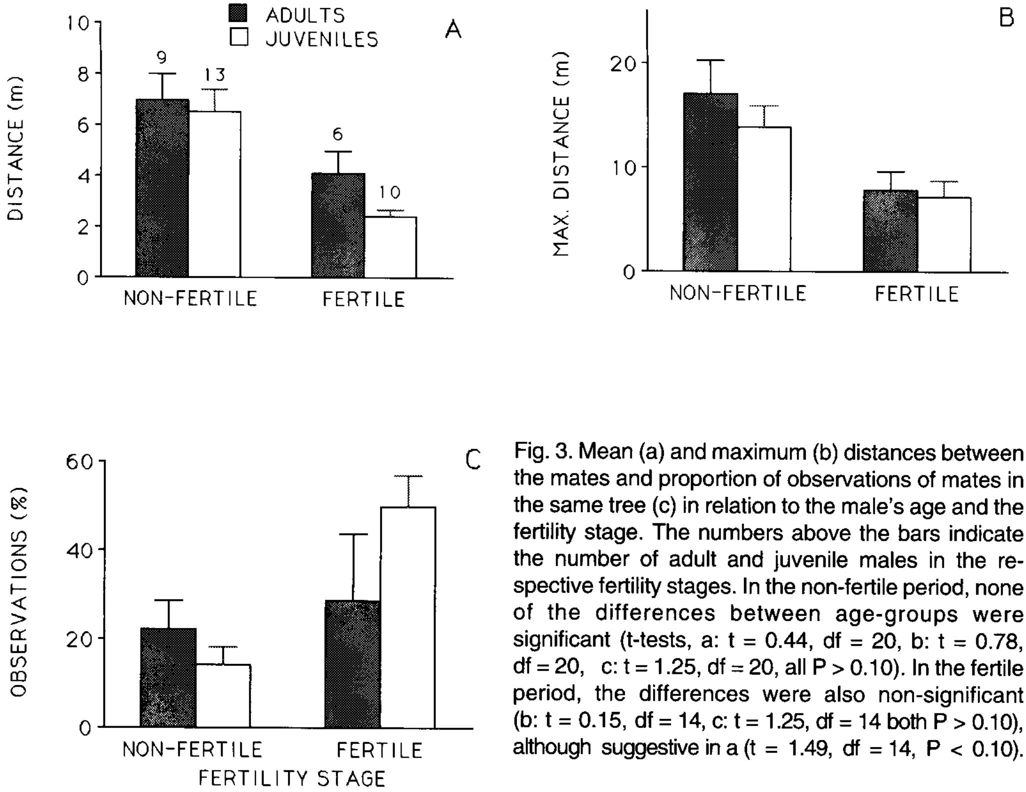

Fig. 3. Mean (a) and maximum (b) distances between the mates and proportion of observations of mates in the same tree (c) in relation to the male's age and the fertility stage. The numbers above the bars indicate the number of adult and juvenile males in the respective fertility stages. In the non-fertile period, none of the differences between age-groups were significant (t-tests, a: t = 0.44, df = 20, b: t = 0.78, df = 20, c: t = 1.25, df = 20, all $P > 0.10$). In the fertile period, the differences were also non-significant (b: t = 0.15, df = 14, c: t = 1.25, df = 14 both $P > 0.10$), although suggestive in a (t = 1.49, df = 14, $P < 0.10$).

it could also be a purely methodological phenomenon, caused by avoidance of forest-living territorial species as study objects, due to difficulties in making accurate observations.

In the Willow Tit mate guarding seems to be fairly intense. This might suggest that the opportunities for EPCs are high. Active seeking of EPCs by females could be one factor promoting the EPC potential, which in turn might make intensive guarding advantageous. In the absence of proper evidence, however, this idea must remain at the level of speculation. Nevertheless, female Black-capped Chickadees seem to seek EPCs in order to copulate with males of superior quality (Smith 1988). Females have been noted to be selective when accepting EPCs in other species as well (Fredrick 1987, Aguilera & Alvarez 1989). Social rank seems to be a good indicator of quality in the Willow Tit, since winter survival is better in high-ranking than in low-ranking birds (e.g. Koivula & Orell 1988). Since the Willow Tit is a resident species living in small coherent flocks in winter, birds might well be able to recognize the rank of both their flock members and neighbours (c.f. Smith 1988).

Provided that the pattern is similar in the Willow Tit and the Black-capped Chickadee, one could suspect that dominant males, which are always adults in mixed-aged flocks (e.g. Hogstad 1989), most probably obtain additional matings. Subordinate juvenile males would most probably suffer from cuckoldry. Besides the rank, age could be an indicator of survival ability. That adult males obtain more EPCs and juveniles suffer more often from cuckoldry has been confirmed in several species (Røskaft 1983, Westneat 1987a, Brooker et al. 1990, but see Sherman & Morton 1988). Furthermore, if the main benefit of EPCs from the female's point of view is the "good genes", one could expect that females paired with adult good-quality males are less willing to accept additional matings.

A logical assumption would be that mate guarding is most beneficial to juvenile males, whereas in adults a lower guarding intensity is expected. Although, our results do not support this idea, there was a trend for juvenile males to guard their mates more intensively than the adults. However, only one variable gave a suggestive result. Also, our material did not allow us to separate the possible effects of other factors than age. For example, the timing of the breeding might affect the risk of cuckoldry and thus cause differences in the intensity of guarding by males of different ages. Therefore, further data collection may be worthwhile. Moreover, experimental removal of adult and juvenile males and simultaneous measurement of a female's tendency to accept EPCs would be of interest.

To sum up, male Willow Tits seemed to guard their mates during the fertile period and the most probable explanation is avoidance of cuckoldry. However, this study (like most others) relies on an observational approach, and in a strict sense, there may be alternative explanations. Surprisingly, there have been only a few mate guarding studies using an experimental approach (but see Björklund & Westman 1983, Møller 1987b). Potentially, two kinds of experimental design could be to prove the effectiveness (or the opposite) of mate guarding. One, employed by Björklund & Westman (1983) for the Pied Flycatcher (*Ficedula hypoleuca*) and by Møller (1987b) for the Swallow, consists of lowering the intensity of guarding by removing the males for a short time. Unfortunately, capturing the birds is often time-consuming and sometimes practically impossible. As far as territorial species are concerned, another possibility could be to induce variation in the threat of cuckoldry by using artificial "intruders" and to monitor their effect on mate guarding intensity.

Selostus: **Puolison vartiointikäyttäytyminen territoriaalisella metsälajilla hömötiaisella**

Teoriassa lintulajeilla, joilla molemmat emot huoltavat jälkeläisiään, koiraat, jotka kykenisivät hedelmöittämään muiden kuin oman puolisonsa munia saattaisivat omata valintaedun "uskollisiin" koiraisiin nähden. Nykyisin tiedetäänkin monilla aiemmin monogamisiksi luulluilla lajeilla esiintyvän parisiteen ulkopuolisia paritteluja (PUP), jotka johtavat myös hedelmöittymiseen. Kun PUP:ja esiintyy, voidaan myös olettaa kehittyvän strategioita, joiden avulla koiras pystyy varmistamaan huoltamiensa poikasten isyyden. Linnuilla yleisin tällainen strategia on puolison vartiointi, joka yleisimmässä muodossaan ilmenee koiraan ja naaraan pysyttelynä yhdessä naaraan ollessa hedelmöittymiskykyinen.

Tutkimme yhden pesimäkauden (1990) aikana mahdollisten PUP:jen ja puolison vartioinnin esiintymistä hömötiaisella jota on perinteisesti pidetty tyypillisesti monogamisena lajina.

Havaitsimme ainoastaan neljä parittelua, joista kaksi oli tulkittavissa PUP:ksi. Näissä kahdessa tapauksessa äskettäin puolisonsa menettäneet naaraat parittelivat naapurireviirin koiraan kanssa. Kuvasimme puolison vartiointia mittaamalla puolisoiden välisen etäisyyden 15 sekunnin välein, jolloin myös otimme huomioon puolisoiden sijainnin ruokailupuissa, ts. ruokailivatko ne samassa vai eri puissa. Kun linnut vaihtoivat olinpaikkaa, rekisteröimme sukupuolten järjestyksen kun ne lähtivät liikkeelle. Sukupuolten välinen etäisyys oli pienimmillään naaraan ollessa fertiilissä vaiheessa kuvattiinpa etäisyyttä keskiarvoilla tai maksimietäisyyksillä (kuvat 1a,b). Sukupuolet viettivät myös tällöin enemmän aikaa samoissa ruokailupuissa kuin ennen tai jälkeen fertiilin vaiheen (kuva 1c). Fertiilissä vaiheessa koiraat pitivät etäisyydet lyhyinä seuraamalla naarasta sen vaihtaessa ruokailupaikkaa ja pidättäytymällä itse aloittamasta paikanvaihtoja. Ennen ja jälkeen fertiilin vaiheen sukupuolten välillä ei ollut eroa paikanvaihtoaloitteen teossa (kuva 2).

Nuorten koiraiden puolisoiden on havaittu muilla (lähisukuisillakin) lajeilla, osallistuvan vanhojen koiraiden naaraita useammin PUP:hin. Teoriassa nuorille koiraille olisi edullista panostaa vartiointiin vanhoja koiraita enemmän, etenkin, jos niiden omat mahdollisuudet osallistua PUP:hin olisivat pienet. Nuoret hömötiaiskoiraat näyttivätkin vartioivan naarastaan vanhoja intensiivisemmin, mutta erot ikäluokkien välillä eivät olleet merkitseviä lukuun ottamatta naaraan kanssa samassa puussa vietetyn ajan osuutta.

Hömötiaiskoiraat siis ilmeisesti vartioivat naaraitaan niiden ollessa fertiilejä. Vartioinnin lisäksi puolisoiden lähekkäisyydellä on olemassa vaihtoehtoisia selityksiä kuten soidinruokinta, vähentynyt predaatioalttius, naaraan suojelu muilta koirailta ja korkea parittelutiheys, jotka kuitenkaan hömötiaisen tapauksessa eivät päde. Koska emme havainneet "täydellisiä" PUP:ja, ilmiön todellinen luonne jää kaipaamaan varmistamista, johon kokeellinen vartiointi-intensiteetin tai PUP-uhan manipulointi tarjonnee parhaat mahdollisuudet.

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References

Aguilera, E. & Alvarez, F. 1989: Copulations and mate guarding of the Spoonbill (Platalea leucorodia). — Behaviour 110:1–22.

Alatalo, R. V., Gottlander, K. & Lundberg, A. 1987: Extra-pair copulations and mate guarding in the polyterritorial Pied Flycatcher, Ficedula hypoleuca. — Behaviour 101:139–155.

Alatalo, R. V., Gustafsson, L. & Lundberg, A. 1984: High frequency of cuckoldry in Pied and Collared Flycatcher. — Oikos 42:41–48.

Beecher, M. D. & Beecher, I. M. 1979: Sociobiology of Bank Swallows: reproductive strategy of the male. — Science 205:1282–1284.

Birkhead, T. R. 1979: Mate guarding in the Magpie Pica pica. — Anim. Behav. 27:866–874.

— 1982: Timing and duration of mate guarding in Magpies Pica pica . — Anim. Behav. 30:277–283.

Birkhead, T. R., Atkin, L. & Møller, A. P. 1987: Copulation behaviour of birds. — Behaviour 101:101—138.

Birkhead, T. R., Johnson, S. D. & Nettleship, D. N. 1985: Extra-pair matings and mate guarding in the Common Murre, Uria aalge. — Anim. Behav. 33:608–619.

Björklund, M. & Westman, B. 1983: Extra-pair copulation in the Pied Flycatcher (Ficedula hypoleuca), a removal experiment. — Behav. Ecol. Socibiol. 13:271–275.

— 1986: Mate-guarding in the Great Tit: tactics of a territorial forest-living species. — Ornis Scand. 17:99–105.

Bray, O. E., Kennelly, J. J. & Guarino, J. J. 1975: Fertility of eggs produced on territories of vasectomized Red-winged Blackbirds. — Wilson Bull. 87:187–195.

Brooker, M. G., Rowley I., Adams, M. & Baverstock, P. R. 1990: Promiscuity: an inbreeding avoidance mechanism in asocially monogamous species. — Behav. Ecol. Sociobiol. 26:191–199.

Buitron, D. 1983: Extra-pair courtship in Black-billed Magpies. — Anim. Behav. 31:211–220.

Carlson, A., Hillström, L. & Moreno, J. 1985: Mate guarding in the Wheatear Oenanthe oenanthe. — Ornis Scand. 16:113–120.

Day, R. W. & Quinn, G. P. 1989: Comparison of treatments after an analysis of variance in ecology. — Ecological Monographs 59:433–463.

Fitch, M. A. & Shugart, G. W. 1984: Requirements for a mixed reproductive strategy in avian species. — Am. Nat. 124:116–126.

Frederick, P. C. 1987: Extrapair copulations in the mating system of the White Ibis (Eudocimus albus).— Behaviour 100:170–201.

Gavin, T. A. & Bollinger, E. K. 1985: Multiple paternity in a territorial passerine: the Bobolink. — Auk 102:550–555.

Gladstone, D. E. 1979: Promiscuity in monogamous colonial birds. — Amer. Natur. 114:546–557.

Goodburn, S. F. 1984: Mate guarding in the Mallard Anas platyrhynchos. — Ornis Scand. 15:261–265.

Hobson, K. A. & Sealy, S. G. 1989: Mate guarding in the Yellow Warbler Dendroica petechia. — Ornis Scand. 20:241–248.

Hogstad, O. 1989: Social organization and dominance behaviour in some Parus species. — Wilson Bull. 101:254–262

Koivula, K. & Orell, M. 1988: Social rank and winter survival in the Willow Tit Parus montanus. — Ornis Fennica 65:114–120.

Krebs, J. R. 1970: The efficiency of courtship feeding in the Blue Tit Parus caeruleus. — Ibis 112:108–110.

Lumpkin, S. 1981: Avoidance of cuckoldry in birds: the role of the female. — Anim. Behav. 29:303–304.

McKinney, F., Derrickson, S. R. & Mineau, P. 1983: Forced copulation in waterfowl. — Behaviour 86:250–294.

Mineau, P. & Cooke, F. 1979: Rape in the lesser Snow Goose. — Behaviour 70:280–291.

Møller, A. P. 1985: Mixed reproductive strategy and mate guarding in a semi-colonial passerine, the Swallow Hirundo rustica. — Behav. Ecol. Sociobiol. 17:401–408.

— 1987a: Behavioural aspects of sperm competition in Swallows (Hirundo rustica). — Behaviour 100:92–104.

— 1987b: Mate guarding in the Swallow Hirundo rustica: an experimental study. — Behav. Ecol. Sociobiol. 21:119–123.

— 1988: Female choice selects for male sexual tail ornaments in the monogamous Swallow. — Nature 332:640–642.

Orell, M. & Ojanen, M. 1983: Breeding biology and population dynamics of the Willow Tit Parus montanus. — Ann. Zool. Fennici 20:99–114.

Power, H. W., Litovich, E. & Lombardo, M. P. 1981: Male Starlings delay incubation to avoid being cuckolded. — Auk 98:386–389.

Quinn, T. W., Quinn, J. S., Cooke, F. & White, B. N. 1987: DNA marker analysis detects multiple maternity and paternity in single broods of the Lesser Snow Goose. — Nature 323:392–394.

Røskaft, E. 1983: Male promiscuity and female adultery by the Rook Corvus frugilegus. — Ornis Scand. 14:175–179.

Sherman, P. W. & Morton, M. L. 1988: Extra-pair fertilizations in Mountain White-crowned Sparrows. — Behav. Ecol. Sociobiol. 22:413–420.

Smith, S. M. 1988: Extra-pair copulations in Black-capped Chickadees: the role of the female. — Behaviour 107:15–23.

Trivers, R. L. 1972: Parental investment and sexual selection. — In: Campbell, B. (ed.). Sexual selection and descent of Man 1871–1971. Aldine, Chicago, pp. 135–179.

Westneat, D. F. 1987a: Extra-pair fertilizations in a predominantly monogamous bird: genetic evidence. — Anim. Behav. 35:877–886.

— 1987b: Extra-pair copulations in a predominantly monogamous bird: observations of behaviour. — Anim. Behav. 35:865–876.