Effects of male removal on reproductive success and provisioning in the Eurasian Treecreeper (*Certhia familiaris*)

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In biparental bird species the optimal level of parental care of one member of the pair generally depends on its mate's strategy. In monogamy, a predicted response to reduced parental care by one parent is incomplete compensation by its partner. The importance of male parental care has been suggested to vary also according to environmental conditions during breeding. From our previous studies, double-brooded male Eurasian Treecreepers (*Certhia familiaris*) were found to desert their nests more often during second broods, when food conditions were generally good. Here, we studied the importance of male parental care in this species, by testing the effects of male removal on the parental behavior and reproductive success during the first broods, when food is scarcer. The aim was to determine the degree to which female parents could increase their workload to compensate for the male absence. We did this by measuring feeding rate, and the size and composition of food loads of widowed and paired females. Food abundance was measured within Treecreeper territories, immediately after fledging, as a measure of territory quality relative to the breeding success of both paired and widowed females. Our results showed that widowed females increased their feeding rate enough to compensate for the loss of their mate. However, widowed females produced fewer young, which were also of lower nestling weight, than control pairs. The success of the second brood, in the same breeding season, was also lower among widowed females with new males than among the control females, despite all experimental females having the opportunity to re-nest.

1. Introduction

Birds exhibit a considerable variation in the extent to which males contribute to the care of young (e.g., Silver *et al.* 1985). The need for male care has traditionally been used to explain the prevalence of social monogamy in birds (Lack 1968, Wittenberger 1979). Following Emlen and Oring's (1977) suggestion that monogamy in birds is maintained because two parents are required to

rear young successfully, paternal care is expected to increase offspring survival and/or growth (e.g., Lozano & Lemon 1995).

Theoretical models predict that the optimal response to a reduction of investment by one parent is for the partner to increase investment (Chase 1980, Houston & Davies 1985, Winkler 1987, McNamara *et al.* 1999). This compensatory behavior is expected to be incomplete if cooperation is to remain as a stable strategy. Otherwise cheaters or deserters would gain greater fitness benefits, which would lead to uniparental care (Houston & Davies 1985, Winkler 1987). Field experiments generally support this prediction, showing that widowed parents attempt to compensate for the loss of their partner parental care, but compensation is usually incomplete (Wolf *et al.* 1988; Bart & Tornes 1989; Dunn & Hannon 1992; Meek & Robertson 1994, Markman *et al.* 1995, 1996). Such compensation behavior is either a female strategy to cope with partner loss or is simply her inability to work any harder to compensate fully for the lack of her partner. However, in most cases, the reproductive success of widowed individuals has been lower (e.g., Wolf *et al.* 1988; Bart & Tornes 1989; Davies & Hatchwell 1992; Meek & Robertson 1994, Whittingham *et al.* 1994; Markman *et al.* 1995, 1996), though many studies have observed no clear effects on the reproductive success (Wolf *et al.* 1988, Bart & Tornes 1989, Dunn & Hannon 1992, Snoeijs *et al.* 2005). The discrepancy between these findings may lie in the differences in environmental conditions during the experiments and variation in male care according to the ecological environment. For instance, male care may be less important at times or sites with a good food supply (Wittenberger 1982, Bart & Tornes 1989, Dunn &d Robertson 1992, Whittingham & Robertson 1994).

The level of parental care can be seen as an evolutionary strategy optimizing the costs and benefits related to parental investment and mating efforts. When an individual spends time and energy in parental care, it may sacrifice opportunities to improve its reproductive success by pursuing additional matings (Trivers 1972, Maynard Smith 1977). In double-brooded species, the opportunities for re-mating are generally good, and the costs and benefits of brood desertion may change in subsequent breeding attempts. In the Eurasian Tree-

creeper (*Certhia familiaris*) paternal care is common during the first brood when food abundance is generally low (Kuitunen *et al.* 1996, J tti *et al.* 2003, 2007).

With the first brood, the extent of male activity in feeding seven-day-old nestlings was also positively correlated with the average mass of the nestlings. During the second broods, males often deserted their brood (Kuitunen *et al.* 1996), when food was more abundant and the temperatures warmer, but the reasons for their desertion was unclear. However, these earlier results support the idea that males of monogamous, altricial bird species may make important contributions to raising young, especially during periods when it is difficult for the female to do so alone.

To date, there are only a few studies comparing avian breeding success between widowed and paired females in relation to feeding activity and food supply to chicks in the territory (Sasv i 1986, Lozano & Lemon 1995). In addition, studies combining the effects of male removal and food supply on foraging behavior, parental care and reproductive success are lacking. We have earlier reported the results of male removal on female foraging behavior (Aho *et al.* 1997). Here, we report the results of the second part of the male-removal experiment. We studied the effects of male removal in the early nestling stage on maternal care, food supply and breeding success during the first broods, when food is relatively scarce. As a measure of parental investment, we used feeding rates, load sizes and the composition of loads. We also investigated whether the amount of available food in a territory was related to breeding success in paired and widowed Treecreepers, and how male removal affects the production of second broods during the same breeding season.

2. Material and methods

The Eurasian Treecreeper is a cavity-nesting, double-brooded, insectivorous passerine that breeds throughout the northern coniferous zone (Kuitunen 1987, Suhonen & Kuitunen 1991a). Females incubate the eggs and males usually feed the incubating females. During any one season, the first broods are fed by both sexes, but the second broods are usually fed by females alone (Kuitunen

et al. 1996). The environmental conditions during first and second broods may vary considerably, being generally more favorable for the second broods (Kuitunen 1989). The food supply in the territories is relatively easy to measure quantitatively (Kuitunen 1989), as Treecreepers forage exclusively on tree trunks (Suhonen & Kuitunen 1991a).

Field work was done at the Konnevesi Research Station in Central Finland (62 7' N, 26 0' E) during the summer of 1993. The study area is covered mainly by forests dominated by the conifers Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), with some birches (*Betula* spp.) and other deciduous tree species as a mixture. Approximately 50 pairs of Treecreepers breed annually in specially designed nest-boxes (see Kuitunen 1987), from a total of 80 to 90 boxes. Each breeding pair had access also to extra nest-boxes for a second breeding attempt.

Data on laying date, clutch size and date of hatching were collected for each nesting attempt. For the experiment we chose sixteen territories, which formed eight pairs of control and experimental territories with the same hatching dates. The diameter of spruce trunks is considered to be one critical determinant of Treecreeper foraging site selection (Suhonen & Kuitunen 1991b). Here we used several criteria (the proportions of different tree species, density of trees, and size distribution of trees) in order to choose similar Treecreeper territories for control and experimental groups, with no differences in any of these variables between the treatment groups.

In the experimental territories, we caught breeding females during incubation and removed males when the nestlings were five days old, after females had ceased to brood them. The adult birds were sexed from morphological criteria taken during capture, e.g. bill length, wing length and the presence of a brood patch in females (Suhonen & Kuitunen 1991a, 1991b, M. Kuitunen unpublished data). The males were transported approximately 100 kilometers, released and they did not return to their breeding sites. The control birds ($n = 8$) were caught during the same time period as the corresponding experimental birds, but were then released again within their own territory. The birds were individually marked with aluminum and colored rings. At the same time, we studied the effects

of male removal on the foraging behavior of females (Aho *et al.* 1997).

Feeding frequencies and food load sizes were measured using a small video camera installed beside the nest entrance. The size of each load was determined in relation to the bill length of the feeding parent from the video tapes. The prey included in the food loads were identified to family level, if possible, and the relative proportions of spiders, dipterans, caterpillars, and pupae were counted, they being the invertebrate groups most commonly identified from the loads. From a total time of two hours video playback per nest, we used the period of one hour (beginning 30 minutes after the start of the tape) to determine both feeding frequencies and food load sizes. Reproductive success for each nest was determined by weighing the nestlings just before fledging (at the age of 12 days) and by counting nestling survival to the fledging stage.

Just after fledging, we collected arthropod samples from six tree trunks that were randomly selected from trees larger than 30 cm in diameter within 20–30 m range from the nest in each territory. The trunk surface at the height of 0.5–1.5 m was cleaned by 12 V battery-operated vacuum-cleaners (see Kuitunen 1989), the diameter of each trunk was measured and the results were afterwards transformed to correspond to a trunk area of 1 m^2. Invertebrates larger than 1 mm in size were identified to the family level. The mean number and body length of the food items on six trunks in each territory were used as indicators of the amount of food remaining on tree trunks in each territory. The vacuum-cleaning was always carried out during good weather conditions. In two experimental nests all the nestlings died before the behavioral and reproductive parameters were recorded. We also failed to obtain video data for one additional experimental and one control nest. The sample sizes in paired comparisons of feeding behavior were i) seven paired males and females, and five paired and widowed females, and ii) mean nestling weights from six experimental and control territories, as none of the perished experimental nests were included in the sample. For comparisons of all other reproductive parameters and of the food abundance, the sample sizes were eight pairs of experimental and control nests.

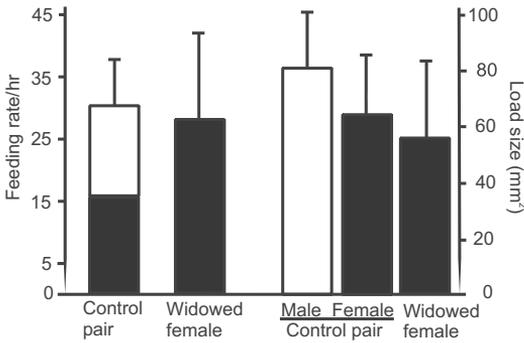The differences in all behavioral variables and

Fig. 1. Mean feeding rate/hour (95% CI) and mean load size (95% CI) of control pairs (N = 7 females and 7 males) and widowed females (N = 5). White bars = males, black bars = females.

in reproductive success between experimental and control birds, and the differences in food abundance between control and experimental territories were tested by paired t-tests. The effects of food abundance on the mean nestling weight and brood weight were analyzed by linear regression. All the proportional values were transformed by arc sin square root transformation for the analysis. For the statistical analysis SPSS 12.0 was used.

3. Results

There were no significant differences between the feeding activity of control males and females (Fig. 1; paired t-test; $t = 0.31$, df $= 6$, $P = 0.77$). The feed-

ing rates of widowed females were on average higher than in control females, but again the difference was not statistically significant (Fig. 1; $t = 2.27$, df $= 4$, $P = 0.085$). There were no statistical differences in feeding rate between widowed females feeding their young and control females and males together (Fig. 1; $t = 0.17$, df $= 4$, $P = 0.88$). Mean food-load size did not differ significantly between widowed females and control females ($t = 1.23$, df $= 4$, $P = 0.29$) or between control males and females (Fig 1; $t = 1.23$, df $= 6$, $P = 0.27$).

As regards the food composition of loads, control females delivered spiders slightly more often to their nestlings than did the widowed females, though there was no significant difference (Fig. 2; $t = 2.27$, df $= 4$, $P = 0.086$). However, the combined loads of control females and males contained spiders significantly more often than the loads of the widowed females ($t = 3.13$, df $= 4$, $P = 0.035$) and they carried dipterans more frequently to their nestlings than the widowed females (Fig. 2; $t = 2.73$, df $= 4$, $P = 0.052$). There were no significant differences in the frequencies of caterpillars and pupae present in the food loads of control pairs compared to widowed females (Fig. 2).

3.2. Breeding success and food supply

In two out of eight treatment nests all the nestlings died. All control nests produced fledged offspring, and consequently the mean number of fledged
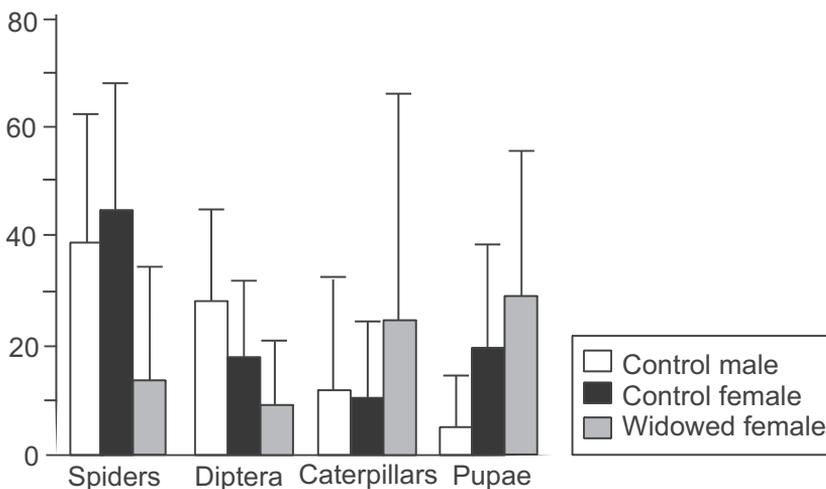

Fig. 2. Mean frequency (95% CI) of spiders, dipterans, caterpillars and pupae in the food loads of control males (N = 7) and females (N = 7), and widowed females (N = 5).

Table 1. Mean clutch size, number of hatched nestlings, number of fledglings in the first and second broods and total number of offspring produced in a breeding period between control and experimental nests of the Eurasian Treecreeper. $N = 8$ in all cases; paired t-test.

Variable	Control Mean (SD)	Experiment Mean (SD)	Test t	P
Clutch size	5.90 (0.64)	5.60 (0.52)	1.00	0.350
No of nestlings	5.90 (0.64)	5.30 (0.89)	1.67	0.140
No. fledglings, 1st brood	5.75 (0.46)	3.38 (2.39)	2.75	0.029
No. fledglings, 2nd brood	3.50 (2.93)	0.80 (2.12)	2.62	0.034
Total no. offspring	9.25 (3.28)	4.13 (3.60)	3.10	0.017
No. dead nestlings	0.10 (0.40)	1.90 (2.42)	1.94	0.093

Table 2. Food supply in the control and experimental territories (arthropods/1 m² of tree trunk surface). $N = 8$ in all cases; paired t-test.

	Control Mean (SD)	Experiment Mean (SD)	Test t	p
No. arthropods	15.4 (6.2)	13.4 (5.4)	0.63	0.55
No. spiders	11.9 (5.1)	8.5 (3.7)	1.44	0.19
Length of arthropods (mm)	2.66 (0.61)	2.60 (0.42)	0.23	0.82
Length of spiders (mm)	1.91 (0.19)	2.01 (0.36)	0.62	0.56

young was higher in control than in experimental nests (Table 1). Nestling mortality (mean number of nestlings that died before fledging) was on average higher in experimental than in control nests (Table 1). In addition, the experimental nestlings were of lower fledging weight than nestlings of control nests (Fig. 3a; $t = 3.36$, df = 5, $P = 0.02$). Consequently, the weight of the whole brood was on average 15.5 g higher in control nests (Fig 3b; $t = 3.27$, df = 5, $P = 0.02$).

Neither the density of arthropods, or spiders (preferred prey items) nor the average body length of all invertebrates (or spiders) differed between the experimental and the control territories during the period after fledging (Table 2). A regression of mean nestling weight on the food abundance showed that the absolute number of invertebrates was not significantly related to the nestling weight or brood weight either in the experimental ($r^2 = 0.12$, $F_{1,4} = 0.53$, $P = 0.51$; $r^2 = 0.36$, $F_{1,6} = 3.34$, $P = 0.12$, respectively) or in the control ($r^2 = 0.003$, $F_{1,5} = 0.01$, $P = 0.92$; $r^2 = 0.51$, $F_{1,5} = 5.16$, $P = 0.07$, respectively) territories. However, when we divided the actual number of food items by the number of hatched young, and regressed the mean nestling weight on this (relative food abundance per chick) there was a significant positive effect of food abundance on brood weight (Fig. 3b) but not on mean nestling weight (Fig. 3a) in the experimental territories. If the two perished nests were excluded from the analysis, the relationship between food and brood weight was still positive though no longer significant ($r^2 = 0.2$, $F_{1,4} = 1.11$, $P = 0.35$). In control territories, the brood weight decreased as the food abundance increased (Fig 3b), since two control pairs had small clutch sizes (five eggs compared to six or seven eggs of the other pairs) in territories with relatively high food abundance/chick (Fig 3b). Food abundance per chick did not affect mean nestling weight in control territories (Fig 3a).

3.3. Effects on the production of second clutches

Two of the eight widowed females started a second clutch, compared with six of eight females among the control pairs. This difference was not statistically significant (Fisher exact test; $P = 0.13$).
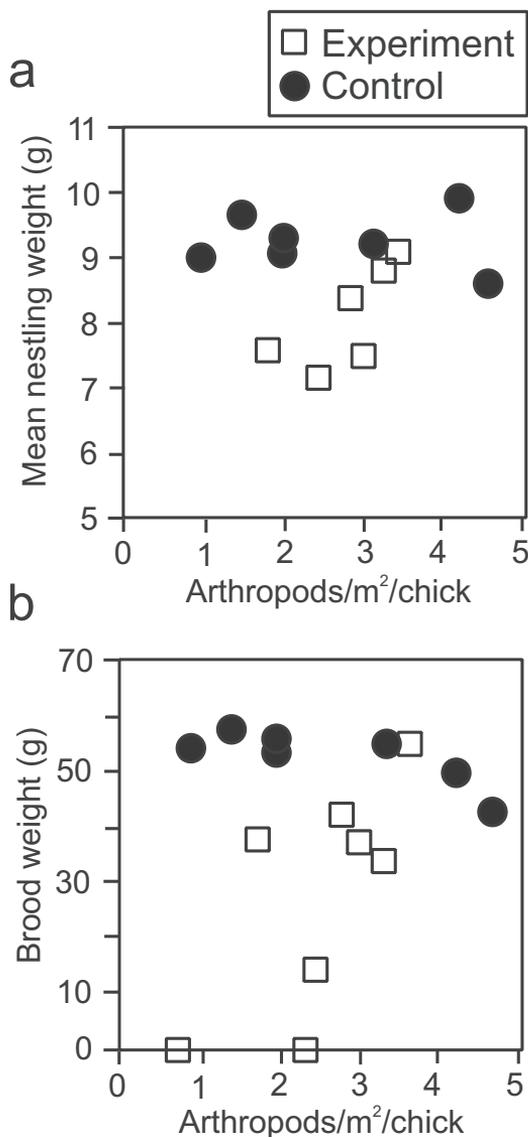
Fig. 3. Mean (a) nestling weight and (b) brood weight in relation to food abundance per chick on tree trunks in experimental and control territories of Eurasian Treecreepers. The regression values for experimental broods are (a) mean nestling weight: $r^2 = 0.51$, $F_{1,4} = 4.16$, $P = 0.11$, (b) brood weight: $r^2 = 0.49$, $F_{1,6} = 5.81$, $P = 0.05$, and for control broods (a) mean nestling weight; $r^2 = 0.006$, $F_{1,5} = 0.03$, $P = 0.87$, (b) brood weight: $r^2 = 0.65$, $F_{1,5} = 9.39$, $P = 0.03$.

However, only one of the experimental females produced a successful second clutch, while all six control pairs succeeded to produce fledglings (Fisher $P = 0.041$). Consequently, the total number of fledglings produced during that breeding season was higher in the control than in the experimental nests (Table 1). The change in body weight of the two experimental females between first and second broods was, on average –0.20 (0.5 SD) g, and of the six control females –0.23 (0.29 SD) g. A new male was observed to be present in every experimental territory after the removal of the original male. The time until the new male was first seen in the territory varied between two hours to two days following the removal of the original male. All ew males attempted to court with the female, but none were seen to feed the nestlings of the removed males.

4. Discussion

In the present study, male removal clearly had negative effects on the breeding success of the Treecreepers; widowed females produced fewer fledglings that were also of lower weight than those of control pairs. Since body mass is a good estimate of the condition (itness of the young (Gustafsson & Sutherland 1988, Tinbergen & Boerlijst 1990, Magrath 1991, Linden *et al.* 1992), the success of widowed females was lower both in terms of the number and quality of produced offspring. Our results indicate that male parental care enhances breeding success in Treecreepers. We did the experiment during the first clutches, when food abundance in Treecreeper territories is low (Kuitunen 1989), and when both parents usually feed the nestlings (Kuitunen *et al.* 1996). The negative fitness effects of male removal during the first clutch, and the absence of males during the second clutches (Kuitunen *et al.* 1996) give indirect support for the suggestion that male parental care may be most beneficial at times of low food abundance (Wittenberger 1982, Bart & Tornes 1989, Dunn & Robertson 1992, Whittingham & Robertson 1994).

In addition, the weight of the first brood, of widowed females was higher when there was more food available in the territory per chick. However, this positive relationship was mainly due to the failed nests, suggesting, rather, an association between food and the success of the brood. When both parents fed the nestlings, brood weight was, surprisingly, lower in association with more abun-

dant food. However, the food supply did not have any detectable effects on mean nestling weight of control pairs. In fact, the reduction in brood weight with food abundance was due to two pairs that had the lowest clutch sizes among the control pairs, indicating an effect simply of clutch size. In contrast, the clutch size of widowed females was independent of food abundance, and the observed patterns in mean nestling weight and brood weight cannot be explained by clutch size.

It has also been observed that individual pairs of animals show great flexibility in their patterns of parental investment, in response to both natural and experimental changes in conditions of their breeding environment (e.g., Clutton-Brock 1991, Davies 1992). In the present study, widowed females increased their maternal effort following male removal, by almost doubling their provisioning rates compared to control females (Fig. 1). In spite of this, and most likely due to a low sample size, the difference was only suggestively significant. However, the observations showed that widowed females could compensate for the mate loss in terms of feeding rate, by providing the nestlings with as high rate of provisioning as control females and males together (Fig. 1).

Given that male removal was conducted during the post-incubation period (implying no effects of incubation-feeding of females by males), the lower number and mean weight of nestlings in experimental nests indicated that provisioning compensation by loan females to chicks was not complete. Although there were no significant differences in the food load sizes of widowed and control females, the loads of widowed females were on average smaller. Also, the composition of loads between widowed females and control pairs differed. Widowed females carried spiders and dipterans to the nestlings less often than control birds, possibly as a result of foraging in different sites. Widowed females and paired males forage almost exclusively on lower parts of tree trunks, while control female use all portions of the trunks equally (Aho *et al.* 1997). In Treecreeper territories, arthropod abundance and diversity may differ due to heterogeneity in the architectural structure of the tree (Gunnarsson 1996), so that paired birds, that exploit a greater proportion of the trunk, may discover a more abundant but more variable food supply than widowed females. Also, the number

and length of spiders have been positively correlated with needle density (e.g., Gunnarsson 1990, Suhonen *et al.* 1992), which is generally lower in lowest parts of spruce trunks. This may explain the greater proportion of spiders in the food loads of control birds compared to the widowed females. Meanwhile, widowed females spent less time foraging on each trunk and on each bout, indicating that there were time constraints on females in the absence of male help (Aho *et al.* 1997). This may have affected their decision as to where to forage, with possible effects on the quality of foraged food (see also Wright *et al.* 1998).

In Treecreepers, 77% of the biomass and energy content of nestling food consists of spiders and harvestmen, and spiders are most frequent (90%) in the loads carried to the nestlings (Kuitunen & T m 1983, Suhonen & Kuitunen 1991a). Spiders may be the preferred food items by the Treecreepers, and may therefore be of greatest value as a source of food. The low frequency of spiders in the food loads of widowed females together with a smaller load size may also have contributed to the lower breeding success of widowed females (Brodmann *et al.* 1997).

Additional reasons for higher nestling mortality in experimental nests could be: i) reduced nest defence either by males or widowed females (e.g., Montgomerie & Weatherhead 1988, Markman *et al.* 1995); ii) increased maternal effort by widowed females, so reducing their own condition and their ability to lay and rear a successful second clutch; iii) new males (that quickly arrived to sing and court widowed females) were either of lower uality were less experienced or less assured of paternity, than the original males, and so could not or would not adequately contribute to the care of the young. There are few data to either support or refute any of these effects in Treecreepers, but our observations showed that the change in body weight of the two experimental females that laid a second clutch was on average the same as the weight change of control females, showing no indication of a reduction in conditions (point i. Meanwhile, no new males were observed to feed the nestlings of either brood, or the female as may be consistent with point ii.

In conclusion, our results indirectly support the idea that the males of monogamous, altricial bird species may help in raising the young, espe-

cially during periods with low food abundance. The compensation of mate loss by widowed females seems to be incomplete, although their provisioning rate, supports theories of parental investment (Houston & Davies 1985, Winkler 1987). In Eurasian Treecreepers, the need for two parents to successfully rear young may favor monogamy during the first broods, whereas better food conditions later in the season may promote brood desertion and even polygyny in the second broods (Whitfield and Tomkovich 1996), though there is no published evidence for the latter. There are no supported explanations for male desertion in Eurasian Treecreepers, but strategies that conserve energy with respect to long-term survival (Ratnieks 1996), molt constraints (Svensson and Nilsson 1997), or that assess the alue of second broods according to late hatching (e.g. Perrins 1965), or male uncertainty in paternity (e.g. Davies and Hatchwell 1992), are potential avenues of interest (Kuitunen et al 1996).

Koiraan poistamisen vaikutus jälkeläistuottoon ja poikasten kasvattamiseen puukiipijällä (*Certhia familiaris*)

Lintulajeilla, joilla molemmat puolisot osallistuvat poikasten hoitoon, yksilön optimaalinen hoitosatsaus riippuu puolison strategiasta. Monogamiassa, jossa vain toinen puoliso hoitaa poikaset, puolison vähentynyt osallistuminen poikasten hoitoon saattaa johtaa hoitavan vanhemman osittaiseen kompensaatioon. Koiraan osallistuminen poikasten hoitoon saattaisi vaihdella myös pesimäaikaisten olosuhteiden vaihtelun mukaan. Aiempien tutkimuksiemme perusteella kaksi poikuetta kesässä kasvattavat puukiipijäkoiraat hylkäävät pesänsä todennäköisemmin jälkimmäisellä pesimiskerralla, jos ravintotilanne on hyvä. Tässä tutkimuksessa selvitimme koiraan poiston vaikutusta emon käyttäytymiseen ja jälkeläistuottoon heikossa ravintotilanteessa.

Tavoitteemme oli määritellä, missä määrin naaras kykenee nostamaan poikasten hoitosatsaustaan ja siten kompensoimaan puuttuvaa koirasta. Tätä varten mittasimme ruokintafrekvenssiä sekä pesälle tuodun ravinnon kokoa ja koostumusta, vertailemalla leskiä (naaraita, joiden puoliso oli kokeellisesti poistettu) kontrollinaaraisiin (joiden puoliso osallistui poikasten huoltoon). Ravinnon määrä reviirillä arvioitiin välittömästi poikasten pesästä lähdön jälkeen reviirin laadun määrittelemiseksi näiden erilaisten naaraiden välillä. Tuloksemme osoittivat, että lesket nostivat ruuantuontifrekvenssiään kompensoidakseen puuttuvan koiraan panosta. Lesket kuitenkin tuottivat vähemmän ja kevyempiä pesäpoikasia kuin kontrollinaaraat. Saman pesimäkauden toisen pesimäyrityksen menestys oli sekin alempi leskillä, jotka olivat löytäneet uuden koiraan, kuin kontrollinaarailla, vaikka kaikilla koenaarailla (leskillä) oli mahdollisuus uusintapesintään.

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