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Nest defence of Eurasian Treecreeper *Certhia familiaris* against the Great Spotted Woodpecker *Dendrocopos major*: only one parent is needed

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The theory of parental care predicts that paternal nest defence should be equal to maternal care in monogamous species. We tested this prediction on the Eurasian Treecreeper *Certhia familiaris*, using a stuffed model of the Great Spotted Woodpecker *Dendrocopos major*. The Great Spotted Woodpecker is a genuine predator of the Treecreeper because it eats Treecreepers' eggs and nestlings. It can also destroy a whole nestbox by pecking. The Woodpecker model was attached to a one-metre-long stick and placed in front of a nest box. We followed the behaviour of adult Treecreepers against the model during a period of five minutes. These trials were carried out with Treecreepers during the first or early brood and during the second or late brood, when nestlings were about two weeks old. Both the male and female invested equally in the nest defence during the first brood. During the second or late brood most of the males were absent during the nest defence. When the male was present and defended its later or second brood, nest defence behaviour did not vary between male and female. For the first brood the females had a shorter mean distance to the predator model than the males. In general, the nest defence of Treecreeper parents was composed mostly of high-pitched alarm calls used to silence the nestlings, which supports the silence hypothesis. Our results also support the effectiveness hypothesis, i.e. one parent is as effective as two parents, because in nest defence one parent can silence the nestlings without its mate.

1. Introduction

Nest defence is an important factor of fitness in many bird species (see Montgomerie & Weatherhead 1988). Many characteristics of adult birds have been found to affect the nest defence intensity of parents: sex, viability (condition), experience, interaction between sexes, earlier costs of breeding and the option for re-nesting. As nestlings grow older, they will become more valuable to their parents and consequently the defence intensity of parents will often increase, because it is less likely that a new brood can be raised in time (Andersson *et al.* 1980).

According to the empirical findings of parental care, monogamous bird species have biparental care, where both parents share the breeding duties equally (Trivers 1972). Both the male and female are needed during breeding, because one parent alone cannot raise the offspring. In true monogamy the future benefits from survival of their offspring are the same for the male and female, and so biparental care can remarkably improve the reproductive success of these birds (for example, Alatalo *et al.* 1988, Wolf *et al.* 1990).

The Eurasian Treecreeper (hereafter Treecreeper) *Certhia familiaris*, is a monogamous passerine bird species showing biparental care. It breeds in natural cavities and also in special nest boxes. Especially Treecreeper nests in natural cavities suffer from heavy nest predation from the Great Spotted Woodpecker *Dendrocopos major* and from mustelids *Mustelidae* (Kuitunen & Aleknonis 1992), but Treecreepers nesting in boxes also suffer from nest predation (Huhta *et al.* 2003). Additionally, mustelids pose a threat to Treecreeper adults, but woodpeckers do not.

In our earlier work we have shown that 70% of male Treecreepers did not feed the offspring of the second brood at all (Kuitunen *et al.* 1995), while for the first brood males participated in chick feeding in most nests. Evidently the greater food supply (mostly spiders) available during the second brood than during the first brood enabled females to feed the offspring alone. In this study, we used a woodpecker model to observe how the Treecreeper parents shared the nest defence duties during the first and second broods.

With Treecreepers as the model species we tested two separate hypotheses: (1) The effectiveness hypothesis predicts that one parent does not take part in the nest defence, when the other parent is as effective as both parents together in defending the nest (Winkler 1992). According to this hypothesis, male or female Treecreepers alone could silence their nestlings without the investment of the other parent. This hypothesis is closely related to the second one. (2) The silence hypothesis predicts that the high-pitched warning calls of Treecreepers should silence nestlings and that this is enough to protect the cryptic nest. This is important, especially when the brood gets older and louder, thus making it more vulnerable to predation. Many bird species use a special call to silence their nestlings rather than immediately engaging in nest defence in the presence of a predator (East 1981, Knight & Temple 1986).

2. Materials and methods

This study was conducted in 60–100-year-old coniferous and mixed managed forests in the vicinity of the Konnevesi Research Station in Central Finland (62°37′N 26°20′E) during the summers of 1991 and 1992. There were about 60 nest-box (special boxes for Treecreeper) territories and each territory had two nest boxes, one for the first clutch and one for the second. We used mist nets to trap breeding females at the nest during the end of incubation, and males when they were feeding their offspring. The birds were individually marked with aluminium and coloured rings. The throat of the parents was coloured to distinguish the females from the males. The adult birds were sexed by morphological measurements; for example, bill length and the presence of females' brood patch (Kuitunen unpublished data).

Treecreepers' nest defence behaviour was studied using 15 pairs of the early brood (17 May–3 June 1991) and 17 pairs of the late brood (14 June–14 July 1991). Only seven of the pairs altogether bred twice during the same breeding period. In 1992 we studied seven new pairs of the early brood (4–8 June) and six new pairs of the late brood (7–13 July).

Nest defence measurements were done when the nestlings were 13–15 days old, i.e. a couple of days before fledging. At this age nestlings are quite vulnerable to predators, because they are generally noisy (personal observ.). We used a stuffed Great Spotted Woodpecker as a predator model. The model was wired to a one-metre-long wood stick, which was put up at the front of the nest box about 20 cm away from the two side entrance holes. Observations were made from a shelter with the naked eye or binoculars at a distance of 10–40 m from the nest on sunny or cloudy days, but not on rainy days. Data were recorded into a dictaphone and later transcribed.

We started each measurement period (later called trial) as soon as we saw or heard one of the parents calling, to be sure that it had noticed the predator. The tape-recorded measurement period lasted for 5 minutes. Generally, the arrival time was different for the male and female, so the trial was performed separately for both parents. Arrival time is the time from setting up the predator model until the parent arrived and started to display (Tables 1 & 2).

Mobbing rate is the attack or fluttering behaviour of the Treecreeper towards the predator model during the five-minute period. The distances of parents from the predator were measured, and after the trial the mean, the minimum, and the maximum distance during the trial were recorded. The mean distance from the predator is the mean value of the bird–predator distance at every fifteen seconds during the trial. The minimum distance is the shortest distance of the Treecreeper from the model during the trial. The maximum distance is the longest distance of the parent during the trial.

Table 1. Nest defence of female and male Treecreepers against the Woodpecker model during the early and late broods.

Variables	Early brood			Late brood			Mann-Whitney U test	
	Mean	SD	N	Mean	SD	n	Z	P
Arrival time (s)								
Female	240	230	17	157	147	16	2.25	0.02
Male	286	302	20	251	159	9	0.19	0.85
Mobbing rate (n)								
Female	0.5	1.1	17	0.4	0.6	16	0.14	0.89
Male	1.6	2.4	20	0.7	1	9	0.87	0.38
Minimum distance(m)								
Female	0.7	0.9	17	2.3	3.2	16	2.29	0.02
Male	0.8	0.4	20	5.2	2.4	9	0.68	0.49
Average distance (m)								
Female	4.5	2.8	17	6	4.4	16	1.17	0.24
Male	9.3	8.4	20	5.2	2.4	9	0.68	0.49
Maximum distance (m)								
Female	11.6	12.1	17	10.6	10.8	16	0.56	0.58
Male	20.4	16.1	20	10.6	8.1	9	1.06	0.29
In the box (n)								
Female	0.4	0.6	17	0	0	16	1.71	0.09
Male	0.4	0.6	20	0	0	9	1.25	0.21
Call rate (n/min)								
Female	40.3	18.8	17	42.7	19.6	16	0.41	0.68
Male	42.6	18.2	20	33.8	20.9	9	0.92	0.36

Table 2. Nest defence comparison between males and females during the early brood in the Woodpecker trials.

Variables	Female		Male					
	Mean	SD	Mean	SD	T	Df	r_s	P
Arrival time (s)	312	236	355	319	–1.27	14	0.80	0.23
Mobbing rate (n)	0.6	1.2	1.8	2.7	–1.69	14	0.50	0.11
Minimum distance (m)	0.7	1.0	0.5	0.3	0.53	14	0.36	0.60
Average distance (m)	4.6	3.0	10.5	9.4	–2.27	14	–0.37	0.04
Maximum distance (m)	12.1	12.7	22.7	17.3	–2.19	14	–0.31	0.05
In the box (n)	0.5	0.6	0.5	0.6	0.00	14	0.39	1.00
Call rates (n/min)	37.8	18.0	41.9	19.1	–0.99	14	0.67	0.34

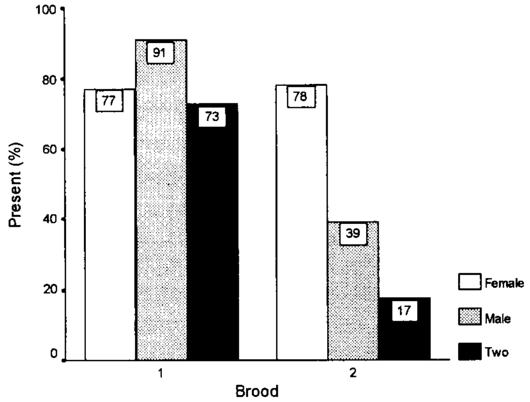

Fig. 1. The presence of female (white columns) and male (shaded columns) Treecreepers in nest defence during the early (1) and late broods (2). Black columns (two) are the percent of cases where both parents were present. There is no difference in the presence of females between broods (χ_1^2 = 0.09, P = 0.77), while the presence of male decreases during the late broods (χ_1^2 = 16.0, P = 0.0001). There were 22 pairs in the early brood and 23 pairs in the late brood.

We also recorded the number of the parents' visits into the nest box ('In the box' in Tables 1 & 2).

The call rate is the mean value per minute from the number of the tjii-warning calls during the five-minute period (Tables 1 & 2). At each nest, we waited for about 20 minutes to make sure the parents were present or absent. During the trial, we also observed the level of quieting that resulted after the parents' alarm call: Is the high-pitched call enough to silence the offspring in the nest? Generally, the two-week-old nestlings made some noises (chirr) in the nest box. In our observations, offspring in all nests made some chirr sounds before the parents were present and made alarm calls.

The presence of the male and female was analysed using the χ^2-test. We used the Mann-Whitney U test to test the possible differences between the nest defence behaviour of the male and female between the first and second broods (Table 1). The paired t-test was used to test differences between male and female Treecreepers in nest defence and the Spearman rank correlation was used to test the similarities of nest defence between the male and female (Table 2).

3. Results

Female and male Treecreepers defended their nest together in 16 out of 22 nests of the early brood and only four out of 23 nests of the late broods (χ_1^2 = 16.2, P < 0.001; Fig. 1). At four nests the female was absent during the trial on the early brood. Two males did not take part in the nest defence during the trial on the early brood, although one of them participated in feeding the nestlings.

In trials on the late brood, five females did not defend the nestlings at all. In all five cases, the male defended the nest alone, but we did not know whether these males had a successful first nest. In general, however, males' effort -in defending the late brood was significantly lower than that of females (Fig. 1). Males were absent at 14 out of 23 nests. In all of the cases where the first nesting was successful, the male was absent during the trial on the second brood (n = 7).

Females showed no differences in their nest defence between the early and late broods (Table 1). The only exception to this was the minimum approach distance, which was, on average, shorter for the early brood than for the late brood. The arrival time of females during the trial on the early brood was an average of 83 seconds longer than for the late brood. One explanation for the difference in the arrival times could be that females spent more time foraging in May when the food supply was less, than later in summer when more food was available. The nest defence behaviour of males did not differ between the broods, if the male was present (Table 1).

We found only one significant difference in nest defence between mates, if both of them had taken part in the nest defence (Table 2). The average distance of females to the predator model was shorter than that of males during the trial on the early brood. Males and females arrived at the nest almost at the same time (Spearman rank correlation, N = 16, P = 0.01, see Table 2).

In most cases (91% for the early brood and 96% for the late brood), the warning calls of parent Treecreepers silenced the nestlings in the nest boxes right from the beginning and the nestlings were quiet during the entire trial. Two of 22 parents during the trial on the early brood and only one parent of 23 nests during the trial on the late brood did not have enough hard intensity in their warning calls to silence their offspring.

4. Discussion

Male and female Treecreepers defended their nests in the same pattern during trials on the first or early broods according to the monogamous biparental care predictions, but during trials on the second or late broods, males were absent in 83% of the cases. The monogamous female Treecreeper incubates eggs alone (Kuitunen 1987) and also feeds nestlings more often than the male (Kuitunen *et al.* 1995).

This nest defence study was done during the nestling phase, when nest defence activity is assumed to be the strongest and the nestlings are the most valuable to their parents because of their age (Andersson *et al.* 1980, Grieg-Smith 1980, Montgomerie & Weatherhead 1988). Two-week-old Treecreeper nestlings are very noisy and near fledging. As a consequence, at this age, they are at their most vulnerable to predators like the Stoat *Mustela erminea*, the Least Weasel *Mustela nivalis*, and the Great Spotted Woodpecker. During this phase of breeding, an effective nest defence is required.

The nest defence intensity of an individual bird compared with that of two birds together would influence the risk taking of parent birds. If a pair is twice as effective as one bird alone, then the parents, or perhaps even more individuals of the same species, should work together. If a pair is less effective than one bird, the hypothesis is that one member of the pair should fly away. This has been observed in Tree Swallows *Tachycineta bicolor* (Winkler 1992). So we could assume that one parent is absent when the intensity of the nest defence is mild. Predators can indirectly decrease nest defenders' fitness, if the cost of nest defence has a negative effect, for example energy or time costs, or if the disturbance of the predator decreases the survival of nestlings (Wheelwright & Dorsey 1991).

There is a limited amount of food available on tree trunks early in the spring during the first brood (Kuitunen 1989, Kuitunen *et al.* 1995). Females alone cannot find enough living spiders and insects to feed the brood. This could be the most important reason for the presence of males during the first brood. With the higher amounts of food available later in summer, females are able to feed the young unassisted. On the other hand, males might be seeking to re-nest with the same female within a breeding season by engaging in body-guarding behaviour, like male Great Tits *Parus major*, which have been seen to invest more in the first brood (Curio *et al.* 1984). So the female could get to know the quality of the male, or, by this behaviour, the male might cheat the female in order to re-nest.

Also, it could be assumed that birds with cryptic nests should defend their offspring less. Parents should change their behaviour depending on the circumstances. For example, a nest should be defended more aggressively in spring when trees are leafless, than later in a season when there is much leaf cover. On the other hand, the cryptic nest may also be revealed by the more intense begging behaviour of nestlings as the breeding season progresses. For this reason, many bird species use a specific call to silence their nestlings (Grieg-Smith 1980, East 1981, Knight & Temple 1986), rather than immediately engaging in nest defence, after the predator has noticed the nest.

The Treecreeper nest is normally quite cryptic in a crevice of a tree or between the bark and the tree trunk. This could explain the nest defence behaviour of Treecreepers, which does not appear to be very active. The nest defence of Treecreepers consists of alarm calls: high-pitched, narrow frequency calls: tjii. These calls are difficult to locate, and Treecreepers are hard to observe in thick spruce forests, and, at the same time, the nestlings in the cryptic nest become quiet. We have shown that over 90% of nests were silenced by one or both parent Treecreepers. Thus, parents have done enough to defend their nest, if they can silence their offspring from a long distance away before a predator arrives too close to the nest or finds it. Parents with high-pitched alarm calls do not expose the nest or themselves to the nearby predator. In the present nest predation simulation we could also expect that the predator model has not noticed the nest and wounded the nestlings, although the distance between the nest and the predator model was short, only 20 cm. The anxious calls of nestlings should surely increase the nest defence, for example the mobbing rates. We sometimes noticed that Treecreeper parents displayed injury feigning, if the nestling screamed in our hands. For example, Great Tits are quiet and seem not to want to expose their nests to a predator, though other birds nearby react to the predator (Windt *et al.* 1990). This could also be the reason why the nest defence of the Treecreeper is quiet, too.

In this study we clarified nest defence differences between first and second broods and between early and late broods. For Treecreepers, offspring produced as early as possible are likely to be the most valuable based on recruits (Kuitunen 1987). The offspring produced earlier in the breeding season have more chances of surviving to the next breeding season than do the later ones, which do not have enough time to mature before migration or to survive a cold winter period. This could also be a reason why the male is absent during the second or the late brood. Also, males might join the first fledged broods and protect these more valuable offspring by giving alarm calls and by leading them to better foraging areas. Why does the male not come back to feed the second brood like, for example, the American Robin *Turdus migratorius* does (Weatherhead & McRae 1990), even though the first brood is probably already dispersed and fledglings independent? One possible explanation could be that males have an earlier moulting season than females. But the greater availability of food on tree trunks probably has some influence on the absence of the male during the second and late brood (Kuitunen 1989, Kuitunen *et al.* 1995). In general, the female can raise the offspring of the late brood alone.

In summary, we could conclude that during the second and late brood the male Eurasian Treecreeper is mostly useless and a flexible resource in the nest defence, because one parent alone is enough to silence the offspring in the nest, which is consistent with the silence and the effectiveness hypotheses. But a probable reason(s) for the absence of the male during the second or late brood could be either the earlier preparation of males for the cold winter period than that of females and/or the increasing amount of food available on tree trunks during the breeding period (Kuitunen *et al.* 1995).

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Selostus: **Puukiipijän pesänpuolustuskäyttäytyminen käpytikkaa vastaan: vain toinen vanhemmista tarvitaan**

Monogaamisilla lintulajeilla, joilla koiras ja naaras huolehtivat yhdessä jälkeläisistään, voidaan olettaa koiraan ja naaraan pesänpuolustuksen olevan samankaltaista ja molempien vanhempien osallistuvan yhtä aktiivisesti jälkeläisten puolustamiseen. Testasimme tätä oletusta puukiipijällä. Käytimme täytettyä käpytikkaa petomallina. Käpytikka on puukiipijän todellinen vihollinen, se syö munia ja poikasia ja se tuhoaa niin luonnonpesiä kuin pesäpönttöjäkin. Käpytikka ei kuitenkaan saalista emoja. Tutkimus on toteutettu Keski-Suomessa Konneveden tutkimusaseman ympäristössä. Pesänpuolustuskokeet on tehty poikasten ollessa hieman alle kaksiviikkoisia, lähellä pesästä lähtöä, jolloin poikaset ovat vielä haavoittuvia ja nälkäisinä ne helposti paljastavat olinpaikkansa pedoille. Käpytikkamalli asetettiin puolentoista metrin mittaiseen keppiin pesäpönttöä vasten, minkä jälkeen odotettiin emojen saapumista pesälle. Emojen saavuttua keräsimme sekä koiraan että naaraan käyttäytymistietoja noin viiden minuutin ajan varhaisilta pesiltä touko-kesäkuun vaihteessa ja myöhäisiltä pesiltä kesä-heinäkuun vaihteessa. Suurin eroavuus koiraan ja naaraan käyttäytymisessä oli koiraan puuttuminen kokonaan suurimmalta osalta myöhäisempiä poikueita. Pareilla, joilla tunnettiin varma ensimmäinen poikue, koiraat puuttuivat toiselta poikueelta kokonaan. Puukiipijän pesänpuolustus koostuu pääosin korkeista tjii-varoitusäänistä, joiden tarkoitus on hiljentää poikaset pesässä, jotta pesä ei paljastuisi pedolle. Tämä puolustuskäyttäytyminen havaittiin lähes kaikilla pesillä. Tuloksemme tukee hiljennys-hypoteesia, jonka mukaan korkeaa ja hankalasti paikallistettavaa varoitusta käytetään poikasten hiljentämiseen. Lisäksi koiraan poissaolo myöhäisiltä pesiltä tukee tehokkuus-hypoteesia, jonka mukaan poikasten hiljentämiseen riittää yksi emo. Puukiipijäkoiraan kannattaa siis pysyä varhemmin tuotetun ja paremmin hengissä säilyvän poikueen mukana sen lentopoikasvaiheessa. Koiraan poissaoloon myöhäisiltä pesueilta voi kenties vaikuttaa koiraan varhaisempi sulkiminen ja valmistautuminen talvea varten. Lisäksi naaras näyttää selviävän yksin myöhäisten uusintapesyiden poikasten hoidosta puiden rungoilla lisääntyneen ravinnon turvin kesän edetessä. Ensimmäisen eli varhaisen ja toisen tai myöhäisen uusintapesyeen (jos koiras oli mukana) poikueen kohdalla koiras ja naaras käyttäytyivät petoa kohtaan pääsääntöisesti samankaltaisesti, mm. molemmat puolisot saapuivat puolustamaan pesää hyvin samanaikaisesti.

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