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Characteristics and level of aggression by female Pied Flycatchers at different distances from the nest hole

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Proposed reasons for female aggression include defence of nest site or food resources on their territory, prevention of intraspecific brood parasitism or infanticide, or monopolisation of male's contribution to feeding of young. Here I investigate the characteristics and the level of aggression of Pied Flycatcher (*Ficedula hypoleuca*) females at different distances from the current nest site during the nest building and egg laying period. A live female was presented in a cage 1, 10, 20 and 40 m away from the nest box of the females and the behaviour of the focal females was recorded. In total, we conducted 76 presentations (19 per distance category). The time spent by females at their own nest box increased significantly with the decreasing distance of the intruded female. This suggests that females used staying at their own nest box as a defence when an intruder was very close. Female aggressive behaviour was concentrated around the nest site and decreased gradually as the distance from the nest hole increased. The main reason for female aggression seems to be the need to defend their own nest site against intruders. However, this does not totally exclude the importance of other reasons for female aggression. Both the intensity and characteristics of female–female aggression were dependent on the distance from the current nest site. This should be taken account when different studies on the level of female aggression are compared.

1. Introduction

Avian females often behave aggressively against conspecific females during breeding (reviewed by Slagsvold & Lifjeld 1994). The proposed reasons for female aggression include (1) the defence of nest site or (2) the food resources on their territory (e.g. Gowaty 1981, Yasukawa & Searcy 1981, Leffelaar & Robertson 1985, Gowaty & Wagner 1988), (3) the prevention of intraspecific brood parasitism (Gowaty & Wagner 1988, Hobson & Sealy 1990, Petrie & Møller 1991) or (4) infanticide (Veiga 1990, 1992), or (5) the monopolisation of the male contribution to feeding the young (von Haartman 1969, Yasukawa & Searcy 1982, Gowaty & Wagner 1988, Hobson & Sealy 1989).

The standard methods in female–female aggression studies have been female model or caged female presentations. In these methods, either a female model or a live female in a cage has been exposed to a focal female near the nest site. The distance to the nest site has commonly varied from less than 1 m to 30 m (Slagsvold & Lifjeld 1994). However, female reactions have never been stud-

ied as a function of distance to the current nest site. These types of studies are important especially when different studies are compared.

Von Haartman (1956) studied the aggressive behaviour of hole breeding Pied Flycatcher (*Ficedula hypoleuca*) males and observed that territorial encounters between males were most frequent near the nest. More than half the fights occurred closer than 10 m from the nest hole. This observation contrasted with the behaviour of open-nesting species which defend contiguous territories, and was interpreted as a defence of nest hole itself, rather than any particular area around the nest site.

The Pied Flycatcher is a small (12–13 g) migratory passerine species (Lundberg & Alatalo 1992). The females are observed to be aggressive towards conspecific females during breeding (von Haartman 1956, Alatalo & Lundberg 1984, Breiehagen & Slagsvold 1988, Slagsvold et al. 1992). The Pied Flycatcher is one of the most thoroughly studied species in respect of female–female aggression (Breiehagen & Slagsvold 1988, Slagsvold et al. 1992, Rätti et al. 1994, Dale & Slagsvold 1995, Kilpimaa et al. 1995).

Here I investigate by experimentation the characteristics and the level of aggression of Pied Flycatcher females at different distances from the current nest site during the nest building and egg laying period. Three of the hypothesis (see above) predict a pattern of aggression where aggressive encounters are concentrated near the nest hole, since the nest itself, or its contents, is defended. These are the nest site defence, the prevention of brood parasitism and the prevention of infanticide hypotheses. The food resource and male parental care hypotheses predict a more evenly distributed aggression pattern. The relevance of hypothesis in explaining the female aggression pattern will be discussed.

2. Methods

Field work was carried out at the Konnevesi Research Station (62°37'N, 26°20'E) in central Finland in 1993 and 1994. The study area consisted of coniferous forest mixed with birch. Every third day, we followed the existing nest boxes to detect arriving Pied Flycatchers.

During the nest building and egg laying period, we presented a live female in a cage 1, 10, 20 and 40 m away from the nest box of females. The cage hung at a height of 1.5 m. During a presentation, we first recorded the time before the female appeared. If the female did not appear within 30 min, we interrupted the presentation. In the presentations, we used six adults and one yearling female which were captured just after their arrival. The caged females were provided with live meal worms during trials. These females were released after the presentations were completed.

Observations were done by binoculars from the distance of 20 to 40 m depending on the visibility around the site of presentation. When the female appeared, we recorded the time she spent at the different distances from the cage over five minute period. The respective zones were from 5 to 2 m, closer than 2 m, and on the cage (i.e. the female was sitting on the cage). For the analysis of maximal response we scored female behaviour: a female got a score 3 if she landed on the top of the cage, 2 if she approached closer than 2 m, and 1 if she approached closer than 5 m (cf. Breihagen & Slagsvold 1988). We assumed that the female's approach to the caged female and time spent near the cage reflects her motivation to aggressive encounter (cf. Breihagen & Slagsvold 1988, Slagsvold & Sætre 1991, Sætre & Slagsvold 1992). Furthermore, we recorded the time spent at her own nest box and whether her male was present or not. All trials were conducted between 06:00–18:00 in good weather conditions from 22 May to 12 June.

Statistical analyses were performed using the SPSS for Windows 6.1.3 program. Two-tailed probabilities are used throughout.

3. Results

Forty-four of the presentations were conducted during the nest building phase and 32 during egg laying. In total, we conducted 76 presentations, i.e., 19 per distance category, and in 41 of them the focal female appeared. There was no significant difference in any of the measured variables between these two nesting phases (Mann-Whitney Test, $P > 0.10$ for all). The result was also similar in a study by Breiehagen and Slagsvold (1988).

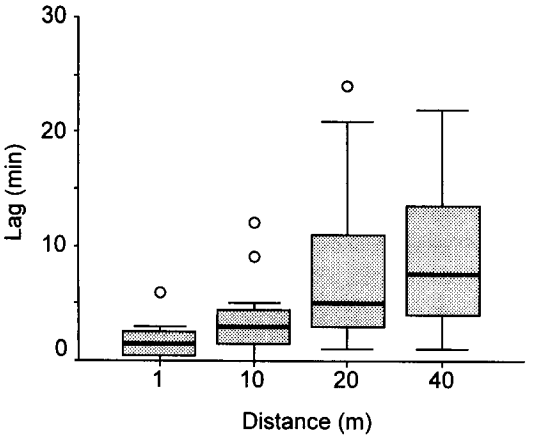

Fig. 1. The time lag before female appearance at different distances. The horizontal thick line is the median, the box shows interquartile range, bars indicate range, and dots denote outliers.

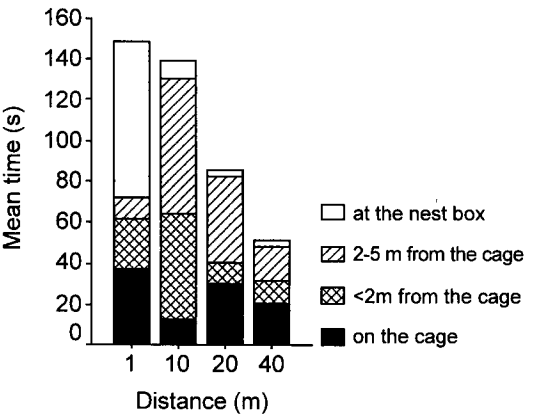

Fig 2. The mean time spent at different zones by females over 5 minutes when a caged female was presented at different distances from their nest box.

Therefore, I present here combined results to get a bigger sample size per distance category.

The number of appearing females decreased only slightly with increasing distance (12, 11, 10 and 8 out of 19; $\chi^2 = 1.85$, P = 0.60). However, the lag before appearance increased significantly with increasing distance (Fig. 1, $r_s = 0.58$, P < 0.001, N = 41). The major factor influencing the appearance of a female was the time of the presentation. In the presentations before noon 73% (N = 48) of the females appeared; in the presentations after noon only 21% (N = 28) of the females appeared ($\chi^2 = 16.86$, with continuity correction, P < 0.001).

The influence of distance and the time of presentation on female appearance was further analyzed by logistic regression analysis. Again, the time had a significant effect while the distance did not (Wald = 6.85, P = 0.01 and Wald = 1.33, P = 0.25, respectively). The interaction between distance and time was not statistically significant (Wald = 0.60, P = 0.44). Nevertheless, the intensity of aggression of appeared females was not significantly correlated with the time (Spearman rank correlations for combined data after ranking the observations within each distance category, P > 0.05 for all, N = 41).

The behaviour of females was very variable when they appeared. Some females approached the cage immediately and showed aggression by raising their feathers. Some of them landed directly on the top of the cage and tried to peck a caged female. Some females did not seemingly pay any attention towards the intruder. Usually, females were silent but some gave warning calls.

Thirty-one females out of 41 showed response (scorings 1–3) to the presence of a caged female. The maximal response decreased significantly with increasing distance from the nest box (Table 1, $r_s = -0.35$, P = 0.02, N = 41). However, neither the recorded times spent in different zones nor total response (time spent closer than 5 m) differed significantly with respect to distance (Fig 2, Kruskal-Wallis, P > 0.10 for all).

The time spent by females at their own nest box increased significantly with the decreasing distance of an intruding female (Fig 2, $r_s = -0.47$, P = 0.002, N = 41). In fact, this behaviour was

Table 1. Maximum aggression scores shown by focal females during presentation. In parenthesis, the results where nest box visits of two females are included in score category 2 (see text for details).

Maximum aggression score	Distance (m)			
	1	10	20	40
3 (on the cage)	5	2	1	1
2 (< 2m)	4 (6)	5	2	1
1 (2–5 m)		3	4	3
0 (> 5 m)	3 (1)	1	3	3

almost exclusively observed at the closed distance category. Usually the visits at the nest box were accompanied by other expressions of aggression. However, in the closest distance category there were two females which showed no other behaviour than staying a considerable time at their nest box (120 and 285 s). The mean length of nest box visits decreased significantly with increasing distance ($r_s = -0.52$, $P = 0.04$, $N = 16$). Thus, females seemed to use staying at their nest box as defence of the nest site especially when the intruder was very close. Two females at a distance of 40 m visited their nest box without showing any direct aggression against an intruder. These visits were very short ($\bar{x} = 12.5$ s) and may not be considered as a form of aggression or nest site defence. Except these two individuals, all other females that visited nest box approached the caged female as well.

In the closest distance category the intruder was put up at 1 m from the nest box, and thus the females at her own nest box could also be categorised into approaching closer than 2 m from the intruder. If staying at their own nest box is included into the zone closer than 2 m, the total response (time spent closer than 5 m) would be negatively correlated with the distance (Fig 2, $r_s = -0.41$, $P = 0.01$, $N = 41$) and the negative correlation between maximal response and distance would be even more significant (Table 1, $r_s = -0.49$, $P = 0.01$, $N = 41$).

The influence of a male presence on female aggression was tested by first ranking the observations within each distance category and then the test was run for combined data. There were no difference in any of the measured female aggression variables when the male was or was not present (Mann-Whitney U-test, $P > 0.20$ for all, $N = 16$ and $N = 25$).

4. Discussion

The majority of the females showed some response to a caged female intruder. They approached the cage and showed aggression by raising their feathers. Usually the females were silent but some of them gave warning calls. Still behaviour of females was very variable. Their response towards an intruding caged female ranged from no reaction at all to seemingly very aggressive. Some females did not pay any attention towards the intruder, while some others landed directly on the top of the gage and tried to peck a caged female.

Female showed aggressive behaviour more often before noon. In the afternoon most females did not appear at all during the 30 minute waiting period. Still, the intensity of aggression by appeared females did not decrease during the day. Female activities, e.g., nest building and egg laying, at their nest box are concentrated in the early hours of the day, and therefore they were not so vigilant and their defence of the nest site was relaxed in the afternoon. There was gradual weakening in the response towards longer distances but still many females approached the intruder, even at the distance of 40 m. Several other factors, including female age and condition, may explain variation in female responses but they were not examined.

Females seemed to use staying at their own nest box as a defence when the intruder was very close. There was a significant increase in the time spent by females at their own nest box with the decreasing distance of an intruding female. In fact, this behaviour was almost exclusively observed at the closest distance category. Usually the visits at the nest box were accompanied by other expressions of aggression. This behaviour has observed in earlier studies in the Mountain Bluebird (Power & Doner 1980) and in the Pied Flycatcher (Slagsvold et al. 1992) where a model/caged female has put close to the nest box of a focal female.

Female aggressive behaviour was concentrated around the nest site and decreased gradually as the distance from the nest hole increased. The observed pattern is similar to that observed earlier in male Pied Flycatchers (von Haartman 1956). In addition, the lag before reaction increased significantly with distance. Three of the proposed hypotheses clearly suggest this kind of pattern of aggression. These are: the prevention of brood parasitism, the prevention of infanticide and the nest site defence hypotheses. In all these hypothesis the nest itself, or its contents, is defended.

The prevention of egg dumping is a potential

explanation for female aggression. In the Pied Flycatcher egg dumping, however, is a very uncommon event. Egg dumping has only once been documented (Gelter & Tegelström 1992), and therefore, it is not a very likely explanation for female–female aggression in the Pied Flycatcher. Another explanation is the prevention of infanticide. There was no difference in female response between the nest building and egg laying phase (cf. Breihagen & Slagsvold 1988). This suggests that the value of the nest site is the same in both breeding stages, which speaks against infanticide prevention. It could be argued that in the case of infanticide prevention aggressions during the egg laying period should be more pronounced, but this was not the case. Also, there are no observations on infanticide in the Pied Flycatcher.

Thus, it seems that one of the main reasons for female aggression is the need to defend their own nest site against intruders. This hypothesis got additional support from the observation that females defend their nest hole by staying at it. Also, female Pied Flycatchers are aggressive against Great Tits, which compete over same nest holes with Pied Flycatchers (Slagsvold 1975, own obs.). Nest holes are a scarce resource and there is vigorous competition over them (see Dale et al. 1992, Dale & Slagsvold 1995). Losing the nest site would be one of the worst scenarios for the breeding female.

However, this does not exclude the importance of the other reasons for female aggression. Though the food resource hypothesis does not predict a concentrated pattern of female aggression, the aggressive behaviour during earlier nesting phases may well serve as a defence of food resources since aggressions limit breeding density and may decrease breeding synchrony between close neighbours. Also, the aggression may help the female to monopolize male parental care, though in this case female aggression is not predicted to concentrate near the nest hole but rather around the male. However, we did not find any difference in the level of female aggression when the male was present.

These kind of cage experiments should be interpreted cautiously (see Rätti et al. 1995). The situation where the intruder is in a cage is unnatural. The caged female can not escape or fight back. This may cause the escalation as well as cessation of aggressive encounters. Therefore, cage experiment data should be used to estimate the overall aggression level with caution. Further studies are needed to assess the level and characteristics of female aggression in more natural conditions. Both the intensity and characteristics of female-female aggression were dependent on the distance from the current nest site. This should be taken account when different studies are compared for level of female aggression.

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Selostus: **Kirjosiepponaaraan aggressiivisuus eri etäisyyksillä pesäkolosta**

Lintunaaraiden aggressiivisuuteen on esitetty monta eri syytä kuten pesän tai reviirin ravintovarojen puolustus, pesäloisinnan ja munien tuhoamisen estäminen tai koiraan ruokinta-avun monopolisoiminen. Tässä artikkelissa esitetään tulokset tutkimuksesta, jossa tutkitaan kirjosiepponaaraan aggressiivisuuden ilmentymistä ja tasoa eri etäisyyksillä pesäkolosta pesänrakennuksen ja muninnan aikana. Elävä naaras esitettiin kirjosiepponaaraille häkissä 1, 10, 20 ja 40 metrin päässä pesäkolosta yhteensä 76 kertaan (19 esitystä/etäisyys) ja kohdenaaraiden käyttäytyminen havainnoitiin.

Naaraiden pesäkolollaan viettämä aika lisääntyi etäisyyden lyhentyessä. Näin ollen naaraat näyttävät käyttävän pesäkololla oloa puolustaessaan pesäkoloaan lähellä olevaa tunkeilijaa vastaan. Naaraiden aggressiivisuus keskittyi pesäkolon lähistölle ja väheni etäisyyden lisääntyessä. Pääasiallinen syy naaraan aggressiivisuuteen näyttää olevan nimenomaan pesäkolon puolustaminen, joskaan muitakaan syitä aggressiivisuuteen ei voida sulkea pois. Sekä naaraiden aggressiivisuuden ilmentyminen että taso riippuivat etäisyydestä pesäkoloon, joten tämä on otettava huomioon vertailtaessa eri tutkimuksia keskenään.

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