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Nest-attenders in the Pied Flycatcher (*Ficedula hypoleuca*) During Nestling Rearing: A Possible Case of Prospective Resource Exploration

ULF OTTOSSON,¹ JOHAN BÄCKMAN, AND HENRIK G. SMITH
Department of Animal Ecology, Lund University, S-223 62 Lund, Sweden

ABSTRACT.—Visits to nest holes by birds other than their owners is a familiar phenomenon for students of breeding biology. In this study, we evaluate that behavior using a transponder reading system. Eighty-five males and females were fitted with transponders at the end of the incubation period or just after hatching. Nest boxes were fitted with transponder readers from just after hatching until all nestlings fledged. That system revealed 123 visits by birds to nest boxes other than their own, a visit being defined as at least one visit to a separate nest box on a separate day. Males were more often detected at other nests than females (53% of males vs. 29% of females visited) and males on average made more visits than females did (4.8 vs. 2.5 visits). However, both males and females devoted time to visiting other nests while still feeding nestlings. That behavior is more common than previously suspected and is consistent with birds prospecting for future nest sites or investigating patch reproductive success.

Individuals of many bird species reoccupy a familiar area in successive years, but within a population the extent of that breeding philopatry may vary between age and sex classes (Greenwood and Harvey 1982). In many cases birds, once established, continue to breed in the same territory throughout their lives. Individuals that disperse between breeding seasons most often do that to obtain a territory of higher quality (e.g. Harvey et al. 1979, Bensch and Hasselquist 1991, Haas 1998). The decision to move can be based on the individual's current breeding success or territory quality (Switzer 1997), but information about quality of nearby territories could also be used (Boulinier and Danchin 1997).

A migrating bird may face additional difficulties. Upon arrival, the territory might be occupied or its suitability drastically changed. For example, a secondary cavity nester may find its old nest hole destroyed or occupied by a con- or heterospecific bird (Lundberg and Alatalo 1992). If early breeding is advantageous (Price et al. 1988), a migrant bird arriving at the breeding grounds should be expected to minimize time spent in search of a nesting site (Alatalo et al. 1982, Slagsvold et al. 1988, Pärt 1995). However, because nest sites differ in quality (e.g. As-

kenmo 1984, Pärt and Gustafsson 1989), previous information about site quality might minimize time required to find a good nest site.

Nest visitors, different from the breeding pair, are relatively common at active nests of several bird species, for example goldeneyes (*Bucephala* sp., Eadie and Gauthier 1985), Tree Swallows (*Tachycineta bicolor*, Lombardo 1985, 1986, 1987; Stutchbury and Robertson 1987) and European Starlings (*Sturnus vulgaris*, H. G. Smith pers. obs.). Normally, those attendants do not interact with the breeding birds. In Tree Swallows, nest attendants visited several nestboxes and were especially attracted to preferred breeding localities (Lombardo 1987). Sexually mature attendants at nests during the early breeding period may be searching for possible breeding opportunities (e.g. Leffelaar and Robertson 1985, Stutchbury and Robertson 1987), extra-pair fertilizations (Westneat et al. 1990), or opportunities to lay parasitic eggs (Rohwer and Freeman 1989). Later during the breeding cycle attendants may be individuals exploring future nest sites (c.f. Lombardo 1987) or trying to interrupt the breeding attempt to get their own chance (c.f. Check and Robertson 1991, Hansson et al. 1997).

The Pied Flycatcher (*Ficedula hypoleuca*) is a small, migratory, monogamous, or facultatively polygynous bird breeding in tree holes and nest boxes (Lundberg and Alatalo 1992). A female produces one clutch per season that she incubates alone, but parents divide nestling feeding approximately equally (Alatalo et al. 1988). In this article, we describe the exploratory behavior of Pied Flycatchers during nestling rearing.

Methods.—The study was carried out during the breeding seasons of 1995 and 1997 in small woodlots surrounded by agricultural land surrounding the Revinge area ~20 km east of Lund in southern Sweden (55°41'N, 13°27'E). More than 200 equally sized nest boxes were erected on trees ~150 cm above the ground at irregular intervals, normally with a distance of >50 m between adjacent nest boxes.

Females were trapped during the last days of the incubation period or just after hatching, whereas males were trapped just after hatching. All birds were banded with an aluminum band and fitted with a transponder glued to two color-bands. In 1995, 33 adults (16 males and 17 females) and in 1997, 52 adults (24 males and 28 females) from 20 and 28 nest

¹ Present address: 18A, rue de Mamer, L-8280 Kehlen, Luxembourg. E-mail: ottosson@village.uu.net.lu

TABLE 1. Number (percentage) of visits to nest boxes other than the one a bird was breeding in by male and female Pied Flycatchers before and after the last recording of the bird in its own nest. Successful nests produced fledgling, whereas unsuccessful nests were either depredated or abandoned.

	Before		After	
	Success-ful	Unsuccess-ful	Success-ful	Unsuccess-ful
Females	8 (57.1)	6 (35.3)	9 (60.0)	9 (11.8)
Males	6 (42.9)	11 (64.7)	6 (40.0)	67 (88.2)

boxes, respectively, were fitted with transponders. Beginning just after hatching until the last nestling had left the nest box, we attached a transponder reading system (Trovan[®] Trovan Ltd., United Kingdom) to a number of nest boxes (for details see Ottosson et al. 1998). The transponder system allowed us to record all visits by transponder-marked flycatchers to a nest box. Number of available readers was 12 in 1995 and 20 in 1997. We fitted as many nest boxes as possible with transponder readers. Of known breeding attempts in nest boxes in the study area, about half were fitted with transponder readers in 1995 and almost all in 1997. Because of technical problems and predation, number of days a nest box was fitted with a working transponder reader varied from a few h up to 16 days.

Often a visit by a transponder-marked flycatcher to a nest-box included multiple readings with short intervals. In this paper, we defined a "visit" as readings at separate nest boxes or on separate days.

Results.—Eighty-five adults were recorded making 132 different visits to nest boxes other than their own. Note that all visits were made to nest boxes containing nestlings. Only in one case was it possible that the male was visiting his secondary female's nest box. Single individuals were detected at up to four different nest boxes other than their own, and individual nest boxes were visited by up to seven different individuals other than the breeding pair. Visits during nestling rearing occurred during feeding pauses that normally were <1 h long (range 9–101 min). Distance between the box in which a bird was breeding and the one it visited ranged from 60 m to almost 3 km (mean 675 m). During the time the attendant's nest contained nestlings, distance to visited nest boxes ranged from 60 to 920 m (mean 317 m).

Parents visited boxes other than their own both before and after the nest in their own box ceased to be active (Table 1). For successful nests, all readings of parents in different nest boxes were within 10 days after fledging of their own nestlings, the period when offspring are still dependent on parental care (Lundberg and Alatalo 1992, Cramp and Perrins 1993). For unsuccessful nests, 94% of readings of par-

ents in different nest boxes were made during the nestling stage up to 10 days after their nest failed. A higher proportion of males (52.5%) than females (28.9%) were detected at nests other than their own (G-test, $G = 5.99$, $P = 0.014$). Each male detected at another's nest also made a higher number of detected individual visits (4.8/male to on average 2.1 nest boxes) than did females (2.5/female to on average 1.6 nest boxes; separate variance t-test, $t = 2.13$, $df = 25.4$, $P = 0.043$). After predation or abandonment, visitation rate at foreign nests seemed to increase for males, but not for females (Table 1).

Discussion.—This study clearly shows that adult Pied Flycatchers visit nest boxes other than their own during the nestling and postbreeding periods. Even while feeding nestlings, at least some breeding birds devote time to visiting nest boxes up to 700 m away. The phenomenon of nest attenders is well known (e.g. Eadie and Gauthier 1985, Lombardo 1985, Stutchbury and Robertson 1987), but it is often assumed that visitors are young or nonbreeding individuals seeking breeding opportunities (e.g. Lombardo 1987). This study demonstrates that breeding individuals of both sexes regularly visit nests of other pairs.

Nest visitation may lead to current or future fitness benefits. For females, intraspecific brood parasitism is a possible reason to visit other nest sites (Yom-Tov et al. 2000). However, because all visits in this study occurred when the visited nests contained nestlings, that is highly unlikely. For males, pursuit of extrapair copulations is a possible fitness benefit (Alatalo et al. 1984, Lifjeld et al. 1991). However, because females at visited nests were postfertile, that seems unlikely. Birds could be prospecting for alternative breeding sites in case the current reproductive attempt failed. However, we did not detect any bird producing a replacement brood after failure during the nestling period. Furthermore, that fitness benefit cannot explain why birds visited nests during the period they reared dependent fledglings, because the probability a replacement clutch will be produced then is extremely low (Lundberg and Alatalo 1992). However, our results are compatible with birds prospecting for future nest sites (Eadie and Gauthier 1985) or investigating patch reproductive success (Doligez et al. 1999).

In the Pied Flycatcher, rapid establishment at a nest site after arrival in spring confers a fitness advantage (Slagsvold et al. 1988, Wiggins et al. 1994). In a natural situation, a returning Pied Flycatcher can find its nest hole destroyed or occupied by another individual (e.g. Källander 1994). In that situation, it may be difficult to quickly locate a new nest site, especially because natural nest holes might be difficult to find. By locating a large number of potential breeding sites with the aid of nestling begging sounds the year before, a bird may drastically reduce the time needed to find new nest sites. Alternatively, a bird may visit other nests to monitor the average

breeding success of a patch, to use that when making decisions about future breeding dispersal (Doligez et al. 1999). The best time to assess quality of a nest site is when it is active and contains nestlings. In the Pied Flycatcher, males arrive on the breeding grounds before females (Lundberg and Alatalo 1992). Males locate a nest hole and then attract females to that nest hole using song (Eriksson and Wallin 1986). Thus, locating a suitable breeding site may be more difficult for males than females. That is consistent with our observation that males more often visited other nests than did females.

It may be argued that males already have substantial information about additional nest holes, because they often occupy multiple nest holes early in the season (Lundberg and Alatalo 1992). However, frequent use of nest boxes in studies of Pied Flycatchers (Lundberg and Alatalo 1992) may result in an underestimation of difficulties of locating suitable nesting sites. First, supplying nest boxes in high numbers may reduce intra- and interspecific competition for nest holes. Second, nest boxes may be much easier to locate than natural nest holes. When searching for natural nest holes, the sound of begging nestlings might be an efficient key.

In the Pied Flycatcher, females are more likely than males to disperse after a failed breeding attempt (Harvey et al. 1984). The reason that males, but not females, increased their visitation rate after breeding failure may thus be because females disperse to other localities where they try to locate future better breeding sites.

Whatever the reason, the important result in this study is that both males and females, during nestling rearing, devote time to visiting nest boxes other than their own.

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Copulatory Behavior of American Avocets and Black-necked Stilts

TEX A. SORDAHL¹

Department of Biology, Luther College, Decorah, Iowa 52101, USA

ABSTRACT.—I recorded details of 231 copulations of American Avocets (*Recurvirostra americana*) and 39 copulations of Black-necked Stilts (*Himantopus mexicanus*) in northern Utah. Those data are presented as quantitative descriptions of the copulatory behavior of each species, complementing and clarifying qualitative descriptions in the literature. I observed no qualitative differences between copulatory behavior of avocets and stilts. Small quantitative differences may be related to differences in morphology and habitat preference. Across the family Recurvirostridae, the distinctive copulatory displays of avocets (*Recurvirostra* spp.) and stilts (*Himantopus* spp.) seem relatively uniform, but the behavior of the monotypic Banded Stilt (*Cladorhynchus leucocephalus*) of Australia appears to differ somewhat from typical recurvirostrid copulatory behavior. Attempted copulation

with inanimate objects has been reported for at least 6 of the 10 recurvirostrid species.

Avocets and stilts (Charadriiformes: Recurvirostridae) exhibit eye-catching ritualized mating behaviors that have been described qualitatively for a majority of the world's species (Cramp and Simmons 1983, Marchant and Higgins 1993, Robinson et al. 1997, 1999). Their copulatory behavior includes a sequence of stereotypic elements arranged in pre- and postcopulatory displays. Copulatory behavior in recurvirostrids is relatively easy to observe because it typically occurs in shallow water with little vegetation to obscure the view. Pairs of some species have been estimated to copulate about seven times per day (Gibson 1978, Marchant and Higgins 1993). Nevertheless, there have been no quantitative studies of that behavior.

Gibson (1971) and Hamilton (1975) described copulatory behavior of the American Avocet (*Recurvirostra americana*). Hamilton (1975) noted that the oth-

¹ E-mail: sordahl@luther.edu