Commentary

Do pied flycatchers prefer nest boxes with old nest material?

Markku Orell, Seppo Rytkönen & Kirsi Ilomäki

Orell, M., Rytkönen, S. & Ilomäki, K., Department of Zoology, University of Oulu, Linnanmaa, FIN-90570 Oulu, Finland

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Møller (1989) and Lindén & Møller (1989) drew attention to a possible bias included in the nestbox data when estimating life history parameters of birds. They emphasized that these data represent an unnatural situation which the hole nesting birds are not usually facing. Removal of the old nest material before the breeding season will release the birds from the ectoparasite load or considerably reduce it. Therefore, the estimates of fitness-related traits may not be universally applicable. Parasites can be an important cause of reproductive failures, including delayed development of young, premature fledging and increased mortality (e.g. Moss & Camin 1970, Brown & Brown 1986, Møller 1991). Furthermore, parasite load, population density and predation pressure may interact and significantly affect reproductive success, offspring quality and their subsequent survival.

We know of only a few species that regularly clean the nest-box before building a new nest, e.g., the starling *Sturnus vulgaris* (Feare 1984) and the house wren *Troglodytes aedon* (Thompson & Neill 1991). The species most commonly used in nest-box studies, the great tit *Parus major*, the blue tit *P. caeruleus* and the pied flycatcher *Ficedula hypoleuca* do not clean the box before building a nest. The majority of the information on population dynamics and factors affecting re-

productive success in passerine birds is based on work carried out with these three species. Thus, if the lack of parasite load in nest-box studies has significantly contributed to the outcome of the work, knowledge on factors governing the reproduction of the passerine species may be distorted.

Ectoparasites in nest boxes

If ectoparasites have detrimental effects on the reproductive success of a pair, hole-breeding species should prefer clean boxes. The work of Thompson & Neill (1991), who did not find house wrens preferring clean nestboxes to those containing old nests, stimulated our experiments with the pied flycatcher. First, we tested the above hypothesis by providing pied flycatchers with a choice between (1) a clean box and one containing a nest with parasites from the previous year, and a choice between (2) boxes containing an artificial nest and a nest from the previous year. We also tested (3) the effect of ectoparasites on the quality and quantity of the fledglings.

The experiment was carried out in Oulu (65°N, 25°30′E), Northern Finland in the spring of 1992 and 1993. The study area consisted of a variety of young and middle-aged forests. The habitats

included pure deciduous forests with birch, (Betula spp.), predominating, mixed forests of birch, Norway spruce, (Picea abies), and Scots pine, (Pinus sylvestris), and mixed coniferous forests with spruce and pine.

The pied flycatcher is a species that breeds in a variety of habitats provided there are nesting holes available. By putting up nestboxes it is easy to get pied flycatchers to settle and breed in sufficient numbers.

We used boxes with a bottom area of 144 cm² and a cavity height of 25 cm. The diameter of the entrance varied between 32 and 36 mm. Altogether 30 pairs of boxes, with south-facing entrances, were placed along a forest road. The boxes were located in the habitats preferred by pied flycatchers (Lundberg & Alatalo 1992) in deciduous and mixed forests. The boxes in each pair, situated no more than 1.5 m apart from each other, were attached at a height of 1.6 m. To minimize the possible effects of polyterritorial polygyny (e.g. Lundberg & Alatalo 1992), the box pairs were located at least 200 m apart.

Before the pied flycatchers arrived in 1992, one box of each pair was randomly assigned and provided with a pied flycatcher nest from the previous year. In 1992 the other boxes were empty and in 1993 provided with an artificial nest. When the old nests were transferred a lot of hen fleas (Ceratophyllus gallinae) were apparent in the debris. Together with bird flies (Ornithomya sp.) this species is the main ectoparasite sucking blood from hole nesting passerines in our study area. The existence of parasites was confirmed by adding about 50 fleas to each nest before the arrival of pied flycatchers in 1992. To prevent great tits from occupying the boxes the entrances were closed until the first pied flycatcher males arrived in the study area.

To find out the occupancy and to collect data on breeding performance, the boxes were checked at sufficient intervals, at least once a week. The following information was gathered in 1992; start of laying, clutch size, time of hatching, number of hatched and fledged young. When the nestlings were 13 d old they were ringed, weighed (0.1 g accuracy; using a Pesola spring balance) and wing and tail lengths were measured to the nearest 1 mm (Svensson 1970, Busse & Kania 1970). The tarsus length was measured to the nearest

0.1 mm with a dial caliper (Svensson 1970). During these visits adults were captured and ringed and the biometrical measurements were taken. In 1993, only information for clutch size and the start of laying was collected.

To test the possible effect of ectoparasites on reproductive success, the parasites were destroyed in half of the occupied nests in 1992. This was done by temporarily moving the 0–1 d old chicks and spraying the randomly assigned nest with 0.3% pyrethrine powder. Pyrethrine kills invertebrates but is harmless to vertebrates (see also Møller 1991).

Results

All the 8 pied flycatcher pairs that bred in the study area chose the boxes with old nests in 1992. The probability of having such an extreme distribution by chance is low (Sign test, 2-tailed, P = 0.008), if the birds select the nest box at random. Hence, this result suggests that the pied flycatchers actively chose the boxes containing old nests.

However, it is possible that pied flycatchers selected the box with an old nest because of the nest material available which would reduce the female's nest-building effort for the current breeding attempt. In the choice between an old and an artificial nest, 11 females out of 14 chose the box containing an old nest in 1993. Although the difference between the observed and random distribution remained just below the level of significance (Sign test, two tailed, P = 0.058), it is probable that the pied flycatchers prefer boxes with old nests.

The 8 females started laying on average on 31 May (range 26 May - 2 June) and the clutch size averaged out at 6.4 eggs (6–7) in 1992. The males attended their broods during the whole breeding period of 1992, implying that all the nests were owned by primary females (Alatalo et al. 1981). The corresponding values for egg laying and clutch size were 25 May (23–31 May) and 6.6 eggs (n = 12) in 1993. (Note that the 2 nests deserted during egg laying were excluded here, because the start of laying was uncertain.) These figures correspond well with reports on the pied flycatcher in the Oulu area (Ojanen et al. 1978, Ojanen & Orell 1982).

Discussion

Why did pied flycatchers prefer nest boxes with old nests? Migratory birds breeding in extreme northern conditions are highly time-constrained. The suitable season in our study area for breeding and postnuptial moult before the autumn migration is not as short as in Finnish Lapland. However, long distance migrants, like pied flycatchers (e.g. Moreau 1972), obviously have little time for the phases of high energy requirement even at the latitude of Oulu. An indication of shortage of time in the summer schedule is that a substantial proportion of the population begin to moult while still breeding in some years (Ojanen & Orell 1982). Pied flycatcher females are therefore presumably short of time when searching for a nesting hole (Alatalo et al. 1981).

Choosing a hole with an old nest can be adaptive, i.e. the parents may save time, in two ways. First, females do not have to collect as much nest material as when settling in a clean hole. However, the result of our second experiment suggests that this hypothesis is not unambiguously valid. Second, birds can choose the breeding territory without time consuming comparisons by using the old nest as an indicator of a good nesting place. Additionally, in natural conditions an empty hole is often a result of nest predation, and may thus indicate an unsafe breeding place. It might be possible that birds use old nest material, or other traces like faeces of nestlings, or even fleas, as a clue to the success of the previous nesting attempt. The result of both our experiments lend support to this hypothesis.

Table 1. Clutch size, number of fledglings, weight, and body dimensions (mean \pm *SD*) of the pied flycatcher broods with and without exposure to ectoparasites (n = 4 broods in both groups, t-test, P > 0.1 in all comparisons).

Ectoparasites:	present	absent
Clutch size	6.00 ± 0.00	6.75 ± 0.50
No. of fledglings	6.00 ± 0.00	6.25 ± 0.96
Weight (g)	14.27 ± 0.32	14.70 ± 0.59
Wing length (mm)	49.54 ± 4.12	47.53 ± 2.14
Tarsus length (mm)	17.60 ± 0.12	17.66 ± 0.40

In this context, the contribution of the ectoparasites to the breeding success must also be considered. Our results on broods with and without fleas revealed no difference in the quality and quantity of nestlings (Table 1), suggesting no disadvantage to breeding in "dirty" boxes. It is possible that in their natural densities fleas do not pose a great threat to the breeding success of the pied flycatchers in our study area (see also Thompson & Neill 1991, Johansson & Albrecht 1993). Sustaining and tolerating a substantial burden of parasites may have evolved during the course of evolution of the pied flycatcher. This does not deny the fact that parasites have a contribution to the life-history strategies of birds. It is possible that there is a latitudinal gradient in the prevalence of parasites, which could also explain the lack of response in our experiment compared to those carried out in more southern areas. Further experiments are needed to solve these possibilities. Information of the annual variation in the occurrence of ectoparasites is also needed before we can judge how important selective factors they are in shaping the reproductive strategies of hole-nesting birds.

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