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Ectoparasite affects choice and use of roost sites in the great tit, *Parus major*

PHILIPPE CHRISTE, ANNE OPPLIGER & HEINZ RICHNER*
Zoology Department, University of Bern, CH-3032 Hinterkappelen, Switzerland
and
Zoology Department, University of Lausanne, CH-1015 Lausanne, Switzerland

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Abstract. Many diurnal bird species roost at night in holes. As a regular visitor of a hole they are therefore a welcome host for several species of ectoparasites. The interactions of ectoparasites with the behaviour, life-history traits and population demography of their hosts are largely unknown. In the present study the effects of the haematophagous hen flea, *Ceratophyllus gallinae*, on the great tit's choice of winter roost site were investigated experimentally. Three experiments tested (1) whether great tits prefer a clean nestbox to one containing an old, but parasite-free nest, (2) whether they prefer a parasite-free nestbox to one infested with the haematophagous hen flea, and (3) whether they prefer not to use a nestbox when there is only an infested box available in their territory. In the first experiment there was no discrimination and both kinds of boxes were used equally often. In the second experiment the great tits clearly preferred to roost in the box without ectoparasites. In the third experiment a significantly higher proportion of the infested nestboxes were not used for roosting compared with the parasite-free boxes. Recently the validity of the conclusions drawn from nestbox studies where the naturally occurring detrimental ectoparasites are eliminated by the routine removal of old nests between breeding seasons has been questioned. This study shows that ectoparasites affect host behaviour and therefore lends support to that criticism.

Great tits and many other bird species use natural holes or nestboxes as a night roost in winter (Kluijver 1952; Perrins 1979; Winkel & Hudde 1988). At outside air temperatures below 0°C the birds roosting in a box benefit by saving at least 10% of the energy expended through the night (Kendeigh 1944, 1961). Does hole roosting also have costs?

Great tits are a common host of ectoparasitic fleas (Harper et al. 1992) which survive from one breeding season to the next inside the nestbox. The risk of infestation therefore increases by the habit of hole roosting in winter, unless birds can detect (Du Feu 1992) and successfully avoid infested holes. Since nest holes are often a limited resource and birds that avoid an infested hole may have to sleep outside and bear the energetic costs proposed by Kendeigh (1961), birds may therefore trade off costs and benefits incurred by hole roosting.

Fleas have detrimental effects on the reproductive success of great tits (Richner et al., in press), and from this it can be expected that the birds' behaviour will be affected by this ectoparasite. The onset of reproduction is also significantly delayed in infested nests (Oppliger et al., in press). In natural nests the fleas survive in the nest inside their cocoons from one breeding season to the next (Bates 1962; Humphries 1967, 1968), and emergence is triggered by rapid increases in temperature and by mechanical stimulation as provided by a roosting or nesting bird (Humphries 1968). Active ectoparasites in old nests are most common early in spring but can be found in lower numbers at all times of the year. Infestation with fleas may imply direct effects on the host, but also the risk of infesting a nest that he builds anew in spring.

In the present study on the great tit we investigated the effect of a common ectoparasite of tits (Harper et al. 1992), the haematophagous hen flea, *Ceratophyllus gallinae*, on choice and use of nestboxes as a night roost.

GENERAL METHODS

We carried out the study during the winter of 1991–1992, in a forest surrounding the campus of the University of Lausanne, Switzerland. A population of great tits uses the nestboxes which were

*To whom all correspondence should be addressed.

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provided in 1989. We inspected the nestboxes for roosting birds either by opening the nestbox (experiment 1), or with a dental mirror (experiments 2 and 3) fitted with a 6-volt light bulb on its back. The inspections took place between 2100 hours and midnight.

In the breeding season of 1989, in clean new nestboxes and without any manipulation of fleas, over 80% of all nests were naturally infested with the hen flea. The adult fleas lay their eggs in the nests of birds. The larvae are not haematophagous and feed on the debris and the digested and undigested blood taken by adult fleas. Many adult fleas leave with the nestlings, dozens of fleas at a time wait at the entrance hole for visitors, and hundreds remain over the winter inside the nest in cocoons, attached to the nesting material until the beginning of the breeding season.

In the experiments described below, nests were either infested with fleas, or the fleas were eliminated by heat-treatment of the nests. For the latter purpose the nests were taken out of the nestbox, put in a closed plastic bag to prevent loss of humidity, and treated for 5 min inside a microwave appliance. This procedure was carried out in the field and a transportable 220-volt generator was used to feed the microwave appliance.

To avoid pseudoreplication of data only one complete inspection of all available nestboxes was analysed.

EXPERIMENT 1

Design

Experiment 1 was designed to test whether great tits prefer to roost in a clean nestbox to one containing a parasite-free nest. After the breeding season of 1990 we provided in each of 45 territories of great tits a pair of nestboxes, hung beside each other at a distance of 0·3–1 m. One box of each pair was clean, the other one contained an old, heat-treated and hence parasite-free nest. All of these boxes were inspected once between the middle of January and middle of February 1991. In one of the pairs a starling, *Sturnus vulgaris*, was found roosting and the pair is therefore excluded from the analysis, thus giving a sample size of 44 pairs of boxes.

Results

In 35 of the 44 pairs of boxes one of the two boxes was occupied by a roosting great tit. None of the pairs was simultaneously occupied by more than one bird. Seventeen birds roosted in the box of a pair that contained the nest, and 18 birds roosted in the empty box of a pair. Thus, the birds did not prefer or avoid (binomial test, $P=0{\cdot}99$) roosting in a box containing an old nest that was parasite-free.

EXPERIMENT 2

Design

In this experiment we tested whether great tits prefer to roost in a parasite-free nestbox to one infested with the haematophagous flea. After the middle of February 1991, in 30 of the pairs of boxes described above, one box was infested with approximately 20 fleas. In 15 of these 30 pairs of boxes the fleas were injected into the box with the nest and in the other 15 pairs they were put into the clean box (Fig. 1). A third group of 15 pairs of nestboxes was kept free of parasites and used for another experiment during breeding. All pairs of nestboxes were inspected on 21 March. A starling roosted in the parasite-free box of one pair. This pair is excluded from the analysis, and the sample size is therefore 29 pairs of boxes.

Results

In 13 of the 29 pairs of boxes a great tit was found roosting in one of the two boxes. None of the pairs was simultaneously occupied by more than one bird. Altogether, 12 birds roosted in the parasite-free box of a pair (Fig. 1), and only one bird chose the infested box. This preference for the parasite-free nestbox of a pair is highly significant (binomial test, $P=0{\cdot}006$).

EXPERIMENT 3

Design

In the third experiment we tested whether birds prefer not to use a nestbox when there is only an infested box available in their territory (and thus in the absence of a suitable roosting site may have to roost outside). We therefore removed, after the end of the breeding season of 1991, one of the boxes of each of the pairs described in the above experiments, leaving only one nestbox per territory. Among 43 nestboxes used for the present experiment, a randomly chosen sample of 21 nestboxes

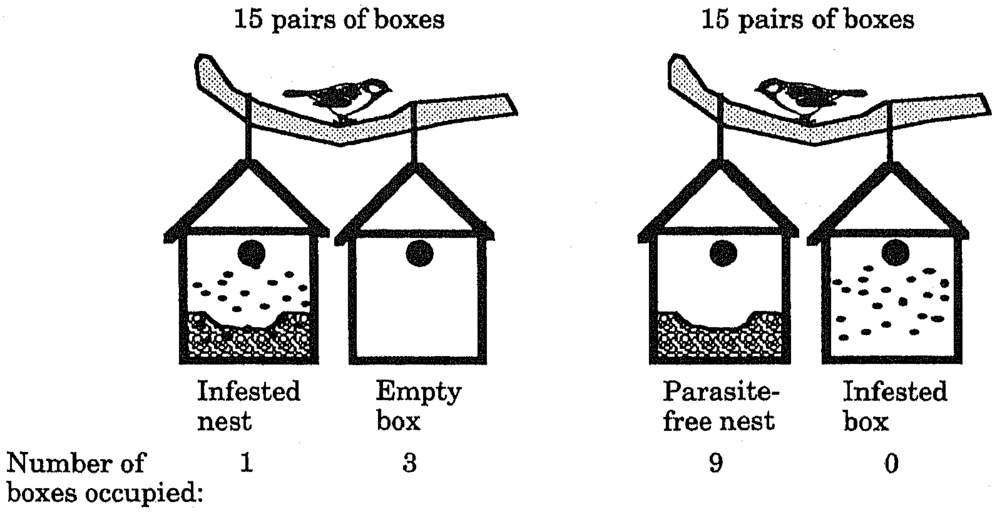

Figure 1. In 30 pairs of nestboxes one box contained an old nest. In 15 pairs the haematophagous hen fleas were injected into the box with the nest, and in 15 pairs into the box without the nest. All boxes were then inspected for roosting great tits.

Table I. Night roosting by great tits in infested and parasite-free nestboxes when only one box was offered in a territory

	Great tit	
Nestbox	Roosting	Absent
Parasite-free	15	6
Infested	6	16

was furnished with one half of a heat-treated old nest of a great tit. Another sample of 22 nestboxes was provided with one half of an infested nest. The other half of the nest was used for other experiments. Nestboxes were inspected with a dental mirror on 16 January 1992.

Results

A two-way frequency table of nestbox occupation versus presence or absence of parasites shows that great tits roosted preferentially in parasite-free nestboxes and avoided the infested ones (Table I). Thus nestbox occupation by a roosting great tit significantly (Fisher exact test, $P=0{\cdot}006$) depends on the presence or absence of the ectoparasites.

DISCUSSION

The present study shows that a common ectoparasite influences the choice and use of nestboxes as night roosts in great tits. Thompson & Neill (1991), to their surprise, found that house wrens, *Troglodytes aedoni*, do not prefer a clean nestbox to one that contains an old nest. In our first experiment great tits had the choice between a clean box and a box containing a parasite-free nest and also showed no preference. In the second experiment we introduced the haematophagous hen flea and there the tits showed a clear preference for the parasite-free box. Thus, Thompson & Neill's (1991) result may simply be explained by the absence of ectoparasites, for which they did not control.

Despite the fact that ectoparasites are naturally common in birds and mammals that regularly use the same natural cavity for roosting or breeding, the effects of ectoparasites on behaviour, reproduction, life-history traits, population genetics, and demography of birds are poorly understood. This is mainly because most of the studies on hole-nesting birds have been carried out in regularly cleaned nestboxes, and because of a general lack of experimental studies investigating this specific host–parasite interaction. Hole-nesting birds breeding in nestboxes have been studied over decades in many countries and the findings from these studies have greatly influenced our ecological and evolutionary thinking. Recently, the validity of the results from nestbox studies has been questioned (Møller 1989), and has led to a controversial discussion (Koenig et al. 1992; Møller 1992). Møller (1989) pointed out that the load of detrimental ectoparasites may be considerably reduced in nestbox studies by the annual cleaning of boxes by the researchers, and hence that their effects on nest choice, mate choice, reproductive success and nestling growth have been ignored. We have shown elsewhere that the haematophagous hen flea affects reproductive success (Richner et al., in press) and timing of reproduction in great tits (Oppliger et al., in press). This and the present study suport Møller's (1989) contention that the effects of ectoparasites on their hosts should be evaluated. The findings from carefully designed experiments should be integrated in our present understanding of bird ecology, behaviour and evolution of life-history traits.

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