Oecologia (1994) 98:147–149

ORIGINAL PAPER

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Ectoparasites, nest site choice and breeding success in the pied flycatcher

Received: 31 January / Accepted: 10 March 1994

Abstract It has recently been suggested that nest box studies might bias the measurement of behavioural and life-history traits, because the removal of old nests may reduce the load of ectoparasites. This experimental artefact may have notable effects on nest site choice and breeding success in cavity-breeding birds. We tested (i) if pied flycatchers *Ficedula hypoleuca* prefer clean nest boxes and (ii) if old nest material affects the number of parasites and the breeding success of pied flycatchers. In the first experiment we offered birds one cleaned nest box and one nest box with old nest material from the previous year. The two nest boxes were placed in very similar sites near each other. In this experiment all pied flycatchers clearly preferred "dirty" nest boxes. In the second part of the study we distributed clean nest boxes and dirty ones on the same study area. After breeding was over we counted the number of fleas *Ceratophyllus gallinae* in the nest material. This flea species was the most abundant and probably the most hazardous parasite in the nests. Surprisingly, we found that there were significantly more fleas in the nest boxes with nests of the current year only than in the boxes with nests of both current and previous year. This might explain the preference for the dirty boxes. However, our results do not indicate that the number of fleas affects breeding success in the pied flycatcher.

Key words Breeding success · Ectoparasitism *Ficedula hypoleuca* · Nest box studies · Nest site selection

Introduction

Since the pioneering work of David Lack (1954) numerous studies of cavity-breeding birds have played an important role in the development of ecological and evolutionary theory. However, Møller (1989, 1992) recently drew attention to a possible artefact in measurements of life-history traits in these nest box studies. He argued that removal of old nest material before the breeding season markedly reduces the load of ectoparasites. If these nest parasites cause mortality and decrease growth of offspring, results originating from nest box studies might be biased in an important way.

Ectoparasites negatively affect their hosts and host reproduction (e.g. Rothschild and Clay 1952), and they have been shown to reduce the attractiveness of nest sites to birds (Moss and Camin 1970; Brown and Brown 1986; Møller 1990). To the contrary, Thompson and Neill (1991) have recently shown that house wrens *Troglodytes aedon* did not prefer nest boxes from which old nest material has been removed to those containing old nests. These birds, however, removed old nests before building their own and so reduced irritation from parasites.

Old nest material may also offer benefits for breeding birds. Erckmann et al. (1990) hypothesized that the presence of old nests in which chicks had been successfully raised could be used as a cue indicating nest site quality. The presence of old nest material may also decrease the time taken for nest building and so reduce costs of this behaviour (Møller 1990; Conrad and Robertson 1993).

Although the pied flycatcher is one of the most studied bird species in behavioural and evolutionary ecology (see review by Lundberg and Alatalo 1992), there is very little information on the effect of ectoparasites on the reproduction of this species. In this study we investigated two specific questions: (i) Does old nest material have any influence on nest site choice of pied flycatchers? (ii) Does the old nest material affect the number of parasites, and breeding success of pied flycatchers?

Methods

Study site and study animals

The study was carried out in Noormarkku (61° N, 21° E), western Finland, during 1991. The study area was coniferous forest domi-

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nated by spruce *Picea abies*, with a mixture of pine *Pinus silvestris* and few deciduous trees birch *Betula pubescens* and aspen *Populus tremulus*. The pied flycatcher is a migratory cavity-nesting passerine of middle and northern Europe. It arrives at the breeding grounds during May and egg laying begins in late May or at the beginning of June (Lundberg and Alatalo 1992).

Nest box choice

In the first experiment we offered birds two nest boxes, which were placed in very similar sites 4 meters apart. We randomly put previous-year nest material of pied flycatchers into one nest box and left one nest box clean. The boxes were distributed just before the arrival of the pied flycatchers. The height from entrance to bottom, width, and diameter of entrance of the wooden nest-boxes were 15 cm, 10*10 cm, and 3.0 cm, respectively. Nest-boxes were placed 1.5 m from the ground. The distances between nest box pairs ($n = 12$) were about 100 meters in the study area. We measured breeding parameters and number of fleas in the nests (see methods below) and used the results in the analyses of breeding success.

Number of fleas and breeding success

In the second part of the study we distributed 22 cleaned nest boxes (clean nest boxes) and 22 nest boxes with old nest material from the previous year (dirty nest boxes) on the same large homogenous study area just before the arrival of the pied flycatchers. To ensure sufficient and independent replication we first chose a site for each nest box and then randomly determined treatment of the box. Nest boxes were about 100 m from each other. Nests were inspected every day to determine breeding parameters, nest building, laying, hatching, and fledging. Nestlings were weighed when they were 9 days old with a Pesola spring balance. After breeding we collected all nest material from the nest boxes and using a dry funnel method (28*28 cm) we extracted invertebrates from the nests. The flea *Ceratophyllus gallinae* was the most abundant and probably the most hazardous parasite in the nests.

Results

Eight pied flycatcher females occupied nest boxes in the nest choice experiment. All these birds clearly preferred dirty nest boxes (sign test, two-way $P = 0.008$). The clean boxes in the pairs remained empty. The remaining four pairs of boxes were occupied by great tits *Parus major*, which seemed to prefer clean boxes (4/0).

There were clearly more fleas in the clean nest boxes ($x = 639$, SE = 193.6, $n = 7$) than in the dirty ones ($x = 138$, SE = 32.8, $n = 19$) ($U = 22$, two-tailed $P = 0.011$) (Fig. 1). The dirty boxes of the nest choice experiment ($n = 8$) were included in the analyses as their number of fleas did not differ from the dirty boxes of the second study ($n = 11$) (see Material and methods) ($U = 26$, $P = 0.149$).

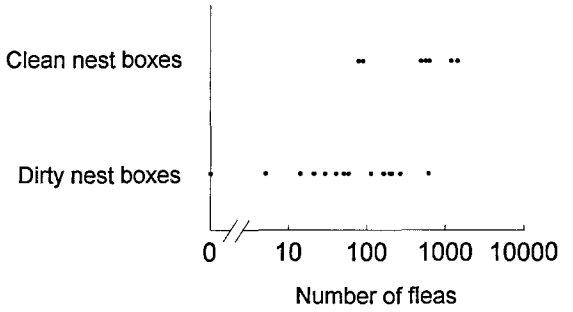

Fig. 1 Number of fleas *Ceratophyllus gallinae* in clean nest boxes (old nest material removed) and dirty boxes (with old nest material of previous year) after breeding of pied flycatchers

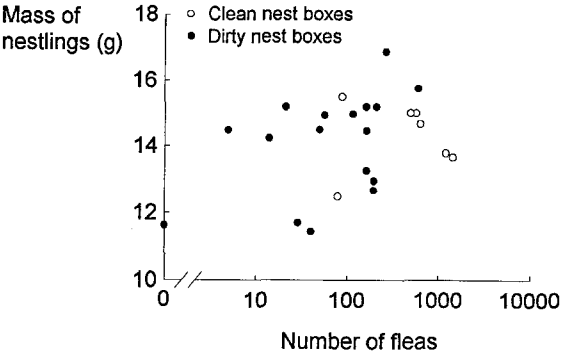

Fig. 2 Correlation between the number of fleas in nests after the end of the breeding season and mass of nestlings when 9 days old

The number of fleas did not affect breeding success of pied flycatchers. There was no significant correlation between number of fleas and mass of nestlings (partial correlation, controlled for the number of nestlings, $r = 0.38$, $n = 24$, $P = 0.067$) (Fig. 2) and number of fledglings (Pearson correlation, $r = 0.02$, $n = 28$, $P = 0.920$). The number of fleas was log-transformed to approach a normal distribution.

Time of nest building was significantly shorter among birds breeding in the clean boxes (Table 1). The other breeding characteristics, the number of eggs, the number of hatchlings, the weight of nestlings, or the number of fledged young did not differ between the clean and the dirty nest boxes. Neither did the laying date of the first egg which may greatly affect other breeding characters of pied flycatchers (Lundberg and Alatalo 1992) (Table 1).

Table 1 Breeding characteristics of pied flycatchers in different types of nest boxes

	Clean boxes			Dirty boxes				
	x	SE	n	x	SE	n	U	P
Clutch size	6.22	0.22	9	6.20	0.18	20	93	0.906
Brood size at hatching	6.22	0.22	9	5.95	0.17	20	73.5	0.451
Brood size at fledging	5.22	0.76	9	5.50	0.37	20	87	0.906
Laying date of the first egg[a]	8.78	1.12	9	8.60	0.60	20	76.5	0.540
Mass of nestlings, g[b]	14.3	0.34	8	14.1	0.38	17	65.5	0.907
Time of nest building, days	4.71	0.42	7	6.94	0.62	17	18.5	0.010

[a] Days since 31 May
[b] Nestlings were weighed when 9 days old

Discussion

In our experiment pied flycatchers did not avoid nest boxes containing old nest material; rather, they seemed to prefer dirty ones. Our results, and the almost identical findings of Orell et al. (1993) are not in agreement with other studies (Brown and Brown 1986; Møller 1990), which found that old nest material with ectoparasites may reduce attractiveness of nest sites. Moreover, we did not find, as earlier supposed (Møller 1989, 1990, 1992), that old nest material increased the number of ectoparasites in nests and decreased the breeding success of cavity-breeding birds. In contrast, ectoparasites seem to affect reproduction success of other birds, especially swallows *Hirundo rustica* and house martins *Delichon urbica* (Møller 1990; de Lope and Møller 1993; de Lope et al. 1993).

The preference for "dirty" nest boxes was not surprising as old nest material in our experiment tended to decrease the parasite load of nest boxes. It seems that new nests of pied flycatchers are not primarily infested by fleas *Ceratophyllus gallinae* from old nests. We suggest that characteristics of the micro-habitat (humidity, temperature, invertebrate predators) are different in nest boxes with old nest material and boxes with new material only. It is the task of future work to find out how environmental conditions affect interactions between invertebrate species in the nest material during the whole breeding season of birds.

If nest parasites cause any cost for breeding birds (Hart 1992), it will be advantageous to choose a breeding site with old nest material, where densities of parasites seem to be lower. An alternative explanation could be that birds prefer dirty nest boxes because old nest material is a cue indicating a good breeding site, where breeding has been successful in the previous year (Erckmann et al. 1990; Thompson and Neill 1991).

Old nest material in the nest boxes may also change duration of nest building, which may reduce the risk of predation and the time and energy spend on building. On the contrary, nest building by pied flycatchers seemed to take longer if there was old nest material in their boxes. A possible reason for this may be that female pied flycatchers attempt to remove parasites or try to disturb parasites with a different quantity or quality of nest material (Clark and Mason 1985, 1988). However, the longer duration of building did not affect the start of egg laying of pied flycatchers, which should be the most marked cost of prolonged nest building (Lundberg and Alatalo 1992).

Old nest material may also lower the depth of nest holes, which may affect the preference for holes in many cavity-nesting species (Edington and Edington 1972; Nilsson 1984; Johnsson et al. 1993). The lower depth may be useful for incubating female pied flycatchers, which like to escape from nest boxes when disturbed. However, this hypothesis was not supported by other experiments, where changes in depth of nest boxes were also controlled for (K. Olsson, unpub. data).

Our results do not support earlier assumptions that old nest material must decrease the attractiveness of a nest site and breeding success in cavity-breeding birds (Møller 1989). However, the contradictory results confirm earlier suggestions that this phenomenon must be carefully considered in all nest box studies of birds.

Acknowledgements We thank R. V. Alatalo, J. van Es, A. P. Møller, K. Olsson and P. Siikamäki for valuable comments on the manuscript. We are also greatly thankful to A. Mappes, M. Mappes and S. Salminen for their assistance in the field and A. Innala who prepared the nest boxes. J. Haimi kindly advised on extraction of fleas. Stockholm University provided good facilities to finish this work. The study was supported by grants from Alfred Kordelin Foundation, Nordisk Forkersutdanningsakademi, Ornithological Society of Pori and University of Jyväskylä.

References

Brown CR, Brown MB (1986) Ectoparasitism as a cost of coloniality in cliff swallows *Hirundo pyrrhonata*. Ecology 67: 1206–1218

Clark L, Mason JR (1985) Use of nest material as insecticidal and anti-pathogenic agents by the European starling. Oecologia 67: 169–176

Clark L, Mason JR (1988) Effect of biologically active plants used as nest material and the derived benefit to starling nestlings. Oecologia 77: 174–180

Conrad KF, Robertson RJ (1993) Clutch size in eastern phoebes *Sayornis phoebe*. I. The cost of nest building. Can J Zool 71: 1003–1007

Edington JM, Edington MA (1972) Spatial patterns and habitat partition in the breeding birds of an upland wood. J Anim Ecol 41: 331–357

Erckmann WJ, Beletsky LD, Orians GH, Johnsen T, Sharbaugh S, D'Antonio C (1990) Old nests as cue for nest-site selection: an experimental test with red-winged blackbirds. Condor 92: 113–117

Hart BL (1992) Behavioral adaptations to parasites – an ethological approach. J Parasitol 78: 256–265

Johnsson K, Nilsson SG, Tjernberg M (1993) Characteristics and utilization of black woodpecker *Dryocopus martius* holes by hole-nesting species. Ibis 135: 410–416

Lack D (1954) The natural regulation of animal numbers. Clarendon Press, Oxford

Lope F de, Møller AP (1993) Effects of ectoparasites on reproduction of their swallow hosts: a cost of being multi-brooded. Oikos 67: 557–562

Lope F de, Gonzalez G, Prez JJ, Møller AP (1993) Increased detrimental effects of ectoparasites on their bird hosts during adverse environmental conditions. Oecologia 95: 234–240

Lundberg A, Alatalo RV (1992) The pied flycatcher. T & A D Poyser, London

Møller AP (1989) Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? Oikos 56: 421–423

Møller AP (1990) Effects of parasitism by a haematophagous mite on reproduction in the barn swallow. Ecology 71: 2345–2357

Møller AP (1992) Nest boxes and the scientific rigour of experimental studies. Oikos 63: 309–311

Moss WW, Camin JH (1970) Nest parasitism, productivity, and clutch size in purple martins. Science 168: 1000–1003

Nilsson SG (1984) The evolution of nest-site selection among hole-nesting birds: the importance of nest predation and competition. Ornis Scand 15: 167–175

Orell M, Rytkönen S, Ilomäki K (1993) Do pied flycatcher prefer nest boxes with old nest material? Ann Zool Fennici 30: 313–316

Rothschild M, Clay T (1952) Fleas, flukes and cuckoos: a study of bird parasites. Collins, London

Thompson CF, Neill AJ (1991) House wrens do not prefer clean nestboxes. Anim Behav 42: 1022–1024