

± 0.4 days between the third- and fourth-hatched chicks. If these limited data are representative (no other detailed information is available), all chicks are well separated in the pattern of size differences initially produced within broods by hatching asynchrony. First-laid eggs averaged 2.6% less than second-laid eggs in volume, but it seems safe to infer that this difference must be of little importance in reducing the initial body-mass difference between first- and second-hatched chicks.

In conclusion, egg volume seems to remain constant after the first-laid egg in clutches of Great Crested Grebes not adding to the size hierarchy of chicks arising from asynchronous hatching. In addition, many authors argue that the increase in size of the second-laid egg relative to the first-laid found in clutches of many bird species may be related to morphological or physiological constraints on the size of the first-laid egg (e.g., Parsons 1976, Leblanc 1987, Arnold 1991). Hence, no adaptive hypothesis seems necessary to explain intra-clutch variation in egg volume of Great Crested Grebes.

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PIED FLYCATCHERS PREFER TO NEST IN CLEAN NEST BOXES IN AN AREA WITH DETRIMENTAL NEST ECTOPARASITES¹

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Key words: Ectoparasitism; hole-nesting birds; nest box studies; nest site selection; *Ficedula hypoleuca*.

Møller (1989, 1992) pointed out a number of possible artifacts in nest box studies due to the common practice of removing old nests from nest boxes. There are apparently few bird species that remove old nest material before breeding (Møller 1989). Therefore, birds choos-

ing previously used cavities for nesting could be exposed to higher levels of infestation by nest ectoparasites than birds choosing empty holes for breeding. Theory predicts that if reproductive costs due to nest ectoparasites are severe, birds should select empty cavities or remove old nest material before breeding (Møller 1989, 1992; but see Thompson and Neill 1991, Davis et al. 1994). Several studies have tested this prediction and failed to demonstrate discrimination of dirty/parasitized boxes in areas where the nest ectoparasites have few detrimental effects on birds' fitness (Thompson and Neill 1991, Orell et al. 1993, Davis et al. 1994, Mappes et al. 1994). Two studies were con-

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ducted with Pied Flycatchers (*Ficedula hypoleuca*), a common hole-nesting passerine with a wide distribution range in the Palearctic (Cramp and Perrins 1993). After finding no effect of nest box condition (dirty vs. clean) on nest box choice, or of ectoparasites on nestling growth in a northern population of flycatchers, Orell et al. (1993) hypothesized that in southern latitudes, with presumably higher abundance of ectoparasites, Pied Flycatchers could behave differently in order to avoid the detrimental effects of ectoparasitism. Here, we show that in the southern Europe, where the premise of reproductive costs caused by ectoparasites is fulfilled (Potti and Merino 1994, Merino and Potti 1995), Pied Flycatchers prefer empty, clean nest boxes over nest boxes with old nest material.

METHODS

The experiments were conducted in central Spain where Pied Flycatchers have been studied since 1984 (e.g., Potti and Montalvo 1991). There were 175 nest boxes (internal dimensions 11 × 11 × 17 cm, entrance hole 3.2 cm) in approximately 100 ha, with a mean distance between adjacent nest boxes of 25 m. Nests of Pied Flycatchers from the 1992 breeding season were defaunated in Berlese funnels for 48 hr, and then dismantled in search of other ectoparasites not obtained by this method (see Merino and Potti 1995). After this, nest material was placed, trying to reshape it in a form similar to natural nests, before the breeding season of 1993 inside 20 nest boxes, leaving two empty nest boxes between each manipulated nest box with old nest (see Table 1). The experiment was repeated in a different part of the study area in 1994, using 13 unmanipulated nests which had been left untouched over the non-breeding season (Table 1), in an attempt to simulate conditions in nature (see Møller 1989). Some of these nests had been parasitized by fleas, mites and blowflies in 1993, although we did not check for their presence before the experiment. However, we may assume that some life stages of these ectoparasites overwintered in the nest material and were present in low numbers, as supported by earlier studies (Merino 1993). In this year, only one empty nest box was available for the birds between two nest boxes with old nests.

Immediately after the arrival of males from spring migration we checked nest boxes every other day to record any change in disposition of the nest material and the progress of nest building. We considered as occupied nests those where laying began. Nest boxes occupied by tits (*Parus* spp.) were excluded from all computations. To control for between-year differences, the laying date was standardized as the deviation from the yearly mean.

Statistical tests are two-tailed. The Yates correction was applied in chi-square tests.

RESULTS

In 1993, Pied Flycatchers occupied more often empty nest boxes than boxes with old nests (Fig. 1a), although this preference was not statistically significant (*t*-test comparing an observed proportion versus that expected by chance, $t = 0.73$, 34 df, $P = 0.47$). However, many ($n = 11$, 55%) of the nest boxes where old nests had been placed were almost completely emptied, and

TABLE 1. Number (*n*) of experimental (provided with an old nest) and control (empty) nest boxes in each study year. Also shown are numbers of boxes occupied by tits (*Parus* spp.).

Nestbox	1993			1994		
	<i>n</i>	Used by tits	Available	<i>n</i>	Used by tits	Available
Experimental	20	0	20	13	2	11
Control	39	6	33	17	0	17

in another 20% of nest boxes, the nest material was partly removed.

In 1994, Pied Flycatchers rejected using nest boxes with old nests (Fig. 1a), although the availability of empty nest boxes was lower in the experimental area ($t = 2.95$, 14 df, $P = 0.01$). Only two nest boxes containing old nest material were used and both were from the late period of the laying season, one of them being a replacement clutch of a female that first chose an empty neighbor nest box and abandoned after being captured by us. No nest material was apparently removed from experimental boxes in this year.

Overall, there was a preference of Pied Flycatchers for empty nestboxes (log-linear analysis; log-likelihood $\chi^2 = 10.03$, 1 df, $P = 0.0015$) and this effect was independent of year (log-likelihood $\chi^2 = 2.43$, 1 df, $P = 0.1189$).

As effects of parasites may differ depending on breeding phenology (Merino and Potti 1995), we examined if choice of nest boxes is affected by the date of laying. When nests are divided into early and late in relation to standardized laying date (above and below the mean), there was a clear preference for empty nest boxes in the late period ($\chi^2_1 = 10.32$, $P = 0.001$), while that preference is not statistically significant in the early half of the breeding season ($\chi^2_1 = 2.19$, $P = 0.14$; Fig. 1b).

DISCUSSION

Our data demonstrate that Pied Flycatchers prefer to nest in empty nest boxes. Although studies with this passerine species in northern Europe found the opposite (Orell et al. 1993, Mappes et al. 1994), in none of them was there strong pressure by nest ectoparasites to make adaptive the choice of clean nest boxes. The opposite is true in our population, where nest-dwelling mites (Acari), blowflies and fleas have been shown to decrease nestling growth (tarsus length and mass) and survival (Merino 1993, Potti and Merino 1994, Merino and Potti 1995). Choice of a clean cavity for breeding is obviously adaptive in these circumstances (e.g., Oppliger et al. 1994, Richner et al. 1994).

Alternatively, birds seem able to ascertain whether nest boxes, either as roosting cavities (Christe et al. 1994, Merilä and Allander 1995) or breeding holes (Oppliger et al. 1994), are parasitized or not. This perceptual factor may be involved in our study in the high rate of rejection of nest boxes with old nests in 1994, and is also suggested by the fact that no nest material was removed by the birds that year. On the contrary,

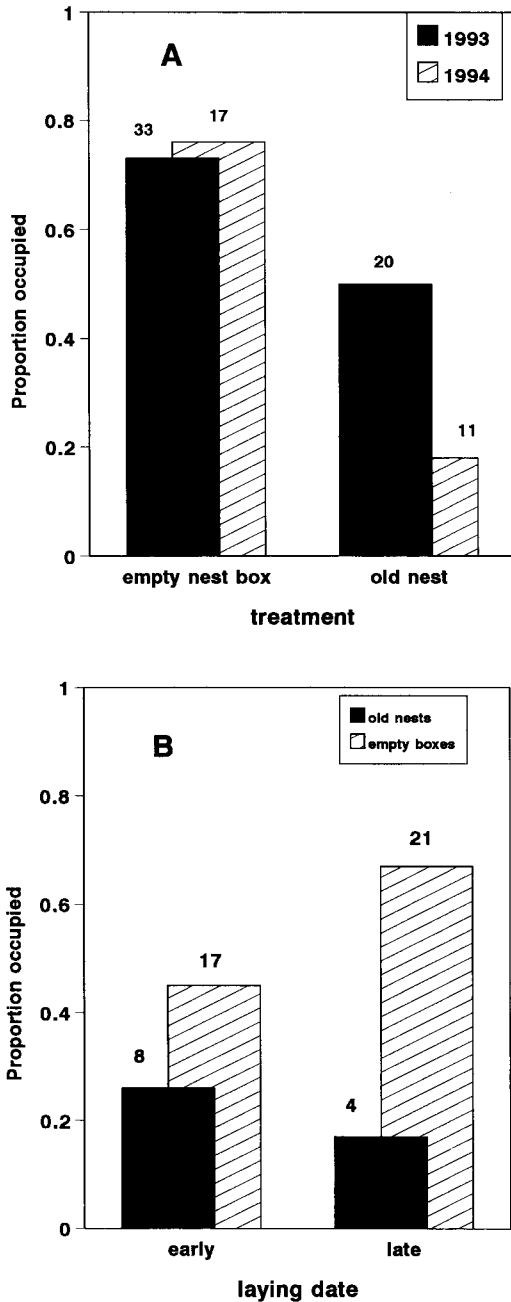


FIGURE 1. Proportion of nest boxes occupied by Pied Flycatchers in relation to (A) experimental treatment in two years; (B) lay date and experimental treatment, data from 1993–1994 combined.

old nest material was removed in at least 75% of nest boxes with old nests in 1993, maybe because that year they were not exposed to the risk of being parasitized (Thompson and Neill 1991, Christie et al. 1994). We

suspect Pied Flycatcher males removed the nest materials, although we did not witness one instance. However, we have strong evidence that male Pied Flycatcher regularly remove nest material as, contrary to females for which we lack observations, we have seen males removing nest materials in other years in nest boxes owned by other Pied Flycatcher pairs who did not complete nest-building there, and also in nest boxes disputed to Blue Tits (*Parus caeruleus*). Rejection of nest boxes with old nests in the second half of the season may be due to a stronger selection on later arrived females to choose clean available options, as occupation of dirty nest boxes prolongs the time spent building and may therefore delay start of egg laying (Mappes et al. 1994). Time constraints are important in the breeding biology of Pied Flycatchers due to a lower probability of recruitment with the advancing season (Potti and Montalvo 1991, Lundberg and Alatalo 1992). The hazards of late breeding on old nests due to the increase of some nest ectoparasite populations with the advancing season (e.g., blowflies in some years, Merino and Potti 1995) may be another factor selecting for choice of nest site.

If given a choice Pied Flycatchers exposed to reproductive costs due to nest ectoparasites in southern Europe prefer to breed in unparasitized nest boxes. Furthermore, Pied Flycatchers are capable of readily remove old nest material, at least when this is not parasitized. Møller's (1989) warnings urging ecologists to take into account nest ectoparasites when studying nest site selection, reproductive success and nestling growth, among others, are substantiated by our results. Also, our data lend support the suggestion (Orell et al. 1993) that latitudinal differences in the occurrence of harmful ectoparasites may be associated with latitudinal differences in anti-parasitic behaviors.

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MOBBING OF EASTERN SCREECH-OWLS: PREDATORY CUES, RISK TO MOBBERS AND DEGREE OF THREAT¹

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Key words: *Cultural tutoring; Eastern Screech-Owl; kin selection; mobbing behavior; Otus asio; predatory cues.*

Avian mobbing of raptorial birds is a common response to potential threat and may warn prey and teach naive individuals about the danger or deter predation (Altmann 1956; Vieth et al. 1980; Frankenberg 1981; Curio et al. 1978, 1983). Birds are important prey of Eastern Screech-Owls (*Otus asio*) in the spring nesting season (Van Camp and Henny 1975, Turner and Dimmick 1981, Gehlbach 1994); and frequent mobbers of the owls are those songbirds most often eaten, including permanent residents and males (Gehlbach 1994). Studies of screech-owls suggest that mobbing is most intense in the spring-early summer nesting period (Altmann 1956; McPherson and Brown 1981; Shedd 1982, 1983; Chandler and Rose 1988; Gehlbach 1994).

Eastern Screech-Owls sing two seasonally distinct songs (Hough 1960, Ritchison et al. 1988). Their monotonic trill is a nest-site advertisement and family-contact song, primarily while nesting in spring-early summer, whereas the descending trill is a territorial defense signal largely in late summer-fall (Gehlbach 1994). Mobbing songbirds orient to these songs and

owl nest and roost sites (McPherson and Brown 1981, Chandler and Rose 1988, Gehlbach 1994). Mobbing is often seen near active nests, where the owls do most monotonic singing and hunting, so it may be keyed to site or song. Despite such focus, fledgling screech-owls in the nest area are seldom mobbed and then only mildly, presumably because they do not kill birds (Gehlbach 1994).

If the mobbers of Eastern Screech-Owls correctly assess risk as some European birds do (Curio et al. 1983), males and permanent residents should respond to the owls' monotonic trills more often, longer, or more intensely than its descending trills, especially in the spring near nests. Also, they should mob adult owls more than fledglings. These postulates have not been tested, and some experimental variables have been confounded in the past. Earlier investigators, for example, induced mobbing with tapes of combined songs (McPherson and Brown 1981) or did not mention the song(s) they used (Shedd 1982, 1983; Chandler and Rose 1988).

Because we conducted mobbing experiments in an area where Eastern Screech-Owls and their avian prey had been studied (Gehlbach 1994), we devised very specific tests. We wanted to know if mobbers correctly assess risks of predation by recognizing certain visual (plumage, nest-site area) and auditory (song) cues with respect to the seasonal variation in these cues. Previously, this has not been possible with any raptor, nor has mobbing been tested as regards the relative jeopardy or reproductive investment of specific mobbers

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