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Effect of old nest material on nest site selection and breeding parameters in secondary hole nesters — a review

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Abstract. Hole nesting birds, due to the long lasting nature of cavities, use their nest sites for many years. Therefore, they may face the problem of the presence of nest material from previous breeding seasons. For a long time, the problem of old nest presence was not addressed in studies of this group of birds because nestboxes, a useful tool in studies of hole nesters, were cleaned by investigators, with old nests removed before each breeding season. In this review, the available results of experiments related to the effects of old nests on hole nesting birds are collected, recapitulated and discussed. The possible effects of old nests on nest site choice and breeding parameters, such as phenology, clutch size, fledging condition, as well as on ectoparasite numbers in a new nest, are presented. The findings show that studies on the problem of old nests started to be conducted mainly in the early 1990's, and to date more then thirty papers have been published related to this topic. The most frequent subjects of such studies in Europe were the Pied Flycather *Ficedula hypoleuca*, Blue and Great Tits *Cyanistes caeruleus*, *Parus major*, and European Starling *Sturnus vulgaris*, while in North America — the House Wren *Troglodytes aedon* and Eastern Bluebird *Sialia sialis*. The analysis of existing papers reveals that a majority of studies did not find any significant effect of old nest presence on nest site selection. In most papers, the presence of old nests did not influence birds' breeding parameters. Worse reproductive output in nestboxes containing old nests was found very rarely, and in particular seasons or study areas. Data on ectoparasite occurrence in relation to the presence of old nest material were presented only in a few papers. Fewer fleas were found in new nests built in artificially cleaned sites compared to sites containing old nests. The abundance of mites and blow fly larvae was not related to nestbox treatment. The results of this review suggest that there is no clear pattern of effects of old nest presence on hole nesters' breeding. It seems that the location of the study area, which influences the time available for birds' reproduction, is especially important for migratory species, and the impact of the ectoparasites dominating in a given study area may influence obtained results. This paper also suggests the direction of future work in this topic. Of most importance are studies carried out in natural tree holes, as the decomposition rate of old nest material could be much higher in such cavities than in nestboxes, and studies providing detailed descriptions of the costs and benefits of nest site cleaning behaviour of the birds themselves.

Key words: cavity nesters, hole nesting birds, old nests, nest site cleaning behaviour, reuse, ectoparasites, nestboxes

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INTRODUCTION

A nest is a structure built by birds for egg-laying, incubation and chick-rearing. It is abandoned after the young fledge. Its preservation in good condition to the next breeding season depends on the disintegration and decomposition rate, which is due, for example, to atmospheric factors, fungi, bacteria, etc. Some birds, especially those that are long-lived, build large nests, use them over a long time, repairing and enlarging them, etc. Among small birds, the relatively frequent utilization of old nests is observed in swallows and martins, due to the long lasting nature of their mud structures (e.g. Barclay 1988, Gauthier & Thomas 1993). Other passerine birds, which build open-cup nests, most often construct a new nest every year. But recent data show that, in some cases, these birds also may reuse old nests both during the same season as well as in consecutive breeding seasons (e.g. Cavitt et al. 1999, Friesen et al. 1999, Wysocki 2004). Utilising an entire old nest or its parts is most often connected with saving time needed for nest building (e.g. Gauthier & Thomas 1993), enabling, for example, earlier egg laying (e.g. Conrad & Robertson 1993, Cavitt et al. 1999, Antonov & Atanasova 2003).

A different situation is seen in the case of secondary cavity nesters, because the nest site — a tree hole (or nestbox) — is not synonymous with the nest itself built by the bird. It seems that there is a shortage of nest sites for cavity nesters in many ecosystems, and strong competition may take place (e.g. Newton 1994). As a result, birds are forced to frequently reuse holes. Besides, about 35% of such cavities may be reused each year, even in areas where tree holes are abundant (Sedgwick 1997, Wesołowski 2006). The tree cavities used for nest sites are generally deep, thus birds may build several nests one on top of another. Hence, hole nesting birds may face the problem of the presence of old nests from previous seasons at their nest sites.

Tree holes are hard to access, making studies of them difficult. As a result, the majority of studies on cavity nesters are carried out with the help of nestboxes. These artificial nest sites were made to attract and increase the number of insectivorous birds in forests and orchards (Campbell & Lack 1985). Many species readily accept them, and so they became an excellent tool for studies of this group of birds, allowing a great amount and variety of data to be gathered (Campbell & Lack 1985).

Old nests from previous seasons are most often removed by researchers in studies conducted with the use of nestboxes, probably because it was assumed that such old material may negatively influence bird reproduction. This practice became so common that it was often not even mentioned in descriptions of study methods. Møller (1989) was the first who brought this lack of important information to the attention of the scientific community. However, it seems that old nests present in nest sites do not always negatively affect breeding birds. Sometimes there are benefits to using old nests.

There are several hypotheses attempting to explain the behaviour of old nest reuse (e.g. Cavitt et al. 1999). Most of them are related to open-cup nesting birds, and are not suitable for hole nesters. However, there are at least four sets of issues explaining possible influences the presence of old nests may have on the breeding biology of cavity nesters (Table 1):

1. Old nests increase the pressure of ectoparasites and pathogens. Various groups of ectoparasites may find good conditions to develop and over-winter in nest material remaining in nest sites between seasons or breeding attempts. Therefore, their abundance in a new nest built on old material could be much higher than in the sites without such an old nest (e.g. Rendell & Verbeek 1996a). Ectoparasites may then attack new owners of a cavity and their nestlings, weakening them both, directly by blood sucking, as well as indirectly by transferring various pathogens (e.g. Proctor & Owens 2000).

Additionally, an old nest is very frequently covered by the faeces of nestlings from previous seasons, or of the birds roosting there during winter. It may also contain dead nestlings, etc. All these factors may act as a good ground for bacteria and other pathogen development, which may infect a new host or its nestlings.

All this suggests that hole nesters may avoid sites with an old nest, and that birds' breeding parameters could be worse in nests built in cavities with old nest material in comparison with sites lacking an old nest.

2. Old nests increase the pressure of predators. Most cavity nesting bird species build their nests one on top of another. Thus, the presence of an old nest leads to shallower nest sites, and decreases the distance between the hole entrance and eggs/nestlings. This so called 'danger distance' (Wesołowski 2002) determines the ability of predators to penetrate holes, and the shorter the distance, the greater the chance that a breeding attempt may fail due to predation (e.g. Alatalo et al. 1991, Wesołowski 2002).

Assuming that the presence of an old nest increases ectoparasite pressure, Møller (1989) also suggests that nestlings weakened by blood sucking arthropods may beg for food louder or more intensively (see e.g. Christe et al. 1996a),

Table 1. Problems related to the presence of old nest material and their possible impact on nest site choice and breeding parameters of hole nesting birds.

Problem	old nest present	old nest absent
Ectoparasite abundance	⇑	⇓
nest site choice	avoided	preferred
breeding parameters	worse	better
Predator pressure	⇑	⇓
nest site choice	avoided	preferred
breeding parameters	worse	better
Investments in nest building	⇓	⇑
nest site choice	preferred	avoided
breeding parameters	better	worse
Information about the site	+	—

which may reveal the nest site to predators, leading to breeding failures. It was found that adult birds compensate ectoparasite pressure by increasing the number of their trips with food for nestlings (e.g. Bouslama et al. 2002, Bańbura et al. 2004), which can also reveal nests to predators, as well as expose adult birds to predators (e.g. Lima & Dill 1990, Martin et al. 2000).

Nevertheless, all this suggests that the presence of an old nest in the nest site may directly enhance predation. On the other hand, the presence of an old nest may indicate that the site had been already used at least once during a breeding season. Some predators may remember sites where they forage and visit them from time to time, so using a site that has existed for some time may also increase the probability of brood failures (Sonerud 1985, Nilsson et al. 1991, Sorace et al. 2004).

In such a case, birds' reactions may be manifested in nest site choice — holes containing old nests should be avoided, and breeding success should be higher in sites without old nests.

3. Old nests serve as an informative cue for breeding birds. Hole nesting birds are unable to assess predation risk for new, unknown nest sites (e.g. Pöysa et al. 2001). Predators plundering broods leave behind characteristic evidence of their activity to the structure of nests in holes (e.g. Walankiewicz 2002). Therefore, the presence of an old nest with signs of successful fledging could help birds assess the quality of sites and territories (Erckmann et al. 1990, Olsson & Allander 1995). This is especially important for migratory birds, which have a shorter time for territory and site evaluation before the commencement of breeding. In this situation, the presence of old nests mostly influences nest site choice.

4. Time and energy savings and other benefits during new nest building. As the total amount of nest material used may influence the breeding results of hole nesters (e.g. Alabrudzińska et al. 2003), for instance, due to better thermoinsulation or better water absorption in the cavity (Wesołowski et al. 2002), the presence of old nest material could benefit birds. Those pairs of hole nesters that are able to reuse old material may build nests more quickly. In this way, they would save time or energy, and invest those saved resources for the later stages of the same reproductive attempt (Reid et al. 2000).

Thus, this factor may lead to both a preferences for sites with old nest material and better reproduction results.

While considering all these sets of issues, it seems that the presence of old nest material in nest holes may impose both the costs as well as benefits on birds breeding in such sites, which can be manifested later in various aspects of their breeding biology. Møller (1989) assumed that old nests influence birds only negatively. However, it seems that they should be also considered as a factor capable of providing some benefits for birds.

In the last decade, several papers have been published on the presence of old nest material in nest sites and its effect on the breeding biology of hole nesters, as well as on the abundance of ectoparasites in these nests. The aim of this paper is to collect, recapitulate and discuss all those studies and their findings. In this presentation, the problem of the presence of old nests in nest sites is considered in two ways. First, as nest material remaining from a previous breeding season and its influence on birds' decisions and breeding parameters in a current season, and second, as material from the same season, because the nest from the first breeding attempt could be treated as an old nest with regard to consecutive broods in the same season.

MATERIAL AND METHODS

I searched ISI Web of Science data base for papers that cited Møller's work (1989) on the problem of old nests, as well as by using keywords. In addition to the phrase 'old nest(s)' and 'hole' or 'cavity', I also used 'dirty nestboxes' and 'clean nestboxes', because such terms are very frequently used in descriptions of experiments with nestboxes that either contain or lack old nests respectively. Using similar keywords, I searched for papers in the SCOPUS and SORA (Searchable Ornithological Research Archive) databases. Some papers published earlier, before 1996, were gathered during my studies about the impact of ectoparasites on hole nesters. To ensure that I did not miss any important paper published earlier, I searched Zoological Abstracts. However, 'old nest' was not found in the index, and using the index I also was unable to locate papers that I already knew, so I did not use this source. As a result, it is possible that a few papers published in local journals were not included in this review. However, this is rather unlikely because it seems that at least some of those papers would have been cited in other published studies. To be certain that all available information was reviewed, I went through monographs of particular species of hole nesters in 'The Birds of the Western Palearctic' (Cramp & Perrins 1993, 1994) and 'The Birds of North America' (Poole & Gill 1993–2000).

During the analysis of all papers found, I excluded those concerning rather nest site fidelity problems than old nest presence itself (Aviles et al. 2000), and those on the presence of old nests on nest building during autumn courtship (Pinowski et al. 2006). Several papers focused only on the behaviour of old nest removal by birds were also not considered either, because they did not present the birds' breeding parameters in relation to the presence of the old nest nor to this behaviour (e.g. Marples 1936–37, Kessel 1957, Feare 1984).

RESULTS

I found 31 scientific papers presenting the results of investigations on the effects of old nest material on various aspects of hole nesting birds' breeding biology. Only several publications mentioned the problem of old nest in the title, and almost all of them used nestboxes, with the single exception of a paper describing the fate of old nest material in natural tree cavities (Wesołowski 2000).

Among the papers found, only two were published before 1989, both presenting nestbox occupation in relation to the presence/absence of a nest from a previous breeding season (Jackson & Tate, 1974, Alerstam 1985 after Lundberg & Alatalo 1992). However, these studies were not experiments about the effect of old nest presence, and the way the results were presented caused some problems with their interpretation. Most papers concerning the presence of old nests in nest sites appeared during the 10 years after Møller's (1989) paper was published. Such studies were conducted mostly in Europe at the beginning of this period, and later in North America (Fig. 1).

In the analyses of the effects of old nest presence on hole nesting birds, 12 species were studied in great detail. They were mostly small passerines, with only one non-passerine, the Wood Duck *Aix sponsa* (Utsey & Hepp 1997). In Europe, mainly the Pied Flycatcher *Ficedula hypoleuca*, the Great and Blue Tits *Parus major*, *Cyanistes caeruleus* and the European Starling *Sturnus vulgaris* were studied, whereas in North America, the species investigated included the House Wren *Troglodytes aedon*, Eastern Bluebird *Sialia sialis*, Prothonotary Warbler *Protonotaria citrea*, Tree Swallow *Tachycineta bicolor*, Purple Martin *Progne subis* and Wood Duck *Aix sponsa*. However, only a few of them were studied more frequently and in several locations of their breeding range (Table 2). Nestbox occupation in a consecutive season only after removal of an old nest is mentioned for a few other species (e.g. *Aegolius acadicus*, *A. funereus* — Cannings 1993, Hayward & Hayward 1993), however, more detailed studies about this issue are lacking for these birds. Similar anecdotal information also could be found for the Ash-throated Flycatcher *Myiarchus cinerascens* and Western Bluebird *Sialia mexicana* (Loye & Carrol 1998).

Among the papers published thus far, those concerning nest site choice predominate. Far fewer papers compare other breeding parameters of birds nesting in sites without old nests, i.e. artificially cleaned by investigators, and those containing old nest material from a previous breeding season.

Nest site choice

Almost all papers already published were about the effects of old nests remaining in nest sites after previous breeding seasons. Only three papers studied the impact of a nest from the first breeding attempt on nest site choice in successive broods of the same season (Gowaty & Plissner 1997, Stanback & Dervan 2001, Stanback & Rockwell 2003). Also, only one paper presented how preferences for nest sites with/without old nests may change over several consecutive seasons (Loye & Carrol 1998).

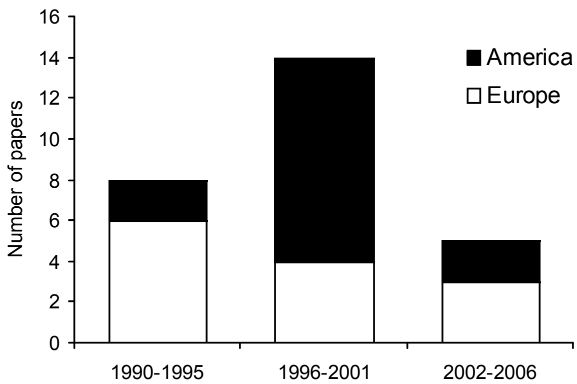

Fig. 1. Number of papers concerning old nests and hole nesting birds published in 1990–2006.

Results of at least 16 planned experiments aimed to determine preferences for nest sites with/without old nest material from a previous season have been published thus far. Two of them (Jackson & Tate 1974, Kozłowski 1992) present only results without describing the experimental procedure, and the results were obtained during the course of conducting other studies. Therefore, these findings should be treated with some caution.

Clear preferences for nest sites without old nests were found in only in four cases, while in five — for sites that contained nest material from a previous breeding season (Table 2). Therefore, the majority of such studies conducted thus far have not found any relationship between the presence/absence of old nest and birds' nest site choice (Table 2). It is a bit surprising that no consistent pattern exists even in a single species. Pied Flycatchers in Scandinavia preferred nest sites that contained old nests, whereas in Spain, the same species more frequently bred in nestboxes without old nests (Table 2). In one paper, Starlings' preferences for clean nest sites were found, whereas in others, such preferences were not observed (Table 2).

However, a detailed analysis of the methods used during experiments which found preferences for nest sites without old nests revealed that such studies were not constructed properly. Nestboxes used in such comparison studies had the same internal dimensions as well as entrance diameter, some of them contained old nests, but the rest were cleaned by investigators who removed old nests. By doing so, the latter nestboxes were made effectively deeper (Fig. 2). Thus, such experiments tested not only the effect of old nest presence itself tested, but primarily possible preferences for deeper sites. Thus, it is difficult to draw any reasonable conclusions from such experiments. In the European Starling, for whom an avoidance of sites with old nest material was found in similar experiments, an additional experiment controlling for nest site depth revealed no preferences in relation to presence of old nests (Mazgajski 2003). Two similar types of experiments were carried out on Tree Swallows, but only the results of the first were presented, when nest site depth was not taken into consideration (Rendell & Verbeek 1996b). Therefore, one cannot determine what choice the birds would make if the effective depth were the same between sites where old nests were present or not.

Table 2. Effect of old nest material on nest site choice of hole nesting bird species. – — avoidance of sites with old nests, + — preferences for sites with old nests, 0 — no clear preferences.

Species	Study area	Nest site choice	Source
Ficedula hypoleuca	Spain	–	Merino & Potti 1995
	Sweden	0	Olsson & Allander 1995
	Sweden	0	Alerstam after Lundberg & Alatalo 1992
	Sweden	+	Mappes et al. 1994
	Sweden	+	Olsson & Allander 1995
	Finland	+	Orell et al. 1993
Parus major	Switzerland	0	Oppliger et al. 1994
	Finland	0	Rytkönen et al. 1998
Cyanistes caeruleus	Poland	–	Koz³owski 1992
	Spain	0	Tomás et al. 2007
Parus sp.	Sweden	0	Olsson & Allander 1995
Sturnus vulgaris	Poland	–	Mazgajski 2003
	Poland	0	Mazgajski 2003
	Poland	0	Koz³owski 1992
	Netherlands	0	Brouwer & Komdeur 2004
Passer montanus	Poland	0	Koz³owski 1992
Passer domesticus	Poland	0	Koz³owski 1992
Tachycineta bicolor	Canada	–	Rendell & Verbeek 1996b
Progne subis	USA, Canada	0	Jackson & Tate 1974
Troglodytes aedon	Wyoming, USA	0	Johnson 1996
	Kentucky, USA	0	Thompson & Neil 1991
	Illinois, USA	+	Pacejka & Thompson 1996
Sialia sialis	Kentucky, USA	+	Davis et al. 1994
Protonotaria citrea	Virginia, USA	0	Blem et al. 1999

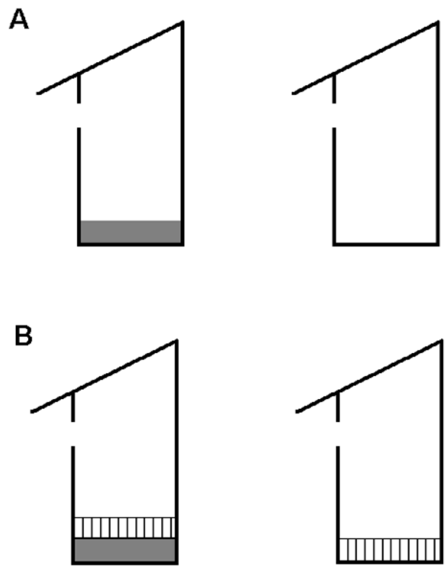

Fig. 2. Effects of an old nest on the effective nestbox depth (A) and the 'danger distance' (B). Grey — old nests, striped - new nests.

In Tree Swallows as well as in Blue Tit, it was found that choosing nest sites with or without old nests was not related to the age of females, which could be connected with intraspecific competition (Rendell & Verbeek 1996b, Tomás et al. 2007), although for the Purple Martin, Hill (after Brown 1997) suggested that older females may prefer nest sites with old nests, which could be related to fidelity for their own previous nest sites.

Only one study investigated how old nests may influence nest site choice over a longer time perspective. The nest site choice of three hole-nesting species analysed together (Ash-throated Flycatcher, Western Bluebird and Tree Swallow) in the second year of nestbox existence was not related to the presence of old nests. However, in the following year — the third year after the nestboxes were hung — these bird species significantly avoided sites that contained old nests after two seasons when nestboxes were not cleaned. Similar results were obtained when Western Bluebird data were analysed separately (Loye & Carrol 1998).

The effect of the nest from a first brood on the next breeding attempt in the same season was studied in a greater detail only for the Eastern Bluebird. Gowaty & Plissner (1997) did not find any clear preference or avoidance of nestboxes containing the nest from a previous breeding attempt within the same season. However, two other papers (Stanback & Dervan 2001, Stanback & Rockwell 2003) revealed that such sites were avoided by this species.

Four papers were found reporting results of experiments that determined if birds' preferences for nest sites are connected with the presence of an old nest itself or the ectoparasites occurring in them (Orell et al. 1993, Oppliger et al. 1994, Olsson & Allander 1995, Rendell & Verbeek 1996b). In those experiments, the old nest material was heated to kill all ectoparasites and/or old nests were infected by a defined number of fleas (Siphonaptera). The results obtained are indefinite. Nestboxes containing Pied Flycatchers' old nests were more frequently used even with the additional increase of fleas in comparison with nestboxes cleaned by investigators before the breeding season (Orell et al. 1993, Olsson & Allander 1995). On the other hand, it was found that Tree Swallows preferred those nestboxes where old nest material was heat-treated (Rendell & Verbeek 1996b). Data on the Great Tit are also contradictory. Oppliger et

Table 3. Effect of old nest material on other aspects of reproduction of hole nesting bird species. 0 — no differences between sites with and without old nests, + — parameters better in nestboxes contained old nests, – — negative effect of old nests, / — results obtained in different seasons or study sites.

Species	Breeding phenology	Clutch size	Number of fledgings	Fledging condition	Breeding success	Source
Ficedula hypoleuca	0	0	0	0		Mappes et al. 1994
	+/0					Olsson & Allander 1995
Cyanistes caeruleus	0	0		0	–	Tomás et al. 2007
Sturnus vulgaris		0	0	0		Brouwer & Komdeur 2004
	–/0	–/0	–/0	0	0	Mazgajski 2007a
Tachycineta bicolor	–/0	0	0	0	0	Rendell & Verbeek 1996b
Troglodytes aedon	0	0			0	Johnson 1996
	0	0	0			Pacejka et al. 1996
	0					Thompson & Neill 1991
Protonotaria citrea	0	0			0	Blem et al. 1999

al. (1994) demonstrated that these birds preferred nestboxes without ectoparasites (fleas) independent of the presence of an old nest. However, when the birds could choose between cleaned boxes and those containing parasite-free nests, no significant preferences were found. But Ollson & Allander (1995) found no preference between cleaned nest sites, those containing infested old nests or those without ectoparasites.

Other aspects of breeding biology

The effect of the presence of old nest material on breeding aspects other than nest site choice was studied much less frequently (Table 3). In the majority of studies, no significant impact of the presence of old nest material was found on the timing of egg laying, clutch size, number of fledglings or their condition, as well as breeding success (Table 3). Only a few papers, mostly in one study area or in a single season, reported significant results. Most frequently in such cases, worse breeding parameters were recorded of pairs that bred in old nest material, although Pied Flycatchers commence egg laying earlier in such locations (Table 3). Hill (after Brown 1997) found that more young fledged from nestboxes that contain old nests only for the Purple Martin, but suggested that such results may be connected to the age differences of females breeding in nestboxes with or without old nest material.

The effect of nest removal after consecutive breeding attempts during the same season was studied only for the Wood Duck. It was found that the total number of broods, eggs laid and young fledged were highest for nestboxes cleaned after each nesting attempt (Utsey & Hepp 1997).

Nest site cleaning behaviour

It should be mentioned that a few bird species breeding in sites with old nests from previous breeding seasons were observed preparing such sites by removing old nest material. Such behaviour was observed in the House Wren (Pacejka et al. 1996), European Starling (e.g. Kessel 1957, Mazgajski et al. 2004), Pied Flycatcher (Merino & Potti 1995), and mentioned for Blue and Marsh Tits (Bailey after Olsson & Allander 1995, Wesołowski 1999), House and Tree Sparrows (Cramp & Perrins 1994, Barlow & Leckie 2000) and Eastern Bluebirds (Gowaty & Plissner 1997).

However, detailed descriptions of old nest removal behaviour are limited. It seems that it leads to increased nest site attractiveness due to 1) reduced ectoparasite load, 2) deepened nest sites, thereby improving the 'danger distance'. Studies of the House Wren have shown that old nest removal by these birds may decrease the number of ectoparasites (e.g. Pacejka et al. 1996). Similar data for European Starling are indefinite (own data), but the amount of old nest material removed was connected with nest site depth, and birds that bred in shallow nest sites removed more material (Mazgajski et al. 2004).

All these studies and anecdotal observations related to birds nesting in sites containing old nests from a previous breeding season. No studies were conducted to determine whether these birds remove old nest material before making another breeding attempt in the same season. The costs and potential benefits of such behaviour also have not been evaluated yet.

Table 4. Relations between old nests presence and abundance of various groups of ectoparasites in new-built nests. 0 — no relation, + — larger number of parasites in sites without old nests, – — larger number of parasites in nests built on old nest material, * — all mites found in nests were taken into consideration.

Species	Fleas (mostly *Ceratophyllus* sp.)	Mites (mostly *Dermanyssus* sp.)	Blow fly *Protocalliphora* larvae	Source
Ficedula hypoleuca	0			Olsson & Allander 1995
	+			Mappes et al. 1994
Parus major	0			Allander 1998
Cyanistes caeruleus	0	0	0	Tomás et al. 2007, pers comm.
Sturnus vulgaris	–	–*		Mazgajski 2007a
		–		Brouwer & Komdeur 2004
Tachycineta bicolor	–	0	0	Rendell & Verbeek 1996a
Troglodytes aedon		0	0	Pacejka et al. 1996
			0	Johnson 1996
Protonotaria citrea		0*		Blem et al. 1999

Presence of ectoparasites and other pathogens

The frequency of occurrence (prevalence) and abundance of ectoparasites in nests built on old nest material from previous breeding seasons and in cleaned nest sites was compared relatively rarely. For a long time, it was assumed that ectoparasites can develop and over-winter in old nest material, and infect and feed on new hosts later in the breeding season — both adult birds as well as their nestlings. Therefore, it was expected that sites without old nests should have a lower number of ectoparasites compared to nests built on old material. However, the number of studies testing this assumption is low. Only a few of the published papers analysed reported that the number of blood sucking fleas and mites was found lower in sites where old nests were removed by investigators (Table 4). Opposing results were presented in one paper — the number of fleas was greater in nests built in cleaned sites (Mappes et al. 1994). However, the abundance of *Protocalliphora* blow fly larvae in nests was not related to the presence/absence of an old nest in the sites (Table 4).

This is related to the life histories of ectoparasites and their host finding behaviour. Fleas over-winter most often as cocoons in old nest material, emerge in early spring, and very frequently wait for a bird host at the hole entrance (Humphries 1968, du Feu 1982). Mites may occur in old nest material also (Rendell & Verbeek 1996a), although clear data on their abundance in nest sites with/without old nest material are rare (Table 4). Flies and their larvae appear only after the nest sites are occupied, although Loye & Carrol (1998) suggested that fly imagines also remained in close proximity to sites used by birds, as well as the flies, in the previous season.

One would assume that the abundance of ectoparasites should increase in successive broods, but no studies have investigated old nest presence from the same season's first breeding attempt in relationship to parasite load. Sometimes the number of ectoparasites is provided from nests after a second brood has used them, but we do not know whether the nestbox was cleaned after the first brood, as this information is not provided in the description of methods (e.g. Gwinner & Berger 2005). Other pathogens have not been considered yet. One study investigated the occurrence of bacteria in old nests of the House Wren (Singelton & Harper 1997), but made no comparison to sites cleaned by researchers.

DISCUSSION

Hole nesting birds very frequently use the same breeding site multiple times (e.g. Sedgwick 1997, Wesołowski 2006, Mazgajski 2007b). Therefore, birds reusing the same cavity every year have to address the problem of the presence of old nests from previous seasons. However, despite the potential importance of this problem for knowledge of hole nesters' ecology and the evolution of this particular breeding strategy, my review indicates that this aspect of birds' breeding ecology has not been studied in great detail. Hole nesting species constitute 4–5% of the entire avifauna both in Europe and North America (Newton 1994), and are very frequently the object of studies. Møller's paper (1989), bringing the practice of neglecting to report the removal old nests in studies using nestboxes to the attention of researchers as a factor potentially influencing results, was very frequently cited. Over 80 papers published between 1996–2006 (data from the ISI Web of Science) cited this work, but still the effect of old nest presence on various aspects of hole nesters' breeding biology remains almost unknown.

The hypothetical costs and benefits of reusing nest sites with a previous season's old nest were briefly presented earlier (cf. Table 1). Thus far, it was commonly believed that the presence of old nests affects birds negatively. However, this review of published papers does not confirm this view (cf Tables 2, 3).

Most papers did not find that nests from previous breeding seasons in the nest site significantly affect birds' nest site choice or breeding parameters. It may be that the main costs related to old nests mentioned earlier, i.e. increased ectoparasite and predator pressure, was not high, or was even decreased by the experimental procedures used. In studies where old nests were heat-treated, birds were found avoiding ectoparasites, and not the nest material itself (Oppliger et al. 1994, Rendell & Verbeek 1996b, but Orell et al. 1993). However, several other studies demonstrated that ectoparasite abundance did not differ between nests built in sites with or without an old nest (Table 4). Apart from this, birds themselves may be evaluating the level of infestation, and avoiding nest sites with a high abundance of ectoparasites (du Feu 1982, Brown & Brown 1986, Loye & Carroll 1991). Thus, the costs of breeding on old nest material as it relates to the presence of ectoparasites would be not so high and controlled by birds. This could explain why it was often not confirmed that the numbers of ectoparasites occurring naturally (not manipulated experimentally) influenced the breeding biology or nestling condition of this bird group (see e.g. review in Mazgajski & Kędra 1997).

In the past (Møller 1989, Hansell 2000), the suggestion that old nest reuse or the presence of an old nest in a nest site should affect birds negatively was always related to ectoparasite pressure. However, precise data describing ectoparasite abundance are rare, and do not confirm this assumption (Table 4). This is why one encounters many explanations in the literature on the lack of an increase of ectoparasite abundance in sites with old nests. First, it is possible that the general number of ectoparasites in birds' nests is relatively low when nest sites are chosen and first broods occur, which are the circumstances most often studied. This could be due to the annual cleaning of nestboxes or the hanging of new ones for the experiments, thus ectoparasites have not managed to multiply in large numbers. Loye & Carrol (1998) suggested that it takes several years for ectoparasites to increase to an abundance that could significantly affect birds negatively.

Second, researchers themselves suggest that old nest removal and nestbox cleaning may not reduce ectoparasite numbers, as many may hide in various crevices of the nestbox (e.g. Rytkönen et al. 1998). This explanation seems rather incorrect, because similar results are found when comparing the number of fleas in European Starling nests in cleaned nestboxes and those newly hung just before the breeding season (Mazgajski 2007a).

Third, it may be that a separate ecosystem develops in the old nest, where the rich fauna of various predators belonging to different animal group live and forage on birds' ectoparasites. Davis et al. (1994) suggest that such organisms could be *Nasonia* wasps. Very frequently, zoophagous Coleoptera from the Staphylinidae and Histeridae families and Salticidae jumping spiders could be found in nestbox nests, and it is suggested that they forage on the avian ectoparasites in great abundance there (Kaczmarek 1991, Pacejka et al. 1996).

Fourth, probably the number as well as pressure of ectoparasites may depend on the birds themselves, in their behaviour of finding and destroying parasites (see e.g. Christi et al. 1996b), or removing old nest material (e.g. Pacejka et al. 1996). It is possible that bringing "green" material to the nest, observed in many species, occurs to control ectoparasites and other pathogens (e.g. Clark 1991, Bańbura et al. 1995, Lafuma et al. 2001, Gwinner & Berger 2005). It should also be remembered that the negative effect of ectoparasites may be compensated by adult birds, for example, by increasing parental expenditures (e.g. Bouslama et al. 2002, Bańbura et al. 2004).

A detailed analysis of the study methods used showed that experiments finding a preference for clean nestboxes had errors in their design. The preferences found there could also be due to the birds' choosing deeper nest sites, thereby avoiding predator pressure. It seems that determining the costs of using nest sites with old nests related to the potential increase of predation cannot be appropriately evaluated in nestbox studies, because the boxes themselves are primarily aimed at improving the safety of the birds nesting there. Besides this, potential predator pressure was often completely eliminated in studies conducted to date by the techniques used in hanging boxes (on smooth metal poles) and protecting them with predatory guards, making access very difficult (Rendell & Verbeek 1996a, Utsey & Hepp 1997, Blem et al. 1999). This may be why no differences were found in the breeding success of birds using boxes with old nest material and those using cleaned nestboxes (cf Table 3).

To date, the presence of old nest material was considered a negative factor affecting birds' breeding, so investigators looked for the costs related to such nest site choice. No possible benefits were considered. Only Davies et al. (1994) suggested that the preference for nestboxes containing old nests found for the Eastern Bluebird may be connected with savings in time and energy when building nests. Similar benefits could be considered for other species, because it was found that birds may react to nest site depth by building smaller nests in shallow locations (own data for the Great Tit), as well as on old nests (Rendel & Verbeek 1996b for the Tree Swallow). Also, Olsson & Allander (1995) found earlier egg laying in nestboxes containing old nests. As nesting phenology in many species may influence clutch size and fledgling number (Wiggins et al. 1994, Barba et al. 1995, Smith 2004, Lahlah et al. 2006), such earlier commencement of laying could be beneficial to birds.

It seems that the presence of old nest material should be considered in terms of both costs and benefits for birds, as well as which of these prevailing factors may affect the study results obtained. In one of the first papers on the problem of old nest presence in nestboxes, Thompson & Neil (1991) suggested that the negative effect of ectoparasites could be compensated by the quality of a site, indicated by the presence of an old nest. Thus, the costs and benefits related to old nest presence may counteract each other, and the reason why results obtained to date in the published papers could not be arranged in any pattern.

At this moment it does not seem possible to provide one or several factors that specifically explain all the results obtained so far, because no single pattern of behaviour has been observed even within one species.

Based on the meagre existing results, it may be that hole nesters' reaction to breeding sites containing old nests depends on specific populations, the type of environment created by the old nests, the predominating group of ectoparasites inhabiting the nest, etc.

Also other factors, such as latitude and duration of breeding season, may influence nest site choice, as completely different decisions must be made by migrant birds breeding in high and low latitudes. The results obtained for the Pied Flycatcher may indicate that for birds with less time for breeding, nest site safety is more important, even if heavily infested with ectoparasites (Orell et al. 1993), as this does not negatively influence nestling growth (e.g. Orell et al. 1993, Eeva et al. 1994).

It cannot be excluded that the preference for sites containing old nests demonstrated so far may be at least partially related to birds' preferences for their own nest sites from previous seasons. It is known that birds change nest sites after a breeding failure, and tend to return to those where their young were raised successfully (e.g. Gowaty & Plissner 1997, Winkler et al. 2004). A preference for a site with the nest from a first breeding attempt of the season especially could be explained by nest site fidelity (Gowaty & Plissner 1997, Stanback & Dervan 2001). Thus, the informative function mentioned as a potential benefit of using a nest site with an old nest from the previous season (Olsson & Allander 1995) could be partially related to nest site fidelity. Also, attachment to its breeding site from the previous season is used to explain the Purple Martin's preference for nestboxes containing old nests, as well as its better breeding success in such nestboxes, as the return rate is observed for older individuals, which achieve better breeding parameters (Hill after Brown 1997).

At the end of this review, it should be mentioned that almost all the data published thus far on the effects of old nests on hole nesting birds were gathered from studies using nestboxes. As breeding parameters, especially clutch size and breeding success, differ between birds using tree holes and nestboxes (e.g. Kuitunen & Aleknonis 1992, Mitrus 2003, Czeszczewik 2004), it should be asked whether the problem of old nest presence also occurs in natural cavities.

Old nests in tree holes. It was found that the material of old nests in natural holes partially or completely decomposes between two consecutive seasons (Wesołowski 2001). However, this study was carried out in a primeval forest, with a high number of saprophytic fungi and other organisms that break down such material. More analogous data are needed to determine if this is a typical pattern for every forest type, as well as to establish the factors influencing the rate of old nest material decomposition. In holes excavated by woodpeckers and used later by other secondary cavity nesters, it seems that the large amount of old nest material of starlings or tits remains there until the new season starts (own data), so even the origin and size of a cavity may influence the decomposition rate of an old nest.

On the other hand, a few species developed the behaviour of removing old nest material, and observations of empty, clean holes noted just before breeding began may be connected with such behaviour (see Wesołowski 2000). However, it should be noted that this behaviour evolved, as birds have had to address the problem of old nest material presence during nest preparation for a very long time.

Old nest material removal has mostly been recorded for the European Starling, House Wren and Pied Flycatcher (e.g. Kessel 1957, Merino & Potti 1995, Pacejka et al. 1996). These species build their nests with dry leaves and grasses, materials that are harder and decompose to a lesser degree in natural holes (Wesołowski 2000). It may be that the material itself used for nest building caused such nest site cleaning behaviour to develop, and at the same time indicates that old nest material present in potential nest sites should be considered an important factor in birds' life histories.

FURTHERS STUDIES

The summary of the existing data on old nests and hole nesters indicates that the problem has still not been precisely investigated, despite the many papers published over the last 15 years.

It is curious that, despite the relative ease of conducting such experiments, many species have not been studied more frequently or in additional areas of their range.

As it has been suggested that the frequency of blood parasitism and birds' immunological responses may be related to geographic location (e.g. Merilä et al. 1995, Møller et al. 2006), a similar situation may be occurring in birds' reactions to old nests and the ectoparasites inhabiting them. Also, the situation of migratory species nesting at low and high latitudes differs, which may be related to the time allotted to find nest sites and breed, and may additionally affect nest site choice.

It's a bit surprising that in Europe, more studies have not been conducted on how such abundant hole nesters, like the Blue Tit, House or Tree Sparrow, react to the presence of old nests. Neither more detailed studies have been conducted of the Purple Martin, though this was suggested more than 30 years ago (Jackson & Tate 1974).

Improving nest site attractiveness by removing old nests or other debris from nestboxes is mentioned for a few species (Cannings 1993, Hayward & Hayward 1993), but no detailed results are quoted. It is also surprising that so few studies on the problem of old nests were conducted for the same breeding season.

Many reservations can be had about how the experiments were conducted thus far. As a result, part of the results obtained may indicate not so much a preference or avoidance of sites with old nests, but rather a choice made based on appropriate size. A correctly designed experiment on the influence of the presence of old nest material must be carefully prepared, with many variables controlled, such as nest site depth or number of ectoparasites. In such studies, it is quite simple to control for nestbox depth, and perhaps also to try to control parasite numbers, if not by infesting the nest with a constant number, then at least by submitting old nests to heat-treatment.

Further studies should not only record such parameters as nest site choice, clutch size, number of fledglings or their condition, but also other data should be considered, such as adults' age and/or condition. These could be indirectly determined by nest weight (Tomas et al. 2006), or number of feeding trips. Also, studies on the effect of old nest presence should be carried out over several years, because the attractiveness of a site may change from season to season (Loye & Carrol 1998). Some costs or benefits of using sites with or without an old nest in one season may be manifested in the adult birds' return rate or survival in the next season.

Little is known about birds' nest site cleaning behaviour itself. We do not know if this is an activity undertaken every year during nest site preparation, or only in some specific circumstances. Almost no data are available about why such behaviour is exhibited, what the impact is of nest site cleaning on current and future reproduction, or on the fitness of the birds involved. For many species, anecdotal information about removing of old nest material could be found (e.g. Cramp & Perrins 1994), but requires verification by intentional observations.

Another issue concerns the fate of old nest material found in natural cavities or holes excavated by woodpeckers. Studies on the decomposition rate of nest material should be carried out more frequently and in various types of tree stands, which would enable researchers to determine the extent to which such data could be useful in studying the problem of old nest presence in nestboxes (see also Wesołowski & Stańska 2001). It should be noted that the decomposition rate of nest material in nestboxes is also unknown, though cellulolytic and keratinolytic fungi have been found in nestbox nests very frequently (Hubalek et al. 1973).

The problem presented here may stimulate further studies, which could lead to understanding these aspects more fully in terms of the evolutionary ecology of hole nesting birds. Clear information on how old nests from previous breeding seasons may influence the current reproduction of birds could be important, not only for the study and protection of hole nesters, but also from an economic point of view. Nestboxes frequently hung in woods and forests are later cleaned every year at considerable financial outlay. Future study results may show that cleaning boxes every second year may suffice, or for particular species, not cleaned at all, potentially leading to saved funds that could be spent on other activities for bird or environmental protection.

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REFERENCES

Alabrudzińska J., Kaliński A., Słomczyński A., Wawrzyniak A., Zieliński P., Bańbura J. 2003. Effects of nest characteristics on breeding success of Great Tits *Parus major*. Acta Ornithol. 38: 151–154.

Alatalo R., Carlson A., Lundberg A. 1991. Polygyny and breeding success of Pied Flycatcher nesting in natural cavities. In: Blondel J., Gosler A., Lebreton J-D., McCleery R. (eds). Population biology of passerine birds. Springer, Berlin Heildelberg, pp. 323–330.

Allander K. 1998. The effects of an ectoparasite on reproductive success in the great tit: a 3-year experimental study. Can J. Zool. 76: 19–25.

Antonov A., Atanasova D. 2003. Re-use of old nests versus the construction of new ones in the Magpie *Pica pica* in the city of Sofia (Bulgaria). Acta Ornithol 38: 1–4.

Aviles J. M., Sanchez J. M., Parejo D. 2000. The Roller *Coracias garrulus* in Extramadura (southwestern Spain) does not show a preference for breeding in clean nestboxes. Bird Study 47: 252–254.

Bańbura J., Blondel J., de Wilde-Lambrechts H., Perret P. 1995. Why do female Blue Tit (*Parus caeruleus*) bring fresh plants to their nests. J. Ornithol 136: 217–221.

Bańbura J., Perret P., Blondel J., Thomas D. W., Cartan-Son M., Lambrechts M. M. 2004. Effects of *Protocalliphora* parasites on nestling food composition in Corsican Blue Tits *Parus caeruleus*: consequences for nestling performance. Acta Ornithol. 39: 93–103.

Barba E., Gil-Delgado J. A., Monros J. S. 1995. The costs of being late: consequences of delaying great tit *Parus major* first clutches. J. Anim. Ecol. 64: 642–651.

Barclay R. M. R. 1988. Variation in the costs, benefits, and frequency of nest reuse by barn swallows (*Hirundo rustica*). Auk 105: 53–60.

Barlow J. C., Leckie S. N. 2000. Eurasian Tree Sparrow (*Passer montanus*). In: Poole A., Gill F. (eds). The Birds of North America, No. 560. The Birds of North America, Inc., Philadelphia, PA.

Blem C. R., Blem L. B., Berlinghoff L. S. 1999. Old nests in Prothonotary Warbler nest boxes: effects on reproductive performance. J. Field Ornithol. 70: 95–100.

Bouslama Z., Lambrechts M. M., Ziane N., Djenidi R., Chabi Y. 2002. The effect of nest ectoparasites on parental provisioning in a north-African population of the Blue Tit *Parus caeruleus*. Ibis 144: E73–E78.

Brouwer L., Komdeur J. 2004. Green nesting material has a function in mate attraction in the European starling. Anim. Behav. 67: 539–548.

Brown C. R. 1997. Purple Martin (*Progne subis*). In: Poole A., Gill F. (eds). The Birds of North America, No 287. The Birds of North America, Inc., Philadelphia, PA.

Brown C. R., Brown M. B. 1986. Ectoparasitism as a cost of coloniality in cliff swallows (*Hirundo pyrrhonota*). Ecology 67: 1206–1218.

Campbell B., Lack E. (eds). 1985. A Dictionary of Birds. T & AD Poyser, Carlton.

Cannings R. J. 1993. Saw-whet Owl. (*Aegolius acadicus*). In: Poole A., Gill F. (eds). The Birds of North America, No 42.. The Birds of North America, Inc., Philadelphia, PA.

Cavitt J. F., Pearse A. T., Miller T. 1999. Brown thrasher nest reuse: a time saving resource, protection from search strategy predators, or cues for nest-site selection? Condor 101: 859–862.

Christe P., Richner H., Oppliger A. 1996a. Begging, food provisioning, and nestling competition in great tit broods infested with ectoparasites. Behav. Ecol. 7: 127–131.

Christe P., Richner H., Oppliger A. 1996b. Of great tits and fleas: sleep baby sleep... Anim. Behav. 52: 1087–1092.

Clark L. 1991. The nest protection hypothesis: the adaptative use of plant secondary compounds by European starling. In: Loye J. E., Zuk M. (eds). Bird-parasite interactions: ecology, evolution, and behaviour. Oxford University Press, pp. 205–221.

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

Cramp S., Perrins C. M. (eds). 1993, 1994. The Birds of Western Palearctic. Vol. VII, VIII, Oxford Univ. Press.

Czeszczewik D. 2004. Breeding success and timing of the Pied Flycatcher *Ficedula hypoleuca* nesting in natural holes and nest-boxes in the Białowieża Forest, Poland. Acta Ornithol. 39: 15–120.

Davies W. H., Kalisz P. J., Wells R. J. 1994. Eastern bluebirds prefer boxes containing old nests. J. Field Ornithol. 65: 250–253.

Eeva T., Lehikoinen E., Nurmi J. 1994. Effects of ectoparasites on breeding success of great tit (*Parus major*) and pied flycatcher (*Ficedula hypoleuca*) in an air pollution gradient. Can. J. Zool. 72: 624–635.

Erckmann W. J., Beletsky L. D., Orians G. H., Johnsen T., Sharbaugh S., D'Antonio C. 1990. Old nests as cues for nest-site selection: an experimental test with Red-winged Blackbirds. Condor 92: 113–117.

Feare C. 1984. The Starling. Oxford Univ. Press.

du Feu C. R. 1982. How tits avoid flea infestation at nest sites. Ringing & Migration 13: 120–121.

Friesen L. E., Wyatt V. E., Cadman M. D. 1999. Nest reuse by Wood Thrushes and Rose-breasted Grosbeaks. Wilson Bull. 111: 132–133.

Gauthier M., Thomas D. W. 1993. Nest site selection and cost of nest building by cliff swallows (*Hirundo pyrrhonota*). Can. J. Zool. 71: 1120–1123.

Gowaty P. A., Plissner J. H. 1997. Breeding dispersal of Eastern Bluebirds depends on nesting success but not on removal of old nests: an experimental study. J. Field Ornithol. 68: 323–330.

Gwinner H., Berger S. 2005. European starling: nestling condition, parasites and green nest material during the breeding season. J. Ornithol. 146: 365–371.

Hanssel M. 2000. Bird nests and construction behaviour. Cambridge Univ. Press.

Hayward G. D., Hayward P. H. 1993. Boreal Owl (*Aegolius funereus*). In: Poole A., Gill F. (eds). The Birds of North America, No. 63. The Birds of North America, Inc., Philadelphia, PA.

Hubalek Z., Balát F., Toukova I., Vlk J. 1973. Mycoflora of birds' nests in nest-boxes. Mycopathologia 49: 1–12.

Humphries D. A. 1968. The host-findings behaviour of the hen flea, *Cerathophyllus galinae* (Schrank). Parasitology 58: 403–414.

Jackson J. A., Tate J. Jr. 1974. An analysis on nest box use by Purple Martins, House Sparrows, and Starlings in Eastern North America. Wilson Bull. 86: 435–449.

Johnson L. S. 1996. Removal of old nest material from the nesting sites of house wrens: effects on nest site attractiveness and ectoparasite loads. J. Field Ornithol. 67: 212–221.

Kaczmarek S. 1991. [Insects from nests of Passeriformes collected in Pomeriania]. WSP Słupsk.

Kessel B. 1957. A study of the breeding biology of the European starling (*Sturnus vulgaris* L.) in North America. Am. Midl. Nat. 58: 257–331.

Kozłowski P. 1992. [Nest-boxes as a site of bird broods in Warsaw urban park]. Acta Ornithol. 27: 21–33.

Kuitunen M., Aleknonis A. 1992. Nest predation and breeding success in Common Treecreepers nesting in boxes and natural cavities. Ornis Fennica 69: 7–12.

Lafuma L., Lambrechts M. M., Raymond M. 2001. Aromatic plants in bird nests as a protection against blood-sucking flying insects? Behav. Proc. 56: 113–120.

Lahlah N., Chabi Y., Bańbura M., Bańbura J. 2006. Breeding biology of the House Martin *Delichon urbica* in Algeria. Acta Ornithol. 41: 113–120.

Lima S. L., Dill L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68: 619–640.

Loye J. E., Carroll S. P. 1991. Nest ectoparasite abundance and cliff swallow colony site selection, nestling development and departure time. In: Loye J. E., Zuk M. (eds). Bird-parasite interactions: ecology, evolution, and behaviour. Oxford University Press, pp. 223–241.

Loye J. E., Carroll S. P. 1998. Ectoparasite behaviour and its effects on avian nest site selection. Ann. Entomol. Soc. Am. 91: 159–163.

Lundberg A., Alatalo R. V. 1992. Pied flycatcher. T. & A. D. Poyser, London.

Mappes T., Mappes J., Kotiaho J. 1994. Ectoparasites, nest site choice and breeding success in the pied flycatcher. Oecologia 98: 147–149.

Marples G. 1936–37. Behaviour of starlings at nest site. Brit. Birds 30: 14–21.

Martin T. E., Scott J., Menge C. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. Proc. R. Soc. Lond. B 267: 2287–2293.

Mazgajski T. D. 2003. Nest site choice in relation to the presence of old nests and cavity depth in the starling *Sturnus vulgaris*. Ethol. Ecol. Evol. 15: 273–281.

Mazgajski T. D. 2007a. Effect of old nest material in nestboxes on ectoparasite abundance and reproductive output in the European Starling *Sturnus vulgaris* (L). Pol. J. Ecol. 55: 377–385.

Mazgajski T. D. 2007b. Nest hole age decreases nest site attractiveness for the European Starling *Sturnus vulgaris*. Ornis Fennica 84: 32–38.

Mazgajski T. D., Kędra A. H. 1997. Are nestling of hole nesting birds affected by ectoparasites — a review. Wiad. Parazytol. 43: 347–355.

Mazgajski T. D., Kędra A. H., Beal K. G. 2004. The pattern of nest-site cleaning by European starling *Sturnus vulgaris*. Ibis 146: 175–177.

Merilä J., Björklund M., Bennett G. F. 1995. Geographic and individual variation in haemetozoan infections in the greenfinch, *Carduelis chloris*. Can. J. Zool. 73: 1798–1804.

Merino S., Potti J. 1995. Pied flycatchers prefer to nest in clean nest boxes in an area with detrimental nest ectoparasites. Condor 97: 828–831.

Mitrus C. 2003. A comparison of the breeding ecology of the Collared Flycatcher *Ficedula albicollis* nesting in boxes and natural cavities. J. Field Ornithol. 74: 293–299.

Møller A. P. 1989. Parasites, predators and nest-boxes: facts and artefacts in nest box studies of birds? Oikos 56: 421–423.

Møller A. P., Martin-Vivaldi M., Merino S., Soler J. J. 2006. Density-dependent and geographical variation in bird immune response. Oikos 115: 463–474.

Newton I. 1994. The role of nest-sites in limiting the numbers of hole-nesting birds: a review. Biol. Conserv. 70: 265–276.

Nilsson S. G., Johnsson K., Tjernberg M. 1991. Is avoidance by black woodpeckers of old nest holes due to predators? Anim. Behav. 8: 439–441.

Olsson K. Allander K. 1995. Do fleas and/or old nest material, influence nest site preference in hole-nesting passerines? Ethology 101: 160–170.

Oppliger A., Richner H. & Christe P. 1994. Effect of an ectoparasite on lay date, nest-site choice, desertion, and hatching success in the great tit (*Parus major*). Behav. Ecol. 5: 130–134.

Orell M., Rytkönen S., Ilomäki K. 1993. Do pied flycatchers prefer nest boxes with old nest material? Ann. Zool. Fenn. 30: 313–316.

Pacejka A. J., Santana E., Harper R. G., Thompson C. F. 1996. House wrens *Troglodytes aedon* and nest-dwelling ectoparasites: mite population growth and feeding patterns. J. Avian Biol. 27: 273–278.

Pacejka A. J., Thompson C. F. 1996. Does removal of old nests from nestboxes by researchers affect mite population in subsequent nests of house wrens? J. Field Ornithol. 67: 558–564.

Pinowski J., Pinowska B., Barkowska M., Jerzak L., Zduniak P., Tryjanowski P. 2006. Significance of the breeding season for autumnal nest-site selection by Tree Sparows *Passer domesticus*. Acta Ornithol. 41: 83–87.

Poole A., Gill F. 1993–2000 (eds). The Birds of North America. The Birds of North America, Inc., Philadephia PA.

Pöysä H., Ruusila V., Milonif M., Virtanen J. 2001. Ability to assess nest predation risk in secondary hole-nesting birds: an experimental study. Oecologia 126: 201–207.

Proctor H., Owens I. 2000. Mites and birds: diversity, parasitism and coevolution. TREE 15: 358–364.

Reid J. M., Monaghan P., Ruxton G. D. 2000. Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. Proc. R Soc. Lond. B 267: 37–41.

Rendell W. B., Verbeek N. A. 1996a. Are avian ectoparasites more numerous in nest boxes with old nest material? Can. J. Zool. 74: 1819–1825.

Rendell W. B., Verbeek N. A. 1996b. Old nest material in nest boxes of tree swallows: effects on nest-site choice and nest building. Auk 113: 319–328.

Rendell W. B., Verbeek N. A. 1996c. Old nest material in nestboxes of the Tree Swallows: Effects on reproductive success. Condor 98: 142–152.

Rytkönen S., Lehtonen R., Orell M. 1998. Breeding Great Tits *Parus major* avoid nestboxes infected with fleas Ibis 140: 687–690.

Sedgwick J. A. 1997. Sequential cavity use in a cottonwood bottomland. Condor 99: 880–887.

Singelton D. R., Harper R. G. 1997. Bacteria in old Hose Wren nests. J. Field Ornithol. 69: 71–74.

Smith H. G. 2004. Selection for synchronous breeding in the European starling. Oikos 105: 301–311.

Sonerud G. A. 1985: Nest hole shift in Tengmalm's Owl *Aegolius funereus* as defence against nest predation involving long-term memory in the predator. J. Anim. Ecol. 54: 179–192.

Sorace A., Petrassi F., Consiglio C. 2004. Long-distance relocation of nestboxes reduces nest predation by Pine Marten *Martes martes*. Bird Study 51: 119–124.

Stanback M. T., Dervan A. A. 2001. Within-season nest-site fidelity in Eastern Bluebirds: disentangling effects of nest success and parasite avoidance. Auk 118: 743–745.
Stanback M. T., Rockwell E. K. 2003. Nest-site fidelity in Eastern Bluebirds (*Sialia sialis*) depends on the quality of alternate cavities. Auk 120: 1029–1032.
Thompson C. F., Neill A. J. 1991. House wrens do not prefer clean nestboxes. Anim. Behav. 42: 1022–1024.
Tomás G., Merino S., Moreno J., Morales J. 2007. Consequences of nest reuse for parasite burden and female health and condition in blue tit, *Cyanistes caeruleus*. Anim Behav. 73: 805–814.
Tomás G., Merino S., Moreno J., Sanz J. J., Morales J., Garcia-Fraile S. 2006. Nest weight and female health in the blue tit (*Cyanistes caeruleus*). Auk 123: 1013–1021.
Utsey F. M., Hepp G. R. 1997. Frequency of nest box maintenance: effects on Wood Duck nesting in South Carolina. J. Wildl. Manage. 61: 801–807.
Walankiewicz W. 2002. Nest predation as a limiting factor to the breeding population size of the Collared Flycatcher *Ficedula albicollis* in the Białowieża National Park (NE Poland). Acta Ornithol. 37: 91–106.
Wesołowski T. 2000. What happens to old nests in natural cavities? Auk 117: 498–500.
Wesołowski T. 2002. Anti-predator adaptations in nesting marsh tits *Parus palustris*: the role of nest-site security. Ibis 144: 593–601.
Wesołowski 2006. Nest-site re-use: Marsh Tit *Parus palustris* decisions in a primeval forest. Bird Study 53. 199–204.
Wesołowski T., Czeszczewik D., Rowiński P., Walankiewicz W. 2002. Nest soaking in natural holes — a serious cause of breeding failure? Ornis Fennica 79: 132–138.
Wesołowski T., Stańska M. 2001. High ectoparasite loads in hole-nesting birds — a nestbox bias? J. Avian Biol. 32: 281–285.
Wiggins D. A., Pärt T., Gustafsson L. 1994. Seasonal decline in collared flycatcher *Ficedula albicollis* reproductive success: an experimental approach. Oikos 70: 359–364.
Winkler D. W., Wrege P. H., Allen P. E., Kast T. L., Senesac P., Wasson M. F., Llambias P. L., Ferretti V., Sullivan P. J. 2004. Breeding dispersal and philopatry in the Tree Swallow. Condor 106: 768–776.
Wysocki D. 2004. Nest re-use by Blackbird — the way for safe breeding? Acta Ornithol. 39: 164–168.

STRESZCZENIE

[Wpływ starego materiału gniazdowego na wybór miejsca na gniazdo i lęgi dziuplaków wtórnych — przegląd badań].

Dziuple w drzewach mogą być wykorzystywane jako miejsca lęgowe przez wiele lat.

W związku z tym, ptaki w nich gniazdujące mogą stawać przed problemem obecności w dziupli materiału gniazdowego z poprzednich sezonów/lęgów. Przez długi czas w badaniach dziuplaków wtórnych problem ten był pomijany, gdyż wykorzystywano skrzynki lęgowe, które były czyszczone przez badaczy.

Obecność starego gniazda może wpływać na ptaki negatywnie w związku z ektopasożytami, które mogą się w nim znajdować, lub poprzez zwiększoną presję drapieżników, gdyż takie gniazdo może spłycać miejsce gniazdowe. Z drugiej strony wpływ ten może być też pozytywny, gdyż materiał starego gniazda może pozwalać na oszczędność czasu i energii w nakładach na budowę nowego gniazda, a także może stanowić informację o jakości danego miejsca lęgowego (Tab. 1).

W pracy zebrano wyniki przeprowadzonych do tej pory eksperymentów mających na celu określenie wpływu, jaki na lęgi dziuplaków może wywierać obecność starego gniazda. Przeanalizowano wpływ na wybór miejsca na gniazdo, parametry reprodukcyjne, oraz liczebność ektopasożytów w gniazdach zbudowanych na starych gniazdach i w skrzynkach lęgowych czyszczonych przez sezonem. Znaczna część prac dotyczących tego zagadnienia powstała w latach 1990-tych (Fig. 1), zestawienie wyników opublikowanych prac wykazało, że w większości z nich nie stwierdzono istotnego wpływu starego gniazda na wybór miejsca lęgowego (Tab. 2). Kilka prac, które wykazały unikanie miejsc ze starymi gniazdami, zostało niewłaściwie przeprowadzonych, ponieważ efektywna głębokość skrzynki lęgowej (stare gniazdo powoduje spłycenie miejsca lęgowego) nie była brana pod uwagę (Fig. 2).

Wyniki większości prac nie wykazują istotnego wpływu starego gniazda na parametry lęgów takie jak termin przystępowania do lęgów, wielkość zniesienia, sukces lęgowy czy kondycja piskląt (Tab. 3). W gniazdach zbudowanych na starych gniazdach więcej jest pcheł i czasem roztoczy, takiej zależności nie stwierdzono dla larw muchówek Protocaliphora (Tab. 4). Mimo dość łatwego sposobu prowadzenia badań, prac poruszających zagadnienie obecności starego materiału gniazdowego w miejscach lęgowych jest ciągle niewiele. Podsumowanie to wskazuje, że obecne dane nie pozwalają jednoznacznie określić wpływu starego gniazda na lęgi dziuplaków. W pracy wskazano nowe kierunki prac i zagadnienia szczególnie ważne w dalszych badaniach. Dokładnymi badaniami powinny zostać objęte dziuple naturalne, gdyż tempo rozkładu materiału gniazdowego może być w nich szybsze niż w skrzynkach lęgowych. Na uwagę zasługuje także zagadnienie czyszczenia miejsc gniazdowych samodzielnie przez ptaki, które mogą wyrzucać stary materiał gniazdowy.