Habitat selection taking nest-box age into account: a field experiment in secondary hole-nesting birds

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Introduction

Initially nest-boxes were created to support hole-nesters and to assist biological control in young forests, plantations, parks and gardens (Lambrechts et al. 2010). Later nest-boxes became valuable in ecological science (Møller 1989, Koenig et al. 1992, Møller 1992, Ekner & Tryjanowski 2008, Langowska et al. 2010, Mainwaring 2011). Due to ease of handling and spatial placement, nest-boxes are often used in ecological experiments, mainly for the study of birds but also for small mammals and insects (e.g. Mazgajski 2003, Garciá-Navas et al. 2008, Lesiński et al. 2009, Langowska et al. 2010). Using boxes may help to better control the impact of stochastic effects such as abiotic factors (e.g. weather, availability of holes) and biotic factors (e.g. predation or competition) (Kluijver 1950, Möller 1989, Möller 1992, Lambrechts et al. 2010).

Use of nest-boxes is the most popular for studying breeding birds (Lambrechts et al. 2013). Finding a suitable nesting site is crucial for the survival of animals. Similarly, a safe roosting site at night, especially during winter, has an impact on survival (Krištín et al. 2001, Ekner & Tryjanowski 2008, Dhondt et al. 2010, Mainwaring 2011). Both in the temperate and (sub)arctic climate zones, night is a critical time for survival during winter, with regard to low temperatures (Pinowski et al. 2006). Hence, in order to avoid adverse weather conditions, birds seek safe roosting sites (Velký et al. 2010). However, despite the apparent importance of winter survival, there have been only a few studies on nest-box selection during this period.

When selecting boxes, birds are guided by safety, as determined by aspect and size of the entry hole, height and construction of nest-boxes (Rendell & Verbeek 1996, Mazgajski 2003), height above the ground (Mazgajski 2002), likelihood of predation (Sonerud 1985, Sorace et al. 2004), habitat (Mänd et al. 2005), size of boxes (Lambrechts et al. 2013) or wood colour.
nest-box age influences where of breeding in great tits Parus preliminary results of the impact of box age on timing cavity selection vary across seasons. We also report accepting that costs and benefits involving choice of suitable place during a winter and breeding initially supposed that there is a difference between the that also might influence box occupation rates. We after controlling for other nest-box characteristics results of a field experiment that aimed to test whether boxes would be a more reliable indicator of habitat quality than new unoccupied boxes. Here we present the quality than new unoccupied boxes. Presence of fresh excrement in the boxes also indicates that the cavity has been occupied recently, and therefore might discourage immigrants or neighbours seeking a new roosting site to use these cavities (Lambrechts et al. 2013). On the other hand, birds might also use old remains in nest-chambers (e.g. old excrement or nests) as an indicator of successful previous breeding attempts so that occupied older boxes would be a more reliable indicator of habitat quality than new unoccupied boxes. Here we present the results of a field experiment that aimed to test whether nest-box age influences where birds will roost or breed after controlling for other nest-box characteristics that also might influence box occupation rates. We initially supposed that there is a difference between the choice of suitable place during a winter and breeding season, also accepting that costs and benefits involving cavity selection vary across seasons. We also report preliminary results of the impact of box age on timing of breeding in great tits Parus major.

Material and Methods
The study was conducted in Poznań (16.93° N, 52.41° E), in western Poland, in the 2009/2010 winter and the 2010 breeding season. The area covers the Morasko campus of Adam Mickiewicz University, about 1.2 km², with three large university buildings and a small forest mainly of Scots pine Pinus sylvestris. Experimental and observational research on cavity nesters have been made in the area since October 2005 (for details on the study area see: Ekner & Tryjanowski 2008).

To study great tits (Ekner & Tryjanowski 2008), one hundred wooden boxes of the same design were attached to trees during October 2005 (hereafter indicated as old boxes). The boxes were erected circa 3 m above the ground, with random inlet orientation. The inner dimension of the box bottom floor was 11 × 11 cm, the internal depth from the inlet to the bottom (inside) was 21 cm, and the diameter of the inlet opening was 33 mm. In mid-December 2009, 30 boxes of the same design and manufacture as the old ones (hereafter indicated as new boxes) were added. At the same time, half of the old boxes were relocated at random in order to eliminate potential influences of predators that might have memorized placements of old boxes (e.g. see Sorace et al. 2004). The old boxes were relocated within the study plot and replaced by new boxes. During relocation, boxes were not affected and their properties not changed. In this study, we choose only old boxes which had no traces of damage, for instance caused by woodpeckers. The distance between both the old and the new boxes varied between eight and 400 m. Since 2005, and prior to the onset of this study, the boxes were checked both during the breeding and winter seasons. Before the onset of the breeding seasons, excrement and insect nests were removed from the old boxes, without removing the nests or nest material from former breeding attempts.

We created three groups of 30 boxes: old boxes never occupied – since 2005 (half relocated), old boxes occupied at least once since 2005 by great tit (half relocated) and new boxes. Shortly before the new nest-boxes were installed, any nests were removed from the old boxes in order to eliminate this influence on bird selection (e.g. by reducing the depth of the nest-boxes). In winter, nest-boxes were checked regularly at 7-day intervals from December 2009 to March 2010 to determine if they were being used. Boxes were classified as occupied for nocturnal roosting if fresh traces of birds in the form of excrement inside the box were seen. In order to avoid birds moving between roosting sites, we did not check the nest-boxes at night (Lambrechts et al. 2013), except once per monthly visits. During the 2010 breeding
season, all boxes were checked weekly from the end of March to the beginning of June. Nest-boxes were classified as occupied if birds started to reproduce and at least one egg was laid. The timing of breeding was classified as the date the first egg was laid. The first day of the breeding season was defined as the day the first egg was laid in the studied population. All tests were two-tailed and results are mentioned in the text as the percentage of occupied nest-boxes, as well as mean ± SE for the other traits.

Results
There was no difference in the frequency of winter occupation (number of nest-boxes where birds spent winter nights) between the three groups of nest-boxes ($\chi^2 = 1.7, df = 2; P = 0.425$, Table 1).

In 2010, birds nested in 30 of the 90 nest-boxes monitored. Twenty six boxes were occupied by great tits (86.7 %). Boxes were rarely occupied by blue tits Cyanistes caeruleus (6.7 %, n = 2), European starlings Sturnus vulgaris (3.3 %) or pied flycatchers Ficedula hypoleuca (3.3 %). In order to standardize the sample, we excluded from additional analyses one box with an enlarged entrance hole that allowed bigger secondary hole-nesters to settle (at least once since 2005 by starlings) and boxes that were occupied by species other than great tits. We then observed in 2010 that the old boxes never occupied between 2005 and 2009 were occupied less frequently by great tits than the other two groups of boxes ($\chi^2 = 4.8, df = 2; P = 0.032$).

The average onset of egg laying occurred nearly more than three weeks earlier in the new boxes erected in December 2009 than in the boxes never occupied during the breeding seasons from 2005 till 2009 (expressed as number of days after the first breeding pair started egg laying in the local population = 1; respectively $12.62 ± 2.16$ vs. $37.20 ± 10.80$; Wilcoxon Test, $Z = –1.977, P = 0.048$; Fig. 1).

Discussion
In one study year, we observed that the occupation rates of cavities varied with nest-box age in a different manner between the winter period (when cavities are mainly exploited for roosting) and the spring period (when cavities are mainly used for nesting). Prior to the breeding season, boxes that differed in age had similar occupation rates and this after controlling for other characteristics of boxes that might influence where birds will roost (e.g. absence of old nests). This is surprising because nest-box exploiters like great tits seem to prefer to roost in boxes without parasites than in boxes where parasites were experimentally added (Christe et al. 1994). Parasites, like fleas, might occur more often in older than in new cavities when the occurrence of parasites is influenced by previous roosting or breeding attempts. Perhaps the conclusions of our winter study would have been different in a study plot where parasites like fleas occur more often. During the breeding season of 2010, new boxes were colonised much earlier than old boxes previously never occupied between 2005 and 2009. These results support other studies that either used nest-boxes as tools (Sonerud 1985, Sorace et al. 2004) or that studied hole-nesters in natural holes (Nilsson et al. 1991, Kotaka & Matsuoka 2002, Mazgajski 2007). The new boxes were colonized much more synchronously than the old boxes previously unoccupied (Fig. 1), as
indicated by the lower standard error of the former. This indicates that the birds indeed preferred the new boxes for breeding, also supporting conclusions from previous studies suggesting that avian box-exploiters prefer new boxes to avoid predators that are able to remember nest sites and revisit them (Sonerud 1985, Sorace et al. 2004). However, in our study, boxes differing in age were located close to one another and the box placements randomized during the study period, hence they had similar probabilities of being visited by predators. Moreover, we rarely observed nest predators in our study plot (unpublished data). Parasites, mainly ectoparasites and blood parasites, are considered to be among the most important factors affecting fitness components (Brown & Brown 1986, review in Moller 1990). As for roosting birds, breeders might prefer new boxes as nesting sites to avoid parasites and/or pathogens from previous roosting or breeding attempts (Christe et al. 1994, Oppliger et al. 1994, Rendell & Verbeek 1996). Surprisingly, we observed that the birds preferred new boxes over the old ones previously unoccupied, which implies that factors other than parasites, like perceived humidity or wood decay indicating cavity vulnerability, might be involved in cavity selection. Obviously, observations in more study years and in more environments that vary in pressures related to predation, parasites or intra-specific competition for cavities will be required to better understand how, why and where cavity age might influence roosting or breeding in avian cavity exploiters. Our experimental study strongly indicates that maintenance procedures of plots where old boxes are replaced by new ones can influence how and where birds will breed. We found that birds bred more frequently in the new boxes and the boxes that were occupied at least once during a former breeding season. Perhaps all the birds preferred to settle in the new boxes, but increased competition might have prevented some individuals to accept these boxes. Thus many individuals might have been excluded from the new boxes and were forced to accept older boxes for breeding. In addition, the birds apparently avoided some old boxes because they were never occupied for at least four years (2006-2009). Perhaps birds memorized information concerning safety or other experiences during former roosting or breeding attempts and when deciding where to settle they choose to avoid some old boxes more frequently than other old boxes (e.g. see Doligez et al. 2003, Danchin et al. 2004).

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Literature


