Folia Zool. – 63 (4): 251–255 (2014)

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

Anna EKNER-GRZYB[1]*, Katarzyna M. ZOLNIEROWICZ[2], Dawid LISICKI[1] and Marcin TOBOLKA[2]

[1] *Department of Behavioural Ecology, Adam Mickiewicz University in Poznań, Umultowska 89, 61-614 Poznań, Poland; e-mail: anna.ekner@gmail.com, lisek88pl@gmail.com*
[2] *Institute of Zoology, Poznań University of Life Sciences, Wojska Polskiego 71C, 60-625 Poznań, Poland; e-mail: kzolnierowicz@gmail.com, marcin_tobolka@o2.pl*

Received 10 April 2014; Accepted 19 January 2015

Abstract. The widespread use of nest-boxes significantly improved our understanding of the ecology and behaviour of secondary cavity-nesting birds. Although former investigations showed that nest-box characteristics (e.g. physical dimensions, material) may determine where birds will roost or breed, biological consequences of the age of nest-boxes have been rarely investigated with field experiments. To test if age of cavities may influence roosting or breeding behaviour in cavity-nesting birds, we created a set-up of three experimental groups of wooden boxes with the same physical dimensions: old boxes that were occupied at least once for nesting during years prior to this study, old boxes that were never accepted for breeding during years prior to this study, and new boxes. Half of the old boxes were relocated within the study plot and replaced by new ones. Box age did not have an impact on occupation rates during the winter period, and therefore did not seem to influence where the birds roosted. However, breeders occupied the old previously unoccupied boxes less frequently than the other boxes. Moreover, birds bred much earlier in new boxes than in the old boxes that were previously never exploited. We discuss when and how cavity age can influence roosting or breeding in nest-box exploiters. Our results strongly suggest that maintenance procedures of plots where old boxes are replaced by new ones can influence how and where birds will breed.

Key words: site selection, great tit, *Parus major*, roosting, secondary cavity-exploiters

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, García-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, Møller 1989, Møller 1992, Lambrechts et al. 2010).

Use of nest-boxes is the most popular for studying breeding birds (Lambrechts et al. 2010, but Mainwaring 2011). 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, depth 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

* *Corresponding Author*

(Browne 2006). Sometimes, the structure and lack of any traces left by other animals in the breeding and roosting sites are important (Rendell & Verbeek 1996, Mazgajski 2003, Ekner & Tryjanowski 2008, Mainwaring 2011). One individual may defend more than one roosting site, probably depending on the distance between different potentially accessible roosting sites (Kluijver 1951).

Nest-box characteristics that influence when and where birds will settle occasionally co-vary with the age of the boxes, so that the relative importance of box age and other aspects of nest-boxes (e.g. placement, content, box-wall characteristics) cannot always be identified. For instance, it was previously hypothesized that predators of birds memorize placement of boxes so that older boxes may have a higher probability to be visited again by these predators. Birds might use cavity age as a proxy of predation risk, which implies that the birds might avoid older boxes potentially memorized by predators and prefer new boxes not memorized by predators (Sonerud 1985, Nilsson et al. 1991, Kotaka & Matsuoka 2002, Sorace et al. 2004, Mazgajski 2007). In addition, new and older boxes might also differ in cavity contents perhaps also influencing box occupation rates (Lambrechts et al. 2010, Lambrechts et al. 2012). For instance, several studies showed that birds prefer clean nest sites above nest sites with remains from previous nesting attempts (Merino & Potti 1995, Amo et al. 2008, Ekner & Tryjanowski 2008). 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 km^2, with three large university buildings and a small forest mainly of Scots pine *Pinus silvestris*. 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.

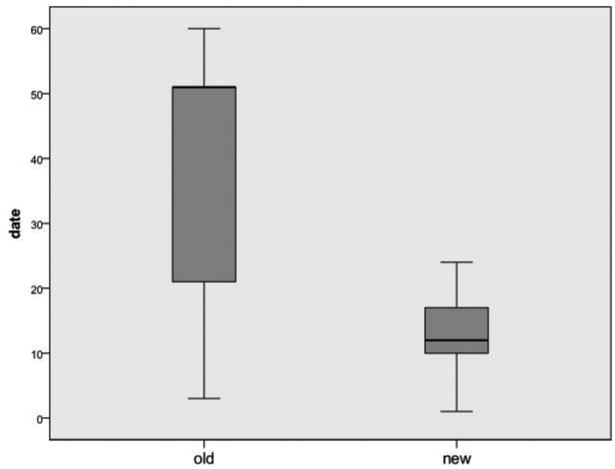

Fig. 1. Date of the first egg laying in nest-boxes: old previously unoccupied boxes and new boxes. 1 is a date when the first pair started egg-laying in the study area.

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 (χ^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

Table 1. Number of nest-boxes (N) occupied by birds during the breeding season (occupancy was classified when birds started laying eggs) and average number of nest-boxes occupied in winter (± SE; occupancy was classified if traces of birds in the form of excrement were seen and were calculated as an average of 10 visits).

Type of nest-boxes	N	Breeding season	Winter
old, not occupied in 2005-2009	30	4	9.3 ± 3.71
old, occupied at least once in 2005-2009	30(29)	12	7.5 ± 2.95
new	30	13	6.4 ± 3.60

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 (χ^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 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 Møller 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).

Acknowledgements

We are grateful to the many students who helped with nest-box monitoring, especially K. Dudek, M. Gawałek, Z. Sajkowska, M. Kalisiak, K. Czarnecka, K. Łosak, T. Grzyb. Tomasz Mazgajski, Tim Sparks and Piotr Tryjanowski critically read previous versions of the manuscript and Marcel M. Lambrechts gave us very useful comments. Native speaker, Nathalie Gilbert has improved the English. Marcin Tobolka and Anna Ekner-Grzyb are a scholarships holder within the project "Scholarship support for PhD students specializing in majors strategic for Wielkopolska's development", Sub-measure 8.2.2 Human Capital Operational Programme, co-financed by European Union under the European Social Fund.

Literature

Amo L., Galván I., Tomás G. & Sanz J.J. 2008: Predator odour recognition and avoidance in a songbird. *Funct. Ecol. 22: 289–293.*

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

Browne S.J. 2006: Effect of nestbox construction and colour on the occupancy and breeding success of nesting tits *Parus* spp. *Bird Study 53: 187–192.*

Christe P., Oppliger A. & Richner H. 1994: Ectoparasite affects choice and use of roost sites in the great tit, *Parus major*. *Anim Behav. 47: 895–898.*

Danchin É., Giraldeau L.A., Valone T.J. & Wagner R.H. 2004: Public information: from noisy neighbours to cultural evolution. *Science 305: 487–491.*

Dhondt A., Blondel J. & Perret P. 2010: Why do Corsican blue tits *Cyanistes caeruleus ogliastrae* not use nest boxes for roosting? *J. Ornithol. 151: 95–101.*

Doligez B., Cadet C., Danchin E. & Boulinier T. 2003: When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Anim. Behav. 66: 973–988.*

Ekner A. & Tryjanowski P. 2008: Do small hole nesting passerines detect cues left by a predator? A test on winter roosting sites. *Acta Ornithol. 43: 107–111.*

García-Navas V., Arroyo L., Sanz J.J. & Díaz M. 2008: Effect of nestbox type on occupancy and breeding biology of tree sparrows *Passer montanus* in central Spain. *Ibis 150: 356–364.*

Kluijver H.N. 1950: Daily routines of the great tit, *Parus m. major* L. *Ardea 38: 99–135.*

Kluijver H.N. 1951: The population ecology of the great tit *Parus m. major* L. *Ardea 39:1–135.*

Koenig W.D., Gowaty P.A. & Dickinson J.L. 1992: Boxes, barns, and bridges: confounding factors or exceptional opportunities in ecological studies? *Oikos 63: 305–308.*

Kotaka N. & Matsuoka S. 2002: Secondary users of great spotted woodpecker (*Dendrocopos major*) nest cavities in urban and suburban forests in Sapporo City, northern Japan. *Ornithol. Sci. 1: 117–122.*

Krištín A., Mihál I. & Urban P. 2001: Roosting of the great tit, *Parus major* and the nuthatch, *Sitta europaea* in nest boxes in an oak-hornbeam forest. *Folia Zool. 50: 43–53.*

Lambrechts M.M., Abouladzé M., Bonnet M., Demeyrier V., Doutrelant C., Faucon V., Prado G., Lidon F., Noell T., Pagano P., Perret P., Pouplard S., Spitaliéry R. & Grégoire A. 2013: Nest-box size influences where secondary-cavity exploiters roost and nest: a choice experiment. *J. Ornithol. 154: 563–566.*

Lambrechts M.M., Adriaensen F., Ardia D.R., Artemyev A.V., Atiénzar F., Bańbura J., Barba E., Bouvier J.C., Camprodon J., Cooper C.B., Dawson R.D., Eens M., Eeva T., Faivre B., Garamszegi L.Z., Goodenough A.E., Gosler A.G., Grégoire A., Griffith S.C., Gustafsson L., Johnson L.S., Kania W., Keišs O., Llambias P.E., Mainwaring M.C., Mänd R., Massa B., Mazgajski T.D., Møller A.P., Moreno J., Naef-Daenzer B., Nilsson J.L., Norte A.C., Orell M., Otter K.A., Park Ch.R., Perrins Ch.M., Pinowski J., Porkert J., Potti J., Remes V., Richner H., Rytkönen S., Shiao M.T., Silverin B., Slagsvold T., Smith H.G., Sorace A., Stenning M.J., Stewart I., Thompson Ch.F., Török J., Tryjanowski P., van Noordwijk A.J., Winkler D.W. & Ziane N. 2010: The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases. *Acta Ornithol. 45: 1–26.*

Lambrechts M.M., Wiebe K.L., Sunde P., Solonen T., Sergio F., Roulin A., Møller A.P., Lopez B.C., Fargallo J.A., Exo K.M., Dell'Omo G., Costantini D., Charter M., Butler M.W., Bortolotti G.R., Arlettaz R. & Korpimäki E. 2012: Nest box design for the study of diurnal raptors and owls is still an overlooked point in ecological, evolutionary and conservation studies: a review. *J. Ornithol. 153: 23–34.*

Langowska A., Ekner A., Skórka P., Tobolka M. & Tryjanowski P. 2010: Nest-site tenacity and dispersal patterns of *Vespa crabro* colonies located in bird nest-boxes. *Sociobiology 56: 375–382.*

Lesiński G., Skrzypiec-Nowak P., Janiak A. & Jagnieszczak Z. 2009: Phenology of bat occurrence in boxes in central Poland. *Mammalia 73: 33–37.*

Mainwaring M.C. 2011: The use of nestboxes by roosting birds during the nonbreeding season: a review of the costs and benefits. *Ardea 99: 167–176.*

Mänd R., Tilgar V., Lõhmus A. & Leivits A. 2005: Providing nest boxes for hole-nesting birds – Does habitat matter? *Biodivers. Conserv. 14: 1823–1840.*

Mazgajski T.D. 2002: Does the great spotted woodpecker *Dendrocops major* select holes for roosting? *Pol. J. Ecol. 50: 99–103.*

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. 2007: Nest hole age decreases nest site attractiveness for the European starling *Sturnus vulgaris*. *Ornis Fenn. 84: 32–38.*

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.*

Møller A.P. 1989: Parasites, predators and nestboxes: facts and artifacts in nest box studies of birds? *Oikos 56: 421–423.*

Møller A.P. 1990: Effect of parasitism by a haematophagus mite on reproduction in the barn swallow. *Ecology 71: 2345–2357.*

Møller A.P. 1992: Nest boxes and the scientific rigour of experimental studies. *Oikos 63: 309–311.*

Nilsson S.G., Johnsson K. & Tjernberg M. 1991: Is avoidance by black woodpeckers of old nest holes due to predators? *Anim. Behav. 41: 439–441.*

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.*

Pinowski J., Haman A., Jerzak L., Pinowska B., Barkowska M., Grodzki A. & Haman K. 2006: The thermal properties of some nests of the Eurasian tree sparrow *Passer montanus*. *J. Therm. Biol. 31: 573–581.*

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

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.*

Velký M., Kaňuch P. & Krištín A. 2010: Selection of winter roosts in the great tit *Parus major*: influence of microclimate. *J. Ornithol. 151: 147–153.*