The design of artificial nestboxes for the study of secondary hole-nesting birds: a review of methodological inconsistencies and potential biases

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Abstract. The widespread use of artificial nestboxes has led to significant advances in our knowledge of the ecology, behaviour and physiology of cavity nesting birds, especially small passerines. Nestboxes have made it easier to perform routine monitoring and experimental manipulation of eggs or nestlings, and also repeatedly to capture, identify and manipulate the parents. However, when comparing results across study sites the use of nestboxes may also introduce a potentially significant confounding variable in the form of differences in nestbox design amongst studies, such as their physical dimensions, placement height, and the way in which they are constructed and maintained. However, the use of nestboxes may also introduce an unconsidered and potentially significant confounding variable due to differences in nestbox design amongst studies, such as their physical dimensions, placement height, and the way in which they are constructed and maintained. Here we review to what extent the characteristics of artificial nestboxes (e.g. size, shape, construction material, colour) are documented in the 'methods' sections of publications involving hole-nesting passerine birds using natural or excavated cavities or artificial nestboxes for reproduction and roosting. Despite explicit previous recommendations that authors describe in detail the characteristics of the nestboxes used, we found that the description of nestbox characteristics in most recent publications remains poor and insufficient. We therefore list the types of descriptive data that should be included in the methods sections of relevant manuscripts and justify this by discussing how variation in nestbox characteristics can affect or confound conclusions from nestbox studies. We also propose several recommendations to improve the reliability and usefulness of research based on long-term studies of any secondary hole-nesting species using artificial nestboxes for breeding or roosting.

Key words: methods, nestboxes, nest sites, passerines, secondary cavity-nesting birds, field experiments, tit, flycatcher, *Ficedula*, *Parus*, *Cyanistes*

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INTRODUCTION

Half of the avian orders use some form of cavity for nesting or roosting (Gill 2007), with up to 30% of the bird species present in some locations being cavity-nesters (Newton 1994, Bai & Mühlenberg 2008). While primary hole-nesters such as woodpeckers are able to excavate their own nest holes in trees, obligate secondary hole-nesters do not have the physical force to drill large holes in hard wood, although some are capable of modifying or enlarging existing cavities in dead or decaying trees (Newton 1994, Schepps et al. 1999, Martin & Norris 2007, Atienzar et al. 2009). Consequently, secondary hole-nesters must rely upon natural tree cavities or unoccupied holes excavated by primary hole-nesters (Martin & Eadie 1999, Remm et al. 2006). Thus, the availability and characteristics of tree holes suitable for secondary hole-nesters is partly influenced by the activity and abundance of primary hole-nesting species, which in turn depend upon the characteristics of the tree species present (e.g. size and age, architecture, hardness) as well as the activity of other taxonomic groups, such as micro-organisms (including fungi), insects, amphibians, reptiles, and mammals (Conner 1977, Wilson et al. 1991, Bednarz et al. 2004, Jackson & Jackson 2004, Ojeda et al. 2007, Wesołowski 2007, Camprodon et al. 2008, Koch et al. 2008, Lambrechts et al. 2008, Matsuoka 2008). Fluctuations in external factors such as ambient temperature and the intensity and direction of wind or rain can also influence the availability and characteristics of holes (e.g. East & Perrins 1988, Walankiewicz 1991, Wesołowski et al. 2002). For instance, persistent strong winds or rain may increase the erosion of existing small cavities, blow branches from trees so that new cavities are created, or blow down dead trees containing cavities.

Each natural hole found in a dead or living tree probably has a unique combination of variables, such as the position, orientation and shape of the entrance hole, and the cavity's material, wall thickness, depth, diameter, floor area, shape, colour, volume, internal surface, light conditions and age (van Balen et al. 1982, Nilsson 1984, East & Perrins 1988, Rendell & Robertson 1989, Carlson et al. 1998, Czeszczewik & Walankiewicz 2003, Wesołowski & Rowiński 2004, Mazgajski 2007b; Table 1). The size or other characteristics of cavities occupied by secondary hole-nesting birds can vary within and between species (Table 1). Studies of these cavities can provide the necessary

background data for the better design of research that uses man-made nestboxes (e.g. Nilsson 1975, 1984, Møller 1989, 1992, Wesołowski 2007).

The use of nestboxes to study secondary hole-nesters

Many secondary hole-nesting species readily breed in man-made artificial cavities, most of which are nestboxes placed against tree trunks, fences or walls, or erected on posts (von Haartman 1969, Kibler 1969, Perrins 1979, Pikula & Beklova 1980, Newton 1994, Lesiński 2000, Zingg et al. 2010). The use of such artificial cavities in avian research has greatly advanced our understanding of breeding behaviour in cavity-nesting species. Nestboxes allow researchers to perform routine monitoring and experimental manipulation of eggs or nestlings, as well as repeatedly capture, identify and manipulate the parents or offspring (e.g. Sanz 1998, Visser et al. 2003, Both et al. 2004, Griffith et al. 2008). The use of nestboxes often increases the local population of secondary hole-nesters available for study, and it may also help to better control, reduce, or eliminate stochastic effects associated with abiotic factors or predation, thus increasing sample sizes and facilitating data analyses or interpretation. Since the pioneering investigations of G. Wolda in the Netherlands (Kluyver 1951, Lack 1955), artificial nestboxes have been used to aid research in a range of sub-disciplines of the behavioural and environmental sciences e.g. behavioural ecology, cognitive ecology, conservation biology, ecotoxicology, evolutionary ecology, functional ecology, molecular ecology, population ecology (e.g. Busse & Olech 1968, Perrins 1979, Lundberg & Alatalo 1992, Koenig et al. 1992, Newton 1994, Schlaepfer et al. 2002, Blondel et al. 2006, Seppänen & Forsman 2007, Slagsvold & Wiebe 2007, Mazgajski 2008, Liedvogel et al. 2009, Mänd et al. 2009, Holveck et al. 2010, Van den Steen et al. 2010, Zingg et al. 2010). Nestbox studies have also contributed significantly to the development of life-history theory in free-ranging organisms (Clutton-Brock 1988, Newton 1989) because of the ease with which manipulations can be performed. Consequently, secondary hole-nesting passerines have become one of the most intensively investigated free-living bird groups of the world (e.g. Riddington & Gosler 1995), and occupy top positions with respect to the total number of papers returned by two ISI Web of Science searches of passerine studies by common and scientific name

Table 1. Mean (± SD) dimensions of natural nest holes in three European hole-nesting species. Ranges in brackets. N — sample size. † — data from different seasons, * — calculated from figures.

Species	Habitat	Country	N	Height above the ground (m)	entrance diameter (smallest value, cm)	holes depth (cm)	bottom area (cm²)	Source
Parus major	deciduous	UK	10–11	2.67 ± 1.53	4.9 ± 2.0*			Edington & Edington 1972
	deciduous	UK	7–10	5.9 (0.4–11)	5.7 ± 2.6; 5.9 ± 1.6†	35.8 ± 25.1; 35.8 ± 29.3†		East & Perrins 1988
	deciduous/mixed	NL	33	2.6 ± 0.9	3.9 ± 1.4		139.2 ± 64.3	van Balen et al. 1982
	deciduous	SE	10–16	2.3	3.5 ± 0.6*	21.0 ± 6.0 (11–32)		Nilsson 1984
	deciduous	SE	20	5.2 ± 2.2	4.5 ± 2.0	15 ± 15	249 ± 189	Carlson et al. 1998
	ash-alder	PL	10	5.2				Wesołowski 1989
	oak-hornbean	PL	27	8.7				Wesołowski 1989
	riverine	EE	14–17	6.5 (2.2–12)	3.8 (2.5–5.5)	20.9 (8.0–45.0)		Remm et al. 2006
	boreal/riparian	MN	16	5.0 ± 2.7	4.1 ± 1.3			Bai et al. 2005
Cyanistes caeruleus	deciduous	UK	10	3.24 ± 1.73	3.1 ± 1.2*			Edington & Edington 1972
	deciduous	UK	13–17	5.5; 7.4 † (0.3–10.3)	5.4 ± 2.6; 5.5 ± 2.5†	22.6 ± 6.96; 24.1 ± 5.71†		East & Perrins 1988
	deciduous	NL	20	4.0 ± 2.4	4.0 ± 1.6		88.5 ± 66.4	van Balen et al.1982
	deciduous/mixed	SE	26	4.3 ± 2.6	2.9 ± 0.7	15 ± 7	130 ± 108	Carlson et al. 1998
	ash-alder	SE	10–11	4.4	3.2 ± 0.8*	13.7 ± 7.1		Nilsson 1984
	oak-hornbean	PL	21	11.1				Wesołowski 1989
	oak-hornbean	PL	81	8.3				Hebda 2007
	oak-hornbean	PL	53	8.8 (1.5–18.7)	2.6	15.3		Remm et al. 2006
	riverine	EE	14–20	5.6 (0.5–12)	2.7 (2.1–3.2)	21.4 (3.5–19.0)		Remm et al. 2006
Ficedula hypoleuca	deciduous	UK	17–18	2.37 ± 1.32	3.9 ± 1.2*			Edington & Edington 1972
	deciduous	SE	29	5.4 ± 2.7	4.5 ± 4.7	14 ± 11	199 ± 177	Carlson et al. 1998
	deciduous/mixed	SE		3.3				Nilsson 1984
	deciduous	SE	105	9.4			(33–735)	Alatalo et al. 1988
	ash-alder	PL	18	6.3				Wesołowski 1989
	oak-hornbean	PL	18					Wesołowski 1989
	oak-hornbean	PL	102–180	8.2 ± 4.6 (1.2–23)	3.5 ±1.1 (1.5–8.5)	19.3 ± 7.6 (6–51)	205 ± 525 (28–2826)	Czeszczewik & Walankiewicz 2003
	riverine	EE	24–27	6.7 (2.0–12.5)	3.8 (2.5–5.7)	16.6 (3.0–45.0)		Remm et al. 2006

(Average number of publications of the two searches in 2010 for cavity-nesters: *Parus major* — 1807, *Sturnus vulgaris* — 1293, *Passer domesticus* — 999, *Ficedula hypoleuca* — 880, *Cyanistes caeruleus* — 756, *Tachycineta bicolor* — 744, *Sialia sialis* — 414 versus non-cavity nesters: *Hirundo rustica* — 663, *Melospiza melodia* — 609, *Agelaius phoeniceus* — 488, *Carpodacus mexicanus* — 335).

However, studies involving birds breeding in nestboxes have been criticized on the grounds that the boxes differ in several ways from natural or excavated cavities, and that avian research in free-ranging populations is overwhelmingly dominated by a few 'classic' model systems. Consequently results derived from these studies may fail to reflect natural variation potentially reducing their general validity or applicability (e.g. Nilsson 1975, Møller 1989, 1992, but see Koenig et al. 1992, Wesołowski 2007). For instance, van Balen et al. (1982) cites the main difference between natural holes and artificial nestboxes erected in the same location as a higher rate of nest failure in natural holes because of water logging or competition from bigger animals, factors that are often excluded when nestboxes are used. Whether nestboxes are safer than natural cavities from nest predators or competitors may depend on differences in height or positioning between artificial and natural cavities (Nilsson 1984, McCleery et al. 1996), or whether protective devices have been added to the nestboxes to reduce predation. For instance, metal plates or wire mesh fitted around the entrance hole of nestboxes may prevent the hole being enlarged by woodpeckers or mammals, and pipes placed in the entrance-hole may prevent predators from reaching the contents. Also, treating wooden nestboxes with chemicals, such as preservatives or pesticides, may prevent them from decay due to fungal rot or burrowing arthropods (e.g. Kibler 1969, Nilsson 1984, McCleery et al. 1996, Miller 2002, Mainwaring & Hartley 2008, Skwarska et al. 2009).

Nestboxes are also designed so that researchers can frequently inspect their contents which may cause rapid changes in the chemical environment within the nest (e.g. CO_2 concentrations influencing attractiveness of flying insects exploiting avian hosts — see Tomás et al. 2008) or micro-climate that do not occur in natural or excavated holes. Nestbox studies may also be prone to biased sampling because they may only be occupied by individuals or species that accept artificial cavities, while the remainder retain a preference for natural or excavated cavities (Dhondt 2007). The proportion of individuals that use either natural or artificial holes may therefore depend on the difference in quality between the two or the distribution of individual preferences for different breeding sites. The interval between the placement of nestboxes and the start of a study may also result in biased sampling. For instance, if nestboxes are initially erected just a few weeks before the start of the breeding season of resident species, non-territorial first-year birds may be attracted to study sites that do not provide opportunities for winter roosting in natural cavities.

While there are many benefits of the intensive study of model species, there is an obvious danger of basing our general understanding of birds on such a small number of cavity-nesting species that share a similar ecology and are mostly located in just one region of the world (Europe). To date, while there are many studies of a variety of hole-nesters in North America they have not dominated the literature to the same extent as have the European studies (e.g. see also Chamberlain et al. 2009). There are whole regions of the world in which nestboxes have never been used, although studies have recently been published on avian nestbox exploiters in Australia (Griffith et al. 2008), Argentina (Massoni et al. 2006, Cockle & Bodradi 2009, Llambias & Fernández 2009), Chile (Moreno et al. 2005, 2007) and China (Wang et al. 2008) (but see for instance older studies in Tryjanowski et al. 2006 and Evans et al. 2009 for New Zealand or Eguchi 1980 for Japan). It should also be pointed out that nestboxes in some countries are widely distributed throughout the countryside by forestry administrations or environmental organizations (e.g. Poland, Spain). For instance, thousands of nestboxes of a specific design have been erected for >50 years in many Polish and Spanish forests, constituting an unavoidable part of the environment for hole-nesters that does not depend on researchers and that may have induced significant selective pressures on populations.

There exist biases in the material used (e.g. nestbox design), the choice of the model species, and the environment (e.g. European woodland) in which research is conducted. The extent to which all this is really a problem is difficult to evaluate since few studies have compared biological aspects of birds which breed in nestboxes and those which breed in natural or excavated cavities at the same location (but see e.g. East & Perrins 1988, Johnson & Kermott 1994, Miller 2002, Llambias & Fernández 2009 and references

therein). However, this issue can be evaluated indirectly by examining whether the characteristics of artificial nestboxes and their occupants differ from those of natural or excavated nest-holes (e.g. Dhondt 2007), and if there are differences, whether these would affect the likelihood of supporting or rejecting a particular hypothesis.

The ecological significance of variation in nestbox characteristics

Several studies indicate that the characteristics of each nestbox influence the physical environment (e.g. ambient temperature, humidity, light reflectance) or biotic environment (e.g. presence and biology of other organisms, parent-offspring interactions) within the nest-chamber, and therefore the development or survival of the eggs or nestlings, or the survival or physical condition of adults using nestboxes for reproduction or roosting (Löhrl 1973, van Balen 1984, Slagsvold & Amundsen 1992, Mazgajski 2007a, Dhondt et al. 2010). The internal size of the nest cavity may also influence clutch size, depending on the size ranges of the nest-chamber or species involved (e.g. Karlsson & Nilsson 1977, Moeed & Dawson 1979, Löhrl 1980, van Balen 1984, Gustafsson & Nilsson 1985, Slagsvold & Amundsen 1992). In Great Tits *Parus major*, for instance, an experiment in which nestboxes were replaced with a different-sized box shortly after the onset of egg laying found that size differences in subsequently-produced clutches may be as large as the variation in clutch size observed across distinct forest types (e.g. > 2 eggs, Löhrl 1973, 1980, Sanz 1998). In Pied Flycatchers *Ficedula hypoleuca*, this may not be related to an adjustment of clutch size to cavity size per se, but could for example result from females laying larger clutches selecting larger cavities for breeding or spending more time to find a large nest cavity (Slagsvold 1987).

Several other variables seem intuitively likely to affect whether a nestbox is occupied, and if so, the success of each breeding attempt. For example, erecting boxes of varying dimensions at the same location has shown that different individuals or species use cavities with different characteristics. The size and position (e.g. height, orientation) of the entrance hole appears to determine which individual or species will occupy nestboxes and how their life-history traits will be expressed in the presence of other organisms (e.g. Kluyver 1951, Nilsson 1984, Barba & Gil-Delgado 1990, Dhondt & Adriaensen 1999, Zingg et al. 2010). For example, large individuals or species cannot enter

small entrance holes or nestbox chambers simply because of physical constraints. Furthermore, smaller individuals or species may prefer to breed in nestboxes with small entrance holes, particularly those located high in trees, to reduce risks related to predation or competition (Löhrl 1970, 1977, Slagsvold 1975, Nilsson 1984, Newton 1994, Sorace & Carere 1996).

A given nestbox type may be preferred in one environment and yet disfavoured in another. For instance, local meteorological effects may influence the preferences for certain nest-cavities with birds avoiding those with holes oriented in the direction of prevailing wind or rain (e.g. Goodenough et al. 2008). Orientation of nests has been found to influence site selection of natural cavities and artificial cavities in Tree Swallows *Tachycineta bicolor* (Rendell & Robertson 1994, Ardia et al. 2006), probably because internal nest temperatures differ as a function of orientation (Ardia et al. 2006). Orientation of occupied nestboxes may also be influenced by the location of conspecifics (Mennill & Ratcliffe 2004). According to Kluijver (1951), cavity preferences may differ between males and females and vary seasonally. Birds may only avoid nestboxes with larger holes in areas with high perceived predation risk (e.g. Sorace & Carere 1996). The cleaning practices of nestboxes may also affect the choice of nestboxes. (Mazgajski 2007a). For example, Pied Flycatchers may gain time benefits in nest building if the old nest is not removed (Orell et al. 1993, Mappes et al. 1994), House Wrens *Troglodytes aedon* may prefer nestboxes containing old nests because they provide evidence of previous success at that location (Johnson 1996, Pacejka & Thompson 1996), or Great Tits may avoid nestboxes containing old nests with many fleas (Rytkönen et al. 1998). Thus, the choice and location of nestbox type may interact with other environmental factors, such as the availability and properties of natural cavities, and significantly influence the outcome of ecological field investigations.

To examine whether scientists working with secondary hole-nesting passerines have acknowledged the significance of variation in nestbox design, we assessed whether nestbox characteristics have been documented in the 'methods' sections of publications or incorporated into statistical analyses of long-term databases. We also discuss how variation in nestbox characteristics can affect or confound conclusions from nestbox studies and propose several recommendations to improve future research.

METHODS

Three papers published over 15 years ago discussed the potential artefacts associated with the use of nestboxes, but also emphasised that many scientists simply did not report what they did with their nestboxes (Møller 1989, 1992, Koenig et al. 1992). Field ornithologists were urged to: 1) improve the design of their nestboxes so that they mimic more closely the characteristics of natural or excavated holes and 2) describe the characteristics of their boxes and the procedures used for maintaining boxes to allow for the exact replication of protocols across studies (see also Kelly 2006). To assess whether subsequent investigations followed these recommendations, we examined the methods section of publications involving the most commonly investigated hole-nesting birds. We divided the papers into two groups: those published before the recommendations of Koenig et al. (1992) and Møller (1992) ("older" publications), and those published from 1992 onwards ("more recent" publications). Based on the recommendations of Møller (1989), we predicted that descriptions of nestbox characteristics would be more frequent among articles published from 1992 onwards. We located relevant publications by using the common or scientific (current or older) names of secondary hole-nesting passerines as key words in the leading electronic databases (ISI Web of Science, Biblio-Vie, BiblioSHS) and also searching the extensive collection of reprints possessed by P. Isenmann (CEFE-Montpellier). We searched the reference section of each of these publications to identify other relevant publications that we had not previously encountered because they were not electronically indexed. We are aware that publications are often not independent units, but we have chosen this entity because it does give the probability that a new reader misses the relevant information in the first paper they read. We surveyed a total of 696 publications from 108 different journals, of which 594 (85%) involved a single species. These publications concerned 12 frequently investigated secondary hole-nesting species, most of which were Eurasian tits (Paridae) or old world flycatchers (Muscicapidae) (Fig. 1).

RESULTS AND DISCUSSION

Our review produced four main results, leading to the overall conclusion that nestbox characteristics are variable and often unreported in the scientific literature and that the significance of these characteristics is often either ignored or underappreciated.

1. Detailed descriptions of nestbox properties are often lacking in recent publications

Around 40% of the older publications (<1992) on passerine secondary hole-nesting birds that we assessed did not provide information on nestbox characteristics and did not reference a former publication providing this information (Fig. 1). This value is even higher (70%) for the verified studies published since 1992. Even when descriptions were provided, they were usually incomplete. For instance, of 94 instances where one nestbox characteristic was mentioned, 58% gave only a broad description of the material used (wood, wood-concrete, concrete), and only 25% gave the diameter of the entrance hole. The tree species used to construct wooden nestboxes or the thickness of the nestbox wall were rarely mentioned (e.g. Michelsons 1958, Delmée et al. 1972, Finch 1989 for exceptions), even though both may influence the thermal or chemical environment of the nest cavity, and thus directly or indirectly affect the physiology of eggs, nestlings or adults (e.g. Kibler 1969, Mertens 1977, 1980, van Balen 1984, Korpimäki 1985, Dawson et al. 2005, García-Navas et al. 2008, Nilsson et al. 2008, Ardia et al. 2009). For instance, there is empirical evidence that invertebrate communities and microorganisms are both affected by their host tree species or its natural compounds, or chemical compounds applied to the wood from which the box was constructed, such as preservatives (e.g. Janzen 1978, Balandrin et al. 1985, Chapuisat et al. 2007, Sipponen et al. 2009, Blondel et al. 2010), and that invertebrate communities in the nest may influence avian life-history traits (e.g. Sengupta 1981, Heeb et al. 2000, Mennerat et al. 2009). Some authors supplied dimensions without specifying whether these refer to the size of the whole box (exterior) or just the nestbox chamber (interior). The biological importance of light incidence inside nestboxes has been ignored for many years, and therefore, rarely, or not reported. For instance, in nestboxes used in several studies in Spain (e.g. Moreno et al. 2006, 2008) the removable frontal lid does not cover the whole front but leaves a slit of 1–1.5 cm which allows luminous conditions within nestboxes. Light conditions within the nestbox chamber may influence the expression of signals possessed by the eggs or
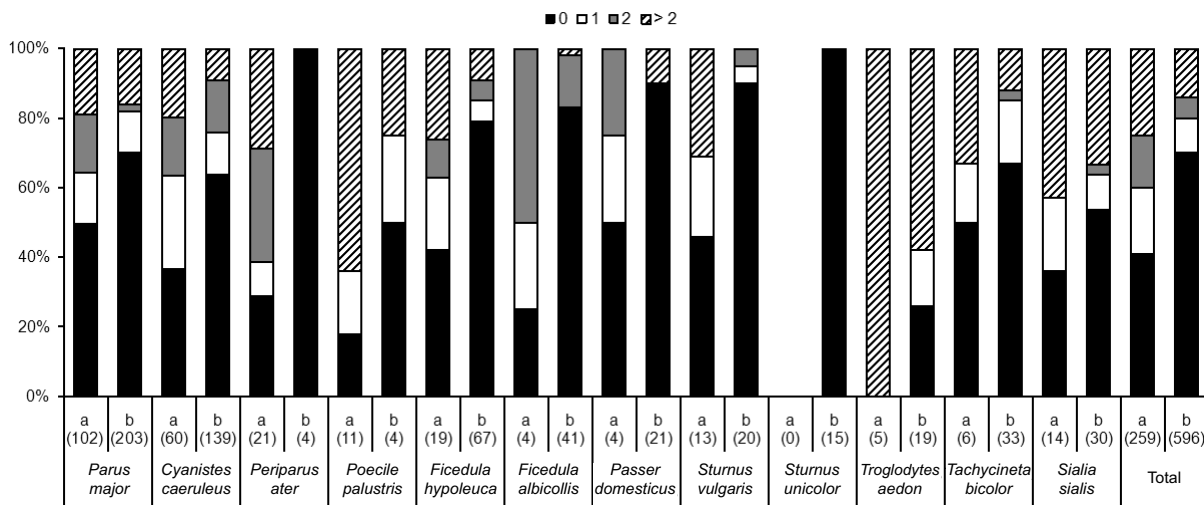
Fig. 1. Percentage of publications describing or citing 0 or more nestbox characteristics in analysed papers in two publication periods: a — < 1992, b — ≥ 1992. The percentage of publications with information on none (0) one (1), two (2) or more than two (>2) nest-box properties are indicated, which includes the publications citing references providing the information in the methods section. Number of papers in parenthesis.

nestlings addressed to parents or social mates (e.g. Holveck et al. 2010). Since natural or excavated tree holes used by secondary hole-nesting birds can be described using at least 10 different parameters (Kibler 1969, van Balen et al. 1982, East & Perrins 1988, Carlson et al. 1998, Remm et al. 2006), perhaps these same parameters could be defined and standardized, then used to describe artificial nestboxes in widely understood details, as architects do when designing buildings.

2. Nestboxes often represent only a small fraction of the properties of natural holes

The nestboxes erected in most study sites are usually identical in shape and dimensions. Although the nestboxes were probably made to a consistent design in order to minimize potential confounding variables and maximize sample sizes (e.g. Drilling & Thompson 1988, McCleery et al. 1996, Llambias & Fernández 2009), the scientific rationale for using a particular type of nestbox, for mounting and positioning them in a particular way, or for protecting them from predators is often not provided. This is a particular problem when nestboxes possess physical properties that significantly differ from those of tree cavities (e.g. Nilsson 1975, Karlsson & Nilsson 1977, Moeed & Dawson 1979, Alatalo et al. 1988, Møller 1989, 1992, Purcell et al. 1997) and nestbox characteristics selected to initiate a long-term study significantly influence the results of ecological investigations (e.g. McCleery et al. 1996, García-Navas et al. 2008).

It should be noted though that the continuity of nestbox characteristics and placements in some study sites can lead to in-depth research where confounding (changeable) factors are controlled (e.g. nestbox orientation, Goodenough et al. 2008).

3. Different research teams often do not use the same nestbox designs and research protocols

Different research groups studying hole-nesting birds in different locations rarely use the same type or size of nestbox, even when studying the same species (see Appendix 1). There may be several economic or scientific reasons for such variation in nestbox design. The material used to construct nestboxes in each location may depend on local availability or price (Moeed & Dawson 1979), or on decisions taken by forestry administrations or environmental organisations without consulting researchers regarding the massive distribution of a certain type of nestbox (e.g. Spain), or may have been proven to be optimal by local ornithological organisations (e.g. Baucells et al. 2003). Consequently, if nestboxes are designed with particular characteristics because of local environmental conditions, such as the use of thick-walled boxes in areas with more extreme weather conditions, then nestboxes should be more variable in species with a larger distributional range. Although we did find large-scale variation in nestbox characteristics among research teams studying the same species, there was little scientific justification for this, as this variation was not intend-

ed to better understand biological consequences of 'nestbox-environment' interactions at broad spatiotemporal scales. Replicates in nestbox design across study sites are currently often segregated instead of properly interspersed. Furthermore, nestbox characteristics may also differ within local populations, as some nestboxes are replaced after several years or different boxes may be erected as new breeding plots are established. However, it has to be noted that nestbox design or placement may be constrained by the need to avoid human predation or destruction of nests in certain countries. For instance, in Spain nestboxes are erected at >3 m above the ground to avoid citizens collecting nests or eggs (but see e. g. nestbox research in orange monocultures in eastern Spain, Monrós et al. 1999), in other areas people collect nestboxes to adorn houses and gardens, and in Kenya people search nestboxes to collect honey.

There are several potential consequences of research teams failing to use the same nestbox design. For example, different nestbox types necessitate the use of different devices for capturing birds. A box opened through the roof (e.g. Wageningen box, van Balen 1984) probably will require a different trapping device than a box opened through a front door (Schwegler type, see www.schwegler-natur.de, Blondel 1985) (Gosler 2004, M. Lambrechts pers. obs.). The use of distinct types of boxes may also influence the time devoted to measuring or manipulating certain traits such as nest characteristics. There may be biological consequences of the different capture or monitoring techniques required for each type of box, since some may be more stressful to the captured birds than others. Furthermore, avian personalities or other phenotypic traits may differ between studies because certain types of nestbox may influence whether they attract relatively "shy" or "bold" individuals (see Garamszegi et al. 2009). In addition, the activity of researchers, such as the frequency of box-monitoring, parent capture and release behaviour (i.e. relative to chick age, and using mist nets or box traps), may all affect the level of desertion or the rate at which parents feed their chicks (and hence growth rates and offspring condition). Direct researcher effects may be limited in populations in which adults are more resistant to disturbance, as a result of conditioning (where individuals become habituated to nestbox design-related research methods over their lifetimes), or even potentially, and perhaps more interestingly, by selection over generations (e.g. Møller 2010).

Wooden nestboxes have to be treated more frequently with chemicals than those built from concrete or a mix of wood and concrete (e.g. Schwegler boxes), and may also have to be replaced more frequently. In long-term studies, replacement boxes should be erected in the same exact location as the previous box or else there may be a change in their local environment, for instance changing the risk of predation (e.g. Sonerud 1989, Sorace et al. 2004) or exposure to weather conditions (e.g. Goodenough et al. 2008). However, keeping the box environment unchanged may not be possible in commercial forests due to frequent habitat alterations by forest practices (see below).

Some unwanted variation in experimental design complicating data interpretation could be avoided using consistent nestbox characteristics across study populations or periods (e.g. "exact" replication of nestbox design, Hurlbert 1984, Hairston 1989, Kelly 2006). For instance, if different study sites containing identical nestboxes, differ significantly in average clutch size, as is the case in Blue Tits (e.g. Isenmann 1987), it is unlikely that the smaller clutch sizes were physically constrained by the size of the nest-cup (e.g. Slagsvold 1989), assuming that geographic variation in clutch size does not result from spatial variation in monitoring protocols. However, the same nestbox set up does not allow us to exclude the hypothesis that the size of the nest cup, physically limited by the size of the nestbox chamber, limits the production of clutches larger than those observed in the nestboxes used. Perhaps a design replicating more than one nestbox type, and standardising monitoring protocols, across study populations or periods could better test some hypotheses dealing with causal relationships between nestbox design and life-history traits.

4. Variation in nestbox characteristics is often ignored in statistical analyses

Nestbox properties may act as confounding factors that should be considered as covariates in statistical analyses of variation in individual or population characteristics. However, most previous comparative studies of phenotypic traits in secondary avian hole-nesters have not included nestbox design as a factor in statistical analyses (e.g. Järvinen 1989, Sanz 1998, 2003, Encabo et al. 2002, Both et al. 2004). This was apparently because variation in nestbox characteristics was assumed to constitute random noise or because

information on nestbox design was unavailable. For instance, the nestboxes used since the 1950s to study tits in Wytham Wood, Oxford, were altered in the 1970s to make them more resistant to damage from Great Spotted Woodpeckers *Dendrocopos major* and to significantly reduce the impact of weasels *Mustela nivalis* entering nestboxes (Perrins 1979). These changes in how nestboxes were constructed (e.g. first from wood then a mixture of wood and concrete) and positioned (initially attached directly on the trunks, later removed from the trunks and suspended from branches) resulted in a rapid temporal shift in life-history traits in Great Tits both at the individual and population level (McCleery et al. 1996, Julliard et al. 1997), a finding apparently ignored in more recent analyses of the long-term database from Oxford. The biological consequences of variation in nestbox design or position could be investigated if future publications would provide details on nestbox characteristics. The non-exhaustive list of designs and positions of nestboxes presented in Table 3 could thus be exploited in future comparative analyses to test for the relative importance of nestbox design and other environmental factors (e.g. population density or composition, presence of other organisms) in the expression of individual life-history traits. Perhaps variation in nestbox characteristics (e.g. nest-chamber size) across most study sites used are often too narrow to become significant confounding factors in many comparative analyses that combine data from different research teams. However, this does not exclude the possibility that variation in nestbox design may become a significant confounding variable when study systems would better reflect the observed variation in characteristics of exploited natural or excavated cavities (see Introduction).

CONSTRAINTS ON REPLICATION OF 'NESTBOX DESIGN — ENVIRONMENT' INTERACTIONS

There are many environmental factors associated with nesting cavities that affect the life-history or phenotypic traits of adults or offspring directly or result from an interaction with the characteristics or position of the nest cavity. For instance, exposure to wind may be a dominant factor in coastal sites, whereas in mountainous terrain or northern regions, variation in altitude and solar exposure may create major environmental differences over small distances. Moreover, the continual growth of trees and forests means that the environment can change significantly during long-term investigations at the same study site. Forest management practices, particularly the removal of old or dead trees that contain excavated or natural holes, will have major effects on the bird species present due to rapid changes in cavity availability, which may influence other biological interactions at intraspecific and interspecific levels (e.g. Newton 1994, Quine et al. 2007, Webb et al. 2007, Wesołowski 2007, Camprodon et al. 2008, Cornelius et al. 2008, Blondel et al. 2010). Habitats shared with humans (e.g. city parks, suburban gardens) during the breeding season may be more likely to be occupied by individuals not disturbed by the presence of human activity (Remacha & Delgado 2009, Møller 2010). The fact that characteristics of the habitat and densities of excavators and secondary hole-nesters may be influenced by anthropogenic activities means that the characteristics of natural cavities used may not (always) mirror the situation in areas that are relatively unaffected by humans, where they still exist. Black-capped Chickadees *Poecile atricapillus*, for example, will readily utilize nestboxes in urban landscapes where natural cavities are scarce, and even accept fairly unusual nesting substrates (e.g. hollow fenceposts, Smith 1991). This same species shows low acceptance of these same nestboxes in mature forests where ample natural nesting sites exist (K. Otter, unpublished data). The same is true for Willow Tits *Poecile montanus*, which do not accept nestboxes in northern Finland (i.e. they excavate new holes in decaying stumps each year, Orell & Ojanen 1983), but readily use special nestboxes filled with coarse saw-dust in southern Sweden (von Brömssen & Jansson 1980). Thus studies of birds nesting in cavities in anthropogenically modified habitat may not be an ideal basis for generalisations about the best design, placement and management of nestboxes. Thus, there are limits to replicating studies in different areas and to what can be and should be included in the description of the study.

Perhaps the existence of logistic constraints on exactly replicated research in free-ranging populations may justify the use of experiments in semi-natural conditions better controlling for possible interactions between nestbox characteristics and the social or physical environment surrounding the boxes (e.g. Kempenaers & Dhondt 1991, Velky et al. 2010, but see Lambrechts et al. 1999). The recommendations presented below are intended to

be a minimum list, and the main purpose of the list is to reduce the likelihood that differences between studies are not an artefact of differences in the characteristics of the nestboxes used. Authors are therefore urged to describe all those aspects of their study sites they consider relevant in comparison to other sites.

List of recommendations

We urge authors, referees and editors to ensure that the following information is accessible or provided in future publications, or at least as an online supplement:

1. Nestbox dimensions (e.g. Table 3). Include a minimum amount of information on nestbox design, including size and position of the entrance hole, thickness and material of nestbox walls, and width, breath, and height of the internal chamber;

2. Location of nestboxes. Report the position of nestboxes (e.g. placed against tree trunks or hanging from a branch attached to a cable or metal hook), including height, supporting structure (tree, wall, post), orientation, the average distance between neighbouring boxes and their density (number of boxes per ha);

3. Maintenance procedures of nestboxes. Report whether and when old nests are removed, and whether nestboxes or nests are treated to remove parasites or microorganisms (e.g. pesticides, micro-wave treatments, rot prevention chemicals). Perhaps most importantly, researchers should report whether nestboxes are cleaned out before each new nesting season (e.g. to remove winter nests from secondary hole-nesting mammals). The use of weather protection devices should also be mentioned. It should be noted if boxes are removed from the study sites between each breeding season. Because old or damaged boxes are often replaced by new boxes, a study site can contain nestboxes differing widely in age, which should be noted.

4. Protection of nestbox occupants. If the nestboxes incorporate any anti-predator features, including devices to reinforce entrance holes (e.g. metal plates), or to prevent predators from entering the nestbox chamber (e.g. pipes to lengthen the entrance) they should be mentioned.

5. Inspection of nestboxes. Report how frequently (and for how long) nestboxes are opened to allow the contents to be inspected, whether they open at the front, side or the roof, and whether any nestbox traps are used to capture the occupants. In addition, it would be useful to know how long the study has been operating in this way, the overall level of desertion of reproductive attempts and the degree of adult and natal philopatry, as these will all potentially contribute to the strength of conditioning or selection on the breeding adults at the site.

6. Study-site characteristics. Report abiotic and biotic factors at local study sites which could conceivably affect 'nestbox-environment' interactions. Report the frequency of artificial holes relative to the frequency of natural or excavated holes, or if this is impossible (e.g. for holes >10 m high or in forest with difficult topography or dense understory) provide at least data about the dominant tree species, age of tree stands, and the proportion of nestboxes occupied. The availability of similar or different nestboxes in the general geographic area should also be given if possible, as people other than researchers erect nestboxes in many countries. To assess the representativeness of the biological samples taken from the nestboxes, a reference survey to assess properties of natural holes could be carried out in each nestbox plot. Research is needed through which information on the phenotypic traits of interest is obtained from breeders in natural or excavated holes and these traits are compared with that of birds breeding in nestboxes. It should also be noted whether there are any particular habitat management practices (e.g. selective logging of trees) or patterns of habitat use (common or occasional recreational areas during the breeding season), which could affect the birds' biology.

PERSPECTIVES

Future research projects dealing with biological consequences of variation in one or more nestbox characteristics could either focus on preferences of birds for particular nestboxes or on the biological consequences of the choice of particular types of boxes. For instance, insectivorous birds which are capable of laying many eggs may prefer to breed in large nestboxes if hole size provides reliable information about tree trunk diameter and canopy size, which could influence the availability of defoliating insects required to rear the chicks. Birds may reduce their clutch size in small nestboxes in order to adjust the number of eggs laid to the size of the nest cup, thereby improving incubation behaviour, reducing sibling competition for limiting space within the nestbox-chamber or reducing problems related to hyperthermia in hot environments (e.g. van Balen 1984). Testing

these competing hypotheses about nestbox choice or adjustment of life-history traits after a nestbox has been accepted will require different types of experimental design, which have been conducted or proposed in former investigations (e.g. Löhrl 1973, 1980, García-Navas et al. 2008). Studies looking at preferences could erect two or more nestbox types close together, such as on the same tree (e.g. Bortolotti 1994) , to better control for variation in environmental factors other than nestbox design. Quantifying parental or territory characteristics at the same time may test whether preferences for particular nestboxes (e.g. of a given orientation) are adjusted to particular phenotypic characteristics of the parents or the territory (e.g. dominant wind direction). Studies looking at the consequences of occupying a particular nestbox type while controlling for biases due to nestbox preferences could allow birds to settle on a territory then change nestbox types. These field studies should ideally avoid experimentally induced biases caused by nest desertion as much as possible. Research protocols should also be adjusted to the life-histories of the biological models involved, which may require preliminary investigations before adequate experimental protocols can be performed. For instance, the consequences of differences in nestbox design for roosting can only be studied in populations where roosting in nestboxes has been confirmed (e.g. Dhondt et al. 2010).

Nestbox characteristics (>10), parental phenotypes (age, behaviour, physiology, morphology, genetics), habitat charactertistics (e.g. presence of other organisms, local climate, light conditions, type of habitat, social factors, resources, population density and composition) and fitness components (e.g. laydate, clutch size, egg characteristics, egg hatching success, brood size, fledging success, offspring phenotypes) may interact in a complex manner, so there are ample opportunities for development of research projects in different parts of the world aimed to better understand these complex relationships. What follows is a short list of topics that could be developed in future research or education projects.

1. The biological consequences of existing variation in nestbox design

Different research teams use replicates in nestbox design that are currently often segregated, so that biological consequences of existing spatial variation in nestbox design cannot always be properly investigated. Existing spatial variation in nestbox design could be redistributed across study sites so that design replicates become properly interspersed. For instance, the effect of differences in nestbox material commonly used (wood versus a woodconcrete mix) could be investigated in local study plots following the experimental designs proposed above (e.g. García-Navas et al. 2008).

2. The biological consequences of nestbox size in heterogeneous environments

Previous field investigations focusing on the life-history consequences of nest-chamber size have usually only compared two nestbox size classes (e.g. Löhrl 1977, van Balen 1984, Slagsvold & Amundsen 1992, but see e.g. Moeed & Dawson 1979, Korpimäki 1985) often without taking environmental or social factors into account. If bigger nestbox chambers would result in larger broods, then smaller nest-chambers which cause birds to produce smaller clutches may improve fledging success because of a reduction in brood size, especially in poor habitat or younger forest patches. If larger boxes would always be preferred regardless of the richness of the habitat, the hypothesis that large nestboxes can become severe ecological or evolutionary traps in poor habitats can be experimentally tested, both at the individual (Schlaepfer et al. 2002, Robertson & Hutto 2006) and population level (Schlaepfer et al. 2002, Mänd et al. 2009). These investigations require simultaneous studies of the proximate mechanisms involved in nestbox choice (e.g. genetic, environmental or historical basis) and the fitness consequences of the choice of a particular nestbox type in different environmental conditions (e.g. many versus few food resources).

3. The biological consequences of the nestbox chemical environment

The biological consequences of variation in the types of wood used for the construction of nestboxes have to our knowledge not been experimentally investigated. In North America, Western Red Cedar *Thuja plicata* is often advocated for nestboxes on hobbyist websites. This wood is commonly used to line trunks and wardrobes due to the aromatics it omits deterring moths, and it likely has an effect on insect colonization of nestboxes as well. The different types of wood (e.g. oak versus pine versus exotic) and the chemical compounds they contain may influence the species assemblage of invertebrates and microorganisms that colonize nestboxes, and thereby potentially interact with the avian

occupants. These effects may be intensified in older nestboxes that are not cleaned by researchers or are rarely opened for monitoring.

4. Nestbox design, perceived microclimate and biological consequences

Several nestbox characteristics, such as wall thickness, or the material (e.g. García-Navas et al. 2008) or colours used for the construction of nestboxes, may influence the nature and stability of the nest microclimate and therefore the functioning and interactions amongst organisms occupying these cavities. The nestbox characteristics which are more likely to insulate parents, eggs and offspring against these environmental fluctuations will likely differ across latitudes or altitudes, which could be investigated with both observational and experimental approaches, also within the framework of climate change. If the presence of old nests favours roosting conditions in winter (Pinowski et al. 2006), then nestbox maintenance procedures may influence climate-bird interactions at the time of nestbox occupation (e.g. García-Navas et al. 2008 for arguments in the methods).

5. Effects of different combinations of nestbox characteristics

An experimental design using different nestbox characteristics as treatments should ideally alter box characteristics in such a way that the 'optimal' nestbox shape for given individuals, territories, populations or habitats can be identified with high precision. This approach calls for field experiments combining different nestbox properties to better reflect variation in natural or excavated holes exploited. It would require a large increase in the number of nestbox types to be erected within or across study plots. As an example, a design combining three classes in wall thickness, cavity depth and cavity width (small, intermediate, and large values), varying independently of each other among nestboxes, would require 27 different nestbox types. In addition, each type should be sufficiently replicated either within or across study populations for the quantification of intra-nestbox type (random) variation. These boxes should ideally be erected "randomly" in a local plot following the designs A1-A3 described in Hurlbert (1984) or experimental designs proposed above. Such an experiment would provide unique opportunities for the study of phenotypic plasticity in life-history traits, with

nest-cavity characteristics perhaps to be considered as physical constraints imposed on the plasticity of nest building-dependent life-history traits. Such a project has been conducted before (Korpimäki 1985).

6. Nestbox design and nest building

Secondary hole-nesters accepting cavities initially created by other species often have more complex nests than do primary hole-nesters. If nests from secondary hole-nesters are adjusted in response to shortcomings in nest-cavity characteristics, the consequences of interactions between nest structure or composition and nestbox characteristics could also be investigated. For instance, bigger nests may be built in artificial nestboxes with a thinner or colder nestbox wall (e.g. Nager & van Noordwijk 1992), perhaps to provide more efficient protection against meteorological fluctuations in colder environments (Pinowski et al. 2006). Larger nests appear to be sexually selected in birds in general (e.g. Soler et al. 1998), and small hole chambers may prevent the full expression of this phenotypic trait. Larger nests built in larger/deeper nestboxes (cf. Mazgajski & Rykowska 2008) may also contain and develop larger populations of ectoparasites (e.g. Tripet & Richner 1997) or other invertebrates. All this suggests that causal relationships between nestbox characteristics, nest characteristics and avian characteristics may be complex, deserving further study.

7. Research protocols, avian selection and conditioning

Different research teams do not always use the same procedures for catching birds or monitoring nestbox contents. What are the effects of research-group dependent behaviours on bird populations breeding or roosting in artificial nestboxes? Do different regimes of catching and monitoring result in different levels of brood desertion or condition? If adults are caught in a nestbox while feeding chicks, are they more cautious when entering the nest in the future, relative to birds caught in a mist-net outside the box? Perhaps these research-group effects may lead to consistent differences in fitness components across study sites or research groups. Avian conditioning to researcher effects over the lifetime of an individual, or selection over time, with adults that better cope with researcher disturbance having higher reproductive success and passing on these personalities to their offspring, could also be investigated.

8. Increased standardization and communication

With the development of the internet and the global real-time availability of information across all researchers, much more attention should be paid to the construction of standardized protocols over large geographic areas (e.g., http://golondrinas.cornell.edu). Project-specific websites and list-serves can help in all aspects of broadly based collaborations, from standardization of nestbox plans and construction to the design and execution of experiments to objectively evaluate changes to those designs.

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STRESZCZENIE

[Modele skrzynek lęgowych używanych do badań dziuplaków wtórnych: ich wpływ na uzyskiwane wyniki oraz niespójności metodyczne]

Szerokie wykorzystywanie sztucznych miejsc gniazdowych, jakimi są skrzynki lęgowe w badaniach dziuplaków, szczególnie drobnych gatunków wróblowych, doprowadziło do znacznego zwiększenia naszej wiedzy o ich ekologii, fizjologii i zachowaniu. Skrzynki lęgowe ułatwiają kontrole lęgów, eksperymentalne zabiegi, którym poddawane są jaja lub pisklęta oraz chwytanie, identyfikowanie i eksperymenty na ptakach dorosłych. Z drugiej strony tak częste wykorzystywanie sztucznych miejsc lęgowych prowadzi do powstania jak do tej pory pomijanego, ale potencjalnie istotnie wpływającego na uzyskiwane wyniki, efektu samych skrzynek — ich wymiarów, wysokości umieszczenia, sposobu konstrukcji, otwierania czy konserwacji.

W pracy podsumowano, w jakim zakresie publikacje naukowe dotyczące dziuplaków wtórnych dokumentują charakterystykę skrzynek lęgowych wykorzystywanych do badań (wymiary, kolor, materiał, z którego są wykonane itd.). Do analizy publikacje podzielono na te opublikowane przed i po roku 1992, ponieważ w tym roku ukazały się drukiem dwie prace zalecające m. in. dokładne opisywanie stosowanych skrzynek lęgowych. Należało zatem przyjąć, że w nowszych pracach (po 1992) właściwości skrzynek (wymiary, materiał, z którego są wykonane itd.) powinny być opisywane dokładniej. Jednakże analiza rozdziałów opisujących metody w łącznie 696 publikacjach wykazała, że w pracach publikowanych po 1992 informacje dotyczące wykorzystywanych w badaniach skrzynek są jeszcze bardziej fragmentaryczne (Fig. 1).

W pracy zwrócono uwagę, że skrzynki lęgowe są najczęściej ujednolicone, a ich charakterystyka odzwierciedla tylko część cech dziupli naturalnych. Należy pamiętać, że w przypadku dziupli naturalnych, zmienność, szczególnie wymiarów wewnętrznych, czy wysokości, na której są umieszczone, jest bardzo duża zarówno pomiędzy poszczególnymi gatunkami dziuplaków, jak i w obrębie tego samego gatunku (Tab. 1). Prócz tego analiza cech skrzynek lęgowych używanych przez różne zespoły badaczy wykazała, że nawet przy prowadzeniu badań na tym samym gatunku, stosowane skrzynki i metody mogą bardzo się różnić. Dużą wartością pracy jest zestawienie charakterystyk skrzynek lęgowych stosowanych do badań najpospolitszych dziuplaków, przede wszystkim w Europie (Apendyks 1).

W pracy podano listę typowych cech, charakteryzujących używane w badaniach skrzynki lęgowe, które powinny być zamieszczane w publikacjach. W pracy wyjaśniono konieczność prezentowania takich informacji, podając przykłady, jak charakterystyka skrzynek lęgowych wpływa na dziuplaki. Na zakończenie przedstawiono kilka generalnych zagadnień związanych ze zmiennością wykorzystywanych do tej pory skrzynek lęgowych, które należałoby poddać badaniom.

Appendix 1. Characteristics of artificial nestboxes exploited by hole-nesting passerine birds for breeding or roosting. Abbreviations: Nestbox position: H — height above the ground (in m), O — entrance orientation (r = random, a = all same direction, with direction in parentheses, o = other), ST — nestbox substrate (t = tree, f = fence, b = building, p = post, aw = attached to a branch with a hook or wire away from hard substrate); Nestbox characteristics (all in cm): EHD — entrance hole diameter, WT — wall thickness; NBCS — nestbox chamber size (internal height x width x depth, in the case of circular bottom diameter (diam.) is provided), D — distance between lower edge of entrance hole to bottom of nest chamber, M — material used for construction, Source — citation or publication referring to a nestbox type or citation of people that provided data.— lack of data. Species: *P.m.* — *Parus major*, *P. v.* — *Parus varius*, *C.c.* — *Cyanistes caeruleus*, *P.a* — *Periparus ater*, *P.p.* — *Poecile palustris*, *Fh.* — *Ficedula hypoleuca*, *Fa.* — *Ficedula albicollis*.

Species	Period	Study site	Nestbox position			Nestbox design characteristics					Source
			H	O	ST	EHD	WT	NBCS	D	M	
Paridae											
C.c.	2001–2008	Brabtia, DZ	1.5–2	o	t	2.6	2	17.5 x 9 x 11	9	Wood-brown	N. Ziane; Chabi & Isenmann 1997, Ziane et al. 2006
C.c.	2001–2004	EL-Ghorra, DZ	2	o	t	2.6	2	17.5 x 9 x 11	9	Wood-brown	N. Ziane; Chabi & Isenmann 1997; Ziane et al. 2006
P.m., C.c.	1959–2010	Ghent, BE	2.5	-	t	3.0–3.2	-	23 x 9 x 12	16.5	Wood	F. Adriaensen; Dhondt et al. 1984
P.m., C.c.	1978–mid 1980s	Antwerp, BE	2.5/1.5	-	t	2.6/3.2	1.5	23 x 9 x 12	16.5	Pine	F. Adriaensen; Dhondt 2010
P.m., C.c.	Mid 1980s–2010	Antwerp, BE	2.5/1.5	-	t	2.6/3.2	1.5	23 x 9 x 12	16.5	Plywood	F. Adriaensen; Dhondt 2010
P.m., C.c.	-	Antwerp, BE	-	-	t	2.6/3.0	1.5	23.5 x 9 x 12.5	16.5	Wood (green)	M. Eens
C.c.	1982–2004	Hrvatsko Zagorje, HR	-	-	-	2.9	-	23 x 12 x 12	-	Spruce	Dolenec 2007
P.m., C.c.	2005–2010	Olomouc, CZ	~1.6	a (S)	t	3.2	2	22.5–25.5 x 11.5 x 13	17.5	Spruce	V. Remeš; Matysiokova & Remeš 2010
P.m.	1995–2010	Kilingi-Nõmme, EE	1.5–2	o	t	3.5–4.0	2.4	30 x 11 x 11	17–19	Wood	R. Mänd; Mänd et al. 2005
P.m., C.c., P.a, P.p.	-	Rødhus, DK	1–2	r	t	2.8/3.2	1.5	25 x 15 x 15	20	Spruce	A. P. Møller; Møller et al. 2010
P.m., C.c.	1976–2010	Oxford, UK	-	-	aw	2.6/3.2	3 2	17–18 x 12 diam	13/14	Schwegler 2M	A. Gosler; Perrins 1979, McCleery et al. 1996
P.m., C.c.	1988–1993	Sussex, UK	-	-	-	≤ 3.18 (1991–93:2.86)	2.2	13.8–17.8 x 10 x 11	8.5	Pine	M. Stenning; Stenning 2008
P.m., C.c., P.a, P.p.	1949–1990	Gloucestershire (Dean), UK	-	-	-	2.8	1.9	17.8–25.4 x 12.7 x 10.2	10.8	Rough sawn, Plank	M. Stenning; Campbell 1968; Stenning et al. 1988
P.m., C.c., P.a, P.p.	1990–2010	Gloucestershire (Dean), UK	~3	r	t	2.8	1.8	21 x 11 x 17 Sloping roof	14.2–15.2	5-plywood	A. Goodenough; Goodenough et al. 2008
C.c.	1997–2010	Lancaster, UK	~1	r	t	2.5	2	20 x 15 x 15	12	Sitka spruce	M. Mainwaring; Mainwaring & Hartley 2009

| Species | Period | Study site | Nestbox position | | | Nestbox design characteristics | | | | | Source |
			H	O	ST	EHD	WT	NBCS	D	M	
P.m., C.c.	1991–2010	Harjavalta, FI	~2	r	t	3.2 (1991–96: 3.6–3.8)	2.6	20–22 x 12 x 12	17	Spruce	T. Eeva; Eeva et al. 1994
P.m.	1969–2009	Oulu, FI	1.5 (2.5–4)[1]	r	t	3.2–3.4	2.0–2.2	24 x 12.5 x 12.5 / 24 x 11 x 11	16.5–17.5	Pine	M. Orell; Orell & Ojanen 1983a
C.c.	1998–2009	Oulu, FI	1.5	r	t	2.8	2.2	23 x 8 x 12.5	14	Pine	S. Rytkönen
P.m.	2001–2010	Southeastern Avignon, FR	2	a (SE)	t	3.2	3[2]	17–18 x 12 diam.	13/14	Schwegler B1	J. C. Bouvier; Bouvier et al. 2005
P.m., C.c.	1991–2010	Montarnaud, FR	~2–3[1]	o[1]	t[1]	2.6/3.2	3[2]	17–18 x 12 diam.	13/14	Schwegler B1 or concrete[3]	P. Perret; Dias & Blondel 1996, Lambrechts et al. 2008
P.m., C.c.	1985–1997	Puéchabon, FR	~1.5–3[1]	o[1]	t[1]	2.6/3.2	3[2]	17–18 x 12 diam.	13/14	Schwegler B1 or concrete[3]	P. Perret; Dias & Blondel 1996, Lambrechts et al. 2008
P.m., C.c., P.a.	1976–2010	Ventoux, FR	~2–3[1]	o[1]	t[1]	2.6/3.2	3[2]	17–18 x 12 diam	13/14	Schwegler B1 or concrete[3]	P. Perret; Blondel 1985
P.m., C.c.	1993–2010	Muro, Corsica, FR	~2–3[1]	o[1]	t[1]	2.6/3.2	3[2]	17–18 x 12 diam	13/14	Schwegler B1 or concrete[3]	P. Perret; Lambrechts et al. 2004
P.m., C.c., P.a.	1976–2010	Pirio,Corsica, FR	~2–3[1]	o[1]	t[1]	2.6/3.2	3[2]	17–18 x 12 diam.	13/14	Schwegler B1 or concrete[3]	P. Perret; Blondel 1985
P.m., C.c.	1982–2010	Pilis Mountains, HU	1.7	r	t	3.2	3	24 x 11 x 11	15	Black Locust	J. Török
P.m., C.c., P.a., P.p.	1993–2010	Sicily, IT	-	-	-	3.4	1	15 x 10.5 x 15	7.8	Coniferous wood (esp. Fir)	B. Massa; Massa et al. 2004
P.m.	1990–1992	Tyrrhenian coast, Central IT	~3	-	t	3.5/3.7/6	-	22 x 14 x 14 ; 35 x 25 x 25[5]	-	Wood	A. Sorace; Sorace & Carere 1996
C.c.	1996–2003	Sicani Mountains, Madonie, IT	-	-	-	3.2/5	-	20 x 15 x 15 ; 30 x 20 x 20[5]	-	Wood	B. Massa; Sarà et al. 2005
P.m.	Early 1980s–2010	various places, LV	-	-	-	4.5–5.0 triangle	2.5	- x 12 x 12	14	Spruce, Pine, Aspen	O. Keišs; Vilka 1999
P.m., C.c., P.a.	1978–2010	5 districts, LT	-	-	-	3.5	-	23 x 12 x 12	-	Wood	R. Juškaitis; Juškaitis 2006
P.m., C.c.	1955–2010	Oosterhout, NL	2.5	-	t	3.2	1.5	23 x 9 x 12	17	Wood	A. J. van Noordwijk; van Balen 1984
P.m., C.c.	1955–2009	Hoge Veluwe, NL	2	-	t	3.2	1.5	23 x 9 x 12	17	Wood	A. J. van Noordwijk; van Balen 1984
P.m., C.c., P.a.	1955–2010	Vlieland, NL	2.5 (since 1996 partly 1)	-	t	3.2	1.5	23 x 9 x 12	17	Wood	A. J. van Noordwijk; van Balen 1984
P.m., C.c.	1975–2010	Warnsborn/ Westerheide, NL	1/2.5	-	t	3.2	1.5	23 x 9 x 12	17	Wood	A. J. van Noordwijk; van Balen 1984
P.m., C.c.	1983–2010	Buunderkamp, NL	2.5	-	t	3.2	1.5	23 x 9 x 12	17	Wood	A. J. van Noordwijk; van Balen 1984

Continued on the next page

Species	Period	Study site	Nestbox position			EHD	WT	Nestbox design characteristics		M	Source
			H	O	ST			NBCS	D		
P.m., C.c., P.a.	1979–1984 (–1988)	Northern PL	~4	a (SE)	t	3.5	2 [4,5]	29 x 10 x 11	17.5	Wood	W. Kania
P.m., C.c., P.a.	1979–1984 (–1988)	Northern PL	~4	a (SE)	t	4.7	2 [4,5]	37 x 13 x 14	23.3	Wood	W. Kania
P.m., C.c.	1999–2010	Łódź, PL	-	-	-	2.9	2.2	22 x 9 x 10; 30 x 11 x 11; 36 x 13 x 13	12–29	Pine	J. Bańbura; Alabrudzińska et al. 2003
P.m., C.c.	2005–2010	Sekocin, Warsaw, PL	2.5	a	t	2.7/3.2	2.5[8]	22 x 13 x 13	-	Wood	T. Mazgajski; Mazgajski & Rykowska 2008
P.m.	2003–2007	Coimbra, PT	2–3	a	t	2.8	1.5	18.5 x 13 x 12	16.5	Wood	A. C. Norte; Norte et al. 2008, 2010
P.m.	2004–2007	Coimbra, PT	2–3	a	t	3	2	18 x 12 x 15	14	Wood	A. C. Norte; Norte et al. 2008, 2010
P.m.	1979–2010	South Karelia, RU	1.5–1.8	o	t	3–3.4	2.4	26 x 10–12 x 10–12	15–16	Pine, Spruce	A. Artemyev; Artemyev 2008
P.m. P. v.	2007–2010	Hongreung, Seoul, KR	1.2–1.8	r	aw	3/3.5	2	25–30 x16 x 15	13.5	Douglas fir	C. R. Park
P.m..	2009–2010	Seogwipo City, KR	1.2–1.8	r	aw	3/3.5	2	27.5 x 16 x 15	13.5	Douglas fir	C. R. Park
P.m.	2005–2010	Catalonia, ES	3–5	o	aw	4	1.5–2	35 x 13 x 15[5]	24	Scotch pine, recycled transport pall	J. Camprodon; Baucells et al. 2003
C.c., P. p.	2005–2010	Catalonia, ES	3–5	o	aw	2.5	1.5-2	26 x 11 x 9[5]	25	Scotch pine, Recycled transport pall	J. Camprodon; Baucells et al. 2003
P.m., C.c., P.a, P.p.	1999–2010	Catalonia, ES	3–5	o	aw	2.6/3	1.0–2	25 x 10 x 15	18	Scotch pine, recycled transport pall	J. Camprodon; Baucells et al. 2003
P.m.,C.c., P.a. P. p.	1999–2004	Catalonia, ES	3–5	o	aw	3.1	2	26.5 x 10.1 x 19.4[8]	-	GACO 2000 Pine, recycled transport pall	J. Camprodon; Camprodon et al. 2008
P.m.	-	Sagunto, ES	-	-	-	3.2	1.5	18.5 x 10.6–11.6 x 10.6–12.1[4]	8.4–12.64	Pine	E. Barba; Álvarez & Barba 2008
P.m., C.c., P.a.	1984–2010	La Hiruela -Madrid, ES	2–4	r	t	3.5	1.5	17.5–19.5 x 11.5 x 13	10	Pine	J. Potti; Potti 2009
P.m., C.c., P.a.	1989–2010	Valsain, ES	3–5	r	aw	3.5	1.5	17.5–19.5 x 11.5 x 13[7]	10	Pine	J. Moreno; Merino et al. 2000, Sanz et al. 1993, 2000
P.m., C.c., P.a.	-	Göteborg, SE	-	-	-	3.2	1–3	17–18/21 x 12 diam.	15.5	Birch trunk	B. Silverin
C.c., P.p.,	1983–2010	Revinge, SE	~1.5	r	t	2.6	2.2	20 x 7.8 x 9.5	13	Spruce	J. Å. Nilsson; Nilsson & Smith 1988

Species	Period	Study site	Nestbox position			EHD	WT	Nestbox design characteristics			Source
			H	O	ST			NBCS	D	M	
P.m.	1991–2010	South Skåne, SE	~1.5	r	t	3.4	2.2	24 x 9.5 x 12.4	16	Spruce	J. Å. Nilsson; Nilsson & Källander 2006
P.m., C.c.	1980–2010	Gotland, SE	1.5–1.7	r	t	3.2	2	25–30 x 10 x 10	20	Pine	L. Gustafsson
P.m., C.c.	1989–1997	Basel, CH	-	-	-	2.8/3.2	c. 1.8	22 x 12 x 15	20	Wood	B. Naef- Daenzer; Naef-Daenzer & Keller 1999
P.m., C.c.	1985–1992	Birsfelder Hard, Basel, CH	2.5		t	3.2	1.2	23 x 9 x 12	17	Wood/ concrete	A. J. van Noordwijk
P.m., C.c., P.a.	1985–1992	Blauen, Basel, CH	2.5	-	t	3.2	1.2	23 x 9 x 12	17	Wood	A. J. Van Noordwijk
P.m., C.c., P.a.	1992–1994	Celerina, CH	-	-	-	2.6/3.2	3[2]	18 x 12 diam.	c.15	Schwegler, Wood-concrete	B. Naef-Daenzer; Mattes et al. 1996
P.m.	1990–2010	Bern, CH	-	-	-	3	-	- x 12.5 x 12.5	21	Wood	Heeb et al. 1996
P.a.	1999–2005	Guan-Yuan, Taiwan	~3	a	t	3	0.9	18 x 13 x 13[5]	13	Lauan, Plywood	M. T. Shiao; Shiao et al. 2009
P.a.	2004–2005	Guan-Yuan, Taiwan	~3	a	t	4.5	0.9	18 x 13.5 x 13.5[6]	11	Lauan Plywood	M. T. Shiao; Shiao et al. 2009
Muscicapidae											
F.h.	Mid 80s–1987	Antwerp, BE	2.5	-	t	3.2	1.5	23 x 9 x 12	16.5	Plywood	Dhondt et al. 1987
F.a.	2005–2010	Olomouc, CZ	~1.6	a (S)	t	3.2	2	22.5–25.5 x11.5 x 13	17.5	Spruce	V. Remes; Matysiokova & Remes 2010
F.h.	1995–2010	Kilingi-Nõmme, EE	1.5–2	o	t	3.5-4.0	2.4	30 x 11 x 11	17–19	Wood	R. Mänd; Mänd & Tilgar 2003
F.h.	1949–1990	Gloucestershire (Dean), UK	-	-	-	2.8	1.9	21.6x12.7x10.2 Roof (17.8-25.4)	10.8	Rough sawn Plank	M. Stenning; Campbell 1968; Stenning et al. 1988
F.h.	1990–2010	Gloucestershire (Dean), UK	~3	r	t	2.8	1.8	21 x 11 x 17 Sloping roof	14.2–15.2	5-plywood	A.Goodenough; Goodenough et al. 2008
F.h.	1991–2010	Harjavalta, FI	~2	r	t	3.2 (1991–96:3.6–3.8)	2.6	20–22 x 12 x 12	17	Spruce	T. Eeva; Eeva et al. 1994
F.a.	1982–2010	Pilis Mountains, HU	1.7	r	t	3.2	3	24 x 11 x 11	15	Black Locust	J. Török
F.h.	Early 1980s–2010	various places, LV	-	-	-	4.5–5.0 triangle	2.5	- x 12 x 12	14	Spruce, Pine, Aspen	O. Keišs; Vilka 1999
F.h.	1978–2010	5 districts, LT	-	-	-	3.5	-	23 x 12 x 12	-	Wood	R. Juškaitis; Juškaitis 2006
F.h.	1955–2010	Hoge Veluwe, NL	2	-	t	3.2	1.5	23 x 9 x 12	17	Wood	A. J. van Noordwijk; van Balen 1984
F.h.	1975–2010	Warnsborn/ Westerheide,NL	2.5/1	-	t	3.2	1.5	23 x 9 x 12	17	Wood	A. J. van Noordwijk; van Balen 1984
F.h.	1983–2010	Buunderkamp,NL	2.5	-	t	3.2	1.5	23 x 9 x 12	17	Wood	A. J. van Noordwijk; van Balen 1984

Species	Period	Study site	Nestbox position			EHD	Nestbox design characteristics				Source
			H	O	ST		WT	NBCS	D	M	
F.h.	1979–1984 (–1988)	Northern PL	~4	a (SE)	t	3.5	2[5]	29 x 10 x 11	17.5	Wood	W. Kania
F.h.	1979–1984 (–1988)	Northern PL	~4	a (SE)	t	4.7	2[5]	37 x 13 x 14	23.3	Wood	W. Kania
F.h.	2005–2010	Sekocin, Warsaw, PL	2.5	a	t	3.2	2.5[8]	22 x 13 x 13	-	Wood	T. Mazgajski; Mazgajski & Rykowska 2008
F.h.	1979–2010	South Karelia, RU	1.5–1.8	o	t	3–3.4	2.4	26 x 10/12 x 10/12	15–16	Pine, spruce	A. Artemyev; Artemyev 2008
F.h.	1984–2010	La Hiruela, Madrid, ES	2–4	r	t	3.5	1.5	17.5–19.5 x 11.5 x 13	10	Pine	J. Potti; Potti 2008
F.h.	1989–2010	Valsain, ES	3–5	r	aw	3.5	1.5	17.5–19.5 x 11.5 x 13[7]	10	Pine	J. Moreno; Moreno et al. 2006, 2008
F.a.	1980–2010	Gotland, SE	1.5–1.7	r	t	3.2	2	25–30 x 10 x 10	20	Pine	L. Gustafsson
F.h.	1985–1992	Blauen, Basel, CH	2.5	-	t	3.2	1.2	23 x 9 x 12	17	Wood	A. J. van Noordwijk
Passer domesticus											
	-	Lexington, Kentucky, USA	2–4	o	b	3.9	1.9	28 x 14.1 x 14.1	16	Pine (white)	I. Stewart; Westneat et al. 2002
Sturnus vulgaris											
	-	Antwerp, BE	-	-	-	5	1.5	30.25 x 13.5 x 16	19	Wood-brown	M. Eens
	-	Warsaw, PL	4	r	t	4.7–5	2.5[8]	- x 12–13 x 15	22	Wood	T. Mazgajski; Mazgajski 2007
	1900–2009	Scania, SE	~2/~3.5	-	t	5.0	2.0–2.4	36 x 13 x 13	24	Spruce	H. G. Smith; Smith 1995
Troglodytes aedon											
	1980–2010	McLean County, Illinois, USA	~1.5	r	p	3.2	1.85[5]	22 x 8.4/8.8 x 9	13	Coniferous (brown/redwood)	C. Thompson; Drilling & Thompson 1988
	1989–2010	Big Horn, Wyoming, USA	~1.5	-	p	2.54	2	18 x 10 x 10	13	Cedar	L. S. Johnson; Johnson 1996
Tachycineta bicolor											
	1997–2010	UWM Field Station, WI, USA	~1.5	o	p	4	1	20.3–25 x 13 x 13	13	Plywood	L. Whittingham, P. Dunn; Whittingham & Dunn 2000
	-	Queen's, Ontario, CAN	-	-	-	4	1	20.3–25 x 13 x 13	13	Plywood	P. Dunn; Rendell & Robertson 1993
	-	Prince George, BC, CAN	-	-	-	3.2	1.5	23–30 x 13.5 x 12.5	13	Plywood	R. D. Dawson; Dawson et al. 2005

Details on nestboxes design for other *Tachycineta* can be found on http://golondrinas.cornell.edu/Data_and_Protocol/NestBoxDesignCentimeters.html

Comments:

[1] Height, orientation and placement of nestboxes may be influenced by the position of trees or branches used to erect nestboxes. Height of nestboxes may also differ between study sites or study periods in a given region (1969–1988, One nestbox colony in Oulu);

[2] Schwegler boxes have a removable front panel which is thinner (1.5–1.8 cm) than the wall thickness of the main body;

[3] Some self-made nestboxes consist of concrete or unstandardised mixtures of concrete and wood (P. Perret, Montpellier, pers. comm.);

[4] Self-made wooden nest-boxes are usually not "identical" in structure. For instance E. Barba measured a sample of 10 boxes of which the average values are provided in this table. Nestboxes may also differ in shape because they come from different suppliers (e.g. Álvarez & Barba 2008);

[5] Nestboxes all have a permanently mounted trapdoor (e.g. a sliding sheet-metal piece mounted under a redwood piece) over the entrance. The result is that the entrance hole is deeper than the nestbox wall (e.g. box wall thickness of 1.8 + 2.0 cm redwood trapdoor = 3.8, C. Thompson pers. comm.). Nestboxes all also have an elongated entrance channel in some study sites (one out of two nestboxes in northern Poland, W. Kania, pers. com.);

[6] Some boxes have been constructed to attract specific species (e.g. short-toed tree creeper *Certhia brachydactyla*, nuthatch *Sitta europaea*, Italian sparrows *Passer italiae*, common dormouse *Muscardinus avellanarius*, or green-backed tits *Parus monticolus*), but also exploited by other secondary hole-nesters (e.g. blue, great, or coal tit);

[7] Some nestboxes have a slit (1–1.5 cm) between the roof and the frontal lid increasing light conditions inside the nestbox chamber (J. Moreno pers. comm.);

[8] In some nestbox types, a small peace of wood has been added under the entrance hole inside the nestbox chamber, i.e. a small table reinforcing the nest-box also used by adults before visiting the nest;

[8] In some nestbox types, the front wall is thicker than the other walls (e.g. front wall 5 cm, other walls 2.5 cm, e.g. Mazgajski & Rykowska 2008); Most nest-boxes have circular entrance holes (but see e.g. O. Keišs).

Source (In alphabetic order, full list available on request):
Alabrudzińska et al. 2003. Acta Ornithol. 38: 151–154; Álvarez & Barba 2008. Acta Ornithol. 43: 3–9; Artemyev 2008. Moscow, Nauka, pp. 1–267 (In Russian); Baucells et al. 2003. Lynx Edicions, Barcelona; Blondel 1985. J. Anim. Ecol. 54: 531–556; Bouvier et al. 2005. Environ. Toxicol. Chem. 24: 2846–2852; Campbell 1968. Forestry 41: 27–46; Camprodon et al. 2008. Acta Ornithol. 43: 17–31; Chabi Y., Isenmann P. 1997. Alauda 65: 13–18; Dawson et al. 2005. Oecologia 144: 499–507; Dhondt et al. 1984. Ibis 126: 388–397; Dhondt et al. 1987. Gerfault 77: 333–339; Dhondt 2010. J. Anim. Ecol. 79: 257–265; Dias & Blondel 1996. Ibis 138: 644–649; Dolenec 2007. Wilson J. Ornithol. 119: 299–301; Drilling & Thompson 1988. Auk 105: 480–491; Eeva et al. 1994. Can. J. Zool. 72: 624–635; Goodenough et al. 2008. Ethol. Ecol. Evol. 20: 375–389; Heeb et al. 1996. J. Anim. Ecol. 65: 474–484; Johnson 1996. J. Field Ornithol. 67: 212–221; Juškaitis 2006. Folia Zool. 55: 225–236; Lambrechts et al. 2004. Oecologia 141: 555–561; Lambrechts et al. 2008. Russ. J. Ecol. 39: 516–522; Mainwaring & Hartley 2009. Behav. Proc. 81: 144–146; Mänd & Tilgar 2003. Ibis 145: 67–77; Mänd et al. 2005. Biodiv. Conserv. 14: 1823–1840; Massa et al. 2004. Ital. J. Zool. 71: 209–217; Mattes et al. 1996. Ornithol. Beob. 93: 293–314; Matysiokova & Remes 2010. Ibis 152: 397–401; Mazgajski 2007. Pol. J. Ecol. 55: 377–385; Mazgajski & Rykowska 2008. Acta Ornithol. 43: 49–55; McCleery et al. 1996. J. Anim. Ecol. 65: 96–104; Merino et al. 2000. Proc. Roy. Soc. Lond. 267: 2507–2510; Møller et al. 2010. J. Anim. Ecol.79: 777–784; Moreno et al. 2006. J. Avian Biol. 37: 555–560; Moreno et al. 2008. Ethology 114: 1078–1083; Naef-Daenzer & Keller 1999. J. Anim. Ecol. 68: 708–718; Nilsson & Källander 2006. J. Avian Biol. 37: 357–363; Nilsson & Smith 1988. J. Anim. Ecol. 57: 917–928; Norte et al. 2008. Auk 125: 943–952; Norte et al. 2010. Condor 112: 79–86; Orell & Ojanen 1983. Ann. Zool. Fenn. 20: 77–98; Perrins 1979. British Tits, Collins, London; Potti 2008. Acta Oecologica 33: 387–393; Potti 2009. J. Ornithol. 150: 893–901; Rendell & Robertson 1993. Ibis 135: 305–310; Sarà et al. 2005. J. Zool. 265: 347–357; Sanz et al. 1993. Ardeola 40: 155–161; Sanz et al. 2000. Oecologia 122: 149–154; Shiao et al. 2009. Auk 126: 906–914; Smith 1995. Proc. R. Soc. Lond. B 260:45–51; Sorace & Carere 1996. Ornis svecica 6: 173–177; Stenning et al. 1988. J. Anim. Ecol. 57: 307–317; van Balen 1984. Ardea 72: 163–175; Vilka 1999. Vogelwelt 120: 223–227; Westneat et al. 2002. Condor 104: 598–609; Whittingham & Dunn 2000. Mol. Ecol. 9: 1123–1129; Ziane et al. 2006. Acta Ornithol. 41: 163–169.

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