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REVIEW

Nest box design for the study of diurnal raptors and owls is still an overlooked point in ecological, evolutionary and conservation studies: a review

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Abstract The use of artificial nest boxes has led to significant progress in bird conservation and in our understanding of the functional and evolutionary ecology of free-ranging birds that exploit cavities for roosting and reproduction. Nest boxes and their improved accessibility have made it easier to perform comparative and

experimental field investigations. However, concerns about the generality and applicability of scientific studies involving birds breeding in nest boxes have been raised because the occupants of boxes may differ from conspecifics occupying other nest sites. Here, we review the existing evidence demonstrating the importance of nest box design to individual life-history traits in three falcon (Falconiformes) and seven owl (Strigiformes) species, as well

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as the extent to which publications on these birds describe the characteristics of exploited artificial nest boxes in their “Methods” sections. More than 60% of recent publications did not provide any details on nest box design (e.g. size, shape, material), despite several calls >15 years ago to increase the reporting of such information. We exemplify and discuss how variation in nest box characteristics can affect or confound conclusions from nest box studies and conclude that it is of overall importance to present details of nest box characteristics in scientific publications.

Keywords Falcons · Nest boxes · Owls · Raptors · Secondary cavity-nesting birds

Zusammenfassung Durch den Einsatz künstlicher Nisthilfen konnten im Vogelschutz große Erfolge erzielt werden. Darüber hinaus ermöglichte der vereinfachte Zugang zu Nestern und Altvögeln eine Vielzahl vergleichender und experimenteller Feldstudien, so dass funktionelle Zusammenhänge wie auch evolutionsbiologische Aspekte im Freiland bearbeitet werden konnten. Auf der anderen Seite wurden aber auch immer wieder Zweifel geäußert, ob und inwieweit sich an Nistkasten-Populationen gewonnene Daten verallgemeinern lassen. Nistkastenbrüter bzw. eine Vielzahl verschiedener biologischer Parameter können sich in vielfacher Weise von in Naturnestern brütenden Vögeln unterscheiden. Aufbauend auf einer umfangreichen Literaturrecherche wird am

Beispiel von drei Greifvogel- (Falconiformes) und sieben Eulenarten (Strigiformes) der Einfluss des Nistkastendesigns auf individuelle life history traits untersucht. Zugleich wurde analysiert, ob und inwieweit die Charakteristika der genutzten Nistkästen im Methodenkapitel der Publikationen angeführt wurden. Obwohl bereits vor über 15 Jahren mehrfach darauf hingewiesen wurde, dass Details zu den verwendeten Nistkästen beschrieben werden sollten, fanden sich in über 60% der aktuellen Publikationen keinerlei Angaben bspw. zu Größe, Form oder auch dem Material der Kästen. Anhand ausgewählter Beispiele wird der Einfluss verschiedener Nistkastencharakteristika auf verschiedene Parameter, bspw. die Gelegstärke, den Bruterfolg, die Belastung mit Parasiten, Interaktionen zwischen Arten etc., dargestellt und diskutiert. Deutlich wird, dass es in wissenschaftlichen Publikationen unerlässlich ist, die eingesetzten Nisthilfen detailliert zu beschreiben.

Introduction

Many secondary cavity-nesting animals (vertebrates, invertebrates) that exploit natural cavities for roosting or breeding also use holes in buildings, or occupy human-made constructions (e.g. artificial stick nests, nest boxes) attached to tree trunks, fences, walls, utility poles, or posts. This is also the case for secondary cavity-nesting members of the Falconiformes and Strigiformes orders (Village 1983; Korpimäki 1984; Toland and Elder 1987; Schönn et al. 1991; Bortolotti 1994; Doody 1994; Gehlbach 1994a, b; Pomarol 1996; Valkama and Korpimäki 1999; Sullivan et al. 2003; Franco et al. 2005; Beasley and Parrish 2009; Steenhof and Peterson 2009; Charter et al. 2007; van Nieuwenhuysse et al. 2008; Costantini et al. 2009; López et al. 2010; Riegert et al. 2010). Nest boxes are artificial cavities that have been designed to attract secondary cavity-nesters for roosting or breeding. The widespread use of nest boxes can halt population declines or can considerably increase a local population, especially in environments where cavity-forming trees are missing or abandoned buildings have become unavailable (Hamerstrom and Hamerstrom 1973; Arlettaz et al. 1991; Schönn et al. 1991; Exo 1992; Solonen 1993; Johnson 1994; Newton 1994; Petty et al. 1994; Ravussin et al. 2001; Löhmus 2003; Meyrom et al. 2009; Arlettaz et al. 2010; but see Klein et al. 2007).

The use of nest boxes has also advanced the understanding of functional and evolutionary aspects of life-history traits in local populations. Nest boxes can facilitate access to nest cavities and their contents, and therefore allow routine monitoring and handling of eggs or nestlings, as well as repeated trapping, identifying and

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sampling nesting birds or their offspring (Korpimäki 1987a, b, 1988a, b, 1993; Schönn et al. 1991; Exo 1992; Tella et al. 2000; Brommer et al. 2003; Smallwood et al. 2009). Using nest boxes as tools may also help to better control stochastic influences associated with abiotic factors, conspecifics or heterospecifics, thus increasing sample sizes for monitoring and scientific research, but at the cost of missing information on such stochastic influences that constitute an important area of research in modern ecology (Koenig et al. 1992; Møller 1989, 1992, 1994). For instance, comparative and experimental research has been facilitated in the fields of behavioural, environmental, evolutionary, demographic and conservation sciences when populations or species rapidly accept artificial nest boxes for reproduction (Korpimäki 1984; Clutton-Brock 1988; Newton 1989; Sonerud 1989; Dijkstra et al. 1990; Gard and Bird 1990; Exo 1992; Wiehn and Korpimäki 1997, 1998; Roulin et al. 1998; Fargallo et al. 2001; Bortolotti et al. 2002; Laaksonen et al. 2004; Klein et al. 2007; Butler et al. 2009; Santolo and Yamamoto 2009; Smallwood et al. 2009; Arlettaz et al. 2010; Charter et al. 2010a; but see Kirk and Hyslop 1998 for difficulties of large-scale monitoring). Nest boxes have also been erected for control of rodents by farmers (Duckett 1991; Meyrom et al. 2009; but see Valkama et al. 2005).

Møller (1989, 1992), and Koenig et al. (1992) discussed in detail the potential artefacts associated with the use of nest boxes in birds and advised field researchers to (1) ameliorate the design of nest boxes aimed to attract secondary cavity-nesters so that they mimic more closely the characteristics of natural or preferred nesting sites, and (2) describe in detail 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). A symposium on falcons and owls organised by Gehlbach (1994a; coordinator) subsequently concluded that nest boxes were adequate substitutes for natural cavities and that information gathered on population size and productivity was unbiased. However, because new data show some significant effects of box characteristics on life-history traits in avian species, including members of the Strigiformes and Falconiformes, we believe that Møller's (1989, 1992) and Koenig et al.'s (1992) recommendations are still relevant, and that it is important to assess whether subsequent studies have improved their reporting and justification of the design and placement of boxes. Therefore, we first review the existing evidence demonstrating the importance of nest box design to individual life-history traits in free-ranging falcons and owls, and secondly verify the extent to which publications on these birds describe the characteristics of exploited artificial nest boxes in their "Methods" sections.

Effects of nest types on life-history parameters in free-ranging populations

Differences between nest boxes and other nest sites

Concerns about the generality and applicability of studies involving birds breeding in nest boxes have been raised because the occupants of boxes may differ from conspecifics occupying other nest types (Korpimäki 1984; Møller 1989, 1992, 1994; Hayward et al. 1992; Petty et al. 1994; Charter et al. 2007; van Nieuwenhuyse et al. 2008; Lambrechts et al. 2010). Research results are likely to be influenced by the tools used (e.g. nest boxes vs. other nest sites), the choice of model species (those that can be investigated more easily), and/or logistics (nest accessibility to human observers). The validity of ecological and evolutionary conclusions from data gathered using nest boxes is difficult to assess because the performance of pairs that occupy nest boxes is rarely compared to pairs that use other nest types at the same location following appropriate sampling designs (Hurlbert 1984; Hairston 1989). In principle, potential biases can be evaluated by examining whether the characteristics of artificial nest boxes and their occupants differ from those of other nest types, and whether any such differences would affect the likelihood of supporting or rejecting the hypotheses to be tested. Hayward et al. (1992), for instance, discussed in detail the potential sampling biases that may exist between owls occupying nest boxes and the target population occupying other nest types.

Although several field studies on falcons and owls did not find statistically significant differences in life-history traits between artificial and natural cavities (e.g. Gehlbach 1994a), other investigations focusing on the same species reported variation in clutch size, hatching success and/or fledging success across distinct nest types, including artificial nest boxes. For instance, larger clutches being laid in nest boxes which are relatively larger than other types of nest sites (cavities in buildings or trees) have been observed in Barn Owls (*Tyto alba*) in Norfolk, England (Johnson 1994), Tengmalm's Owls (*Aegolius funereus*) in western Finland (Korpimäki 1984), and Eurasian Kestrels (*Falco tinnunculus*) in Rome (G. Dell'Omo, personal communication). Hatching success of Barn Owl eggs in Venezuela was higher in boxes compared to natural cavities because the eggs broke less frequently (Lander et al. 1991). Other studies have reported either that fledging success was greater in boxes relative to natural cavities (e.g. van Nieuwenhuyse et al. 2008 studying Little Owls, *Athene noctua*) or that there was no significant difference in productivity between boxes, buildings and trees (Barn Owls; Johnson 1994). One study on Lesser Kestrels (*F. naumanni*) found that the fledging success in nest boxes

did not differ from that recorded in nests located in attic cavities, but was lower than that in nests located in wall cavities (Bux et al. 2008). Sometimes, the effect of boxes may first appear when nestlings try to fledge. For example, in North America, radio-tagged Barn Owl fledglings from marsh locations survived their first flight better than those that fledged from offshore nest boxes or duck blinds (Bendel and Therres 1993). Such studies demonstrate the importance of recording the use of and measuring the characteristics of breeding places other than nest boxes, which can vary greatly depending on location.

Whether nest boxes are safer than other cavities or stick nests may depend on differences in size, height or position between different nest types, the types of protective devices added to nest boxes, and/or nest box relocation across years (Sonerud 1989, 1993; Fargallo et al. 2001; Charter et al. 2007; van Nieuwenhuyse et al. 2008; López et al. 2010; but see Korpimäki 1993). For instance, some species breeding in smaller nest cavities may have fewer surviving fledglings because the cavities are too cramped to allow nestlings to practise motor skills prior to fledging (Klein et al. 2007). Because most Tawny Owl (*Strix aluco*) fledglings finish their first flight from the nest at a lower height, a relatively lower nest position in combination with absence of perches near the entrance hole might increase the risk for fledglings sitting on the ground, perhaps also making them more vulnerable to mammalian predators, such as red foxes *Vulpes vulpes* (Sunde 2005). However, *Strix* and Scops Owl *Otus scops* fledglings regularly leave the nest before they can fly properly, perhaps to disperse as soon as possible to reduce the risk of small carnivores (e.g. *Martes* sp.) depredating the whole brood (T. Solonen; R. Arlettaz and A. Sierro, personal communication). In Eurasian Kestrels from Finland, Germany, Spain, and Israel, breeding success was higher in closed-type nests (nest boxes or cavities in buildings or walls) than in open-type nests (pre-existing stick nests), presumably because open nests are more vulnerable to predation, extreme weather conditions, or other environmental factors (Korpimäki 1983; Kostrzewa and Kostrzewa 1997; Fargallo et al. 2001; Charter et al. 2007; see also Carrillo and González-Dávila 2009 for other study sites).

Differences among nest box types

The way nest boxes are designed, positioned, monitored and maintained may influence a cocktail of abiotic and biotic factors in the nest box chamber at the timing of roosting or breeding. Nest box parameters will probably also interact with external environmental factors expressed differently in different regions (food abundance, weather, nest-site availability, presence of other organisms), and markedly influence the outcome of ecological field

investigations. In this context, researchers may inadvertently control or exaggerate the effect of some of these factors on the population or on the studied trait by using specific nest box designs or materials. Nest box design can also affect nest box choice and the development and survival of the eggs or nestlings, or the survival and physical condition of adults exploiting nest boxes (Korpimäki 1985; Bortolotti 1994; Charter et al. 2007; Butler et al. 2009; López et al. 2010; Zingg et al. 2010).

In this context, the internal size of the nest cavity may influence clutch size, depending on the size ranges of the nest chamber, the local population, the species, or the external environments monitored. Tengmalm's Owls from a Finnish study population produced larger clutches in medium-sized and large nest boxes than in small nest boxes during vole peak years, apparently because there are more stored prey in the larger nest box types (Korpimäki 1985). This relationship was not observed in years with severe food constraints. The amount of food stored in artificial nest boxes may therefore influence egg formation directly if females consume these stores before or during the period of egg development, or they can perhaps be used as a cue (Durant et al. 2010) required to anticipate the abundance of food available at the time of rearing nestlings (Hörnfeldt et al. 1990). However, López et al. (2010) studying the same species in the Pyrenees Mountains did not find a significant relationship between clutch size and nest box size, perhaps because of small sample sizes or interactions with key environmental factors that were not taken into account. Valkama and Korpimäki (1999) did not find differences in clutch size or brood size at fledging with respect to nest box size (small, intermediate or large) in Eurasian Kestrels from western Finland, whereas Charter et al. (2007) reported somewhat larger clutches or larger broods with more fledglings in smaller nest boxes than in larger ones. However, Charter et al. (2007) studied Kestrels in nest boxes designed to attract Barn Owls. Clutch size, brood size at fledging and nest success were all unaffected by box size in American Kestrels (*F. sparverius*) from Saskatchewan, Canada (Bortolotti 1994), although the American Kestrels apparently preferred the larger nest boxes provided in choice experiments. Clearly, clutch size–nest box size relationships, and the underlying mechanisms causing these relationships, vary between local study populations within species or across species settled in the same or different geographic regions (see Charter et al. 2007).

Several other nest box variables seem to affect the occupation and breeding success of a nest box. The size of the entrance hole obviously determines which individuals or species will occupy nest boxes and hence how their life-history traits will be expressed in the presence of other organisms (Bavoux et al. 1991; Valdez et al. 2000; López

et al. 2010). While larger-bodied species require large entrances, smaller individuals or species may prefer to breed in nest boxes with small entrance holes to reduce risks related to predation or competition. The dimensions of the nest box characteristics apparently influence interactions between Eurasian Kestrels and Barn Owls in Israel (Charter et al. 2007, 2010b), between Tawny Owls and Tengmalm's Owls in southern Finland and Spain (Solonen 1993; López et al. 2010), between Tengmalm's Owls, Ural Owls (*S. uralensis*) and Eagle Owls (*Bubo bubo*) in western Finland (Hakkarainen and Korpimäki 1996), between Barn Owls and Tawny Owls in northeast England (Petty et al. 1994), and between Eurasian Kestrels and Tawny Owls in Rome (D. Costantini and G. Dell'Omo, personal communication). In western Finland, Tengmalm's Owls mostly avoided breeding in the largest boxes (internal diameter 26–35 cm, entrance hole 15–18 cm) probably because Ural Owls could have entered them and physically removed the Tengmalm's Owls (Hakkarainen and Korpimäki 1996).

A more subtle impact of entrance hole size on hetero-specific intrusion was found for Tawny Owls in Denmark. Here, the prevalence of blood parasites (*Leucozytozoon*, *Trypanosoma*) was much higher for Tawny Owl nestlings in boxes with a wide entrance hole (30 cm × 40 cm as designed for Eurasian Kestrels) compared to those from natural cavities or nest boxes with a narrow entrance (15 cm diameter) (P. Sunde, unpublished data). While as yet untested, it is possible that insect vectors, and perhaps ectoparasites, may have easier access or can more easily detect larger entrances, or perhaps parents block the entrance hole when insect vectors are noticed. In addition, large entrance holes in small and shallow nest box chambers could increase the probability of premature fledging, for instance when nestlings are disturbed by the intrusions of heterospecifics or by humans which possibly increase stress levels (Roulin et al. 2010).

Local weather may influence the preferences for certain nest cavities with birds avoiding those with entrance holes oriented in the direction of prevailing rain or wind (Exo 1981; Sullivan et al. 2003). Orientation of the entrance influences site selection of natural cavities and artificial cavities in American Kestrels, possibly because internal nest temperatures differ as a function of orientation (Balgoyen 1990; Butler et al. 2009). In a rural ecosystem in Israel, the number of fledged young per breeding attempt and the hatching success of Eurasian Kestrels nesting in large nest boxes decreased with increasing rain (Charter et al. 2007). On the other hand, overheating of boxes during heat waves may cause hyperthermia or mortality of entire broods of Barn Owls and Kestrels (Meyrom et al. 2009). In hot environments, Barn Owls apparently prefer to settle in cooler than in warmer nest boxes where they also produce more fledglings per breeding attempt (Charter et al. 2010c).

Prey stored in nest boxes decompose more rapidly late in the season, i.e. when nest box environments become warmer, perhaps reducing availability of optimal prey for broods produced late in the season (A. Roulin, personal communication). It is also possible that decaying prey items such as rodents which are vectors or hosts of microorganisms causing disease (Combes 2001), or sources of ectoparasites, may be more or less likely to transmit the infection to the nest box occupants, depending on the micro-climate (e.g. Fargallo et al. 2001 for ectoparasites), or the types of prey (e.g. sick vs. healthy; Temple 1986; Valkama et al. 2005) influencing pathogen reproduction. Because falcons and owls do not add their own nest material to cavities, the presence of old nest material in a box or the experimental addition of sawdust or wood chips may improve insulation and hence the attractiveness of the site, especially in environments with more extreme weather conditions (López et al. 2010). In addition, old nest material not removed from nest chambers may increase the probability that ectoparasites develop in the nest box chamber, possibly influencing avian breeding success (Møller 1994; Roulin et al. 2007).

The reporting of nest box design in recent publications

Methods

To examine whether recent literature sources (national and international scientific journals, book chapters, proceedings of scientific meetings) reported details on nest box design and position, we examined the “Methods” sections of publications involving the most commonly investigated cavity-nesting falcons and owls in Europe and North America (Table 1) following similar approaches as those presented in Lambrechts et al. (2010). We divided the literature sources into two categories: those published before the publications of the Gehlbach symposium (“older” papers published before 1995), and those published from 1995 onwards (“more recent” publications). Based on the recommendations of Møller (1989, 1992, 1994), we predicted that descriptions of nest box characteristics would be more frequent among articles published after 1994. Publications were classified according to research category of the journal of publication (ornithology vs. ecology vs. others, including zoological, behavioural and physiology-oriented papers) and the 5-year impact factor from 2009 following the criteria presented on the Web of Knowledge. For journals that have changed their name (*Journal für Ornithologie* replaced by *Journal of Ornithology*, *Ornis Scandinavica* replaced by *Journal of Avian Biology*, *Holarctic Ecology* replaced by *Ecography*), the latest impact factors available were used. We predicted that nest box

Table 1 Percentage of publications describing or citing zero or more nest box characteristics in analysed papers during two periods: <1995 and 1995 or later

Taxonomic name	Period	Source numbers	Nest box characteristics described or cited (%)			
			0	1	2	>2
Falconiformes						
<i>Falco naumanni</i>	<1995	–	–	–	–	–
	≥1995	3	33.3	0	0	66.7
<i>Falco sparverius</i>	<1995	21	66.7	4.8	0	28.6
	≥1995	42	38.1	2.4	4.8	54.8
<i>Falco tinnunculus</i>	<1995	13	61.5	0	0	38.5
	≥1995	61	73.8	16.4	0	9.8
Strigiformes						
<i>Aegolius funereus</i>	<1995	34	35.3	8.8	2.9	52.9
	≥1995	26	57.7	0	3.8	38.5
<i>Athene noctua</i>	<1995	18	72.2	11.1	0	16.7
	≥1995	11	90.9	0	0	9.1
<i>Otus asio</i>	<1995	12	83.3	0	0	16.7
	≥1995	5	40.0	0	0	60.0
<i>Otus scops</i>	<1995	0	0	0	0	0
	≥1995	4	50.0	0	0	50.0
<i>Strix aluco</i>	<1995	4	50.0	0	0	50.0
	≥1995	29	79.3	0	0	20.7
<i>Strix uralensis</i>	<1995	4	100.0	0	0	0
	≥1995	10	100.0	0	0	0
<i>Tyto alba</i>	<1995	10	40.0	0	10.0	50.0
	≥1995	28	64.3	0	0	35.7
Total	<1995	116	57.8	5.2	1.7	35.3
	≥1995	221	65.2	5.0	1.4	28.5

The percentages of publications with information on none (0), one (1), two (2) or more than two (>2) nest box characteristics are indicated

descriptions would be more detailed in publications dealing with ornithology or ecology, assuming nest box design would be considered as an important environmental key factor for the development or expression of individual life-history traits or population dynamics (see above). We predicted more detailed descriptions of nest boxes in publications with lower 5-year impact factors, presuming these journals could provide more space per article. We also recorded other information about the publication, including the name of the first author, the number of authors, the number of institutional addresses, the country in which the research was performed, and the focal species. Lastly, we categorised the research topic of the paper as focusing on reproductive attributes (i.e. data focused on events within the nest box: eggs, incubation, brood size, chick phenotypes, nestling growth or behaviour, breeding success, parental care behaviour with nestlings) or not (i.e.

data focused on information obtained outside the nest boxes: adult vocal behaviour, population dynamics, dispersal behaviour, working effort, winter roosting behaviour, foraging behaviour, diet composition, survival after fledging, pair formation, presentation of trapping device).

We located relevant publications by using the scientific or common names of species as key words in leading electronic databases (ISI Web of Science, Biblio-Vie, BiblioSHS, CEFE-CNRS library; September–November 2010). We also searched the extensive collection of reprints possessed by collaborators working on these species. We searched the reference section of each of these publications to identify other relevant publications mentioned in the “Methods” sections. Only publications indicating nest boxes have been used as tools were included in the literature survey, which makes this survey conservative, due to the possibility that many publications may not have reported nest box use. We are aware that publications from the same team are often not independent units, but we have chosen to not include team as a factor because this reflects the probability that a student gathers information in the first paper she or he reads, regardless of the author’s previous publication record, and because it allows comparison with the nest box study review on passerines presented in Lambrechts et al. (2010).

To model the probability whether or not a paper addressed nest box information, we performed a series of general linear mixed models with a logit link function and a binary error distribution (PROC GLIMMIX; conducted by P. Sunde). Because many of the random effects (journal name, first author name, country, and focal species) were inter-correlated and inclusion of all random effects did not allow all models to converge, all random effects were analysed to select the most informative one. First author accounted for a plurality of the variation ($Z = 3.14$, $P = 0.002$; all others $P > 0.09$), so this random effect was included in all subsequent analyses on fixed effects. We then ran a series of fixed effect analyses with each fixed effect (time period, journal category, journal impact factor, and research topic) as the sole fixed effect, and one model with all fixed effects included simultaneously. Then, because it is possible that several of these categories may interact with each other (e.g. only ornithological journals may have increased reporting of nest box characteristics after the 1994 symposium), we ran another series of analyses with all second order interactions of the aforementioned fixed effects. All statistics were performed using SAS 9.2 (Cary, NC, USA).

Lack of reporting of nest box characteristics

Thirty-seven percent (95% confidence interval: 30–45%) of the sources verified addressed nest box information (a total

of 337 literature sources; Table 1). No fixed effect, either alone or when included in the statistical model with all fixed effects, significantly predicted the probability that a paper included any nest box parameter descriptions (6 variables tested: all $F < 2.42$, all $P > 0.12$). Within models that included the interactions of two fixed effects (additional 6 models tested), one interaction (period \times research topic) significantly predicted whether a paper included any nest box parameter descriptions ($F_{3,327} = 3.06$, $P = 0.028$), while all others were not significant at the $\alpha = 0.05$ level (all $F < 2.56$, all $P > 0.079$). The final model that utilised the significant interaction showed no significant effect of period ($F_{1,292} = 0.06$, $P = 0.81$), but significant effects of both research topics ($F_{1,327} = 4.20$, $P = 0.041$) and the interaction between period and research topic ($F_{1,327} = 5.14$, $P = 0.024$; Fig. 1). Given that 12 reasonably independent models were tested, at least one P value ≤ 0.028 would appear by chance alone with 29% probability [$1 - (1 - 0.028)^{12}$]. Rigorously, the single significant result can therefore be considered a random event. This conclusion would not change if the obtained P values were adjusted for multiple tests (Chandler 1995).

The statistical analysis of the published literature, together with the information presented in Table 1, strongly indicate that nest box design has often remained underreported in the literature. This conclusion is also based on the following observations.

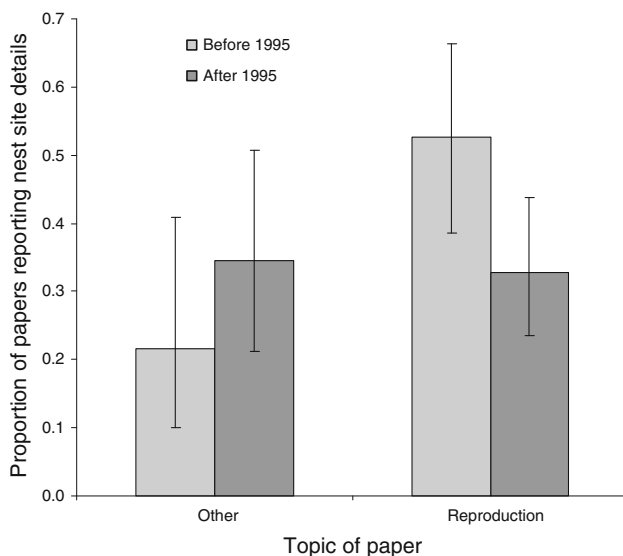


Fig. 1 Proportion of literature sources (error bars are 95% confidence intervals) that report nest box descriptions as a function of time period published and the paper's research topic. There was a significant interaction between period and research topic. Post hoc tests revealed significant differences between periods for papers about reproduction ($P = 0.026$) and between topics for papers published before 1995 ($P = 0.006$)

Detailed descriptions of nest box design are rarely available in publications

Box descriptions provided were often incomplete or imprecise, reporting dimensions without specifying whether these referred to the size of the whole box (exterior) or just the nest box chamber (interior). Thus, the thickness of the nest box wall was often not reported (see Korpimäki 1985; Eschenbauch et al. 2009 for exceptions), despite some researchers working with owls recognising that wall thickness may influence the thermal environment of the nest box chamber and hence winter survival, egg-hatching success or nestling survival in extreme environmental conditions (Korpimäki 1984, 1985; Johnson 1994).

Other aspects of box construction, such as the material used (e.g. metal, plastic, or wooden) were even less frequently reported than size (but see, e.g., Ravussin et al. 2001; van Nieuwenhuyse et al. 2008). Only some authors reported whether there were drainage holes in the bottom as used by the team of G. Dell'Omo to study Eurasian Kestrels. Such factors could have a significant impact on the conditions in which eggs are incubated or nestlings reared, and perhaps influence the duration that nestlings stay in the nest (Knötzsch 1978; Wendt 1978; Illner 1979). Also, no scientific justification was provided for the wood types used to construct the nest boxes, even though it is possible that wood chemistry affects the decomposition rate of prey stored in nest boxes or influences the invertebrate communities there (Philips and Dindal 1977). The volatile or other chemical compounds emitted by the wood used to construct nest boxes, perhaps in interaction with the micro-climate inside the nest box chamber, may influence functioning or development of eggs, nestlings, or adults, although very few studies have looked at this in birds of prey (see Ontiveros et al. 2008; Lambrechts et al. 2010 for details).

In addition to the box characteristics themselves, the type and amount of substrates added to the box by researchers, such as wood shavings, sawdust or vegetation, were rarely described, as illustrated in studies of American Kestrels (Hamerstrom and Hamerstrom 1973; Bortolotti 1994; Rohrbaugh and Yahner 1997; Beasley and Parrish 2009; Eschenbauch et al. 2009; Santolo and Yamamoto 2009; Steenhof and Peterson 2009), although the types and maintenance procedures of these substrates may significantly influence nest sanitation or comfort for nestlings or adults (Møller 1994; Roulin et al. 2007; López et al. 2010). For instance, Wimberger (1984) suggested that greenery added to line nests of open-nesting raptors of genera *Accipiter*, *Buteo* and *Pernis* may also improve nest sanitation. Perhaps wood chips emitting aromatics (Eucalyptus or pine; e.g. see Ontiveros et al. 2008) added in wooden nest boxes possess chemical properties impacting the

health and physiology of individuals at the time of reproduction.

The impact of nest box design on aspects of intraspecific or interspecific communication has also been ignored in the published literature, although plumage colours and vocal begging signals are known to be important in Barn Owls (Roulin et al. 2000, 2003), and the potential importance of light intensity inside nest boxes has been recognised for years (Bortolotti 1994). In particular, the size of the entrance hole, the depth of the cavity, the orientation of the box, or its placement relative to other habitat structures may affect internal light levels, but this has to the best of our knowledge rarely been measured in cavities exploited by diurnal species (see Butler et al. 2009 for an exception in American Kestrels). A comparative study on parental behaviour in passerines using nest boxes and Northern Flickers (*Colaptes auratus*) using deep tree cavities found that the parent's ability to detect and feed nestlings depended on ambient light levels, cavity depth, and on nestling coloration (Wiebe and Slagsvold 2009). Therefore, it is probable that light levels also influence a cavity-nesting raptor's ability to detect nestlings, or to remove ectoparasites from the nestlings or nest chamber. The possibility that features of the box influence the sounds involved in vocal communication, such as nestling begging calls, also deserves future study.

Nest boxes often represent a biased fraction of the properties of natural nest-types

Although the nest boxes provided in many local study sites were probably made with a consistent design in order to minimise potential confounding variables and maximise sample sizes (e.g. through a significant reduction of nest predation; Julliard et al. 1997), the scientific arguments for using a particular nest type or for placing them in a particular way (orientation, height above the ground and substrate) is often not provided or not taken into account. Several local long-term studies tried out a limited number of nest box designs to ultimately propose an optimal design that should maximise reproductive output for a given local population or species (Korpimäki 1985, 1987a, b; De Bruijn 1994; van Nieuwenhuysse et al. 2008; G. Dell'Omo, unpublished data). These studies did not always explain in detail why the initial nest box types used had been selected among the many other conceivable alternative nest types, or never published the methods and results of initial studies that provided the arguments for the use of one particular nest box design in a local long-term study. In preliminary investigations, Gehlbach (1994b) selected a small number of nest boxes reflecting as close as possible the range of characteristics of natural cavities exploited in the same region by the model species investigated. In some cases,

unconventional boxes such as those with multiple chambers may be suitable for species like Tawny Owls (P. Sunde, personal communication). Practical reasons impose the use of a small number of nest box type classes, in which only one or two nest box properties are altered (e.g. small vs. intermediate vs. large interior bottom size and entrance hole, controlling for other nest box characteristics). The few studies on nest box orientation that investigated a nest box property as a “continuous” variable currently provide the best examples for more profound investigations on aspects of nest box position where confounding (changeable) factors could be controlled in a more efficient manner (Butler et al. 2009; Charter et al. 2010c).

Nest box designs and research protocols vary across study sites at macro-geographic scales

While a certain research team or monitoring organisation often uses a standard box type across their different study sites, different research groups may use either similar or different box designs without providing a scientific justification. For instance, Hayward et al. (1992) working with Tengmalm's Owls in the U.S.A. used the type of nest box considered to be optimal for reproduction in Tengmalm's Owls from western Finland (Korpimäki 1985). Our review indicated that typically different research groups studying the same species in different locations did not use the same nest box design or protocols (Baucells et al. 2003; van Nieuwenhuysse et al. 2008). For instance, the nest box design proposed to investigate Tengmalm's Owls in Switzerland (Ravussin et al. 2001) and Germany (März 1968) differs significantly from designs used in Finland (Korpimäki 1985) or Spain (López et al. 2010), without providing scientific arguments why the nest box shapes should differ across European regions or countries. According to Ravussin et al. (2001), nest boxes constructed from PVC tubes are more efficient in attracting breeding Tengmalm's Owls than other nest box types, probably because the PVC boxes are more efficient in excluding European pine martens (*Martes martes*) in that study population. Thus, in the course of long-term studies, nest box design or position may be adjusted to local environmental conditions (predation pressures), without necessarily always indicating this in the published literature, perhaps explaining a significant part of the spatiotemporal variation in nest box design currently observed (see case studies in Little Owls; van Nieuwenhuysse et al. 2008).

In some regions, such as southern and central Finland and the eastern Pyrenees, there are a large number of artificial nest boxes erected by well-meaning citizens, including birdwatchers and hunters, and there are no or only a few general standards that are applied for the construction of these nest boxes. Thus, one reason for the lack

of detailed descriptions of artificial nest boxes from certain regions might be their enormous heterogeneity and the difficulty to classify them properly (T. Solonen, personal communication; López et al. 2010), although natural cavities expressing similar or more heterogeneity in structure have been described in some publications on owls (Korpimäki 1984; Gehlbach 1994b; Tomé et al. 2004).

Using different nest box designs probably influences the procedures and the time needed to monitor the occupants of nest boxes. Differences in the ease and frequency of monitoring nest sites could explain some large-scale variation in the accuracy or precision of reported breeding parameters from different geographic sites, for example in American Kestrels (Smallwood et al. 2009). Beasley and Parrish (2009), studying the same species, used a spotting scope to monitor nests in tubes of transmission towers at 30 m above the ground, and a ladder to inspect PVC boxes placed at 4.5 m above the ground, which perhaps caused different levels of stress and disturbance to adults or nestlings. To the best of our knowledge, no one verified scientifically whether diurnal or nocturnal inspections may influence sleeping patterns and breeding or parental activities in the following day(s) or night(s).

Because the detailed procedures of nest box monitoring and maintenance are rarely published, they may not be efficiently transmitted among different research teams even when an effort is made to collaborate. For instance, the team of G. Dell’Omo for many years added dry *Sphagnum* turf at the bottom of nest boxes aimed to attract breeding Eurasian Kestrels around Rome. The nest box design was given to another North Italian research team without providing instructions to add turf or other bedding material inside the nest boxes. In this new North Italian study population, established in 1999, Eurasian Kestrels started to occupy the nest boxes only 3–4 years after they were installed, possibly because the 4-year-old nest boxes contained old sparrow nests which significantly increased the desirability of these nest boxes for breeding Eurasian Kestrels. Thus, at macro-geographic scales, replicates in nest box design and monitoring protocols across study sites are often inconsistent, which precludes a good experimental design (see Hurlbert 1984) when the goal is to compare large geographical areas.

Variation in nest box characteristics is often ignored in statistical analyses

If a single type of nest box is impossible or undesirable to standardise across study sites, one can enter nest box type as a factor in statistical analyses of variation at the individual or population level (Carrillo and González-Dávila 2009), but this has rarely been done, either because the information was unavailable at the time the analyses were done (see Klein

et al. 2007), or because the significance of nest box design has been considered to be negligible (Gehlbach 1994a; Charter et al. 2007). Lack of standardisation or unreported changes in nest box design within local study plots in the course of long-term studies could thus (1) bias inferences on population trends within areas, (2) prevent analyses of temporal trends in population responses to biotic and abiotic factors, and/or (3) compromise meta-analyses and thus the generality of findings. Including nest box design as an environmental key factor in meta-analyses could help to point out outlier populations or gain a better understanding of the statistical noise facing these analyses (see Zuur et al. 2010 for procedures in data exploration).

Concluding remarks

The present literature review on secondary hole-nesting raptors (outlined above) and a recent review on passerines (Lambrechts et al. 2010) provide similar observations and conclusions. Publications or unpublished observations from older and more recent studies (<1995 vs. ≥1995) report that aspects of nest box design (e.g. size of the whole box, internal size of the nest cavity, size of entrance hole, nest box material, presence or absence of drainage holes, wall thickness), location (e.g. nest box height, orientation of entrance hole, substrate to which the box is attached) and/or maintenance procedures (e.g. addition of substrate on the nest box floor) can influence both the probability that a box is occupied and the expression of avian life-history traits of nest box occupants (clutch size, egg hatching success, breeding success, chick phenotype). However, many recent publications do not provide any details on nest box design, despite several published calls to increase reporting of such information. Because the vast majority of avian nest box studies focus on Falconiformes, Strigiformes and Passeriformes, we believe that our general conclusions will not change if other avian nest box exploiters are added to these reviews.

While we encourage interpreting these results with caution, we found that generalist journals with high impact factors were less likely to contain methodological details in more recent publications, presumably because journal editors and reviewers do not always know the burgeoning literature well enough to advise which information should be excluded from short papers, and researchers themselves often underappreciated the significance of box design (e.g. Gehlbach 1994a). Clearly, it is important for rigorous scientific research that the methods are adequately described and fully replicable (Hurlbert 1984; Hairston 1989). Therefore, we urge journals, even those with strict page limits, to encourage the detailed reporting of box design whether in appendices, online supplements, or by citing

former publications which do contain this information. Our recommendations addressed to authors, referees and editors are the same as those for passerine studies, and they include detailed reporting of location and design of boxes, and the detailed description of procedures related to maintenance, protection and inspection of boxes (Lambrechts et al. 2010, p. 10).

In addition to merely reporting box characteristics and protocol details, we encourage more research on how box characteristics and maintenance or monitoring procedures actually influence individual life-history expressions and population dynamics. Most, if not all, of the research projects and experiments proposed for passerines are also applicable to other cavity-nesting birds, although there are certainly logistic constraints which may prevent exact replication of box types and placements in free-ranging populations (see Lambrechts et al. 2010). Also, numerous characteristics of boxes may be acting simultaneously and it may be difficult to tease these apart in free-ranging populations (Bortolotti 1994). However, Korpimäki (1985) and López et al. (2010) showed that the consequences of different combinations of nest box characteristics could indeed be investigated in owls. In general, logistic constraints for experiments with falcons and owls may be more challenging than for passerines because the former group of birds have larger body sizes, larger territories, and higher nest-site positions, and so it is more difficult to obtain sufficient sample sizes. Also, in many cases, and especially in the exploited forest of Europe, there are few suitable natural nesting cavities so it is often difficult to judge what is a “natural” or “optimal” nesting site.

It is probably naïve to think that a single box design or placement for a given species is “optimal” for all situations and all habitats (Charter et al. 2007). In the wild, spatio-temporal fluctuations in weather conditions or predation pressures may favour the maintenance and use of a variety of cavity types (van Nieuwenhuysen et al. 2008). However, it would be informative to study the interaction effects of box characteristics with environmental factors using long-term or large-scale studies. As an aid to this endeavour are nest boxes numbering into the thousands monitored by amateur ornithologists (Saurola 2008) or other citizen science projects. We therefore finally suggest that nest box design is an environmental key factor for individual survival, reproduction, and population dynamics, which could also be investigated in the framework of such large-scale monitoring networks.

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