Clutch-size variation in Western Palaearctic secondary hole-nesting passerine birds in relation to nest box design

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Summary

1. Secondary hole-nesting birds that do not construct nest holes themselves and hence regularly breed in nest boxes constitute important model systems for field studies in many biological disciplines with hundreds of scientists and amateurs involved. Those research groups are spread over wide geographic areas that experience considerable variation in environmental conditions, and researchers provide nest boxes of varying designs that may inadvertently introduce spatial and temporal variation in reproductive parameters.

2. We quantified the relationship between mean clutch size and nest box size and material after controlling for a range of environmental variables in four of the most widely used model species in the Western Palaearctic: great tit *Parus major*, blue tit *Cyanistes caeruleus*, pied flycatcher *Ficedula hypoleuca* and collared flycatcher *F. albicollis* from 365 populations and 79 610 clutches.

3. Nest floor area and nest box material varied non-randomly across latitudes and longitudes, showing that scientists did not adopt a random box design. Clutch size increased with nest floor area in great tits, but not in blue tits and flycatchers. Clutch size of blue tits was larger in wooden than in concrete nest boxes.

4. These findings demonstrate that the size of nest boxes and material used to construct nest boxes can differentially affect clutch size in different species. The findings also suggest that the nest box design may affect not only focal species, but also indirectly other species through the effects of nest box design on productivity and therefore potentially population density and hence interspecific competition.

Key-words: geographic location, habitat, latitude, longitude, nest box floor area, nest box material

Introduction

Hole-nesting birds have played a major role in the development of several fields of ecology, evolution and genetics. This is largely attributable to their willingness to occupy artificial nest boxes in numbers large enough to generate sufficient sample sizes; they are amenable to a range of experimental manipulations; their reproductive parameters are easily quantified; and

adults are easily captured. Thus, studies of life history, population dynamics and many other subjects are to a large extent based on studies of nest box populations of birds (e.g. Kluijver 1951; Perrins 1965; Royama 1969; Löhrl 1973).

Many hole-nesting birds breed across large geographic areas, thereby allowing an examination of how spatial and temporal environmental heterogeneity influences their biology. As an example, clutch size of birds has been found to correlate with latitude, longitude, altitude, intraspecific and interspecific interactions (predation, competition, parasitism), photoperiod, phenology, food availability, body size, energy require-

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ments, parental age, first or second clutch, and climate (e.g. Lack 1947; Royama 1969; Klomp 1970). Furthermore, the risk of hyperthermia may increase in smaller nest holes with over-crowding (Mertens 1977) with negative consequences for reproductive success (Erbeling-Denk & Trillmich 1990). The reason for the focus on the determinants of clutch size is its close association with fitness and its ease of study including experimentation.

However, studies differ in the size of nest boxes they use (Lambrechts *et al.* 2010), and variation in nest box size itself may also affect clutch size (e.g. Löhrl 1973; Karlsson & Nilsson 1977; van Balen 1984). None of the studies of macrogeographic variation in clutch size took the size of nest boxes into account (e.g. Sanz 1997, 1998, 2002; Fargallo 2004), perhaps because details of nest box design were unavailable, or they were considered unimportant (Lambrechts *et al.* 2010). Scientists use nest boxes as a research tool, and ultimately, it is the research goal that determines the design, location and management of boxes. Such information should optimally be provided in scientific publications derived from these studies, although surprisingly this is often not the case (Lambrechts *et al.* 2010). Some studies of nest box breeding birds have even changed box design during the course of a study, with potential consequences for the phenomena under study and the size and composition of the entire study populations and therefore populations of competitors (Møller 1989, 1992; Lambrechts *et al.* 2010).

Clutch size is known to vary significantly with the area of the nest box floor area (e.g. Löhrl 1973; Karlsson & Nilsson 1977; Korpimäki 1984), although the strength of the correlation between clutch size and nest floor area differs among species (van Balen 1984; Purcell, Verner & Oring 1997), study plots (Gustafsson & Nilsson 1985; Slagsvold 1987; Alatalo, Carlson & Lundberg 1988), experiments differing in design characteristics other than box floor area (e.g. Slagsvold 1987; Sorace & Carere 1996), or between studies that either focused on natural or artificial cavities (e.g. Korpimäki 1984; Alatalo, Carlson & Lundberg 1988; Wesolowski 2003). For instance, great tit (*Parus major*) females laid smaller clutches in nest boxes with a smaller box floor area (Graczyk 1967; Löhrl 1973; Karlsson & Nilsson 1977), even when female condition was controlled experimentally (Löhrl 1973, 1980), although the strength of this relationship may depend on the size range of the nest boxes monitored (e.g. Sorace & Carere 1996). In German great tits, the average clutch size was adjusted to experimentally manipulated nest floor area when this was changed between the end of nest building and the first 4 days following the onset of egg laying (Löhrl 1980). In other small passerines, such as pied flycatchers (*Ficedula hypoleuca*), the strength of the relationship between nest floor area and clutch size depended on other nest box characteristics such as the angle of the box on the tree as well as phenotypic characteristics of the breeders (Slagsvold 1987). Thus, observed differences in findings between investigations from the same or different model species could be due to differences in nest box design. Consequently, while there is no doubt that significant advances have been made in a wide range of biological disciplines by studying nest box breeding birds, spatial and tempo-

ral variation in nest box characteristics may introduce unknown bias into studies of breeding biology and life-history variation.

We explicitly analysed the effects of the floor area of nest boxes and nest box construction material on clutch size across the Western Palaearctic, considering 155 study populations of great tits, 121 of blue tits (*Cyanistes caeruleus*), 24 of pied flycatchers and 65 of collared flycatchers (*Ficedula albicollis*) for a total of 79 610 clutches. First, we analysed whether nest box design varied randomly across latitudes, longitudes and altitudes. Secondly, we predicted that clutch size would increase with box floor area independent of other predictors and more strongly in the two tit species having larger clutches than in the two flycatcher species with smaller clutches (Löhrl 1973; Karlsson & Nilsson 1977; van Balen 1984). Thirdly, we predicted an interaction between nest floor area and latitude if latitudinal variation in temperature exaggerated the effect of nest floor area. Finally, we investigated clutch-size variation in relation to latitude, longitude, altitude, year, habitat and urbanization that are all known from previous studies to correlate with clutch size (e.g. Perrins 1979; Glutz von Blotzheim & Bauer 1993; Ahola *et al.* 2009). We included latitude and longitude as covariates because they are well-known predictors of clutch size through their effects on peak food availability and the number of daylight hours available for foraging, and quadratic terms were added to account for nonlinear relationships.

Materials and methods

GENERAL PROCEDURES

We conducted an extensive study of clutch size in hole-nesting birds in the Western Palaearctic relying on collaboration with amateurs and professionals. We contacted participants in a previous exhaustive study of hole-nesting birds (Lambrechts *et al.* 2010). Although the taxonomy of tits and flycatchers is currently under revision, we used these four taxa with similar ecologies without considering that some populations in the Iberian Peninsula, the Canary Islands and North Africa may constitute separate species.

We restricted the analyses to first clutches, or early clutches known to be initiated <30 days after the first egg was laid in a given year to standardize sampling procedures (cf. Nager & van Noordwijk 1995). We assumed that the very small number of unidentified early repeat clutches that usually resulted from perturbations (e.g. Haywood 1993), or lay dates calculated from information obtained from different breeding stages (e.g. Lambrechts *et al.* 1997), did not substantially alter the overall average clutch size per study plot. Second or late clutches were excluded from analyses because they are usually smaller than first or early clutches, even for females not changing nest box within a given breeding season, and they show strong spatial and temporal variation (e.g. Kluijver 1951; Lambrechts *et al.* 2008).

LIFE-HISTORY TRAITS AND ENVIRONMENTAL FACTORS

Information on latitude, longitude and altitude was provided by the authors or found in publications.

Tree species vary significantly in the timing and the amount of invertebrates available for raising offspring. We broadly classified vegetation as 'deciduous' habitat dominated by non-evergreen broad-

leaved deciduous trees (*Alnus, Betula, Carpinus, Citrus, Fagus, Fraxinus, Malus, Quercus,* including *Q. faginea*), 'evergreen' habitat dominated by non-coniferous broad-leaved evergreen trees (*Q. ilex, Q. suber*), 'coniferous' habitat dominated by coniferous trees (*Abies, Cedrus, Picea, Pinus*) or 'mixed' habitats dominated by a combination of the former tree vegetation classes (e.g. deciduous mixed with coniferous).

Scientists classified their study plots as either rural or urban with urban areas being characterized by city parks, gardens and similar habitats in close proximity of humans, while forests, plantations and similar habitats were classified as rural.

Major life-history traits are known to vary among years. For instance, in local study plots, biotic (e.g. resource availability, intraspecific or interspecific interactions) or abiotic factors (e.g. meteorology, climate) can vary substantially among years, perhaps explaining within-plot variation in average clutch size (e.g. Kluijver 1951; Perrins 1965; Both 2000). We used study year in all analyses.

We calculated the internal floor area (in cm²) of nest boxes, using publications (e.g. Lambrechts *et al.* 2010) or additional information provided by participants. The material constituting the nest box was divided into two broad binary classes that are readily distinguishable: wood scored as 1, which includes tree trunks, plywood, board–masonite, or board (e.g. Gustafsson & Nilsson 1985) and concrete scored as 0 (a mixture of cement and other materials; Lambrechts *et al.* 2010). Frequency distributions of the different variables are reported in Supporting Information Tables S1–S2.

STATISTICAL ANALYSES

The basic unit of analysis is mean clutch size and associated predictor variables for a given study site and year. We could not pool means across years because we explicitly wanted to test for effects of year, and because the number of size categories of nest boxes differed among years for a given site. First, we tested whether there was consistent geographic variation in nest floor area and nest box material by relating these two response variables to site (random factor), latitude, longitude and altitude (fixed factors) to test whether scientists showed consistent choice of specific nest box designs across study sites. Next, we investigated the relationship between mean size of first clutches and internal floor area (cm²) of nest boxes after controlling for confounding factors influencing mean clutch size, using mixed models. These mixed models included plot ID as a random effect to account for differences in the number of clutches among plots and species and year (a factor) as fixed effects. Having shown significant two-way interactions between species and predictor variables, we proceeded by developing four species-specific mixed models with plot ID as a random effect (Tables 1–4). The fixed effects were latitude, longitude, quadratic latitude, quadratic longitude, the interaction between latitude and longitude, habitat, urbanization, box material and year. We log$_{10}$-transformed nest bottom area to eliminate the skewed frequency distributions. We originally included altitude in the analysis, but this variable had a very skewed distribution and was highly correlated with a number of other variables such as latitude and longitude.

We weighted the analyses by sample size to account for the fact that the variance of mean clutch size for small sample sizes is larger than the variance of mean clutch sizes for large sample sizes. We present the full models to allow easy comparison of effects among species. We were unable to include all variables in the analysis for collared flycatcher because some of those showed no variation (urbanization and nest box material). We only included interactions that were biologically meaningful and that had been implicated as determinants of clutch size in the four species of hole nesters.

We evaluated the strength of relationships between variables using Pearson's partial product-moment correlation coefficient as a standardized estimate of effect size, relying on Cohen (1988), who suggested that a correlation of $r = 0.10$, accounting for 1% of the variance, is a small effect, a correlation of $r = 0.30$, accounting for 9% of the variance, an intermediate effect, and a correlation of $r = 0.50$, accounting for 25% of the variance, a large effect. In biological questions, main effects account on average for 5–7% of the variance (Møller & Jennions 2002), thus constituting an intermediate effect. We emphasize that effect sizes rely on analyses based on plot by year means thus ignoring any variation within years within plots. Hence, these effect sizes refer to geographic or annual variation in mean clutch size. That said, comparison of effect sizes among factors provides an estimate of the relative amount of variance explained by these different factors. Effects and effect sizes do not imply causation, but simply imply the strength of partial correlations between pairs of variables, and some of these effects may arise as a consequence of correlations with third variables. We report least square means and standard errors for all categories of categorical variables. All analyses were carried out in JMP, version 10.0 (SAS Institute Inc. 2012).

Results

ANALYSES OF NEST FLOOR AREA

Covariation between clutch size and latitude and longitude, respectively, may arise for completely arbitrary reasons if scientists using nest boxes adopt sizes that vary non-randomly with latitude and longitude. Nest floor area showed non-random geographic variation. Nest floor area decreased with latitude [$F = 35.13$, d.f. = 1, 226.1, $r^2 = 0.02$, $P < 0.0001$, estimate (SE) = -0.0069 (0.0012)] and altitude [$F = 4.07$, d.f. = 1, 273.1, $r^2 = 0.0002$, $P = 0.045$, estimate (SE) = -0.0191 (0.0094)], but was independent of longitude ($F = 0.24$, d.f. = 1, 207.8, $r^2 < 0.001$, $P = 0.63$). When we repeated these analyses based on means per site, there was also a significant relationship between nest floor area and latitude ($F = 13.95$, d.f. = 1, 392, $r^2 = 0.03$, $P = 0.0002$, estimate (SE) = -0.00245 (0.0007) and altitude [$F = 72.23$, d.f. = 1, 391, $r^2 = 0.15$, $P < 0.0001$, estimate (SE) = 0.0485 (0.0057)], but was independent of longitude ($F = 1.26$, d.f. = 1, 391, $r^2 = 0.003$, $P = 0.26$). In addition, nest box material was more frequently wood at high latitudes ($\chi^2 = 23041.90$, d.f. = 1, $r^2 = 0.38$, $P < 0.0001$) and eastern longitudes ($\chi^2 = 7113.35$, d.f. = 1, $r^2 = 0.12$, $P < 0.0001$) and at higher altitudes ($\chi^2 = 10124.19$, d.f. = 1, $r^2 = 0.17$, $P < 0.0001$). When we repeated these analyses based on means per site rather than annual means, there was still a significant relationship between nest floor area and latitude ($\chi^2 = 23041.90$, d.f. = 1, $r^2 = 0.38$, $P < 0.0001$), longitude ($\chi^2 = 7811.69$, d.f. = 1, $r^2 = 0.13$, $P < 0.0001$) and altitude ($\chi^2 = 10084.45$, d.f. = 1, $r^2 = 0.17$, $P < 0.0001$). This implies that scientists more frequently put up boxes with larger nest floor area at lower latitudes and altitudes, and boxes made out of wood at high latitudes and eastern longitudes. These factors had small to intermediate effects. Nest floor area differed significantly between wood and concrete nest boxes ($F = 151.44$, d.f. = 1, 2881, $r^2 = 0.003$, $P < 0.0001$), with nest boxes made of wood on average being

Table 1. Mixed model of the relationship between mean clutch size and environmental variables in the great tit. Variance component for the random study site effect was 0·75 (95% CI = 0·52, 0·99) accounting for 10·04% of the total variance. Adjusted R^2 for the model was 0·76. The total number of observations was 29 685 (some clutches did not have information on all variables, thereby reducing sample size from the original 29 826 clutches) and 1481 plot by year means. Least mean squares and their SE are reported for categories of discrete variables

	d.f.	d.f. (denominator)	F	P	Estimate	SE	Effect size
Intercept	1	193·9	14·29	0·0002	6·7262	1·7815	
Latitude	1	124·9	9·97	0·0020	−0·0905	0·0287	0·27
Latitude × Latitude	1	121·3	36·10	<0·0001	−0·0156	0·0026	0·48
Longitude	1	117·6	50·70	<0·0001	0·1071	0·0150	0·55
Longitude × Longitude	1	143·7	1·11	0·29	0·0011	0·0011	0·09
Latitude × Longitude	1	147·2	8·56	0·0040	0·0035	0·0012	0·23
Habitat	3	507·3	4·72	0·0030			0·10
Coniferous					8·78	0·18	
Deciduous					8·97	0·15	
Evergreen					8·29	0·30	
Mixed					9·08	0·18	
Urbanization	1	1299	21·71	<0·0001			0·13
Rural					9·07	0·15	
Urban					8·48	0·19	
Box material	1	280·1	1·27	0·26			0·07
Wood					8·89	0·16	
Concrete					8·67	0·21	
Year	57	1263	5·85	<0·0001			0·29
Altitude	1	140·9	0·66	0·42	0·1057	0·1302	0·07
Nest floor area	1	1046	31·51	<0·0001	2·6645	0·4747	0·17

Table 2. Mixed model of the relationship between mean clutch size and environmental variables in the blue tit. Variance component for the random study site effect was 0·94 (95% CI = 0·63, 1·26) accounting for 12·61% of the total variance. Adjusted R^2 for the model was 0·89. The total number of observations was 20 177 (some clutches did not have information on all variables, thereby reducing sample size from the original 20 229 clutches) and 1124 plot by year means. Least mean squares and their SE are reported for categories of discrete variables

	d.f.	d.f. (denominator)	F	P	Estimate	SE	Effect size
Intercept	1	216·8	6·92	0·0092	5·8407	2·2220	
Latitude	1	120·7	13·29	0·0004	0·0925	0·0254	0·31
Latitude × Latitude	1	108·6	14·86	0·0002	−0·0116	0·0031	0·35
Longitude	1	105·2	7·16	0·0086	0·0416	0·0155	0·25
Longitude × Longitude	1	124·7	3·96	0·0487	−0·0046	0·0023	0·18
Latitude × Longitude	1	106·3	10·84	0·0013	0·0093	0·0028	0·30
Habitat	3	229·5	17·87	<0·0001			0·27
Coniferous					9·29	0·30	
Deciduous					10·22	0·22	
Evergreen					8·89	0·31	
Mixed					10·15	0·27	
Urbanization	1	904·5	0·10	0·75			0·01
Rural					9·67	0·20	
Urban					9·61	0·27	
Box material	1	308	8·69	0·0035			0·17
Wood					9·94	0·24	
Concrete					9·33	0·24	
Year	49	961·3	2·03	<0·0001			
Altitude	1	114·8	0·41	0·52	−0·1145	0·1794	0·06
Nest floor area	1	442·3	0·18	0·67	−0·3381	0·7916	0·02

100 cm^2 (SE = 3), while those made of concrete were on average 130 cm^2 (SE = 2). However, nest box material only accounted for 0·3% of the variance in nest floor area. When we repeated these analyses based on means per site, there was again a significant difference in nest floor area between wood and concrete boxes (χ^2 = 36·88, d.f. = 1, $P < 0·0001$).

We made two mixed model of the relationship between clutch size and environmental variables based on annual means (Table S3) and means per study site (Table S4). The magnitude of effect sizes was similar in the two models, although some of the significant effects in the model based on annual means were no longer significant in the model based on means per study site (e.g. urbanization and nest box material). This is not surprising given the reduction in sample size from 79 610 nests to 3485 mean annual estimates and then to 392 site means. In models with clutch size as the response variable,

Table 3. Mixed model of the relationship between mean clutch size and environmental variables in the pied flycatcher. Variance component for the random study site effect was 0·04 (95% CI = −0·009, 0·09) accounting for 1·54% of the total variance. Adjusted R^2 for the model was 0·84. The total number of observations was 14 031 (some clutches did not have information on all variables, thereby reducing sample size from the original 14 051 clutches) and 288 plot by year means. Least mean squares and their SE are reported for categories of discrete variables

	d.f.	d.f. (denominator)	*F*	*P*	Estimate	SE	Effect size
Intercept	1	49·50	24·11	<0·0001	8·4849	1·7283	
Latitude	1	12·84	7·53	0·0169	−0·0530	0·0193	0·61
Latitude × Latitude	1	10·52	2·12	0·17	−0·0060	0·0042	0·41
Longitude	1	11·10	0·72	0·42	0·0107	0·0126	0·25
Longitude × Longitude	1	12·61	0·56	0·47	0·0013	0·0018	0·21
Latitude × Longitude	1	10·10	0·03	0·86	0·0008	0·0044	0·05
Habitat	2	54·62	0·10	0·91			0·04
			Coniferous		5·55	0·64	
			Deciduous		5·54	0·65	
			Mixed		5·53	0·65	
Urbanization	1	206·9	71·80	<0·0001			0·51
			Rural		5·75	0·65	
			Urban		5·33	0·65	
Box material	1	207·6	1·17	0·28			0·44
			Wood		6·18	0·19	
			Concrete		4·90	1·22	
Year	58	185·7	3·38	<0·0001			
Altitude	1	11·53	1·12	0·31	−0·1869	0·1768	0·30
Nest floor area	1	86·36	0·07	0·79	0·1648	0·6045	0·03

Table 4. Mixed model of the relationship between mean clutch size and environmental variables in the collared flycatcher. Variance component for the random study site effect was 0·00 (95% CI = −0·0011, 0·0044) accounting for 0·16% of the total variance. Adjusted R^2 for the model was 0·37. The total number of observations was 15 504 and 592 plot by year means. Least mean squares and their SE are reported for categories of discrete variables

	d.f.	d.f. (denominator)	*F*	*P*	Estimate	SE	Effect size
Intercept	1	177·2	4·58	0·034	18·0368	8·4426	
Latitude	1	198	2·74	0·10	−0·548	0·1538	0·12
Latitude × Latitude	1	274·1	3·24	0·07	−0·0429	0·0238	0·11
Habitat	2	13·85	0·07	0·94			0·08
			Coniferous		6·15	0·06	
			Deciduous		6·13	0·04	
			Mixed		6·12	0·10	
Year	31	532·2	9·68	<0·0001			
Altitude	1	545·2	3·13	0·08	0·2778	0·3007	0·08
Nest floor area	1	525·6	3·13	0·08	1·1584	0·0238	0·08

we found significant interactions between species and all predictor variables (results not shown for brevity). In particular, clutch size was predicted by the interaction between species and nest floor area (*F* = 115·12, d.f. = 3, *P* < 0·0001), implying that clutch size was related to nest floor area in a species-specific manner. Therefore, we proceeded by investigating the relationships between clutch size and the predictor variables for the four species separately (Tables 1–4).

ANALYSES FOR TITS

The model of clutch size for great tits explained 73% of the variance and that for blue tits 88% (Tables 1–2). Great tits showed a positive relationship between clutch size and nest floor area with an intermediate effect size (Table 1; Fig. 1a). In contrast, blue tit showed no significant correlation between nest floor area and clutch size (Table 2; Fig. 1b). There was a weak, but significant interaction between nest floor area and latitude in the great tit when added to the model in Table 1 [*F* = 8·40, d.f. = 1, 388·4, r^2 = 0·02, *P* = 0·0039, estimate (SE) = 0·2613 (0·0901)]. Inspection of the data showed a positive association between clutch size and nest floor area at high latitudes, but a negative association at low latitudes.

Clutch size of blue tits was significantly larger in wooden than in concrete boxes with an intermediate effect size, while that was not the case in the great tit (Tables 1–2; Fig. 1c). Both great and blue tits showed positive linear relationships between clutch size and latitude of an intermediate effect size, while there were large quadratic effects of latitude implying a reduction in clutch size at high latitudes (Tables 1–2; Fig. 2a). In great and blue tits, there was a significant positive association between clutch size and longitude (Tables 1–2; Fig. 2b). The quadratic

effects of longitude were not significant in either species (Tables 1–2). There was a positive interaction between latitude and longitude in both species (Tables 1–2). Altitude was not a significant predictor of clutch size in any of the species (Tables 1–2). There were significant effects of habitat in both species with clutch sizes being larger in deciduous and mixed habitats than in coniferous and evergreen habitats (Tables 1–2). Great tits showed a strong effect of urbanization (with smaller clutches in urban areas) (Fig. 2c), while blue tits did not (Tables 1–2). Clutch size in the great tit declined with year with an intermediate effect size (Table 1; Fig. 2d), while that was not the case in the blue tit (Table 2). The effect of year averaged more than 1·5 eggs since 1950 [$F = 134·96$, d.f. = 1,1431, $P < 0·0001$, estimate (SE) = $-0·0229 (0·0020)$].

ANALYSES FOR FLYCATCHERS

The model of clutch size for pied flycatcher explained 75% of the variance, while that for collared flycatcher explained only 13%. Nest floor area did not explain a significant fraction of variance in clutch size in either species (Tables 3–4). There was a negative association between latitude and clutch size in pied flycatchers, while only the collared flycatcher showed a quadratic effect of latitude (Tables 3–4). There were no significant differences in clutch size among habitats (Tables 3–4). Pied flycatchers had significantly smaller clutches in urban areas with a large effect size (Tables 3; Fig. 2e). Clutch size increased with year in the collared flycatcher with an intermediate effect size (Fig. 2f), while there was no significant association in the pied flycatcher (Tables 3–4). There was no significant change in clutch size with altitude in either species (Tables 3–4).

Discussion

We have presented the most comprehensive study to date of factors correlated with clutch size in four species of secondary hole-nesting birds in the Western Palaearctic. Although these species constitute some of the most well-known model systems for a number of different fields of biological research, we documented previously unknown heterogeneity. Box material and size varied non-randomly across geographic scales. Nest box

material and nest floor area were significantly correlated with clutch size, with these differences being prominent in some species, but not in others. These patterns held even when controlling for other variables known to affect clutch size in these species such as latitude, longitude, altitude, habitat, urbanization and year. These conclusions are interesting because they suggest that nest box size may represent a hidden source of variation in broad comparative studies not only in clutch size, but also in other life-history traits in these species.

We did not analyse spatial autocorrelation in response or predictor variables nor have previous analyses of geographic variation in clutch size done so (e.g. Sanz 1997, 1998, 2002; Fargallo 2004). Likewise, studies of geographic variation in life-history traits in a climate change context have not considered spatial autocorrelation (Visser *et al.* 2003; Both *et al.* 2004). Although we consider this a shortcoming, we leave this question open for a future study.

We found evidence of non-random variation between box size and material and geographic distribution, hence violating a previously untested assumption of random variation. Therefore, studies of geographic variation in life history should consider nest box design as confounding variables. Clutch size was significantly related to nest floor area, but only in the great tit that laid larger clutches in larger boxes, while the blue tit and the two flycatcher species showed no significant relationships. This difference among species appeared after statistical control for a large number of known predictors of clutch size, although similar conclusions were reached in analyses only including clutch size and nest floor area (results not shown for brevity). Slagsvold (1987) provided an exhaustive list of hypotheses explaining variation in clutch size caused by differences in nest size. In retrospect, we can state that his tests of these hypotheses for pied flycatchers are unlikely to have been particularly powerful, although they were experimental, simply because the pied flycatcher does not show a clear clutch size response to variation in nest floor area, as we have documented here. The two flycatcher species have much smaller clutches than the two tit species, making it unlikely that flycatchers commonly encounter problems of space limitation or adverse nest microclimate at southern latitudes. The difference in relationship between clutch size and nest floor area between great tits and
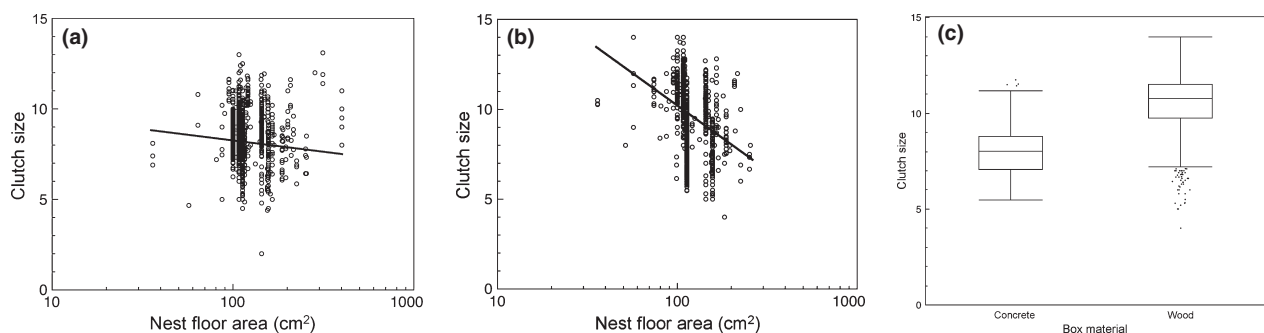

Fig. 1. Clutch size in relation to nest floor area (cm²) in (a) the great tit and (b) the blue tit, and (c) clutch size in the blue tit in wooded and concrete nest boxes. The box plot in (c) shows median, quartiles, 5- and 95-percentiles and outliers. The figures show the raw data. The lines are the linear regression lines.
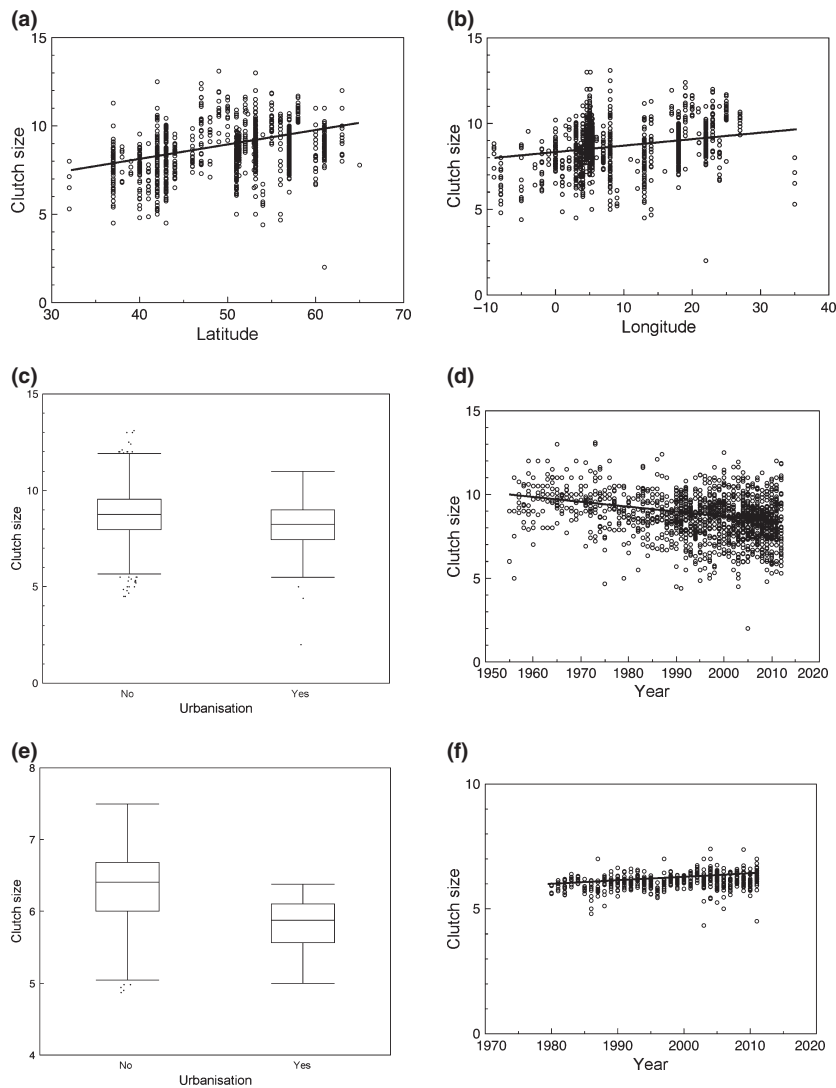
Fig. 2. Clutch size in relation to (a) latitude, (b) longitude, (c) urbanization, (d) year in the great tit, (e) urbanization in the pied flycatcher and (f) year in the collared flycatcher. The box plots in (c) and (e) show median, quartiles, 5- and 95-percentiles and outliers. The figures show the raw data. The lines are the linear regression lines.

blue tits is novel. If hyperthermia is a determinant of the relationship between nest floor area and clutch size, we should expect nest floor area to interact with latitude in determining clutch size because of higher ambient temperatures at low latitude during breeding. Indeed, the interaction between nest floor area and latitude was statistically significant in great tits, but not in the other species. While clutch size in great tits increased with nest floor area at high latitudes, clutch size decreased with nest floor area at low latitudes. These findings are inconsistent with the hyperthermia hypothesis.

Analyses of the four species showed heterogeneous effects of predictor variables (latitude, longitude, altitude, habitat, urbanization, year) as demonstrated by interactions (results not shown for brevity). Many findings reported here replicate previous findings for latitude, longitude and habitat (e.g. Järvinen 1989; Sanz 1997; Fargallo 2004). This lends credibility to our overall findings. However, we note that our analyses did not reproduce a previously reported effect of altitude (Järvinen 1989; Sanz 1997; Fargallo 2004). This is probably due to a combination of uneven distribution of altitudes in our data set combined with strong correlations between altitude and several other variables. Finally, given the much

greater sample size and the larger number of predictors used in our study compared to previously published studies, we consider our study to provide a more reliable conclusion. Many of the effects that we have documented here are unlikely to be due to direct effects of the included variables, but rather may be attributed to density effects, effects of food or effects of photoperiod. For example, while density could be a cause of the quadratic relationships between clutch size and latitude (and longitude), this seems unlikely given that clutch size is density dependent in great tits, but not in pied flycatchers (von Haartman 1971; Alatalo & Lundberg 1984; Ahola *et al.* 2009). Alternatively, the levelling off in clutch size at higher latitudes may be linked to the number of daylight hours. Parent birds at southern latitudes are time constrained by the limited number of daylight hours available for foraging, while conspecifics at northern latitudes may be energy constrained since they do not exploit the long daylight period available for foraging (Lack 1947; Sanz *et al.* 2000). Furthermore, low night temperatures reduce insect activity and hence foraging efficiency at night at high latitudes (Veistola, Eeva & Lehikoinen 2000). The effects of habitat on clutch size cannot be attributed to density effects because there are higher densities

in deciduous habitats where clutch size is also the largest (e.g. Perrins 1979). We suggest that multiple causal factors most likely lead to the patterns detected here.

Interspecific competition for food is intense between great and blue tits (Dhondt 1977, 2011), as is competition between great tits and pied flycatchers (Gustafsson 1987). The interspecific difference in the relationship between clutch size and nest box floor areas that we have documented here may also have implications for competition. In two imaginary scenarios with nest box floor areas of 40 and 400 cm^2, we would expect 2·89 more great tit eggs and with 100% hatching success, a similar number of fledglings per nest in the scenario with large boxes compared to that with small boxes. In other words, there would be relatively higher density of great than blue tits in the scenario with large boxes compared to that with small boxes given that blue tits do not show increasing clutch size with increasing box floor size. Hence, great tits would be at a competitive advantage in the scenario with large boxes, where their average clutch size is larger than that of blue tits, while blue tits would enjoy an advantage when boxes were small – even when everything else was the same. Thus, nest box design may have significant implications for the relative abundance of species and hence for the intensity of interspecific competition (Lambrechts *et al.* 2010).

Wooden nest boxes had larger clutches than concrete boxes in the blue tit, but not in the other three species, and nest material showed non-random geographic variation. Nest box material may affect ambient temperature inside boxes. We hypothesize that blue tits in particular may be relatively more susceptible to hyperthermia than the other three species for a given nest box size simply because their large clutch sizes will cause high internal air temperature, high humidity and high ammonia concentration that increase nestling mortality in small boxes (Erbeling-Denk & Trillmich 1990).

We documented a strong negative correlation between clutch size and year in the great tit, no relationship in blue tit and pied flycatcher, and a weak increase in collared flycatcher. This effect in the great tit amounted to a decline in clutch size by 0·023 eggs per year, or for the 65-year study period a decline of 1·50 eggs. With a mean clutch size of 8·68 eggs (SD = 1·31) for the 1477 great tit samples, 1·5 eggs equal 17% or 1·15 SD units. Four explanations may account for this change. First, if there has been a decline in the abundance of large natural nest holes over time because of intensified forestry (e.g. Sandström 1992; Newton 1994; Carlson, Sandström & Olsson 1998), this should have selected for small clutch size, especially in the species that responds most strongly to the size of nest boxes. Secondly, great tit populations in Scandinavia and elsewhere have increased in abundance during several decades, and this increase in population density is expected to result in reduced clutch sizes due to density dependence (Ahola *et al.* 2009). Thirdly, a greater increase in populations of blue tits compared to great tits in Sweden and elsewhere in Scandinavia would have resulted in more intense competition between blue tits on great tits. Fourthly, climate change may have affected clutch size as females may lay smaller clutches so that they can begin incubation sooner and breed at the optimal time with respect to maximum food demand and maximum food supply (Cresswell & McCleery 2003). However, the long period with continuous decline in clutch size contrasts with climate warming having been particularly strong since 1990 in Europe (IPCC 2007). Obviously, these factors may all have contributed independently to a temporal reduction in clutch size in the great tit (Ahola *et al.* 2009).

Urbanization is known to be associated with higher densities, smaller clutches and longer life span (e.g. Glutz von Blotzheim & Bauer 1993; Hõrak 1993; Chamberlain *et al.* 2009). Here, we documented smaller clutches in urban environments, although only in great tits and pied flycatchers. Reduced clutch size in urban areas may be caused by food limitation exacerbated by intraspecific competition due to high population densities in urban environments caused by elevated adult survival rates (Glutz von Blotzheim & Bauer 1993; Hõrak 1993). Blue tits are common inhabitants of cities just as great tits and pied flycatchers are, but urban blue tits still do not differ in clutch size from their ancestral rural populations. However, great tits have much higher densities in urban than in rural areas, while that is less so in blue tits (Møller *et al.* 2012). Therefore, clutch size in urban great tits is expected to differ from that in rural conspecifics, while that should not be the case in blue tits, as we observed.

In conclusion, we have shown non-random geographic distribution of nest box design. Several aspects of nest boxes explained variation in clutch size of tits, although differently in great and blue tits. The implications of these findings are that the choice of nest boxes by scientists in empirical studies may impact research findings not only by affecting focal species, but potentially also by affecting interspecific interactions.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Frequency distributions of continuous variables from nest box studies of four secondary hole-nesting bird species.

Table S2. Sample sizes and frequency distribution of discrete variables from nest box studies of four secondary hole-nesting bird species.

Table S3. Mixed model of the relationship between mean clutch size and environmental variables in hole nesters based on analysis of annual means per site.

Table S4. Mixed model of the relationship between mean clutch size and environmental variables in hole nesters.