Nest building, sexual selection and parental investment

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Summary

Avian nest building has traditionally been viewed as resulting in natural selection advantages, but it is also been associated with courtship and pair formation. We hypothesize that nest-building activity could be used as a sexually selected display, allowing each sex to obtain reliable information on the condition of the other. In this paper, we test the 'good parent' process in a scenario where nest size is a sexually selected trait. Thus, individuals with more extreme displays (larger nests) might obtain benefits in terms of either parental investment or differential parental investment by the partner. We predicted that: (1) species in which both sexes contribute to nest building have larger nests than those in which the nest is built only by one sex, because both sexes are using the nest-building process as a signal of their quality; (2) species in which both sexes work together in the nest-building process invest more in reproduction, because each can assess the other more reliably than in species where only one sex participates in nest building; and (3) in light of the two preceding predictions, nest size should be positively related to investment in parental care. A comparative analysis of 76 passerine species confirmed that nest size, relative to the species' body size, is larger when both sexes build the nest and that species with a larger nest relative to their body size invest more in reproduction.

Keywords: nest building; parental investment; sexual selection; signal

Introduction

An avian nest is a special construction forming a receptacle in which eggs and young develop. The nest may be an evolutionary compromise between such benefits as insulation from adverse environmental conditions (low temperatures and rain), keeping the eggs (or nestling) warm during incubation (depending on the material used in nest building) and other physical factors (Kern, 1984; Kern and Riper, 1984; Sciurine and Kern, 1980), and such costs as the energy expended in nest building, predation risk during nest building and nest predation due to nest conspicuousness (Slagsvold, 1984, 1989a; Lima, 1987).

The size of a nest is also related to the birds' body size, nest type (open, domed or cavity) and clutch size (see Slagsvold, 1982, 1989a,b). Altitude and latitude also influence the size of a nest in relation to the insulation function (Kern and Riper, 1984). However, much variation in nest-size parameters still remains to be explained.

Nest-building behaviour is often associated with courtship and pair formation in birds because males can use nest sites and nest material to attract a mate. The degree to which this behaviour is used in courtship varies from mere manipulation of a piece of nest material, or display of a potential nest site, to the building of an entire nest by the male (Collias and Collias, 1984). The actual nest-building behaviour is used in displays by polygamous and monogamous bird species (see examples in Collias and Collias, 1984).

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Nest-building behaviour may signal the reproductive condition of individuals and reproductively stimulate a partner (Collias, 1964). This idea has received little attention in the literature on the evolution of nest-building behaviour and, in general, there is very little information on the importance of the nest itself and its role in mate choice (Hoi *et al.*, 1994). For instance, a nest may indicate parental quality, experience or genetic quality (Borgia, 1987), and females could benefit from mating with good nest-building males. However, if nest building is costly (in terms of energy and predation), only individuals in good condition (strong physical condition or high ability to defend the nest) should be able to build large nests (Zahavi, 1987). Thus, nest-building behaviour could provide information to a bird about the quality of a potential partner, and such assessment of mate quality may allow individuals to choose a mate in non-monogamous species, while in monogamous species assessment may also allow partners to invest differentially in reproduction relative to the quality of a mate (Burley, 1986; Møller, 1994). The average nest size of each species may therefore partially depend on whether one or both members of a pair use nest building as a signal of quality for their mate.

It has recently been shown for the magpie (*Pica pica*, Soler *et al.*, 1995) and the black wheatear (*Oenanthe leucura*, Moreno *et al.*, 1994) that individuals with better parental qualities build larger nests. Furthermore, it has been shown experimentally in the black wheatear that (1) morphological adaptations exist for stone-carrying (used in the nest structure), which is an extreme display used in post-mating sexual selection (Møller *et al.*, 1995), and (2) an experimental increase in the number of the stones carried results in increased reproductive success (Soler *et al.*, 1996).

In the present study, we use a comparative approach to test the idea that nest building also gives rise to sexual selection. However, we have restricted ourselves to an examination of the hypothesis based on the good-parent process in sexual selection. Therefore, we have used only species in which both sexes provide parental care of nestlings, because if only one sex tends the nestlings, then traits other than parental ability will inevitably be selected in the process of nest building, such as reduced participation in extra-pair copulation, genetic quality or the size of the nest itself because of related characteristics (thermal insulation, anti-predation, etc.) (Hoi *et al.*, 1994, 1996). Our hypothesis is that one or both members of a pair judge the effort invested by the mate in nest building as a cue to the phenotypic quality of the partner (parental quality in this case), and this information is used for decisions about investment in reproduction.

Hypotheses and predictions

The nest-building behaviour or nest characteristics could be used as a sexually selected display, allowing members of one sex to obtain reliable information on the condition of potential partners, and individuals with more extreme displays (larger nests) would thus obtain benefits in terms of absolute or differential parental investment by the partner.

We made the following predictions based on the good-parent process (see above):

1. Nest size for each species should be optimized by natural selection in terms of cost and benefits, but if no sexual selection process is involved in the resulting nest size, then this optimum should depend on the demands of the eggs and nestlings and not on which or how many individuals were involved in nest building. Thus, any nest-size difference in relation to the number of individual builders indicates an extra cost attributable to sexual selection. Thus, for species in which both sexes contribute to nest building, we predict bigger nests (after controlling for the allometric effect of body size and other variables affecting nest size; see Materials and methods) than for species in which the nest is built only by the female.

2. If nest building is a reliable signal of willingness to invest in parental care, as the good-parent sexual-selection process predicts, then we should expect an increase in parental care for species in

which both sexes build together (both sexes, having information on partner quality, should mutually invest more in reproduction) compared with species in which the female builds alone (only species in which both sexes feed the nestlings are included in the analysis).

3. If the two foregoing predictions are true, then we should, in general, find a direct relationship between nest size and investment in parental care for each species. Therefore, we predict that species which build larger nests (in relation to their body size) should also be those that invest more effort in reproduction.

Materials and methods

In this study, we used the duration of the nestling period relative to body size as an index of parental investment (reported by Perrins, 1987), because this stage is the most conspicuous component of parental care (Winkler and Wilkinson, 1988) and it has been demonstrated experimentally that the amount of parental effort is regulated by the length of the nestling period (Johnsen *et al.*, 1994). Therefore, the duration of the nestling period could be an appropriate measure of parental effort.

The exposure of the nest to predation may also affect the amount of effort that should be devoted to nest building. If the probability of predation is high, selection may favour a small nest to minimize the problem of attracting the attention of nest predators. In addition, the duration of the nestling period is positively related to the risk of nest predation (Bosque and Bosque, 1995), which may interact with nest size and also with which sex builds the nest. To account for this interaction, we (1) corrected nest size for the duration of the nestling period of each species and, to analyse the relationship between nest size and the duration of the nestling period (prediction number 3), (2) we analysed the data including and excluding hole-nesters, because hole-nesting birds have a reduced risk of predation, which has led to the evolution of a long nestling period (Lack, 1968; Bosque and Bosque, 1995).

We calculated clutch size and body size as the average between the maximum and minimum values reported by Perrins (1987). When the sex of the builder contradicted any of the source books used (Harrison, 1975; Perrins, 1987; Cramp, 1985–92; Cramp and Perrins, 1993–94), we used the information only if two references were in agreement. If information was available in only two references, and these were contradictory, we deleted that species from the analysis. We used information if available from only one reference.

The nest-size parameters were taken from Dementiev and Gladkov (1966–68), Haftorn (1971) and Niethammer (1937). We used nest diameter, nest depth, cup volume, nest-material volume and nest thickness as defined in Fig. 1. Nest volume and nest-material volume were estimated as shown in Fig. 1. To reduce the number of nest parameters and the influence of any one variable on the others in the results, we conducted a principal component analysis, which resulted in one factor explaining 75.3% of the variance (eigenvalue = 3.77; the loading factors were 0.903 for nest diameter, 0.797 for nest depth, 0.920 for nest cup volume, 0.920 for nest volume and 0.759 for nest thickness). We use the value of this factor for each species as an estimate of nest size (original variables in Table 1).

A rough measure of geographical distribution was obtained from Dementiev and Gladkov (1966–68), to the nearest five degrees of latitude traversing the middle of the range of the species in the Palaearctic (Table 1).

To control for the possible effect of common phylogenetic descent, we used Felsenstein's (1985) independent comparison method as implemented in a computer program by Garland *et al.* (1993) for the continuous variables, and CAIC (Purvis, 1991) when assessing the influence of the sex involved in nest building (discrete variable) on nest size and duration of the nestling period. This

Nest material = Outer volume - Nest cup volume

Volume = 4/3 Pi a^2 b x

a = smallest radius
b = largest radius
x = fraction of an ellipsoid

Diameter

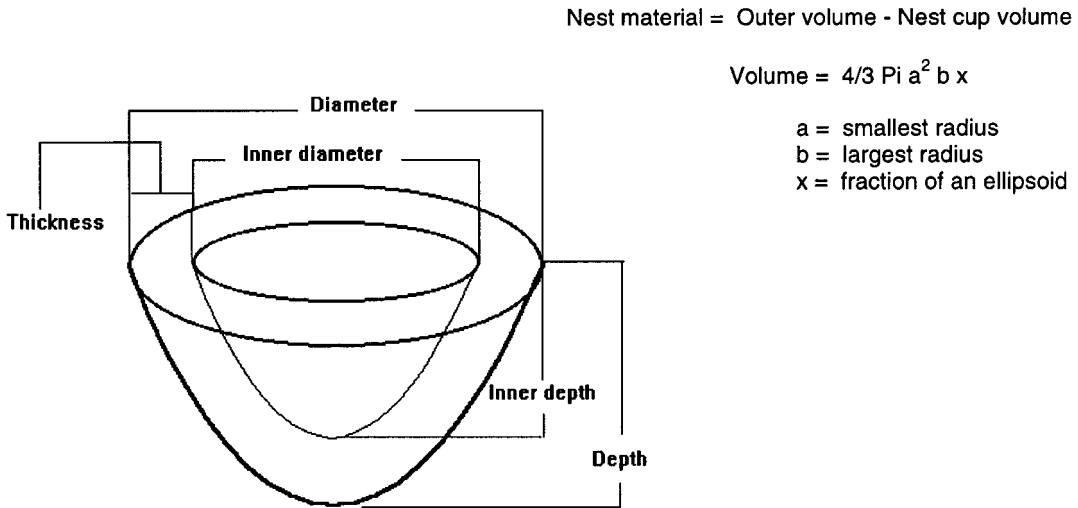**Inner diameter**

Thickness

Inner depth

Depth

Figure 1. Definition of nest measurements and calculation of thickness and volumes.

method finds a set of independent pairwise differences or contrasts, assuming that changes along the branches of the phylogeny can be modelled by a Brownian motion process (successive changes are independent of one another), and that the expected total change (i.e. the sum of many independent changes) is zero (Harvey and Pagel, 1991). That is, the rate of evolutionary change per unit branch length is equal in all branches of the phylogeny (Harvey and Pagel, 1991). To check whether the contrasts were adequately standardized, we plotted the value of the contrasts against the variance of the raw contrasts, but in no case did we find a significant correlation ($P > 0.08$). Therefore, pairwise differences in the phylogenetic tree were considered to be independent of each other (Harvey and Pagel, 1991). The advantage of independent comparison approaches is that, by partitioning the variation appropriately, all contrasts can be used to assess a hypothetical comparative relationship (Harvey and Pagel, 1991).

Nestling periods and nest-size parameters were approximately normally distributed after natural log-transformation, while latitude and clutch size were already normally distributed (Kolmogorov-Smirnov = N.S.).

We used the phylogenetic passerine classification given in Howard and Moore (1991), because the taxonomic classification based on DNA–DNA hybridization techniques of many species in the present study is poor (Sibley and Ahlquist, 1990). In the analysis, we assumed polytomies (multi-way speciation events) between different species within the same genus (see Purvis and Garland, 1993, for problems with polytomies, their implications and possible solutions), and we set all branch lengths of all species to the same length (= 1) (Garland *et al.*, 1993; Purvis and Garland, 1993).

Nest size and the duration of the nestling period are related to body size (see above). To remove this source of variation, we first calculated the slope through the origin for the contrasts of body mass of the species (independent variable) and the contrasts of nest size and duration of the nestling period (dependent variables). Later, we used these slopes to compare the expected values for body size (standardized) for each species and their residuals with the observed values for nest size and duration of the nestling period. We used the standardized residual in all statistical analyses as the value of the nest parameter controlled for body size (Harvey and Pagel, 1991).

Table 1. Sexes building the nest, nest site, latitude, nest parameters, clutch size, body size and duration of the nestling period for Palaearctic passerines

Species	Nest building sex	Nest site	Latitude (°N)	Nest diameter (cm)	Nest depth (cm)	Nest cup volume (cm^3)	Nest material volume (cm^3)	Nest thickness (cm)	Clutch size	Body size (cm)	Nesting period (days)
Galerida cristata	Female	Open	35	7.0	5.0	128	314	2.2	4	17	14
Lullula arborea	Male and female	Open	50	7.0	5.0	128	404	2.8	4	15	12
Alauda arvensis	Female	Open	55	8.0	5.0	209	253	1.0	4	18	19
Eremophila alpestris	Female	Open	65	6.5	5.3	116	251	1.8	4	16	12
Hirundo rustica	Male and female	Semi-hole	50	8.5	4.0	76	189	1.4	5	10	21
Ptyonoprogne rupestris	Male and female	Semi-hole	50	8.7	3.8	149	105	0.6	4	14	26
Anthus novaeseelandiae	Male and female	Open	50	8.0	8.5	285	269	1.2	5	18	16
Anthus spinoletta	Female	Open		6.3	4.0	106	419	2.6	5	17	
Anthus pratensis	Female	Open		6.0	3.7	86	301	1.5	5	14	
Motacilla alba	Female	Semi-hole	50	6.7	4.0	93	150	2.7	6	18	15
Lanius collurio	Male and female	Open	50	7.0	2.5	64	1 009	3.8	6	17	14
Lanius excubitor	Male and female	Open	55	10.0	3.5	183	3 417	7.5	6	24	20
Lanius senator	Male and female	Open	40	7.0	5.5	141	655	3.0	6	17	20
Bombycilla garrulus	Male and female	Open	65	9.0	5.8	246	2 040	6.0	5	18	16
Cinclus cinclus	Male and female	Semi-hole	55	12.2	9.0	460	2 787	7.1	5	18	23
Prunella modularis	Female	Open	55	5.7	3.8	65	493	2.8	5	14	12
Erithacus rubecula	Female	Semi-hole	55	7.0	5.0	128	191	1.4	5	14	14
Luscinia luscinia	Female	Open	55	6.6	5.3	120	489	2.8	5	16	12
Luscinia megarhynchos	Female	Open	45	6.9	5.0	123	673	2.9	5	16	13
Luscinia svecica	Female	Open	55	5.0	5.0	65	467	3.8	6	14	14
Cercotrichas galactotes	Male and female	Open	40	9.5	6.4	299	723	2.7	5	15	

Table 1 *Continued*

Species	Nest building sex	Nest site	Latitude (°N)	Nest diameter (cm)	Nest depth (cm)	Nest cup volume (cm^3)	Nest material volume (cm^3)	Nest thickness (cm)	Clutch size	Body size (cm)	Nesting period (days)
Phoenicurus phoenicurus	Female	Hole	50	6.0	7.0	132	480	2.7	6	14	15
Saxicola torquata	Female	Open	50	6.0	2.8	54	317	2.5	6	12	15
Monticola solitarius	Female	Hole	35	10.0	3.0	157	600	3.5	5	20	17
Turdus torquatus	Male and female	Open	60	19.3	9.7	300	1 825	4.8	5	24	14
Turdus merula	Female	Open	45	8.2	5.3	183	922	4.2	4	25	14
Turdus pilaris	Female	Open	55	10.2	7.0	381	1 472	3.2	5	26	14
Turdus philomelos	Female	Open	55	12.3	5.5	348	187	1.3	4	23	14
Turdus iliacus	Female	Open	55	8.9	5.4	224	647	1.7	6	21	13
Turdus viscivorus	Female	Open	50	10.0	5.5	288	3 968	3.9	4	27	15
Locustella naevia	Male and female	Open	50	5.1	5.1	69	303	2.2	6	13	12
Locustella luscinoides	Male and female	Open	50	6.9	5.0	125	330	2.2	5	14	13
Acrocephalus schoenobaenus	Female	Open	55	6.4	4.1	87	246	1.9	6	13	13
Acrocephalus dumetorum	Male and female	Open	55	5.7	3.7	61	446	2.7	5	12	11
Acrocephalus palustris	Female	Open	50	5.1	5.1	67	388	2.4	5	12	12
Acrocephalus scirpaceus	Female	Open	50	5.0	4.3	56	133	1.4	4	12	12
Acrocephalus arundinaceus	Female	Open	45	7.0	6.9	176	748	1.5	5	19	12
Hippolais icterina	Male and female	Open	55	5.1	4.5	61	223	2.0	5	13	13
Phylloscopus sibilatrix	Female	Semi-hole	55	7.0	3.3	83	1 253	3.4	6	12	12
Phylloscopus collybita	Female	Semi-hole	55	6.0	2.5	47	617	2.3	6	11	14
Phylloscopus trochilus	Female	Semi-hole	55	5.6	4.8	77	522	3.0	7	11	14
Sylvia nisoria	Male and female	Open	50	6.5	5.8	127	337	2.4	5	15	14
Sylvia curruca	Male and female	Open	55	5.9	3.9	55	195	1.7	5	13	11

Table 1 *Continued*

Species	Nest building sex	Nest site	Latitude (°N)	Nest diameter (cm)	Nest depth (cm)	Nest cup volume (cm^3)	Nest material volume (cm^3)	Nest thickness (cm)	Clutch size	Body size (cm)	Nesting period (days)
Sylvia communis	Male and female	Open	55	5.8	4.6	79	240	2.6	5	14	12
Sylvia borin	Male and female	Open	55	5.9	3.8	67	284	2.5	5	14	10
Sylvia atricapilla	Male and female	Open	55	6.1	4.6	87	137	1.8	5	14	12
Regulus regulus	Male and female	Semi-hole	55	5.0	4.4	58	316	2.2	8	9	19
Muscicapa striata	Male and female	Open	50	5.5	4.5	71	391	4.3	5	14	14
Ficedula hypoleuca	Female	Hole	55	6.5	5.0	111	1 360	3.4	7	13	16
Ficedula albicollis	Female	Hole	50	5.2	3.5	49	331	3.3	7	13	15
Tichodroma muraria	Female	Hole	35	7.8	3.8	121	751	3.6	4	16	24
Passer domesticus	Male and female	Hole	55	8.0	10.0	335	1 956	2.3	5	14	15
Passer montanus	Male and female	Hole	55	5.0	3.0	78	904	3.8	5	14	13
Emberiza hortulana	Female	Open	50	6.0	5.0	94	438	2.2	5	16	13
Emberiza aureola	Male and female	Open	60	6.0	4.8	90	137	1.3	5	14	14
Emberiza calandra	Female	Open	50	8.0	5.5	184	381	2.0	4	18	13
Calcarius lapponicus	Female	Open	70	6.0	5.5	104	289	4.0		15	
Frigilla coelebs	Female	Open	55	6.8	3.3	78	264	1.1	5	15	14
Fringilla montifringilla	Female	Open	60	5.8	5.1	88	454	3.0	6	14	14
Serinus serinus	Female	Open	50	5.3	3.5	41	217	2.3	4	11	15
Carduelis chloris	Female	Open	40	6.1	2.9	56	236	2.2	5	14	15
Carduelis spinus	Female	Open	55	5.2	4.0	56	198	1.9	5	12	15
Acanthis flavirostris	Female	Open	65	6.0	5.0	94	182	1.5	6	13	15
Acanthis flammea	Female	Open	60	5.3	1.6	77	94	2.1	5	13	12
Carpodacus erythrinus	Female	Open	55	7.0	5.5	141	1 037	4.0	5	14	14

Table 1 *Continued*

Species	Nest building sex	Nest site	Latitude (°N)	Nest diameter (cm)	Nest depth (cm)	Nest cup volume (cm³)	Nest material volume (cm³)	Nest thickness (cm)	Clutch size	Body size (cm)	Nesting period (days)
Pinicola enucleator	Female	Open	65	7.5	4.5	133	481	3.0	4	20	14
Loxia curvirostra	Female	Open	60	6.3	3.8	77	790	4.1	4	16	21
Loxia pytyopsittacus	Female	Open	60	7.0	6.0	154	925	3.8	3	17	25
Pyrrhula pyrrhula	Female	Open	60	7.6	4.8	145	882	4.7	5	15	14
Coccothraustes coccothraustes	Female	Open	50	7.5	4.5	133	2 061	6.8	5	18	13
Oriolus oriolus	Female	Open	50	10.0	4.5	236	428	1.5	4	24	15
Pica pica	Male and female	Semi-hole	50	17.3	12.2	2 696	11 762	3.4	6	46	25
Corvus monedula	Male and female	Hole	45	12.1	4.8	425	23 973	13.2	5	33	33
Corvus frugilegus	Male and female	Open	55	19.8	12.1	3 036	39 574	11.0	5	46	30
Corvus corone	Male and female	Open	60	20.0	12.5	2 618	49 742	30.0	5	47	31
Corvus corax	Male and female	Open	50	27.6	11.1	4 427	14 103	21.3	5	64	38

We used latitude and clutch size as independent variables in the multiple regression analyses, because both parameters can influence nest size (Kern and Riper, 1984). The size of the nest could also depend on nest type (open, semi-open or hole), because of different levels of predation pressure and physical constraints (see above); therefore, we analysed the prediction both including and excluding hole-nesters.

All tests were two-tailed, except those analysing relationships between contrasts of continuous and discrete variables, when mean values of the contrasts were tested to be significantly different from zero (Purvis, 1991).

Results

Relationships between body size and nest size and duration of nestling period

We found a statistically significant relationship between contrasts in body size and contrasts in nest size ($r = 0.676$, $F_{1,75} = 75.61$, $P < 0.0001$) and between contrasts in body size and contrasts in the duration of the nestling period ($r = 0.366$, $F_{1,71} = 12.49$, $P < 0.001$).

Prediction 1: the nest should be larger when both sexes build. In agreement with this prediction, the analysis of the contrasts of the residual (nest size corrected for body size) revealed that species in which both sexes together build the nest had larger nests than those in which only the female builds the nest (one-tailed *t*-test, $t_8 = 3.013$, $P = 0.008$). This association was also significant when we excluded hole-nesters from the analysis ($t_7 = 2.919$, $P = 0.011$). When we corrected the residual nest size for the duration of the nestling period, the relationships were also significant ($t_6 = 2.312$, $P = 0.03$), even when hole-nesters were excluded from the analysis ($t_6 = 2.922$, $P = 0.013$).

Prediction 2: species in which both sexes participate in nest building should invest more in reproduction. In agreement with the prediction, the analysis of the contrast of the residuals of the duration of nestling period, after controlling for body size, revealed that species in which both sexes built the nest had longer nestling periods than those in which only the female built the nest. However, this relationship was not significant, either when including ($t_7 = 0.890$, $P = 0.202$) or excluding ($t_6 = 1.383$, $P = 0.165$) hole-nesters.

Prediction 3: species with a larger nest relative to their body size should also invest more in reproduction. Hence, in the residual analysis we should find that contrasts of relative nest size are positively correlated with contrasts of the relative duration of the nestling period. We found that the species with longer relative nestling periods have relatively larger nests than those with smaller nest parameters, both when including (Fig. 2, Table 2) and excluding (Table 2) hole-nesters. We used latitude and clutch size contrasts as independent variables in a multiple regression analysis. When we included hole-nesters, the partial regression coefficients were significant for all three independent variables, whereas when hole-nesters were excluded, the partial regression coefficient for latitude was only marginally significant (Table 2).

Discussion

Pair formation in birds is closely related to nest-building behaviour, as evidenced by nest-site choice and the use of nest material by many birds during courtship and pairing (Collias and Collias, 1984). Generally, nest building has been viewed as a result of natural selection. The most important advantage of the nest is perhaps its insulating capacity (Whittow and Berger, 1977; Sciurine and Kern, 1980; Kern, 1984) and the resulting reduction in the energetic cost of incubation (Walsberg and King, 1978; Sciurine and Kern, 1980; Kern, 1984; Kern and Riper, 1984). However, some studies have shown that, although thermal conductance was significantly related to nest mass

All species in the analysis
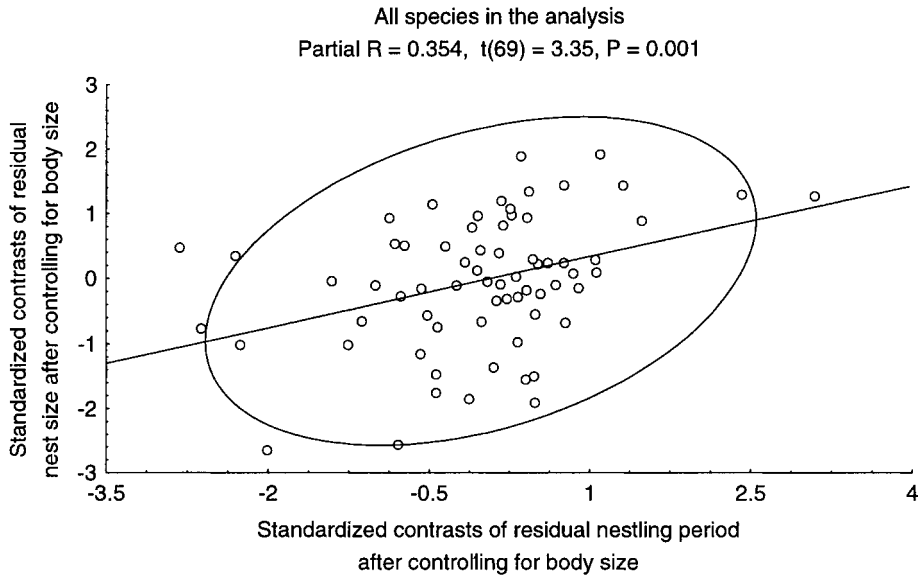Partial R = 0.354, t(69) = 3.35, P = 0.001

Figure 2. Relationship between contrasts of standardized residual nest size and contrasts of standardized residual duration of the nestling period after correcting for body size. Confidence ellipse ($P = 0.01$).

and several nest dimensions, it was not a simple function of nest size (Kern, 1984; Kern and Riper, 1984), but depended instead on the porosity or density of the wall of the nest (Sciurine and Kern, 1980; Kern, 1984; Kern and Riper, 1984). Other natural selection advantages of a large nest include increased stability, and thus greater structural resistance to wind or other environmental hazards, and a reduced risk of eggs or nestlings falling from the nest (Collias and Collias, 1984).

Natural selection would result in an optimal nest size based on environmental factors that are dependent on the demands of eggs and nestlings but independent of the nest builder. If the nest is built only to insulate and protect the clutch and the chicks, there should be no difference in nest size between species in which both sexes cooperate in nest building and those in which only the female builds the nest. However, our results show that nest size does depend on the builder (one or both sexes).

Based on the idea that nest size is merely the result of natural selection pressures, we should expect nests in places with lower temperatures to be larger than in places with higher temperatures, as shown in previous studies (Kern, 1984; Kern and Riper, 1984). We found a significant positive relationship between latitude and nest size (Table 2). However, considerable residual variance needs to be explained. Furthermore, nest size showed a highly significant positive relationship with the duration of the nestling period as predicted by our hypothesis regarding nest-building as sexual selection (prediction 3), and thus a large nest may be a sexually selected trait which allows each member of a pair to assess the parental ability of its partner.

The duration of the nestling period is related to body size and to the risk of nest predation (Bosque and Bosque, 1995). If the probability of nest predation is low, selection may favour a long nestling period. And if young are to remain for a long period in the nest, they need a wide and stable nest. However, when we corrected the nest size for the duration of the nestling period and for body size, significant differences in nest size appeared between species in which the two sexes build together and those in which only the female builds.

Table 2. Results of multiple regression analyses between nest size corrected for body size (dependent variable) and latitude, clutch size and duration of the nestling period of different passerines (including and excluding hole-nesters) in an analysis of independent contrasts

| | Multiple correlation coefficient | | | Independent variables | | | | | |
| | | | | Latitude | | Clutch size | | Nestling period | |
Nest size	R	F	P	β	P	β	P	β	P
Including hole-nesters (df = 3,68)	0.522	8.501	< 0.0001	0.250	0.02	0.255	0.02	0.354	0.001
Excluding hole-nesters (df = 3,60)	0.519	7.380	0.0003	0.188	0.10	0.262	0.02	0.349	0.003

It is difficult to distinguish between the effects of the risk of nest predation and parental investment on the duration of nestling period. However, because the risk of nest predation does not appear to be related to the number of pair members participating in nest building but to the number of trips necessary to transport all nest material, variability in parental investment remains the only likely factor to account for the association of differences in the duration of the nestling period with the number of pair members involved in the nest-building process. Since both sexes cared for nestlings in all species in this study, differential parental investment should be related to the nest-building process, as stated by our second prediction. However, the relationship was not statistically significant. Because of polytomies, when we controlled for common phylogenetic decent, we only obtained eight and seven contrasts when including and excluding hole-nesters, respectively. Because the duration of the nestling period is the result of both parental investment and the risk of nest predation, more data (to increase the degrees of freedom) and a better phylogeny of the species (to reduce the number of polytomies) are needed to reach a firm conclusion regarding the relationship between the duration of the nestling period and which of the sexes builds the nest.

Other hypotheses proposed to explain variation in nest size

1. *Nest size could be a consequence of clutch size, because brood size may be constrained by nest size in passerines* (Slagsvold, 1989a). Our data revealed a significant positive partial regression coefficient between clutch size and nest size, but it was smaller than the partial regression coefficient for the relative duration of the nestling period (Table 2). However, we found no relationship between contrasts of the relative duration of the nestling period and contrasts of clutch size (including hole-nesters: $r = 0.140$, $F_{1,70} = 1.40$, $P > 0.20$; excluding hole-nesters: $r = 0.179$, $F_{1,70} = 2.05$, $P > 0.15$), while contrasts of nest size (corrected for body size) were significantly positively correlated with contrasts of the duration of the nestling period (corrected for body size, Table 2). This agrees with our hypothesis (prediction number 3).

The increase in clutch size in relation to nest size can be explained by the fact that greater ability to nourish offspring is associated with larger clutch size (Lack, 1968; Sæther, 1994). The female can assess mate quality by his nest-building behaviour or nest characteristics, and then adjust clutch size accordingly. Therefore, a large nest-building effort (large nests) is predicted to be related to large clutch sizes and good reproductive success.

There is some evidence in the literature that is consistent with an increasing reproductive success (brood size or breeding success) in larger nests: Slagsvold (1982) found greater breeding success when he increased the size of the nest in the fieldfare (*Turdus pilaris*). Møller (1982) also reported a positive relationship between nest size and clutch size in the barn swallow (*Hirundo rustica*). Moreno *et al.* (1994) showed that bigger nests had higher breeding success in the black wheatear, and that alternative explanations for large nests, such as thermoregulation, were unlikely. Experimental manipulation of the number of stones carried by mated male black wheatears affected the timing and the rate of reproduction by their mates (Soler *et al.*, 1996). Soler *et al.* (1995), studying the magpie, found a positive relationship between nest size and territory quality as well as indirect evidence for a relationship between nest size and parental quality.

2. *Males may use the amount of nest material delivered as a means of obtaining more pair copulations* (Tortosa and Redondo, 1992). In the white stork (*Ciconia ciconia*), Tortosa and Redondo (1992) found a positive relationship between percentage of nest material delivered by individual males and pair copulation rate. However, the copulation rate was simultaneously related to the time spent at the nest, nestling feeding rate by the male and the female, and breeding success. Before laying, the female may be able to assess the foraging efficiency of males by monitoring copulation frequency and, perhaps, by the delivery of nest material (Tortosa and Redondo, 1992). However, experimental food supplementation resulted in larger nests and clutch sizes, and showed that males copulated less during the period preceding maximum female fertility in food-supplemented areas than in non-food-supplemented areas (opposite to the prediction of the frequency of copulations being a reliable signal of foraging efficiency; Tortosa and Redondo, 1992). Therefore, the results agree with our hypothesis that male nest building allows the female to assess the quality of her mate.

Why don't all individuals build a large nest?

Nest size is constrained by different parameters (see Slagsvold, 1989a):

1. *Cost of nest predation*. Nest conspicuousness is related to risk of nest predation (Lack, 1954), and thus large nests appear to suffer more from predation than small nests (Snow, 1978). This is one of the most important constraints on nest size (Collias and Collias, 1984; Slagsvold, 1989a). However, in two experiments (Slagsvold, 1982, 1989b) and two sets of observational data (Pikula, 1979; Soler *et al.*, 1995), predation rate did not differ according to the size of the nests. Although this cost of predation is logical, intraspecific variation in nest size is not related to the risk of nest predation.

2. *Cost of adult predation during the nest-building period*. Another reason why passerines do not build larger nests could be the risk of adult predation while nest building (Collias and Collias, 1984). However, in this scenario, nest size – that is, the capacity of one (or two) individuals to build a large nest – could provide information about the ability of that individual to avoid predation, and also about the risk taken by that individual bird in the nest-building process (in terms of time spent building). Therefore, although risk of nest predation could limit nest size, the result of the trade-off between nest size and risk of predation could be used as a signal of individual quality in sexual selection.

3. *Cost of carrying nest material*. The cost of carrying nest material could also be an important constraint for time and energy reasons. One extreme example of this cost has been described in the black wheatear. This 40 g bird carries, on average, 1.8 kg of stones during an average of 7.8 days, and breeding success is positively related to the number of stones carried (Moreno *et al.*, 1994). The number of stones carried could provide females with an estimate of the mate's provisioning

capacity, and the nest-building signal could prompt females to invest more or less in reproduction (Moreno *et al.*, 1994). Female birds usually invest more than male birds in reproduction (Clutton-Brock, 1991). When both sexes build the nest, it is the male that usually carries the heaviest material and the female who places it in the nest (Collias and Collias, 1984), thus allowing the female to evaluate the working ability of the male.

In conclusion, we hypothesize that nest building has a sexual selection component, and that the trade-off between the costs and the benefits of a large nest could be used by pair members for mutual assessment of phenotypic quality. In accordance with this hypothesis, we found that (1) nest size was larger when the nest was built by both sexes, and (2) parental investment estimated as the relative duration of the nestling period was positively related to relative nest size.

Could sexual selection based on nest-building activity or nest characteristics occur in organisms other than birds?

Nest building is widespread in the animal kingdom (Hansell, 1984) and, therefore, it is possible that sexual selection based on mutual assessment of parental quality from nest-building activity or nest characteristics could occur in organisms other than birds. However, there is little information on nest size and reproductive parameters in organisms other than birds. However, the information we have collected indicates that, in some cases, there may be a relationship between reproductive parameters and size of the nest. For example, beavers (two species of the genus *Castor*), with some lodges reaching 12 m in diameter and 2 m high (Warren, 1927), are monogamous (Bishir *et al.*, 1983). These species could be appropriate ones in which to study the relationships between nest-building activity, size of the nest and the quality of the partner.

In teleost fishes, some species are characterized by parental care for eggs in a nest (Clutton-Brock, 1991; Pitcher, 1993). Usually males defend nests that are used by females for egg laying. According to our hypothesis, females choose their mate (nest) in relation to characteristics of the nest, such as its quality (see references in Pitcher, 1993). Large nests have more eggs and, in some species, male body size is positively correlated with nest measurements and also with the number of eggs in the nest (see references in Hastings, 1988; Kraak and Videler, 1991). Nest defence is one of the most important components of parental care in fish (Clutton-Brock, 1991). If a male occupies a high-quality nest, he is able to defend the nest against other males or predators (when the nest already contains some eggs; Kraak and van den Berghe, 1992). Therefore, nest characteristics are related to the parental ability of males and thus reliably signal male quality.

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