Title: The fecundity costs of building complex nests in birds

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Abstract

Animal nests provide a beneficial environment for offspring development and as such contribute to fitness. Gathering and transporting materials to construct nests is energetically costly, but the life history trade-offs associated with the complexity of nests built are largely unknown. Who contributes to building the nest could also mediate these trade-offs, as building a nest as a couple is expected to be less costly per individual than building alone. Using a comparative analysis on 227 songbird species globally, we found a fecundity cost associated with the type of nest a species builds. Species that build complex dome nests produce fewer broods per year than species building more simple cups or platforms. On the other hand, dome nesting species have larger clutch sizes than open nesting species, but only when the nest is built by a couple and not when females build nests alone. This suggests that building dome nests represents a trade-off with investment in young, especially when females are solely responsible for nest building. More broadly, our results could explain macroevolutionary patterns, such as the recent finding that females more often build open cup rather than dome nests.

Key words

broods per year, clutch size, life history, nest type, reproductive investment

Introduction

Avian nests create favorable conditions for developing offspring whilst also protecting them against predators, meaning they are important structures for reproduction (Hansell, 2000; Mainwaring *et* *al.*, 2014). Whilst nests provide advantages, they are also time consuming and energetically costly to build (Mainwaring & Hartley, 2013). Although there is little experimental evidence, the cost of nest building probably depends on the type of nest a species builds, with open cups or platforms (open nest), being smaller and requiring less cognitive ability to build than the larger and more complex enclosed cups with a roof and side entrance (dome nest; Collias, 1997). For example, current evidence suggest that open nests are simpler to construct, require less building material, are lighter and smaller relative to the builders' body weight, and take less time to build than dome nests (Collias, 1997; Hansell, 2000; Mouton & Martin, 2019; Medina *et al.*, 2022). While dome nests might be more costly to build, they are thought to be an adaptation to extreme environments, offering greater insulation of offspring from unfavorably cold and hot weather conditions and providing protection from solar radiation (Collias, 1997; Martin *et al.*, 2017; Duursma *et al.*, 2018).

Building nests of a certain type, open or dome, may have co-evolved with other life history parameters, such as fecundity. A trade-off in allocation of resources between nest building and fecundity is evident at the species level (Lens *et al.*, 1994; Moreno *et al.*, 2010a). When species that reuse nests were unable to do so, or nests were experimentally removed which forced birds to build new nests, female white storks (*Cionia ciconia*), black wood peckers (*Dryocopus martius*) and blue tits (*Cyanistes caeruleus*) all produced lower clutch sizes or had lower breeding success (Lambrechts *et al.*, 2012; Tobolka *et al.*, 2013; Kosiński & Walczak, 2019; for no effect see Cancellieri & Murphy, 2013). In addition, when pied flycatchers (*Ficedula hypoleuca*) were provided with complete nests, offspring received more provisioning and were larger, suggesting resources were redirected from nest building to developing offspring (Moreno *et al.*, 2010b). Past comparative studies on species of North American Passeriformes and Piciformes found evidence that fecundity can vary with nest type (Martin & Li, 1992; Böhning-Gaese *et al.*, 2000). However, these studies have divided nest type into open and cavity nests (ignoring dome nests), and hence don't focus on the costs of building the nest structure, but rather its placement. Jetz et al. (2008) did consider dome nests (categorizing nests as open, closed or cavity) in their analysis on clutch size and found that clutch size was strongly related to nest type, with cavity nesters producing largest clutches, followed by dome nesting species and open nesting species producing the smallest clutches. However, Jetz et al. (2008) considered only clutch size as a measure of fecundity as it aimed to test the global predictors of clutch size and not the potential fecundity costs of nest building.

Another dimension of fecundity is how many times a species reproduces during each breeding season. Species, or individuals within a species, that produce a single brood would be expected to have larger clutches than those that have multiple breeding attempts. There are several possible reasons why multi-brooded species have smaller clutches. Breeding multiple times may present a trade-off between investment in the current breeding attempt and saving resources for future breeding attempts, it could be to align with more steady resource availability supporting less offspring at once (rather than a single burst), or to avoid predation of entire breeding attempt for the season (Slagsvold, 1982; Crick *et al.*, 1993; Martin *et al.*, 2000). Evidence for females producing larger clutches when investing in a single brood per season has been found in Brown-cheeked Laughing Thrush's (*Trochalopteron henrici*) where females that produce single broods have larger clutches than multi-brooded females (Li *et al.*, 2020). There is some variation as to how multi-brooded species invest in their clutches over the breeding season. Some species such as Eastern Bluebirds (*Sialia sialis*) invest more in the first attempt producing heavier first clutches and lighter second clutches (Robinson *et al.*, 2010). In contrast some species have larger clutch sizes in their subsequent breeding attempts, such as Horned Larks (*Eremophila alpestris*) and White-collared Blackbirds (*Turdus albocinctus*), possibly due to increased food availability later in the season (Du *et al.*, 2014; Fan *et al.*, 2017). While studies have investigated the relationship between clutch size and number of broods per year, it is unknown if the type of nest a species builds affects the trade-off between clutch size and number of broods produced per year. It has been shown that dome nesting species take longer to build their nests, but differences in number of broods per season between nest types are yet to be tested.

One factor that may buffer the possible fecundity costs associated with nest building is sex-specific nest building contributions. In crested tits (*Lophophanes cristatus*), males helping with nest building shortened the period between start of nest building and the start of egg laying, resulting in beneficial earlier fledging dates of young (Lens *et al.*, 1994). More broadly, a recent comparative analysis found that species with females who build nests alone had shorter breeding seasons and therefore less opportunity for subsequent broods (Mainwaring *et al.*, 2021). Furthermore, dome nests were suggested to be particularly costly for females to build alone, as females usually build open nests, with larger and more complex dome nests more commonly being built by female and males together (Mainwaring *et al.*, 2021). While there is some research on the roles of males and females contributing to nest building (Lifjeld *et al.*, 2019; Soler *et al.*, 2019; Mainwaring *et al.*, 2021), we know very little about the life history consequences of these sex-specific investment strategies.

Fecundity is a crucial aspect of avian reproduction, and unsurprisingly, it is related to a suite of different variables. For example, latitude encapsulates trends in fecundity attributed to environmental drivers such as predation rate, length of the breeding season and seasonality of resources, making it a useful umbrella term to control for these effects used in many studies (Griebeler *et al.*, 2010; Jetz *et al.*, 2008). Generally, species at higher latitudes lay larger clutches and produce less broods per year likely due to the more seasonal environment with a short suitable climate and food availability windows for breeding (Cardillo, 2002). Nest predation rates are higher in the tropics selecting for smaller clutches and more broods per year, which is facilitated by the comparatively stable climate (Schemske *et al.*, 2009; Remeš *et al.*, 2012). Another important variable related to fecundity that is not covered by latitude is body size. Larger species also typically have smaller clutches and less broods per year than smaller species (Böhning-Gaese *et al.*, 2000). Therefore, after latitude and body size are taken into account, the type of nest a species builds may have a fecundity cost due to the resources required for nest building.

In this study we use a phylogenetically controlled comparative analysis of 227 songbird species (suborder Passeri) globally to explore whether building more complex and time-consuming nests (e.g. dome nests) incurs a fecundity cost in terms of clutch size or the number of broods species produce per year. In addition, we test whether such effects depend on who contributes to nest building: both the female and the male, or the female alone.

Methods

Data compilation

We built upon the Medina *et al*. (2022) dataset on nest type and time taken to build nests (*N*=277 spp.) of songbird species, and adopted the taxonomy structure from Jetz et al. (Jetz *et al.*, 2012) phylogenies (see Figure 1 for phylogenetic distribution of nest types). We collected data primarily from the Birds of the World website (Billerman *et al.*, 2022) on the number of broods per season, sex of the nest builder and adult body weight, and on clutch sizes primarily from Jetz et al. (Jetz *et al.*, 2008) and Lislevand et al. (Lislevand *et al.*, 2007). When data was unavailable in these sources, we performed a literature search on each of the remaining species (*N* = 37) and extracted data from journal articles and handbooks (for sources see supplementary materials). Nest type built by each species was classified as either dome (nest with a roof or a side entrance; *N*=43) or open (nest with a cup shape or platform; *N*=184) following established procedures (Mouton & Martin, 2019; Medina *et al.*, 2022). We excluded nests that were built inside a cavity because we were interested in the costs of building a structure, not those associated with its placement. Clutch size (defined as the average of the minimum and maximum clutch sizes) and average number of broods per year were used as separate response variables, rather than combined into a measure of fecundity as they have a negative relationship (Böhning-Gaese *et al.*, 2000) which may mask individual effects. Species where the male builds the nest alone were excluded (*N*=8). This was because males building the nest alone is far less common (as in Mainwaring *et al.*, 2021) and as only female birds lay eggs, we would only expect a relationship between nest building and fecundity if the female was involved in nest building.

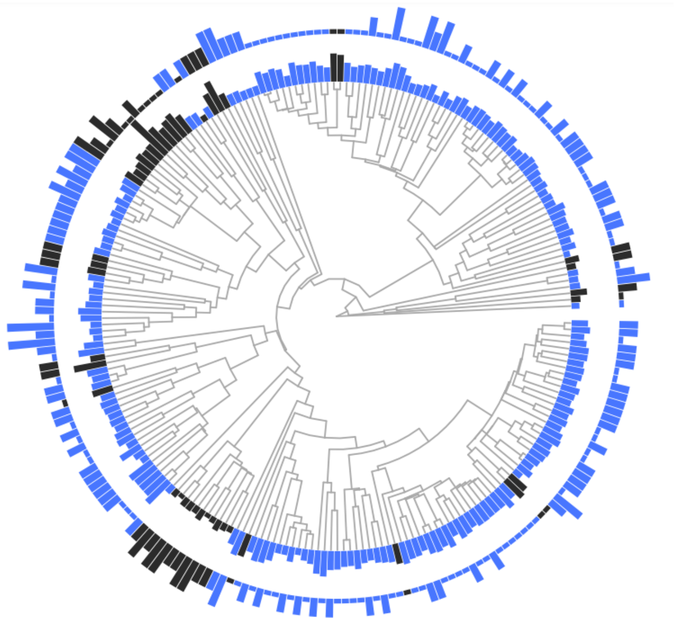

Figure 1. Phylogenetic distribution of open (represented in blue) and dome (represented in black) nests and association with mean clutch size (inner ring) and number of broods per year (outer ring) across 227 songbird species. R package 'ggtree' was used to generate this figure (Yu *et al.*, 2017).

To control for the associations between latitude and body size, and our response variables (clutch size and the number broods per year; Böhning-Gaese *et al.*, 2000), we collected data on the mean latitude for the distribution range of each species (Sheard *et al.*, 2020) and the body weight of the nest builder (an average of the male and female when they built the nest together and the female weight when she solely built the nest [female weight wasn't available in 13% of species that the female built the nest, so we used the average of both sexes]). We also collected information on the length of the breeding season (maximum time range breeding has been recorded to occur, as months) for as many species as possible (*N*=186).

<u>Statistical analysis</u>

The statistical program R was used for all analyses (v. 4.2.0; Team, 2019). The full models consisted of the predictors; nest type (dome or open), nest builder (female or both female and male), latitude (absolute), average body weight of the builder/s (log transformed) and interactions between nest type and nest builder, and body weight and nest builder. The response variables were clutch size (log transformed) or broods per year (average values were rounded to the nearest whole number). Initial models were run using Phylogenetic Generalized Least Squares with the 'caper' package (Orme *et al.*, 2013) and all predictors. We then used the 'dredge' function in the MuMin package (Burnham & Anderson, 2002) to select a best-fitting model by comparing the corrected Akaike Information Criteria (AICc) of the models nested within the full model (see Table S1 for results). The final models consisted of predictors of models within Δ AICc < 2. The *check_model* function in the 'performance' package (Lüdecke et al., 2021) was used to check final models for collinearity between predictors. All variance inflation factors (VIF) values were below 1.5 for the broods per year model. Values for the clutch size model were above 5 so we split the dataset into nests built by females and nests built by both males and females and ran two separate models for this analysis, which reduced the VIF to below 1.5. Final models were run using Bayesian regression models using Stan (BRMS) with the 'brms' package (Bürkner, 2017) to accommodate for ordinal response data and to use a consistent method across all models. All models were run with weakly informative priors calculated with the *get_prior* function in 'brms' package (Bürkner, 2017). We report the credibility intervals for each predictor.

To investigate if nest type is associated with the number of broods produced per year, we used a BRMS with an ordinal cumulative distribution and a probit link function (Bürkner, 2017). This distribution was the most appropriate due to the ordinal distribution of the response variable 'broods per year'. The best model predictor variables from model selection were average body weight of the builder/s (log transformed), nest type (dome or open), nest builder (female or both male and female) and latitude (absolute). This model was run in 4 chains each with 10000 iterations with a warmup of 1000 iterations and thinning of 1.

To test if nest type influences fecundity through clutch size, we built BRMS models with a gaussian distribution and an identity link function (Bürkner, 2017). Due to collinearity between predictors, we split the dataset in two by who built the nest (female or male and female together) and ran a separate model for each sub-set of the data. In both models, the response variable was the mean clutch size (log transformed) and the best model predictors from model selection; nest type (dome or open) and latitude (absolute). To facilitate model convergence, in the final model the predictors (nest type and latitude) were scaled and centered for the dataset of nests built by both the male and female. Both models were run in 4 chains each with 20000 iterations with a warmup of 2000 iterations and thinning interval of 1. This number of iterations was necessary for model convergence.

To control for species phylogenetic relatedness, we generated a maximum clade credibility (MCC) tree to include as a random effect in our analysis, using 1000 phylogenies from birdtree.org (Jetz *et* *al.*, 2012) and the package ‘Phangorn’ (Schliep, 2011). To account for phylogenetic uncertainty we performed each analysis across 100 trees, and used the package ‘coda’ (Plummer *et al.*, 2006) to generate 95% highest posterior density intervals (HPD) for the estimates across 100 trees.

Results

Open nests were built by 81% of species, with the female building the nest alone in 61% of these species. Dome nests were built by the other 19% of species, with the female building the nest alone in 51% of these species.

When the male and female build the nest together, species building dome nests have larger clutches but when the female builds the nest alone, the clutch size didn’t differ between species building dome and open nests (Table 1 and Figure 2). Species at higher latitudes laid larger clutches.

There was no difference in body weight or breeding latitude between open and dome nesting species (Figure S1 and Figure S2), or differences in the length of their breeding season (Figure S3).

Table 1. Results of BRMS models testing the associations between nest type and average clutch size (when the nest is built by the (1) female or (2) the male and female), and (3) average number of broods per year. Estimate and 95% confidence intervals (95% CI) from models with MCC to control for phylogeny. The 95% HPD interval of the estimate was generated across 100 phylogenetic trees.

Response	Predictor	Estimate_{MCC}	$\text{95\% CI}_{MCC}$		$\text{95\% HPD interval}_{100}$	
(1) Clutch size (female data)	Nest type	0.01	-0.15	0.16	-0.03	0.04
	abs(latitude)	0.01	**0.01**	**0.02**	**0.01**	**0.01**
(2) Clutch size (male and female data)	Nest type	-0.10	**-0.16**	**-0.04**	**-0.29**	**-0.28**
	abs(latitude)	0.15	**0.03**	**0.08**	**0.006**	**0.007**
(3) Broods per year	log(weight)	-0.48	**-0.88**	**-0.14**	**-0.54**	**-0.42**
	Nest type	0.96	**0.14**	**2.08**	**0.86**	**1.15**
	Nest builder	-0.54	-1.24	0.02	-0.66	-0.49
	abs(latitude)	-0.03	**-0.04**	**-0.01**	**-0.03**	**-0.02**

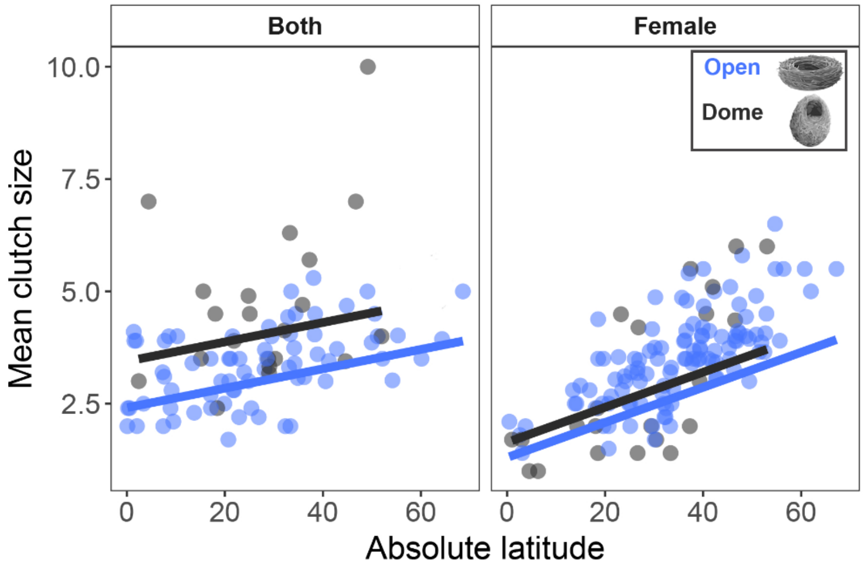

Figure 2. Association between mean clutch size and latitude of species that build dome nests (black) and open nests (blue). Points indicate raw data and lines show the model predictions.

Species that build open nests lay more broods per year than those that build dome nests (Table 1, Figure 3). The number of broods produced per year didn't differ between species in which the female builds the nest and those where the female and male build together. Larger species and those at higher latitudes produced less broods per year.

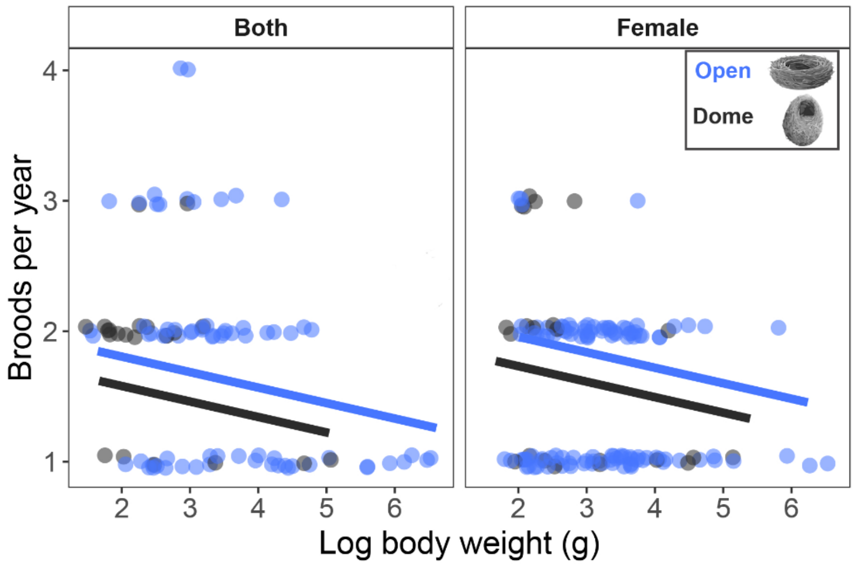

Figure 3. Association between the number of broods a species produces per year and the weight of the species that build dome nests (black) and open nests (blue). Points indicate raw data and lines show the model predictions.

Discussion

We found that building different nest types is associated with fecundity costs, with species building dome nests having less broods per year than species building open cup nests. The effect of nest building on overall fecundity, however, depends on sex-specific nest building contributions. In dome nesting species where both females and males contribute to nest building, the lower number of broods per year may be compensated by producing larger clutch sizes than open nesting species. In species where the dome nest is built solely by the female, clutch size isn't larger than that produced by open nesting species. Therefore, our results suggest there could be an overall fecundity cost to building dome nests when females build the nest (Mainwaring *et al.*, 2021).

Dome-nesting species produced larger clutches than open nesting species when the male and female built the nest together, but clutch size didn't differ with nest type when the female built alone. One hypothesized advantage of enclosed nests is a lower rate of predation due to offspring concealment from predators (Collias, 1997; Hall *et al.*, 2015). Lower predation rates of dome nests could drive selection for larger clutch sizes in dome than open nesting species (Skutch., 1949). Previous research on the benefits of lower predation rates in dome nests hasn't considered who is involved in nest building. Our findings indirectly suggest there could only be lower predation in dome nesting species when the male and female build together, but not when the female builds alone (because there is a larger clutch size only in couples that build domed nests). Alternatively, dome nesting females may be under selection to lay larger clutches due to lower predation, but are unable to do so due to a trade-off in resource allocation between nest building and offspring (Lens *et al.*, 1994; Moreno *et al.*, 2010a). When males also contribute to building the dome nest the cost to the female is likely to be lower than if she built the nest alone, meaning only in such cases are the trade-offs between resource allocation to nest building and egg production relaxed, thereby resulting in a larger clutch.

We found that after controlling for body size and latitude, species that build dome nests have less broods per year than species building open nests, regardless of who builds the nest. It is highly likely that dome nests are more energetically costly and cognitively demanding to build than open nests (Collias, 1997; Hansell, 2000; Mouton & Martin, 2019) which could leave less energy for subsequent breeding attempts. If there is selection for larger clutches in dome nesting species then females may face a trade-off with producing less broods per year to allow for investment in larger clutches (Böhning-Gaese *et al.*, 2000). Another possibility is that dome nests take longer to build as reported in (Medina *et al.*, 2022), and it's possible that there is less time for re-nesting, resulting in fewer broods per year. Producing multiple broods per year is more common when birds successfully fledge a brood early in the breeding season, leaving more time for subsequent renesting (Geupel & DeSante, 1990; Evans Ogden & Stutchbury, 1996; Halupka *et al.*, 2008). Consistent with this idea, we found that species with longer breeding seasons produced more broods per year (Figure S4), however, the differences in number of broods between open and dome-nesting species that we report cannot be explained by differences in length of breeding seasons, because in our dataset the length of their breeding seasons is similar (Figure S3).

Latitude and body size are known to be global drivers of clutch size and number of broods per year (Böhning-Gaese et al., 2000). Consistent with the literature, species at higher latitudes laid larger clutches (Figure 2) and produced less broods per year (Figure S6), which is thought to be because of prominent seasonal variation in food availability and survival (Cardillo, 2002; Jetz et al., 2008). In addition, species at lower latitudes had longer breeding seasons (Ricklefs & Bloom 1977; Wyndham, 1986; Figure S5). Latitude was included in our analysis to control for these trends, and we found no differences in latitude between nest types in our dataset (Figure S2). We also controlled for body size, as consistent with previous studies, species with smaller body size tended to lay larger clutches (but this effect was not statistically significant) and produce more broods per year (Böhning-Gaese et al., 2000; Figure 3). We didn't find a difference in body size between open and dome nesting species in our dataset (Figure S1).

Our study found that building a dome nest has a fecundity cost for species in which the female builds alone. This could explain broad-scale patterns recently reported, where dome nests are less commonly built by females alone (Mainwaring *et al.*, 2021). A pertinent question, therefore, is why some species where the female builds alone build dome nests? There is growing evidence that the benefits of dome nests may be more related to the protective thermal environment than predation (Martin *et al.*, 2017). Hence, the costs of constructing larger dome nests might be lower than having a nest with a suboptimal microclimate. There is evidence that dome nesting species spend less time incubating, suggesting a lower energetic cost associated with incubating at least in colder environments (Martin *et al.*, 2017; Mouton & Martin, 2019). In this instance selection would favor building a dome nest.

Our findings that building dome nests could result in fecundity costs could help explain the repeated transition from dome to open nests in songbirds in mild climates where the thermal benefits of dome nests aren't required (Price & Griffith, 2017; Fang *et al.*, 2018; Medina, 2019). The ancestral state in passerines has been found to be dome nests built by the male and female together (Price & Griffith, 2017; Mainwaring *et al.*, 2021), thus suggesting that in some lineages there was a transition to females building dome nests alone. Future studies could investigate if breeding strategies, such as how monogamous a species is, have selected for females to build nests alone and particularly more complex dome nests.

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Supplementary material

Table of contents

1. Data sources

The handbooks and journal articles used to collect data for this comparative analysis can be found in the supplementary excel data sheet 'Data sources'. The songbird species in this dataset are the species for which we could find information on how long it took to build the nest, clutch size, and the number of broods per year, and there were no geographic restrictions placed on our data collection.

3. Supplementary analysis

Model structure for supplementary models

All models were run with weakly informative priors calculated with the *get_prior* function in 'brms' package (Bürkner, 2017). We included the maximum clade credibility (MCC) tree as a random effect, and for any models with significant predictors, we also ran the same model using a distribution of 100 trees. All models were run in 4 chains each with 10000 iterations with a warmup of 1000 iterations and thinning of 1. We report the credibility intervals for each predictor.

Test for an association between latitude and nest type

To investigate if dome or open nesting species have significantly different weight distributions, we built a BRMS model with a gaussian distribution and identity link function (Bürkner, 2017). The response variable was the average body weight of the builder/s (log transformed), and the predictor variable was nest type (dome or open).

We found no significant difference in body weight of dome and open nesting species (Estimate= -0.00, [95% CI -0.29 – 0.28], Figure S1).

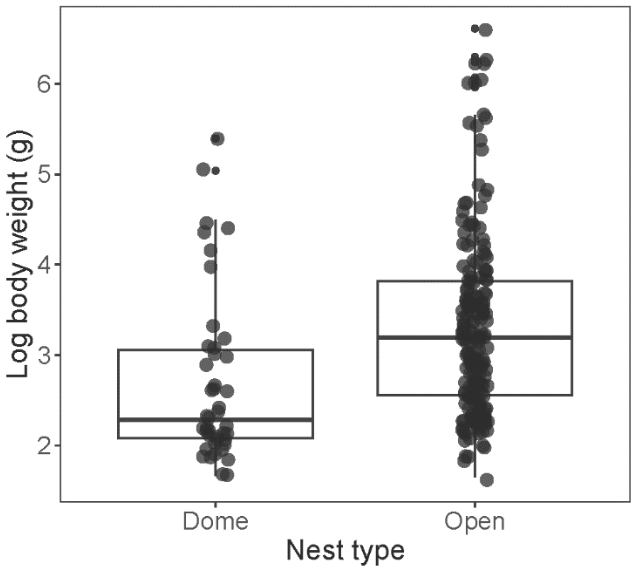

Figure S1. The mean body weight of species that build open and dome nests was not significantly different. The points indicate the raw data, the dark line in each box indicates the median, the upper and lower lines of each box indicate the minimum and maximum quantiles and the whiskers indicate the minimum and maximum data spread.

Test for an association between latitude and nest type

To investigate if dome or open nesting species are distributed across significantly different latitudes, we built a BRMS model with a gaussian distribution and an identity link function (Bürkner, 2017). The response variable was absolute latitude, and the predictor variable was nest type (dome or open).

There was no significant difference in latitude between dome and open nesting species (Estimate= 1.88, [95% CI -4.38 – 8.20], Figure S2).

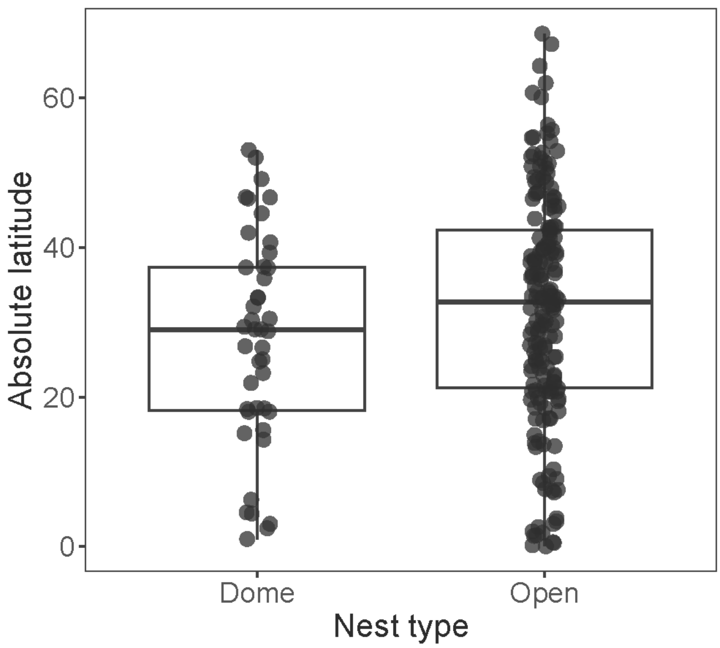

Figure S2. The mean latitude of the distribution range species that build open and dome nests was not significantly different. The points indicate the raw data, the dark line in each box indicates the median, the upper and lower lines of each box indicate the minimum and maximum quantiles and the whiskers indicate the minimum and maximum data spread.

Test for an association between the length of the breeding season and nest type

To investigate if species that build dome or open nests breed for significantly different lengths of time in each year, as this could result in differences in the number of broods, we built a BRMS model with a gaussian distribution and an identity link function (Bürkner, 2017). The response variable was length of breeding season (maximum time range breeding has been recorded to occur, as months [e.g., mid-March to end May = 2.5 months]; *N*=186), and the predictor variable was nest type (dome or open).

Dome and open nesting species breed for the similar lengths of time (Estimate= 0.09, [95% CI -0.30 – 0.11], Figure S3).

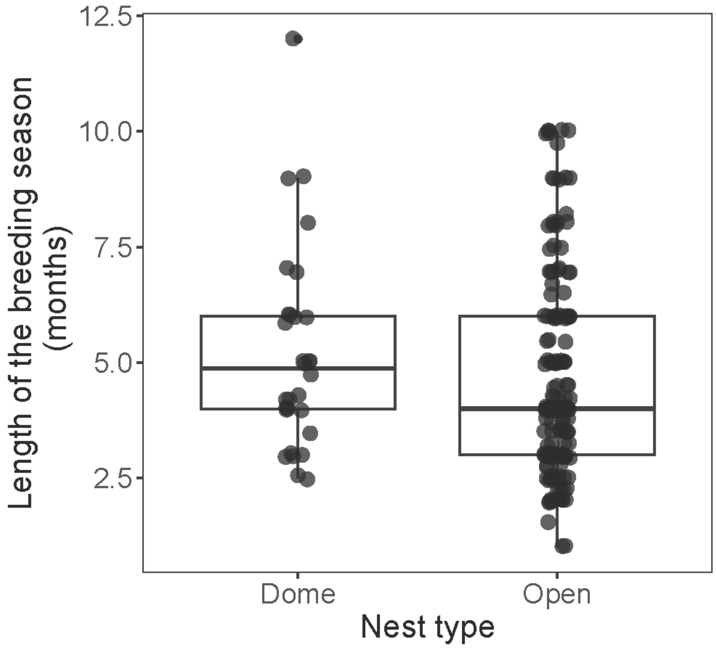

Figure S3. The length of the breeding season did not differ between species that build dome and open nests. The points indicate the raw data, the dark line in each box indicates the median, the upper and lower lines of each box indicate the minimum and maximum quantiles, the whiskers indicate the minimum and maximum data spread and the outlier is shown by the smaller solid point.

Test for an association between length of the breeding season and broods per year

To test for an association between the length of the breeding season and the number of broods a species lays, we built BRMS with a gaussian distribution and an identity link function (Bürkner, 2017). The response variable was the length of the breeding season log transformed, and the predictor variable was broods per year (average values were rounded to the nearest whole number; *N*=186).

There was a significant positive association between the length of the breeding season and broods per year, such that species with longer breeding seasons have more breeding attempts (Estimate= 0.17, [95% CI 0.08 – 0.26], 95% HPD interval = 0.16 to 0.18, Figure S4).

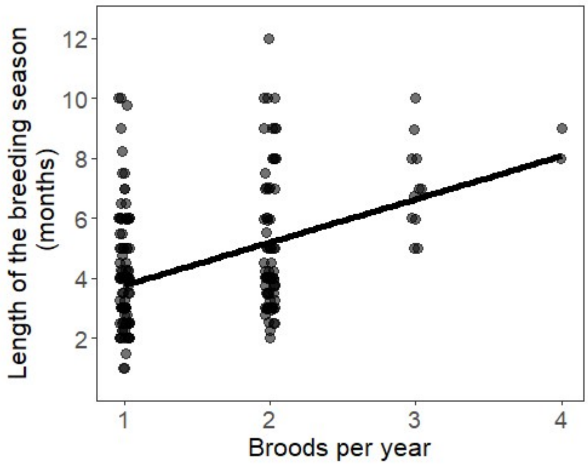

Figure S4. Association between the length of the breeding season and the number of broods a species lays annually.

Test for an association between species latitude and length of the breeding season

To test for an association between the mean latitude for the species distribution and the length of the breeding season, we built a BRMS model with a gaussian distribution and an identity link function (Bürkner, 2017). The response variable was absolute latitude, and the predictor variable was the length of breeding season (*N*=186).

There was a significant negative association between latitude and breeding season length, with tropical species having longer breeding seasons (Estimate= -3.43, [95% CI 7.88 – 11.56], 95% HPD interval = -3.46 to -3.32, Figure S5). Due to this association, we only included latitude in our main models.

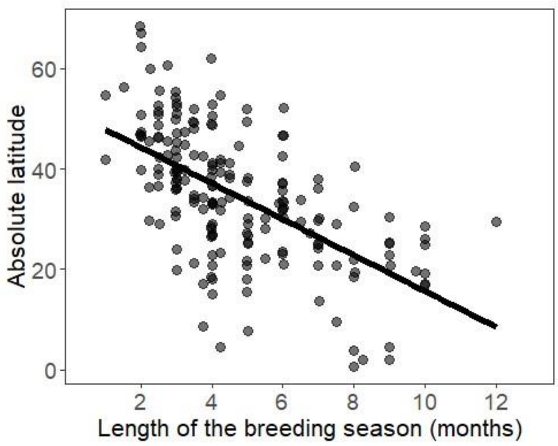

Figure S5. Association between the mean latitude for the species distribution range and the length of the breeding season in months.

4. Model selection results

Table S1. Results of model selection predicting broods per year and clutch size. Predictors are nest type (dome or open), nest builder (female or both female and male), absolute latitude, average body weight of the builder/s (log transformed) and an interaction between nest type and nest builder and between body weight and nest builder. Data for clutch size is split by nest builder so nest builder was not included as a predictor in these models.

Fecundity measure	Rank	Intercept	Latitude	Weight	Nest type	Nest builder	Weight* Nest builder	Nest type* Nest builder	AICc	ΔAICc	Weight
Broods per year	1	2.19	-0.01	-0.12	+	+			323	0.00	0.316
	2	2.27	-0.01	-0.12	+				324.7	1.66	0.14
	3	2.19	-0.01	-0.12	+	+		+	325	1.97	0.12
	4	2.16	-0.01	-0.11	+	+	+		325	2.01	0.12
	5	2.11	-0.01	-0.11		+			325.5	2.53	0.09
	6	2.19	-0.01	-0.11					326.8	3.76	0.05
	7	2.15	-0.01	-0.11	+	+	+	+	326.9	3.94	0.04
	8	2.10	-0.01	-0.11		+	+		327.6	4.62	0.03
	9	1.78	-0.01		+	+			327.7	4.69	0.03
	10	1.73	-0.01			+			329.5	6.53	0.01
Clutch size- both data	1	2.41	0.02		+				268.0	0.00	0.71
	2	2.28	0.02	0.04	+				270.2	2.13	0.25
	3	2.71	0.02						275.0	6.91	0.02
	4	3.00			+				276.2	8.14	0.01
	5	2.77	0.02	-0.02					277.1	9.04	0.01
	6	2.88		0.04	+				278.3	10.24	0.00
	7	3.38							284.4	16.33	0.00
	8	3.50		-0.04					286.4	18.38	0.00
Clutch size- female data	1	1.38	0.04						287.4	0.00	0.38
	2	1.30	0.04		+				287.5	0.13	0.36
	3	1.45	0.04	-0.02					289.5	2.06	0.14
	4	1.39	0.04	-0.02	+				289.6	2.20	0.13
	5	2.54							337.3	49.87	0.00
	6	2.44			+				337.7	50.27	0.00
	7	2.76		-0.06					339.1	51.71	0.00
	8	2.68		-0.07	+				339.5	52.07	0.00

5. Supplementary figure

Association between the number of broods a species produces per year and latitude (from analysis in main text)

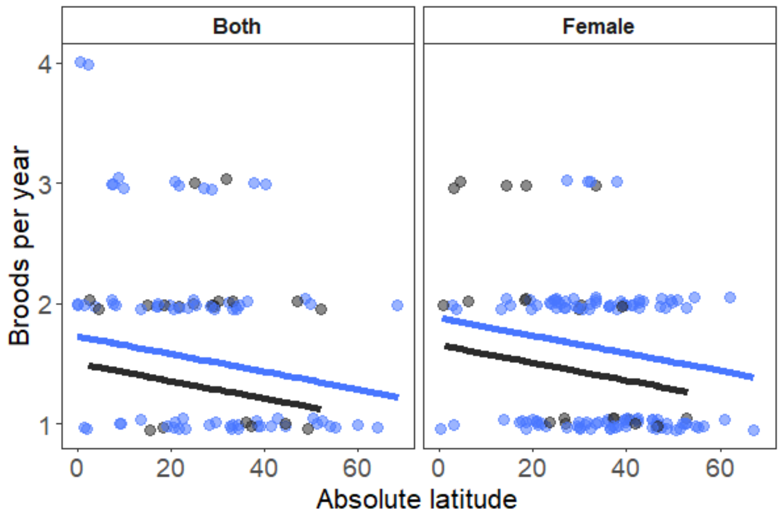

Figure S6. Association between the number of broods a species produces per year and latitude of species that build dome nests (black dots) and open nests (blue dots). Points indicate the raw data and lines show the model predictions.

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