

The evolution of enclosed nesting in passerines is shaped by competition, energetic costs, and predation threat

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ABSTRACT

Many avian species breed in enclosed nests that may provide better protection against predation and climatic conditions compared to open nests and are generally associated with larger clutch sizes and slower offspring growth. Here we show that different enclosed nesting strategies are each linked to behaviors with very different costs and benefits on a macroevolutionary scale. Using a detailed dataset of nest structure and location from the order Passeriformes, we employed phylogenetic comparative methods to evaluate (1) how predation, competition, design complexity, and energetic costs have shaped evolutionary transitions between different nesting strategies, and (2) whether these strategies also have distinct relationships with life-history traits. We find that flexible strategies (i.e., nesting in both open and enclosed sites) as well as energetically demanding strategies are evolutionarily unstable, indicating the presence of underlying ecological tradeoffs between antipredator protections, construction costs, and competition. We confirm that species with enclosed nests have larger clutch sizes and longer development and nestling periods compared to open nesters, but only species that construct enclosed nests rather than compete for preexisting cavities spend more time incubating and are concentrated in the tropics. Flexible strategies prevail in seasonal environments and are linked to larger clutches—but not longer development—compared to nesting in the open. Overall, our results suggest that predation, competition, and energetic costs affect the evolution of nesting strategies, but via distinct pathways, and that caution is warranted when generalizing about the functions of enclosed nest designs in birds.

Keywords: cavity nests, competition, domed nests, enclosed nests, life history, macroevolution, nest-building, predation

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LAY SUMMARY

- Many birds raise their young in enclosed nests, which likely offer protection from predators and climatic conditions. We currently know little, however, about why some species build their own enclosed nests, while others adopt existing cavities.
- Using a broad-scale, comparative approach with data from more than 4,000 passerine species (order Passeriformes), we evaluate how predation, competition, nest complexity, and energetic costs have shaped the evolution of these different enclosed nesting strategies.
- We find that both flexible and energetically costly enclosed nesting strategies are disfavored on evolutionary timescales. We also show that enclosed nesters have larger clutches and longer developmental periods irrespective of whether they compete for or build their nests.
- Our study highlights that different types of enclosed nesting strategies are linked to different sets of evolutionary costs and benefits.

La evolución de los nidos cerrados en los paseriformes está moldeada por la competencia, los costos energéticos y la amenaza de depredación

RESUMEN

Muchas especies de aves crían en nidos cerrados que pueden proporcionar una mejor protección contra la depredación y las condiciones climáticas en comparación con los nidos abiertos, y generalmente se asocian con tamaños de nidada más grandes y un crecimiento más lento de las crías. Aquí mostramos que diferentes estrategias de anidamiento en nidos cerrados están vinculadas a comportamientos con costos y beneficios muy diferentes a escala macro-evolutiva. Utilizando un conjunto de datos detallado sobre la estructura y la ubicación de los nidos del orden Passeriformes, empleamos métodos comparativos filogenéticos para evaluar (1) cómo la depredación, la competencia, la complejidad del diseño y los costos energéticos han dado forma a las transiciones evolutivas entre diferentes estrategias de anidamiento; y (2) si estas estrategias también tienen relaciones distintas con los rasgos de la historia de vida. Encontramos que las estrategias flexibles (i.e.,

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anidar tanto en sitios abiertos como cerrados), así como las estrategias energéticamente exigentes, son evolutivamente inestables, lo que indica la presencia de compensaciones ecológicas subyacentes entre las protecciones contra depredadores, los costos de construcción y la competencia. Confirmamos que las especies con nidos cerrados tienen tamaños de nidada más grandes y períodos de desarrollo y crianza más largos en comparación con las especies que anidan en nidos abiertos, pero solo las especies que construyen nidos cerrados en lugar de competir por cavidades preexistentes pasan más tiempo incubando y están concentradas en los trópicos. Las estrategias flexibles prevalecen en entornos estacionales y están vinculadas a tamaños de nidada más grandes, pero no a un desarrollo más largo, en comparación con el anidamiento en lugares abiertos. En general, nuestros resultados sugieren que la depredación, la competencia y los costos energéticos afectan la evolución de las estrategias de anidamiento, pero a través de vías distintas, y que se debe tener precaución al generalizar sobre las funciones de los diseños de los nidos cerrados en las aves.

Palabras clave: competencia, construcción de nidos, depredación, historia de vida, macro-evolución, nidos abovedados, nidos cerrados, nidos en cavidades

INTRODUCTION

The majority of bird species build or adopt a nest as part of their reproductive cycle (Hansell 2000, Collias and Collias 2016). Bird nests vary greatly in their design and location, from simple scrapes on the ground to elaborate, multi-chambered structures in trees (Collias 1997). In comparative studies, it is common to broadly divide nest types into “enclosed” or “open” nests, indicating, respectively, the presence or absence of a roof connected to the sides of the nest (e.g., Jetz et al. 2008, Stoddard et al. 2017, Cooney et al. 2020, Mainwaring and Street 2021). Such enclosed nests, however, can be achieved by several, very different strategies. The category of enclosed nests typically includes species that adopt or excavate cavities in trees, rock, or earth, as well as those that construct a closed, domed structure from plants and other materials. Some of these diverse enclosed nesting strategies are thought to result from similar selection pressures (e.g., all types of enclosed nests have been linked to increased protection from predators as they render nest contents and the attending parent less conspicuous; Lack 1948, Alerstam and Hogstedt 1981, Auer et al. 2007). Furthermore, recent studies have suggested that enclosed nests provide more favorable microclimates for offspring development and result in higher reproductive outcomes compared to open nests due to thermoregulatory benefits, especially in harsh environments (Rhodes et al. 2009, Martin et al. 2017, Duursma et al. 2018). However, some selection pressures are likely specific to different enclosed nesting strategies. In particular, obligate cavity nesters (i.e., those reliant on preexisting cavities) face strong intra- and inter-specific competition for nest sites (e.g., Martin and Li 1992, Martin 1993) in comparison to facultative cavity nesters and dome-nest builders. The extent to which these different types of enclosed nests evolve in response to similar or distinct selection pressures remains underexplored at the macroevolutionary scale.

Predation threat is an important cause of offspring mortality in birds and therefore strongly affects the evolution of reproductive traits (Ricklefs 1969, Fontaine and Martin 2006). Species with enclosed nests generally exhibit larger clutch sizes (Lack 1948, Slagsvold 1982, Lima 1987, Auer et al. 2007, Jetz et al. 2008) and longer developmental periods (Ricklefs 1968, Martin and Li 1992, Martin 1995; but see Cooney et al. 2020 or Barve and Mason 2015 where no correlation was found), which is thought to result from lower rates of nest predation (Alerstam and Hogstedt 1981, Remeš and Martin 2002). A general theory suggests that if birds minimize the energetic demands required to fight off or avoid predators, they can instead invest in nourishing larger clutches (Cody 1966). An alternative hypothesis by Skutch (1949) to explain this correlation posits that parental activity at the nest increases the risk of predation by making nest sites more conspicuous—the use of safer, enclosed habitats can therefore lead to higher

feeding rates of young. Studies of families containing a variety of nesting strategies provide some evidence that predation threat might have driven the evolution of enclosed nests and associated reproductive traits. For example, ground-nesting species of Old World babblers (Timaliidae) are more likely to build roofed nests, whereas species that build higher up in more protected locations tend to construct more open structures (Hall et al. 2015). Similarly, an experiment using artificial Ovenbird (*Seiurus aurocapilla*) nests suggested that constructing domed nests rather than open cups in habitats with high predation is associated with survival benefits (Linder and Bollinger 1995). On a broad scale, dome-nesting species tend to be more prevalent in low latitudes (Martin et al. 2017, McEntee et al. 2018), which might reflect the global gradient in predation threat, with increased offspring mortality rates towards the tropics (Ricklefs, 1969, Snow, 1978, Matysioková and Remeš 2022). In addition, dome nesters have been found to be smaller compared to open nesters, which indicates that the rapid changes in body temperature associated with small size can be offset by the thermoregulatory benefits of building an enclosed nest (Martin et al. 2017). Moreover, a recent meta-analysis showed that larger passerine species are exposed to lower daily predation rates irrespective of nest type, which is thought to reflect their ability to fight off a wider range of predators (Unzeta et al. 2020) and might allow them to adopt open nesting strategies in greater numbers compared to small species.

Suitable nest cavities can be a limiting resource for obligate cavity nesters (Von Haartman 1957, Cockle et al. 2011). The aggression and breeding dynamics of Western (*Sialia mexicana*) and Mountain bluebirds (*S. currucoides*), for example, suggest that competitive advantages gained by obtaining nesting cavities come at a cost of higher investment in parental care (Duckworth and Badyaev 2007). Furthermore, competition for nest sites with Great Tits (*Parus major*) has been shown to lead to increased adult mortality in populations of migratory flycatchers (*Ficedula hypoleuca*; Samplonius and Both 2019). On macroevolutionary time-scales, such interactions could have a pronounced effect on the evolution of these species. In particular, a phylogenetic comparative study of more than 3,000 passerine species revealed that evolutionary transitions out of hole-nesting into open or domed nests were more frequent than those into hole-nesting, indicating that competitive interactions might hinder the adoption of this strategy (Zenil-Ferguson et al. 2022). Larger species could be more likely to retain obligate cavity-nesting as a trait because they might outcompete other species for suitable nest locations, whereas smaller birds would need to pursue alternative nesting strategies such as excavation or facultative use of cavities (Barve and Mason 2015)—with a caveat that these species can also utilize a broader range of nesting holes compared to large cavity nesters. Furthermore,

studies of life-history traits in North American and European bird species (Martin and Li 1992, Martin 1993) suggest that the intense competition for nest sites among obligate cavity nesters maximizes reproductive output once the opportunity to breed does arise (also known as the “limited breeding opportunities” hypothesis) and leads to this group having the highest clutch sizes among all types of enclosed nesters. This potential fitness cost of competition in some but not all cavity nesters may explain the contradictory results of some comparative studies examining the relationship between enclosed nesting and avian reproductive traits (e.g., Martin and Li 1992, Cooney et al. 2020).

Other aspects of variation in enclosed nesting strategies may also have consequences on a broad scale. For example, the construction of domed nests may be more energetically costly because they are larger than open nests and take longer to build (Hansell 2000, Mouton and Martin 2019, Medina et al. 2022). More complex nests may have further costs due to specialist behavior and/or morphology (Mainwaring and Hartley 2013). By contrast, the evolution of care in avian systems is thought to be unidirectional (Gardner and Smiseth 2011), with elaborate parental behaviors and large investments in care becoming evolutionarily fixed (Wesolowski 1994). While the pathways of evolution towards complex avian nest structures have yet to be identified, a comparative analysis of 64 species suggests that the ability to construct a cup-shaped nest with sides instead of a platform is linked to an increase in the surface folding and therefore, potentially, the processing capacity of the cerebellum, a part of the brain that supports motor control (Hall et al. 2013), highlighting a potential mechanism for the evolution of more intricate nest types.

Nest types vary widely across all birds. The passerines (order Passeriformes), in particular, are a species-rich clade of birds where more than half of all families include species with enclosed nests that are either adopted or constructed (Collias 1997). Passerine species also vary substantially in the degree of flexibility in their nesting strategy, that is, whether they always nest in cavities or construct domes (i.e., obligate enclosed nesters), or if they can also utilize more open habitats and structures (i.e., facultative enclosed nesters). They are distributed globally across a wide variety of environments, have relatively well-documented reproductive and life-history information (Cornell Laboratory of Ornithology 2020), and have generally comparable nest morphologies across the clade (Hansell 2000). Despite the availability of data on reproductive behavior, large-scale comparative studies in passerines often employ broad categories of nest types (typically open vs. enclosed) that do not account for the diversity of designs and associated reproductive behaviors within these categories (e.g., Jetz et al. 2008, Cooney et al. 2020, Zenil-Ferguson et al. 2022). Here, we use phylogenetic comparative methods to evaluate the importance of predation, competition, design complexity, and energetic costs in the evolution of different enclosed nesting strategies and associated life-history traits in passerines. While the macroevolutionary dynamics of nest types have recently been investigated as part of several large-scale comparative studies using a variety of methodological approaches (McEntee et al. 2018, 2021, Zenil-Ferguson et al. 2022), we seek specifically to assemble a global database of passerine nests, distinguishing between 3 different enclosed nesting strategies: competitive (i.e., species dependent on existing cavities), noncompetitive (i.e., spe-

cies that build or excavate their own enclosed structures), and facultative (i.e., species that nest in both open and enclosed structures/locations); see Methods and Figure 1 for further details.

We first assess whether the transitions between open and enclosed nesters are driven by predation threat or by competition, and which specific types of enclosed nests this shift is mediated by, if any. If predation were a key driver of enclosed nest macroevolution (Ricklefs 1969), we would expect high transition rates away from open nests and facultative nesting strategies, and towards obligate enclosed nesting. By contrast, if competition were making obligate cavity adoption especially disadvantageous (Martin and Li 1992, Martin 1993), we would anticipate high transition rates away from this state, to either open nests, facultative cavity-nesting, or excavation. We also evaluate whether enclosed nests with complex designs evolve from simpler forms (e.g., open/dome → dome and tube or open/cavity → excavation), and whether energetic costs limit this pathway. If the complexity of avian nest types evolves unidirectionally (Wesolowski 1994, Gardner and Smiseth 2011), we would expect to see more transitions towards strategies requiring specialized morphology or nest-building skills than the reverse. By contrast, if these more complex forms were also more energetically and temporally costly (Mainwaring and Hartley 2013, Medina et al. 2022), we would expect transitions into these specialized states to be rarer, and transitions away from these states to be more common.

We further test whether competitive, noncompetitive, and facultative enclosed nesting strategies differ in their geographical distribution and their effect on passerine reproductive traits and body size, while controlling for other potential covariates in our models. We would expect obligate enclosed nesters—and, to a smaller extent, facultative enclosed nesters—to exhibit larger clutches (e.g., Lack 1948, Slagsvold 1982, Lima 1987, Jetz et al. 2008) and longer developmental periods compared to open nesters due to the increased protection afforded by their nest site (including separate analyses of incubation and nestling period; Ricklefs 1968, Martin and Li 1992, Martin 1995, Cooney et al. 2020), with the largest clutch sizes found among cavity-nesting species that are subject to competition (Martin and Li 1992). Species that nest in cavities or construct domes are also predicted to be smaller than open nesters due to the thermoregulatory benefits and protection from predators associated with enclosed nests (Martin et al. 2017, McEntee et al. 2018, Unzeta et al. 2020, Mainwaring and Street 2021)—but this relationship might be absent or reversed in competitive nesters where large body size is advantageous (e.g., Barve and Mason 2015).

METHODS

Nest Classification

Information on passerine nest type was obtained from descriptions and photos or videos in the *Handbook of the Birds of the World* (del Hoyo et al. 2019), the *Birds of North America* (Cornell Lab of Ornithology 2019a), the *Neotropical Birds Online* (Cornell Lab of Ornithology 2019b), the *Birds of the Western Palearctic* (Cramp et al. 2008), and van der Hoek et al. (2017). An “enclosed nest” refers to a space used for breeding that is enclosed on all sides apart from a small entrance hole, including both species that adopt existing cavities

		Nest Location Classification				
		Open <i>n</i> = 3,164	Enclosed by Location			
			Facultative Cavity <i>n</i> = 369	Obligate Cavity <i>n</i> = 444	Excavator <i>n</i> = 128	
Nest Structure Classification	Enclosed by Structure	Open <i>n</i> = 2,715	 <i>n</i> = 2,097	 <i>n</i> = 232	 <i>n</i> = 295/*127	 <i>n</i> = 91/*29
		Partial Dome <i>n</i> = 108	 <i>n</i> = 83	 <i>n</i> = 18	 <i>n</i> = 4	 <i>n</i> = 3
		Dome <i>n</i> = 955	 <i>n</i> = 836	 <i>n</i> = 98	 <i>n</i> = 17	 <i>n</i> = 4
		Dome and Tube <i>n</i> = 171	 <i>n</i> = 148	 <i>n</i> = 21	 <i>n</i> = 1	 <i>n</i> = 1

Figure 1. Diagram showcasing all possible combinations of nest structure and location categories present in the data, with respective sample sizes (nest illustrations by Sally Street). Nest strategies are divided into 4 different groups by location ($n = 4,105$) or by structure ($n = 3,949$). The square of cells highlighted by the bold border indicate nest types enclosed by both location and structure; the red cross in the facultative cavity nester column signifies open nest locations that can also be utilized as part of this strategy. White cells, open nest structures built in open locations ($n = 2,097$); blue cells, facultative nesters ('Partial Dome', 'Facultative Cavity', $n = 333$); yellow cells, competitive enclosed nesters ('Obligate Cavity', $n = 444$); green cells, noncompetitive enclosed nesters ('Dome', 'Dome and Tube', 'Excavator', $n = 1,231$). The sample sizes with an asterisk for obligate cavity nesters and excavators signify cases where the nest structure within the enclosed location is unknown, as these can still be classified as competitive and noncompetitive strategies, respectively, in the absence of this information. Please note that some combinations have very small sample sizes and that categories are collapsed in different ways for different analyses.

or excavate new cavities ("enclosed by location") as well as those that construct a closed structure such as a "dome" or "pouch"-shaped nest ("enclosed by structure"). These enclosed nest types are juxtaposed with "open" nests of species that nest on bare ground or rock, in shallow depressions or in/on vegetation, as well as species that build structures lacking a roof, such as cup or platform nests. The "enclosed by location" category is divided into facultative cavity nesters, obligate cavity nesters, and excavators whereas the "enclosed

by structure" category includes species that construct partial domes, domes, or domes and tubes (keywords for each nest type are described in detail in the next section). These categories are not exclusive; in particular, a single species can have a nest type that is enclosed by both location and structure, such as an obligate cavity nester that constructs a domed structure inside the cavity. For the purpose of elucidating the effect of different nesting strategies on reproductive traits and body size, we introduced another classification of enclosed

nesters (either by structure or location) consisting of 3 exclusive categories. Obligate cavity nesters were categorized as competitive, excavators and dome nesters (including species building a dome and tube) were categorized as noncompetitive, and species that were facultative cavity nesters and/or that built a partial dome were classified as facultative enclosed nesters. If a species was described as an obligate cavity nester and also built a dome within the cavity or, alternatively, its nest structure within the cavity was undescribed, it was included in the category of competitive nesters. While we do note that excavators might be subject to some competition for substrates that are suitable for excavating, these species were classed as noncompetitive because they exhibit greater control over nest location over species that rely on preexisting cavities. Other species where nest design was unknown, ambiguously described or presumed to be similar to a closely related species were excluded from the analysis. An overview of all categories of nest types is shown in [Figure 1](#).

The “enclosed by location” category includes species described as nesting in locations that are covered from all sides with only a small gap for entry and exit (e.g., nesting in a “cavity,” “hole,” “crevice,” “burrow,” “crack,” “tree hollow,” or “cleft”). All of these locations are collectively referred to as “cavities” hereafter. Facultative cavity nesters are species that utilize existing cavities in addition to other, open nesting locations. Obligate cavity nesters are species that nest only in cavities. This includes species where nesting in open or partially enclosed locations has been recorded as rare and only in the absence of available cavities. Excavators are obligate cavity nesters that have been observed as excavating their own nesting cavity in a substrate rather than just utilizing or modifying an existing structure, either in the absence of available cavities or as a primary nesting strategy. If the presence of excavation was not explicitly stated, species where descriptions had keywords such as “digging” and “dug tunnels” were also included in this category because these descriptions strongly implied excavating a cavity. Locations described as “under rock,” “among or under tree roots,” “among boulders/rocks,” “hollow on top of tree stump,” “recess,” “under a ledge,” “under leaves,” or “in building” were categorized as open because these could also indicate an open or partially covered location.

The “enclosed by structure” category includes partial dome, dome, and dome-and-tube structures. Partial dome nesters comprise both species that build structures intermediary between cups and domes (described as “partially domed, roofed, or covered”) as well as those with population-level variation that construct either cups or domes. Dome nesters construct an enclosed structure with an opening that leads to a nesting chamber. These structures could also be described as “purses,” “pockets,” “balls,” or “spheres,” and include nests where the roof component consists of leaves and is stitched to the nesting cup (e.g., tailorbirds from genus *Orthotomus*). In dome-and-tube nesters, the domed structure is complemented with multiple chambers or a tunnel-like entrance to the main nest chamber.

For visualization purposes, nest types were plotted on a maximum clade credibility (MCC) tree using the R package *ggtree* (Yu 2020). The MCC tree was generated from a distribution of 1,000 phylogenetic trees with the Hackett backbone (birdtree.com, Jetz et al. 2012) using the *maxCladeCred* function in the package *phangorn* (Schliep 2011). To quantify the strength of phylogenetic signal in the binary trait of

enclosed nesting, we calculated *D* statistic (Fritz and Purvis 2010) with the *phylo.d* function in *caper* (Orme 2018) on the MCC tree. A *D* value of 1 indicates that trait values are distributed randomly with respect to the phylogeny, whereas a *D* value of 0 corresponds to the phylogenetic dispersion of a binary trait evolving under a Brownian threshold model. Values of *D* > 1 can occur and indicate that species with the same trait values are more distantly related than expected by chance, whereas values < 0 correspond to stronger evolutionary conservatism than predicted by Brownian motion. We ran 2 analyses in which species’ nesting strategies were categorized as either (1) “open location” vs. “enclosed by location” (irrespective of nest structure) or (2) “open structure” vs. “enclosed by structure” (irrespective of nest location).

Life-History, Environmental, and Biogeographical Variables

Information on clutch sizes and duration of parental care was obtained primarily from the *Handbook of the Birds of the World* (del Hoyo et al. 2019), complemented by the *Birds of North America* (Cornell Lab of Ornithology 2019a) and the *Neotropical Birds Online* (Cornell Lab of Ornithology 2019b); whereas adult body mass values were sourced from Dunning (2007) with additions from primary and secondary literature (see Tobias et al. 2022 for a comprehensive dataset). The parental care period was defined as the sum of incubation period (i.e., average number of days from laying the last egg of the clutch until it hatches) and nestling period (i.e., average number of days from hatching until leaving the nest). For both clutch size and parental care periods, we used values described as “mostly,” “usually,” or “typically” characteristic of a species, if specified, or computed averages between maximum and minimum values provided, if not.

Data on migratory behavior were sourced from BirdLife International (2019); this variable was included as a predictor due to its potential effect on reproductive traits. Migratory behavior selects for fast life-history strategies (i.e., large clutches and short development) according to the slow–fast continuum (Stearns 1992) as extended breeding seasons would deplete energy reserves necessary for migration (Jetz et al. 2008, Minias and Włodarczyk 2020). Migratory behavior was a binary variable, with “full migrants” and “altitudinal migrants” coded as migratory and “non-migrants” and “nomads” as non-migratory.

To capture environmental variation affecting the breeding range of each species, we obtained mean annual temperature (BIO1) as well as annual range in temperature (BIO7) from the WorldClim v.2.1 database at 10-min resolution (Fick and Hijmans 2017). Seasonal habitats in temperate latitudes have been linked to high adult mortality rates that select for larger clutches and faster maturation of offspring compared to more stable environments (Ashmole 1963, Jetz et al. 2008, Cooney et al. 2020). In addition, temperature can alter the overall speed of embryonic development by affecting the egg cooling rates within the nest (Reid et al. 2000, Cooper et al. 2005). The species range polygons were sourced from BirdLife International (2019) and intersected with a 0.5° × 0.5° grid in the *letsR* R package (Vilela and Villalobos 2015). We merged the resulting presence–absence matrix with the WorldClim layers and calculated the mean value of each environmental variable per grid cell; these values were then averaged across all cells within a species’ range to obtain a single value per

species. As species nesting in the northern hemisphere are thought to exhibit lower survival rates at high latitudes compared to their southern counterparts due to increased climate seasonality and colder winters (Scholer et al. 2020), we also calculated the coordinates of species range midpoint and determined whether this midpoint is located in the southern or northern hemisphere. The presence–absence matrix was additionally used for visualizing the proportion of competitive, noncompetitive, and facultative enclosed nesters in each grid cell in the *ggplot2* R package (Wickham 2016).

We additionally accounted for island-dwelling because the low predation threat on the islands relative to continental habitats should select for slow life-history strategies and open nest designs (Bosque and Bosque 1995). The insularity variable was obtained by intersecting species range maps with full-resolution landmass shapefiles, GSHHG v2.3.7 (Wessel and Smith 2017). Following the methodology described in Weigelt et al. (2013), Cooney et al. (2020) and Vanadzina et al. (2023a), we selected islands with area > 1 km² and < 2,000,000 km² (i.e., smaller than Greenland) and rasterized this layer using a 0.5° × 0.5° grid in *raster* R package (Hijmans 2021). We obtained a binary estimate of insularity for each species by intersecting the presence–absence matrix with the rasterized island layer; a species was labeled as insular if the overlap between the island layer and the species' range exceeded 90%.

Multistate Analyses of Macroevolutionary Transitions

We used Pagel's Multistate method (Pagel et al. 2004) implemented in BayesTraits v3.0.1 (Pagel and Meade 2017) to (1) evaluate the macroevolutionary dynamics of facultative vs. obligate strategies and to (2) assess the role of complexity and specialization in these dynamics (e.g., whether the evolution of more elaborate or specialized nest types such as dome and tube or excavation are characterized by few to no reversals to simpler nests). To achieve the first objective, we ran 2 models: (1) using “enclosed by location” categories to compare “open locations,” “facultative cavity nesters,” and “obligate cavity nesters (with excavators included),” and (2) using “enclosed by structure” categories to compare “open structures,” “partial domes,” and “domes (including domes and tubes).” To achieve the second objective, we ran the following 2 models: (1) using “enclosed by location” categories to compare “open locations,” “obligate cavity nesters,” and “excavators” (with facultative cavity nesters excluded), and (2) using “enclosed by structure” categories to compare “open structures,” “domes,” and “domes and tubes” (with partial domes excluded). We based all phylogenetic comparative analyses on the MCC tree, scaled by a constant for a mean branch length of 0.1.

Each multistate model was run for 1.1×10^8 iterations with an initial burn-in of 10^7 and was sampled at every 2×10^4 iterations, which resulted in a posterior distribution of 5,000 samples. We ran 3 independent chains per model; all runs produced qualitatively similar results. In all cases, we used a hyper-prior of an exponential distribution (seeding from a uniform distribution on the interval 0–100) for a reversible-jump Markov chain Monte Carlo (MCMC) procedure (Pagel and Meade 2006), which estimates transition rates between states and, at the same time, selects the most appropriate model of evolutionary change by sampling models in pro-

portion to their fit to the data. This procedure can greatly reduce model complexity because it permits variation in the number of transition rates (i.e., for rates to equal one another or to equal zero). The inspection of all traces of parameter estimates in Tracer v1.7.1 (Rambaut et al. 2018) confirmed adequate mixing and effective sample sizes > 2,000.

Bayesian Phylogenetic Mixed Models

To identify factors that determine the global distribution of different strategies of enclosed nesting and to quantify their association with reproductive traits and body size while controlling for potential co-variables, we ran Bayesian phylogenetic mixed models in the R package *MCMCglmm* (Hadfield 2010). We first assessed the effects of temperature and its variability, hemisphere, and island-dwelling on the presence of competitive, noncompetitive, or facultative enclosed nesting as a binary response variable ($n = 4,105$ in all cases). We also produced 5 models of different avian traits as response variables: clutch size ($n = 3,724$ species with available information), total length of developmental period ($n = 1,547$), duration of incubation period ($n = 1,722$), duration of nestling period ($n = 1,675$), and body size ($n = 4,105$). As avian traits are expected to correlate with other aspects of life history in a predictable manner along the slow–fast continuum (Stearns 1992), we included body size as a predictor in models with reproductive traits as response variables (Saether 1987, Jetz et al. 2008) and clutch size in models with developmental duration as response variable (Cooney et al. 2020). In addition to migratory behavior and environmental and biogeographical variables, nest type was included as an explanatory variable with 4 discrete, unordered categories: open (0) nesting vs. competitive (1), noncompetitive (2), or facultative (3) enclosed nesting. See [Supplementary Tables S1–S2](#) for the hypothesized relationships between predictors and response variables based on literature sources and an overview of all model structures.

Reproductive traits, body size, mean annual temperature, and annual temperature variability were log-transformed prior to analysis due to the presence of strong to moderate right skewness in the untransformed data, and all continuous variables were then mean-centered and expressed in units of standard deviation. The variance inflation factor of all non-interaction variables in all models was < 4, demonstrating that multicollinearity was not a concern in these analyses (Dormann et al. 2013) ([Supplementary Table S3](#)). We included phylogenetic relatedness as a random effect to control for the non-independence of traits in species that share common ancestry, using the MCC tree described above. To check whether phylogenetic uncertainty might have an effect on the model outputs, we re-ran the analysis of reproductive traits (i.e., models with clutch size and developmental period duration as response variables) on a distribution of 1,000 hypothesized phylogenetic trees, drawn from the Hackett backbone of the Jetz et al. (2012) bird tree. Following the recommendations in Hadfield (2010) and Villemereuil (2021), we (1) fixed the residual variance to 1 and employed χ^2 prior distributions for phylogenetic variance ($V = 1$, $\nu = 1000$, $\alpha.\mu = 0$, $\alpha.V = 1$) for models with categorical response variables and (2) used inverse-Wishart priors for the phylogenetic and residual variance ($V = 1$, $\nu = 0.02$) for models with continuous response variables. We used diffuse normal priors for fixed effects (mean 0, $V = 10^{10}$) for all models. We ran 3 MCMC

chains on the MCC tree for (1) 6×10^6 iterations, discarding the first 10^6 iterations as burn-in, and sampled every 2,500 iterations for models with categorical response variables; and (2) 7.2×10^5 iterations, discarding the first 1.2×10^5 iterations as burn-in, and sampled every 300 iterations for models with continuous response variables, for a total posterior sample of 2,000 estimates. For the 2 models with full tree distributions, we first conducted a dummy run of 1.2×10^5 iterations on a single tree from the distribution with a burn-in of 2×10^4 and a thinning interval of 50 to determine a start point for the R- and G-structures. We then ran 3 MCMC chains on each phylogenetic tree for 2,400 iterations, discarding the first 400 iterations as burn-in and sampled every 1,000 iterations, for a total posterior sample of 2,000 solutions (2 per tree). The effective sample sizes exceeded 1,000 for all parameters tested. Chain convergence was assessed using Gelman-Rubin statistic, with potential scale reduction values <1.1 for all model outputs. Autocorrelation in chains was determined using function *acf*, with 0.1 used as a target threshold. For each model, we also estimated and reported the (1) “marginal” and (2) “conditional” R^2 values, that is, the proportion of total variance explained by (1) fixed effects and (2) both the fixed and random effects (Nakagawa and Schielzeth 2013).

RESULTS

Phylogenetic Distribution of Enclosed Nesters

Our final dataset contained information on nest location (“open,” “facultative cavity nester,” “obligate cavity nester,” “excavator”) for 4,105 species of passerines and information on nest structure (“open,” “partial dome,” “dome,” and “dome and tube”) for 3,949 species (see Figure 1 for sample sizes). Dome nesters constitute around a third of all species for which nest structure is known (open structure, $n = 2,715$; dome/dome and tube, $n = 1,126$) while obligate enclosed nesters account for 14% of species with known nest location (open location, $n = 3,164$; obligate cavity nester/excavator, $n = 572$). A very small number of species ($n = 18$) have been recorded as obligate cavity nesters that construct a dome or a dome and tube within an enclosed location. The phylogenetic distribution of passerine nest types indicates that enclosed nesters tend to be constrained to specific families, suggesting strong phylogenetic effects (Figure 2). For example, dome nesters dominate among weavers (Ploceidae), estrildid finches (Estrildidae), and sunbirds (Nectariniidae), whereas obligate cavity nesters are prevalent among Old World flycatchers (Muscicapidae) and starlings (Sturnidae). Only a few families exhibit a mix of enclosed nesters by both location and structure (e.g., ovenbirds [Furnariidae], swallows [Hirundinidae], and tyrant flycatchers [Tyrannidae]). The number of species reported as building partial domes is low ($n = 108$) and typically constrained to dome-building families but—in line with an earlier finding in Old World babblers (Timaliidae) where domes were more prevalent on the ground compared to open nests due to increased exposure to predators (Hall et al. 2015)—partial domes also occur among clades where ground-nesting is common (e.g., in larks, Alaudidae; and New World sparrows, Passerellidae). The ability to excavate nesting holes is comparatively rare among species that nest in enclosed locations ($n = 128$) and tends to be associated with obligate cavity nesters (e.g., in ovenbirds and swallows). Dome-and-tube nesters tend to occur in clades where

dome-building already prevails (e.g., in weavers), which suggests that it might follow the evolution of less elaborate domed structures (as per the unidirectional prediction of macroevolutionary transitions). Enclosed nesting is phylogenetically conserved, with a stronger phylogenetic signal in nest structure ($D = -0.26$; $P(D < 1) = 0.00$) compared to location ($D = 0.03$; $P(D < 1) = 0.00$).

Evolutionary Transition Rates Among Nest Types

The two facultative nest enclosure states (“facultative cavity” and “partial dome”) were found to be particularly unstable, with partial domes lost at ~ 27 times the rates that they were gained from open nesting or domes, and a facultative cavity-nesting strategy lost ~ 4 and ~ 8 times faster than gained from obligate cavity-nesting or open nesting, respectively (Figure 3; Supplementary Tables S4 and S5). The facultative cavity-nesting, however, seems to be an important intermediate step between open nests and obligate cavities, as direct transitions between these non-facultative strategies occur at a lower rate compared to the indirect route.

Furthermore, the two nesting strategies that require specialized morphology or nest-building skills (“excavation” and “dome and tube”) were also found to be evolutionarily unstable (Figure 4; Supplementary Tables S6 and S7). The transition from “dome and tube” into “dome” occurred ~ 20 times faster than vice versa and ~ 7 times faster into open nests than from open nests, while the ability to excavate was lost to obligate cavity-nesting at ~ 2 times the rate it was gained (and excavation was not reconstructed to have ever directly evolved from open nests).

Spatial Distribution of Enclosed Nesters

The geographic distribution of passerine nest types (Figure 5) indicates that noncompetitive enclosed nesters (i.e., dome nesters and excavators) are more prevalent in the tropics while competitive nesters (i.e., obligate cavity nesters) do not exhibit a clear latitudinal trend but are concentrated in South America and Central Asia. The output from the categorical models further supports this trend (Supplementary Tables S8 and S9); the presence of noncompetitive nesting correlates with less seasonal environments ($z = -0.521$, $P = 0.012$) and mainland living ($z = -1.138$, $P = 0.005$) while competitive nesting is not linked to any extrinsic factors. Species exhibiting facultative enclosed nesting strategies are concentrated in the higher latitudes of the northern compared to southern hemisphere, and the model output confirms that facultative enclosed nesting is significantly more prevalent in climates with large variability in temperature ($z = 0.646$, $P < 0.001$; Supplementary Table S10).

Enclosed Nesting as a Potential Driver of Variation in Reproductive Traits and Body Size

As documented in many earlier studies (e.g., Lack 1948, Snow 1978), the geographic distribution of passerine clutch size and developmental period is characterized by strong latitudinal gradients, with larger clutches and shorter development found in higher latitudes and in northern hemisphere (Figure 6A, B). We find, after controlling for variation with life history, biogeography, and climate, that species who use enclosed nests (obtained both competitively and non-competitively and including flexible nesters) have larger clutches ($z = 0.199$, $z = 0.266$, and $z = 0.155$, respectively; $P < 0.001$; Figure 6C,

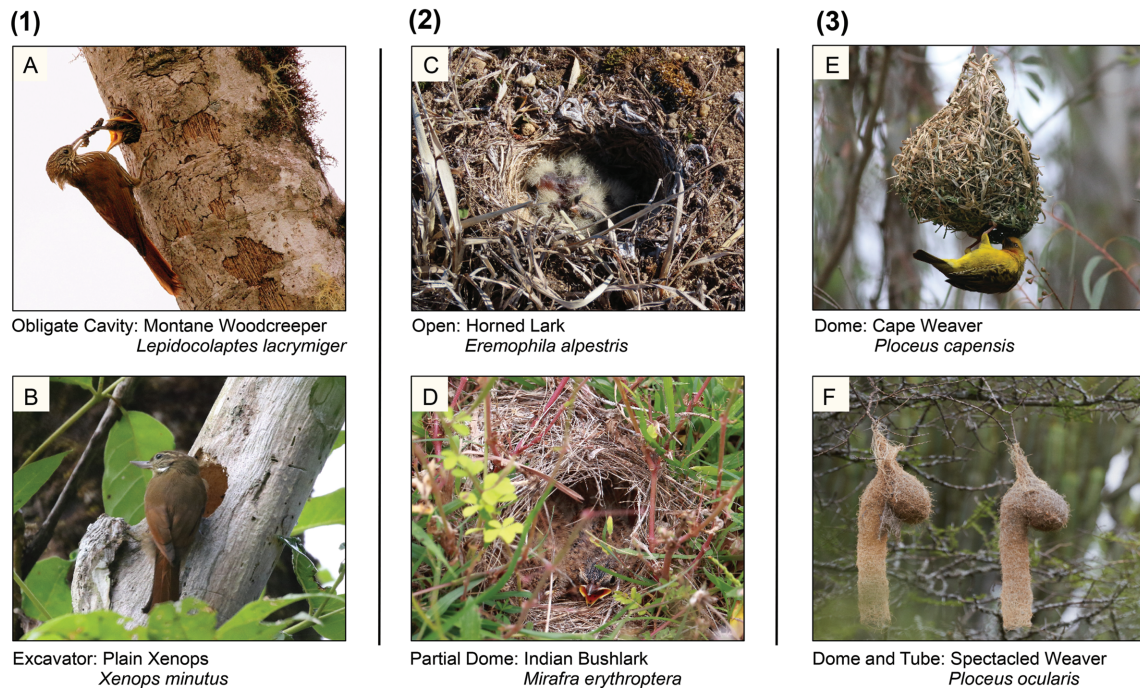
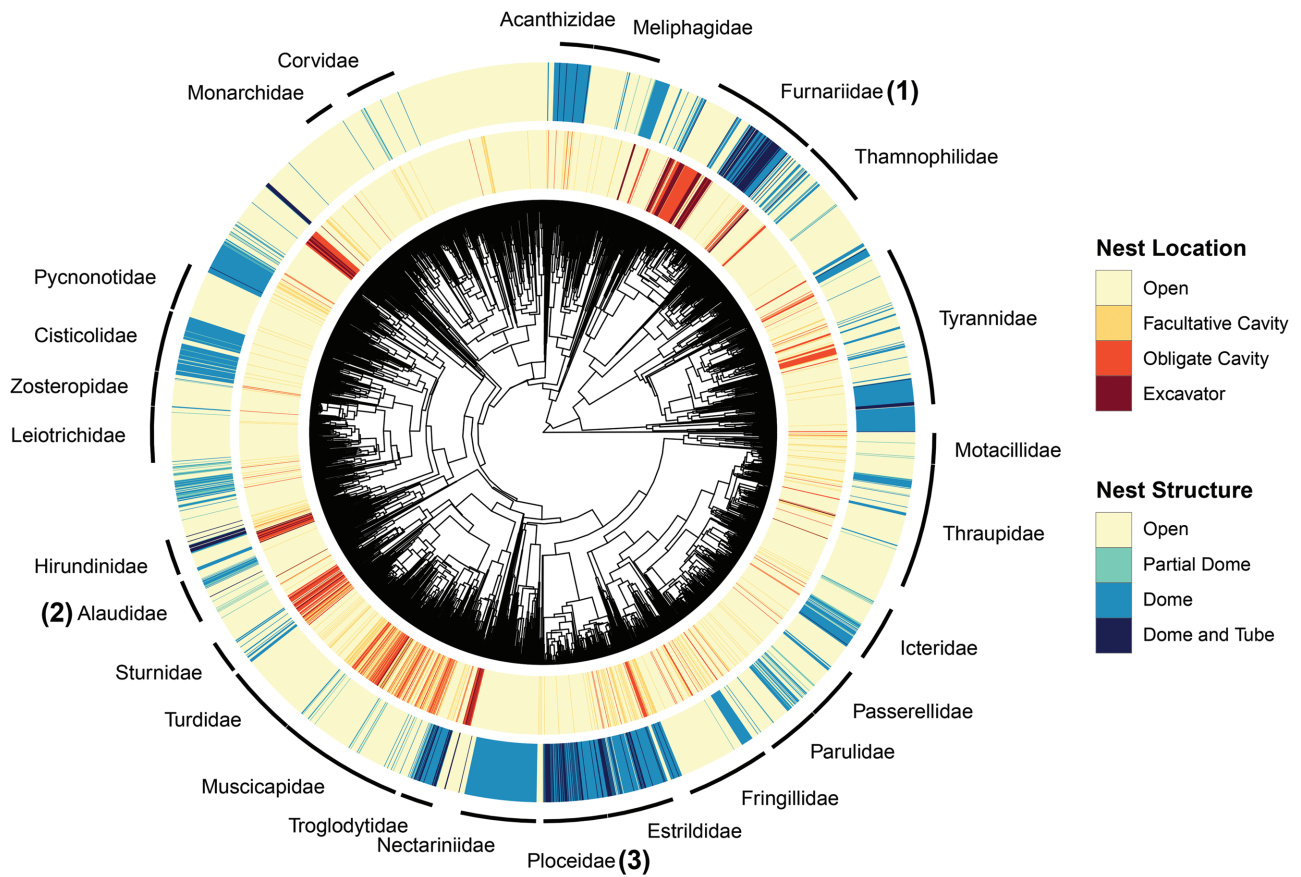


Figure 2. Distribution of nest location and structure in passerines across a maximum clade credibility tree generated from a distribution of 1,000 phylogenies using the Hackett backbone (Jetz et al. 2012), $n = 3,949$ species. For ease of interpretation, only the names of families with records for 50 species or more have been displayed. Examples of different nesting strategies within a single family: (1) Furnariidae, (2) Alaudidae, and (3) Ploceidae. Macaulay Library asset number and photo credit: (A) #204071801, Romuald Mikusek; (B) #203758661 Steve Hampton; (C) #354352041, Rebecca Suomala; (D) #355666611, Shreyas Punacha; (E) #314676881, George Parker; (F) #37329411, Brooke Miller.

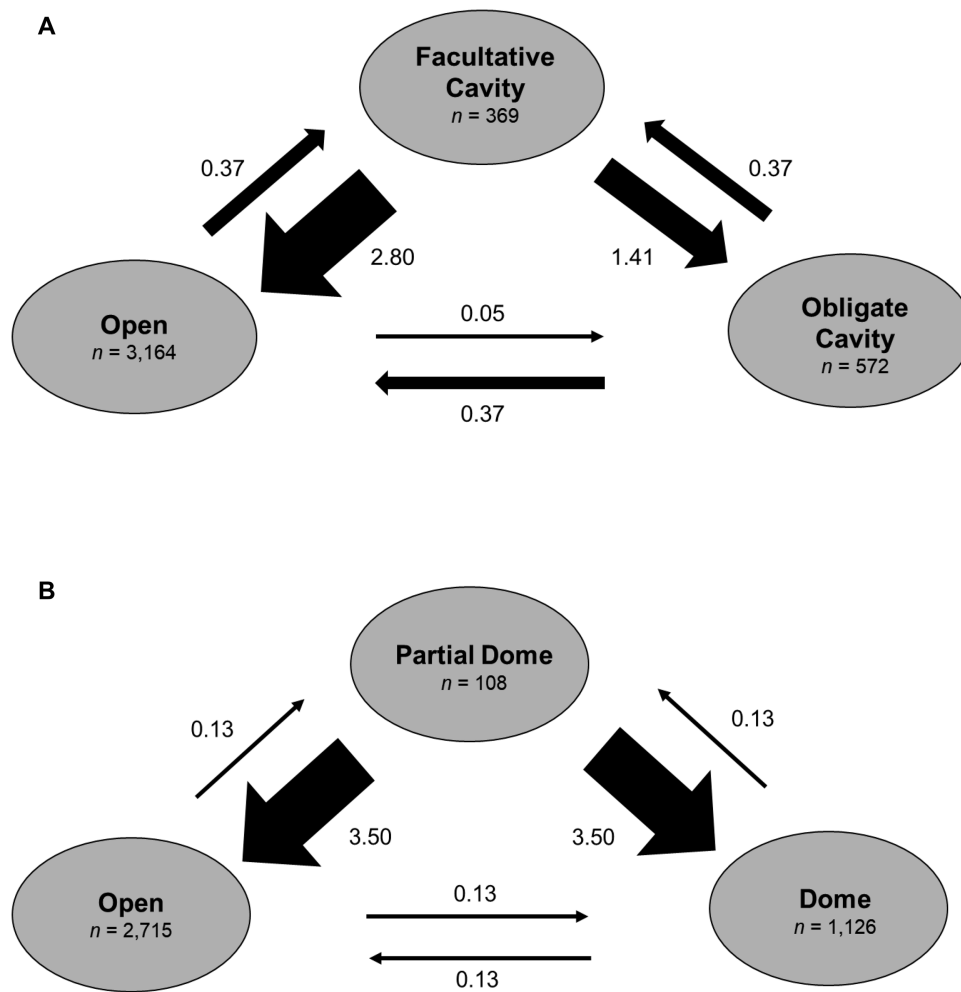


Figure 3. Results from the BayesTraits reversible-jump Markov chain Monte Carlo Multistate analysis testing the evolution of facultative vs. obligate strategies of enclosed nesting across a maximum clade credibility tree generated from a distribution of 1,000 phylogenetic trees from [Jetz et al. \(2012\)](#) using a Hackett backbone. Circles illustrate 3 possible evolutionary states from (A) open location to facultative cavity nester to obligate cavity nester (including excavators) ($n = 4,105$ species) and from (B) open structure to partial dome to dome (including dome and tube) ($n = 3,949$ species). An increase in arrow thickness corresponds to an increase in transition rates with median transition rate provided above each arrow. See [Supplementary Tables S4](#) and [S5](#) for further details.

[Supplementary Table S11](#)). Furthermore, both competitive and noncompetitive enclosed nesting strategies are correlated with longer total development periods ($z = 0.297$ and $z = 0.363$, respectively; $P < 0.001$; [Figure 6D](#), [Supplementary Table S12](#)) and longer nestling periods ($z = 0.391$ and $z = 0.412$, respectively; $P < 0.001$; [Supplementary Table S13](#)), though only noncompetitive strategies are correlated with longer incubation periods ($z = 0.272$, $P < 0.001$; [Supplementary Table S14](#)). There is some evidence that competitive cavity-nesting is associated with an increase in adult body mass compared to other nesting strategies ($z = 0.081$, $P = 0.022$; [Supplementary Table S15](#)). Effect sizes for reproductive traits of noncompetitive enclosed nesters are consistently higher than for competitive enclosed nesters, suggesting that competition for nest sites may indeed be limiting the fitness benefits of an enclosed nest, but these differences are not statistically meaningful as model predictions for these nest types have overlapping 95% credibility intervals. The outputs from models that incorporated phylogenetic uncertainty are qualitatively similar to the main analysis ([Supplementary Tables S16–S17](#)).

DISCUSSION

We demonstrate here that both facultative and energetically costly enclosed nesting strategies, such as excavation and dome-and-tube nests, are evolutionarily unstable. As outlined in the Introduction, both the effects of predation and a unidirectional model of nest-type evolution should result in high transition rates *to* enclosed nesting from other states, whereas energetic costs and the effect of competition predict the opposite (high transition rates away *from* enclosed nesting). Our results, however, do not unequivocally match the predicted effects of any of the 4 potential drivers, instead suggesting the presence of macroevolutionary tradeoffs between these various pressures. We also show that the distribution of noncompetitive and facultative enclosed nesters correlates with seasonality—while obligate cavity nesters exhibit no such association. We find that both competitive and noncompetitive enclosed nesting strategies are generally related to passerine life-history traits, but that only competitive enclosed nesting species have larger body masses compared to open nesters. Taken together, these results underscore the importance of separately analyzing different nesting strategies

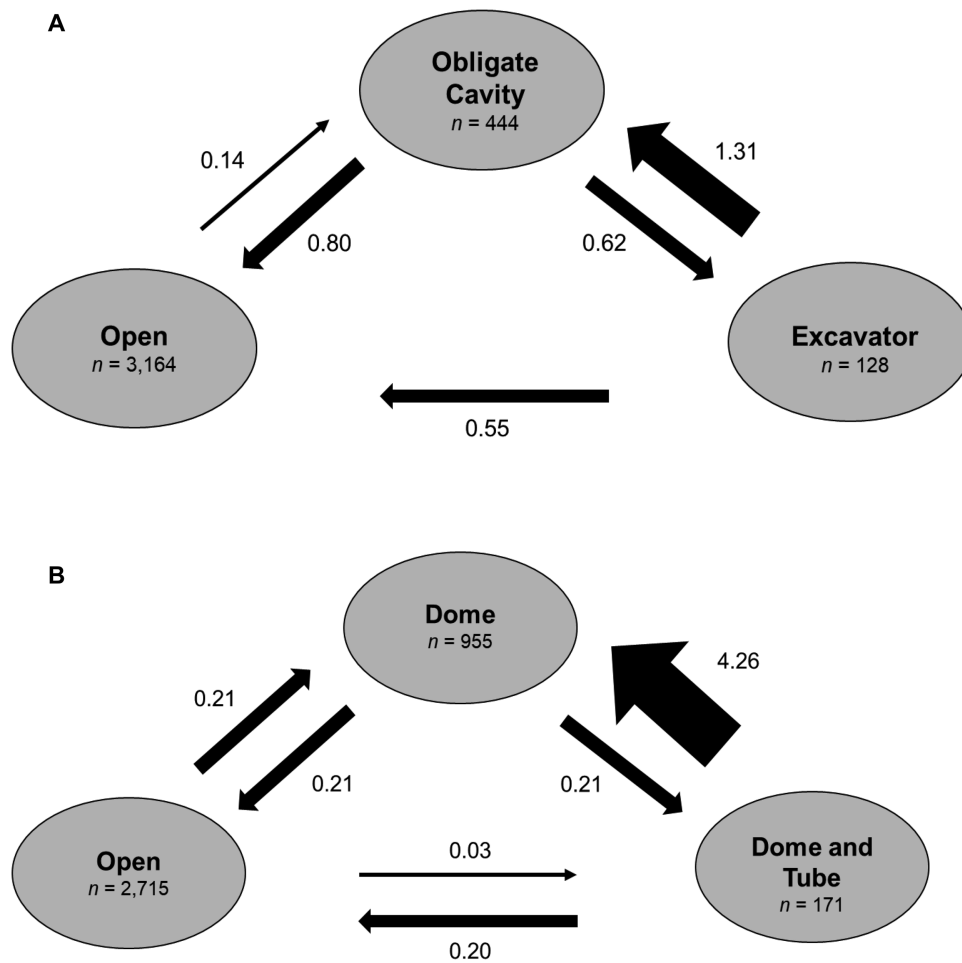


Figure 4. Results from the BayesTraits reversible-jump Markov chain Monte Carlo Multistate analysis testing the evolution of enclosed nesting with regards to complexity and specialization across a maximum clade credibility tree generated from a distribution of 1,000 phylogenetic trees from [Jetz et al. \(2012\)](#) using a Hackett backbone. Circles illustrate 3 possible evolutionary states from (A) open location to obligate cavity nester to excavator (with facultative cavity nesters excluded; $n = 3,736$) and from (B) open structure to dome to dome and tube (with partial domes excluded; $n = 3,841$). An increase in arrow thickness corresponds to an increase in transition rates with median transition rate provided above each arrow. See [Supplementary Tables S6](#) and [S7](#) for further details.

at the macroevolutionary level, and suggest that both predation threat and competition for nest sites, together with high energetic costs of “complex” strategies, have influenced the evolution of this trait.

Our analysis of evolutionary transitions suggests that multiple factors drive the evolution of different enclosed nest types across the passerine order. While the rarity of transitions between open nests and excavation/construction of domes and tubes gives some support to the unidirectional model of nest-type evolution, these complex strategies are also characterized by high rates of loss ([Figure 4](#)). This might reflect the high energetic cost of these strategies, particularly in the absence of specialized excavation morphologies as are found in other orders (e.g., in woodpeckers [Piciformes]; [Bock 1999](#)). The relative stability of dome nesting may represent a balance between the energetic costs and the predator-protection benefits. Furthermore, the lack of direct evolutionary transitions from open nesting to excavation ([Figure 4A](#)) indicates that competitive interactions among obligate cavity nesters might have been the main driving force for the evolution of excavating behavior in this clade. Intraspecific studies suggest that flexibility in nest shape is rare ([Perez et al. 2020](#)), and

indeed relatively few species built partial domes ($n = 108$). In line with [Zenil-Ferguson et al. \(2022\)](#), we find that obligate cavity-nesting is lost to open nesting at higher rates than it is gained ([Figure 3A](#)), which highlights that facultative use of cavities might represent a crucial intermediate stage between these 2 types. It is possible that the evolutionary trends away from partial domes and facultative cavity-nesting reflect the inability of these species to optimize their behavior for one reproductive strategy or another, and thus their inability to maximize their benefits under either syndrome. We also note that this result might be affected by the geographical biases in the reporting of bird life histories ([Culumber et al. 2019](#), [Lees et al. 2020](#)). The diversity of nest types for well-researched species, predominantly from the northern temperate regions, is predicted to be higher, whereas nest descriptions of species that are difficult to observe or access, predominantly from the tropics and southern latitudes, are limited and might not reflect the true flexibility in their nesting strategies.

While noncompetitive nesters exhibit a clear latitudinal gradient in their prevalence, with relatively more species in the tropics, and relatively fewer on islands, no such trend was observed among the competitive nesters. This corresponds

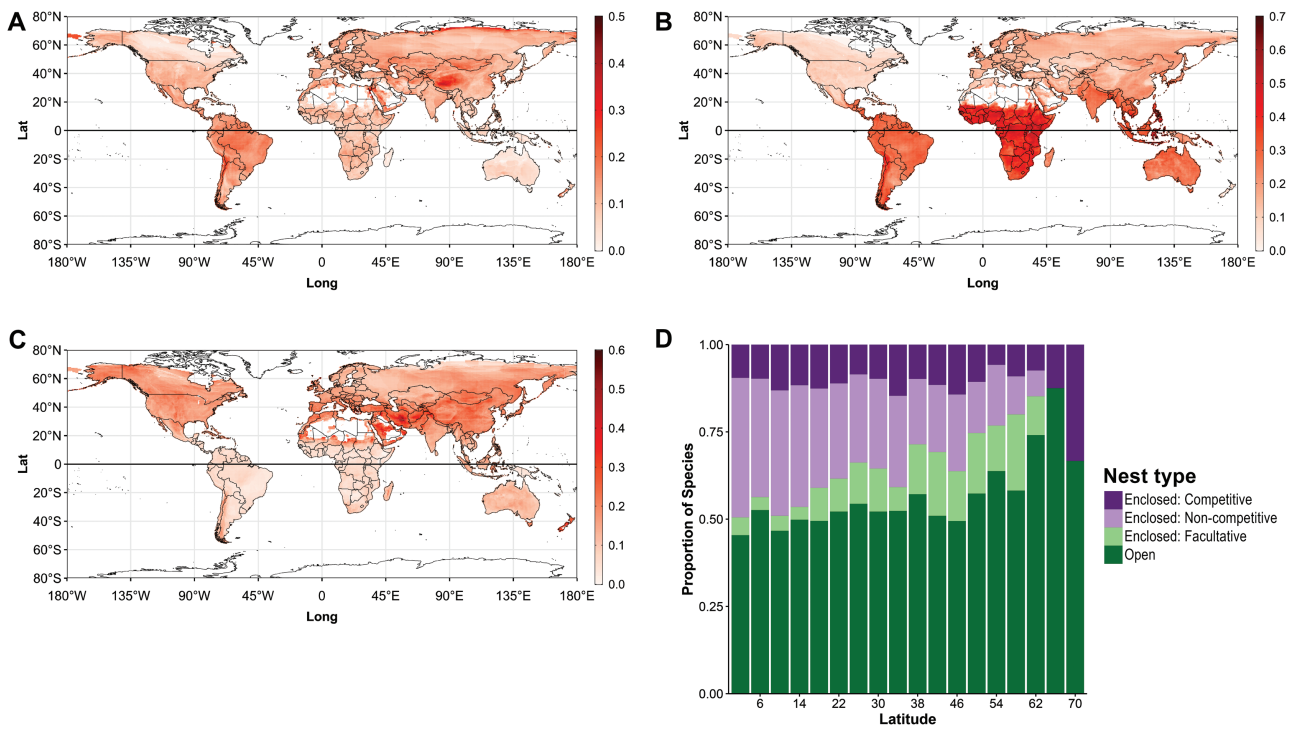


Figure 5. Geographical distribution of (A) enclosed: competitive, (B) enclosed: noncompetitive, and (C) enclosed: facultative nesters per 0.5° grid cell; grid cells with fewer than 10 species have been removed from visualization. (D) Proportion of species exhibiting different nest types mapped across midpoint latitudes of species ranges divided into equal bins, $n = 4,105$ species in total.

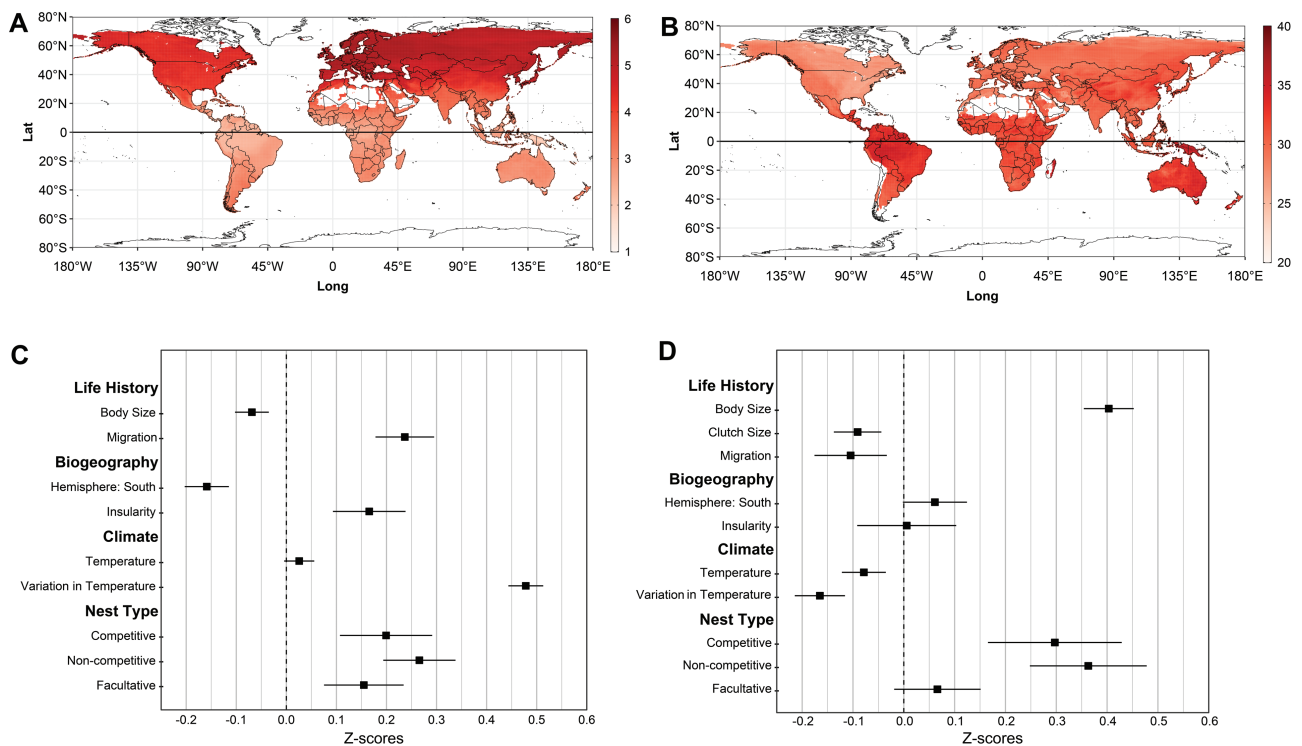


Figure 6. Geographical distribution of average (A) clutch size and (B) developmental period per 0.5° grid cell; grid cells with fewer than 10 species have been removed from visualization. Predictors of variation in average (C) clutch size ($n = 3,724$) and (D) developmental period ($n = 1,547$) were calculated with a Bayesian phylogenetic mixed model. Significant predictors can be identified by a substantial shift from 0. Temperature and Variation in Temperature here refer to annual mean temperature and its range. See [Supplementary Tables S11](#) and [S12](#) for further details.

with the global distribution of dome- and cavity-nesting passerines obtained in other analyses (McEntee et al. 2018). After controlling for shared phylogenetic history and a range of environmental and life-history co-variables, both strategies of enclosed nesting correlated with larger clutch sizes, longer developmental periods, and longer nestling periods. We do not obtain evidence that smaller passerine species are more likely to opt for enclosed nesting strategies compared to larger birds due to thermoregulatory or antipredator benefits (Martin et al. 2017, Unzeta et al. 2020). In addition, the prevalence of enclosed nesters does not correlate with temperature. In line with the trend observed among Old World flycatchers (Barve and Mason 2015), we do find, however, that competitive nesters are larger compared to species exhibiting other nesting strategies, indicating that competition may play a role in modulating this macroevolutionary relationship. Our observation that facultative cavity-nesting is significantly more widespread in seasonal environments compared to the other groups might indicate that some flexibility in nesting strategies is beneficial in dealing with fluctuating environmental conditions. It is also possible that this trend reflects the temperate bias in the observation and reporting of different nesting strategies exhibited by a single species.

Overall, these results suggest that the limited breeding opportunities hypothesis—first proposed to explain variation in clutch size in a small number of European and North American cavity-nesting species (Martin 1993)—might not operate on a broad scale as competitive nesters do not have significantly larger clutches compared to species that do not compete for enclosed nests. There are several potential reasons for this discrepancy. First, the thermoregulatory benefits and better protection from predators afforded by secondary cavities might be offset by an increased parasite load in these locations. For example, an early field study in Sweden showed that obligate cavity nesters exhibited similar rates of nest failure as species nesting in the open—while they benefitted from increased protection from predators, they also suffered greater partial brood losses due to ectoparasites (Nilsson 1986). In species that nest in tree holes, the amount of ectoparasites has been shown to be higher in natural cavities that are used repeatedly over several nesting seasons as opposed to nest-boxes that get replaced or cleaned each year (Møller 1989). In addition, noncompetitive excavators typically dig new cavities for each breeding season and thus have not accrued the same parasite load as species adopting an older cavity (Martin 1993). Second, the large clutch sizes among obligate cavity nesters observed by Martin (1993) could be explained by other factors not included in the original analysis such as environmental variability. In line with previous studies (e.g., Jetz et al. 2008), we show that clutch sizes are larger in more seasonal environments and in migratory birds with fast life-history irrespective of nest type, which implies that the effect observed by Martin (1993) might reflect the composition of species included in the dataset and their geographical distribution rather than the effect of competition. This explanation is further supported by Mönkkönen and Orell (1997) who used a different dataset of cavity-nesting species and failed to find significantly larger clutches among obligate cavity nesters compared to excavators. Third, the impact of competition might vary depending on the nest location (e.g., species that nest in natural tree cavities might be exposed to more intense competition than species that are able to exploit other loca-

tions such as artificial cavities and rock crevices). Evidence from parrots and trogons indicates that shifts from nesting in tree holes to alternative locations are not associated with a drop in clutch size but do lead to longer nestling periods (Brightsmith 2005). The impact of different nest locations on the evolution of life-history traits in obligate cavity nesters has yet to be explored globally. The small number of excavating species among passerines also precludes detailed analysis on whether excavators and dome constructors, grouped as noncompetitive nesters in this analysis, differ in their evolutionary influence on other aspects of species' life history. It would therefore be beneficial to expand the study to all birds to include primary excavators from non-passerine orders—for example, Piciformes (woodpeckers), Psittaciformes (parrots) and others.

Our general findings linking passerine nest type to the length of parental care are in line with earlier studies (e.g., Ricklefs 1968, Martin and Li 1992). It does contrast, however, a recent comparative study assessing the length of developmental periods across all bird species with available data which failed to find any significant difference between nest types after controlling for a number of extrinsic drivers and phylogenetic relatedness (Cooney et al. 2020), potentially due to a difference in phylogenetic scale (order vs. class). Furthermore, our finding that only noncompetitive cavity nesters have longer incubation periods (in contrast with nestling and total developmental periods) may be linked to the abundance of noncompetitive nesters from lower latitudes within our passerine dataset. Field studies have shown that tropical and southern hemisphere birds have lower nest attentiveness (i.e., they spend smaller percentage of time on the nest per sampling duration) compared to northern temperate species, which translates into cooler embryonic temperatures and longer incubation periods independent of predation risk (Martin 2002, Martin et al. 2007). This effect, combined with a further slow-down in cooling rates in enclosed compared to open nests (Lamprecht and Schmolz 2004), could explain the long incubation periods in noncompetitive species. While a reduction in nest predation does not seem to affect the length of incubation among obligate cavity nesters, it is possible that these species differ from open nesters in their pattern of incubation rather than its duration, e.g., by exhibiting more frequent trips to the nest and shorter on-bouts (Conway and Martin 2000). A more complete understanding of global variation in avian life history and reproductive behavior could be used to determine how taxonomic and geographic biases may be affecting these results.

Conclusion

Understanding the underlying causes and consequences of variation in nesting strategies remains a central objective for researchers interested in avian life histories. Here, we find some evidence that increased protection from predators, competition for cavities, and energetic costs of nest-building have together shaped the evolution of different enclosed nesting strategies in passerines, with varying effects on life-history traits.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics statement

Analysis was based on existing data from the literature.

Authors contributions

KV and CS designed the study. KV, SES, and CS collected nest structure and location data; KV collected all other life-history traits and environmental and geographic data. KV performed all analyses. KV and CS wrote the paper, and all authors contributed to subsequent revisions.

Conflict of interest statement

The authors declare no conflict of interest.

Data availability

Analyses reported in this article can be reproduced using the data provided by [Vanadzina et al. \(2023b\)](#).

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