

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

3

4

5 **Abstract**

6

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

25

26 **Keywords:** cavity nests, competition, domed nests, enclosed nests, life history, macroevolution,

27 nest-building, predation

28

29 **Lay Summary**

30

31 • Many birds raise their young in enclosed nests, which likely offer protection from predators
32 and climatic conditions. We currently know little, however, about why some species build
33 their own enclosed nests, while others adopt existing cavities.

34 • Using a broad-scale, comparative approach with data from more than 4,000 passerine
35 species (order Passeriformes), we evaluate how predation, competition, nest complexity and
36 energetic costs have shaped the evolution of these different enclosed nesting strategies.

37 • We find that both flexible and energetically costly enclosed nesting strategies are disfavored
38 on evolutionary timescales. We also show that enclosed nesters have larger clutches and
39 longer developmental periods irrespective of whether they compete for or build their nests.

40 • Our study highlights that different types of enclosed nesting strategies are linked to
41 different sets of evolutionary costs and benefits.

42 **Introduction**

43

44 The majority of bird species build or adopt a nest as part of their reproductive cycle (Collias and
45 Collias 2016, Hansell 2000). Bird nests vary greatly in their design and location, from simple scrapes
46 on the ground to elaborate, multi-chambered structures in trees (Collias 1997). In comparative
47 studies, it is common to broadly divide nest types into ‘enclosed’ or ‘open’ nests, indicating
48 respectively the presence or absence of a roof connected to the sides of the nest (e.g., Jetz et al.
49 2008, Stoddard et al. 2017, Cooney et al. 2020, Mainwaring and Street 2021). Such enclosed nests,
50 however, can be achieved by several, very different strategies. The category of ‘enclosed’ nests
51 typically includes species that adopt or excavate cavities in trees, rock or earth as well as those that
52 construct a closed, domed structure from plant and other materials. Some of these diverse enclosed
53 nesting strategies are thought to result from similar selection pressures – for example, all types of
54 enclosed nests have been linked to increased protection from predators as they render nest
55 contents and the attending parent less conspicuous (e.g., Lack 1948, Alerstam and Hogstedt 1981,
56 Auer et al. 2007). Furthermore, recent studies have suggested that enclosed nests provide more
57 favorable microclimates for offspring development and result in higher reproductive outcomes
58 compared to open nests due to thermoregulatory benefits, especially in harsh environments
59 (Rhodes et al. 2009, Martin et al. 2017, Duursma et al. 2018). However, some selection pressures are
60 likely specific to different enclosed nesting strategies. In particular, obligate cavity nesters (i.e., those
61 reliant on pre-existing cavities) face strong intra- and inter-specific competition for nest sites (e.g.,
62 Martin and Li 1992, Martin 1993) in comparison to facultative cavity nesters and dome-nest builders.
63 The extent to which these different types of enclosed nests evolve in response to similar or distinct
64 selection pressures remains underexplored at the macroevolutionary scale.

65

66 Predation threat is an important cause of offspring mortality in birds and therefore strongly affects
67 the evolution of reproductive traits (Ricklefs 1969, Fontaine and Martin 2006). Species with enclosed

68 nests generally exhibit larger clutch sizes (Lack 1948, Slagsvold 1982, Lima 1987, Auer et al. 2007,
69 Jetz et al. 2008) and longer developmental periods (Ricklefs 1968, Martin and Li 1992, Martin 1995,
70 but see Cooney et al. 2020 or Barve and Mason 2015 where no correlation was found), which is
71 thought to result from lower rates of nest predation (Alerstam and Hogstedt 1981, Remeš and
72 Martin 2002). A general theory suggests that if birds minimize the energetic demands required to
73 fight off or avoid predators, they can instead invest in nourishing larger clutches (Cody 1966). An
74 alternative hypothesis by Skutch (1949) to explain this correlation posits that parental activity at the
75 nest increases the risk of predation by making nest sites more conspicuous – the use of safer,
76 enclosed habitats can therefore lead to higher feeding rates of young. Studies of families containing
77 a variety of nesting strategies provide some evidence that predation threat might have driven the
78 evolution of enclosed nests and associated reproductive traits. For example, ground-nesting species
79 of Old World babblers (Timaliidae) are more likely to build roofed nests, while species that build
80 higher up in more protected locations tend to construct more open structures (Hall et al. 2015).
81 Similarly, an experiment using artificial ovenbird (*Seiurus aurocapilla*) nests suggested that
82 constructing domed nests rather than open cups in habitats with high predation is associated with
83 survival benefits (Linder and Bollinger 1995). On a broad scale, dome-nesting species tend to be
84 more prevalent in low latitudes (Martin et al. 2017, McEntee et al. 2018), which might reflect the
85 global gradient in predation threat, with increased offspring mortality rates towards the tropics
86 (Ricklefs, 1969, Snow, 1978, Matysioková and Remeš 2022). In addition, dome nesters have been
87 found to be smaller compared to open nesters, which indicates that the rapid changes in body
88 temperature associated with small size can be offset by the thermoregulatory benefits of building an
89 enclosed nest (Martin et al. 2017). Moreover, a recent meta-analysis showed that larger passerine
90 species are exposed to lower daily predation rates irrespective of nest type, which is thought to
91 reflect their ability to fight off a wider range of predators (Unzeta et al. 2020) and might allow them
92 to adopt open nesting strategies in greater numbers compared to small species.

93

94 Suitable nest cavities can be a limiting resource for obligate cavity nesters (Von Haartman 1957,
95 Cockle et al. 2011). The aggression and breeding dynamics of western and mountain bluebirds (*Sialia*
96 *mexicana* and *S. currucoides*), for example, suggest that competitive advantages gained by obtaining
97 nesting cavities come at a cost of higher investment in parental care (Duckworth and Badyaev 2007).
98 Furthermore, competition for nest sites with great tits *Parus major* has been shown to lead to
99 increased adult mortality in populations of migratory flycatchers *Ficedula hypoleuca* (Samplonius
100 and Both 2019). On macroevolutionary timescales, such interactions could have a pronounced effect
101 on the evolution of these species. In particular, a phylogenetic comparative study of more than
102 3,000 passerine species revealed that evolutionary transitions out of hole-nesting into open or
103 domed nests were more frequent than those into hole-nesting, indicating that competitive
104 interactions might hinder the adoption of this strategy (Zenil-Ferguson et al., 2022). Larger species
105 could be more likely to retain obligate cavity-nesting as a trait because they might out-compete
106 other species for suitable nest locations, while smaller birds would need to pursue alternative
107 nesting strategies such as excavation or facultative use of cavities (Barve and Mason 2015) – with a
108 caveat that these species can also utilize a broader range of nesting holes compared to large cavity
109 nesters. Furthermore, studies of life-history traits in North American and European bird species
110 (Martin and Li 1992, Martin 1993) suggest that the intense competition for nest sites among obligate
111 cavity nesters maximizes reproductive output once the opportunity to breed does arise (also known
112 as the ‘limited breeding opportunities’ hypothesis) and leads to this group having the highest clutch
113 sizes among all types of enclosed nesters. This potential fitness cost of competition in some but not
114 all cavity nesters may explain the contradictory results of some comparative studies examining the
115 relationship between enclosed nesting and avian reproductive traits (e.g., Martin and Li 1992,
116 Cooney et al. 2020).

117

118 Other aspects of variation in enclosed nesting strategies may also have consequences on a broad
119 scale. For example, the construction of domed nests may be more energetically costly because they

120 are larger than open nests and take longer to build (Hansell 2000, Mouton and Martin 2019, Medina
121 et al. 2022). More complex nests may have further costs due to specialist behavior and/or
122 morphology (Mainwaring and Hartley 2013). By contrast, the evolution of care in avian systems is
123 thought to be unidirectional (Gardner and Smiseth 2011), with elaborate parental behaviors and
124 large investment in care becoming evolutionarily fixed (Wesolowski 1994). While the pathways of
125 evolution towards complex avian nest structures have yet to be identified, a comparative analysis of
126 64 species suggests that the ability to construct a cup-shaped nest with sides instead of a platform is
127 linked to an increase in the surface folding and therefore potentially the processing capacity of the
128 cerebellum, a part of the brain that supports motor control (Hall et al. 2013), highlighting a potential
129 mechanism for the evolution of more intricate nest types.

130

131 Nest types vary widely across all birds. The passerines (order Passeriformes), in particular, are a
132 species-rich clade of birds where more than half of all families include species with enclosed nests
133 that are either adopted or constructed (Collias 1997). Passerine species also vary substantially in the
134 degree of flexibility in their nesting strategy, that is, whether they always nest in cavities or construct
135 domes (i.e., obligate enclosed nesters), or if they can also utilize more open habitats and structures
136 (i.e., facultative enclosed nesters). They are distributed globally across a wide variety of
137 environments, have relatively well-documented reproductive and life-history information (Cornell
138 Laboratory of Ornithology 2020), and have generally comparable nest morphologies across the clade
139 (Hansell 2000). Despite the availability of data on reproductive behavior, however, large-scale
140 comparative studies in passerines often employ broad categories of nest types (typically ‘open’
141 versus ‘enclosed’) that do not account for the diversity of designs and associated reproductive
142 behaviors within these categories (e.g., Jetz et al. 2008, Cooney et al. 2020, Zenil-Ferguson et al.,
143 2022). Here, we use phylogenetic comparative methods to evaluate the importance of predation,
144 competition, design complexity and energetic costs in the evolution of different enclosed nesting
145 strategies and associated life-history traits in passerines. While the macroevolutionary dynamics of

146 nest types have recently been investigated as part of several large-scale comparative studies using a
147 variety of methodological approaches (McEntee et al. 2018, 2021; Zenil-Ferguson et al. 2022), we
148 seek specifically to assemble a global database of passerine nests , distinguishing between three
149 different ‘enclosed’ nesting strategies: competitive (i.e., species dependent on existing cavities),
150 non-competitive (i.e., species that build or excavate their own enclosed structures) and facultative
151 (i.e., species that nest in both open and enclosed structures/locations), see Methods and Figure 1 for
152 further details.

153 We first assess whether the transitions between open and enclosed nesters are driven by predation
154 threat or by competition, and which specific types of enclosed nests this shift is mediated by, if any.
155 If predation were a key driver of enclosed nest macroevolution (Ricklefs 1969), we would expect
156 high transition rates away from open nests and facultative nesting strategies, and towards obligate
157 enclosed nesting. By contrast, if competition were making obligate cavity adoption especially
158 disadvantageous (Martin and Li 1992, Martin 1993), we would anticipate high transition rates away
159 from this state, to either open nests, facultative cavity nesting or excavation. We also evaluate
160 whether enclosed nests with complex designs evolve from simpler forms (e.g., open/dome -> dome
161 and tube or open/cavity -> excavation), and whether energetic costs limit this pathway. If the
162 complexity of avian nest types evolves unidirectionally (Wesolowski 1994, Gardner and Smiseth
163 2011), we would expect to see more transitions towards strategies requiring specialized morphology
164 or nest-building skills than the reverse. By contrast, if these more complex forms were also more
165 energetically and temporally costly (Mainwaring and Hartley 2013, Medina et al. 2022), we would
166 expect transitions into these specialized states to be rarer, and transitions away from these states to
167 be more common.

168

169 We further test whether competitive, non-competitive and facultative enclosed nesting strategies
170 differ in their geographical distribution and their effect on passerine reproductive traits and body
171 size, while controlling for other potential co-variates in our models. We would expect obligate

172 enclosed nesters – and, to a smaller extent, facultative enclosed nesters – to exhibit larger clutches
173 (e.g., Lack 1948, Slagsvold 1982, Lima 1987, Jetz et al. 2008) and longer developmental periods
174 compared to open nesters due to the increased protection afforded by their nest site (including
175 separate analyses of incubation and nestling period; e.g., Ricklefs 1968, Martin and Li 1992, Martin
176 1995, Cooney et al. 2020), with the largest clutch sizes found among cavity-nesting species that are
177 subject to competition (Martin and Li 1992). Species that nest in cavities or construct domes are also
178 predicted to be smaller than open nesters due to the thermoregulatory benefits and protection from
179 predators associated with enclosed nests (Martin et al. 2017, McEntee et al. 2018, Unzeta et al.
180 2020, Mainwaring and Street 2021) – but this relationship might be absent or reversed in
181 competitive nesters where large body size is advantageous (e.g., Barve and Mason 2015).

182

183 **Methods**

184

185 *Nest classification*

186

187 Information on passerine nest type was obtained from descriptions and photos or videos in the
188 Handbook of the Birds of the World (del Hoyo et al. 2019), the Birds of North America (Cornell Lab of
189 Ornithology 2019a), the Neotropical Birds Online (Cornell Lab of Ornithology 2019b), the Birds of the
190 Western Palearctic (Cramp et al. 2008) and van der Hoek et al. (2017). An ‘enclosed nest’ refers to a
191 space used for breeding that is enclosed on all sides apart from a small entrance hole, including both
192 species that adopt existing cavities or excavate new cavities (‘enclosed by location’) as well as those
193 that construct a closed structure such as a ‘dome’ or ‘pouch’-shaped nest (‘enclosed by structure’).
194 These enclosed nest types are juxtaposed with ‘open’ nests of species that nest on bare ground or
195 rock, in shallow depressions or in/on vegetation as well as species that build structures lacking a
196 roof, such as cup or platform nests. The ‘enclosed by location’ category is divided into **facultative**
197 **cavity nesters**, **obligate cavity nesters** and **excavators** while the ‘enclosed by structure’ category

198 includes species that construct **partial domes, domes** or **domes and tubes** (keywords for each nest
199 type are described in detail in the next section). These categories are not exclusive; in particular, a
200 single species can have a nest type that is enclosed by both location and structure, such as an
201 obligate cavity nester that constructs a domed structure inside the cavity. For the purpose of
202 elucidating the effect of different nesting strategies on reproductive traits and body size, we
203 introduced another classification of enclosed nesters (either by structure or location) consisting of
204 three exclusive categories. Obligate cavity nesters were categorized as **competitive**, excavators and
205 dome nesters (including species building a dome and tube) were categorized as **non-competitive**
206 and species that were facultative cavity nesters and/or that built a partial dome were classified as
207 **facultative** enclosed nesters. If a species was described as an obligate cavity nester and also built a
208 dome within the cavity or, alternatively, its nest structure within the cavity was undescribed, it was
209 included in the category of competitive nesters. While we do note that excavators might be subject
210 to some competition for substrates that are suitable for excavating, these species were classed as
211 non-competitive as they exhibit greater control over nest location over species that rely on pre-
212 existing cavities. Other species where nest design was unknown, ambiguously described or
213 presumed to be similar to a closely related species were excluded from the analysis. An overview of
214 all categories of nest types has been provided in Figure 1.

215

216 The 'enclosed by location' category includes species described as nesting in locations that are
217 covered from all sides with only a small gap for entry and exit – e.g., nesting in a 'cavity', 'hole',
218 'crevice', 'burrow', 'crack', 'tree hollow' or 'cleft'. All of these locations are collectively referred to as
219 'cavities' hereafter. Facultative cavity nesters are species that utilize existing cavities in addition to
220 other, open nesting locations. Obligate cavity nesters are species that nest only in cavities. This
221 includes species where nesting in open or partially enclosed locations has been recorded as rare and
222 only in the absence of available cavities. Excavators are obligate cavity nesters that have been
223 observed as excavating their own nesting cavity in a substrate rather than just utilizing or modifying

224 an existing structure, either in the absence of available cavities or as a primary nesting strategy. If
225 the presence of excavation was not explicitly stated, species where descriptions had keywords such
226 as 'digging' and 'dug tunnels' were also included in this category because these descriptions strongly
227 implied excavating a cavity. Locations described as 'under rock', 'among or under tree roots', 'among
228 boulders/rocks', 'hollow on top of tree stump', 'recess', 'under a ledge', 'under leaves', or 'in
229 building' were categorized as open because these could also indicate an open or partially covered
230 location.

231

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

241

242 For visualization purposes, nest types were plotted on a maximum clade credibility (MCC) tree using
243 the R package 'ggtree' (Yu 2020). The MCC tree was generated from a distribution of 1,000
244 phylogenetic trees with the Hackett backbone (birdtree.com, Jetz et al. 2012) using the
245 *maxCladeCred* function in the package 'phangorn' (Schliep 2011). To quantify the strength of
246 phylogenetic signal in the binary trait of enclosed nesting, we calculated D statistic (Fritz and Purvis
247 2010) with the *phylo.d* function in 'caper' (Orme et al. 2018) on the MCC tree. A D value of 1
248 indicates that trait values are distributed randomly with respect to the phylogeny, while a D value of
249 0 corresponds to the phylogenetic dispersion of a binary trait evolving under a Brownian threshold

250 model. Values of D greater than 1 can occur and indicate that species with the same trait values are
251 more distantly related than expected by chance, while values less than 0 correspond to stronger
252 evolutionary conservatism than predicted by Brownian motion. We ran two analyses in which
253 species' nesting strategies were categorized as either 1) 'open location' vs. 'enclosed by location'
254 (irrespective of nest structure) or 2) 'open structure' vs. 'enclosed by structure' (irrespective of nest
255 location).

256

257 *Life-history, environmental and biogeographical variables*

258

259 Information on clutch sizes and duration of parental care was obtained primarily from the Handbook
260 of the Birds of the World (del Hoyo et al. 2019), complemented by the Birds of North America
261 (Cornell Lab of Ornithology 2019a) and the Neotropical Birds Online (Cornell Lab of Ornithology
262 2019b), while adult body mass values were sourced from Dunning (2007) with additions from
263 primary and secondary literature (see Tobias et al. 2022 for a comprehensive dataset). The parental
264 care period was defined as the sum of incubation period, i.e., the average number of days from
265 laying the last egg of the clutch until it hatches, and nestling period, i.e., the average number of days
266 from hatching until leaving the nest. For both clutch size and parental care periods, we used values
267 described as 'mostly', 'usually' or 'typically' characteristic of a species, if specified, or computed
268 averages between maximum and minimum values provided, if not.

269

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

275 variable, with 'full migrants' and 'altitudinal migrants' coded as migratory and 'non-migrants' and
276 'nomads' as non-migratory.

277

278 To capture environmental variation affecting the breeding range of each species, we obtained mean
279 annual temperature (BIO1) as well as annual range in temperature (BIO7) from the WorldClim v.2.1
280 database at 10 min resolution (Fick and Hijmans 2017). Seasonal habitats in temperate latitudes have
281 been linked to high adult mortality rates that select for larger clutches and faster maturation of
282 offspring compared to more stable environments (Ashmole 1963, Jetz et al. 2008, Cooney et al. 2020).
283 In addition, temperature can alter the overall speed of embryonic development by affecting the egg
284 cooling rates within the nest (Reid et al., 2000, Cooper et al., 2005). The species range polygons were
285 sourced from BirdLife International (2019) and intersected with a $0.5^\circ \times 0.5^\circ$ grid in the 'letsR' R
286 package (Vilela and Villalobos 2015). We merged the resulting presence-absence matrix with the
287 WorldClim layers and calculated the mean value of each environmental variable per grid cell; these
288 values were then averaged across all cells within a species' range to obtain single value per species.
289 As species nesting in the northern hemisphere are thought to exhibit lower survival rates at high
290 latitudes compared to their southern counterparts due to increased climate seasonality and colder
291 winters (Scholer et al. 2020), we also calculated the coordinates of species range midpoint and
292 determined whether this midpoint is located in the southern or northern hemisphere. The presence-
293 absence matrix was additionally used for visualizing the proportion of competitive, non-competitive
294 and facultative enclosed nesters in each grid cell in the 'ggplot2' R package (Wickham 2016).

295

296 We additionally accounted for island-dwelling because the low predation threat on the islands relative
297 to continental habitats should select for slow life-history strategies and open nest designs (Bosque
298 and Bosque 1995). The insularity variable was obtained by intersecting species range maps with full-
299 resolution landmass shapefiles, GSHHG v2.3.7 (Wessel and Smith 2017). Following the methodology
300 described in Weigelt et al. (2013), Cooney et al. (2020) and Vanadzina et al. (2023), we selected islands

301 with area $> 1 \text{ km}^2$ and $< 2,000,000 \text{ km}^2$ (i.e., smaller than Greenland) and rasterized this layer using a
302 $0.5^\circ \times 0.5^\circ$ grid in 'raster' R package (Hijmans 2021). We obtained a binary estimate of insularity for
303 each species by intersecting the presence-absence matrix with the rasterized island layer; a species
304 was labelled as insular if the overlap between the island layer and the species' range exceeded 90%.

305

306 *Multistate analyses of macroevolutionary transitions*

307

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

322

323 Each Multistate model was run for 1.1×10^8 iterations with an initial burn-in of 10^7 and was sampled
324 at every 2×10^4 iterations, which resulted in a posterior distribution of 5000 samples. We ran three
325 independent chains per model; all runs produced qualitatively similar results. In all cases, we used a
326 hyper-prior of an exponential distribution (seeding from a uniform distribution on the interval 0–

327 100) for a reversible-jump Markov chain Monte Carlo (MCMC) procedure (Pagel and Meade 2006),
328 which estimates transition rates between states and, at the same time, selects the most appropriate
329 model of evolutionary change by sampling models in proportion to their fit to the data. This
330 procedure can greatly reduce model complexity because it permits variation in the number of
331 transition rates (i.e., for rates to equal one another or to equal zero). The inspection of all traces of
332 parameter estimates in Tracer v1.7.1 (Rambaut et al. 2018) confirmed adequate mixing and effective
333 sample sizes greater than 2000.

334

335 *Bayesian phylogenetic mixed models*

336

337 To identify factors that determine the global distribution of different strategies of enclosed nesting
338 and to quantify their association with reproductive traits and body size while controlling for
339 potential co-variables, we ran Bayesian phylogenetic mixed models (BPMMS) in the R package
340 ‘MCMCglmm’ (Hadfield 2010). We first assessed the effects of temperature and its variability,
341 hemisphere and island-dwelling on the presence of competitive, non-competitive or facultative
342 enclosed nesting as a binary response variable ($n = 4,105$ in all cases). We also produced five models
343 of different avian traits as response variables: clutch size ($n = 3,724$ species with available
344 information), total length of developmental period ($n = 1,547$), duration of incubation period ($n =$
345 $1,722$), duration of nestling period ($n = 1,675$), and body size ($n = 4,105$). As avian traits are expected
346 to correlate with other aspects of life history in a predictable manner along the slow-fast continuum
347 (Stearns 1992), we included body size as a predictor in models with reproductive traits as response
348 variables (Saether 1987, Jetz et al. 2008) and clutch size in models with developmental duration as
349 response variable (Cooney et al. 2020). In addition to migratory behavior and environmental and
350 biogeographical variables, nest type was included as an explanatory variable with four discrete,
351 unordered categories: open (0) nesting, versus competitive (1), non-competitive (2) or facultative (3)
352 enclosed nesting. See Supplementary Material Tables S1-S2 for the hypothesized relationships

353 between predictors and response variables based on literature sources and an overview of all model
354 structures.

355

356 Reproductive traits, body size, mean annual temperature and annual temperature variability were
357 log-transformed prior to analysis due to the presence of strong to moderate right skewness in the
358 untransformed data, and all continuous variables were then mean-centered and expressed in units
359 of standard deviation. The variance inflation factor (VIF) of all non-interaction variables in all models
360 was less than 4, demonstrating that multicollinearity was not a concern in these analyses (Dormann
361 et al. 2013) (Supplementary Material Table S3). We included phylogenetic relatedness as a random
362 effect to control for the non-independence of traits in species that share common ancestry, using
363 the MCC tree described above. To check whether phylogenetic uncertainty might have an effect on
364 the model outputs, we re-ran the analysis of reproductive traits (i.e., models with clutch size and
365 developmental period duration as response variables) on a distribution of 1,000 hypothesized
366 phylogenetic trees, drawn from the Hackett backbone of the Jetz et al. (2012) bird tree. Following
367 the recommendations in Hadfield (2010) and Villemereuil (2021), we 1) fixed the residual variance to
368 1 and employed χ^2 prior distributions for phylogenetic variance ($V = 1$, $v = 1000$, $\alpha \cdot \mu = 0$,
369 $\alpha \cdot V = 1$) for models with categorical response variables and 2) used inverse-Wishart priors for
370 the phylogenetic and residual variance ($V = 1$, $v = 0.02$) for models with continuous response
371 variables. We used diffuse normal priors for fixed effects (mean 0, $V = 10^{10}$) for all models. We ran
372 three MCMC chains on the MCC tree for 1) 6×10^6 iterations, discarding the first 10^6 iterations as
373 burn-in, and sampled every 2500 iterations for models with categorical response variables and 2) 7.2
374 $\times 10^5$ iterations, discarding the first 1.2×10^5 iterations as burn-in, and sampled every 300 iterations
375 for models with continuous response variables, for a total posterior sample of 2,000 estimates. For
376 the two models with full tree distributions, we first conducted a dummy run of 1.2×10^5 iterations
377 on a single tree from the distribution with a burn-in of 2×10^4 and a thinning interval of 50 to
378 determine a start point for the R- and G-structures. We then ran three MCMC chains on each

379 phylogenetic tree for 2,400 iterations, discarding the first 400 iterations as burn-in and sampled
380 every 1,000 iterations, for a total posterior sample of 2,000 solutions (2 per tree). The effective
381 sample sizes exceeded 1,000 for all parameters tested. Chain convergence was assessed using
382 Gelman-Rubin statistic, with potential-scale reduction values less than 1.1 for all model outputs.
383 Autocorrelation in chains was determined using function *acf*, with 0.1 used as a target threshold. For
384 each model, we also estimated and reported the 1) 'marginal' and 2) 'conditional' R^2 values, i.e., the
385 proportion of total variance explained by 1) fixed effects and 2) both the fixed and random effects
386 (Nakagawa and Schielzeth 2013).

387

388 **Results**

389

390 *Phylogenetic distribution of enclosed nesters*

391

392 Our final dataset contained information on nest location ('open', 'facultative cavity nester', 'obligate
393 cavity nester', 'excavator') for 4,105 species of passerines and information on nest structure ('open',
394 'partial dome', 'dome', 'dome and tube') for 3,949 species (see Figure 1 for sample sizes). Dome
395 nesters constitute around a third of all species for which nest structure is known (open structure, $n =$
396 2,715; dome/dome and tube, $n = 1,126$) while obligate enclosed nesters account for 14% of species
397 with known nest location (open location, $n = 3,164$; obligate cavity nester/excavator, $n = 572$). A very
398 small number of species ($n = 18$) have been recorded as obligate cavity nesters that construct a
399 dome or dome and tube within an enclosed location. The phylogenetic distribution of passerine nest
400 types indicates that enclosed nesters tend to be constrained to specific families, suggesting strong
401 phylogenetic effects (Figure 2). For example, dome nesters dominate among weavers (Ploceidae),
402 estrildid finches (Estrildidae) and sunbirds (Nectariniidae), while obligate cavity nesters are prevalent
403 among Old World flycatchers (Muscicapidae) and starlings (Sturnidae). Only a few families exhibit a
404 mix of enclosed nesters by both location and structure (e.g., ovenbirds (Furnariidae), swallows

405 (Hirundinidae) and tyrant flycatchers (Tyrannidae)). The number of species reported as building
406 partial domes is low ($n = 108$) and typically constrained to dome-building families but – in line with
407 an earlier finding in Old World babblers (Timaliidae) where domes were more prevalent on the
408 ground compared to open nests due to increased exposure to predators (Hall et al. 2015) – partial
409 domes also occur among clades where ground-nesting is common (e.g., in larks, Alaudidae; and New
410 World sparrows, Passerellidae). The ability to excavate nesting holes is comparatively rare among
411 species that nest in enclosed locations ($n = 128$) and tends to be associated with obligate cavity
412 nesters (e.g., in ovenbirds and swallows). Dome-and-tube nesters tend to occur in clades where
413 dome-building already prevails (e.g., in weavers), which suggests that it might follow the evolution of
414 less elaborate domed structures (as per the unidirectional prediction of macroevolutionary
415 transitions). Enclosed nesting is phylogenetically conserved, with a stronger phylogenetic signal in
416 nest structure ($D = -0.26$; $p(D < 1) = 0.00$) compared to location ($D = 0.03$; $p(D < 1) = 0.00$).

417

418 *Evolutionary transition rates among nest types*

419

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

427

428 Furthermore, the two nesting strategies that require specialized morphology or nest-building skills
429 ('excavation' and 'dome and tube') were also found to be evolutionarily unstable (Figure 4;
430 Supplementary Material Tables S6, S7). The transition from 'dome and tube' into 'dome' occurred

431 ~20 times faster than vice versa and ~7 times faster into open nests than from open nests, while the
432 ability to excavate was lost to obligate cavity nesting at ~2 times the rate it was gained (and
433 excavation was not reconstructed to have ever directly evolved from open nests).

434

435 *Spatial distribution of enclosed nesters*

436

437 The geographic distribution of passerine nest types (Figure 5) indicates that non-competitive
438 enclosed nesters (i.e., dome nesters and excavators) are more prevalent in the tropics while
439 competitive nesters (i.e., obligate cavity nesters) do not exhibit a clear latitudinal trend but are
440 concentrated in South America and Central Asia. The output from the categorical models further
441 supports this trend (Supplementary Material Tables S8,S9); the presence of non-competitive nesting
442 correlates with less seasonal environments ($z = -0.521, p = 0.012$) and mainland living ($z = -1.138, p =$
443 0.005) while competitive nesting is not linked to any extrinsic factors. Species exhibiting facultative
444 enclosed nesting strategies are concentrated in the higher latitudes of the northern compared to
445 southern hemisphere, and the model output confirms that facultative enclosed nesting is
446 significantly more prevalent in climates with large variability in temperature ($z = 0.646, p < 0.001,$
447 Supplementary Material Table S10).

448

449 *Enclosed nesting as a potential driver of variation in reproductive traits and body size*

450

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

457 <0.001, Figure 6c, Supplementary Material Table S11). Furthermore, both competitive and non-
458 competitive enclosed nesting strategies are correlated with longer total development periods ($z =$
459 0.297 and $z = 0.363$, respectively; $p < 0.001$; Figure 6d, Supplementary Material Table S12) and
460 longer nestling periods ($z = 0.391$ and $z = 0.412$, respectively; $p < 0.001$, Supplementary Material
461 Table S13), though only non-competitive strategies are correlated with longer incubation periods (z
462 $= 0.272$, $p < 0.001$; Supplementary Material Table S14). There is some evidence that competitive
463 cavity nesting is associated with an increase in adult body mass compared to other nesting strategies
464 ($z = 0.081$, $p = 0.022$; Supplementary Material Table S15). Effect sizes for reproductive traits of non-
465 competitive enclosed nesters are consistently higher than for competitive enclosed nesters,
466 suggesting that competition for nest sites may indeed be limiting the fitness benefits of an enclosed
467 nest, but these differences are not statistically meaningful as model predictions for these nest types
468 have overlapping 95% credibility intervals. . The outputs from models that incorporated
469 phylogenetic uncertainty are qualitatively similar to the main analysis (Supplementary Material
470 Tables S16-S17).

471

472 **Discussion**

473

474 We demonstrate here that both facultative and energetically costly enclosed nesting strategies, such
475 as excavation and dome-and-tube nests, are evolutionarily unstable. As outlined in the introduction,
476 both the effects of predation and a unidirectional model of evolution should result in high transition
477 rates *to* enclosed nesting from other states, while energetic costs and the effect of competition
478 predict the opposite (high transition rates away *from* enclosed nesting). Our results, however, do not
479 unequivocally match the predicted effects of any of the four potential drivers, instead suggesting the
480 presence of macroevolutionary trade-offs between these various pressures. We also show that the
481 distribution of non-competitive and facultative enclosed nesters correlates with seasonality – while
482 obligate cavity nesters exhibit no such association. We find that both competitive and non-

483 competitive enclosed nesting strategies are generally related to passerine life-history traits, but that
484 only competitive enclosed nesting species have larger body masses compared to open nesters.
485 Taken together, these results underscore the importance of separately analyzing different nesting
486 strategies at the macroevolutionary level, and suggest that both predation threat and competition
487 for nest sites, together with high energetic costs of 'complex' strategies, have influenced the
488 evolution of this trait.

489

490 Our analysis of evolutionary transitions suggests that multiple factors drive the evolution of different
491 enclosed nest types across the passerine order. While the rarity of transitions between open nests
492 and excavation/construction of domes and tubes gives some support to the unidirectional model of
493 nest type evolution, these complex strategies are also characterized by high rates of loss (Figure 4).
494 This might reflect the high energetic cost of these strategies, particularly in the absence of
495 specialized excavation morphologies as are found in other orders, e.g., in woodpeckers (Piciformes)
496 (Bock 1999). The relative stability of dome nesting may represent a balance between the energetic
497 costs and the predator-protection benefits. Furthermore, the lack of direct evolutionary transitions
498 from open nesting to excavation (Figure 4a) indicates that competitive interactions among obligate
499 cavity nesters might have been the main driving force for the evolution of excavating behavior in this
500 clade. Intraspecific studies suggest that flexibility in nest shape is rare (Perez et al. 2020), and indeed
501 relatively few species built partial domes ($n = 108$). In line with Zenil-Ferguson et al. (2022), we find
502 that obligate cavity nesting is lost to open nesting at higher rates than it is gained (Figure 3a), which
503 highlights that facultative use of cavities might represent a crucial intermediate stage between these
504 two types. It is possible that the evolutionary trends away from partial domes and facultative cavity
505 nesting reflect the inability of these species to optimize their behavior for one reproductive strategy
506 or another, and thus their inability to maximize their benefits under either syndrome. We also note
507 that this result might be affected by the geographical biases in the reporting of bird life histories
508 (Culumber et al. 2019, Lees et al. 2020). The diversity of nest types for well-researched species,

509 predominantly from the northern temperate regions, is predicted to be higher, while nest
510 descriptions of species that are difficult to observe or access, predominantly from the tropics and
511 southern latitudes, are limited and might not reflect the true flexibility in their nesting strategies.

512

513 While non-competitive nesters exhibit a clear latitudinal gradient in their prevalence, with relatively
514 more species in the tropics, and relatively fewer on islands, no such trend was observed among the
515 competitive nesters. This corresponds with the global distribution of dome- and cavity- nesting
516 passerines obtained in other analyses (McEntee et al. 2018). After controlling for shared
517 phylogenetic history and a range of environmental and life-history co-variables, both strategies of
518 enclosed nesting correlated with larger clutch sizes, longer developmental periods, and longer
519 nestling periods. We do not obtain evidence that smaller passerine species are more likely to opt for
520 enclosed nesting strategies compared to larger birds due to thermoregulatory or anti-predator
521 benefits (Martin et al. 2017, Unzeta et al. 2020). In addition, the prevalence of enclosed nesters does
522 not correlate with temperature. In line with the trend observed among Old World flycatchers (Barve
523 and Mason 2015), we do find, however, that competitive nesters are larger compared to species
524 exhibiting other nesting strategies, indicating that competition may play a role in modulating this
525 macroevolutionary relationship. Our observation that facultative cavity nesting is significantly more
526 widespread in seasonal environments compared to the other groups might indicate that some
527 flexibility in nesting strategies is beneficial in dealing with fluctuating environmental conditions. It is
528 also possible that this trend reflects the temperate bias in the observation and reporting of different
529 nesting strategies exhibited by a single species.

530

531 Overall, these results suggest that the ‘limited breeding opportunities’ hypothesis – first proposed to
532 explain variation in clutch size in a small number of European and North American cavity-nesting
533 species (Martin 1993) – might not operate on a broad scale as competitive nesters do not have
534 significantly larger clutches compared to species that do not compete for enclosed nests. There are

535 several potential reasons for this discrepancy. First, the thermoregulatory benefits and better
536 protection from predators afforded by secondary cavities might be offset by an increased parasite
537 load in these locations. For example, an early field study in Sweden showed that obligate cavity
538 nesters exhibited similar rates of nest failure as species nesting in the open – while they benefitted
539 from increased protection from predators, they also suffered greater partial brood losses due to
540 ectoparasites (Nilsson 1986). In species that nest in tree holes, the amount of ectoparasites has been
541 shown to be higher in natural cavities that are used repeatedly over several nesting seasons as
542 opposed to nest-boxes that get replaced or cleaned each year (Møller 1989). In addition, non-
543 competitive excavators typically dig new cavities for each breeding season and thus have not
544 accrued the same parasite load as species adopting an older cavity (Martin 1993). Second, the large
545 clutch sizes among obligate cavity nesters observed by Martin (1993) could be explained by other
546 factors not included in the original analysis such as environmental variability. In line with previous
547 studies (e.g., Jetz et al. 2008), we show that clutch sizes are larger in more seasonal environments
548 and in migratory birds with fast life history irrespective of nest type, which implies that the effect
549 observed by Martin (1993) might reflect the composition of species included in the dataset and their
550 geographical distribution rather than the effect of competition. This explanation is further supported
551 by Mönkkönen and Orell (1997) who used a different dataset of cavity-nesting species and failed to
552 find significantly larger clutches among obligate cavity nesters compared to excavators. Third, the
553 impact of competition might vary depending on the nest location, e.g., species that nest in natural
554 tree cavities might be exposed to more intense competition than species that are able to exploit
555 other locations such as artificial cavities and rock crevices. Evidence from parrots and trogons
556 indicates that shifts from nesting in tree holes to alternative locations are not associated with a drop
557 in clutch size but do lead to longer nestling periods (Brightsmith 2005). The impact of different nest
558 locations on the evolution of life-history traits in obligate cavity nesters has yet to be explored
559 globally. The small number of excavating species among passerines also precludes detailed analysis
560 on whether excavators and dome constructors, grouped as non-competitive nesters in this analysis,

561 differ in their evolutionary influence on other aspects of species' life history. It would therefore be
562 beneficial to expand the study to all birds to include primary excavators from non-passerine orders,
563 e.g., Piciformes (woodpeckers), Psittaciformes (parrots) and others.

564

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

585

586

587 **Conclusion**

588

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

594

595

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797 **Figure Legends**

798

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

811

812 **Fig. 2** Distribution of nest location and structure in passerines across a maximum clade credibility
813 tree generated from a distribution of 1,000 phylogenies using the Hackett backbone (Jetz *et al.*,
814 2012), $n = 3,949$ species. For ease of interpretation, only the names of families with records for 50
815 species or more have been displayed. Examples of different nesting strategies within a single family:
816 (1) Furnariidae, (2) Alaudidae, (3) Ploceidae. Macaulay Library asset number and photo credit: A,
817 #204071801, Romuald Mikusek; B, #203758661 Steve Hampton; C, #354352041, Rebecca Suomala;
818 D, #355666611, Shreyas Punacha; E, #314676881, George Parker; F, #37329411, Brooke Miller.

819

820 **Fig. 3** Results from the BayesTraits reversible-jump Markov chain Monte Carlo (MCMC) Multistate
821 analysis testing the evolution of facultative versus obligate strategies of enclosed nesting across a
822 maximum clade credibility tree generated from a distribution of 1,000 phylogenetic trees from Jetz

823 *et al.* (2012) using a Hackett backbone. Grey circles illustrate three possible evolutionary states from
824 (A) 'open location' to 'facultative cavity nester' to 'obligate cavity nester (including excavators)' ($n =$
825 4,105 species) and from (B) 'open structure' to 'partial dome' to 'dome (including dome and tube)'
826 ($n = 3,949$ species). An increase in arrow thickness corresponds to an increase in transition rates with
827 median transition rate provided above each arrow. See Supplementary Material Tables S4 and S5 for
828 further details.

829

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

839

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

844

845 **Fig. 6** Geographical distribution of average (A) clutch size and (B) developmental period per 0.5° grid
846 cell; grid cells with fewer than 10 species have been removed from visualization. Predictors of
847 variation in average (C) clutch size ($n = 3,724$) and (D) developmental period ($n = 1,547$) calculated
848 with a Bayesian phylogenetic mixed model. Significant predictors can be identified by a substantial

849 shift from 0. 'Temperature' and 'Variation in Temperature' here refer to annual mean temperature
850 and its range. See Supplementary Material Tables S11 and S12 for further details.