

1 Ecology, phylogeny, and the evolution of developmental 2 duration in birds

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30 from all authors.

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32 **Data accessibility:** Code and data will be made available via Figshare Digital Repository upon
33 acceptance.

34 **ABSTRACT**

35 The duration of the developmental period represents a fundamental axis of life history variation in
36 animals, yet broad insights regarding the drivers of this diversity are currently lacking. Here using
37 embryological data combined with information on incubation and fledging periods for 3096 species,
38 we test key mechanistic and adaptive explanations for the evolutionary diversification of
39 developmental durations in birds. First, using data on embryonic development for 20 model species,
40 we show that developmental phases associated primarily with growth are longer and more variable
41 than earlier phases, consistent with a role for allometric constraint in determining the duration of
42 development. Second, using phylogenetic comparative methods, we find that avian developmental
43 durations retain a strong imprint of deep evolutionary history, and that after accounting for these
44 effects, body size differences among species explain less variation (5-22%) in developmental period
45 lengths than previously thought. Finally, by collecting data for a suite of potential explanatory
46 variables, our analyses reveal broad-scale ecological correlates of developmental durations,
47 including variables associated with the relative safety of the developmental environment (e.g. nest
48 height, insularity) and pressures of breeding phenology (e.g. migration). Overall, our results reveal
49 that the combined effects of species' body size, ecology, and phylogenetic history can account for
50 62-93% of the variation in developmental durations across birds, providing broad-scale quantitative
51 insight into the relative importance of mechanistic constraints, adaptive evolution and evolutionary
52 constraints in shaping the diversification of this key life-history trait.

53

54 INTRODUCTION

55 A fundamental goal in ecology and evolution is to explain the vast diversity of life-history strategies
56 observed in nature (1-3). The duration of the developmental period represents a fundamental axis of
57 life history variation (4) and varies from days to several years among animal species. Attempts to
58 explain variation in developmental duration across species typically fall into two broad categories
59 (5). A first set of hypotheses, focusing on the role of mechanistic constraints, predict that
60 developmental periods vary among species largely as a result of negative scaling between mass-
61 specific growth (metabolic) rates and body size (6-8). In other words, larger species grow relatively
62 slower compared to smaller species and therefore take longer to develop. Alternatively, a second
63 set of hypotheses emphasise the role of selection and adaptation in generating interspecific
64 differences in developmental durations. These adaptive ideas stem from classic life-history
65 evolution theory (2, 4, 9) and assume that the external context of the organism drives the
66 evolutionary optimisation of growth rates (and hence developmental period), within the constraints
67 imposed by size and other assumed trade-offs (5). However, despite both sets of hypotheses being
68 rooted in robust theoretical arguments, confidence in each is undermined by a lack of broad-scale
69 empirical support and uncertainty exists regarding the relative importance of different factors for
70 explaining broad-scale variation in developmental rates, particularly after accounting for
71 phylogenetic effects (10).

72 Here we address this problem by conducting a global-scale phylogenetic comparative
73 analysis of avian developmental periods and other life history traits. Birds are particularly suited for
74 such analyses because accurate information on the duration of major avian developmental periods
75 (incubation and fledging) is available for many species, as well as for many relevant aspects of
76 species' biology, ecology and distribution. In addition, detailed data on embryonic developmental
77 stages are available for several taxonomically-diverse bird species, permitting the integration of
78 large-scale comparative analyses with fine-scale investigation into differences in species'
79 developmental rates. To quantify broad-scale variation in overall developmental period length
80 across birds we follow previous studies [e.g. refs. (11-14)] and use the sum of incubation and
81 fledging periods, thereby capturing variation in both pre-natal and post-natal development rates.
82 Furthermore, by combining data on incubation and fledging duration, we are able to define a second
83 variable, which we refer to as the *incubation fraction*. This variable captures differences among
84 species in the balance between prenatal (incubation) and postnatal (fledging) development periods
85 and is calculated as the duration of the incubation period divided by the total developmental
86 duration (incubation + fledging). This is useful because in birds, as in other animals, the proportion
87 of prenatal to postnatal development varies among species, raising important questions regarding
88 the factors explaining these differences (e.g. developmental mode, predation risk, etc.) (15, 16).
89 However, while the importance of such factors have been examined in some taxa (17-27), their
90 importance is rarely tested at broad phylogenetic scales.

91 To test key mechanistic and adaptive explanations for the evolutionary diversification of
92 developmental durations in birds, we collected data from two different sources. First, we extracted
93 standardised estimates of developmental timepoints from a taxonomically-diverse sample of 20 bird
94 species with existing information on embryonic development. We predicted that if mechanistic
95 constraints related to growth rates play an important role in determining avian developmental
96 durations, then developmental phases associated primarily with growth should be longer and more
97 variable across species than earlier phases concerned mostly with cell differentiation and body plan
98 formation. Second, we compiled information on incubation and fledging durations for a total of 3096
99 bird species from 176 families and 39 orders, and combined this in a phylogenetic comparative
100 framework with comprehensive data for a suite of variables that have previously been linked to
101 avian developmental durations (17-27). Specifically, we tested variables related to species' body
102 mass, life history, parental care, nesting behaviour, ecology, ambient climate and biogeography.
103 This two-scale approach—combining detailed observations of embryonic development with a
104 broader comparative dataset—allows us to (i) to identify the phase(s) of avian development
105 contributing most to inter-specific differences in developmental duration, (ii) investigate the strength
106 of phylogenetic signal in trait values, and (iii) directly test and compare the relative importance of
107 multiple potential underlying factors for determining developmental period length. Specifically, we
108 use this approach to quantify the relative roles of mechanistic constraints and species' ecology in
109 shaping the evolution of avian developmental durations at a global scale.

110

111 **RESULTS AND DISCUSSION**

112 A central prediction of mechanistic explanations for variation in developmental durations is that
113 bigger species take relatively longer to develop. This is because growth is fuelled by metabolism
114 which scales negatively with body size, such that larger species have lower relative metabolic rates
115 than smaller species, and thus take proportionally longer to develop (6-8). A corollary of this is that if
116 mechanistic constraints related to growth rate and body size during ontogeny represent an
117 important rate-limiting step in offspring development, then phases of development associated with
118 growth should be more variable across species, and account for a greater proportion of total
119 developmental time, than non-growth periods.

120 To test the prediction that growth periods represent the longest and most variable phases of
121 offspring development, we conducted a fine-scale analysis of developmental rates in a
122 taxonomically diverse set of species ($n = 20$) with existing information on the timing of key
123 developmental stages (Fig. S1, Appendix S1). Specifically, we examined four distinct phases in
124 avian ontogeny spanning both pre-hatching (incubation) and post-hatching (fledging) periods (Fig.
125 1A). Phases 1 and 2, defined on the basis of Hamburger-Hamilton (HH) stages 1-24 and 25-32,
126 respectively, correspond to periods of chick embryogenesis. These early stages of prenatal
127 development consist primarily of cell differentiation and embryo formation rather than absolute

128 growth (28), and we therefore consider these as “non-growth” phases. In contrast, phases 3 and 4,
129 corresponding to HH33 to hatching and hatching through to fledging, are primarily concerned with
130 periods of prenatal (phase 3) and postnatal (phase 4) growth of existing structures (see
131 Supplementary Material for extended justification of these developmental phases). We used this
132 framework to investigate variation in the duration and partitioning of avian offspring development.

133 We found that the durations of developmental stages associated with embryogenesis
134 (phases 1 and 2) account for only a small proportion of the variance in overall developmental
135 duration across species (Fig. 1B). At these early stages of development, all bird embryos –
136 regardless of species identity and eventual adult body size – are of comparatively similar size and
137 therefore expected to have approximately similar growth rates (Fig. 1B). In contrast, the durations of
138 growth phases (phases 3 and 4) are longer and more variable than non-growth phases and account
139 for a far greater proportion of the variance in developmental duration among species (Fig. 1B). The
140 longer duration of growth phases relative to embryogenesis phases is consistent with the well-
141 characterised phenomenon of declining growth rates over ontogeny, caused by decreases in the
142 ratio of energy acquisition to energy loss as developing organisms increase in size (5). Furthermore,
143 greater variance in the duration of growth phases relative to non-growth phases (as indicated by
144 coefficient of variation scores; Fig. 1B) is also consistent with greater size-related effects on the
145 later stages of development. As development progresses, offspring of different species become
146 increasingly different in size and therefore exhibit far greater disparity in relative growth rates
147 compared to earlier stages of development.

148 Our observation that the developmental phases associated primarily with growth are longer
149 and more variable than earlier non-growth phases predicts that body size should explain a
150 significant amount of variation in developmental durations due to metabolic scaling rules. To test
151 this idea more broadly, we collected data on developmental durations (incubation and fledging
152 periods) for 3096 bird species covering the breadth of the avian phylogeny (Fig. 2A). In our dataset,
153 overall developmental durations ranged from ~20 days in some passerine species (e.g. *Volatinia*
154 *jacarina*) to >350 days in some seabird lineages (e.g. *Diomedea*). Likewise, estimates of the
155 proportion of development allocated to incubation relative to fledging (i.e. the incubation fraction)
156 also varied markedly across species, ranging from ~0.15 (e.g. *Struthio camelus*) to >0.95 in certain
157 landfowl and shorebird species (e.g. *Megapodius pritchardii*, *Synthliboramphus wumizusume*)
158 (Appendix S1).

159 Before addressing relationships with body size, we first quantified the extent of phylogenetic
160 signal in avian developmental durations. Phylogenetic signal measures the degree to which
161 variation in species’ trait values covaries with phylogenetic relatedness and when estimated using
162 Pagel’s λ model (29) varies on a scale from 0 (species trait values are unrelated to phylogeny) to 1
163 (species trait values follow Brownian motion expectations). Fitting Pagel’s λ model to our dataset,
164 we found that developmental variables exhibited strong phylogenetic signal, with λ values [95% CI]

165 of 0.93 [0.91, 0.94] and 0.86 [0.83, 0.89] for developmental duration and incubation fraction,
166 respectively. This reflects a pervasive pattern in our dataset, that species within clades tend to
167 exhibit similar developmental durations and incubation fractions (Fig. 2A), such that on average
168 closely related species have more similar trait values than more distantly related species.

169 Against this backdrop, we used phylogenetic regression (30) and variance partitioning
170 techniques (31) to test the relationships between body size and avian developmental duration, and
171 to compare the contributions of predictor variables (body size) and variance components
172 (phylogenetic effects) to the overall fit of the model. Using this approach, as predicted we found that
173 overall developmental duration is positively related to body size across bird species (Fig. 2B).
174 Furthermore, for incubation fraction we found that the offspring of larger-bodied species have
175 proportionally shorter incubation periods relative to fledging periods (Fig. 2C), presumably reflecting
176 energetic and/or ecological constraints associated with laying and/or developing in larger eggs. In
177 both cases, we used adult body mass values as our index of body size across species, which we
178 consider to represent a useful albeit imperfect proxy for offspring size at the end of development.
179 However, we note that results were similar when we use an alternative proxy for offspring size
180 (initial egg mass) (Appendix S1). Variance partitioning revealed that the partial R^2 values associated
181 with these phylogenetically-adjusted allometric relationships were 0.22 and 0.05 for developmental
182 duration and incubation fraction, respectively. In contrast, the partial R^2 values associated with the
183 phylogenetic (covariance) components of each model were far greater: 0.79 and 0.59, respectively.

184 The significant relationships we observe between body size and developmental durations
185 are in line with our predictions based on embryological data and provide broad empirical support for
186 the role of size-related constraints in determining both the duration and partitioning of avian
187 developmental periods (6-8). However, after accounting for phylogenetic effects, we found that the
188 importance of body size for explaining variation in developmental durations across birds was
189 surprisingly low, particularly considering that early tests implied that as much as 85% of inter-
190 specific variation in incubation period could be explained by body size effects (32-34). In contrast,
191 our comparatively low estimates for the variance explained by body size (5-22%) support the
192 conclusion that, while important, allometric constraints play a more minor role in determining the
193 length and partitioning of avian developmental periods than once thought (10). Instead, our
194 quantitative estimates indicate that a greater proportion of the variance in avian developmental
195 durations is attributable to phylogenetic history rather than body size. This finding is apparent in the
196 observation that species within clades typically share similar developmental duration values that are
197 largely unrelated to variation in body size both within and between clades (Fig. 2 and Fig. S2).

198 The existence of substantial mass-independent differences in developmental periods among
199 bird lineages is intriguing, as it raises questions regarding the relative importance of mechanistic
200 constraints versus adaptation in generating interspecific diversity in avian developmental periods.
201 However, such questions have yet to be addressed at broad scales (10). The idea that selection and

202 adaptation play an important role in driving the evolution of developmental periods is rooted in
203 classical life-history optimisation theory, the central tenet of which is that species adapt their life-
204 history strategies to maximise fitness within particular ecological contexts (2, 4, 9). A range of
205 factors have been suggested to be important in driving the evolution of developmental duration,
206 many of which relate to either (i) constraints imposed by environmental or ecological limits to the
207 resources available for reproduction, or (ii) selection imposed by increased mortality of parents
208 and/or offspring. Field studies focusing on one or a few species have provided critical insight into
209 relationships between ecology, selection and variation in developmental periods (17-27), but the
210 restricted nature of these studies, combined with their often-conflicting results, have made broad
211 conclusions difficult to draw. To test the relative importance of adaptation in explaining broad-scale
212 variation in developmental periods, we studied the individual and combined effects of 16 variables
213 related to behavioural, ecological, environmental, and life-history variation across species (plus
214 body size) that have previously been linked to patterns of selection acting on avian developmental
215 periods (17-27) (Fig. 3).

216 Our analyses revealed several important correlates of variation in avian developmental
217 durations. First, after testing each predictor separately (see Fig. S3-6), we found strong
218 relationships between several variables and developmental duration and incubation fraction across
219 species (Appendix S1). By combining all significant single predictors in multi-predictor models, we
220 were then able to identify sets of important predictors with unique effects that are independent of
221 phylogeny. We found that, in addition to being larger, species with longer overall developmental
222 durations tend to be longer lived, with smaller clutches, bi-parental care, elevated nest heights,
223 vertebrate-eating/scavenging dietary niches, and pelagic foraging ecologies (Fig. 3; Appendix S1).
224 These species also tend to be non-migratory and have more equatorial and insular breeding-range
225 distributions. For incubation fraction (Fig. 3A; Appendix S1), in addition to the negative relationship
226 with body size, we found that species with proportionally longer incubation periods tend to have
227 uniparental parental care, are typically insectivorous and nocturnal, and have more polar breeding-
228 range distributions. In both cases, broadly similar effects were found using initial egg mass as an
229 alternative proxy for body size (Fig. S7; Appendix S1). Partial R^2 values for these models indicated
230 that, after controlling for phylogenetic and body size effects, the unique effects of 'ecological'
231 variables included in multi-predictor models accounted for ~12% and ~4% of the variance in
232 developmental duration and incubation fraction, respectively (Table 1). Interestingly, the magnitude
233 of these effects were similar to those associated with body size (Table 1), implying that ecological
234 and allometric effects (as measured here) explain roughly equivalent proportions of variation in
235 developmental durations among bird species. Nonetheless, the variance associated with
236 phylogenetic components indicated that phylogenetic effects remained a dominant source of
237 variation in these models (Table 1). In total, these models incorporating body size, ecological, and

238 phylogenetic effects accounted for 62-93% of the variation in developmental durations across
239 species.

240 These results have several important implications. Most notably, they show that behavioural
241 and ecological variation among species can explain a significant amount of variation in
242 developmental durations across species, consistent with an important role for selection in driving
243 the evolution of avian developmental durations (4). In particular, three main 'ecological syndromes'
244 appear to be associated with variation in developmental durations. First, longer developmental
245 durations are generally associated with factors that presumably increase the safety of the
246 developmental environment from predation threat or other mortality risks, such as nesting in
247 relatively inaccessible sites (nest height), on islands (insularity), or having more than one parent to
248 provide for and protect the offspring (biparental care). The idea that nesting in safe places may relax
249 selection for rapid development is consistent with work by Remeš & Martin [ref. (21)], who found
250 nestling growth rates to be positively associated with predation rates across passerines. Second,
251 factors linked to phenological effects, such as breeding at temperate latitudes, insectivory, and
252 migratory ecology, tend to be associated with shorter developmental durations. In species where
253 reproductive success is driven largely by an individual's ability to coincide their reproduction with
254 peak seasonal food availability (4, 35, 36), the need to operate within a tight timeframe to avoid
255 phenological mismatch is likely to select for rapid development (37). Third, several of the patterns
256 we observe are also consistent with the importance of trade-offs between reproduction and survival
257 for determining variation in avian developmental strategies. For example, shorter developmental
258 periods in species with short lifespans and large clutches are consistent with selection for 'fast' life
259 histories and greater investment in reproduction (independent of body size) (38, 39), while longer
260 developmental periods among species with vertebrate hunting/scavenging diets are potentially
261 explained by selection for slower development to mitigate costs associated with limited and/or
262 unpredictable food availability (40, 41).

263 Furthermore, by considering predictors of incubation and fledging period separately, our
264 results provide further insight into the patterns of selection generating underlying divergence in
265 overall developmental duration and pre- versus postnatal allocation (Fig. 3, Appendix S1). For
266 instance, our finding that nocturnal species have larger incubation fractions than diurnal species is
267 seemingly driven by nocturnal species having relatively long incubation periods rather than
268 particularly short fledging stages. This makes sense if lower daytime parental activity
269 disproportionately reduces nest predation risk during the incubation period relative to the fledging
270 period (26), thus relaxing selection for rapid development inside the egg. Similarly, the longer
271 developmental periods of pelagic species are largely driven by relatively long incubation periods,
272 which may be a consequence of selection for advanced development at hatching (22) or lower rates
273 of egg predation due to inaccessible breeding locations (39). In contrast, our results show that
274 species with uniparental care tend to have overall shorter developmental durations (and greater

275 incubation fractions) largely because of reduced fledging durations. This is consistent with
276 predictions for evolutionary associations between single parent care and short post-hatching
277 offspring development periods (4, 42), but the direction of causality remains unclear. On the one
278 hand, uniparental care may generate selection for rapid post-hatching offspring development to
279 reduce the burden of care, but on the other hand short post-hatching periods may facilitate
280 desertion by one of the parents (typically the male), implying a reversal in the direction of cause and
281 effect (43).

282 Finally, our results challenge several assumptions regarding relationships between
283 developmental durations and other factors at broad scales. In particular, ambient climate is
284 predicted to shape broad-scale patterns of developmental rates in birds via its effect on egg
285 temperature and parental behaviour (10). However, after controlling for the effect of other factors,
286 we found no evidence that variation in environmental conditions (temperature and precipitation) was
287 related to developmental duration across species. This finding supports the view that offspring are
288 to a large extent buffered from variation in ambient environmental conditions by parental
289 adaptations such as nest design, incubation efficiency, and provisioning rate (24, 44, 45).
290 Surprisingly, we also found no significant relationships with developmental mode (precocial, semi-
291 precocial, altricial) or nest type (cavity, closed, open, mixed). This is despite strong expectations for
292 significant associations (15, 46-48) and seemingly large differences between groups in the raw data
293 (see Fig. S3-6). We attribute these negative results to the effect of correcting for phylogenetic non-
294 independence among species in our models. Variation in developmental mode and nest type have
295 likely independently evolved only a limited number of times across the avian phylogeny (49) and so
296 their effect on developmental durations cannot be disentangled from underlying patterns of shared
297 evolutionary history and/or ecology (31). Thus, although developmental mode and nest type appear
298 to co-vary with developmental durations, the generally assumed view that precocial species have
299 longer developmental durations and greater incubation fractions (i.e. prenatal developmental) than
300 altricial species is not supported when phylogenetic effects are taken into account. Greater clarity
301 on whether factors such as developmental mode directly influence the evolution of developmental
302 durations or are simply associated at broad scales via phylogenetically conserved constraints will
303 likely come from integrating data on equivalent traits from other groups (e.g. all vertebrates) to
304 generate sufficient independent phylogenetic replication to conclusively test these relationships.

305 Overall, our study reveals key drivers of developmental durations across the breadth of the
306 avian phylogeny, providing broad, quantitative insight into the relative importance of mechanistic
307 constraints and ecologically-mediated selection in explaining variation in key life-history traits.
308 Furthermore, our results highlight the pervasive impact of phylogenetic history in shaping variation
309 in species' developmental durations. The close association between developmental duration,
310 species' traits, and phylogeny implies a strong signal of evolutionary conservatism, both in terms of
311 species' developmental durations and the combinations of factors ('syndromes') that co-evolve with

312 them, echoing the conclusions from other large-scale phylogenetic analyses of avian life history
313 traits (39, 49). While birds provide sufficient evolutionary replication to investigate the importance of
314 many factors, phylogenetic constraints and evolutionary conservatism makes it difficult tease apart
315 the effects of other, less labile, traits. Thus, a potentially fruitful avenue of future research would be
316 to address these questions over even broader phylogenetic scales in order to better address the
317 effects of body size, species' traits, and phylogenetic constraints (e.g. mutation rates) on the
318 evolutionary diversification of developmental durations.

319 MATERIALS AND METHODS

320

321 **Data.** We collected information on the timing of embryonic development for 20 species using data
322 available in the primary literature (see Appendix S1 for references). For each species with existing
323 data, we extracted information on the time taken for embryos to reach sequential stages of the
324 Hamburger-Hamilton (28) scale, which represents a standard approach for describing and
325 comparing rates of embryonic development across bird species (50). To ensure consistent
326 measurements across species, one of us (NH) re-staged embryo development using data provided
327 in the original publication. In cases where an alternative staging approach was used, we re-staged
328 embryo development according to the Hamburger and Hamilton (28) scale using detailed
329 descriptions and photographs provided in the original publication. In cases where a range of time
330 points were reported for reaching a given stage, we used the average.

331 We collected information on prenatal (incubation) and postnatal (fledging) period lengths
332 (days) for 3096 bird species listed in Appendix S1 from ref. (51) and major ornithological reference
333 works (52). Following ref. (51), we define incubation period as the time (in days) between when the
334 egg is laid and when it hatches, and fledging period as the time taken (in days after hatching) for
335 offspring to be capable of flight (or for some species, leaving the nest). These variables have been
336 used extensively in the comparative avian life history literature and represent standardised
337 measurements of avian developmental periods that are broadly comparable across all bird species
338 (51). Furthermore, the sum of incubation plus fledging time represents a commonly-used metric for
339 species' 'total development period' that integrates variation in both pre- and postnatal development
340 times (11-14). While we acknowledge that in some bird lineages individuals continue to grow after
341 fledging, we argue that in most cases post-fledging growth accounts for a relatively minor proportion
342 of offspring development and as such the combined duration of incubation plus fledging periods
343 represents an informative metric of the total development time.

344 To improve data quality we removed clear outliers that must reflect measurement error (i.e.
345 incubation lengths < 8 or > 90 days; $n = 6$). In addition, we also assessed the extent of within-
346 species variability in development period estimates (where available) relative to the extent of
347 variation across all species by calculating repeatability (i.e. intra-class correlation) coefficients (53).
348 Our dataset contained an average of 1.54 (range 1 to 9) measurements per species for incubation
349 period and 1.47 (range 1 to 9) measurements per species for fledging period. Based on this data,
350 estimated repeatability coefficients were 0.984 (95% CI = [0.982, 0.985]) for incubation period and
351 0.944 (95% CI = [0.939, 0.949]) for fledging period, implying low variability in estimates of
352 developmental periods within species relative to variation between species. We therefore calculated
353 mean values of incubation and fledging period per species (when multiple values were available)
354 and from this calculated variables capturing total developmental duration (incubation + fledging) and
355 incubation fraction [incubation / (incubation + fledging)].

356 Data on adult body mass (g), initial egg mass (g), generation length (days), clutch size,
357 developmental mode (precocial, semi-precocial, altricial), parental care (uniparental, biparental),
358 brood parasitism (parasite, non-parasite), minimum nest height (m), nest type (cavity, closed, open,
359 mixed), habitat (forest dependency: high, medium, low, none), diet (omnivore, fruit/nectar,
360 invertebrate, plant/seed, vertebrate/fish/scavenger), foraging (pelagic, non-pelagic), nocturnality
361 (nocturnal, diurnal) and migration (sedentary, migratory) were extracted from standard avian trait
362 databases (51, 54, 55) or scored directly from the literature [primarily ref. (52)]. Geographical
363 variables, including temperature, precipitation, latitudinal midpoint, and insularity (continental,
364 insular), were based on maps of species breeding distributions from <http://www.datazone.birdlife.org>
365 (Version 9) combined with global climate (56) and landmass datasets (57). Further details of data
366 compilation methods are given in the Supplementary Material. The full dataset, along with
367 associated sample sizes, can be found in Appendix S1.

368

369 **Phylogeny.** Our analyses are based on the taxonomy and phylogenies of ref. (58), which currently
370 represent the only available ‘complete’ species-level phylogenetic hypothesis for all birds. To
371 provide a phylogenetic framework for the species in our dataset ($n = 3094$), we downloaded 1000
372 ‘full’ trees (those containing all 9,993 species) from <http://www.birdtree.org>, which we then pruned to
373 leave only the species represented in our dataset. We then used this tree distribution to generate a
374 maximum clade credibility (MCC) tree, which provided the phylogenetic framework for our analyses.

375

376 **Analyses. Staging data.** We categorized avian development into four discrete phases spanning
377 both prenatal (embryonic; based on the descriptions of Hamburger & Hamilton [ref. (28)]) and
378 postnatal (fledging) periods (Fig. 1A), and calculated the time taken for individuals to reach the end
379 of each phase. Specifically, we estimated the time required for embryos to reach HH24 (phase 1),
380 HH33 (phase 2), to hatch (phase 3) and finally to fledge (phase 4). To estimate the time points
381 associated with reaching HH24 and HH33, we fitted curves of the form $y = \exp(a + b \cdot x)$ using the R
382 function ‘nls’ to describe the relationship between embryonic stage (x) and time (y) (Fig. S1). This
383 allowed us to accurately infer time points associated with HH24 and HH33, even when such data
384 were not explicitly reported in the original publication. Data on the later time points (hatching and
385 fledging) were extracted either from the relevant staging paper directly or else imported from our
386 broader comparative dataset.

387 **Allometric analyses.** We tested the relationship between adult body size and
388 developmental period variables using phylogenetic linear regression (30), controlling for
389 phylogenetic relatedness by estimating Pagel’s lambda. For each variable, we also fit a model in
390 which intercepts were estimated separately for major taxonomic groups (> 20 spp.) in order to
391 generate mass-adjusted estimates of relative developmental durations (Fig. S2).

392 **Multi-predictor models.** We used the same phylogenetic regression approach described
393 above to test the relationship between predictor variables and variation in our developmental
394 variables. First, we fitted individual (i.e. single) predictor models using all available data for each
395 predictor. We then combined all individually important predictors into a multi-predictor model. In all
396 cases, predictors were considered to be important if model support values dropped by >2 units (i.e.
397 $\Delta AIC > 2$) when the predictor was dropped from the model (59), with larger ΔAIC values indicating
398 greater statistical support for the importance of a predictor. We checked for evidence of multi-
399 collinearity among predictors in our multi-predictor models using variance inflation factors (VIF) and
400 found no evidence of severe ($VIF > 10$) or even moderate ($VIF > 5$) multi-collinearity in any of our
401 models (median VIF = 1.80; range = 1.01 – 4.13). R^2 values for full models (including phylogenetic
402 effects) and partial- R^2 values associated with predictors were calculated using the 'R2.lik' function in
403 the R package 'rr2' (31).

404

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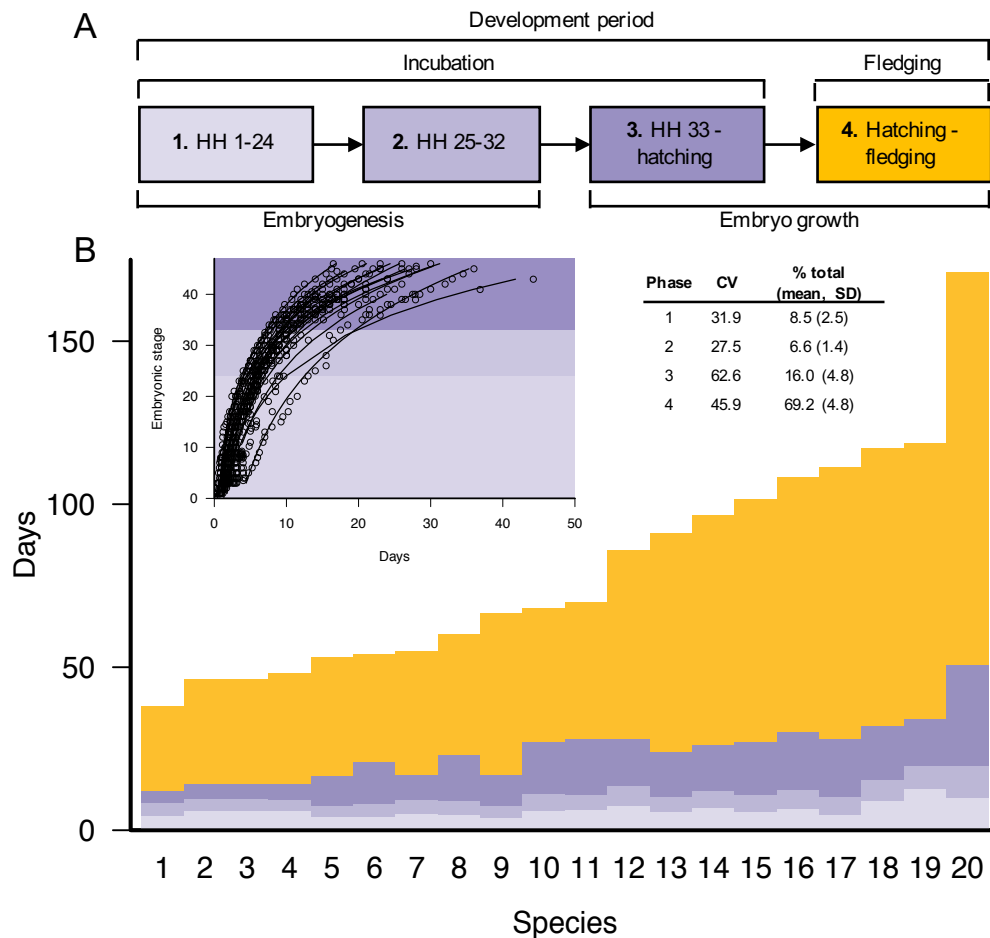


Fig. 1. The duration of avian developmental phases. A, schematic illustrating four distinct phases of avian ontogeny. Phase 1 and phase 2 corresponding to Hamburger-Hamilton stages (HH) 1-24 and 25-32, respectively, represent embryonic developmental stages primarily associated with embryogenesis (i.e. non-growth). In contrast, phases 3 (HH33 to hatching) and 4 (post-hatching fledging period) correspond to developmental periods consisting largely of growth. B, stacked bar chart showing time intervals associated with phases 1 to 4 for 20 bird species for which information on the timing of embryonic developmental stages was available, with species are ordered by total developmental duration. Species codes are shown in Fig. S1. Inset graph shows the staging data and fitted curves used to estimate the time points separating phases 1-3. Inset table reports the coefficient of variation (CV) and percentage of total developmental period length (% total) accounted for by each of the four phases.

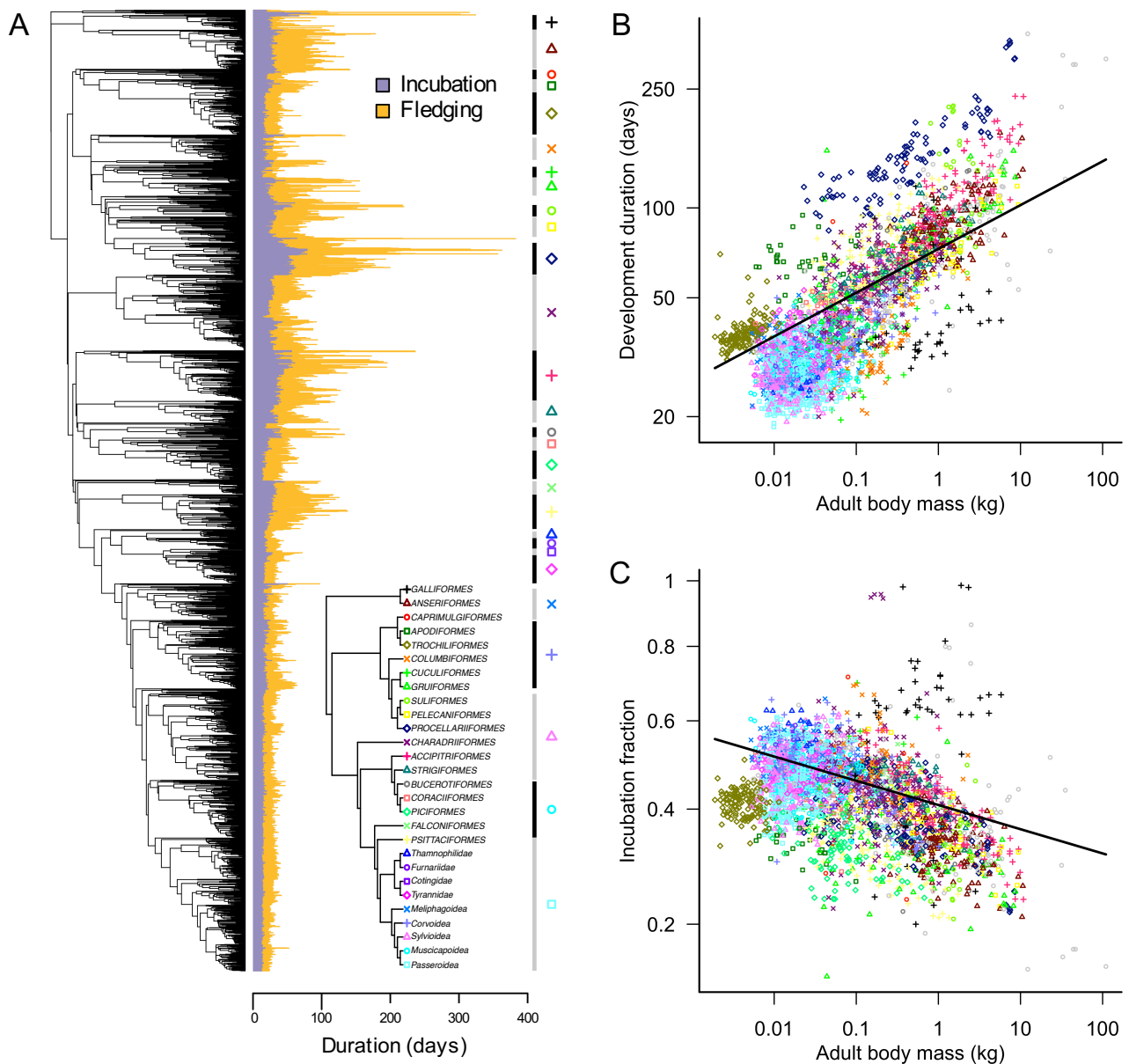


Fig. 2. The diversity, phylogenetic distribution and allometry of development periods in birds. A, The phylogenetic distribution of incubation, fledging and overall development (incubation + fledging) period across 3096 species of birds. Inset tree schematic indicates the relationships among major taxonomic groups (>20 spp.) and provides a key for the plotting symbols used throughout the figure. B and C, allometric relationships of (log-transformed) development period length (B) and (square root-transformed) incubation fraction (C) with (log-transformed) adult body mass. Lines indicate the regression lines estimated by phylogenetically-controlled regression.

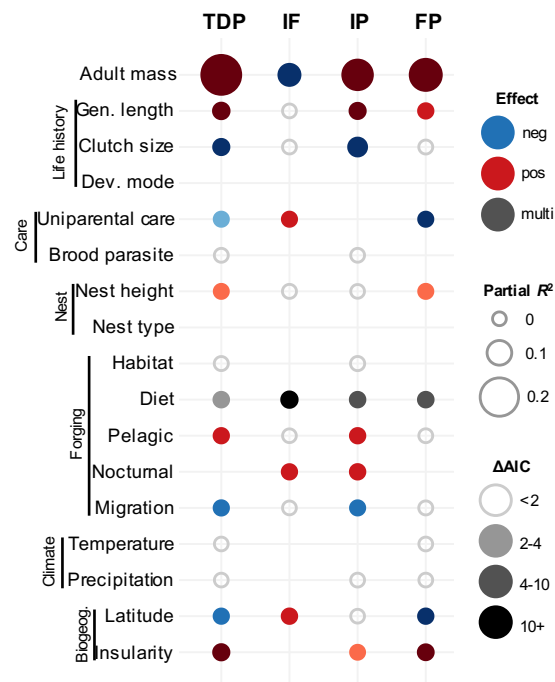


Fig. 3. Predictors of the duration and partitioning of developmental period lengths in birds. A, Phylogenetically-controlled multi-predictor models of total developmental period (TDP), incubation fraction (IF), incubation period (IP) and fledging period (FD). Unfilled circles indicate factors that were significant as single predictors but not significant in a multi-predictor model. Gaps indicate factors that were not significant ($\Delta AIC > 2$) as single predictors as single predictors and were therefore not included in the multi-predictor model. Note: factors with filled grey points (e.g. Diet) represent categorical variables with >2 ('multi') levels. ΔAIC values indicate the change in model support when the focal predictor was dropped from the model, with larger ΔAIC values indicating greater support for the importance of a predictor. Sample sizes (number of species) for the models were 1665, 1685, 1935, 1665 for TDP, IF, IP, and FP, respectively.

Model component	TDP	IF	IP	FP
Body size	0.18	0.05	0.12	0.13
'Ecology'	0.12	0.04	0.11	0.06
Phylogeny	0.62	0.43	0.70	0.52
Full model	0.91	0.62	0.93	0.84

Table 1. (Partial) R^2 values for model components explaining variation in avian developmental durations. Partial R^2 (individual components) and R^2 (full model) values are derived from phylogenetic multi-predictor models of total development period (TDP), incubation fraction (IF), incubation period (IP) and fledging (FP). Sample sizes and predictor sets are the same as those given in Fig. 3.

1 Supplementary material for

2

3 **Ecology, phylogeny, and the evolution of developmental**
4 **duration in birds**

5

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12

13

14 **1 Supplementary methods**

15 16 **1.1 Extended justification for avian developmental phases**

17
18 According to Hamburger and Hamilton (1951), stages 1-24 of embryo development (our 'Phase 1'; Fig.
19 1A) are described exclusively in terms of embryogenesis – specifically the formation and organisation
20 of the fundamental body plan. During this time (up to incubation day 4 in the chicken), changes in the
21 embryo are characterised primarily by the number of somites, and then, once somites become difficult
22 to see due to the development of the mesoderm, the development of limb-buds, visceral arches, and
23 other externally visible structures. Similarly, stages 25-32 (incubation day 4-8 in the chicken; our 'Phase
24 2') are also characterised by rapid developmental changes in the wings, legs, and visceral arches, and
25 can therefore also be considered as part of embryogenesis, as the differentiation of body structures
26 (e.g. toes, mandible, etc.) is still ongoing.

27 In contrast, from stage 33 onwards, chick development is described primarily in terms of growth,
28 rather than embryogenesis. Specifically, between stages 33-38 (incubation day 8-12 in the chicken),
29 Hamburger and Hamilton describe changes in feather germs and eyelids to distinguish stages, both of
30 which are already present in the developing embryo. Furthermore, from stage 38 (day 12 in the chicken)
31 onwards, Hamburger and Hamilton explicitly state that no new structures are formed, and that chick
32 development primarily comprises the growth of structures that already exist. Thus, from stage 38
33 onwards, Hamburger and Hamilton exclusively use measurements of beak and toe length (i.e. growth)
34 to distinguish stages. We decided to include stage 33-38 into this 'growth' phase (our 'Phase 3')
35 because although Hamburger and Hamilton were not exclusively using growth measurements to
36 differentiate stages at this point, they were still using descriptions of growth based on existing structures
37 only. Thus, we consider chick development from stage 33 to hatching (our 'Phase 3'), and from hatching
38 to fledging (our 'Phase 4'), to constitute growth, in contrast to stages 1-32, which we consider to
39 represent embryogenesis.

40 41 **1.2 Predictor variables**

42
43 Data on mean adult body mass (g), egg mass (g), clutch size, diet (omnivore, fruit/nectar, invertebrate,
44 plant/seed, vertebrate/fish/scavenger), foraging (pelagic, non-pelagic) and nocturnality (nocturnal,
45 diurnal) were extracted directly from Wilman et al. (2014) and Myhrvold et al. (2015). We used the
46 literature [primarily del Hoyo et al. (1992–2011) and Starck (1993)] to assign species to broad categories
47 capturing variation in developmental mode (precocial, semi-precocial, altricial), parental care
48 (uniparental, biparental), brood parasitism (parasite, non-parasite), nest type (cavity, closed, open,
49 mixed). Nest height (m) was recorded as the (minimum) distance between the base of the egg cup and

50 the ground for a given species reported in the literature. We extracted information on generation length
51 (days), habitat (forest dependency: high, medium, low, none) and migration (sedentary, migratory) from
52 <http://www.datazone.birdlife.org> following the approaches described in Cooney et al. (2018). Briefly,
53 regarding species' habitat classifications, in the BirdLife dataset species are assigned to one of four
54 broad habitat categories, depending on whether they "do not normally occur in forests", or exhibit "low",
55 "medium" or "high" levels of forest dependency. Similarly, BirdLife categorise species as "not a migrant",
56 "nomadic", "altitudinal migrant" or "full migrant". We converted this classification system into a binary
57 variable capturing broad differences in species' migratory tendencies, categorising each species as
58 'non-migratory' or 'migratory' (nomadic, altitudinal migrant or full migrant).

59 Variables relating to species' geographical distributions are based on bird breeding range maps
60 provided by BirdLife International and NatureServe (version 9; <http://www.datazone.birdlife.org>),
61 rasterised to 1° resolution. Following Jetz et al. (2008), we calculated average range-wide temperature
62 and precipitation values for the warmest quarter (bio10 and bio18), extracted from the WorldClim2
63 database (Fick and Hijmans 2017), and we calculated species mean (absolute) breeding-range latitude
64 values directly from grid cell occurrences.

65 Finally, insularity was determined by comparing species range maps to a dataset of global
66 landmasses (GSHHG v2.3.6; <http://www.soest.hawaii.edu/pwessel/gshhg/>), and we defined insular
67 species as those with >95% of their range occurring on islands as defined by Weigelt et al. (2013). Prior
68 to analysis, incubation fraction was square-transformed, and the following variables were log-
69 transformed: incubation, fledging and total developmental duration, adult body mass, generation length,
70 clutch size and nest height. The full dataset, along with associated sample sizes, can be found in
71 Appendix S1.

72

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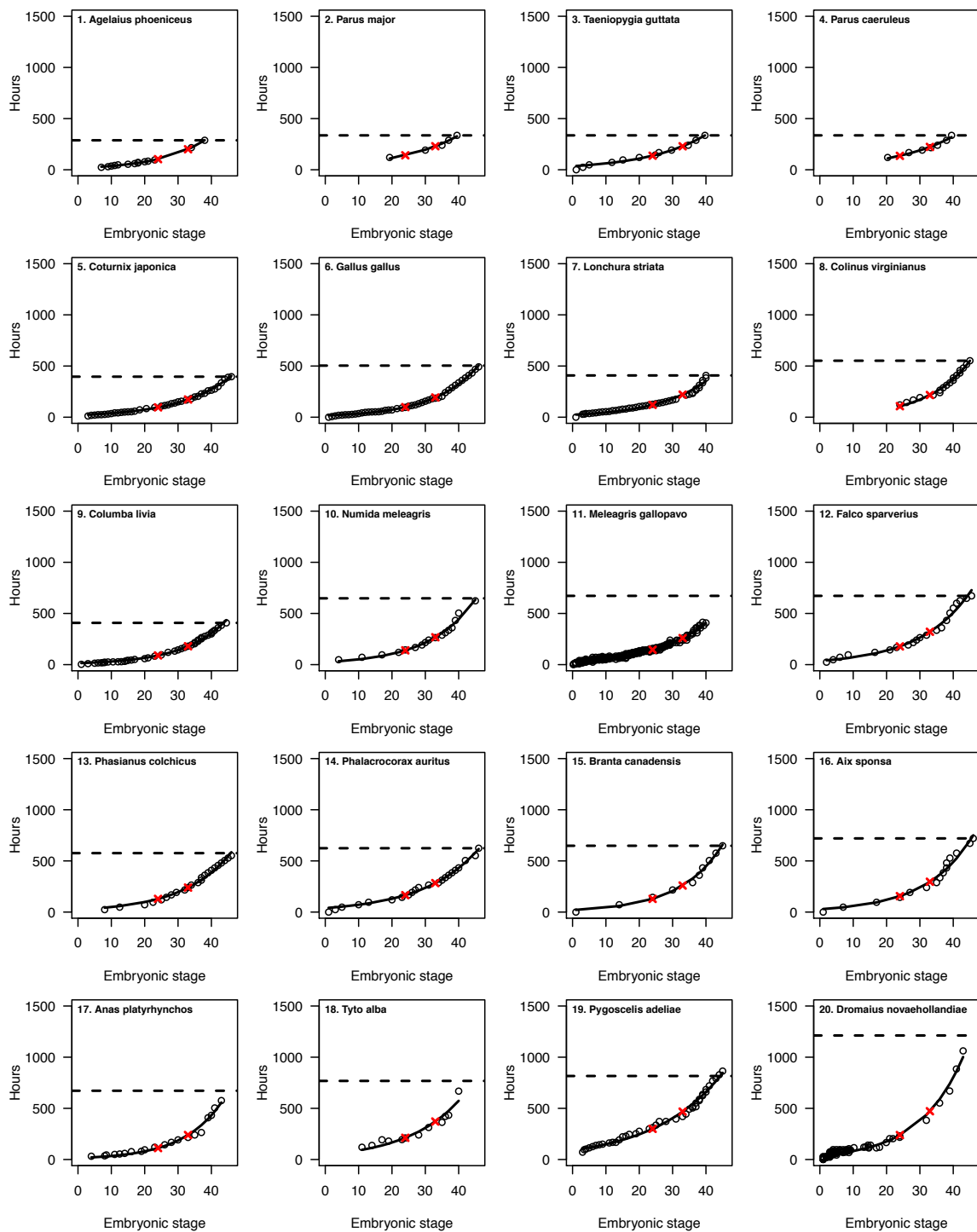


Fig. S1. Individual embryonic development curves for 20 bird species. Points are observed data, and fitted lines come from fitting an equation of the form $y = \exp(a + b \cdot x)$. Red crosses indicate the estimated time at which species reach embryonic stage 24 and 33, respectively. Dotted line indicates the hatching time, as reported from the relevant literature.

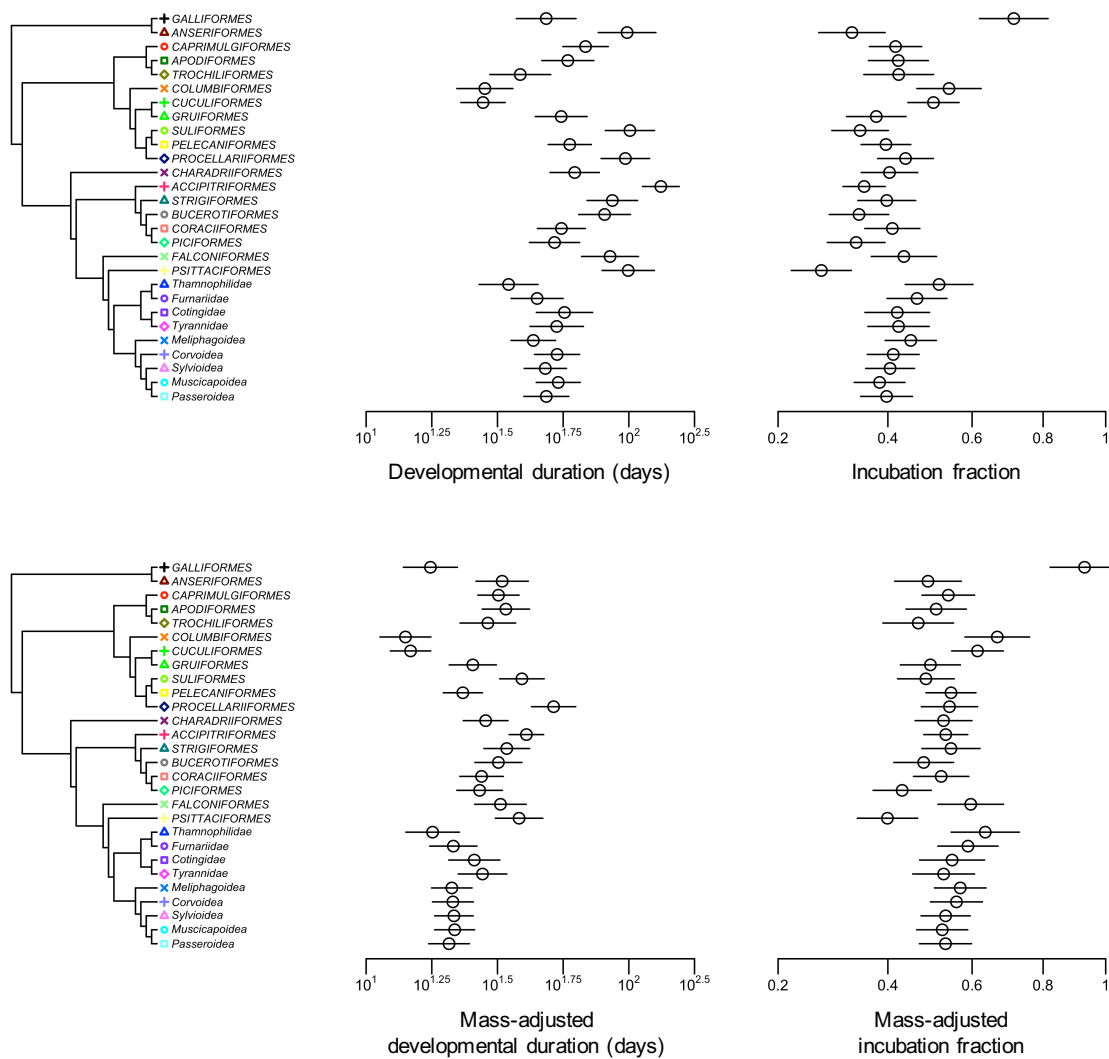


Fig. S2. Variation in developmental durations of major avian clades. Relative developmental duration and incubation fraction values represent the y-intercepts from a model of the form $y = a + b (\log \text{mass})$ in which major avian clades (>20 spp.) were permitted to have unique intercepts (but parallel slopes). Horizontal lines indicate standard errors.

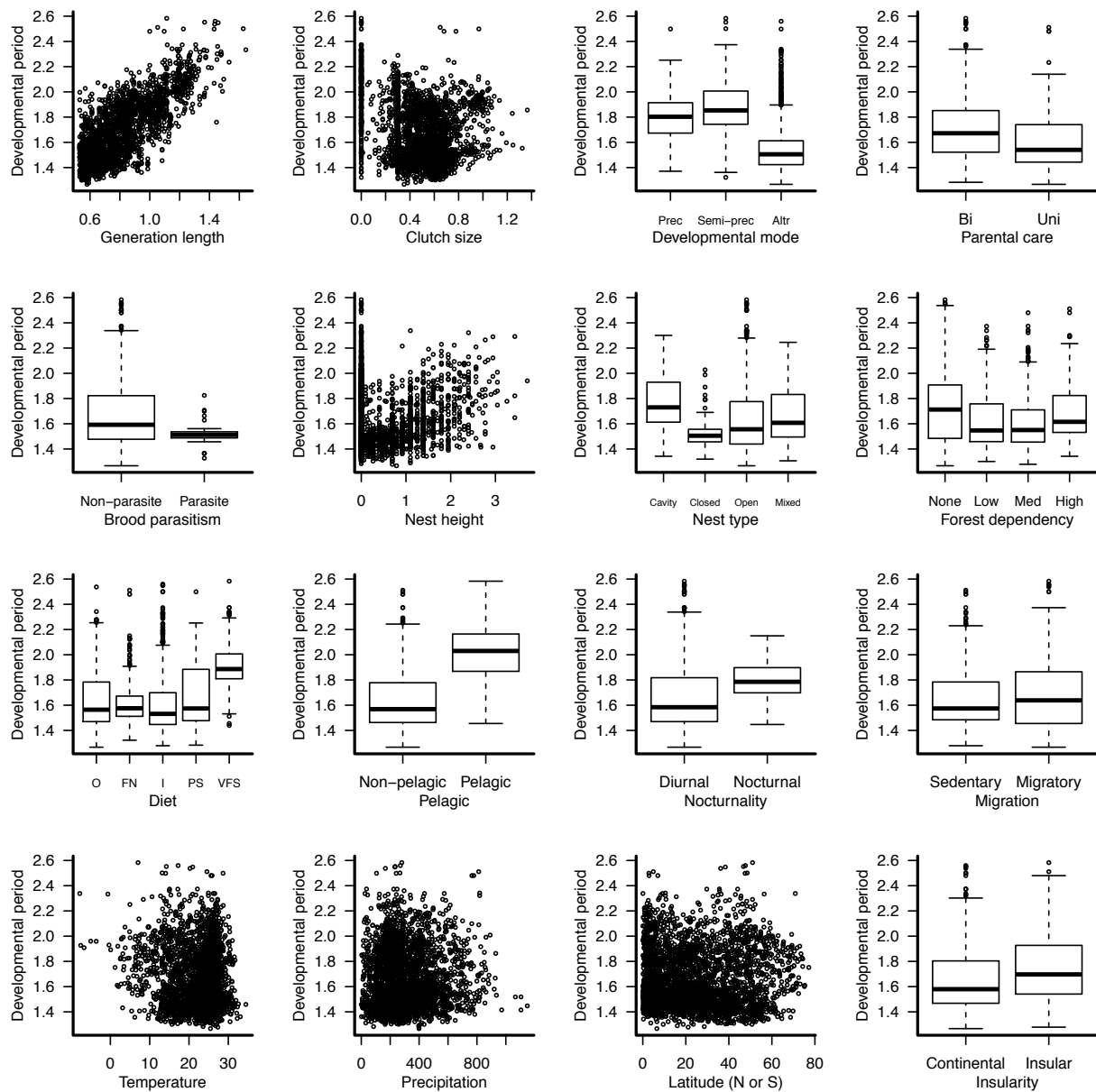


Fig. S3. Relationships between (log₁₀-transformed) total developmental period length and individual predictor variables. Sample sizes and regression statistics can be found in Appendix S1.

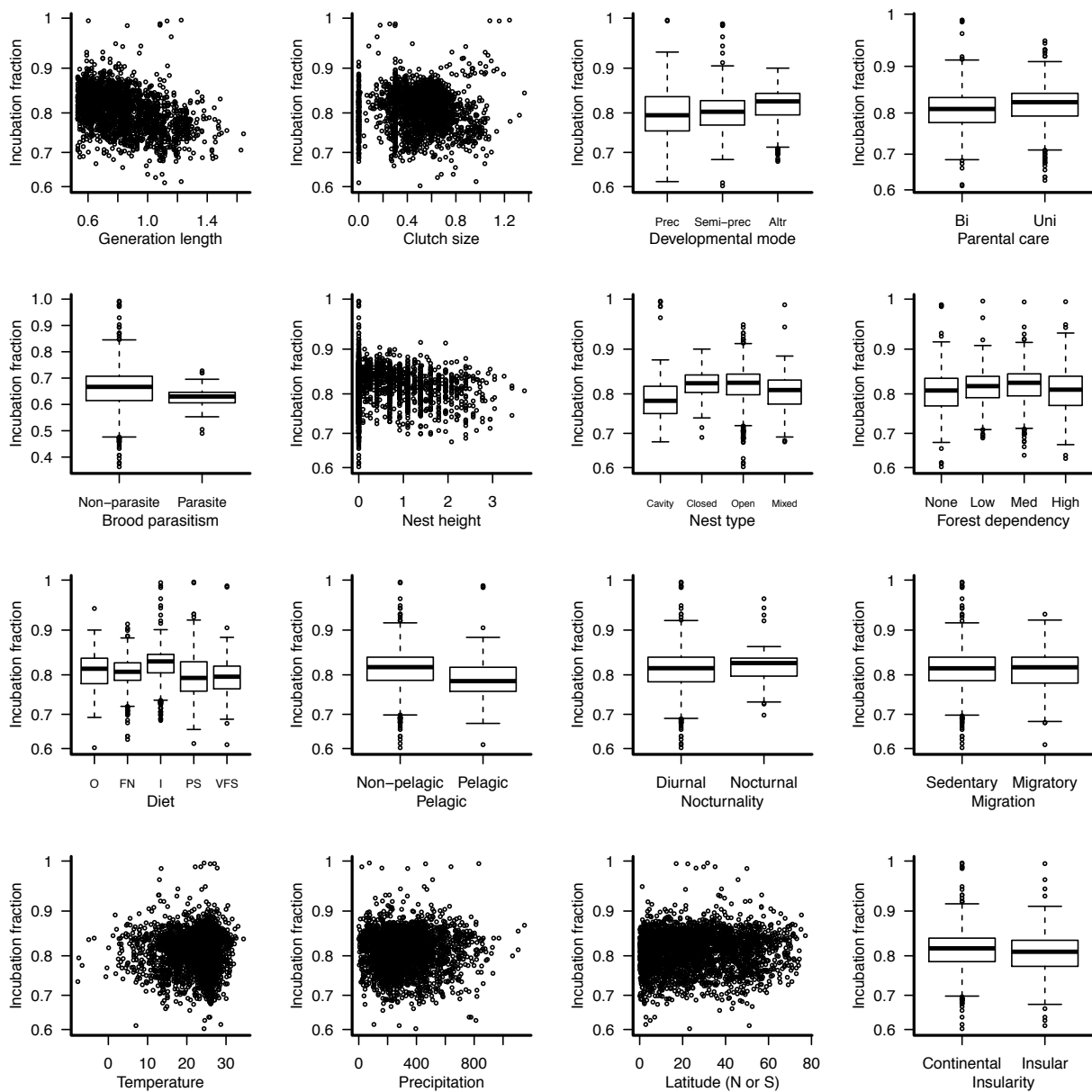


Fig. S4. Relationships between (square root-transformed) incubation fraction and individual predictor variables. Sample sizes and regression statistics can be found in Appendix S1.

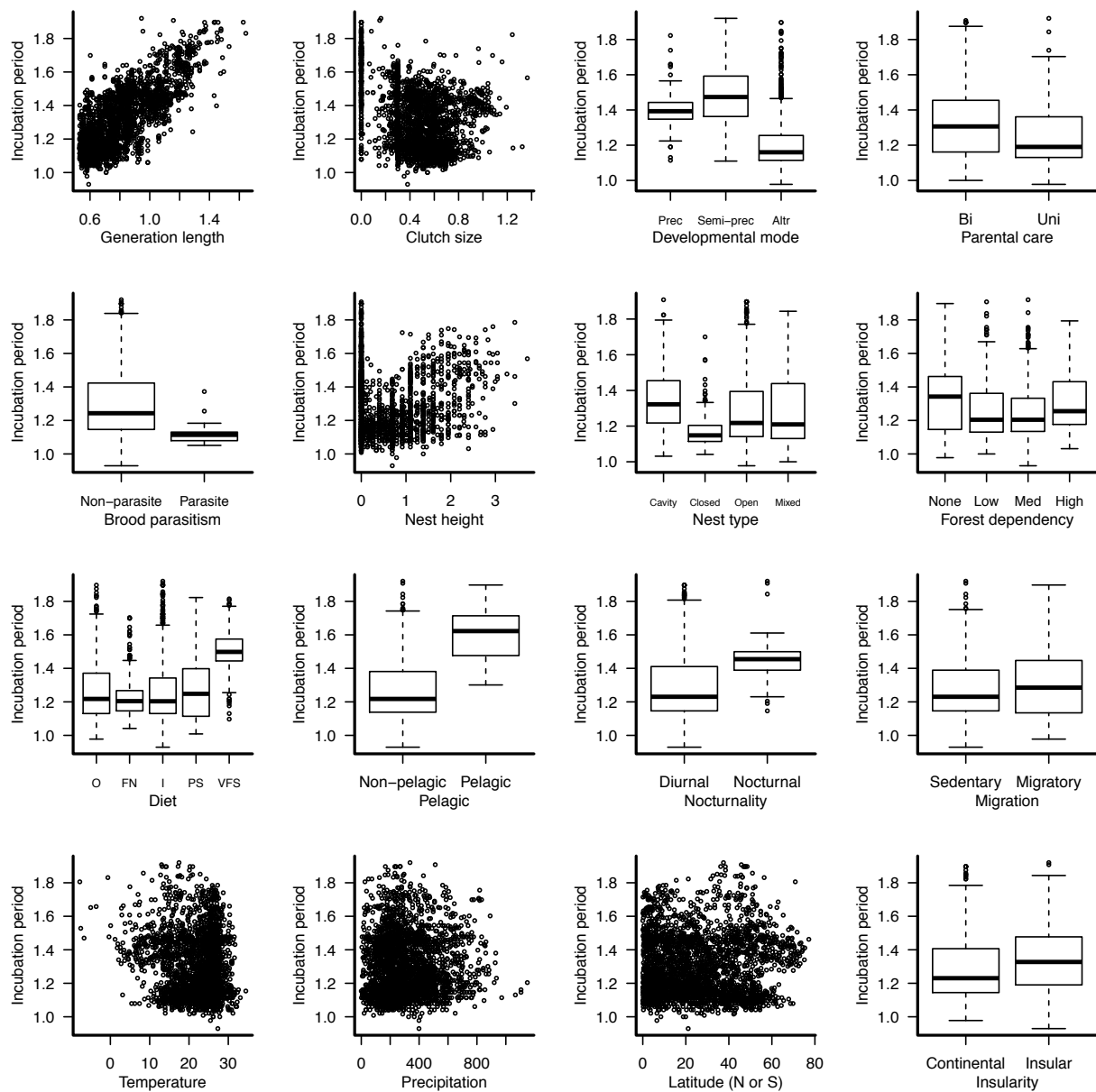


Fig. S5. Relationships between (log₁₀-transformed) incubation period length and individual predictor variables. Sample sizes and regression statistics can be found in Appendix S1.

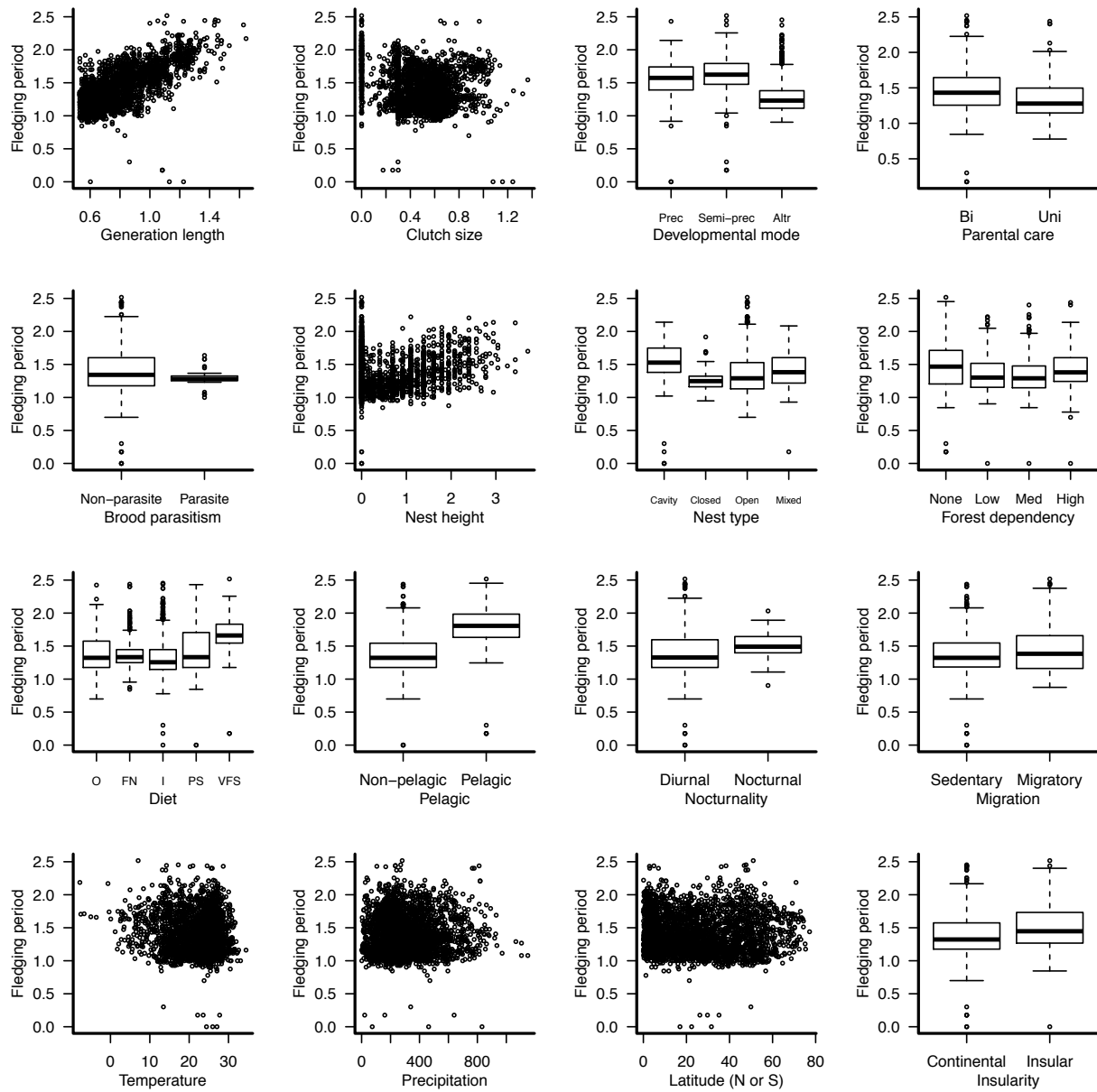


Fig. S6. Relationships between (log₁₀-transformed) fledging period length and individual predictor variables. Sample sizes and regression statistics can be found in Appendix S1.

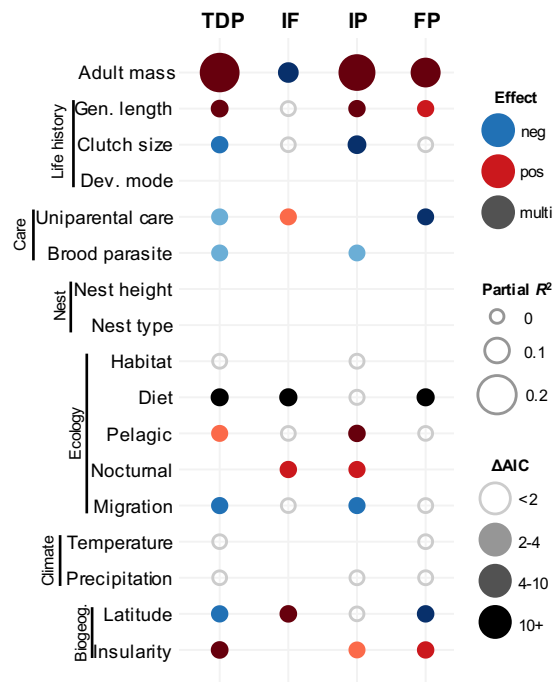


Fig. S7. Predictors of the duration and partitioning of developmental period lengths in birds using egg mass as a proxy for (fledgling) body size. A, Multi-predictor models of total developmental period (TDP), incubation fraction (IF), incubation period (IP) and fledging period (FP). Unfilled circles indicate factors that were significant as single predictors but not significant in a multi-predictor model. Gaps indicate factors that were not significant ($\Delta AIC > 2$) as single predictors and were not included in the multi-predictor model. Note: factors with filled grey points (e.g. Diet) represent categorical variables with >2 ('multi') levels. ΔAIC values indicate the change in model support when the focal predictor was dropped from the model, with larger ΔAIC values indicating greater support for the importance of a predictor. Sample sizes (number of species) for the models were 2327, 1988, 1988, 2017 for TDP, IF, IP, and FP, respectively.