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Disentangling the avian altricial-precocial spectrum: Quantitative assessment of developmental mode, phylogenetic signal, and dimensionality

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Abstract :

The altricial-precocial spectrum describes patterns of variation in avian developmental mode that greatly influence avian life histories. Appraising a given species' position on this spectrum is therefore fundamental to understanding patterns of avian life history evolution. However, evaluating avian developmental mode remains a relatively subjective task reliant on untested assumptions, including the notion that developmental strategies are distributed along a single dimension of statistical variation. Here, we present a quantitative multivariate framework that objectively discriminates among meaningfully different modes of avian development. We gathered information on seven hatchling and post-hatching traits for up to 4000 extant bird species, and find that most traits related to developmental mode show high phylogenetic signal and little intraclade variation, allowing unknown values to be reliably interpolated. Principal component analyses (PCAs) of these traits illustrate that most variation in hatchling state can be quantified along one dimension of trait space. However, our PCAs also reveal an important second dimension explaining variation in post-hatching behavior, enabling factors related to hatchling state and post-hatching behavior to be disentangled. In order to facilitate future macroevolutionary studies of variation in avian developmental strategies, as well as explorations of covariation between developmental mode and other aspects of avian biology, we present PC scores for 9993 extant avian species.

Keywords : Birds, developmental mode, down cover, eye opening, hatchling, life history

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Introduction

Variation in avian developmental patterns has long been a major focus of ornithologists. Hatchling appearance and post-hatching behavior differ markedly across extant avian diversity (Figure 1), ranging from the immediate independence of hatchling megapodes, to the blind and naked hatchlings of woodpeckers that remain in their nest until they can fly. This variation has traditionally been described by categorizing species along a spectrum ranging from “altricial” (comparatively immature hatchlings in need of substantial parental care) to “precocial” (relatively advanced hatchlings capable of early independence). The importance of this spectrum in dictating aspects of avian lifestyles has been widely acknowledged (e.g., Starck 1993; Starck and Ricklefs 1998*a*), and the altricial-precocial spectrum has been associated with numerous important biological variables, including those related to life history (e.g., Ricklefs 1979; Sotherland and Rahn 1987; Vleck and Vleck 1987; Temrin and Tullberg 1995; Ricklefs et al. 1998; Thomas and Székely 2005; Deeming 2007; Deeming and Birchard 2007; Karlsson and Lilja 2008; Sibly et al. 2012; Birchard and Deeming 2015, 2015; Mytiai et al. 2017), physiology (e.g., Vleck and Vleck 1987; Ar and Tazawa 1999), morphology (Botelho et al. 2015; Mytiai et al. 2017; Shatkovska and Ghazali 2017; Shatkovska et al. 2018), brain size/development (Bennett and Harvey 1985; Starck 1993; Iwaniuk and Nelson 2003; Charvet and Striedter 2011) and behavior (Shatkovska and Ghazali 2017).

Studying variation in patterns of development requires metrics enabling comparisons of developmental mode across species. Significant work has been devoted to categorizing developmental mode, with efforts aimed at determining how many categories should be considered, the variables that should be used to define those categories, and how to differentiate among categories (Nice 1962; Ricklefs 1979, 1983; Starck 1993; Starck and Ricklefs 1998c). For example, the most recent in-depth work on this hierarchization recommended eight categories (Starck and Ricklefs 1998c), although most comparative analyses have used simplified schemes ranging from two (precocial/altricial) to four (precocial/semiprecocial/semialtricial/altricial) (e.g., Garamszegi et al. 2007; Sibly et al. 2012; Cooney et al. 2020). Traits characterizing a hatchling's down cover, eye state (open or closed), locomotor abilities, nest attendance, and parental care are often considered in these classifications. Unfortunately, as recognized by many practitioners, unambiguously defining these categories is challenging (Starck and Ricklefs 1998c), and identifying limits between categories can be especially subjective. Delineating among categories may rely on arbitrary decisions regarding the relative importance placed on certain traits, such as hatchling down cover vs. hatchling eye state, and category assignment may also be circular, relying on *a priori* assumptions of the category a given species should belong to. For example, hatchling down cover has been a controversial criterion for distinguishing between altricial and non-altricial taxa; although "hatching naked" is considered a key criterion identifying altricial species (Starck 1993; Starck and Ricklefs 1998c), the many representatives of Passeriformes that hatch partially covered with down are still considered altricial. To accommodate this variation, a solution has been to create two subcategories of altricial species based on the presence or absence of down (Starck 1993). However, there is a significant degree of variation in the extent of down covering among passeriform hatchlings (e.g., see Wetherbee 1957), raising questions about whether further consideration should be given to the variation observed among downy species.

Nearly forty years ago, Ricklefs (1983), referring to the categories defined by Nice (1962), suggested that "Nice's eight-category scheme may eventually be replaced by a quantitative, metrical classification". In an attempt to quantitatively describe variation in development patterns, Starck and Ricklefs (1998*b*) developed a metric integrating proxies of tissue maturation (dry matter content) for different organs at hatching. Although particularly pertinent to characterizing hatchling state, this metric is unfortunately only available for a few dozens of species (61 in Starck and Ricklefs 1998*b*), and ignores post-hatching development, which also exhibits substantial variation across species and is often used to inform characterizations of developmental mode. As such, qualitative schemes attempting to discretize the altricial-precocial spectrum remain the standard.

Here, we aim to provide quantitative indices of variation in developmental mode across birds, based on multivariate ordinations of seven chick traits. A primary objective is to provide a quantitative metric available for most (if not all) extant avian species that will be amenable to incorporation into large-scale comparative analyses as a continuous variable. We also aim to test two key assumptions arising from the extensive literature on avian developmental mode. First, development-related traits are often assumed to be highly conserved within higher taxonomic groups, to the point where intraclade variation at the traditional 'family' level is seen as negligible (Nice 1962; Ricklefs 1983; Ricklefs and Starck 1998b; Starck and Ricklefs 1998c; Botelho and Faunes 2015). To our knowledge, this assumption has never been formally tested, so we address it here. Second, the hierarchical classification of developmental mode categories relies on the expectation that developmental strategies are distributed along a single dimension of statistical variation. Although attempts have been made to test this assumption (see Ricklefs and Starck 1998), it remains to be clearly demonstrated or refuted.

The altricial-precocial spectrum aims to describe the diversity of developmental patterns observed among extant birds. Traditionally, however, it has focused on patterns of development that can be discerned from phenotypic observations of chicks. This spectrum therefore does not directly consider differences in pre-hatching development, although embryonic development has obvious consequences bearing on the characteristics of hatchlings (Ricklefs and Starck 1998a). The spectrum also aims to integrate aspects of variation in both hatchling state and post-hatching development, although the strength of association between these factors is unclear. An ability to statistically distinguish between factors related to hatchling state and post-hatching development would be particularly valuable in order to enable the assessment of their relative influence on variables related to avian growth and lifestyle. For example, the relatively slow growth of precocial taxa with respect to altricial taxa could alternatively be explained by multiple mechanisms, such as the advanced state of precocial hatchling maturity and an associated trade-off between hatchling maturity and growth (Ricklefs 1979; Ricklefs et al. 1994), the high post-hatching energy expenditure associated with the active lifestyles of precocial chicks, or both (Ricklefs 1979; Ricklefs et al. 1994). Distinguishing between these mechanisms requires isolation of the influence of hatchling state from post-hatching behavior, which is only possible if they are not too strongly interdependent. By testing the dimensionality of variation in developmental mode across birds, we aim to determine whether it is possible to statistically distinguish between variation in hatchling state and post-hatching development across the altricial-precocial spectrum, or whether these two stages of chick development should be summarized along a single axis of variation.

We gathered information on seven variables characterizing hatchling state and post-hatching behavior for over 4,000 extant bird species, covering most major taxonomic groups and geographic regions. These variables (down cover, eyes at hatching, age at eye opening, locomotion, feeding ability, nest attendance, and post-nest behavior) have been classically considered in the determination of developmental mode categories (e.g., Nice 1962; Starck and Ricklefs 1998c). For each variable we first calculated phylogenetic signal and intraclass correlation coefficients (ICC) for avian clades recognized at the family and order level by recent taxonomies. We then performed principal component analyses (PCAs) including the different variables to determine the dimensionality of variation in developmental patterns, and to extract species scores from these principal component (PC) axes that could be used as quantitative metrics of developmental mode. We investigated how different combinations of variables affected PCA outputs, performing PCAs that either included or excluded descriptors of post-hatching behavior. To determine whether factors related to pre- and post-hatching development could be distinguished from one-another, we compared the performance of the PCA axes at predicting a variable normally only affected by pre-hatching development (degree of tissue maturation at hatching) vs. a variable that should be affected by both pre- and post-hatching development (chick growth rate). We hypothesized that, if the effects of pre- and post-hatching development could not be isolated, these contrasting PCAs would predict the degree of tissue maturation at hatching and chick growth rate similarly. By contrast, if these stages could be isolated, we expected the degree of tissue maturation at hatching to be better predicted by the hatchling PCA, and growth rate to be better predicted by the PCA incorporating both hatchling and post-hatching traits. Finally, since most developmental traits exhibited very little variation within families and high phylogenetic signal, we estimated indices of developmental modes (both including or excluding post-hatching characteristics) for the 9,993 extant bird species included in the taxonomy employed by Cooney et al. (2017).

Methods

Traits assessed

To characterize variation in patterns of avian development, we extracted information on seven traits: hatchling down cover, eye state at hatching, age at eye opening, hatchling locomotor activity, hatchling feeding ability, ratio of time spent in the nest to age at first flight (hereafter, *nest attendance*), and post-nest behavior. Complete details on our scoring system for all variables is provided in Supplementary Table 1 (Supp. Table 1). Below, we provide an abridged description of our scoring methodology.

Hatchling *down cover* is highly variable across species. To capture this variation, we used a scoring system with 4 categories, from naked (0) to fully covered with down (3). To characterize eye state at hatching, we constructed two variables, a binary one determining whether the eyes are open on hatching day (hereafter *eyes at hatching*) and a continuous variable characterizing the age (in days) at which the hatchling's eyes open (hereafter *age at eye opening*). Locomotor activity (hereafter *locomotion*) was coded as a binary variable (1 for species in which hatchlings usually walk or swim within the first 24 hours post-hatching, 0 otherwise), as was *feeding ability* (0 for hatchlings fed by adults, 1 for self-feeding hatchlings).

To characterize the behavior and environment of chicks after hatching, we considered the acquisition of flight as a marker of the end of the chick life stage. We first measured the proportion of time chicks spend in the nest before being able to fly as the ratio of the time spent in the nest to the age at first flight (*nest attendance*). Obviously, flightless species could not be scored directly for this variable. However, the hatchlings of many flightless species included in our dataset leave their nest very soon after hatching (e.g., hatchlings of the Greater Rhea *Rhea americana* or the Guam Rail *Hypotaenidia owstoni*). In these cases, species were assigned a score of 0 for nest attendance. For penguins (Spheniscidae), we used the age at first swim to mark the end of the chick life stage instead of age at first flight, as it is similarly indicative of a life-stage transition in this clade. Nest attendance was not estimated for the remaining flightless species (e.g., Kakapo *Strigops habroptila*), and these species were excluded from analyses considering this variable.

In addition to the typical precocial (leave nest early and follow parents) vs. altricial (do not follow parents but stay in nest) dichotomy, most developmental mode classifications recognize a separate category for species in which chicks leave the nest early but do not follow their parents until they are able to fly. For example, the chicks of some gull and tern species (Laridae) leave their nest just a few days after hatching, but stay in the nest area where they are fed by their parents until they are able to fly. Traditionally, only a very restricted set of family-level clades are considered to attend the "nest area" after leaving the nest (e.g., Laridae, Stercorariidae, Phoenicopteridae). However, this behavior is actually more widespread. For example, the chicks of many Passeriformes, including most larks (Alaudidae), also leave their nest long before being able to fly, and spend several days waiting for adults to feed them around the nest area. We thus constructed a separate variable (hereafter, *post-nest behavior*) distinguishing between species in which hatchlings follow their parents or are independent once they leave the nest (score of 0), and hatchlings that stay around the nest area waiting to be fed (score of 2). Some birds spend most of their pre-flight period in their nest, but still leave their nest shortly before being able to follow their parents. To distinguish species that only spend a short period out of their nest waiting to be fed, we attributed a score of 1 to species spending more than 80% of their preflight period in the nest, but which are unable to follow their parents or forage independently immediately after leaving the nest. A score of 2 was therefore restricted to species spending at least 21% of their post-nest, pre-flight period waiting to be fed out of the nest.

We elected to exclude two variables that are sometimes considered in assessments of avian developmental mode: brooding behavior and food showing by adults. Brooding behavior is often used to estimate the degree of homeothermy at hatching. However, this variable is influenced by a diversity of factors, including abiotic ones (e.g., climatic conditions), and homeothermy is much more strongly affected by body size than by differences in development patterns (Visser 1998), making this trait less relevant to the assessment of variation in development patterns. In addition, quantifying brooding behavior can be particularly subjective. With the notable exception of megapodes (Megapodiidae), some shorebirds (Scolopacidae), and the only obligately brood-parasitic duck (*Heteronetta atricapilla*, see Supp. Mat. 1), chicks of virtually all bird species are brooded. Although the duration of brooding varies, properly quantifying this variation to obtain comparable estimates across a wide range of species requires detailed behavioral data that are rarely available. The amount of time spent brooding can vary significantly within and between days, and often decreases as chicks mature (Billerman et al. 2020). As a result, neither the number of brooding days nor the amount of time spent brooding on a given day can reliably summarize variation in brooding behavior across a wide taxon sample. With regard to food showing behavior, determining whether parents engage in food showing can be challenging and not exempt from subjectivity. Most precocial species (e.g., Anatidae, Phasianidae) lead their chicks to appropriate settings for foraging, and in many cases, social learning or facilitation is likely involved in a chick's acquisition of appropriate feeding behaviors. In species where parents do not directly feed their chicks, determining whether parents actively show food items to their chicks can be particularly challenging, with substantial opportunity for false negatives. To limit the potential for uncertainty and subjectivity when scoring feeding ability, we decided to exclude food showing behavior as a trait in our analyses. Therefore, we only distinguish between direct beak-to-beak feeding by adults, and self-feeding.

Data sources

We used the taxonomy of the IOC World Bird List version 10.2 (Gill et al. 2020) as a reference to build our developmental trait database. Information on each trait was obtained from a diversity of sources. We first extracted all information available in the main regional handbooks covering Australia, New Zealand and Antarctica (Marchant and Higgins 1990, 1993; Higgins and Davies 1996; Higgins 1999; Higgins et al. 2001, 2006; Higgins and Peter 2002), Africa (Fry et al. 1982-2013), Asia (Ali and Ripley 1968-1974; Roberts 1991-1992; Wells 2007), the Western Palearctic (Cramp and Perrins 1977-1994) and North America (Billerman et al. 2020). No handbook was available for Central and South America, and in order to limit this geographic (and taxonomic) bias, we extracted information from Skutch (1954*a*, 1960*b*, 1969*c*). In addition, we extracted information from 16 family-level monographs (Delacour and Amadon 1973; Taylor and van Perlo 1998; Harris and Franklin 2000; Holyoak 2001; Short and Horne 2001; Davies 2002; Kushlan and Hancock 2006; Nelson 2006; König and Weick 2008; Feare and Craig 2010; Kirwan and Green 2011; Erritzøe et al. 2012; Clement and Rose 2015; Greeney 2018; Gregory 2020) and two field guides focused on bird chick descriptions (Harrison 1975, 1978). Since we aimed to limit taxonomic bias and maximize the phylogenetic breadth of our database, we also extracted all information available from the birdsoftheworld website (Billerman et al. 2020) for a minimum of 10 species per family, and for all species in families containing fewer than 10 species. For families for which we still had no information, we then conducted a search on the Web of Science, using keywords corresponding to "Genus species" AND ("breeding" OR "reproduction" OR "chick*" OR "nest*") for each taxon, and extracted information from articles directly describing hatchlings. We also opportunistically extracted data from references providing information on other species (see Supp. Mat. 2 for an exhaustive list of our sources). In addition, we collected information provided in the family introductions of the Handbook of the Birds of the World (del Hoyo et al. 1992-2020), and we consulted the birdsoftheworld website (Billerman et al. 2020) for all species for which we had data for at least one trait, and extracted any additional information available.

In total, we extracted all information available on the birdsoftheworld website for 6,359 species, covering all 251 extant family-level clades and all 40 extant order-level clades recognized by the IOC World Bird List version 10.2 (Gill et al. 2020). Our final dataset gathers information on at least one of the traits of interest for 4,041 different species from 238 families across all 40 orders. Importantly, the number of species for which a given trait was available strongly varied across traits (ranging from a minimum of 1,477 for age at eye opening to a maximum of 3,872 for feeding ability; see also Table 1). Despite our effort to limit sampling biases, significant differences in research effort across geographic areas and taxa (Ducatez and Lefebvre 2014) affected our dataset construction. For some areas (e.g., North America and Europe), hatchlings of almost all breeding species have been described in detail, whereas for other areas (e.g., the Neotropics), many remain undescribed (see also Xiao et al. 2017). Nonetheless, our ability to cover most bird families suggests that we were generally able to limit the potential effects of this geographic bias.

Analyses

Phylogenetic and taxonomic signals

To estimate the phylogenetic signal of the traits we considered, we built phylogenetic generalized linear mixed models (PGLMM) with Markov chain Monte Carlo (MCMC) techniques using *R* (R Core Team 2020) and the *R* package MCMCglmm (Hadfield 2010). This package allows variables to be modeled with a diversity of distributions, including ordinal ones (required for both down cover and post-nest behavior). The variable of interest was included as the response variable, and phylogenetic signal was calculated as the ratio $V_P/(V_P+V_R)$, where V_P is the variance explained by phylogeny and V_R is the residual variance.

We then aimed to assess whether intraclade variation in hatchling traits at the order and family levels was sufficiently negligible to allow these taxonomic levels to be used as references in global comparative analyses. Towards this aim, we built GLMMs with the same response variables, but including taxonomic order or taxonomic family (following the IOC World Bird List version 10.2; Gill et al. 2020) instead of phylogeny as random variables to estimate their intraclass correlation coefficient (ICC). We estimated ICCs as the proportion of variance explained by each of these taxonomic levels by calculating the ratio $V_O/(V_O+V_R)$ or $V_F/(V_F+V_R)$, where V_O is the variance explained by order and V_F is the variance explained by family. To determine the importance of variation among families within the same order, we also built models including both order and family as random effects, and extracted the relative contribution of order and family using the ratios $V_O/(V_O+V_F+V_R)$ or $V_F/(V_O+V_F+V_R)$. We ran the latter analysis after excluding the 23 orders that only include a single family, since family and order levels are confounded in these clades.

We used ordinal distributions for down cover and post-nest behavior, binomial distributions ('multinomial2' in MCMCglmm) for locomotion, feeding ability, eyes at hatching and nest attendance (coded as a percentage), and a normal distribution for the log-transformed age at eye opening. For each model, MCMC chains were run for 215,001 iterations with a burn-in interval of 15,000 to ensure satisfactory convergence. A total of 1,000 iterations were sampled to estimate parameters from each model. We checked that autocorrelation levels among samples were lower than 0.1. Following Hadfield (2010) we used uninformative priors **(**$V = 1$, $\nu = 0.002$), and fixed the covariance structure for models with an ordinal distribution.

Data for each trait were available for different sets of species, so we could not directly compare coefficients obtained for the different traits using our full dataset. Therefore, to allow directly comparable coefficients to be estimated, we also ran models on the restricted set of species for which all traits of interest were available (considering the binary variable "eyes at hatching" instead of "age at eye opening", since it was available for more species). Finally, since the major clade Passeriformes accounts for more than half of all extant bird diversity at both the species and family levels (Oliveros et al. 2019), we re-ran all analyses excluding Passeriformes in order to assess the extent to which our results were driven by taxa within this highly diverse clade. Conversely, we also calculated phylogenetic signal and family ICCs of the different traits within Passeriformes when excluding all non-passeriforms.

For our comparative analyses we used the composite topology from Cooney et al. (2017), which combines "stage 2 Hackett" Maximum Clade Credibility trees from Jetz et al. (2012) with the backbone topology and clade age estimates from Prum et al. (2015). Because aspects of the taxonomy employed by Prum et al. (2015) and Cooney et al. (2017) differ from the most recent version of the IOC taxonomy (e.g., due to recent splits acknowledged by the IOC but not included in the phylogeny), some species included in our dataset were not covered by the phylogeny. We thus ran all analyses twice, alternately excluding all species that were not directly included in the phylogeny, or including them by swapping them for their closest extant relative in the topology based on information provided on the IOC list (Gill et al. 2020) or the birdsoftheworld website (Billerman et al. 2020). Since most of these instances were the result of recent species splits, this usually involved swapping the "new" species with its unsplit precursor taxon. We removed two recently extinct species from New Zealand from our analyses as their phylogenetic position remains unclear (the Laughing Owl *Sceloglaux albifacies*, and the South Island Piopio *Turnagra capensis*). Nonetheless, we present estimates of available developmental characteristics for these taxa in our database (see Supp. Dataset 1).

Principal component analyses

To determine whether the different traits characterizing avian developmental patterns could be projected unidimensionally, we conducted several principal component analyses (PCAs). We first ran a PCA considering 6 of the 7 collected variables (eyes at hatching was redundant with age at eye opening, so we excluded the former and assigned a score of 0 for age at eye opening to species hatching with open eyes). All six variables were available for a total of 1,144 species, and hereafter this analysis is referred to as *Chick PCA*. Passeriformes is only one of 40 extant order-level clades, but accounts for more than 50% of all extant bird species and recognized family-level clades. To test whether Passeriformes was driving the Chick PCA outputs, we re-ran this PCA excluding Passeriformes. We then performed a PCA focused on the four traits describing chicks on the day of hatching (down cover, locomotion, feeding ability and eyes at hatching). Hereafter this analysis is called the *Hatchling PCA*. We also re-ran the Hatchling PCA excluding Passeriformes.

To compare the performance of the Chick and Hatchling PCA axes for predicting hatchling tissue maturation and chick growth rate, we extracted indices of hatchling tissue maturation and growth rate from Starck and Ricklefs (1998*b*, 1998*c*). In these studies, the authors estimated hatchling tissue maturation from the dry matter content of six different tissues in hatchlings of 61 bird species. Extracting the first component of a PCA considering the dry content of these six tissues, Starck and Ricklefs (1998*b*) then calculated a normalized index of lean dry fraction corrected by hatchling body mass (I_P) to compare tissue maturation across species. We used this I_P index, available for 47 species included in our PCAs, as the hatchling tissue maturation index (I_P scores increase with hatchling tissue maturation; see Starck and

Ricklefs (1998*b*) for more information on the calculation of this index). With regard to growth rate, we used two different indices. We first used the growth constant estimated from logistic growth functions (K_L), compiled from dozens of studies by Starck and Ricklefs (1998*c*). This growth constant is available for 1,117 cases across 557 species, including 727 cases representing 295 species that overlap with those included in our PCAs. We also used the t_{10}-t_{90} interval (growth period between 10% and 90% of asymptotic size) as another metric of growth rate from Starck and Ricklefs (1998*c*), to test for consistency in our results. This metric was available for 123 species (198 cases) included in our PCAs. Fast-growing species are associated with higher scores for K_L but lower scores for t_{10}-t_{90}.

We built six linear models with the *lm* procedure in *R* (R Core Team 2020), including I_P as a response variable and either the first, the second or the two first axes of the Chick PCA, or the first, the second or the two first axes of the Hatchling PCA. We then compared the AICc of these models to determine which PCA axes best predicted hatchling tissue maturation. Similar models were built with either K_L or t_{10}-t_{90} as response variables, and we also included species as a random effect since several growth rate estimates existed for some species. We used the *lme* procedure from the package nlme (Pinheiro et al. 2018) to build these linear mixed models. We compared these models using AIC since the sample sizes were sufficiently large. We used maximum likelihood to compare the AIC of mixed models with different fixed effects, but restricted maximum likelihood to estimate the parameters of the best models (Zuur et al. 2009). The three response variables were log-transformed to meet homoscedasticity assumptions.

Since most traits showed little variation within families (see results), we then built PCAs at the family level, after summarizing trait values for each family. When species with different scores occurred within a single family, we averaged these different scores (e.g., if a family included some species with a down cover score of 1, and others with a score of 2, the family was assigned a score of 1.5). Since each family was represented by a single value, the family-level PCAs were less affected by potential taxonomic biases than the species-level analyses, where some families are overrepresented, and others only represented by one or a few species. Finally, we estimated PCA scores as indices of developmental mode for each of the 9,993 species included in the phylogeny based on their phylogenetic position.

Results

Phylogenetic signal, order and family intraclass correlation coefficients (ICCs)

Down cover, locomotion, feeding ability, eyes at hatching and post-nest behavior all exhibited extremely high phylogenetic signal (>0.99, with very narrow 95% credibility intervals for all subsets of species, see Table 1, Figure 2 and Supp. Table 2). Phylogeny thus explained a remarkably high proportion of the variation in hatchling traits. The phylogenetic signal was slightly lower for nest attendance (0.97 or 0.98 in most analyses, though only 0.88 to 0.92 within Passeriformes), and even lower for the age at eye opening in species hatching with closed eyes (0.89 globally, 0.95 in non-Passeriformes, and 0.69 to 0.70 within Passeriformes).

The proportion of variance in hatchling traits explained by either taxonomic family or taxonomic order was also very high (>0.99 for eyes at hatching, locomotion, and feeding ability; 0.98 to 0.99 for down cover), demonstrating that most variation occurs among family-level or order-level clades, and that variation within such clades can mostly be ignored when estimating hatchling traits. Note that within Passeriformes, the family-level ICC for down cover was 0.91, underlining that there was some variation in down cover within passeriform families, whereas the family-level ICC for down cover was >0.99 in non-Passeriformes. The ICC of post-hatching traits, i.e., age at eye opening (0.70 to 0.83 for species hatching with closed eyes), nest attendance (0.85 to 0.94) and post-nest behavior (0.89 to 0.93), were lower than those of hatchling traits for both family-level and order-level clades. Family ICCs were even lower within Passeriformes for these three variables (0.26 to 0.37 for the age at eye opening; 0.49 to 0.63 for nest attendance; 0.65 to 0.76 for post-nest behavior), suggesting that these traits are particularly evolutionary labile within passeriform families.

Finally, models including both order-level and family-level clades show that most of the variation in developmental traits occurs at the order level. However, these analyses also underscore that some variation exists among families within individual orders, especially in traits such as down cover (order ICC: 0.90 to 0.98; family ICC: 0.02 to 0.11) feeding behavior (order ICC: 0.67 to 0.81; family ICC: 0.19 to 0.36) and nest attendance (order ICC: 0.81 to 0.82; family ICC: 0.12 to 0.14; see Table 1 and Supp. Table 2 for more details). Note that for post-nest behavior, the models including both order and family in the random structure failed to properly estimate the two variances together even when changing prior specifications to more informative ones, after transforming post-nest behavior into a binary variable, or after substantially increasing the number of iterations (up to 2 million) and burn-in interval (up to 200,000) for the MCMC chains. Credibility intervals in such analyses were always broad and uninformative, e.g., with ICCs varying between 0.01 and 0.98, with autocorrelation levels among lags for variance estimates exceeding 0.1. Therefore, for this variable we only provide ICCs for models including either family or order as random effects. Note that globally, except for differences between Passeriformes and non-Passeriformes, results were highly consistent across subsets of data (see Table 1 and Supp. Table 2). Some examples of within-family and within-order variation, as well as exceptions, are presented in Supp. Mat. 1. These may be useful for future studies investigating the selective forces affecting developmental traits.

Species-level PCA

We built a first PCA considering the full suite of six developmental traits (hereafter, *Chick PCA*) available for 1,144 species. The first principal component had an eigenvalue of 3.7 and explained 61% of the total variance (Table 2, Fig. 3). Five of the six variables projected onto this first axis, which segregated species that are less mature at hatching and leave their nest close to the age of their first flight (negative chick PC1 scores), from species with more mature hatchlings that leave their nest long before being able to fly (positive chick PC1 scores, see Figure 3). The second principal component, with an eigenvalue of 1.1, explained 18.4% of the variance. Its main contributor was post-nest behavior, and this axis mostly separated species that are either independent or able to follow their parents after leaving the nest (negative chick PC2 scores) from species that stay in the nest area after leaving their nest (positive chick PC2 scores).

Our results therefore suggest that most variation in traits related to developmental mode can be summarized along one primary dimension of statistical variation. However, they also emphasize that some post-hatching characteristics classically used to determine developmental mode are partly independent from other developmental traits. Running a separate PCA on hatchling traits (hereafter, *Hatchling PCA*) confirmed the finding that hatchling characteristics are unidimensional: the Hatchling PCA included down cover, eyes at hatching, locomotion and feeding ability, and its first principal component axis explained 77.6% of the variance (with an eigenvalue of 3.1), while the second principal component exhibited a much lower eigenvalue (0.5; see Figure 3). We ran the Hatchling PCA considering all 1,936 species for which we had information on these four traits, and found that restricting the sample to the 1,144 species considered in the Chick PCA yielded very similar results (see Table 2 and Supp. Fig. 1). Although the first principal component of the Chick and Hatchling PCAs were highly correlated (Spearman rank correlation: $\rho = 0.972$; $p < 0.001$), the correlation was lower between the second axes ($\rho = 0.702$; $p < 0.001$). Running the same PCAs excluding Passeriformes yielded very similar results (Table 2, Supp. Fig. 1).

To determine whether the effects of hatchling state and post-hatching conditions are confounded or additive, we then explored how the Chick and Hatchling PCAs performed at predicting hatchling tissue maturation (expected to be predicted by hatchling characteristics only) and growth rate (expected to be better predicted by both hatchling and post-hatching characteristics). As expected, the index of hatchling tissue maturation was better predicted by the components of the Hatchling PCA, based on hatchling traits only. Indeed, the best model predicting tissue maturation included the two components of this PCA (ΔAICc with the second-best model = 8.2, Table 3). Species with higher hatchling PC1 scores (and thus, on the ‘precocial’ side of the spectrum) exhibited higher tissue maturation scores (estimate = 0.072 ± 0.007, $t = 10.461$, $df = 44$, $p < 0.001$). Hatchling PC2 scores were also positively associated with tissue maturation (estimate = 0.040 ± 0.012, t = 3;263, df = 44, p = 0.002). The latter result is likely explained by the fact that downy hatchlings capable of self-feeding tend to exhibit a greater degree of tissue maturity than downy hatchlings that are unable to feed themselves (see Fig. 3).

In contrast, growth rate was better predicted by the components of the Chick PCA. This result was consistent regardless of whether we considered logistic growth rate estimates (K_L) or estimates of the t_{10}-t_{90} interval (growth period between 10 and 90% of asymptotic size). The best model predicting growth rate included the first two components of the Chick PCA (ΔAIC with the second-best model = 20 for K_L, 10.4 for t_{10}-t_{90}, see Table 3). Species with higher Chick PC1 scores (and thus, on the 'precocial' side of the spectrum) grew more slowly (K_L: estimate = -0.165 ± 0.014; t = -11.754, df = 292, $p < 0.001$; t_{10}-t_{90}: estimate = 0.196 ± 0.026; t = 7.767, df = 120, $p < 0.001$). By contrast, growth rate increased with scores on Chick PC2 (K_L: estimate = 0.101 ± 0.018; t = 5.482, df = 292, $p < 0.001$; t_{10}-t_{90}: estimate = -0.134 ± 0.026; t = -5.198, df = 120, $p < 0.001$), with species remaining in the nest area to be fed by adults after leaving the nest growing faster than species that follow their parents immediately after leaving the nest. Hatchling tissue maturation was thus better predicted by the components of the Hatchling PCA, and growth rate by the components of the Chick PCA.

We then estimated the phylogenetic signal, family-level ICC and order-level ICC for the first two components of both the Chick (with n = 1,144 species) and the Hatchling (n = 1,936 species) PCAs (Table 4). We used the same model specifications as for the variable *age at eye opening* (see Methods) and found that the phylogenetic signal of each of the four PC axes was higher than 0.9 (see Table 4). Family emerged as the most reliable taxonomic level at which to provide estimates of a species' PC scores, since the highest ICCs were obtained at this level for each of the 4 PCs. Note, however, that although family-level ICCs were high for the first principal components of both Chick and Hatchling PCAs (both ICC > 0.97), they were lower for the second principal components. In particular, family was a relatively poor predictor of the second PC axis of the Chick PCA (ICC = 0.66, *vs* 0.86 for the second PC axis of the Hatchling PCA). The latter result is in line with the low family-level ICC of post-nest behavior, a main contributor to the second PC axis of the Chick PCA (post-nest behavior is not included in the Hatchling PCA). Family thus emerges as a particularly robust taxonomic level at which to infer unknown variables related to hatchling-stage developmental mode, but is not as reliable for assessing post-hatching characteristics.

We then re-built these Chick and Hatchling PCAs, but based on family-level instead of species-level characteristics. PCA outputs were very similar to those obtained in the species-level analyses (see details in Table 2, Fig. 4 and Supp. Fig. 2). In addition, PCA scores calculated at the species and family levels were strongly correlated, especially for the first principal components (Chick PCA: PC1, Spearman $\rho = 0.977$; $p < 0.001$; PC2, Spearman $\rho = 0.727$; $p < 0.001$; hatchling PCA: PC1, Spearman $\rho = 0.940$; $p < 0.001$; PC2, Spearman $\rho = 0.882$; $p < 0.001$). Note also that, as for species-level PCAs, including or excluding Passeriformes had no major effect on family-level PCA outputs (Table 2, Supp. Fig. 2).

Assembly of a developmental mode dataset for all extant bird species

For each of the 9,993 species included in the phylogeny (Cooney et al. 2017), we present scores for the first two axes of both the Chick and Hatchling PCAs, considering both species-level and family-level PCAs (Supp. Dataset 2 – see also Table 5 for a brief guideline on the use of these scores in comparative analyses). We could directly calculate the species-level PCA scores for the subset of species for which all trait data were available, and the remaining species were assigned the same scores as their closest relatives for which all trait data were available. In our complete species-level dataset (Supp. Dataset 2) we delineate between scores based on complete species trait values, and those estimated from a species' closest relative with complete trait data. Further, we provide the phylogenetic distance (computed as total time-scaled phylogenetic branch length extracted from the topology of Cooney et al. 2017) to the closest relative with complete trait data as an index of confidence in the accuracy of these estimated scores, with greater confidence associated with shorter distances (Supp. Dataset 2).

Discussion

Quantifying variation in avian developmental mode is fundamental to understanding the influence of development on the evolution of disparate lifestyles across the avian crown group (Ricklefs 1979; Starck 1993; Starck and Ricklefs 1998c). By compiling an extensive dataset of traits related to the state of chicks at and after hatching, we first show that hatchling traits exhibit very high phylogenetic signal, and little intra-clade variation at the order and family levels. Post-hatching characteristics were more variable within these higher-level clades, though they still exhibited high phylogenetic signal. Additionally, our analyses allowed us to demonstrate the unidimensionality of hatchling state variation, since most variation in hatchling traits was captured by a single dimension of principal component trait space. By contrast, post-hatching characteristics did not all project along this same dimension, revealing that the full spectrum of relevant developmental mode characteristics cannot be fully captured by a unidimensional range of values.

Although expected (Nice 1962; Ricklefs 1983; Ricklefs and Starck 1998b; Starck and Ricklefs 1998c; Botelho and Faunes 2015), the generally high phylogenetic conservatism of traits characterizing developmental mode had, to the best of our knowledge, never been formally tested. Here, we confirm that all the developmental traits considered, as well as the principal components quantifying developmental mode itself, exhibit high phylogenetic signal, corroborating the expectation that life history traits in general are strongly determined by phylogenetic history (Böhning-Gaese and Oberrath 1999; Blomberg et al. 2003; Pienaar et al. 2013). Traits characterizing the phenotype of chicks at hatching exhibited especially high phylogenetic signal, to the point where intraclade variation at the family level was limited and generally negligible. Since most variation in avian developmental traits occurs among taxonomic orders, and most phylogenetic divergences among extant order-level bird clades appear to have occurred during the Paleogene Period (~66-23 MYA; (Feduccia 1995; Jarvis et al. 2014; Claramunt and Cracraft 2015; Prum et al. 2015; Berv and Field 2018; Kimball et al. 2019; Field et al. 2020; Kuhl et al. 2021), this long-term retention of developmental traits may imply their canalization relatively early in crown bird evolutionary history, following an interval of more pronounced variation coinciding with the post-Cretaceous diversification of crown birds.

Despite limited variation within taxonomic families overall, we nonetheless identified some patterns of variation that provide relevant targets for future research aimed at identifying selective pressures driving the evolution of traits related to developmental mode within family-level clades. For example, down cover at hatching varied within several passeriform families, providing an interesting opportunity to test for the effect of environmental variables that may explain the emergence and maintenance of this variation (e.g., nest type, climatic variables, etc.). To stimulate this research, we provide the raw data for each trait considered in our study (Supp. Dataset 1), and underline what we believe are some of the most relevant exceptions and patterns of variation to investigate in Supp. Mat. 1. Our illustration of greater evolutionary lability of post-hatching as compared to hatchling characteristics was also in line with the recent discovery that fledging period exhibits lower phylogenetic signal than incubation period, suggesting that developmental constraints are stronger during the embryonic period, while post-hatching characteristics are more sensitive to selective pressures (Minias and Włodarczyk 2020). Some post-hatching traits, including age at eye opening, may also be subject to greater measurement error, partly explaining their apparently lower phylogenetic signal than others. For example, the eye-opening process can sometimes take several days, from the appearance of an eyelid slit to the full opening of the eye (Billerman et al. 2020). However, in most chick descriptions only a single estimate for the age at eye opening is provided, and authors may differ in their criteria for recognizing eye-opening, potentially adding noise in the assessment of this variable. Nevertheless, post-hatching development and growth are known to be directly impacted by environmental factors, including within species (e.g., Stodola et al. 2010). Disturbance, food availability, and climatic conditions can all have important impacts on chick development (Zotier 1990; Martin 1995; Stodola et al. 2010), while the conditions encountered during embryonic development may be better buffered against environmental variation (Deeming 2002; Hepp et al. 2015; Minias and Włodarczyk 2020), potentially explaining differences in phylogenetic and taxonomic signal among hatchling-stage and post-hatching traits.

Most variation in hatchling state could be quantified along one dimension of trait space, confirming an assumption that had not been formally tested at such a broad scale (see Starck and Ricklefs 1998*b*). This result was highly consistent: it held regardless of the inclusion of the highly diverse passeriform clade, whether or not we restricted our analyses to taxa included in the taxonomy used by Cooney et al. (2017), whether or not post-hatching traits were included or excluded from our principal component analyses, and regardless of whether variation was investigated across species or across families. It was also in line with the demonstration, based on a limited sample of 61 species, that variation in hatchling tissue maturation is mostly unidimensional (Starck and Ricklefs 1998c). Importantly, however, post-hatching conditions did not necessarily project on this same dimension of trait space. In particular, post-nest behavior – a variable identifying species that leave their nest early but are unable to follow their parents – was mostly independent from the other traits and projected on a different principal component axis. So far, this variable has been considered as a means of categorizing a few groups of birds (mostly within Charadriiformes) as semi-precocial instead of fully precocial (Nice 1962; Starck and Ricklefs 1998c). However, our dataset reveals that this behavior is much more widespread across extant bird diversity, since the chicks of species representing 16 order-level clades and 40 different family-level clades are known to leave their nest early in development to spend an important amount of time in the nest area, waiting to be fed without being able to follow their parents (see Supp. Dataset 1).

The finding that our post-nest behavior variable was independent from the main axis of developmental variation suggests that the effects of hatchling state and post-hatching characteristics can, to some extent, be statistically disentangled. Accordingly, the principal components of PCAs including or excluding post-hatching characteristics performed differently when predicting traits affected by either hatchling characteristics, or by both hatchling and post-hatching characteristics: the Hatchling PCs (derived from hatchling traits only) were better predictors of hatchling tissue maturation than the Chick PCs (derived from both hatchling and post-hatching traits). In turn, both of the investigated proxies of growth rate were better predicted by the Chick PCs than by the Hatchling PCs, underlining that both hatchling and post-hatching traits affect chick growth rate, in line with both theoretical expectations and empirical evidence (Ricklefs 1983, 1984; Martin 1995; Ricklefs and Starck 1998b,b; Williams and Groothuis 2015). This ability to differentiate between the effects of hatchling state and post-hatching conditions raises interesting possibilities. For example, a better understanding of the constraints and adaptations shaping the evolution of pre- and post-hatching development may prove highly valuable for developing a more mechanistic view of the evolution of avian life history strategies (e.g., see Cooney et al. 2020).

The strong phylogenetic signal and limited intraclade variation of traits determining developmental mode allowed us to generate new quantitative metrics (extracted from PCAs including or excluding post-hatching characteristics) for 9,993 extant bird species as tools for future comparative analyses (Supp. Dataset 2). These scores were either calculated directly, when all traits were available, or were estimated based on a species' phylogenetic position. We found that family-level analyses captured slightly more variation than order-level analyses, and thus also provide estimates of developmental mode for each of the 9,993 species based on their family scores. The first component of each PCA showed particularly high taxonomic and phylogenetic signal (all > 0.9), making estimates based on family or phylogenetic position particularly reliable. By contrast, the family intraclass correlation coefficient (ICC) of the Chick PCA's second axis was much lower (0.66), and estimates of species scores on this axis should therefore be taken with caution. In general, for comparative analyses at the species level, we recommend using estimates based on a species' phylogenetic position (as all exhibited $\lambda > 0.9$), and suggest running analyses based both on the full dataset with all estimated species values, and on the subset of species for which PCs were calculated from actual trait values. Species in the latter group are clearly identified in our dataset for this purpose. Choosing whether to use chick or hatchling PCs depends on the objectives of an analysis; that is, whether the consideration of post-hatching conditions is relevant to the question being investigated (see Table 5). Comparing the effects of the PCs from both the Chick and Hatchling PCAs could also be of interest if analyses aim at testing whether hatchling state and post-hatching conditions have additive effects on a given variable, as was the case for growth rate.

The new metrics provided here have several advantages over previous classification schemes of developmental mode. Most importantly, their quantitative nature means that no subjective decisions are needed to determine limits among developmental mode categories. Moreover, these metrics are not dependent on *a priori* expectations that some clades belong to particular developmental mode categories. However, these metrics also have important limitations. Fundamentally, they are dependent on the variables initially included in our PCAs, and additional variables could have been included in order to take other aspects of avian development, such as brooding behavior, into account. Similarly, the scoring system that we developed for each variable could impact the output of the PCAs. We favored a system allowing us to score an important number of species based on the information available in the literature, which involved simplifying some variables (e.g., by introducing a binary score for locomotion). Undoubtedly, more detailed, and ideally quantitative, scores for such variables would be valuable. We also made the important decision of ignoring the role of phylogeny in shaping relationships among traits in the construction of our PCAs. Correcting for phylogenetic non-independence when measuring associations among traits exhibiting high phylogenetic conservation is particularly challenging, since phylogenetic position and trait values can easily be confounded (e.g., see Cooney et al. 2020). Our attempt to perform phylogenetic PCAs illustrates this issue, as traits such as eyes at hatching and feeding ability emerged as completely independent despite their obvious association. These two traits exhibit extremely high phylogenetic signal ($\lambda > 0.99$), suggesting that developmental trait variation cannot easily be statistically distinguished from phylogenetic relatedness. Instead of correcting for phylogeny and obtaining components that would have been difficult to interpret, we focused on a descriptive approach of the associations among traits while ignoring phylogenetic non-independence. Ultimately, researchers interested in the structure of associations between developmental mode and other components of avian lifestyle variation should bear in mind the phylogenetic signature of developmental mode.

Traits characterizing pre-hatching development are so tightly associated that several divergent aspects of hatchling biology (e.g., vision, locomotion, feeding ability) evolve along one single dimension of variation. Although it might be tempting to interpret variation in hatchling state as the consequence of altricial chicks hatching at an earlier stage of development than precocial ones (Vleck and Vleck 1987; Augustine et al. 2019), empirical evidence shows that species with different developmental modes pass through the same stages of embryonic development (and thus hatch at the same stage, see Hamburger and Hamilton 1951; Ricklefs and Starck 1998*b*). Instead, hatchling state seems to primarily reflect differences in tissue maturation at hatching (Ricklefs and Starck 1998a). The maturation of different tissues seems constrained to evolve in a coordinated way (i.e. adhering to a concerted instead of a mosaic pattern), giving rise to the unidimensionality of hatchling state demonstrated here. By contrast, post-hatching characteristics, though influenced by hatchling state, are more evolutionarily labile. By investigating the dimensionality of developmental mode and providing quantitative indices and information on traits characterizing developmental mode for the vast majority of extant avian diversity, we hope to stimulate further research into how variation in developmental strategy has shaped avian diversification patterns (e.g., see Thomas et al. 2006) and affected the evolution of avian lifestyles (Starck and Ricklefs 1998a; Sibly et al. 2012).

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Table 1. Phylogenetic signal and intra-class coefficients (ICC) for family-level and order-level clades (either included in separate models, or together in the same model) for six traits describing birds soon after hatching. We built phylogenetic generalized linear mixed models with the MCMCglmm procedure in *R*, using either phylogeny, order, family, or family and order as random effects. We then estimated ICCs as the ratio of variance explained by the variable of interest (e.g., family) divided by the total variance (see text for details). *Down cover* is an ordinal variable (varying from 0 = naked to 3 = fully covered with down), as is *post-nest behavior* (varying from 0 = follows parents or forages independently after leaving the nest; 1 = stays in the nest area where it is fed by adults after leaving the nest, but spends more than 80% of its preflight period in the nest; 2 = stays in the nest area where it is fed by adults after leaving the nest, spends less than 80% of its preflight period in the nest). *Locomotion*, *feeding ability*, and *eyes at hatching* are binary variables. *Nest attendance* is a proportion (100 * nesting duration / age at first flight), and *age at eye opening* is a continuous variable. Note that for *age at eye opening*, only species exhibiting closed eyes at hatching were considered, since the difference between species hatching with closed vs open eyes was already taken into account with the *eyes at hatching* variable. CI Inf/CI Sup = lower/upper bounds of the 95% credibility interval; n Orders, Families and Species = number of orders, families and species included in each model. Results presented here consider all species in our dataset (except two for which phylogenetic position could not be assessed with enough confidence, see Methods). Species that were not included in the phylogeny were attributed the same tips as their closest relatives on the tree. Variations of these analyses focused on i) only the species included in the phylogeny; ii) species for which all trait data were available; and iii) only Passeriformes or non-Passeriformes. Those results are presented in Supplementary Table 2 (see also Figure 2b).

Coefficient	Random effect	Response variable	ICC	CI Inf	CI Sup	n Orders	n Families	n Species
Phylogenetic signal	Phylogeny	Down cover	**0.9940**	0.989	0.996	40	215	2614
	Phylogeny	Locomotion	**0.9999**	0.992	1.000	40	231	3547
	Phylogeny	Feeding ability	**0.9998**	0.994	1.000	40	237	3872
	Phylogeny	Eyes at hatching	**0.9999**	0.986	1.000	39	206	2082
	Phylogeny	Age at eye opening	**0.8950**	0.855	0.929	23	128	750
	Phylogeny	Nest attendance	**0.9730**	0.994	1.000	39	191	1914
	Phylogeny	Post-nest behavior	**0.9913**	0.970	0.994	40	192	1965
Order ICC	Order	Down cover	**0.9840**	0.964	0.994	40	215	2614
	Order	Mobility	**1.0000**	0.996	1.000	40	231	3547
	Order	Feeding ability	**1.0000**	0.988	1.000	40	237	3872
	Order	Eyes at hatching	**1.0000**	0.990	1.000	39	206	2082
	Order	Age at eye opening	**0.8330**	0.703	0.909	23	128	750
	Order	Nest attendance	**0.8490**	0.778	0.922	39	191	1914
	Order	Post-nest behavior	**0.9324**	0.843	0.975	40	192	1965
Family ICC	Family	Down cover	**0.9840**	0.978	0.990	40	215	2614
	Family	Mobility	**1.0000**	0.998	1.000	40	231	3547
	Family	Feeding ability	**0.9999**	0.996	1.000	40	237	3872
	Family	Eyes at hatching	**1.0000**	0.997	1.000	39	206	2082
	Family	Age at eye opening	**0.7050**	0.620	0.758	23	128	750
	Family	Nest attendance	**0.9250**	0.908	0.954	39	191	1914
	Family	Post-nest behavior	**0.9093**	0.848	0.938	40	192	1965
ICCs for family and order included in the same models	Order	Down cover	**0.8990**	0.800	0.966	17	192	2330
	Family		**0.1090**	0.028	0.180			
	Order	Mobility	**0.9670**	0.917	0.989	17	208	3259
	Family		**0.0320**	0.012	0.084			
	Order	Feeding ability	**0.8110**	0.602	0.913	17	214	3527
	Family		**0.1860**	0.087	0.393			
	Order	Eyes at hatching	**0.9580**	0.910	0.984	17	184	1908
	Family		**0.0420**	0.016	0.091			

	Order	Age at eye opening	**0.8790**	0.741	0.958	13	118	673
	Family		**0.0370**	0.012	0.090			
	Order	Nest attendance	**0.8160**	0.624	0.916	17	169	1712
	Family		**0.1440**	0.057	0.272			

Table 2. Outputs of principal component analyses (PCAs) conducted on traits characterizing bird chicks at or after hatching. Eigenvalues and % variance explained are provided for the first two axes of each PCA. A total of 10 PCAs were conducted, considering either species-level or family-level characteristics, using different sets of variables. The variables included in each PCA are identified with an X in the corresponding column (DC = *down cover*; L = *locomotion*; FA = *feeding ability*; EH = *eyes at hatching*; AEO = *age at eye opening*; NA = *nest attendance*; PNB = *post nest behavior*). PCAs used to estimate species' developmental strategy scores (Supp. Dataset 2) are in bold. An alternative version of the species-level Hatchling PCA was built on a reduced dataset (*Hatchling PCA reduced dataset*), which only considered the set of species included in the Chick PCA to obtain directly comparable scores for the Hatchling PCA and Chick PCA. In addition, each PCA was run a second time after excluding passeriform species and families, to test whether excluding this highly diverse order-level clade affected PCA outputs. PC1 = Principal Component 1; PC2 = Principal Component 2; n = number of species or families included in the PCA.

	eigenvalue		% variance										
PCA	PC1	PC2	PC1	PC2	Passeriformes	n	DC	L	FA	EH	AEO	NA	PNB
Species-level													
Chick PCA	**3.7**	**1.1**	**61.1**	**18.4**	**included**	**1144**	**X**	**X**	**X**		**X**	**X**	**X**
Hatchling PCA	**3.1**	**0.5**	**77.6**	**13.3**	**included**	**1936**	**X**	**X**	**X**	**X**			
Hatchling PCA reduced dataset	3.0	0.6	74.5	15.3	included	1144	X	X	X	X			
Chick PCA – non-Passeriformes	3.4	1.2	56.2	19.3	excluded	864	X	X	X		X	X	X
Hatchling PCA – non-Passeriformes	2.8	0.7	70.7	17.0	excluded	1066	X	X	X	X			
Hatchling PCA reduced dataset – non-Passeriformes	2.7	0.8	67.0	18.7	excluded	864	X	X	X	X			
Family-level													
Chick PCA	**3.69**	**1.12**	**61.5**	**18.71**	**included**	**197**	**X**	**X**	**X**	**X**		**X**	**X**
Hatchling PCA	**2.91**	**0.65**	**72.8**	**16.24**	**included**	**207**	**X**	**X**	**X**	**X**			
Chick PCA – non-Passeriformes	3.43	1.13	57.2	18.79	excluded	105	X	X	X	X		X	X
Hatchling PCA – non-Passeriformes	2.72	0.75	68.06	18.63	excluded	105	X	X	X	X			

Table 3. Comparison of the performance of Chick and Hatchling PCA axes (see Table 2) in predicting hatchling tissue maturation (I_P) and two indices of chick growth rate: K_L, a growth constant estimated from logistic growth curves and the t_{10}-t_{90} interval, the growth period between 10% and 90% of asymptotic size. These indices were obtained from Starck and Ricklefs (1998*c*, 1998*b*). We built 3 models for each response variable / PCA combination, and compared the different models using either AIC (for the two growth rate indices) or AICc (for tissue maturation, since the sample size was relatively small for this variable (n = 47)). Since we had several growth rate estimates for some species (n records > n species), we used mixed models including species as a random effect for models with each of the two growth rate estimates as response variables.

Response variable	Explanatory variables	AIC($_c$) for models with Hatchling PCA	AIC($_c$) for models with Chick PCA	n species	n records
Tissue maturation index (I_P)	Body mass, PC1 and PC2	**-113.07**	-96.00	47	47
	Body mass and PC1	-104.89	-97.13		
	Body mass and PC2	-56.37	-56.65		
Growth rate K_L	Body mass, PC1 and PC2	327.86	**307.84**	295	727
	Body mass and PC1	338.37	334.81		
	Body mass and PC2	423.64	417.52		
Growth rate t_{10}-t_{90}	Body mass, PC1 and PC2	56.06	**43.99**	123	198
	Body mass and PC1	67.33	67.14		
	Body mass and PC2	97.49	92.83		

Table 4. Phylogenetic signal and intraclass correlation coefficients (ICC) for order and family levels for the first two components of the Chick PCA (based on 6 traits characterizing chicks at hatching and post-hatching behavior) and of the Hatchling PCA (based on 4 traits characterizing chicks at hatching). CI Inf = lower bound of the 95% credibility interval; CI Sup = upper bound of the 95% credibility interval. The posterior mean of the ICC coefficients is in bold. All coefficients were estimated from mixed models using the MCMCglmm procedure in *R*.

Coefficient	Random effect	Response variable	ICC	CI Inf	CI Sup	n Orders	n Families	n Species
Phylogenetic signal	Phylogeny	PC1 - Chick PCA	**0.9680**	0.961	0.976	37	152	1144
	Phylogeny	PC2 - Chick PCA	**0.9178**	0.887	0.945	37	152	1144
	Phylogeny	PC1 - Hatchling PCA	**0.9349**	0.927	0.947	39	201	1936
	Phylogeny	PC2 - Hatchling PCA	**0.9042**	0.888	0.919	39	201	1936
Order ICC	Order	PC1 - Chick PCA	**0.9103**	0.876	0.949	37	152	1144
	Order	PC2 - Chick PCA	**0.4508**	0.361	0.628	37	152	1144
	Order	PC1 - Hatchling PCA	**0.9445**	0.902	0.960	39	201	1936
	Order	PC2 - Hatchling PCA	**0.7075**	0.616	0.811	39	201	1936
Family ICC	Family	PC1 - Chick PCA	**0.9758**	0.968	0.980	37	152	1144
	Family	PC2 - Chick PCA	**0.6626**	0.583	0.712	37	152	1144
	Family	PC1 - Hatchling PCA	**0.9740**	0.968	0.979	39	201	1936
	Family	PC2 - Hatchling PCA	**0.8633**	0.831	0.884	39	201	1936
ICCs for family and order included in the same models	Order	PC1 - Chick PCA	**0.9010**	0.837	0.962	17	132	1029
	Family		**0.0586**	0.029	0.124			
	Order	PC2 - Chick PCA	**0.2283**	0.002	0.450	17	132	1029
	Family		**0.3804**	0.260	0.594			
	Order	PC1 - Hatchling PCA	**0.9212**	0.844	0.964	17	179	1775
	Family		**0.0578**	0.025	0.115			
	Order	PC2 - Hatchling PCA	**0.5531**	0.359	0.761	17	179	1775
	Family		**0.3082**	0.167	0.473			

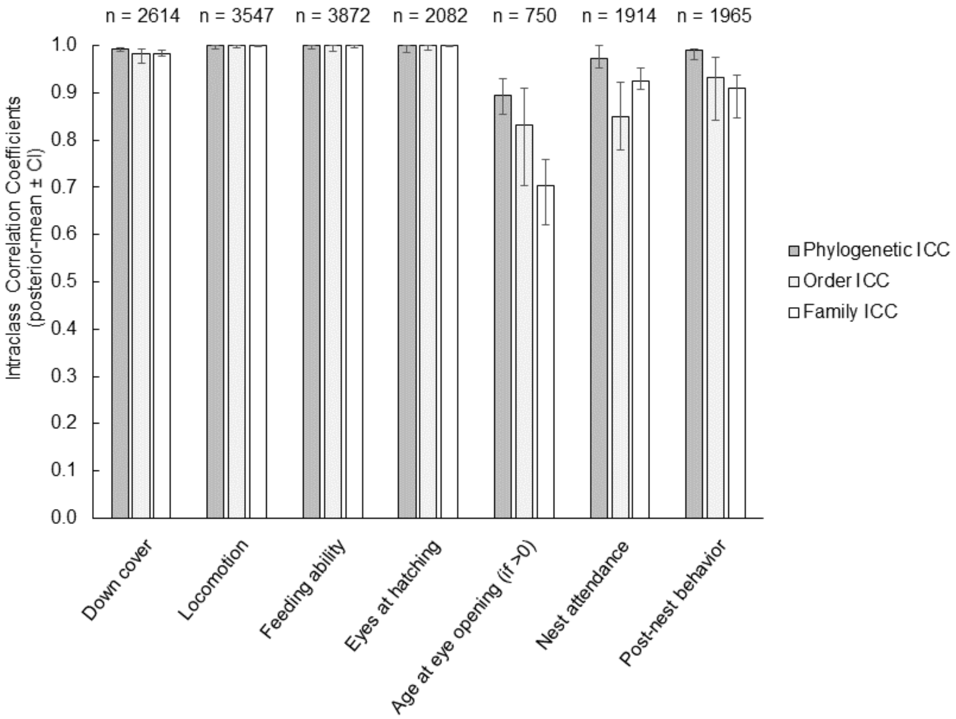
Table 5. Description of developmental mode indices and guideline for their use in comparative studies. Note that these indices were calculated at both the species and family levels – authors should select species- or family-level indices depending on the scale of taxonomic variation they are interested in.

	Description	General use	Examples
Chick PC1	segregates species that are less mature at hatching and leave their nest close to the age of first flight (negative scores), from species with more mature hatchlings that leave their nest long before being able to fly (positive scores)	Chick PC1 should be used when a unique quantitative estimate of developmental mode is needed. It is the most integrative index of avian developmental mode, representing the highest proportion of variance across 6 traits	test how developmental mode constrains variation in life history strategies
Chick PC2	segregates species that are either independent or able to follow their parents after leaving the nest (negative scores) from species that stay in the nest area after leaving their nest (positive scores)	Both Chick PC1 and Chick PC2 should be considered for analyses aiming to include maximal variation in hatchling and post-hatching traits	test whether post-nest behavior has effects that are additive to or confounded with global developmental mode on, e.g., growth rate or chick survival
Hatchling PC1	segregates species that are less mature at hatching (negative chick PC1 scores) from species with more mature hatchlings	Hatchling PC1 captures most of the variation in hatchling traits and should be selected when a unique quantitative estimate of hatchling maturity (but not post-hatching traits) is required	test how hatchling maturity affects nesting and brooding behavior
Hatchling PC2	segregates species that are fully covered with down but unable to feed on their own (positive scores) from species that either hatch naked or hatch covered with down but are able to feed alone (negative scores)	Both Hatchling PC1 and Hatchling PC2 could be included in analyses aiming to include maximal variation in hatchling traits; however, note the low eigenvalue (0.5) and % of variance (13%) explained by Hatchling PC2, making this PC challenging to directly interpret	

Note: For authors aiming to compare the importance of hatchling maturity vs. both hatchling maturity and post-hatching traits, analyses should compare models considering Chick PC1 (or both Chick PC1 and Chick PC2) with models considering Hatchling PC1 (or both Hatchling PC1 and Hatchling PC2). See our example in the main text, comparing the effects of these PCs on growth rate and hatchling tissue maturation.

Figure 1. Contrasting states of development on the day of hatching in three species of birds. Left: the Wood Duck (*Aix sponsa*; Anseriformes: Anatidae) hatches with open eyes, fully covered with down, leaves the nest soon after hatching, and is immediately able to swim and feed by itself. Middle: the Brown Noddy (*Anous stolidus*; Charadriiformes: Laridae) hatches with open eyes and fully covered with down, but stays in or around the nest until fledging and is fed by its parents. Right: the American Robin (*Turdus migratorius*; Passeriformes: Turdidae) hatches blind with sparse down on its upperparts, stays in the nest until fledging, and is fed by its parents (photo credits: SD).

Figure 2. Phylogenetic signal and intraclass correlation coefficients (ICC) for family- and order-level clades for seven traits characterizing birds at and shortly after hatching. **a)** Phylogenetic signal, order ICC, and family ICC calculated from the entire dataset (number of species indicated on top of the bars). **b)** Family ICC in non-Passeriformes and Passeriformes (number of species indicated on top of the bars). The variable *age at eye opening* excludes species for which eyes were already open on hatching day, since the variable *eyes at hatching* already differentiates between species hatching with eyes open or closed. Values provided are posterior means ± credibility intervals, calculated from (phylogenetic) GLMMs built with MCMCglmm. The different subsets of data provided remarkably similar results. We thus present the results of models considering the largest number of species, i.e. all species with information for the trait of interest, including species that were not included in the phylogeny.


n = 2614
n = 3547
n = 3872
n = 2082
n = 750
n = 1914
n = 1965
Intraclass Correlation Coefficients (posterior-mean ± CI)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Down cover
Locomotion
Feeding ability
Eyes at hatching
Age at eye opening (if >0)
Nest attendance
Post-nest behavior
Phylogenetic ICC
Order ICC
Family ICC

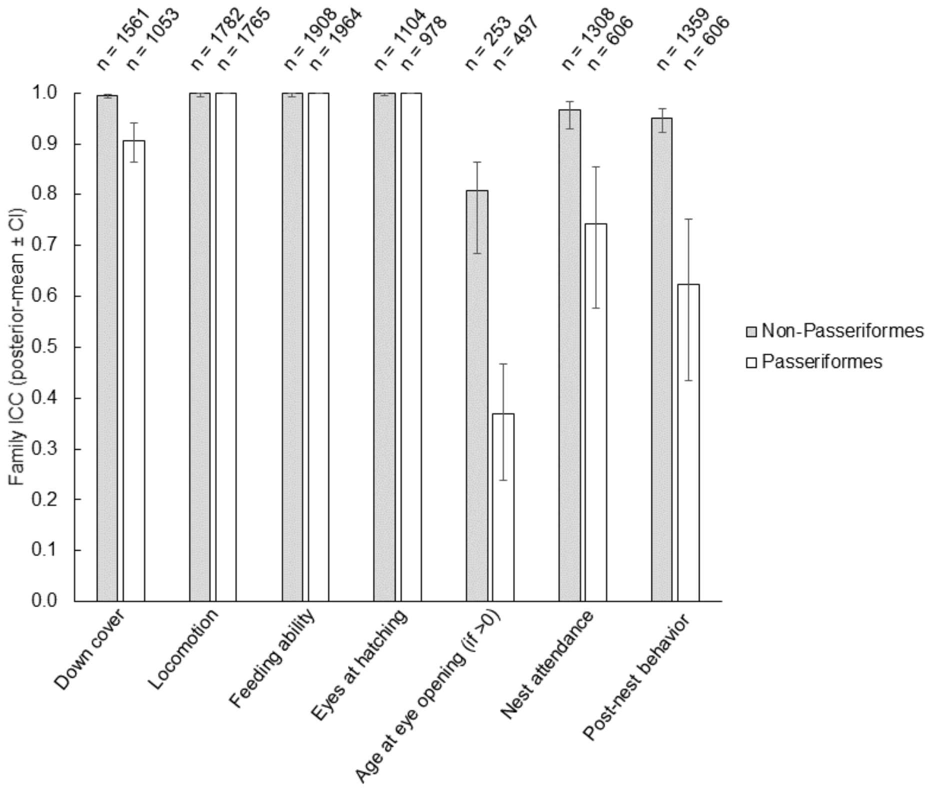
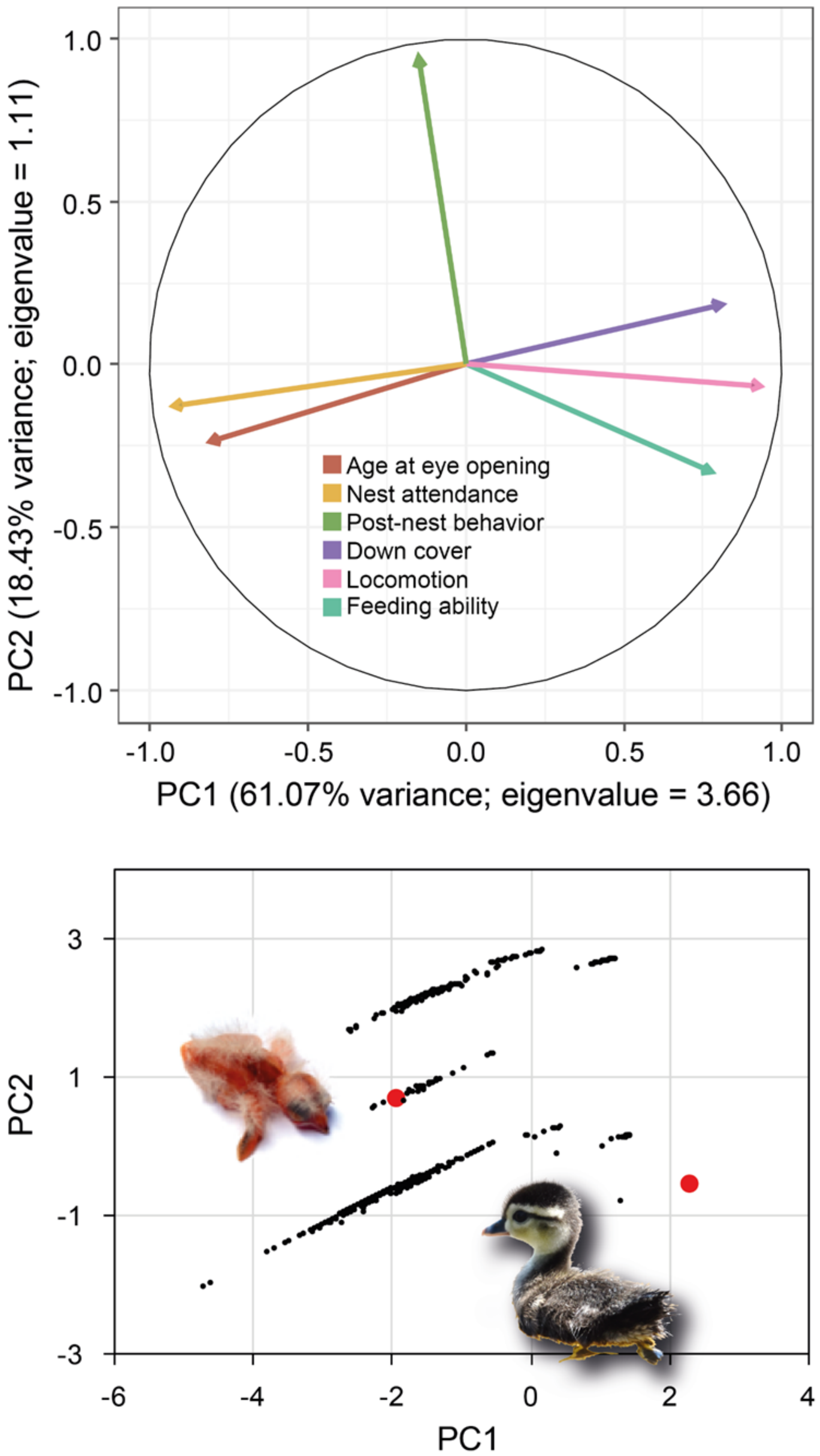
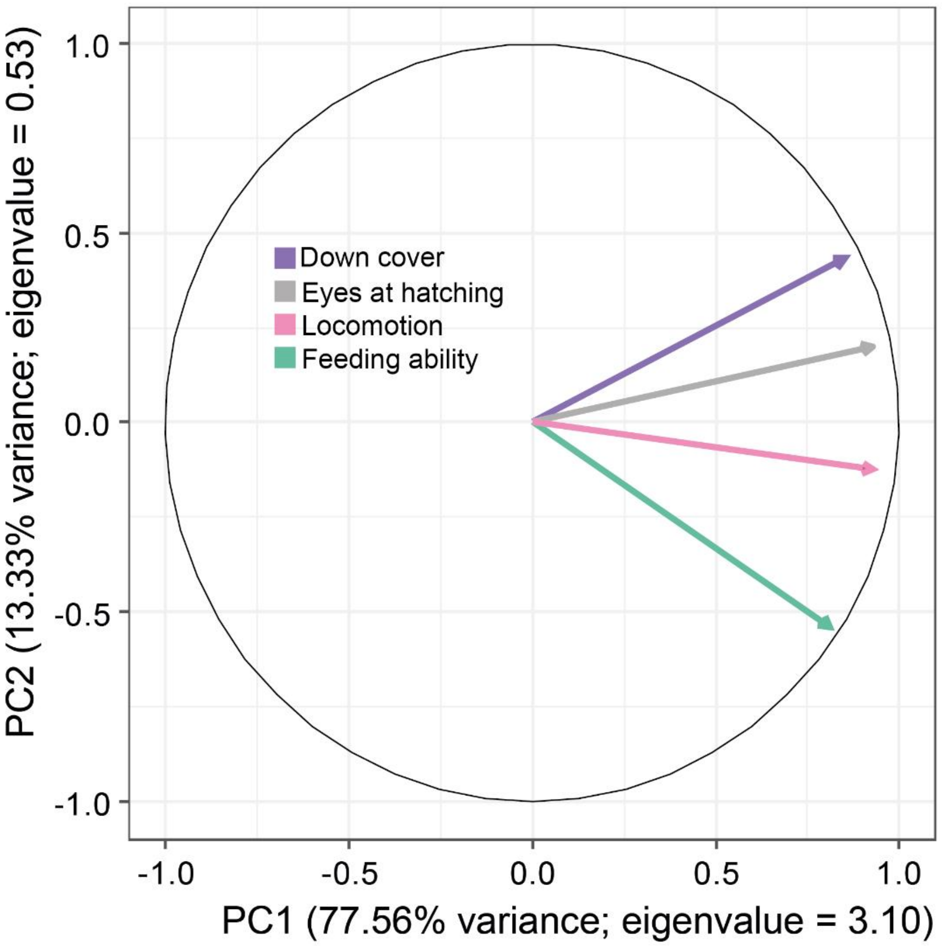

n = 1561
n = 1053
n = 1782
n = 1765
n = 1908
n = 1964
n = 1104
n = 978
n = 253
n = 497
n = 1308
n = 606
n = 1359
n = 606
Family ICC (posterior-mean ± CI)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Down cover
Locomotion
Feeding ability
Eyes at hatching
Age at eye opening (if >0)
Nest attendance
Post-nest behavior
Non-Passeriformes
Passeriformes

Figure 3. Principal component analyses (PCAs) on traits characterizing bird species at and/or shortly after hatching. **a)** Species-level Chick PCA based on six traits characterizing hatchlings and post-hatching behavior (n = 1,144 species) – note that the apparent distribution of species along three discrete bands is explained by post-nest behavior, an ordinal variable with three states (varying from 0 to 2), which is the main contributor to Chick PC2; **b)** Species-level Hatchling PCA based on four traits characterizing hatchlings (n = 1,936 species). Shown here are variable projections (top) and species coordinates (bottom). The eigenvalue and % of variance explained by each principal component (PC1 and PC2) are also shown. See text and Table 2 for details. Note that several species are often represented by a single point as they may combine the same scores for every trait included in a given PCA (i.e., fewer than 1,936 discrete data points are visible due to overlap of identical scores). This is especially true for PCAs based on fewer variables (e.g., panel b). The photo insets provide examples of birds on their hatching day, illustrating variation in hatchling traits across species; species represented by photo insets are indicated with a red dot. Photo insets: *a) right*, a Wood Duck *Aix sponsa* (Anseriformes: Anatidae); *a) left* a Red-winged Blackbird *Agelaius phoeniceus* (Passeriformes: Icteridae); *b) right* a Hooded Merganser *Lophodytes cucullatus* (Anseriformes: Anatidae); *b) left* an American Robin *Turdus migratorius* (Passeriformes: Turdidae) (all photo credits: SD). We re-ran these PCAs considering different subsets of species and obtained remarkably similar results (see Supp. Fig. 1).

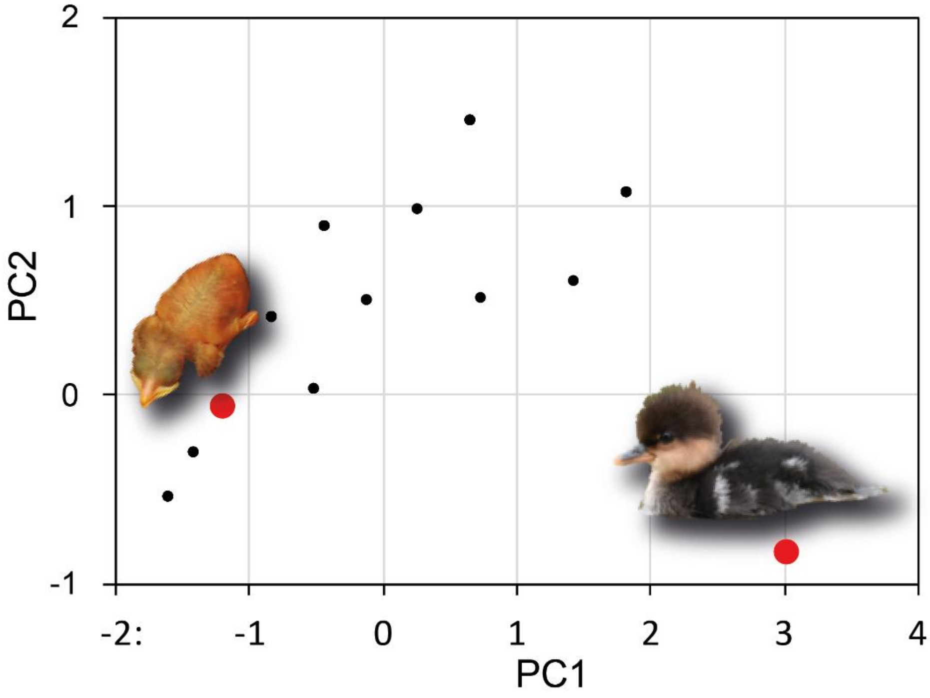


1.0
0.5
0.0
-0.5
-1.0
PC2 (18.43% variance; eigenvalue = 1.11)
-1.0
-0.5
0.0
0.5
1.0
PC1 (61.07% variance; eigenvalue = 3.66)
Age at eye opening
Nest attendance
Post-nest behavior
Down cover
Locomotion
Feeding ability
3
1
-1
-3
PC2
-6
-4
-2
0
2
4
PC1

a)



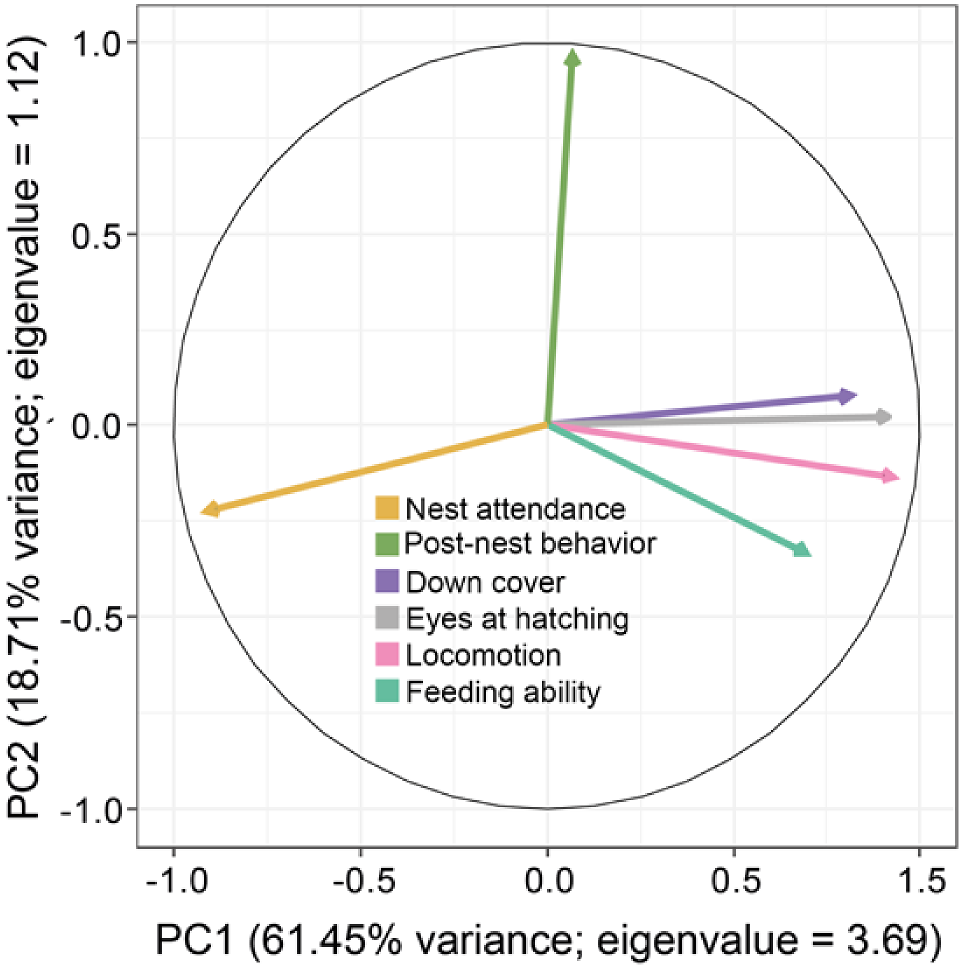
Down cover
Eyes at hatching
Locomotion
Feeding ability
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
PC2 (13.33% variance; eigenvalue = 0.53)
PC1 (77.56% variance; eigenvalue = 3.10)

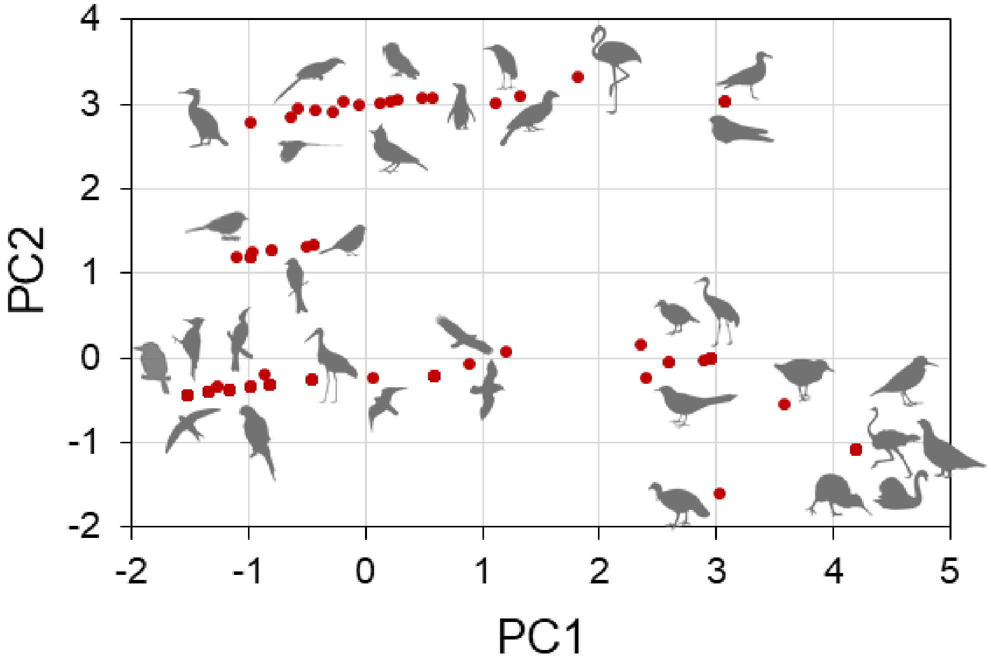


2
1
0
-1
PC2
-2:
-1
0
1
2
3
4
PC1

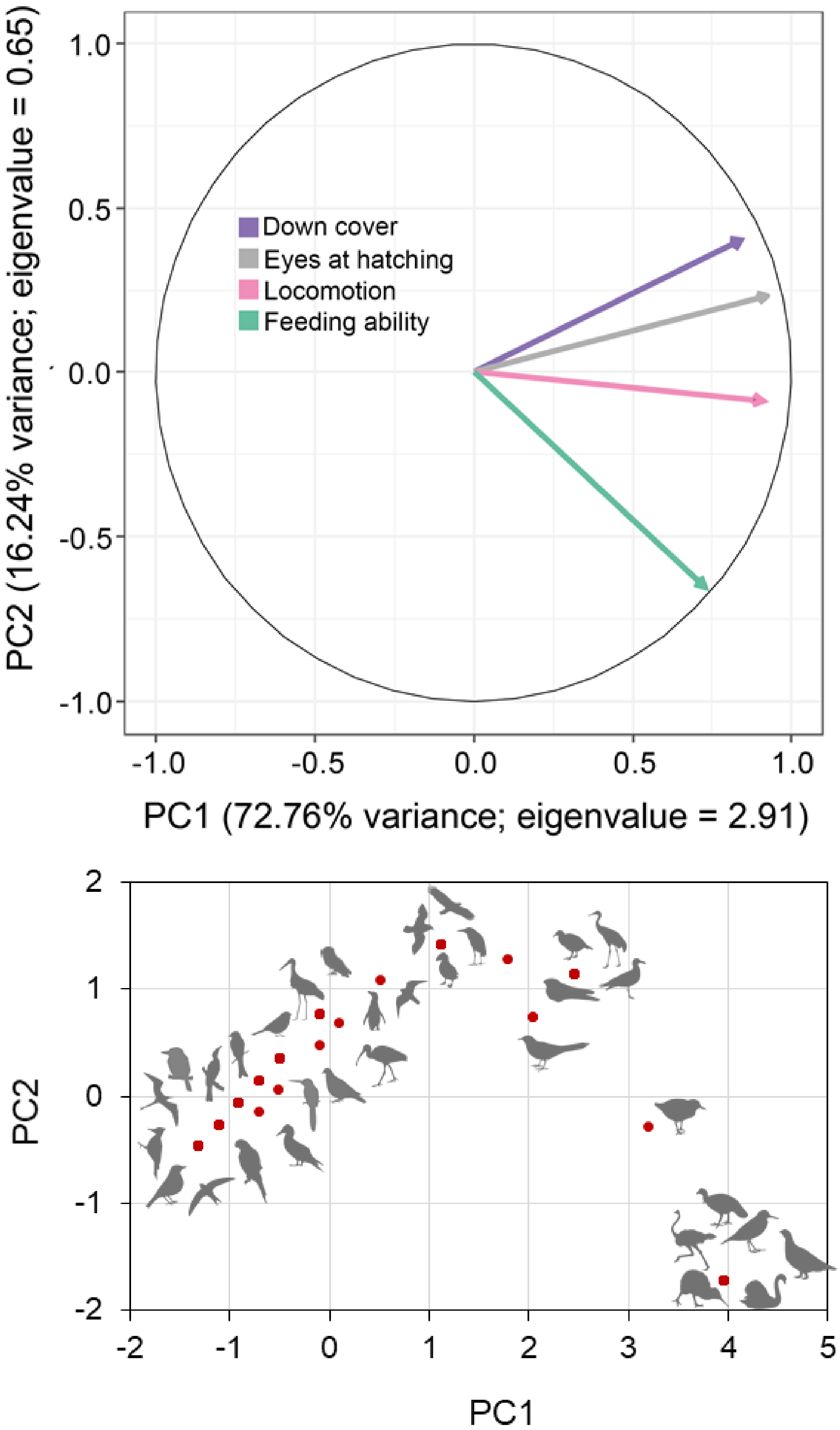
b)

Figure 4. Principal component analyses (PCAs) on traits characterizing bird families at and/or shortly after hatching. **a)** Family-level Chick PCA based on six traits characterizing hatchlings and post-hatching behavior (n = 197 families); **b)** Family-level Hatchling PCA based on four traits characterizing hatchlings. Shown here are variable projections (left) and family coordinates (right). The eigenvalue and % of variance explained by each principal component (PC1 and PC2) are also shown. See text and Table 2 for details. The PCAs were built using different subsets of families which provided remarkably similar results (see Supp. Fig. 1). Silhouettes on the right panel illustrate the position of some family-level clades. All are under a public domain license from phylopic.org. Alternative versions of the same figures providing family names instead of silhouettes on the right panels are provided in Supp. Fig. 1.


1.0
0.5
0.0
-0.5
-1.0
PC2 (18.71% variance; eigenvalue = 1.12)
-1.0
-0.5
0.0
0.5
1.5
PC1 (61.45% variance; eigenvalue = 3.69)
🟧 Nest attendance
🟩 Post-nest behavior
🟪 Down cover
⬜ Eyes at hatching
🟥 Locomotion
🟩 Feeding ability


4
3
2
1
0
-1
-2
PC2
-2
-1
0
1
2
3
4
5
PC1

a)


Down cover
Eyes at hatching
Locomotion
Feeding ability
PC2 (16.24% variance; eigenvalue = 0.65)
PC1 (72.76% variance; eigenvalue = 2.91)
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
PC2
PC1
2
1
0
-1
-2
-2
-1
0
1
2
3
4
5

b)

Supplementary Materials

Supplementary Material 1: Selected examples of variation in avian developmental traits. Studying the evolution of traits that exhibit high phylogenetic signal can be especially challenging since trait variation and phylogeny are mostly confounded. To help disentangle these factors, we have identified notable exceptions and portions of the phylogeny where intraclade variation in developmental traits is more pronounced. We hope these examples will provide relevant targets for future studies aiming to identify selective pressures acting on the evolution of avian developmental traits. Although we highlight several notable examples here, additional examples can be found in our full dataset.

Supplementary Material 2: Full list of the references used to build the dataset.

Supplementary Material 3: Additional methods

Phylogenetically-corrected PCAs: We also conducted phylogenetically-corrected PCAs using the 'phyl.pca' procedure from the phytools package (Revell 2012), but these yielded particularly inconclusive outputs with some variables that are obviously correlated estimated to be independent and projecting on different axes. For example, feeding ability and eyes at hatching are unlikely to be independent of one-another as all species hatching with closed eyes are fed by their parents, yet these variables projected on different phylogenetically-corrected PCA axes. Such artefactual outputs are likely the result of the extremely high phylogenetic signal of most of the traits included in the PCAs, making it particularly challenging to take phylogenetic non-independence into account while identifying meaningful associations among traits. In addition, although the axes obtained with phylogenetic PCAs are phylogenetically transformed, the scores are not, making them generally difficult to interpret (see also Uyeda et al. 2015, Collyer and Adams 2021). For the sake of concision, we do not present the results of these phylogenetic PCAs (see discussion).

Collyer, M. L., and D. C. Adams. 2021. Phylogenetically aligned component analysis. Methods in Ecology and Evolution 12:359–372.

Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–223.

Uyeda, J. C., D. S. Caetano, and M. W. Pennell. 2015. Comparative analysis of principal components can be misleading. Systematic Biology 64:677–689.

Supplementary Figure 1. Figures illustrating species-level PCAs (see Table 2 in the main text). Both variable projections (left panel) and species graphs (right panel) are shown for each PCA. Each set of figures illustrates a different PCA: **1a)** illustrates the Hatchling PCA on a dataset reduced to the same taxon sample as the Chick PCA (see Table 2); **1b)** illustrates the Chick PCA when excluding Passeriformes; **1c)** illustrates the Hatchling PCA when excluding Passeriformes, and **1d)** illustrates the Hatchling PCA on a dataset reduced to the same taxon sample as the Chick PCA and excluding Passeriformes. As with Figure 3 (see main text), on the species graphs, note that a single dot often represents several species if they share the exact same set of trait scores.

Supplementary Figure 2. Figures illustrating family-level PCAs (see table 2 in the main text). Both variable projections (left panel) and family coordinates (right panel) are shown for each PCA. Each set of figures illustrates a different PCA: **2a)** same as Figure 4a, but providing family names instead of silhouettes; **2b)** same as Figure 4b, but providing family names instead of silhouettes; **2c)** illustrates the Chick PCA when excluding passeriform families and **2d)** illustrates the Hatchling PCA on a dataset reduced to the same taxon sample as the Chick PCA and excluding passeriform families. Note that, on the family graph, a single dot often represents several families if they share the exact same set of trait scores.

Supplementary Table 1: **Description of the scoring methodology for each of the variables describing hatchling characteristics and post-hatching conditions.** Note that only some examples are listed; for a more exhaustive list, see the Supplementary Dataset.

Supplementary Table 2: Phylogenetic signal and intra-class coefficients (ICC) for family-level and order-level analyses (either included in separate models, or together in the same model) for seven traits describing birds soon after hatching. In these tables, we present the results of the same analyses as presented in Figure 2, but on different subsets of species. **2a**: Only species with complete trait data are included. This includes species that were not listed in the phylogeny, which were assigned the same tips as their closest relatives included in the tree. **2b**: All species with any trait information are included, but species that were not listed in the phylogeny are excluded. **2c**. Only species with complete trait data are included, and species that were not listed in the phylogeny are excluded. **2d**. Passeriformes are excluded, all non-Passeriformes with any trait information are included, including those not included in the phylogeny. **2e**. Passeriformes are excluded, only non-Passeriformes with complete trait data are included and species that were not listed in the phylogeny are included. **2f**. Passeriformes are excluded, all non-Passeriformes with any trait information are included except species that were not listed in the phylogeny, which are excluded. **2g**. Passeriformes are excluded, only species with complete trait data are included, except species that were not listed in the phylogeny, which are excluded. **2h**. Non-Passeriformes are excluded, all Passeriformes with any trait information are included, including those that were not included in the phylogeny. **2i**. Non-Passeriformes are excluded, only Passeriformes with complete trait data are included and species that were not included in the phylogeny are included. **2j**. Non-Passeriformes are excluded, all Passeriformes with any trait information are included except species that were not included in the phylogeny which are excluded. **2k**. Non-Passeriformes are excluded, only species with complete trait data are included, except species that were not listed in the phylogeny, which are excluded.

Supplementary Dataset 1. Dataset including 4,041 different bird species used for the analyses, including raw data for 7 hatchling and post-hatching traits.

Supplementary Dataset 2. Quantitative indices of developmental modes estimated for 9,993 species listed in the taxonomy from Jetz et al. (2012). The principal components of the Hatchling and Chick PCAs are provided, estimated both at the species and family level.