The evolutionary convergence of avian lifestyles and their constrained co-evolution with species' ecological niche

Paola Laiolo[1,2*], *Javier Seoane*[3], *Juan Carlos Illera*[1], *Giulia Bastianelli*[1], *Luis María Carrascal*[4], *José Ramón Obeso*[1]

[1] *Research Unit of Biodiversity (UO, CSIC, PA), Universidad de Oviedo, 33600 Mieres, Spain*

[2] *Department of Life Sciences and Systems Biology, Universitá di Torino, 10123 Torino, Italy*

[3] *Terrestrial Ecology Group, Departamento de Ecología, Universidad Autónoma de Madrid, 28049 Madrid, Spain*

[4] *Museo Nacional de Ciencias Naturales (MNCN-CSIC), 28000 Madrid, Spain*

Short Title: Evolutionary convergence of life histories

[*] Corresponding author: Paola Laiolo, paola.laiolo@csic.es

Abstract

The fit between life histories and ecological niche is a paradigm of phenotypic evolution, also widely used to explain patterns of species co-occurrence. By analyzing the lifestyles of a sympatric avian assemblage we show that species' solutions to environmental problems are not unbound. We identify a life-history continuum structured on the cost of reproduction along a temperature gradient, as well as habitat–driven parental behaviour. However, environmental fit and trait convergence are limited by niche filling and by within-species variability of niche traits, which is greater than variability of life histories. Phylogeny, allometry and trade-offs are other important constraints: lifetime reproductive investment is tightly bound to body size and the optimal allocation to reproduction for a given size is not established by niche characteristics but by trade-offs with survival. Life histories thus keep pace with habitat and climate but under the limitations imposed by metabolism, trade-offs among traits and species' realized niche.

Key-words: Life-history trade-offs, phylogenetic comparative method, realized niche, reproductive allocation

1. Introduction

The relationship among life histories, physiology, phylogeny and niche characteristics is central to understanding not only how phenotypes evolve with the environment and connect with energy fluxes and material cycles [1,2], but also patterns of species distribution and co-occurrence [3]. Classically, this relationship has been analyzed in terms of the biotic and abiotic processes that fuel the diversity of life history strategies and the intrinsic structural rules that bind them. The main objective has been to identify either the former or the latter, and less frequently their interaction, an intricate task in natural communities cloaked in environmental and biological complexity. One of the most intuitive constraints is the basic allometric rule that places life history differentiation along the so-called mouse-to-elephant, or yeast-to-sequoia, axis. Larger species have longer life spans and generation times as it takes longer for large species to grow, but lower specific allocation in reproduction and slower relative growth rates [4]. For some traits, the relationship to body size has a predictable shape: growth or the rate of reproductive mass production have been shown scale approximately to 3/4 power of body size, as predicted for metabolic rates by the Metabolic Theory of Ecology [2,5]. The 3/4 power scaling is based on the idea that a fractal-like branching network supplies resources to cells [2], while rates proportional to surface area or structural body volume should result in an exponent ranging from 2/3 to 1, as predicted by the theory of Dynamic Energy Budgets [6].

However, substantial deviations from equations are produced by characteristics of a species' ecological niche, such as interspecific competition [7] and trophic specialization [8], but also by trade-offs in the allocation of limited resources among competing functions [9]. These trade-offs impinge upon a second dimension of life-history variation, the cost of reproduction, i.e. the reduction in future reproduction or survival resulting from current

investment in reproduction [10,11]. Hence, at a similar body size, organisms that develop slowly and die older tend to allocate less to reproduction than those with short maturation and lifespan. At the level of species, this dynamic linkage is also known as the slow-fast lifestyle continuum or pace-of-life syndrome, rooted in the classic concept of *r*/*K*-selection [12]. Within this general framework, the evolutionary history of lineages is a potential constraint dictating the options for differentiation, and traits of more closely related species often display similar patterns of variation [13,14]

It is along these axes that natural selection operates. Components of the species' ecological niche, such as habitat structure, food supply, predation, disease or physical stresses favor different lifestyles and combinations of life histories, and foster their variation. Two major extrinsic drivers have been suggested for explaining (or maintaining) the life history continuum: food predictability and mortality patterns. Unpredictable resources such as food and light, and high mortality attributable to external factors, tend to favor fast growth, high reproduction rates and risky lifestyles [15,16]. The investment in parental care and self-maintenance reflects responses to perceived risks and environmental stresses: high juvenile mortality or reduced recruitment may yield greater allocation in offspring quality than quantity, while the opposite may hold for high adult extrinsic mortality [17,18].
Several comparative studies on animals have analyzed, mostly separately, the above-mentioned eco-evolutionary processes. However, the relative influences of trade-offs in allocation of limited resources, specific environmental variables such as climate and habitat, scaling relationships and competition for niche space have rarely been addressed and combined in empirical works on life history evolution. Trade-offs among traits, especially those between reproduction and survival, can cause deviations in allometric equations of reproductive biomass production rates if, for instance, resources are saved from reproduction and redirected to self-maintenance, and thus future reproduction, in large or long-lived

species. In these conditions, we expect that a measure of investment that accounts for energy allocated to self-maintenance should fit equations better than that of reproductive biomass production rate per year. Moreover, when studying the ecological context of life history evolution, the limitation imposed by local competitors on species distribution is an important source of deviation from optimality, though most life history thinking is based on the assumption that species occupy their fundamental niche. Competition among species can distort our appreciation of phenotype-habitat matching in old environments, in which niche filling has taken place through immigration from the outside (e.g. continental areas) rather than having been generated *in situ* (e.g. volcanic islands) [19].

In this study, we adopt the approach of considering all species in a sympatric assemblage for studying the degree of differentiation of life history traits. We examined whether the influence of the above listed pathways of life history differentiation can be distinguished in a pool of almost one hundred breeding birds broadly differing in size and pace of life, and in which congeners tend to segregate spatially. We deconstruct an elevation gradient into its climate and habitat clines of variation, as indicators of environmental harshness, disturbance and productivity [18,20], and address their influence on the rate of reproductive biomass production, egg number and weight, life expectancy and parental care attributes. We used phylogenetic comparative methods that model stabilizing selection around optima modelled on environmental variables that change over time, because these capture realistically the relationship between traits and environmental agents of selection [14,21,22]. Although we focus on interspecific patterns, we accounted for intraspecific variability, i.e. trait variance and covariance within species, since the differentiation of populations through local adaptation is an inherent aspect of niche and life history evolution [23]. This is especially true along elevation gradients, which fuel intraspecific adaptive differentiation [24-26]. We test the following: (i) Whether the allometric exponent

approximates 0.75 for the slope of the regression line between body mass and reproductive productivity [2]. (ii) Whether the annual investment in reproductive traits is higher where unreliable food resources are available, or higher risk of predation is perceived [27], and if low levels of habitat-dependent predation-risk can prolong parental care [16,18]. (iii) Whether trade-offs among traits and limiting similarities among co-existing species condition the degree of allometric and environmental fit, in terms of adjustment to allometric equations, rates of adaptation, and contribution of environmental variation. For the latter, we split the dataset and its phylogeny into two groups: one formed by species that do not coexist with a congener in this species pool (with a phylogeny with deeper branches) and another that groups congeneric species, with higher levels of biological similarity and presumably also interspecific competition. In comparative studies, the usual way to test the robustness of inferences is to statistically transform phylogeny branch lengths and simulate trait measurement errors [28,29]. We perform this exercise with natural variances and biologically-transformed phylogenies, to test assumptions and predictions that were formulated neglecting these aspects.

2. Methods

Ecological characteristics were obtained for 94 species of a terrestrial avian community breeding in NW Spain, which includes common birds of the western Palearctic that assembled by immigration from outside the region. Bird ecological niche was studied in the field along a wide environmental gradient, in an area of 16,000 km^2 ranging from 120 to 2,620 m in elevation. Here deciduous forests, shrubberies, grasslands, rocks and screes are the main habitat types (ESM, figure S1). A total of 2,347 survey plots of 3.14 ha each were established, in which we recorded the abundance of birds, elevation and habitat characteristics. For each species, we calculated the average covers of forest, grassland, shrub and rocks in occurrence plots, where we also estimated the average annual temperature and

its range, and the annual accumulated precipitation and its range (details in the ESM, table S1). The variance associated with these averages was also estimated. These continuous descriptors were used as indicators of variation in selective regimes to infer phenotypic adaptation.

Ideally, we should estimate life history and phenotypic traits *in situ* as well, but this is notoriously difficult for even a single species. We mostly used published information on mean adult mass and life history traits of birds of the western Palearctic (see the ESM, table S2). We also accounted for the average migration distance and its variance, since migration strategy is an important driver of avian life histories [8]. Life histories were quantified in terms of eggs laid per year (clutch size × brood number), egg mass, the rate of reproductive biomass production per year (hereafter productivity, egg mass × clutch size × brood number; [8]), time (per year) spent incubating (time to hatching × brood number), time (per year) spent caring for nestlings (time from hatching to fledging × brood number), and reproductive life expectancy. The latter was estimated as [2-(1-adult survival)]/2 × (1-adult survival) [30] and was used as a measure of lifespan instead of maximum longevity, because it is less sensitive to sampling effort as it is based on capture-recapture survival models [albeit the two lifespan proxies are highly correlated ($r_S = 0.6$, $t_{74} = 6.19$, $p < 0.001$)]. The lifetime production of reproductive biomass was obtained as the product of life expectancy and the annual rate of reproductive biomass production.

We obtained mean trait values for all species (94) with the exception of life expectancy, known only for 77 species; variance values were obtained for all body mass and reproductive variables, and for 63% - 85% of the species for the rest of the variables (ESM, table S2). Missing variances were substituted with the average variance of the rest of the species [31]. Variances were either obtained from the literature on a single population (the case for survival estimates) or calculated using population trait values reported for each species (the

remaining phenotypic variables) (ESM, table S2). The variance of variables that are the product of traits (e.g. egg number, annual and lifetime productivity, incubation and nestling times) was calculated by summing trait variances and covariances within species, with the following formula (an example for two traits): $\sigma^2_{1\times2} = \frac{\sigma_1^2}{\mu_1^2} + \frac{\sigma_2^2}{\mu_2^2} + 2 \cdot \frac{\sigma_1}{\mu_1} \cdot \frac{\sigma_2}{\mu_2} \cdot \rho_{12}$; where σ_1 and σ_2 are the standard deviations and μ_1 and μ_2 the means of variable 1 and 2, and ρ_{12} is their coefficient of correlation [32]. We obtained the correlation coefficient for 6 - 8 species per trait, and the average of species' values was used for species in which the correlation was unknown. Notably, we found that ρ differed significantly from zero in the case of egg weight vs. clutch size, and clutch size vs. survival only (ESM, table S2). All variables were $\log_{10}$-transformed to attain a normal distribution, estimate allometric coefficient appropriately and obtain independent variances from the means [33]. This transformation implies that an originally lognormal distribution with variance σ^2 and mean μ is transformed into a normal distribution, with mean = $\mathbf{Log_{10}}\ (\mu^2/\sqrt{(\sigma^2 + \mu^2)}\ )$ and variance = $\mathbf{Log_{10}}\left(1 + \frac{\sigma^2}{\mu^2}\right)$ [31]. The above $\log_{10}$-transformed means and variances were used as trait mean value and measurement error, respectively, in comparative analyses.

To model trait evolution on species phylogeny we downloaded 10,000 trees from www.bird.tree.org [34] for the species included in our dataset. We chose the backbone tree based on Ericson et al. [35] to obtain a 50% majority rule consensus tree in which branch length is represented by the proportion of nucleotide substitutions (ESM, figure S2). Being a sympatric assemblage of species, the phylogenetic relationship among them should capture differentiation mechanisms limited by niche similarities [19]. We first quantified the

influence of phylogeny on variation in each trait by means of *K* statistics [28], to assess whether traits conserved a phylogenetic signal and whether predictors (body mass, migration strategy and ecological parameters) were not changing too fast with respect to the rate of adaptation of life histories, a condition in which adaptive variation cannot take place [22]. When *K* approaches 1, trait evolution follows a purely neutral, drift-mutation model (also known as Brownian motion (BM) model) in which the differentiation between lineages increases with the time since they diverged (the longer the time, the greater the change). When $K < 1$ closely related species are less similar than expected because rates of evolution are fast under strong directional or disruptive sexual selection [36], or stabilizing selection hampers deviations through time from optimal trait values (a case of the Ornstein-Uhlenbeck (OU) process) [37]. When $K > 1$, close relatives are more similar than expected under a purely neutral model of evolution [28].

Allometric scaling of annual and lifetime productivity was estimated by phylogenetic regressions weighting differences in variances due to within-species variation in both productivity and body mass. We followed the methods proposed by Ives et al. [31] and Hansen & Bartoszek [38], which differently account for predictor variance [39].We then analyzed the determinants of life history optima in the traits that were less constrained by phylogeny (egg number, life expectancy, incubation and nestling times, see Results). We modeled variation as a sum of the random noise and a deterministic pull toward particular states determined by niche characteristics, migration distance, and allometry with body mass, again accounting for trait variance [22,37]. The linear influence of predictors was not assessed on traits but on the 'primary' optima, the optimal states where all ancestral constraints were lost following an OU process [37]. The OU model mathematically expresses an evolutionary process in the presence of natural selection, in which different lineages, or successive branches within a lineage, are subject to the same selective regime (e.g. a common

environment) [21]. It expresses the change in trait X by time t as $dX(t)= -\alpha[X(t) -\theta]dt + s\,dB(t)$, where α measures the rate of adaptation towards the optimum trait value θ, $X(t)$ is the current trait value, s is the standard deviation of random change and $dB(t)$ is white (random) noise dB by time t [37]. When the current trait approaches the optimum, adaptation to a particular niche has taken place [22,37]. The adaptive potential of a trait can be predicted by its adaptation rate α, which measures the rate of adaption contingent on all past niche influences. It can be also appreciated by comparing the relationship of the trait with predictors under the influence of both adaptation and phylogenetic inertia (evolutionary regression) with the relationship free of phylogenetic constraints, in which the trait evolves fast enough to adjust to predictor changes (optimal regression) [22]. A possible explanation for why optimal regressions are steeper than evolutionary regressions is that the trait in question is undergoing strong directional selection but is highly constrained, for instance because it concurrently keeps pace with other traits [14]. Poor environmental fit can also occur in species occupying their realized niche, rather than the environment maximizing demographic rates in the absence of competition. To envisage these potential mismatches we modeled life history variation and allometric scaling in a dataset that included species that do not co-occur with congeners (44 species), and then in one grouping species of the same genus (50 species) (ESM, figure S2).

To assess the fit of models including different combinations of the predictor variables, we used the Akaike information criterion corrected for sample size (AIC_c), considering as equally probable those models separated by less than two AIC_c points from the model with the lowest AIC_c (i.e. $\Delta AIC_c < 2$ [40]). In models, the contribution of each predictor was based on Type II SS, and the phylogeny was specified to be non-ultrametric. Analyses were done in R 3.2.0 with the packages *ape* [41], *phytools* [42] and *slouch* [43].

3.Results

Variables associated with mass were by far more conserved (K >>1) along the phylogeny than life history and niche traits (K < 1; figure 1). This suggests that the latter traits may have undergone a more remarkable divergence in the terminal branches or, alternatively, may be subject to higher environmental variation (or within species variation) than morphology. Phylogenetic signal was higher among non-congeners than among groups of congeners in mass-related traits, but niche and life histories changed roughly at similar rates in the two assemblages. This result again suggests that these traits may have evolved faster than morphology (interaction assemblage × variable type in a comparison of K indices: $F_{2,28}$ = 3.61, p = 0.04). However, niche traits, unlike life histories, where characterized by large within-species variance in both assemblages (comparisons among the three categories of traits: $F_{2,28}$ = 7.30, p = 0.0028) (figure 1).

Annual productivity increased with body mass, but more slowly than expected: slopes were 0.57 as obtained by the regression method of Ives *et al.* [31], and 0.56 by the method of Hansen & Bartoszek [38], differing significantly from the expected value of 0.75 (t > 5.89, p < 0.001). Remarkably, the optimal regression slope (free of constraints) for annual productivity predicted by the latter method was extremely close to predictions (0.74 ± 0.05 SE), but evolutionary equations also adjusted to this value when productivity was measured across birds' lifespans. Slopes for lifetime productivity were 0.79 and 0.81 according to Ives et al. [31] and Hansen & Bartoszek [38] methods, respectively, and none differed from 0.75 (t < 1.57, p > 0.11) (figure 2). The above results hold when splitting the assemblage, and no significant difference emerged between equations obtained with congeners' and non-congeners' assemblages, either regarding annual productivity (t = 0.17, p = 0.9) or lifetime productivity (t = 1.66, p = 0.1) (table 1).

Life histories with low but significant phylogenetic signal (0 < K < 1) were modeled on niche characteristics, migration distance and body mass. We excluded temperature range

from the predictors, a trait with no phylogenetic signal (figure 1) and thus supposedly too labile for traits to keep pace with [22]. We also excluded accumulated precipitation, which was correlated with the rest of the predictors ($0.22 < r_S < 0.59$; $p < 0.05$). For egg number and life expectancy, adaptive models where optima were determined by body mass, temperature and /or migration distance performed best by AIC_c criteria (ESM, table S3). Thus, large species, breeding in cold climates and migrating long distances, survived longer but laid fewer eggs, while species inhabiting shrub vegetation laid more eggs (figure 3; table 2). The best models explaining the durations of incubation and nestling phases included the positive relationship to body mass and rocky habitats, and also shrub habitats for the former variable (figure 3; table 2; ESM, table S3). Steeper slopes of egg numbers with predictors were expected by the optimal regressions with respect to the relationships constrained by phylogeny (evolutionary regressions), while for the rest of the variables equations largely overlapped (table 2). Adding life expectancy (which trades off with egg number) to the other predictors of egg number increased both adaptation rates ($\alpha = 5.33$) and the match between evolutionary and optimal allometric slopes, as estimated by the dataset of species of known survival (optimal vs. evolutionary slopes of egg number on body mass in models including life expectancy: -0.17 ± 0.06 *vs.* 0.12 ± 0.04; $t = 0.85$, $p = 0.39$; excluding life expectancy: -0.37 ± 0.07 *vs.* 0.19 ± 0.03; $t = 2.04$, $p = 0.04$).

The environmental fit of life history traits, as measured in terms of relative variance explained by predictors, tended to be higher in the assemblage of species that does not coexist with a congener, especially in parental care variables, when centering on the common models that best explained variation in both assemblages (table 1; ESM, table S3). Among non-congeners, egg number and incubation time showed faster adaptation to the environment than groups of congeners (table 1). The opposite occurred for life expectancy and nestling time,

although their adaptation rate was high in both assemblages as compared to that of egg number (table 1, 2).

4. Discussion

We found an echo of historical, physiological and environmental filters in the life histories of this pool of species. Results are in agreement with theoretical predictions for the 3/4 power scaling of reproductive biomass production rates with body mass [2], provided the investment in self-maintenance (measured through life expectancy) is accounted for as a source of expenditure. In spite of a substantial within-species variation in niche traits, our results highlight a certain degree of optimization of life histories, supported by significant relationships between life history optima and habitat or climate aspects of species niche. The match between life history and the environment increases among species that do not share their niche space with a congener, suggesting that competition may limit our appreciation of the environmental fit of traits in natural populations.

The comparison of phylogenetic signal among traits reveals a signal deeply rooted in the phylogeny in the case of mass-related variables, consistent with the hypothesis drawn with dated avian phylogenies of early and rapid body size differentiation followed by competition-driven stasis [19,43]. On the other hand, bird ecological characteristics do not exhibit a strong phylogenetic signal in either terminal (congeners) or in deeper branches (non congeners), although they maintain a significant historical footprint. Niche differences may have evolved later than morphology and may be highly adaptive, but can also depend more on the local ecological context and environmental (i.e. not genetic) variation. The latter hypothesis is substantiated by a variance more than ten-fold that of the rest of the traits, a circumstance that lowers K and agrees with results obtained in other animal groups [28]. The low variances and Ks of life histories suggest instead a pattern of reduced environmental variation but high levels of evolutionary malleability, especially in parental care variables, as

if adaptations to specific conditions involved some but not all members of a lineage. It is worth noting that our sampling protocol may have accentuated differences among variances, since these were derived from population means for body size and most life histories, and from individual values for niche traits. However, the abundant evidence of ecotypic differentiation through species Palearctic distribution [44] and the local extent of niche data, should have limited the magnitude of this bias.

Since productivity traits were strongly influenced by phylogeny and body mass, they were not regressed on niche variables, because the latter are too evolutionarily labile for productivity to track their changes while keeping pace with phylogeny and body mass [14]. However, the difference between the allometric equations of annual and lifetime productivity is informative in that it highlights a link between the compensatory allocation to distinct vital functions, namely the cost of reproduction, and the scaling rules governing resource uptake and redistribution in individual organisms. Sibly & Brown [2] and Sibly *et al.* [7] identified such a link in the annual productivity of birds and mammals, but our results show that the largest birds do not invest in annual reproduction as expected from their size, so that the relationship does not fit expectations in any of the assemblages considered. It is instead the overall reproductive biomass production across bird adult life that that adjusts to predictions, revealing a simple mechanistic link that can be used for quantitative predictions based on life history trade-offs and allometry. As further evidence, adding trade-offs to life expectancy in models of egg number revealed the "optimal" adjustment of egg number to body mass (i.e. the optimal and evolutionary regressions of egg number and body mass coincide), while ecological predictors were unable to demonstrate this (table 2). Future work should however assess the compliance of these relationships with the theoretical framework defined by the chief metabolic theories in ecology, the Metabolic Theory of Ecology and the theory of

Dynamic Energy Budgets, which have different models for maintenance and assimilation parameters [45].

Once accounting for phylogeny and body mass variation, we did find contrasting suites of correlated life histories favored along the environmental gradient. The result of decreasing egg number and increasing life expectancy in birds breeding in colder conditions is in line with results obtained along elevation gradients [27]. Cold climate augments the metabolic requirements of chicks [46] and may drive the evolution of a syndrome of smaller reproductive effort but higher investment per offspring, with implications for juvenile and subsequently adult survival. Life history theory also predicts that environmental uncertainty should foster the allocation in offspring number [11,47], thus explaining why shrubberies, a secondary habitat that undergoes high levels of natural disturbance, are inhabited by species laying large numbers of egg [48]. The balance between present and future reproduction tilts more strongly towards the future (survival) in species migrating longer distances, confirming the trade-off, described in several animal groups, between migration and reproductive investment and its long-term implications for the rest of the life histories [1]. Ultimately, habitat has a relevant influence on parental care traits and we interpret this result as being partly associated with predation risk, which typically differs among habitats and is one of the major determinants of avian parental strategies [18]. The prolongation of parental care is risky since it increases the probability that eggs and young will be preyed upon. Thus, we expect this to evolve when predation pressure on eggs or nestlings is low, or when selection on parents favors the reduction of attentiveness [16]. Most rupicolous species nest in virtually inaccessible cliffs, a behavior that reduces selection for rapid development and high parental nest attentiveness [13].

All in all, these results suggest that the spatial and ecological co-occurrence of species fosters the evolutionary convergence of their life histories. The analysis of life history and

niche differences in the assemblages of congeners and non-congeners, however, suggests that trait values, especially those associated with parental care, are closer to their environmental optimum in the latter assemblage, which includes species of more ancient relationships and reduced similarity. This finding does not obviously imply that congeners display maladaptations, and we also exclude incomplete adaptation and ongoing niche filling, since congeners are not of recent origin, nor have they recently colonized this continental mountain chain. Other factors, we did not consider as implicit predictors, may separate traits from their habitat-driven optima. We point to competition among similar, closely related, species as a candidate factor capable of segregating species that share habitat associations and intrinsic traits. This is because congeners occupy different elevation bands in our study area [20], as in other mountain regions where competition is an important community structuring mechanism [19], but often share life histories [13]. Undoubtedly, we have made simplified assumptions on competition among congeners, and diluted similarities within genera with dissimilarities among them in the analyses. More realistic analyses should explicitly model variation in species that share the greatest similarities, and account for species relative abundances and competition asymmetry. Alternative explanations are indeed plausible, for instance the extreme variability of niche variables, which may *per se* explain the little contribution of environmental variables to life history diversification. To our knowledge, this is the first study on this subject accounting for within-species variation, and thus the first that calls for caution when over- or under-stressing the importance of measurement error in such comparative analyses. Importantly, not all variables have the same variance and significant trends are highlighted even with predictors with large errors (e.g. figure 3), but high levels of environmental variation may undeniably slow down or hamper evolutionary processes of adaptation [49].

In conclusion, we evaluated competing models of life history evolution along species phylogeny and assessed the degree of environmental fit and the lag separating traits from their environment-driven optima. We show that lifetime reproductive biomass production is a good indicator of species' structural limits on metabolic expenditure since it accounts indirectly for the physiological costs of self-maintenance in long-lived species. We also hypothesize that within-species variation and competition for niche space may separate life histories from their habitat and climate-driven optima. Beyond these major constraints and limiting factors, lifestyles appear to have coevolved with species' ecological niche, as an outcome of evolutionary convergence, and this results in guilds of species sharing life histories, and not only similarities in morphology and foraging habits.

Ethics

Bird surveys were done in accordance with national legislation and under permit of access to the protected areas of the Cantabrian Mountains (Picos de Europa National Park: CO/09/0515/2009-10; CO/09/033/2011; CO/08/058/2012; CO/09/016/2013; CO/09/097/2014; Asturias Government: 2008/054047; Cantabria Government: 3501).

Data availability

Datasets are available in the ESM (table S2).

Competing interests

We have no competing interests

Author's contribution

P.L. designed the study. P.L., J.R.O., J.S. performed field work. P.L., J.C.I., J.R.O., G.B., L.M.C. prepared the dataset. P.L. analyzed data and wrote the manuscript, with contributions of the rest of authors.

Acknowledgements

We thank A Segura and L Meléndez for help during fieldwork, S Young for improving the English, JH Brown, SF Dobson and two anonymous reviewers for their useful comments on a former version of the manuscript.

Funding

This work was supported by the Spanish Ministry of Economy and Competitiveness (CGL2009-11302; CGL2011-28177; CGL2014-53899-P; Ramón y Cajal program) and *Fundación Biodiversidad*.

References

1. Roff D. 1992 *Evolution of life histories: theory and analysis*. Springer Science & Business Media.

2. Sibly RM, Brown JH. 2007 Effects of body size and lifestyle on evolution of mammal life histories. *Proc .Natl. Acad. Sci. USA* **104**, 17707-17712.

3. Kraft NJB, Godoy O, Levine JM. 2015 Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl. Acad. Sci. USA* **112**, 797-802.

4. Dobson FS. 2007 A lifestyle view of life-history evolution. *Proc. Natl. Acad. Sci. USA* **104**, 17565-17566.

5. Enquist BJ, West GB, Charnov EL, Brown JH. 1999 Allometric scaling of production and life-history variation in vascular plants. *Nature* **401**, 907-911.

6. Kooijman SALM. 2000. *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press, Cambridge.

7. Muller-Landau HC et al. 2006 Testing metabolic ecology theory for allometric scaling of tree size, growth and mortality in tropical forests. *Ecol. Lett.* **9**, 575-588.

8. Sibly RM et al. 2012 Energetics, lifestyle, and reproduction in birds. *Proc. Natl. Acad. Sci. USA* **109**, 10937-10941.

9. Sibly RM, Grady JM, Venditti C, Brown JH. 2014 How body mass and lifestyle affect juvenile biomass production in placental mammals. *Proc. R. Soc. Lond. Ser. B.* **281** 20132818. ISSN 0962-8452

10. Williams GC. 1966 Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* **916**, 687-690.

11. Stearns SC. 1989 Trade-offs in life-history evolution. *Funct. Ecol.* **3**,259-268.

12. Ricklefs RE, Wikelski M. 2002 The physiology/life-history nexus. *Trends Ecol. Evol.* **17**, 462-468.

13. Bennett PM, Owens IP. 2002 *Evolutionary ecology of birds: life histories, mating systems, and extinction*. OUP, Oxford, United Kingdom.

14. Pienaar J, Ilany A, Geffen E, Yom-Tov Y. 2013 Macroevolution of life-history traits in passerine birds: adaptation and phylogenetic inertia. *Ecol. Lett.* **16**, 571-576.

15. Obeso JR. 2002 The costs of reproduction in plants. *New. Phytol.* **155**, 321-348.

16. Martin TE. 2002 A new view of avian life-history evolution tested on an incubation paradox. *Proc. R. Soc. Lond. Ser. B.* **269**, 309-316.

17. Clutton-Brock TH. 1991 *The evolution of parental care*. Princeton University Press.

18. Martin TE. 1995 Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monog.* **65**, 101-127.

19. Price TD et al. 2014 Niche filling slows the diversification of Himalayan songbirds. *Nature* **509**, 222-225.

20. Laiolo P, Illera JC, Meléndez L, Segura A, Obeso JR. 2015 Abiotic, biotic and evolutionary control of the distribution of C and N isotopes in food webs. *Am. Nat.* **185**, 169-182.

21. Butler MA, King AA. 2004 Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *Am. Nat.* **164**, 683-695.

22. Hansen TF, Pienaar J, Orzack SH. 2008 A comparative method for studying adaptation to a randomly evolving environment. *Evolution* **62**, 1965-1977.

23. Kawecki TJ, Ebert D. 2004 Conceptual issues in local adaptation. *Ecol. Lett.* **7**, 1225-1241.

24. Bastianelli G, Seoane J, Álvarez-Blanco P, Laiolo P. 2015 The intensity of male-male interactions declines in highland songbird populations. *Behav. Ecol. Sociobiol.* **69**, 1493-1500.

25. Laiolo P, Illera JC, Obeso JR. 2013 Local climate determines intra- and interspecific variation in sexual size dimorphism in mountain grasshopper communities. *J. Evol. Biol.* **26**, 2171-2183.

26. Laiolo P, Obeso JR. 2015 Plastic responses to temperature vs. local adaptation at the cold extreme of the climate gradient. *Evol. Biol.* **42**, 473-482.

27. Badyaev AV, Ghalambor CK. 2001 Evolution of life histories along elevational gradients: trade-off between parental care and fecundity. *Ecology* **82**, 2948-2960.

28. Bloomberg SP, Garland T, Ives AR. 2003 Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717–745.

29. Revell LJ, Harmon LJ, Collar DC. 2008 Phylogenetic signal, evolutionary process, and rate. *Syst. Biol.* **57**, 591-601.

30. Botkin DB, Miller RS. 1974 Mortality rates and survival of birds. *Am. Nat.* **108**, 181-192.

31. Ives AR, Midford PE, Garland T. 2007 Within-species variation and measurement error in phylogenetic comparative methods. *Syst. Biol.* **56**, 252-270.

32. Goodman LA. 1960 On the exact variance of products. *J. Amer. Statist. Assoc.* **55**, 708-713.

33. Lande R. 1981 Models of speciation by sexual selection on polygenic traits. *Proc. Natl. Acad. Sci. USA* **78**, 3721-3725.

34. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012 The global diversity of birds in space and time. *Nature* **491**, 444-448

35. Ericson PGP et al. 2006 Diversification of Neoaves: integration of molecular sequence data and fossils. *Biol. Lett.* **2**, 543-547.

36. Gavrilets S. 2000 Rapid evolution of reproductive barriers driven by sexual conflict. *Nature* **403**, 886–889.

37. Hansen TF. 1997 Stabilizing selection and the comparative analysis of adaptation. *Evolution* **51**, 1341–1351.

38. Hansen TF, Bartoszek K. 2012 Interpreting the evolutionary regression: the interplay between observational and biological errors in phylogenetic comparative studies. *Systematic Biology* **61**, 413-425.

39. Garamszegi LS. 2014 Uncertainties due to within-species variation in comparative studies: Measurement errors and statistical weights. In: M*odern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology* (Ed: Garamszegi LS). Springer-Verlag Berlin. Pp: 157-200.

40. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: a practical information-theoretic approach*. Springer Science & Business Media.

41. Paradis E, Claude J, Strimmer K. 2004 APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289-290

42. Revell LJ. 2012 phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217-223.

43. Harmon LJ et al. 2010 Early bursts of body size and shape evolution are rare in comparative data. *Evolution* **64**, 2385-2396.

44. Millien V, Lyons S, Olson L, Smith FA, Wilson AB, Yom-Tov Y. 2006 Ecotypic variation in the context of global climate change: revisiting the rules. *Ecol. Lett.* **9**, 853-869.

45. van der Meer J. 2006 Metabolic theories in ecology. *Trends Ecol. Evol.* **21**, 136-140.

46. Schekkerman H, Visser GH. 2001 Prefledging energy requirements in shorebirds: energetic implications of self-feeding precocial development. *Auk* **118**, 944–957

47. Simons AM. 2007 Selection for increased allocation to offspring number under environmental unpredictability. *J. Evol. Biol.* **20**, 813-817.

48. Böhning-Gaese K, Halbe B, Lemoine N, Oberrath R. 2000 Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. *Evol. Ecol. Res.* **2**, 823-839.

49. Price TD, Qvarnstrom A, Irwin DE. 2003 The role of phenotypic plasticity in driving genetic evolution. *Proc. R. Soc. Lond. Ser. B.* **270**, 1433–1440.

Figure and Table captions

Fig. 1. Values of the K statistics measuring phylogenetic signal in the set of variables considered in this study. Significant phylogenetic effects are marked with asterisks (* $p <$ 0.05; ** $p < 0.01$; *** $p < 0.001$). The plots on the right indicate the average values of K (top) and variances (bottom) of mass-related variables (body mass, egg mass, lifetime and annual productivity), life history variables (egg number, adult life expectancy, incubation and nestling time), and ecological traits (climate, habitat and migration variables) in the assemblage of species that do not coexist with a congener and in groups of congeneric species.

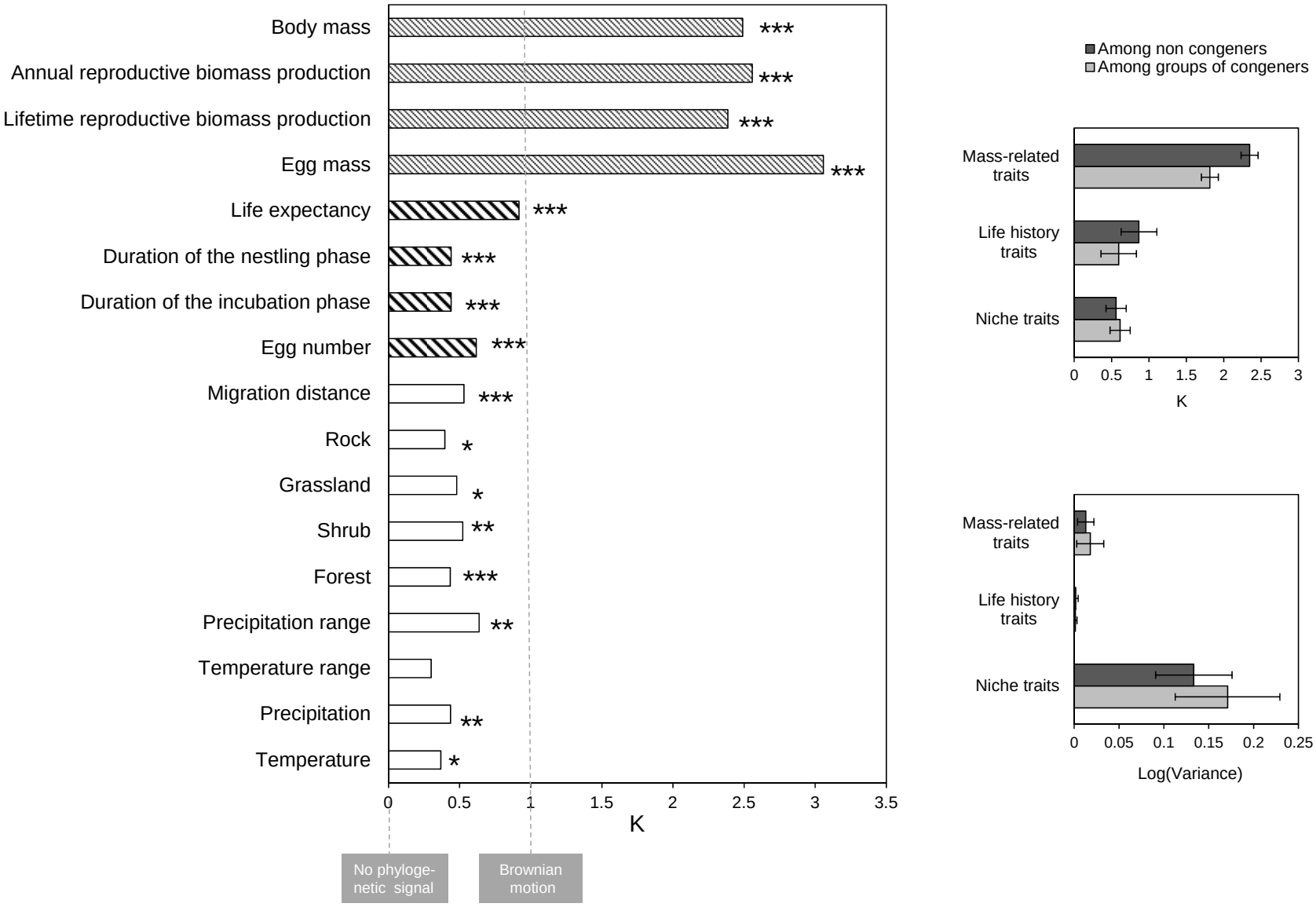
Fig. 2. Relationship between lifetime reproductive biomass production and body mass, as expressed on a logarithmic scale. Each dot represents the mean value of a species, and variances are also shown as error bars. Phylogeny does not constrain this relationship since the slope of the evolutionary regression, indicating the influence of body mass and phylogenetic inertia, and that of the optimal regression, free of phylogenetic constraints, coincide and equal 0.81 ± 0.04 ($R^2 = 0.88$).

Fig. 3. Plots depicting variation in egg number along the temperature gradient (left) and in nestling times driven by habitat (right). Dots represent species' residuals partialling out the effect of other predictors influencing traits; the error bars of x- and y-variables represent that of raw $\log_{10}$-transformed variances. The significant evolutionary regressions, indicating the influence of predictors and phylogenetic inertia, are also shown.

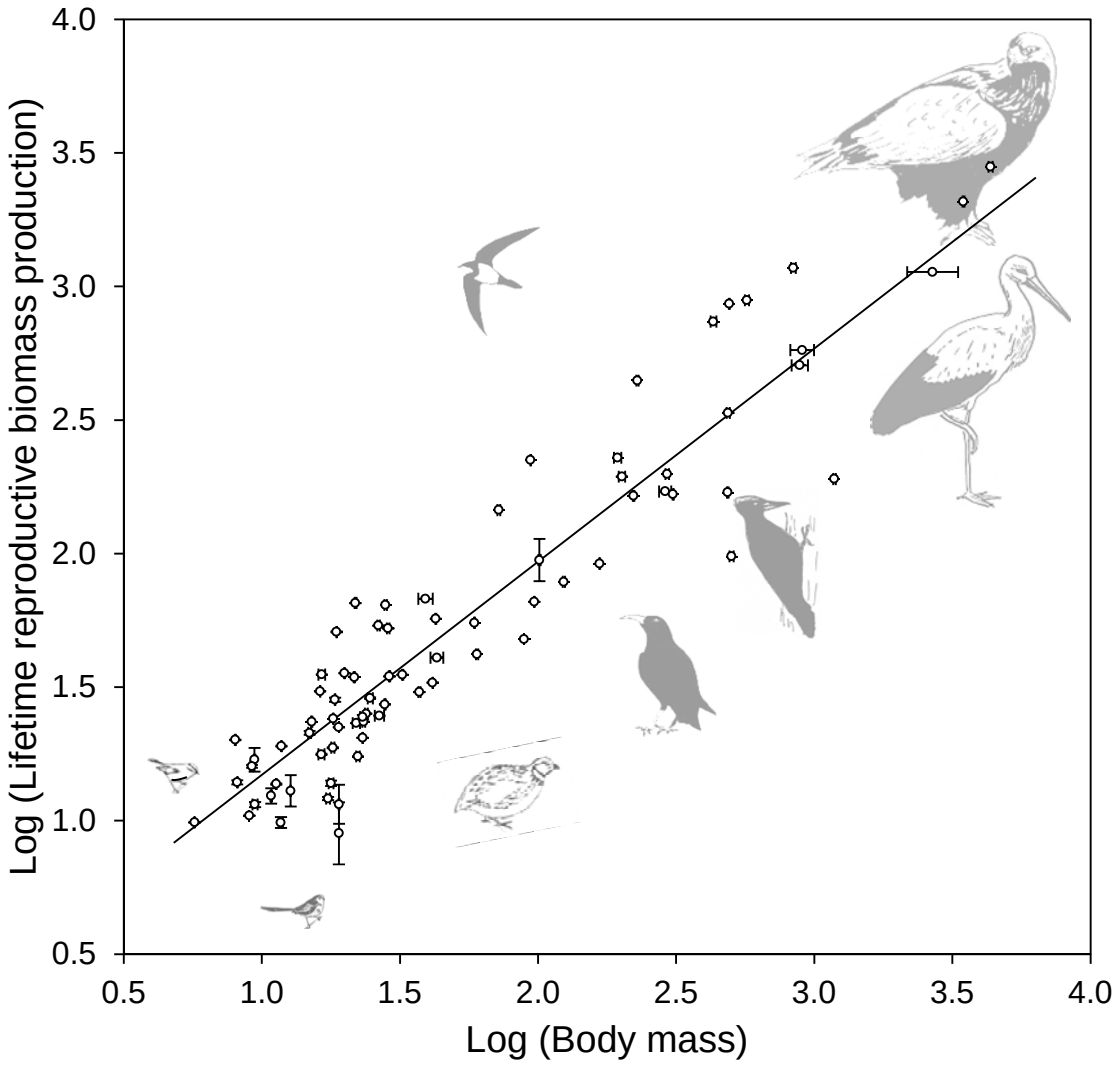
Table 1. Relationships between productivity traits and body mass, and between life histories and body mass and niche characteristics, in the entire community of birds, in the assemblage formed by groups of congeners, and in the assemblage formed by non-congeners. Allometric slopes ± standard errors, trait adaptation rate α (indicating independence from ancestral values) and model coefficients of determination (R^2) are also shown. We report the models with the highest performance based on AIC_c criteria and that included the same set of variables in the three assemblages (see also the ESM, table S3). Since data were $\log_{10}$-transformed prior to analyses, estimates should be interpreted in this scale.

Table 2. Summary of the parameter estimates (± standard errors) of the best models explaining life history variation across the entire dataset. Life history optima were modeled on combinations of body mass, migration distance and niche variables. Optimal slopes indicate the expected adaptive variation of traits as these were free of phylogenetic constraints, while evolutionary slopes indicate the observed variation due to both adaptation and phylogeny. The value of α measures trait dependence on ancestral values (the higher the α, the higher the rate of change and the lower the inertia). When more than one model best fitted the data, the model with the largest number of parameters is shown here; alternative models are listed in the ESM, table S3. Since data were $\log_{10}$-transformed prior to analyses, estimates should be interpreted in this scale.

1 Fig. 1.


Body mass
Annual reproductive biomass production
Lifetime reproductive biomass production
Egg mass
Life expectancy
Duration of the nestling phase
Duration of the incubation phase
Egg number
Migration distance
Rock
Grassland
Shrub
Forest
Precipitation range
Temperature range
Precipitation
Temperature
***
***
***
***
***
***
***
***
*
*
**
***
**
**
*
0
0.5
1
1.5
2
2.5
3
3.5
K
No phyloge-netic signal
Brownian motion
Among non congeners
Among groups of congeners
Mass-related traits
Life history traits
Niche traits
0
0.5
1
1.5
2
2.5
3
K
Mass-related traits
Life history traits
Niche traits
0
0.05
0.1
0.15
0.2
0.25
Log(Variance)

2 Fig. 2


Log (Lifetime reproductive biomass production)
Log (Body mass)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0

3

4

Fig.3

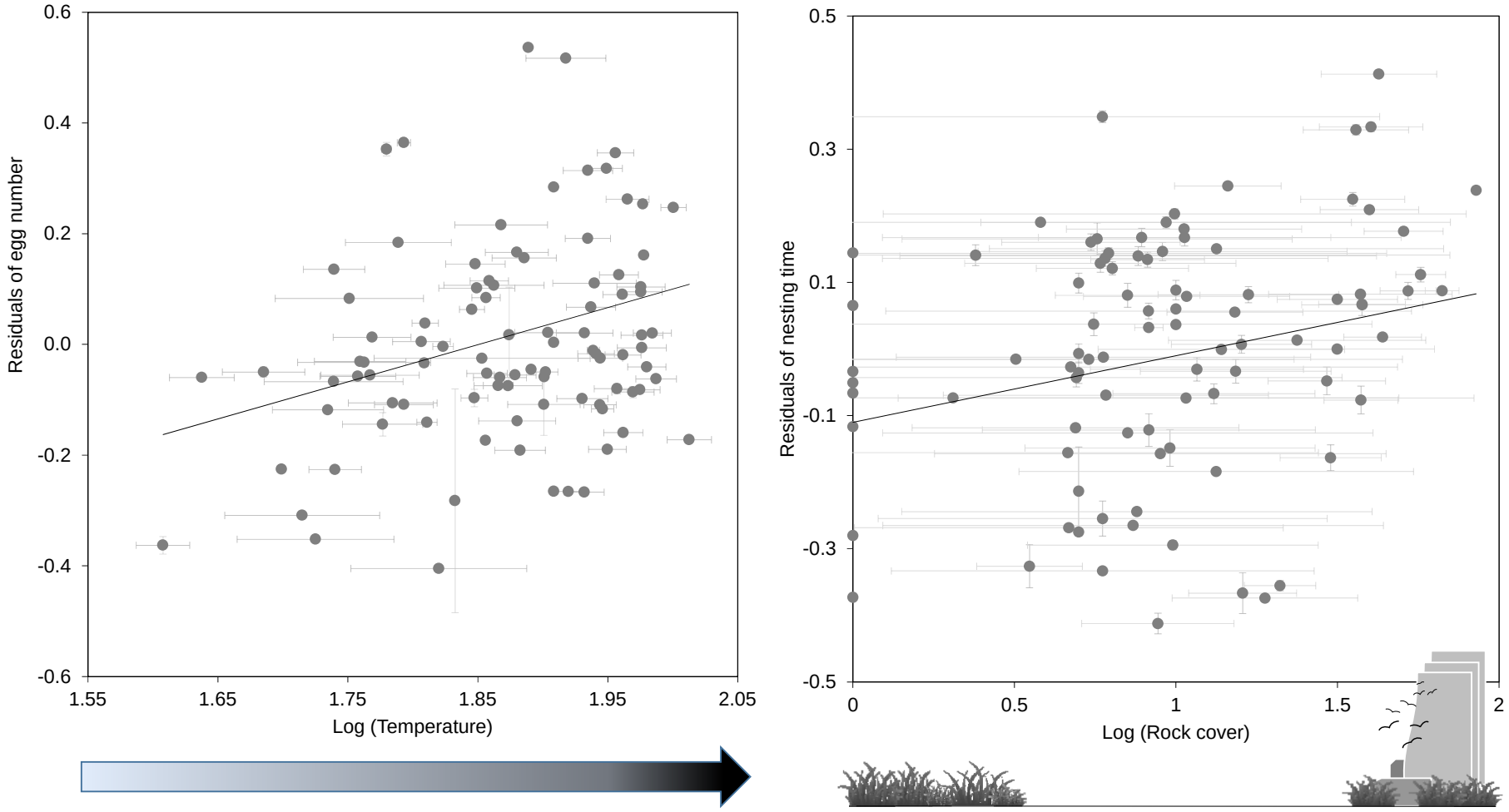

Residuals of egg number
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
1.55
1.65
1.75
1.85
1.95
2.05
Log (Temperature)
Residuals of nesting time
0.5
0.3
0.1
-0.1
-0.3
-0.5
0
0.5
1
1.5
2
Log (Rock cover)

Table 1. Relationships between productivity traits and body mass, and between life histories and body mass and niche characteristics, in the entire community of birds, in the assemblage formed by groups of congeners, and in the assemblage formed by non-congeners. Allometric slopes ± standard errors, trait adaptation rate α (indicating independence from ancestral values) and model coefficients of determination (R^2) are also shown. We report the models with the highest performance based on AIC_c criteria and that included the same set of variables in the three assemblages (see also the ESM, table S3). Since data were $\log_{10}$-transformed prior to analyses, estimates should be interpreted in this scale.

	Entire community		Among groups of congeners		Among non-congeners	
Model	*Allometric slope*		*Allometric slope*		*Allometric slope*	
Lifetime productivity ~ Body mass	0.81 ± 0.04		0.72 ± 0.05		0.85 ± 0.06	
Annual productivity ~ Body mass	0.56 ± 0.03		0.53 ± 0.04		0.54 ± 0.04	
Model	α*	R^2	α*	R^2	α*	R^2
Incubation time ~ Body mass + Rock cover	23.1	0.156	17.3	0.109	34.7	0.439
Nestling time ~ Body mass + Rock cover	12.6	0.201	17.3	0.166	10.0	0.334
Egg number ~ Body mass + Temperature	0.43	0.315	2.89	0.339	29.0	0.398
Life expectancy ~ Body mass + Temperature	13.9	0.513	69.3	0.637	13.9	0.677

* Since branch length in our phylogeny is represented by the proportion of nucleotide substitutions, thus total tree height = 1, α is expressed in this unit. A $\alpha = 0.69$ (i.e. ln(2)) means that it takes the distance separating the root from the tip of our phylogeny to lose half of the ancestral influence, and a null α characterizes an evolutionary model without adaptive change (BM model).

Table 2. Summary of the parameter estimates (± standard errors) of the best models explaining life history variation across the entire dataset. Life history optima were modeled on combinations of body mass, migration distance and niche variables. Optimal slopes indicate the expected adaptive variation of traits as these were free of phylogenetic constraints, while evolutionary slopes indicate the observed variation due to both adaptation and phylogeny. The value of α measures trait dependence on ancestral values (the higher the α, the higher the rate of change and the lower the inertia). When more than one model best fitted the data, the model with the largest number of parameters is shown here; alternative models are listed in the ESM, table S3. Since data were $\log_{10}$-transformed prior to analyses, estimates should be interpreted in this scale.

	Egg number	Life expectancy	Time spent incubating	Time spent caring for nestlings
α*	0.60	9.90	23.10	12.6
Body mass (optimal)	-0.90 ± 0.16	0.29 ± 0.04	0.09 ± 0.02	0.14 ± 0.04
Body mass (evolutionary)	-0.18 ± 0.03	0.23 ± 0.03	0.08 ± 0.01	0.12 ± 0.03
Migration distance (optimal)	-0.26 ± 0.08	0.02 ± 0.02	-	-
Migration distance (evolutionary)	-0.06 ± 0.02	0.01 ± 0.01	-	-
Temperature (optimal)	2.06 ± 0.84	-0.80 ± 0.26	-	-
Temperature (evolutionary)	0.63 ± 0.17	-0.66 ± 0.21	-	-
Shrub cover (optimal)	0.34 ± 0.16	-	-	-
Shrub cover (evolutionary)	0.08 ± 0.03	-	-	-
Rock cover (optimal)	-	-	0.05 ± 0.03	0.11 ± 0.05
Rock cover (evolutionary)	-	-	0.04 ± 0.03	0.10 ± 0.04
R^2	0.357	0.477	0.156	0.201

* Since branch length in our phylogeny is represented by the proportion of nucleotide substitutions, thus total tree height = 1, α is expressed in this unit. A $\alpha = 0.69$ (i.e. ln(2)) means that it takes the distance separating the root from the tip of our phylogeny to lose half of the ancestral influence, and a null α characterizes an evolutionary model without adaptive change (BM model).