

Energetics, lifestyle, and reproduction in birds

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Contributed by James H. Brown, April 24, 2012 (sent for review December 8, 2011)

Theoretical and empirical studies of life history aim to account for resource allocation to the different components of fitness: survival, growth, and reproduction. The pioneering evolutionary ecologist David Lack [(1968) *Ecological Adaptations for Breeding in Birds* (Methuen and Co., London)] suggested that reproductive output in birds reflects adaptation to environmental factors such as availability of food and risk of predation, but subsequent studies have not always supported Lack's interpretation. Here using a dataset for 980 bird species (Dataset S1), a phylogeny, and an explicit measure of reproductive productivity, we test predictions for how mass-specific productivity varies with body size, phylogeny, and lifestyle traits. We find that productivity varies negatively with body size and energetic demands of parental care and positively with extrinsic mortality. Specifically: (i) altricial species are 50% less productive than precocial species; (ii) species with female-only care of offspring are about 20% less productive than species with other methods of parental care; (iii) nonmigrants are 14% less productive than migrants; (iv) frugivores and nectarivores are about 20% less productive than those eating other foods; and (v) pelagic foragers are 40% less productive than those feeding in other habitats. A strong signal of phylogeny suggests that syndromes of similar life-history traits tend to be conservative within clades but also to have evolved independently in different clades. Our results generally support both Lack's pioneering studies and subsequent research on avian life history.

David Lack's classic account of ecological adaptations for breeding in birds (1) influenced generations of evolutionary ecologists who have had the benefit of more data and better methods of analysis (e.g., refs. 2–11). Subsequent studies, however, have not always supported Lack's conclusions about the primary importance of factors that affect birds directly, such as predation risk and food availability, and indirectly, such as seasonality (2, 6, 12, 13).

Subsequent to Lack's classic study, life-history theory explored adaptive resolutions of trade-offs in allocation of limited time, energy, and material resources to survival, growth, and reproduction (e.g., refs. 14–16). Here we use a larger dataset and improved phylogenetic analyses to document how reproductive output varies with body size and other aspects of avian lifestyle, such as parental care, diet, foraging mode, and migratory status. As our measure of reproductive output, we use the rate of production of reproductive biomass, termed *productivity* hereafter, and calculate for each species as (egg mass) \times (number of eggs per clutch) \times (clutch frequency, i.e., number of successful clutches per year) all divided by body mass. Egg production is fueled by metabolism, so the mass-specific rate of productivity should scale negatively with body size, roughly similarly to mass-specific metabolic rate (17). Furthermore, environmental limits on energy supply and physiological and ecological limits on metabolic energy expenditure should result in predictable trade-offs in energy allocation. Finally, these trade-offs should be strongly related to phylogeny because avian lifestyles (syndromes of adaptive physiological and behavioral traits) are evolutionarily conservative and widely shared among species within a clade. These considerations lead to the following predictions: (i) productivity decreases with increasing body mass, reflecting the effect of mass-specific

metabolic rate on the rate of energy allocation to reproduction (18); (ii) productivity exhibits a strong signal of phylogeny, deeply rooted in the tree, reflecting shared lifestyle traits inherited from common ancestors; (iii) productivity decreases with increased levels of parental care, reflecting a trade-off in energy allocation between producing eggs and providing for the growth and survival of hatchlings; and (iv) productivity increases with increased extrinsic mortality, so that high investment in reproduction compensates for risky lifestyles (3, 19, 20).

To evaluate these predictions, we compiled and analyzed Dataset S1 on body size, life-history traits, and other attributes of lifestyle for 980 bird species. The lifestyle traits are shown in Table S1.

Results

Prediction (i): Productivity Decreases with Increasing Body Size. The effect of body size is shown in Fig. 1A, which plots productivity as a function of body mass on logarithmic axes for 966 species by monophyletic order (Fig. S1). Across all birds and in all orders with data for >10 species, productivity decreased with increasing body size, supporting Prediction (i) (bivariate correlations, all $P < 0.05$). Note also that the relationship between productivity and body mass was distinctly curvilinear; the slope of the best-fit quadratic regression decreased continuously with body size, from -0.23 for birds weighing <10 g to -0.52 for birds weighing $>1,000$ g. This curvilinearity was shown by a significant quadratic as well as a linear effect in our phylogenetically explicit analysis [see below; phylogenetic general linear model (PGLM): $-0.0727 \pm \text{SE } 0.0098$ and $-0.0872 \pm \text{SE } 0.0479$, respectively] (Table 1). We calculated an index of mass-corrected productivity for each order by fitting parallel quadratic regression lines for each order to the data in Fig. 1A and by taking the intercept (Fig. 1B). Birds of the same size differed as much as 10-fold in productivity—from low productivities of nightjars, swifts, and hummingbirds (Caprimulgiformes-Apodiformes) and tube-nosed seabirds (Procellariiformes) to high productivities of waterfowl (Anseriformes), landfowl (Galliformes), and rails, cranes, and relatives (Gruiformes-Cuculiformes) (Fig. 1B).

Prediction (ii): Productivity Is Strongly Affected by Phylogeny. Differences among orders in Fig. 1 suggests that much of the variation in productivity is associated with phylogeny. We used our avian supertree to generate a PGLM that explicitly incorporates phylogenetic relationships. The phylogenetic influence was strong ($\lambda = 0.88$ on the scale of 0 for no signal to 1 for maximal signal strength).

Author contributions: R.M.S., C.C.W., N.A.W., C.V., and J.H.B. designed research; R.M.S., C.C.W., N.A.W., C.V., W.J., and J.H.B. performed research; R.M.S., C.C.W., N.A.W., C.V., and J.H.B. analyzed data; and R.M.S., C.C.W., N.A.W., C.V., W.J., and J.H.B. wrote the paper.

The authors declare no conflict of interest.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1206512109/-DCSupplemental.

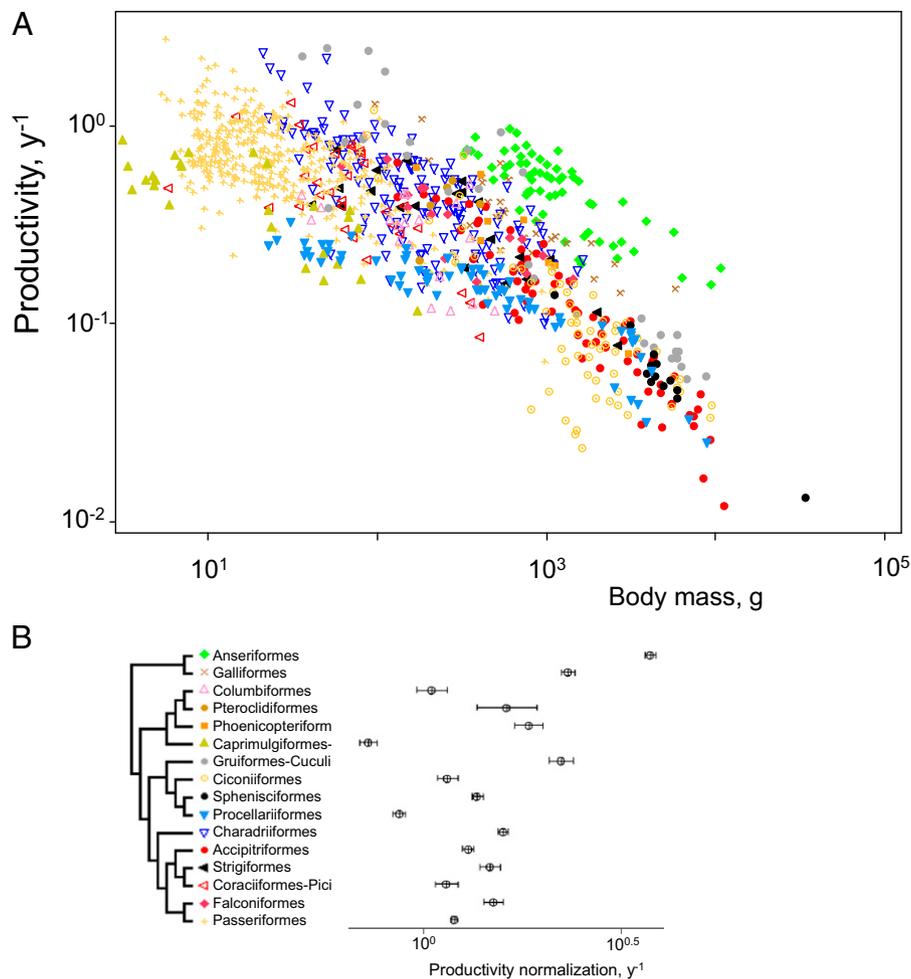


Fig. 1. Productivity in relation to body mass and evolutionary history. (A) Productivity plotted against body mass with one point/species. Productivity is measured as grams of eggs per grams adult female per year, i.e., y^{-1} . Only orders with five or more species are shown. (B) Phylogenetic relationships and relative productivities of orders, quantified as y -intercepts after fitting parallel curved lines of form: $y = a + b (\log \text{mass}) + c (\log \text{mass})^2$. Horizontal bars indicate SEs. Together, A and B show the strong effects of both body size and phylogeny on productivity.

Predictions (iii) and (iv): Productivity Is Strongly Associated with Lifestyle Traits, Reflecting Trade-Offs in Allocation.

The PGLM also identified strong effects of lifestyle traits. Variation in productivity was associated with developmental mode, breeding system, migratory status, diet, foraging time, habitat, and nest type as shown in Table 1 and illustrated in Fig. 2 and Fig. S2. Each of these

Table 1. Significance of the factors affecting productivity in the phylogenetic general linear model

Source	df	D	P
Mass	1	3.4	0.066
Mass ²	1	54.9	0.000
Developmental mode	2	29.5	0.000
Breeding system	6	19.1	0.004
Migratory status	1	26.5	0.000
Diet	6	26.0	0.000
Foraging time	2	7.5	0.024
Foraging habitat	4	33.1	0.000
Nest type	3	6.6	0.085

Significance was tested after other factors were accounted for; D is the likelihood-ratio statistic. The PGLM accounted for 57% of the variance with 26 df; the error df were 953.

factors accounted for significant variation ($P < 0.05$) except nest type, which was marginally significant ($P = 0.085$).

So productivity varied not only with body size and phylogeny, but also with intrinsic lifestyle characteristics related to parental care, supporting Prediction (iii). These relationships reflect fundamental trade-offs in energy allocation. Productivity was lower in species with more posthatching parental care. Species with precocial offspring that feed, locomote, and thermoregulate immediately after hatching invested more energy in eggs and hence had higher productivity than species that have semiprecocial and altricial hatchlings and devote substantial energy to parental care (Fig. 2A, $P < 0.001$; P values here and below refer to phylogenetically adjusted pairwise comparisons given in Table S3). Productivity was also lower in species with female-only parental care than in biparental, male-only and cooperatively breeding species (Fig. 2B, $P < 0.05$), supporting the prediction that females invest more in eggs when other individuals, either males or members of social groups, contribute to incubation, feeding, and care of offspring.

Other patterns reflected trade-offs between reproduction and survival, supporting Prediction (iv). Predictably, migratory species allocated more energy to reproduction: 14% higher productivity than nonmigrants (Fig. 2C, $P < 0.001$). Migration allows breeding in seasonal environments with abundant resources (13, 21–23), but at the cost of increased mortality (24,

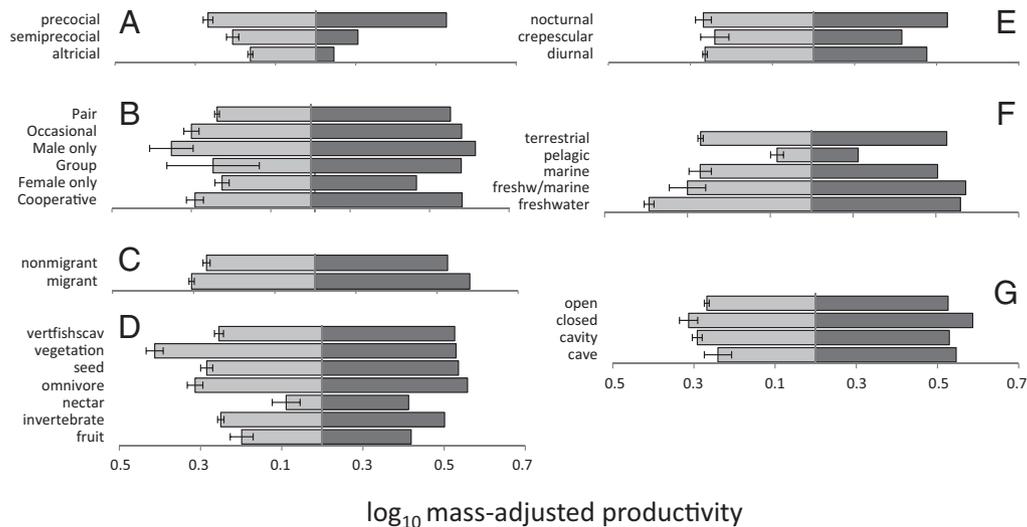


Fig. 2. Effects of lifestyle factors on productivity. The light bars on the left show the quantitative effect of each trait on productivity after adjusting for body size and the effects of other traits but not phylogeny. The dark bars on the right show the effect after accounting for these and also for phylogeny. Error bars on the left are SEs calculated from the residuals. For pairwise significance tests, see *SI Materials and Methods*. (A) Developmental mode. (B) Breeding system. (C) Migratory status. (D) Diet. (E) Foraging time. (F) Foraging habit. (G) Nest type.

25). Frugivores and nectarivores and crepuscular and pelagic foragers had significantly lower productivities than species with other diets and foraging modes ($P < 0.05$, $P < 0.01$, and $P < <0.001$, respectively; Fig. 2D–F). Birds that feed on energy-rich nectar or fruit or on the abundant insects available just at twilight can apparently satisfy their food requirements by spending little time foraging. This may also reduce exposure to predators, contributing to relatively low mortality rates and correspondingly low productivities. Pelagic foragers had the lowest productivities (Fig. 2F), which Lack (1) attributed to the high energetic costs of commuting between foraging areas and nesting islands, but low mortality is a more parsimonious explanation. Some pelagic seabirds with low productivity nest close to productive foraging waters, so energy expenditure on foraging flights should be modest. However, all pelagic seabirds spend their time at sea or on remote islands with few or no predators, so mortality rates should be low. Indeed, they have among the longest life spans known for birds (26–28).

Discussion

A limitation of our study is that egg production is only a part of the energy investment of parents in reproduction. In addition to producing eggs, females of many bird species expend energy on territorial defense, nest construction, incubation, foraging to feed offspring, and anti-predator defenses. The parental investment of the female parent may also be supplemented by contributions of the male parent and other members of a social group, depending on the breeding and social system. Failure to include these other components of energy investment in reproduction might appear to be a major problem for a study intended to test the above predictions, understand patterns of resource allocation in relation to lifestyle traits, and extend life-history theory.

Of course it would be ideal to have complete quantitative energy budgets, broken down into categories of reproduction and survival. Unfortunately, such data are available for only very few species (e.g., ref. 29) because they require measurements of energy income and expenditure for all activities throughout life. Furthermore, although such data would be desirable, they are not essential to addressing many of the important conceptual

questions of life-history theory. The life history satisfies conservation of energy, so the energy income from foraging, F , must be balanced by energy expenditure, E , on growth, G , maintenance and survival, S , and reproduction, R ; therefore, $F = E = G + S + R$ (3, 7, 30). Furthermore, energy expenditure on reproduction, R , is the sum of nest building, N , egg laying, P , incubation, I , and parental care, C (feeding and protection of offspring); therefore $R = N + P + I + C$. These conservation of energy relationships form the basis for the qualitative predictions that we made and evaluated here. So, for example, a bird species with a diet or a migratory pattern that provides access to a greater energy supply (i.e., with a higher F) can—all else being equal—devote more energy to reproduction (a higher R). A female that invests heavily in egg production (a higher P), necessarily has less to invest in parental care (a lower C); and if a male parent or helper provides much of the parental care, the female parent with lower C can invest more in eggs (a higher P).

Most of our results can be interpreted as supporting the predictions based on fundamental allocation trade-offs. Birds that live fast and die young have higher productivity (i.e., some combination of larger eggs and/or larger and more frequent clutches) than those that experience lower rates of mortality. This is seen not only in the effect of body size, with small birds being more productive than large ones, but also in lifestyle traits that affect risk of predation and other sources of mortality. Productivity is also affected by trade-offs among life-history traits, such as less investment in eggs when hatchlings are altricial or cared for only by the female.

Our results directly support or at least are consistent with most earlier studies (2, 6, 9, 12, 31, 32). Most previous quantitative analyses of avian life history have emphasized the effects of just one or a few variables and have focused on variation within a single species or a clade of closely related species. Sometimes this has led to debates between authors who have obtained different results. Our results suggest that most of the patterns documented in these different studies are supported by a broad analysis across all birds.

The restricted scope of earlier studies makes it difficult to disentangle the relative influences and interacting effects of specific

environmental variables, such as temperature, productivity, and nest predation; broad geographic factors, such as latitude and elevation; and trade-offs in allocation of limited resources, such as between eggs and posthatching parental care. Our analysis also cannot address this limitation because we consider only life-history and lifestyle traits. Our results do, however, clarify how these traits have affected the evolution of avian life histories. We show significant associations between productivity and many aspects of avian lifestyle that affect reproductive investment, either directly as a result of allocation trade-offs, or indirectly as a result of variation in extrinsic mortality. These relationships remain strong even after accounting for the pervasive effects of body size and phylogenetic relationships.

The close association between life history and phylogeny, made possible by our new supertree for phylogenetic relationships (Fig. S1) across all birds, indicates not only that most members of order-level clades tend to exhibit syndromes of similar life-history traits inherited from their common ancestors, but also that multiple independent evolutions of these syndromes occurred in the ancestors of contemporary birds. For example, an association between high productivity and precocial hatchlings is characteristic not only of the sister clades waterfowl (Anseriformes) and landfowl (Galliformes), but also of the more distantly related flamingos and grebes (Phoenicopteriformes-Podicipediformes); gulls, terns, and shorebirds (Charadriiformes); and rails and cranes (two families of Gruiformes-Cuculiformes). Somewhat similarly, nectarivores and frugivores with relatively low productivities and long life spans include hummingbirds (in the Caprimulgiformes-Apodiformes) and sunbirds and contingas (in the Passeriformes).

Our focus on the effects of body size, phylogeny, and lifestyle offers a mechanistic understanding of life-history variation in birds. It also raises questions about the timing and consequences of key trade-offs in the evolution of bird lineages and about the effects of factors such as climate and seasonality—and hence latitude and elevation, which can be addressed when additional high-quality data from undersampled taxa (e.g., Coraciiformes-Piciformes and several families of Passeriformes) and regions (e.g., the tropics) become available.

Materials and Methods

Data. Information on clutch size, egg mass, clutch frequency, and various life-history and lifestyle traits for 980 bird species listed below were based on select datasets in refs. 6 and 13 and on major ornithological online reference works (Handbook of Birds of the World, Animal Diversity Web at <http://animaldiversity.ummz.umich.edu/site/index.html>; All About Birds, Cornell Laboratory of Ornithology at <http://www.allaboutbirds.org>). Because adult body mass calculated as the average of male and female is more widely available than female mass, we used the former. Clutch frequency is subject to intraspecific variation, which is not accounted for here. Availability of data resulted in inclusion of a disproportionate number of birds of northern latitudes, which means, for example, that our dataset (Dataset S1) includes fewer species that have small clutches (13), are nonmigratory, and are

frugivores or nectarivores (33) than would be representative. These limitations should not greatly affect the results, but additional data for under-represented taxa and regions would be desirable.

Analyses. Allometry of production. Because productivity is defined as biomass production per unit of body mass, plotting this measure as a function of female mass has the disadvantage that ratios of random numbers regressed against their denominator will necessarily yield negative correlations (34). We nonetheless use this ratio for several reasons (following ref. 35): (i) The problem of spurious correlation is not serious when the correlation between numerator and denominator is high (36) as it is in our data; $r = 0.91$. (ii) The slope calculated using mass-specific productivity was less than that for whole-organism productivity by exactly 1 as predicted: -0.377 compared with 0.623 , respectively, and the latter was significantly <1 . (iii) Using mass-specific values did not affect calculated coefficients, SEs, and significance levels of other variables. (iv) Using mass-specific values allows ready biological interpretation and direct comparisons with previous work (17, 37, 38), without compromising the testing of hypotheses.

Phylogenetic tree. We created a supertree for the 980 species of birds (Fig. S1) that were included in our dataset on productivity (Dataset S1). These birds represent 116 families and therefore require a near-comprehensive higher-level phylogeny of birds. Given the well-known challenges of estimating the deep nodes in the bird tree, as a starting point for our supertree we used the most rigorous available estimate of bird phylogeny, the 169-taxon, 19-locus tree of ref. 39. Starting with the phylogram presented in figure 3 of ref. 39, we assigned each of the 980 taxa in Dataset S1 to one of 23 well-supported monophyletic clades ($>70\%$ maximum-likelihood bootstrap in figure 2 of ref. 39), using taxonomy as a guide. We searched GenBank for mitochondrial DNA data from any of the species in each set and retained the longest available sequence for each species–gene combination. For each set, we included at least one pair of taxa that were also included in the tree (39) and could therefore be used for scaling branch lengths. We aligned the sequences for each set and gene, checked the alignments by eye, and then consolidated alignments into a supermatrix for each set as described in *SI Materials and Methods*. In this way, we produced a complete, time-scaled supertree that was based on slowly evolving nuclear DNA at deep nodes and fast-evolving mitochondrial DNA at the tips. Although our tree undoubtedly contains minor topological errors due to gene-tree/species-tree conflicts, model mis-specification, and insufficient data, phylogenetic regression is expected to be robust to tree mis-specification, especially at the tips of the tree (40).

GLM and PGLM. We used a phylogenetic generalized least-squares multiple regression approach (41, 42) implemented in the program BayesTraits (43) while simultaneously estimating the parameter λ to quantify the “phylogenetic signal” (41, 44). The categorical life-history factors were incorporated using a standard “dummy” or “treatment” contrast coding.

ACKNOWLEDGMENTS. We thank P. Bennett and I. Owens for sharing datasets used in Bennett and Owens (2002) and thank K. Bohning-Gaese, F. S. Dobson, and T. E. Martin for helpful comments on the manuscript. We also thank all original field data collectors and authors of primary and secondary literature that formed the basis of our datasets and without which the analyses would not have been possible. R.M.S. and J.H.B. were supported by National Science Foundation Research Coordination Network Grant DEB-0541625; C.V. was supported by The Leverhulme Trust Early Career Fellowship (Grant ECF/2009/0029); and W.J. was supported by National Science Foundation DEB-1026764 and DBI-0960550.

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