Introduction

There is enormous variation in life-history among species and across regions, which ecologists have long sought to explain [1–3]. One trait of particular interest is the number of eggs laid per nest (clutch size) by birds, which is central to avian reproductive effort and probably the best-recorded animal life-history trait. The causes of its substantial variation have fascinated behavioural, ecological, and evolutionary biologists for more than 60 years [2,3], but remain highly debated [4–6]. Life-history theory aims to discover the factors that determine intra- and inter-specific variation in life-history traits. This discipline has recently benefited from observational and experimental studies that have quantified important trade-offs, reaction norms, and phenotypic plasticity of the variation within populations and species [7,8]. However, this work is limited in its ability to explain the tremendous interspecific and geographic variation in life-histories—from warblers to raptors, and from the tropics to the poles. Inspired by David Lack’s original observations [3], comparative biologists have documented that clutch size tends to be conserved within clades and often co-varies with intrinsic (biological) attributes such as body size, nesting development, and nest type. At the same time, others have pointed to extrinsic (environmental) influences on clutch size with respect to latitude [1,2], gradients of resource availability, and seasonality [4,9,10], and between biogeographic regions. Lack [3,11] hypothesised that clutch size may be determined by food abundance during the breeding period, per se, and that northern species have large clutches because daylight periods during the breeding season are longer than those in the tropics. In contrast, seasonality of food abundance is suggested to be linked to clutch size by two alternative mechanisms. Classical life-history theory predicts that high seasonality in the temperate regions, causing high adult mortality, will lead to the evolution of high investment in current reproduction and large clutch sizes because the likelihood to survive until the next breeding season is low [5]. Alternatively, Ashmole [9] argued that high adult mortality in the temperate regions reduces population density, increases per-individual resource availability in the breeding season, and allows temperate birds to nourish large clutches [4,12].

Critically, like these suggested extrinsic drivers, clades and their intrinsic traits that may affect clutch size are also not randomly distributed along environmental gradients or realms. Consequently, separate viewpoints focusing on just intrinsic or extrinsic drivers have limited the unification and generalization of our understanding of life-history variation. Here we present an analysis that integrates these perspectives and we assess the variation in clutch size across species and assemblages worldwide. We compiled information on clutch size and other intrinsic (body mass, migratory behavior, development mode, nest type, diet) and extrinsic attributes (latitude, temperature, precipitation, net primary productivity, seasonality, and realm) for a total of 5,290 species of landbirds. This allows us to develop and test a first global model of clutch size that integrates existing viewpoints of life-history variation.

Results/Discussion

While clutch sizes vary over a large range, more than half of all birds lay 2 or 3 eggs (mode: 2, median: 2.8; Figure 1). The right-skewed frequency distribution indicates that from a global perspective, the large clutch sizes of northern temper-
Author Summary

Why do some bird species lay only one egg in their nest, and others ten? The clutch size of birds is one of the best-studied life-history traits of animals. Nevertheless, research has so far focused either on a comparative approach, relating clutch size to other biological traits of the species, such as body weight; or on a macroecological approach, testing how environmental factors, such as seasonality, influence clutch size. We used the most comprehensive dataset on clutch size ever compiled, including 5,290 species, and combined it with data on the biology and the environment of these species. This approach enabled us to merge comparative and macroecological methods and to test biological and environmental factors together in one analysis. With this approach, we are able to explain a major proportion of the global variation in clutch size and also to predict with high confidence the average clutch size of a bird assemblage on earth. For example, cavity nesters, such as woodpeckers, have larger clutches than open-nesting species; and species in seasonal environments, especially at northern latitudes, have larger clutches than tropical birds. The findings offer a bridge between macroecology and comparative biology, and provide a global and integrative understanding of a core life-history trait.

ate bird species—few in numbers, but most frequently studied in life-history research [5,13,14]—are in fact unusual. This highlights the importance for a perspective that extends to the tropics [15]. We find that a key intrinsic factor that distinguishes clades in their typical clutch size is the mode of development [16–19]. Precocial species, with their more mobile offspring, have much larger clutches (̄x = 4.49, N = 864 species) than altricial species (̄x = 2.85, N = 4,426; t = 21.73, p < 0.001). This may be the result of the shorter and less intensive parental care required by precocial young, thus reducing the fitness costs of additional offspring and allowing parents to raise larger clutches [18,19]. Development mode is phylogenetically highly conserved (in our dataset there is no altricial versus precocial variation below the family level), and we note that its consequences and associated selection pressures likely influence other intrinsic effects on clutch size.

Because of the prevalent influence of development mode and its high collinearity with other potential predictors of clutch size (Table S1), we assessed all intrinsic effects in combination (for single-predictor results, see Table S2). A previously noted negative effect of body mass on clutch size [20] is only weakly borne out across the global avifauna for altricial species (Table 1 and Figure 2). From a global perspective, altricial migrants have larger clutches than nonmigrants, especially when extrinsic effects are not accounted for (see below), which is different from studies that do not include tropical species [17,21,22]. Another strong intrinsic determinant of clutch size is nest type [23–25]. Cavity nesters, which are naturally exposed to lower rates of nest predation, tend to have larger clutch sizes than open nesters, and species with half-open nests are in between (Figure 2). Finally, clutch size also varies by diet [3], with granivores and omnivores laying larger clutches than frugivores and nectarivores.

A second suite of constraints on life histories arises from extrinsic factors characterizing the environment of species. One popular “catch-all” surrogate is latitude, which captures much of the global environmental variation because energy availability becomes more seasonal and is usually reduced at higher latitudes. An increase in clutch size toward the poles has long been noted [1,2] and is confirmed by our data (Table S1). The extensive geographical coverage of our data allows us to disentangle the various environmental trends underlying latitude. We use environmental information integrated across the global breeding distribution of each species to quantify the average extrinsic conditions characterizing its broad-scale niche. Specifically, we evaluate the seasonal difference between summer and winter temperatures (TempMax – TempMin, averaged over 3-mo periods), which emerges as the strongest extrinsic predictor: clutch sizes are smallest in species inhabiting relatively aseasonal environments and increase linearly with temperature seasonality (Figure 2). When this seasonality is controlled for, energy availability in the breeding season (NPPMax) has a very weak positive effect on clutch size. This supports the idea that seasonality in resource conditions has a much stronger effect on clutch size than the absolute level of resources in the breeding season [4,9,10,26]. Even though fine-scale variation in productivity may limit NPPMax as estimate of per-individual energy availability during the breeding season, the consistently weak trend over a wide range of environments offers little support for Lack’s original hypothesis [3,11]. Finally, after accounting for these two environmental variables, only a limited biogeographic signal (variable Realm) remains: birds of Australasia, the Afrotropics, and especially Oceania tend to have smaller clutch sizes than birds of other regions. While the strong deviation in Oceania may arise from a potential oversampling of species with large clutches (data were available for only 17% of species, compared to 57% elsewhere), the life-history strategies of island taxa may be partially shaped by higher population densities and elevated intraspecific competition [27,28].

Intrinsic and extrinsic life-history determinants do not act in isolation, and our analytical approach allows us to assess their respective contribution in combination. In the joint model, all five intrinsic and three extrinsic predictors so far discussed emerged as significant (Table 1 and Figure 2). All
Under phylogenetic control, the extrinsic portion of the membership, the relative strength of the intrinsic compared to the extrinsic and most of the intrinsic variables continue to have very strong effects. This is not true for migratory tendency and diet, which are closely tied to climatic conditions (Table S1). After accounting for temperature seasonality in the combined model, these variables retain relatively little residual effect. This suggests that the larger clutches of altiricial migrants arise at least in part from their occupying morphological, physiological, and ecological niches and as a consequence exhibit conservatism in both life-history traits and their intrinsic and extrinsic correlates [29]. Over 90% of the variation in key life-history traits in birds occurs at the level of families and higher [30]. We therefore tested the ability of our combined model to predict variability of clutch size in a phylogenetic nested model that takes into account the order and family membership of the species. The results confirm the strong phylogenetic constraints on many intrinsic predictors of clutch size. After accounting for clade membership, the relative strength of the intrinsic compared to the extrinsic model in the cross-species analysis is reversed. Under phylogenetic control, the extrinsic portion of the model offers stronger predictions ($r^2 = 0.26$) than the more phylogenetically conserved intrinsic part ($r^2 = 0.21$), and the latter does not improve overall model fit as much (delta Akaike information criterion (AIC) of 305 and 983 to full model, respectively). Extrinsic predictors appear orthogonal to phylogeny and the outstanding importance of temperature seasonality is confirmed. As expected, biogeographic realm membership, which is tightly linked to clade-specific biogeographic history, loses importance in the phylogenetic model. Accounting for the phylogenetic variation at the order and family level explains substantial additional variation, increasing $r^2$ to 0.68 (Figure 3B).

The geographic context of our data allows us to test the ability of a comparative analysis to predict a global ecological pattern [31]. Specifically, we evaluate how well predictions for each species from our combined cross-species and phylogenetic model fit the observed average (geometric mean) clutch size in 2,521 bird assemblages of 220 × 220-km size. This provides a test of whether the proposed integration of intrinsic and extrinsic factors is able to recreate observed geographic gradients. Observed average clutch sizes across assemblages show a remarkably strong geographic gradient from an average of 4.5 eggs at the high northern latitudes to just over two eggs in the tropics (Figure 4A). We find that our combined cross-species model successfully predicts this geographic pattern (Figure 3C), with a slope almost indistinguishable from 1 ($\Delta_{\text{Observed}} = 0.092 + 0.99$ (s.e. = 0.004) $\times_{\text{Predicted}}$).

### Table 1. Integrated Models of Clutch Size across 5,290 Bird Species

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Category</th>
<th>Cross Species</th>
<th>Nested Phylogenetic</th>
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<tr>
<td></td>
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<tr>
<td>Fruits and Nectar</td>
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Multi-predictor models based on only intrinsic (Intr, biological) or extrinsic (Extr, environmental) predictors, or both combined (Both). The $\Delta$AIC (delta AIC) columns list the increase in Model AIC when a predictor is dropped. All potential interactions between Precocial and continuous predictors were explored. The null models AICs were $-2,204$ for cross species and $-5,545$ for nested phylogenetic model. $r^2$ fixed indicates proportion variance explained by predictor variables, $r^2$ Order and $r^2$ Family indicate the proportion variance of observed values explained by those predicted when additionally the random effects of Order and Family nested in Order are fitted. $r^2$ Model is a binary variable indicating migratory behaviour, Temp$_{max}$ – Temp$_{min}$, and NPP$_{max}$ quantify temperature seasonality and peak net primary productivity across species’ geographic range. In the two categorical variables Diet and Realm, contrasts were specified as “treatment” and each level related to the baseline category (Vertebrates and Nearctic, respectively). doi:10.1371/journal.pbio.0060303.t001
Figure 2. Partial Residual Plots for the Combined Intrinsic-Extrinsic Model of Clutch Size

This plot (also called component + residual plot, response: Comp + Res) illustrates the relationship between a predictor and the response given other predictors in the model (specifically, it is a plot of $r_i + b x_i$ versus $x_i$, where $r_i$ is the ordinary residual for the $i$th observation, $x_i$ is the $i$th observation and $b$ is the regression coefficient estimate). For Mass, the solid line and solid symbols refer to altricial species, the dashed line and open symbols to precocial species. To visualize the interaction with Precocial, we excluded that variable for the two interacting predictors (Mass, Migrant) in the calculation of $r_i$.

Abbreviations in Diet: Vert, vertebrates; Invert, invertebrates; Mixed, omnivore; PlaSee, plants and seeds; FruNect, fruits and nectar. In Realm: NeA, Nearctic; NeT, Neotropics; PaA, Palearctic; AfT, Afrotropics; InM, IndoMalaya; Aus, Australasia; Ocn, Oceania. In Migrant: Non-mig, non-migrant. For further details, see Table 1 (cross-species model Both).

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The phylogenetic nested model provides an even better fit ($r^2 = 0.98, F = 129,800$). This exceptional match is confirmed by a visual inspection of the geographic patterns (Figure 4B). It illustrates the statistical strength that assemblage attributes, averaged across species, can achieve even when underlying detectable trends across species are weaker. Geographic trends in the attributes of assemblages (e.g., mean assemblage clutch size) are affected by species' different geographic range sizes, as wide-ranging species occur in a disproportionate number of assemblages and thereby dominate geographic patterns [32]. Geographic trait patterns based on assemblage averages therefore carry a signal of both trait and range size variation across space. Consequently, models of eco-geographic patterns confound correlates of trait variation with correlates of species distributions and range size (and their respective patterns of spatial autocorrelation). For an understanding of potential extrinsic determinants of trait variation, we therefore advocate the use of a comparative approach for biological inference. Additionally testing whether a model can predict geographic patterns allows validation and bridges to the eco-geographic perspective.

Our findings on 56% of the world's landbirds empirically support recent theoretical work that highlighted the importance of food seasonality via adult mortality on clutch size [26,33]. Highly seasonal environments can cause increased adult mortality [34], e.g., because birds have to survive low temperatures and resource conditions in situ or because they have to migrate, which carries risks and costs. Additional effects on population density and, indirectly, per-individual resource availability in the breeding season, then combine to make seasonality of resources the predominant driver of clutch size variation across geographic gradients [26,33]. The significance of mortality, in this case mostly of offspring, for the evolution of clutch size is also expressed in the most important intrinsic determinant: nest type. Closed-nesters are subject to much smaller rates of nest predation or loss [23,24], and nest safety may influence clutch size through clutch size–dependent nest predation [35] or the effect of chick survival on adult density [4,9]. Nest type is phylogenetically conserved (its importance decreases strongly when phylogeny is addressed, Table 1), and it is clearly an intrinsic attribute. But its importance may itself be modulated by extrinsic constraints connected to mortality, such as nest predation pressure. This illustrates yet further the strong link between environmental conditions and the evolution and geographic distribution of biological traits such as nest type, which in turn affect life-history traits. Intricate disruptions of such trait associations may arise from climate change and its differential consequences for extrinsic vs. intrinsic determinants.

This study confirms many of the previously asserted correlates of clutch size, but moreover demonstrates how life-history traits are jointly determined by the interplay of intrinsic biological traits, the phylogenetic affinities, and the environment of a species. Understanding these interactions is
vital for gauging broad-scale life-history consequences of future climate change and their potential impacts on biodiversity. Our findings call for a combination of traditional cross-species comparative analyses with spatial and macroecological approaches to gain a more integrative, conceptual understanding of life-history variation. Using this approach offers a compelling integration of the intrinsic and extrinsic determinants of trait variation that help understand long-noted eco-geographic patterns and critical linkages in a world of change.

Materials and Methods

Data. We obtained the minimum and maximum clutch size data for 5,290 landbird species from a range of literature sources (see Tables S4–S6 and [36] for detailed overview). In this compilation, we did not include brood parasites, as their clutch size is difficult to define (female birds usually spread a large number of eggs over many host nests) and is obviously exposed to very different selection pressures. We also excluded predominately pelagic and marine species, because the environmental data in the analysis (see below) prevent a straightforward comparison with predominantly terrestrial species. We calculated the species-typical clutch size as the geometric mean of the typical minimum and maximum clutch size (for an evaluation of intraspecific variation, see below). For the same species, we compiled data on species-typical values of potential intrinsic determinants (development mode, body mass, migratory behavior, nest type, diet) from the literature (see Tables S4–S6 for details). We classified species into precocial (newly born young are relatively mobile, covered in feathers, and independent) and altricial (newly born young are relatively immobile, naked, and usually require care and feeding by the parents). Mass information (body mass in grams) was compiled from a variety of sources and averaged across up to four sources, and, if they differed, across sexes. Diet data came from the dataset described in [36]. Species dietary preferences were first recorded across nine major diet categories, and species were subsequently assigned to one out of five primary diets (vertebrates, invertebrates, fruits or nectar, other plant material or seeds, and omnivore). We were able to compile data on nest type data for 2,816 species in the analysis and for all 1,293 genera. Based on these data, we scored nest type according to levels of nest cover as follows: 1, open (e.g., no nest, cup, scrape, saucer, platform); 2, half-open nest (e.g., pendant, sphere, dome, pouch, crevice); 3, closed (cavity, burrow). This nest cover score only showed minor variation within genera, and across the 2,816 species with data the average genus score was an adequate surrogate for the species-level score (Nest type(genus) = -0.00 + 1.00 × nest
Avian Clutch Size across Species and Space

Sample text for the supporting information section.
Table S6. List of All Literature Sources Consulted
Found at doi:10.1371/journal.pbio.0060303.s006 (186 KB DOC).

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Author contributions. WJ conceived and designed the experiments. WJ analyzed the data. WJ, CHS, and KBG contributed reagents/materials/analysis tools. WJ, CHS, and KBG wrote the paper.

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References

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