ORIGINAL ARTICLE

Interspecific pairwise relationships among body size, clutch size and latitude: deconstructing a macroecological triangle in birds

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ABSTRACT

Aim Ecogeographical 'rules', large-scale patterns in ecological variables across geographical space, can provide important insights into the mechanisms of evolution and ecological assembly. However, interactions between rules could obscure both the observation of large-scale patterns and their interpretation. Here, we examine a system of three variables interrelated by ecogeographical rules – the latitudinal increase in body size within closely related homeotherms (Bergmann's rule), the negative allometry of clutch size (Calder's rule) and the latitudinal increase in clutch size (Lack's rule) – in a global dataset of birds.

Location Global.

Methods We used linear regressions and meta-analysis techniques to quantify the three rules across clades and through the taxonomic hierarchy. Path analysis was used to quantify interactions between rules at multiple taxonomic levels, as a function of both phylogenetic inheritance of traits and indirect feedbacks between the three rules. Independent contrasts analyses were performed on four clades with available phylogenies, and the taxonomic partitioning of variation in each trait was quantified.

Results Standardizing across all clades, Lack's and Bergmann's rules were supported at all taxonomic levels, with Calder's rule being supported at the order level. Lack's rule was consistently stronger and more often detected than the other two rules. Path analysis showed that the indirect effects often outweighed the direct effects of Calder's rule at the genus level and Bergmann's rule at the order level. Strong interactions between Calder's and Bergmann's rules led to a trade-off between the rules depending on taxonomic resolution.

Main conclusions We found strong interactions between Bergmann's, Lack's and Calder's rules in birds, and these interactions varied in strength and direction over the taxonomic hierarchy and among avian clades. Ecogeographical rules may be masked by feedbacks from other, correlated variables, even when the underlying selective mechanism is operating. The apparently conflicting pairwise relationships among clutch size, body size and latitude illustrate the difficulty of interpreting individual pairwise correlations without recognition of interdependence with other variables.

Keywords

Allometry, Bergmann's rule, birds, Calder's rule, Lack's rule, macroecology, positive semidefinite condition.

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INTRODUCTION

A large body of research dating back to the 19th century has shown evidence for consistent relationships between ecological variables across geographical space (Lomolino *et al.*, 2006; Gaston *et al.*, 2008). These so-called ecogeographical 'rules' are often observed both within and among species and across lineages. Here we focus on three of the most familiar

interspecific relationships in birds: (1) Bergmann's rule, the pattern of increasing body size within closely related homeotherms towards colder (higher) latitudes (Bergmann, 1847); (2) the tendency for clutch size to increase with latitude, which we refer to as Lack's rule (Lack, 1947); and (3) the negative allometry between body size and clutch size, which we term Calder's rule (Calder, 1984).

Collectively, Bergmann's, Lack's and Calder's rules form an interrelated triangle of relationships (Fig. 1). Traditionally these rules have been examined as simple, bivariate relationships based on the assumption that the degree of correlation between two variables accurately reflects the strength of the evolutionary drivers (but see Jetz *et al.*, 2008). However, because two of these ecogeographical relationships are positive while one is negative (Fig. 1), indirect and direct effects between variables may act in opposite directions, effectively masking some relationships while strengthening others (Cartron *et al.*, 2000). Specifically, the possible values of the correlation coefficients are limited by the positive semidefinite (PSD) condition of correlation matrices. In a system of three variables, with two positive and one negative correlation, not all pairwise correlations can be strong (Brown *et al.*, 2004). Although interactions between ecogeographical rules could obscure both the observation of large-scale patterns and their mechanistic interpretation, these potential interactions remain poorly understood (Gaston *et al.*, 2008).

Bergmann's rule has been documented both within and among many bird species (James, 1970; Buehler, 2000; Jackson & Ouellet, 2002; Jackson *et al.*, 2002), and even the house sparrow (*Passer domesticus*) has rapidly evolved a latitudinal body size cline since its introduction to North America (Murphy, 1985; Johnston & Selander, 2008). Large-scale studies at the intraspecific (Ashton, 2002; Meiri & Dayan, 2003) and interspecific (Blackburn & Gaston, 1996; Blackburn *et al.*, 1999; Cardillo, 2002) levels have generally found larger body sizes at higher latitudes, although the interspecific pattern probably reflects both body size adaptation within lineages and lineage turnover across the latitudinal gradient (Meiri &

Thomas, 2007; Olson *et al.*, 2009). Bergmann (1847) originally proposed that, within closely related homeotherms, body size is larger in colder latitudes than in warmer latitudes because large size improves heat conservation via a lower surface area to volume ratio. However, there are many other possible mechanisms that could lead to the same empirical pattern, including patterns of migration (Blackburn & Gaston, 1996; Ramirez *et al.*, 2008; Olson *et al.*, 2009) or that large-bodied species are more resistant to starvation (Calder, 1984; Linstedt & Boyce, 1985). Additionally, the pattern could be affected by strong interactions with a third, correlated variable, such as clutch size.

It has long been recognized that clutch size tends to increase with latitude both between and within species of birds (Rensch, 1938; Lack, 1947, 1948; Ashmole, 1963; Cody, 1966; Kulesza, 1990). For example, the mean clutch size of northern flicker (*Colaptes auratus*) populations increases by about one egg for every 10° increase in latitude (Koenig, 1984). Here we refer to this pattern as Lack's rule in recognition of David Lack's original observations of the pattern and its hypothesized mechanism (Lack, 1947). Several explanations have been proposed for Lack's rule, including day length (Lack, 1947), seasonality of resource supply (Ashmole, 1963) and a trade-off between clutch size and number of clutches per year (Perrins, 1977). While these explanations apply to intraspecific patterns of latitudinal variation in clutch size, as they are based on mechanisms that maximize the reproductive output of individual birds (see Lack, 1947; Perrins & Moss, 1975), it is also consistent with this reasoning that Lack's rule is observed at the interspecific level (Cody, 1966; Ricklefs, 1980; Griebeler & Böhning-Gaese, 2004). If natural selection on clutch size occurs at multiple levels of biological organization, effects across species should be consistent with effects within species. Recent work supports the importance of environmental seasonality (and associated seasonality of mortality) on interspecific patterns of clutch size at a global scale (Jetz *et al.*, 2008).

A negative relationship between clutch size and body size has been observed at the interspecific level in both birds (Ar & Yom-Tov, 1978; Saether, 1987; Cartron *et al.*, 2000; Jetz *et al.*, 2008) and mammals (Millar, 1981; Charnov, 2001; Charnov & Ernest, 2006). Here we refer to this pattern as Calder's rule, for W. A. Calder's pioneering work on avian allometry (e.g. 'clutch sizes are inversely related to [body] size'; Calder, 1984, p. 250 and table 9-1). Calder's rule is often explained as a consequence of a loose trade-off between fecundity and longevity (Charnov & Ernest, 2006). Mass-specific rates of production scale inversely with body size (Brown & Sibly, 2006), and this relationship may represent a fundamental constraint on the rate at which biomass can be produced (Sibly & Brown, 2007). While Calder's rule is commonly observed at higher taxonomic levels, we are unaware of any observations of the relationship at the intraspecific level in birds or mammals. This is not surprising, however, given that intraspecific variation in body size is modest compared to higher taxonomic levels and variation is limited by strong stabilizing selection within species (Covas *et al.*, 2002).
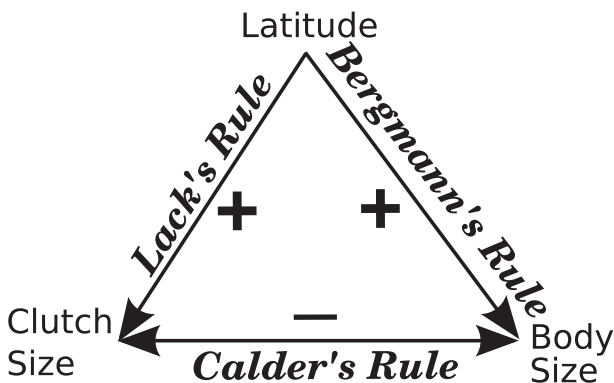

Figure 1 Schematic diagram showing the hypothesized relationships between Lack's rule, Bergmann's rule and Calder's rule in birds. Single-headed arrows represent direct causal effects on dependent variables and the double-headed arrow is a correlation.

Recently, Gaston *et al.* (2008) suggested that study of the interactions between ecogeographical rules could be a significant step towards a synthetic understanding of these pervasive patterns. In the triangle of interactions among body size, clutch size and latitude there is an apparent conflict between the three rules. If Bergmann's rule drives the system then we would expect to observe small clutch sizes at high latitudes, while if Lack's rule dominates it would indirectly produce small body sizes at high latitudes. The trade-offs between conflicting direct and indirect effects in the system may also vary across levels of taxonomic organization, as the three rules tend to vary in strength over the taxonomic hierarchy. Here we examine the relationships among clutch size, body size and latitudinal distribution in a large avian dataset. We use path analysis to quantify interactions between Lack's, Calder's and Bergmann's rules through the taxonomic hierarchy, as a function of both phylogenetic inheritance of traits and indirect feedbacks between the three rules. Do the three rules in this system interact equally or does one rule drive the others? In other words, which came first the chicken, the egg or latitude?

MATERIALS AND METHODS

Data

We gathered data from the literature on clutch size, latitudinal distribution and body size for 1458 species of birds across 409 genera, 25 families and 10 orders (data and references are given in Appendix S1 in Supporting Information). All references used for this study consisted of global treatments of taxonomic groups, with morphological and reproductive information and distribution maps. We limited our analysis to taxonomic groups for which we had data for at least 90% of species. Species restricted to islands were excluded as both body size and clutch size are known to be affected by island living (Klomp, 1970; Clegg & Owens, 2002; Olson *et al.*, 2009). Taxonomy and classification as either altricial or precocial follows references given in Appendix S1. Although there is substantial intraspecific variation in clutch size and body size in many species, and some species are found across a wide range of latitudes, our analysis collapses each trait to a single variable in order to include data for as many species and higher taxa as possible.

We used body length (cm) as a measure of body size, in accordance with previous work showing that the cube of body length is proportional to body mass in birds (Peters, 1983; see Appendix S2). Body length was log-transformed prior to analysis. For clutch size, we used modal clutch size, or the mean of clutch sizes provided (< 20% of species). Since our focus was on interactions between rules, and not necessarily on inferring underlying environmental mechanisms, we used latitude as a proxy for temperature and seasonality, consistent with classic studies (Lack, 1947; Cody, 1966; James, 1970; Koenig, 1984). We estimated the median absolute latitude of each species' breeding range from distribution maps following Cartron *et al.* (2000). For species found in both the Northern and Southern Hemispheres, absolute latitude was calculated as the mean of the northern latitudinal midpoint and the southern latitudinal midpoint, which reflects a species' average dispersion from the equator. We used the latitude of species breeding ranges in order to associate both clutch-laying and body size with a common latitudinal point. If migratory species tend to be small-bodied, as demonstrated in the New World (Ramirez *et al.*, 2008), use of breeding ranges here provides a conservative test of Bergmann's rule.

Analyses

To quantify the strength of the three rules, we measured the interspecific correlations between log body length, clutch size and latitude for species within genera (where $n > 10$ species), species within families, and species within orders using linear regression. We tested for significant overall correlations for each rule at each taxonomic level with standard meta-analysis techniques. Using Fisher's Z-transformation of the correlation coefficient and weighting by sample size, we calculated the weighted common correlation (Z_+) for each rule at each level of taxonomic resolution and tested for a difference from zero (Hedges & Olkin, 1985).

We used path analysis to assess the relative importance of direct and indirect causal paths for each rule at different taxonomic levels. Unlike statistical techniques such as multiple regression where variables are either dependent or independent, path analysis allows the specification of a variable as both a predictor and dependent on other variables (Kline, 2005). The system sketched in Fig. 1 was used as our path model, where clutch size and body size are both dependent on latitude, and there is a negative correlation between them. Path coefficients were computed from the correlation coefficients (given in Table 1), using the following system of equations (Alwin & Hauser, 1975):

$$r(L, B) = p(L, B) + p(L, C) \times p(C, B)$$
$$r(L, C) = p(L, C) + p(L, B) \times p(B, C)$$
$$r(B, C) = p(B, C)$$

where r is the Pearson correlation coefficient between two traits, p is the path coefficient and L, B and C refer to latitude, log body size and clutch size, respectively. We used the path coefficients to decompose correlations into direct and indirect effects, corresponding to direct and indirect paths reflected in the arrows in the model. Since the value of any compound path is the product of its path coefficients, we multiplied the appropriate path coefficients to find the indirect effects. The strengths of indirect and direct effects were compared in each avian group to determine if one ecogeographical rule tends to drive the system. For example, in a given family Bergmann's rule may appear weak due to conflicting interactions with Lack's rule. In this case indirect effects of latitude acting through clutch size on body size may cancel out the direct effect of latitude on body size, despite a positive correlation between body size and latitude.

We also examined the influence of taxonomic and phylogenetic structure on the three rules. We quantified the

Table 1 Pearson correlation coefficients between body size and latitude (Bergmann's rule), clutch size and latitude (Lack's rule) and body size and clutch size (Calder's rule) in birds. No analyses were conducted for Apodiformes and Passeriformes at the order level due to insufficient sampling; for other groups, sampling (*n*) includes ≥ 90% of species.

Group	*n*	Bergmann's rule	Lack's rule	Calder's rule
Apodiformes	–	–	–	–
Apodidae/Hemiprocnidae	57	0.44	0.18*	−0.08
Apus	14	0.44	0.25	−0.01
Collocallia	15	−0.35	0.25	−0.30
Anseriformes	147	0.16*	−0.24*	−0.28*
Anatidae	143	0.20*	−0.30*	−0.26*
Anas	37	0.12	0.30(*)	0.1
Anser	10	−0.52	−0.44	0.52
Ciconiiformes	99	0.05	0.42*	−0.16*
Ardeidae	49	0.10	0.62*	0.02
Egretta	12	0.55(*)	0.32	−0.13
Threskiornithidae	43	0.00	0.43*	0.09
Falconiformes	229	0.07	0.43*	−0.55*
Accipitridae	177	0.08	0.47*	−0.47*
Accipiter	26	0.22	0.77*	0.05
Buteo	25	0.40*	0.64*	0.57*
Circus	13	−0.49(*)	0.91*	−0.60*
Falconidae	51	0.33*	0.26(*)	0.45*
Falco	37	0.42*	0.35*	−0.09
Galliformes	171	−0.06	0.49*	−0.29*
Cracidae	39	−0.08	0.24	−0.54*
Odontophoridae	19	0.03	0.59*	−0.39(*)
Phasianidae	107	0.23*	0.59*	−0.02
Francolinus	30	0.18	0.42*	0.36(*)
Tetraonidae	18	0.13	−0.23	0.11
Passeriformes	–	–	–	–
Corvidae	84	−0.12	0.24*	0.16
Corvus	30	−0.19	0.41*	0.09
Cyanocorax	12	0.32	−0.19	0.14
Turdidae	116	0.01	0.78*	0.17(*)
Catharus	12	0.51(*)	0.94*	0.66*
Monticola	11	0.30	0.30	0.38
Turdus	52	0.07	0.87*	0.01
Zoothera	21	0.35	0.67*	0.20
Piciformes	197	0.14*	0.62*	0.00
Capitonidae	52	0.28*	0.26(*)	0.04
Megalaima	17	0.29	0.60*	0.01
Picidae	121	0.20*	0.65*	0.07
Melanerpes	15	0.71*	0.76*	0.56*
Picoides	31	0.41*	0.54*	0.04
Picus	11	0.56(*)	0.83*	0.51
Ramphastidae	19	−0.11	−0.03	−0.03
Psittaciformes	169	0.22*	0.36*	−0.27*
Amazona	20	−0.47*	0.32	−0.53*
Sphenciformes	17	0.51*	−0.32	−0.69*
Strigiformes	83	0.13	0.50*	−0.27*
Strigidae	77	0.14	0.57*	−0.33*

Significant linear regressions: *$P < 0.05$; (*)$P < 0.10$.

importance of taxonomy in each rule (as a proxy for phylogeny in the absence of a well-resolved phylogenetic tree) by incorporating taxonomy as a nested random effect in a generalized linear mixed-effects model of the entire dataset. These results were compared with a non-taxonomic model on the same variables. Models were fitted to each pairwise relationship using packages lme4 (function *lmer*) and stats (function *glm*) in the R statistical environment (R Foundation for Statistical Computing, 2008), and the Akaike information criterion (AIC; Burnham & Anderson, 2002) was used to identify the preferred model for each rule. We also quantified the partitioning of variation in body size, clutch size and latitude among hierarchical taxonomic levels using mixed-model nested ANOVAs for each trait. Trait values were the dependent variables, and the taxonomic classifications (order/family/genus) were the nested independent variables. Tests were run using the package lme4 (function *lmer*) in R.

To test for the influence of shared evolutionary history on ecogeographical rules, we performed phylogenetic independent contrasts analyses on three groups of birds for which recent phylogenetic trees were available. For the Corvidae, we used a maximum-likelihood tree from Ericson *et al.* (2005), which was based on three genes (cytochrome *b*, myoglobin and *β*-fibrinogen). The tree included 17 of the 24 corvid genera in our dataset (Fig. S1a). For the Falconidae, we used a maximum-likelihood phylogeny inferred from combined molecular and morphological datasets from Griffiths (1999), which included all of the falconid genera in our dataset (Fig. S1b). We used a phylogeny of the Galliformes, which included representatives of all galliform families except the Megapodidae (Kimball *et al.*, 1999). The tree was based on cytochrome *b* nucleotide data and included 26 of the 59 non-megapode galliform genera in our database (Fig. S1c). Since each tree was resolved only to the genus level, we used a polychotomous phylogeny for species within each genus. Internal branch lengths were estimated from the published trees, while a constant arbitrary value was assigned to each of the terminal branches.

We used Felsenstein's (1985) method of independent contrasts to test for relationships between clutch size, log body length and latitude that remain after accounting for phylogeny. Contrasts were calculated using the PDAP package (Midford *et al.*, 2008) implemented in MESQUITE version 2.5 (Maddison & Maddison, 2008). Contrasts were standardized and positivized on the *x*-axis following the methods of Garland *et al.* (1992) and linear regressions through the origin were performed. We compared our results with the analogous independent contrasts analysis conducted for Strigidae by Cartron *et al.* (2000).

RESULTS

Quantifying the three rules

Although support for each rule varied among clades, generally each rule was more widespread towards higher taxonomic

levels (Table 1). Bergmann's rule was supported in about one-third of genera, one-third of families and half of the orders (Fig. S2). A reverse Bergmann's rule was observed in two genera (*Circus* and *Amazona*). Lack's rule was supported in the majority of genera, families and orders (Fig. S3). A reverse Lack's rule was observed in one family (Anatidae), leading to a reversal of the rule at the order level (Anseriformes) as well. We found support for Calder's rule in only two genera, while the rule was reversed in four genera. However, support for the rule increased towards higher taxonomic levels, with support in about half of families and 90% of orders (Fig. S4). No difference in support for Lack's and Calder's rules was found when altricial and precocial species were analysed separately (cross-species linear regression; Lack's rule altricial: $n = 1045$, slope $= 0.034 \pm 0.003$, $r^2 = 0.14$, $P < 0.001$; Lack's rule precocial: $n = 342$, slope $= 0.042 \pm 0.009$, $r^2 = 0.05$, $P < 0.001$; Calder's rule altricial: $n = 1045$, slope $= -1.000 \pm 0.157$, $r^2 = 0.04$, $P < 0.001$; Calder's rule precocial: $n = 342$, slope $= -3.168 \pm 0.959$, $r^2 = 0.03$, $P < 0.01$).

Overall, meta-analysis revealed significant support for Bergmann's rule at all taxonomic levels (genera: $Z_+ = 3.78$, $P = 0.02$; families: $Z_+ = 4.50$, $P < 0.01$; orders: $Z_+ = 3.53$, $P = 0.04$; Fig. 2a). Lack's rule was also strongly supported at all taxonomic levels (genera: $Z_+ = 13.09$, $P < 0.01$; families: $Z_+ = 14.80$, $P < 0.01$; orders: $Z_+ = 13.47$, $P < 0.01$; Fig. 2b). Overall, Calder's rule was only supported at the order level (genera: $Z_+ = 2.09$, $P > 0.50$; families: $Z_+ = -3.41$, $P < 0.06$; orders: $Z_+ = -9.91$, $P < 0.01$; Fig. 2c).

Path analysis of direct and indirect effects

Using path analysis to partition direct and indirect effects in the system of interacting rules, we found Lack's rule to have the strongest direct effects of the three rules at the genus, family and order levels (Fig. 3). Lack's rule was overridden by negative indirect effects in only one group, the Sphenisciformes, where there was little variation in clutch size (one to two eggs per clutch) and the other rules were quite strong. Direct effects for Bergmann's rule were relatively strong at the genus level (Fig. 3a), but negative indirect effects of latitude on body size increased in strength towards higher taxonomic levels (Fig. 3b,c). Negative indirect effects ($L \rightarrow C \rightarrow B$) outweighed direct effects of latitude on body size (Bergmann's rule; $L \rightarrow B$) in three orders (Ciconiiformes, Falconiformes and Strigiformes) and four families (Accipitridae, Odontophoridae, Strigidae and Threskiornithidae). Calder's rule was quite weak at the genus level (Fig. 3a), but increased dramatically in strength towards higher taxonomic levels (Fig. 3b,c).

Taxonomic and phylogenetic structure

Linear mixed-effects models showed that taxonomy is an important component of the three rules. Taxonomic models provided an improved fit over non-taxonomic models for Bergmann's and Lack's rules for all species in the dataset without significantly altering the slopes of the relationships
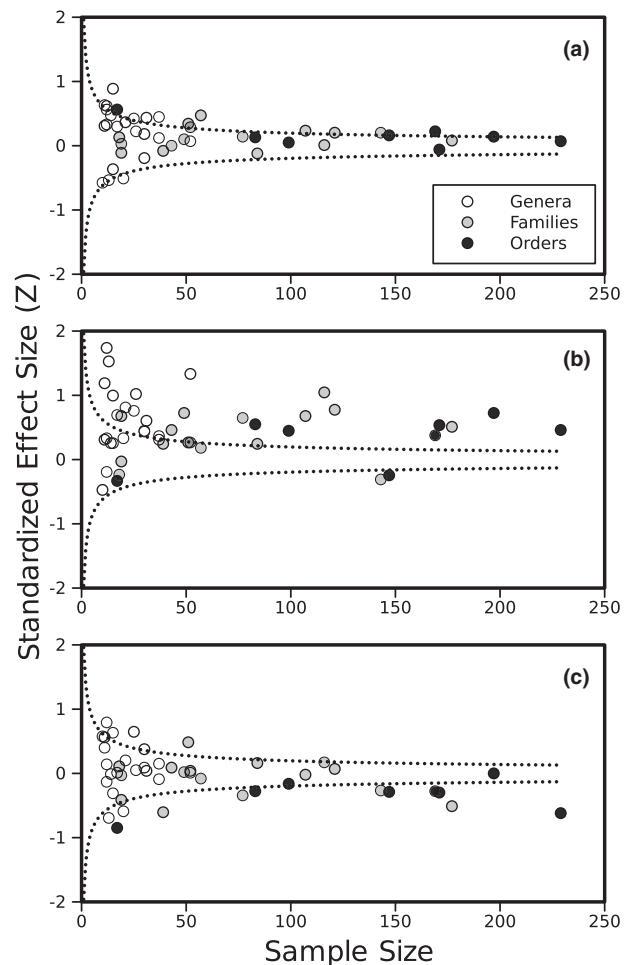

Figure 2 Standardized effect size (Z) versus sample size for (a) Bergmann's, (b) Lack's and (c) Calder's rules in 21 genera, 16 families and 8 orders of birds. Dotted lines show upper and lower critical values for Z with sample size (two-tailed test, $\alpha = 0.05$).

(Table 2). For Calder's rule the taxonomic model was a better fit to the data and also provided support for a negative relationship between clutch size and body size where the cross-species model did not.

Variation in body size, clutch size and latitude are unequally distributed over the taxonomic hierarchy (Table 3). Variation in clutch size and body size was highest at the order level, suggesting that these traits are substantially phylogenetically conserved. Latitude was most variable at the level of individual species, an indication that individualistic ecological processes have a major influence on latitudinal distribution of bird species.

Regressions on phylogenetic independent contrasts (PIC) and raw regressions consistently showed the same relationships to be strongest in each clade – Lack's rule in Corvidae, Galliformes and Strigidae, and Calder's rule in the Falconidae (based on r^2 values; Table 4). Regressions on PIC supported Lack's rule in three of the four studied clades, while Calder's rule was supported in two clades and Bergmann's rule was supported in one clade. For the Corvidae, PIC results matched the raw regressions for this group; Lack's rule and Calder's rule
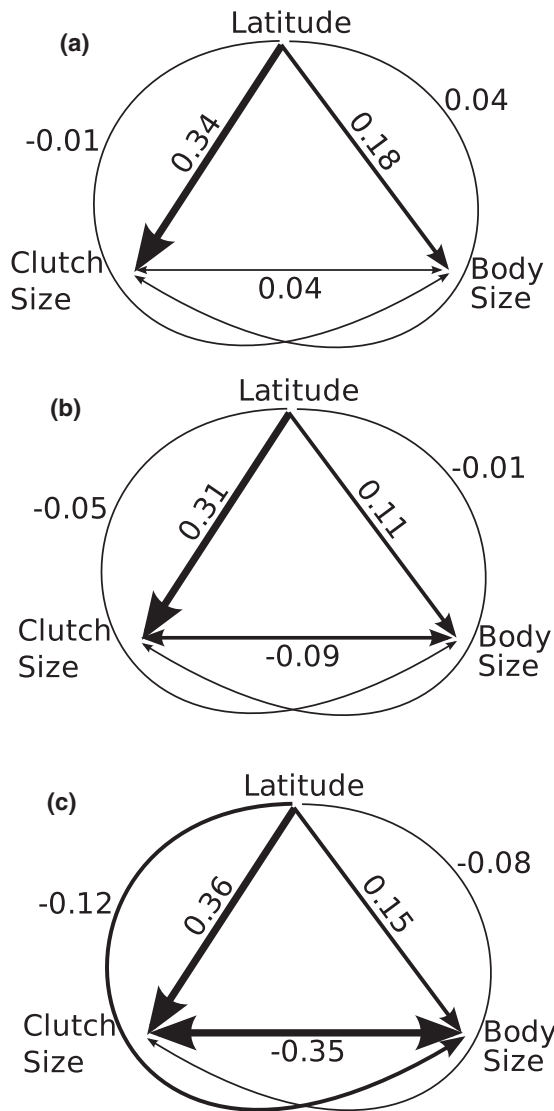
Figure 3 Path diagrams for relationships between Lack's rule, Bergmann's rule and Calder's rule in birds showing coefficients for mean direct and indirect effects at the (a) genus ($n = 21$), (b) family ($n = 16$) and (c) order ($n = 8$) levels. The width of lines and arrows is proportional to the absolute magnitude of the corresponding path coefficients.

were supported. In the Falconidae, PIC analysis did not support Lack's or Bergmann's rules, in contrast to the raw regression results. However, support for Calder's rule remained strong. The PIC analysis on the Galliformes found no support for Calder's rule but maintained support for Lack's rule. Finally, as reported by Cartron *et al.* (2000), PIC regressions found Lack's and Bergmann's rules in the Strigidae but did not support Calder's rule.

DISCUSSION

We found strong interactions between Bergmann's, Lack's and Calder's rules in birds, and these interactions vary in strength

Table 2 Results of generalized linear models quantifying taxonomic effects on ecogeographical rules in birds. All relationships are significant ($P < 0.05$); ΔAIC is the difference in AIC between the two models ($\text{AIC}_{\text{cross-species}} - \text{AIC}_{\text{taxonomic}}$) for each rule. Taxonomy significantly improved model fit for each rule.

		Cross-species model	Taxonomic model	
	n	Slope $\pm$ SE	Slope $\pm$ SE	ΔAIC
Bergmann's rule	1457	0.003 ± 0.000	0.001 ± 0.000	2678
Lack's rule	1389	0.057 ± 0.004	0.034 ± 0.002	1849
Calder's rule	1389	0.709 ± 0.285	-0.013 ± 0.357	1848

Table 3 Results of nested ANOVAs on variation of clutch size, body size and latitude in birds through the taxonomic hierarchy ($\text{d.f.}_{\text{order}} = 9$, $\text{d.f.}_{\text{family}} = 15$, $\text{d.f.}_{\text{genus}} = 366$, $\text{d.f.}_{\text{residual}} = 998$). Deviance (DE) accounted for in each taxonomic level is given, with %DE in parentheses. The largest proportion for each variable is given in bold type. After accounting for higher taxonomic levels, residual variation represents the variation between individual species in a genus.

	Order	Family	Genus	Residual
Clutch size	4076 (**45%**)	1653 (18%)	2370 (26%)	998.3 (11%)
Log body size	41.2 (**50%**)	11.3 (14%)	25.5 (31%)	4.48 (5%)
Median latitude	61785 (17%)	34413 (10%)	116842 (34%)	142332 (**40%**)

and direction over the taxonomic hierarchy and among avian clades. While overall support was strong for both Bergmann's and Lack's rules at all levels of biological organization, and for Calder's rule at the order level (Fig. 2), substantial variation was found between clades in the strength and interactions of ecogeographical rules. For example, Bergmann's rule was reversed in *Circus* and *Amazona* and Lack's rule was reversed in Anatidae and Anseriformes. These reversals were not attributable to conflicting indirect effects and therefore may reflect genuine exceptional macroecological patterns in these groups.

Each rule was detected with increasing frequency towards higher (more inclusive) taxonomic levels. The simplest explanation for this pattern is based on the statistical power of linear regression analysis. With a large sample size and sufficient range of variation in the traits, significant correlations may be detected at higher taxonomic levels even though the correlation is relatively weak. The observation of strong interactions between rules, coupled with issues of statistical power at low taxonomic levels, introduces the notion of a 'threshold of detection' for ecogeographical rules. Pairwise relationships may be undetectable when variation is too low or when conflicting processes are very strong, even when an underlying selective mechanism is operating.

Table 4 Pairwise linear regression results for ecogeographical rules in birds showing regressions on phylogenetic independent contrasts (PIC) and analogous results from raw data (rounded to four significant figures).

	Group	n	Bergmann's rule		Lack's rule		Calder's rule	
			Slope ± SE	r^2	Slope ± SE	r^2	Slope ± SE	r^2
PIC	Corvidae	71	−0.000 ± 0.001	0.01	0.022 ± 0.009*	0.08	1.371 ± 1.586(*)	0.02
	Falconidae	17	0.001 ± 0.001	0.03	0.011 ± 0.008	0.12	−3.735 ± 1.756*	0.22
	Galliformes	104	0.001 ± 0.001	0.01	0.091 ± 0.018**	0.20	0.857 ± 1.975	0.00
	Strigidae	70	0.001 ± 0.001(*)	0.04	0.049 ± 0.008**	0.33	−1.023 ± 1.603	0.01
Raw	Corvidae	112	0.001 ± 0.000	0.00	0.018 ± 0.008*	0.06	1.512 ± 0.904(*)	0.02
	Falconidae	50	0.003 ± 0.001*	0.08	0.015 ± 0.007(*)	0.06	−2.239 ± 0.781**	0.13
	Galliformes	231	−0.000 ± 0.000	0.00	0.112 ± 0.017**	0.18	−4.542 ± 1.334**	0.05
	Strigidae	76	0.002 ± 0.002	0.01	0.055 ± 0.009**	0.31	−2.532 ± 0.777**	0.11

Significance codes: **$P < 0.01$, *$P < 0.05$, (*)$P < 0.10$.

The three rules do not interact equally. Both meta-analysis and path analysis showed Lack's rule to be the strongest rule at all taxonomic levels. Clutch size varies considerably among species and across regions and is subject to strong selective pressures (Bennett & Owens, 2002; Jetz *et al.*, 2008). Although precocial and altricial birds differ substantially in clutch size and reproductive allocation (Starck & Ricklefs, 1998), both groups showed a nearly parallel increase in clutch size with latitude (see Results). In addition, although there is a strong phylogenetic component, clutch size may be slightly less phylogenetically constrained than body size (Table 3), making it more readily adaptable to local conditions.

Factors hypothesized to influence interspecific patterns of clutch size fall into four main categories. First are proximate environmental constraints, including: (1) length of day (Lack, 1947); (2) distance from nest to feeding grounds (seabirds that forage close to shore tend to lay more eggs than those foraging far offshore; Lack, 1968; Weimerskirch, 2001); and (3) abundance of resources relative to breeding population densities (Ashmole's seasonality hypothesis; Ashmole, 1963; Ricklefs, 1980; Hussell, 1985). Most of these factors could be captured to a large extent by latitude. Second are constraints based on predation, where predation pressure selects for smaller clutch size because large broods tend to be noisier and attract more predators (Skutch, 1949; Cody, 1966; Slagsvold, 1982). The extent to which latitude reflects a gradient in predation pressure is unclear. Third, constraints based on nest size (Slagsvold, 1982) and nest type (open cup versus cavity nesters; Jetz *et al.*, 2008) have also been recognized. Finally, clutch size has been hypothesized to be influenced through trade-offs with other life-history traits, including life expectancy of the adults but also, among others, egg size and body size (Williams, 1966; Figuerola & Green, 2006). Here we treat latitude as only a surrogate variable for broad environmental conditions, but the strength and ubiquity of Lack's rule both within and among species suggests that for many birds clutch size may be closely regulated by the local breeding environment (Jetz *et al.*, 2008). The latitudinal increase in clutch size may in some cases be masked or even reversed through life-

history trade-offs, but overall clutch size seems to be directly selected in response to proximate constraints.

Bergmann's and Calder's rules appear to trade-off in strength over the taxonomic hierarchy, with Bergmann's rule stronger for species within genera and Calder's rule stronger at the order level. The trade-off comes from the shifting of strength from direct effects of latitude on body size ($L \rightarrow B$) within genera, to the negative indirect pathway from latitude to body size ($L \rightarrow C \rightarrow B$) at higher taxonomic levels (Fig. 3). The indirect pathway was strong enough to outweigh the direct Bergmann's rule in Accipitridae, Strigidae and Threskiornithidae, and in the orders to which these families belong. Direct effects were also swamped in the Odontophoridae, but not in the Galliformes as a whole. In these groups, spanning wide latitudinal and body size ranges, clutch size appears to be more tightly regulated by latitude than is body size. Bergmann's rule may be strongest and most readily observed among closely related species, where other ecological and life-history traits are similar (Olson *et al.*, 2009), and where body size is an important niche for climate adaptation (Diniz-Filho *et al.*, 2007). Within higher taxonomic levels Bergmann's rule probably reflects a combination of local adaptation and taxonomic turnover across latitude (Meiri & Thomas, 2007; Olson *et al.*, 2009).

The strength and direction of the allometry of clutch size (Calder's rule) depends on the level of taxonomic resolution. In our meta-analysis the rule was significant only at the order level, and the rule was reversed in more genera (positive correlation, 4/21) than supported it (negative correlation, 2/21). Perhaps this should not be surprising considering that positive relationships are observed within many invertebrates and ectothermic vertebrates, and are attributed to an effect of non-asymptotic growth allowing older, larger females to produce larger clutches (Fitch, 1970; Shine, 1988; Du *et al.*, 2005). The extent to which this effect occurs in birds is unknown. Additionally, in many genera any relationship between body size and clutch size may be masked if stabilizing selection limits variation in the two variables (Table 3). The strong order-level Calder's rule pattern may not result from a common selective mechanism, as genera show a variety of

patterns (Fig. S4). The overall negative relationship may instead reflect turnover of lower taxa through the spectrum of body size and clutch size as each taxon maximizes its production relative to the constraints (Sibly & Brown, 2007). Furthermore, a negative Calder's rule was detectable across all species in the dataset only after controlling for differences between taxonomic groups (Table 2).

The complicated relationships among body size, clutch size and latitude at different levels of taxonomic resolution are largely due to the way that the three factors are interrelated. Consequently, they form a paradoxical or conflicting triangle of direct and indirect relationships. Because of the positive semidefinite condition of correlation matrices (Brown *et al.*, 2004), the pairwise correlations predicted by the three rules cannot simultaneously all be strong. If an analysis has sufficient statistical power (i.e. sufficient sample size and range of variation in all variables) the three rules may be detected by significant correlations, even though some of these correlations may be relatively weak. However, the strengths of the underlying processes vary among taxonomic groups and environmental settings, and not all avian groups show the expected relationships. Conflicting direct and indirect relationships obviously complicate the process of inferring biological mechanisms from simple correlations.

A recent *Science* perspective proposed that conflicting interactions, rather than cooperation, may be a common thread across all complex systems (Binder, 2008). Many complex macroecological patterns are probably interrelated with other patterns that may indirectly feed back on each other. Thus, caution is urged when testing for rules that lie in a larger nexus of interrelated patterns, some of them negative and therefore potentially operating in opposition. The apparently conflicting pairwise relationships among clutch size, body size and latitude illustrate the difficulty of interpreting individual pairwise correlations without recognition of possible interdependence with other important variables (Brown *et al.*, 2004; Holt & Slade, 2004). For this reason, we advocate the use of multivariate techniques to tease apart macroecological systems of potentially conflicting interactions.

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REFERENCES

Alwin, D.F. & Hauser, R.M. (1975) The decomposition of effects in path analysis. *American Sociological Review*, **40**, 37–47.

Ar, A. & Yom-Tov, Y. (1978) The evolution of parental care in birds. *Evolution*, **32**, 655–669.

Ashmole, N.P. (1963) The regulation of numbers of tropical oceanic birds. *Ibis*, **103b**, 458–473.

Ashton, K.G. (2002) Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Global Ecology and Biogeography*, **11**, 505–523.

Bennett, P.M. & Owens, I.P.F. (2002) *Evolutionary ecology of birds*. Oxford University Press, New York.

Bergmann, C. (1847) Über die Verhältnisse der Wärmekönomie der Tiere zu ihrer Grösse. *Göttinger Studien*, **1**, 595–708.

Binder, P.M. (2008) Frustration in complexity. *Science*, **320**, 322–323.

Blackburn, T.M. & Gaston, K.J. (1996) Spatial patterns in the body sizes of bird species in the New World. *Oikos*, **77**, 436–446.

Blackburn, T.M., Gaston, K.J. & Loder, N. (1999) Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions*, **5**, 165–174.

Brown, J.H. & Sibly, R.M. (2006) Life-history evolution under a production constraint. *Proceedings of the National Academy of Sciences USA*, **103**, 17595–17599.

Brown, J.H., Bedrick, E.J., Ernest, S.K.M., Cartron, J.-L.E. & Kelly, J.F. (2004) Constraints on negative relationships: mathematical causes and ecological consequences. *The nature of scientific evidence* (ed. by M. Taper and S. Lele), pp. 298–308. University of Chicago Press, Chicago.

Buehler, D.A. (2000) Bald eagle (*Haliaeetus leucocephalus*). *The birds of North America online* (ed. by A. Poole). Cornell Laboratory of Ornithology, Ithaca. Available at: http://bna.birds.cornell.edu/bna/species/506/ (accessed 21 April 2009).

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. Springer-Verlag, New York.

Calder, W.A., III (1984) *Size, function, and life history*. Harvard University Press, Cambridge, MA.

Cardillo, M. (2002) Body size and latitudinal gradients in regional diversity of New World birds. *Global Ecology and Biogeography*, **11**, 59–65.

Cartron, J.-L.E., Kelly, J.F. & Brown, J.H. (2000) Constraints on patterns of covariation: a case study in strigid owls. *Oikos*, **90**, 381–389.

Charnov, E.L. (2001) Evolution of mammal life histories. *Evolutionary Ecology Research*, **3**, 521–535.

Charnov, E.L. & Ernest, S.K.M. (2006) The offspring-size/clutch-size trade-off in mammals. *The American Naturalist*, **167**, 578–582.

Clegg, S.M. & Owens, I.P. (2002) The 'island rule' in birds: medium body size and its ecological explanation. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 1359–1365.

Cody, M.L. (1966) A general theory of clutch size. *Evolution*, **20**, 174–184.

Covas, R., Brown, C.R., Anderson, M.D. & Brown, M.B. (2002) Stabilizing selection on body mass in the sociable weaver

Philetairus socius. Proceedings of the Royal Society B: Biological Sciences, **269,** 1905–1909.

Diniz-Filho, J.A.F., Bini, L.M., Rodriguez, M.A., Rangel, T.F. & Hawkins, B.A. (2007) Seeing the forest for the trees: partitioning ecological and phylogenetic components of Bergmann's rule in European Carnivora. *Ecography*, **30,** 598–608.

Du, W., Ji, X. & Shine, R. (2005) Does body volume constrain reproductive output in lizards? *Biology Letters*, **1,** 98–100.

Ericson, P.G.P., Jansen, A.-L., Johansson, U.S. & Ekman, J. (2005) Inter-generic relationships of the crows, jays, magpies and allied groups (Aves: Corvidae) based on nucleotide sequence data. *Journal of Avian Biology*, **36,** 222–234.

Felsenstein, J. (1985) Phylogenies and the comparative method. *The American Naturalist*, **125,** 1–15.

Figuerola, J. & Green, A.J. (2006) A comparative study of egg mass and clutch size in the Anseriformes. *Journal für Ornithologie*, **147,** 57–68.

Fitch, H.S. (1970) Reproductive cycles in lizards and snakes. *University of Kansas Museum of Natural History Miscellaneous Publications*, **52,** 1–247.

Garland, T.J., Harvey, P.H. & Ives, A.R. (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology*, **41,** 18–32.

Gaston, K.J., Chown, S.L. & Evans, K.L. (2008) Ecogeographical rules: elements of a synthesis. *Journal of Biogeography*, **35,** 483–500.

Griebeler, E.M. & Böhning-Gaese, K. (2004) Evolution of clutch size along latitudinal gradients: revisiting Ashmole's hypothesis. *Evolutionary Ecology Research*, **6,** 679–694.

Griffiths, C.S. (1999) Phylogeny of the Falconidae inferred from molecular and morphological data. *The Auk*, **116,** 116–130.

Hedges, L.V. & Olkin, I. (1985) *Statistical methods for meta-analysis*. Academic Press, Orlando, FL.

Holt, R.D. & Slade, N. (2004) Constraints come in many colors. *The nature of scientific evidence* (ed. by M. Taper and S. Lele), pp. 308–315. University of Chicago Press, Chicago.

Hussell, D.J.T. (1985) Clutch size, daylength and seasonality of resources: comments on Ashmole's hypothesis. *The Auk*, **102,** 632–634.

Jackson, J.A. & Ouellet, H.R. (2002) Downy woodpecker (*Picoides pubescens*). *The birds of North America online* (ed. by A. Poole). Cornell Laboratory of Ornithology, Ithaca. Available at: http://bna.birds.cornell.edu/bna/species/613/ (accessed 21 April 2009).

Jackson, J.A., Ouellet, H.R. & Jackson, B.J.S. (2002) Hairy woodpecker (*Picoides villosus*). *The birds of North America online* (ed. by A. Poole). Cornell Laboratory of Ornithology, Ithaca. Available at: http://bna.birds.cornell.edu/bna/species/702/ (accessed 21 April 2009).

James, F. (1970) Geographic size variation in birds and its relationship to climate. *Ecology*, **51,** 365–390.

Jetz, W., Sekercioglu, C. & Böhning-Gaese, K. (2008) The worldwide variation in avian clutch size across species and space. *PloS Biology*, **6,** e303.

Johnston, R.F. & Selander, R.K. (2008) House sparrows rapid evolution of races in North America. *Urban ecology: an international perspective on the interaction between humans and nature* (ed. by J.M. Marzluff, E. Shulenberger, W. Endlicher and M. Alberti), pp. 315–320. Springer-Verlag, New York.

Kimball, R.T., Braun, E.L., Zwartjes, P.W., Crowe, T.M. & Ligon, J.D. (1999) A molecular phylogeny of the pheasants and partridges suggests that these lineages are not monophyletic. *Molecular Phylogenetics and Evolution*, **11,** 38–54.

Kline, R.B. (2005) *Principles and practice of structural equation modeling*, 2nd edn. Guilford Press, New York.

Klomp, H. (1970) The determination of clutch-size in birds. *Ardea*, **58,** 1–124.

Koenig, W.D. (1984) Geographic variation in clutch size in the Northern Flicker (*Colaptes auratus*): support for Ashmole's hypothesis. *The Auk*, **101,** 698–706.

Kulesza, G. (1990) An analysis of clutch-size in New World passerine birds. *Ibis*, **132,** 407–422.

Lack, D. (1947) The significance of clutch size. Parts I and II. *Ibis*, **89,** 302–352.

Lack, D. (1948) The significance of clutch size. Part III. Some interspecific comparisons. *Ibis*, **90,** 25–45.

Lack, D. (1968) *Ecological adaptations for breeding in birds*. Methuen, London.

Linstedt, S.L. & Boyce, M.S. (1985) Seasonality, fasting endurance, and body size in mammals. *The American Naturalist*, **125,** 873–878.

Lomolino, M.V., Sax, D.F., Riddle, B.R. & Brown, J.H. (2006) The island rule and a research agenda for studying ecogeographic patterns. *Journal of Biogeography*, **33,** 1503–1510.

Maddison, W. & Maddison, D. (2008) *Mesquite: a modular system for evolutionary analysis, version 2.5*. Available at: http://www.mesquiteproject.org/ (accessed 25 October 2008).

Meiri, S. & Dayan, T. (2003) On the validity of Bergmann's rule. *Journal of Biogeography*, **30,** 331–351.

Meiri, S. & Thomas, G.H. (2007) The geography of body size – challenges of the interspecific approach. *Global Ecology and Biogeography*, **16,** 689–693.

Midford, P., Garland, T.J. & Maddison, W. (2008) *PDAP: PDTREE: a translation of the PDTREE application of Garland et al.'s phenotypic diversity analysis programs, version 1.13*. Available at: http://www.mesquiteproject.org/pdap_mesquite (accessed 25 October 2008).

Millar, J.S. (1981) Pre-partum reproductive characteristics of eutherian mammals. *Evolution*, **35,** 1149–1163.

Murphy, E.C. (1985) Bergmann's rule, seasonality and geographic variation in body size of house sparrows. *Evolution*, **39,** 1327–1334.

Olson, V.A., Davies, R.G., Orme, C.D.L., Thomas, G.H., Meiri, S., Blackburn, T.M., Gaston, K.J., Owens, I.P.F. & Bennett, P.M. (2009) Global biogeography and ecology of body size in birds. *Ecology Letters*, **12,** 249–259.

Perrins, C.M. (1977) The role of predation in the evolution of clutch size. *Evolutionary ecology* (ed. by B. Stonehouse and C. Perrins), pp. 181–191. University Park Press, Baltimore, MD.

Perrins, C.M. & Moss, D. (1975) Reproductive rates in the great tit. *Journal of Animal Ecology*, **44**, 695–706.

Peters, R.H. (1983) *The ecological implications of body size.* Cambridge University Press, Cambridge.

R Foundation for Statistical Computing (2008) *R: A language and environment for statistical computing, version 2.8.1.* Available at: http://www.r-project.org/ (accessed 22 December 2008).

Ramirez, L., Diniz-Filho, J.A.F. & Hawkins, B.A. (2008) Partitioning phylogenetic and adaptive components of the geographical body-size pattern of New World birds. *Global Ecology and Biogeography*, **17**, 100–110.

Rensch, B. (1938) Some problems of geographical variation and species-formation. *Proceedings of the Linnean Society of London B: Biological Sciences*, **150**, 275–285.

Ricklefs, R.E. (1980) Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. *The Auk*, **97**, 38–49.

Saether, B.-E. (1987) The influence of body weight on the covariation between reproductive traits in European birds. *Oikos*, **48**, 79–88.

Shine, R. (1988) The evolution of large body size in females: a critique of Darwin's 'fecundity advantage' model. *The American Naturalist*, **131**, 124–131.

Sibly, R.M. & Brown, J.H. (2007) Effects of body size and lifestyle on evolution of mammal life histories. *Proceedings of the National Academy of Sciences USA*, **104**, 17707–17712.

Skutch, A.F. (1949) Do tropical birds raise as many young as they can nourish? *Ibis*, **100**, 1–30.

Slagsvold, T. (1982) Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia*, **54**, 159–169.

Starck, J.M. & Ricklefs, R.E. (1998) *Avian growth and development: evolution within the altricial precocial spectrum.* Oxford University Press, New York.

Weimerskirch, H. (2001) The demography of seabirds and its relationship with the marine environment. *Biology of marine birds* (ed. by E.A. Schreiber and J. Burger), pp. 115–135. CRC Press, Boca Raton, FL.

Williams, G.C. (1966) Natural selection, the costs of reproduction, and a refinement of Lack's principle. *The American Naturalist*, **100**, 687–690.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Figure S1 Phylogenetic trees used in independent contrasts analysis for (a) Corvidae, (b) Falconidae and (c) Galliformes.

Figure S2 Linear regression results for Bergmann's rule in birds: log body length versus midpoint of latitudinal range, with species as data points within (a) genera, (b) families and (c) orders.

Figure S3 Linear regression results for Lack's rule in birds: median clutch size versus midpoint of latitudinal range, with species as data points within (a) genera, (b) families and (c) orders.

Figure S4 Linear regression results for Calder's rule in birds: median clutch size versus log body length, with species as data points within (a) genera, (b) families and (c) orders.

Appendix S1 Data table and references for clutch size, body length and latitudinal midpoint for all bird species used in the analysis.

Appendix S2 Analysis of the relationship between body length and body mass in birds.

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