

Constraints on patterns of covariation: a case study in strigid owls

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In a system of intercorrelated variables, the sign and strength of pairwise relationships must conform to a mathematical constraint affecting the entire system. The constraint exists as a property of all correlation matrices, the positive semi-definite (PSD) criterion. We illustrate its implications with a case study of covariation among clutch size, body size, and latitude in the Strigidae. Our analyses indicate that clutch size and body size among strigid owls increase with latitude, while clutch size decreases with body size. The PSD provides a framework to explain the existence of this apparent macroevolutionary paradox. It also shows why the three relationships are never detected concurrently when using simple regressions or independent contrasts. In a system with three intercorrelated variables, the PSD criterion may allow one pairwise relationship to be negative even if the other two relationships are positive. However, the correlation coefficients cannot all be strong. Whenever the PSD criterion may constrain covariation, care should be exercised in inferring evolutionary or ecological processes from patterns of correlation.

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Ecologists, particularly those who address large-scale or evolutionary questions, rely extensively on the repeated occurrence of patterns to infer both their general nature and the operation of underlying mechanisms (Brown and Maurer 1989, Gaston and Blackburn 1999). In the past, exceptions to an ecogeographic rule or to a global pattern of species diversity have been used to argue against the significance of such a pattern or the mechanistic explanation proposed for it (e.g., McNab 1971, Stevenson 1986, Geist 1987, Gaston et al. 1998). Yet, the possibility exists that the mechanism is operating but its effects are obscured by another, stronger mechanism through interrelationships with other variables. This is especially likely when a correlation analysis is used to infer relationships among multiple variables, and some of the correlations are negative (Brown et al. in press).

From a mathematical perspective, limits on the magnitude of covariation can arise due to the positive semi-definite (PSD) criterion, a property of all correlation matrices (Rao 1973: 107, Jobson 1992: 571, 629,

Brown et al. in press). The PSD criterion constrains all eigenvalues and the determinant of each principal minor in a correlation matrix to values greater than or equal to zero (Jobson 1992: 571). Although the mathematical underpinnings of the PSD criterion are described in detail elsewhere (Brown et al. in press), it may be useful to illustrate it here with two simple examples. In the case of a 3×3 matrix of correlation coefficients, when all three variables are perfectly correlated, all three correlation coefficients must be $+1$, or two must be -1 and one must be $+1$; it is a mathematical impossibility for two to be $+1$ and one to be -1 . When only one of the correlation coefficients is negative, at least one of the pairwise correlations must be less than perfect (Fig. 1). Another example that can be quantified is when all correlation coefficients are equal. Then, the constraint on the correlation coefficients of the correlation matrix can be expressed by the following formula:

$$-1/(1-n) \leq r \leq 1, \quad (1)$$

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where r are the correlation coefficients and n is the number of variables. Whereas no constraint operates on the possible values of r if the relationships are positive, in the case of negative relationships, there is a lower bound which deviates away from -1 and towards 0 as n increases. For example, in the case of three variables the lowest possible value is -0.5 , and in the case of 11 variables it is -0.1 . Note that these are the limits on the possible values of correlation coefficients. The proportion of variation explained by a correlation is given by the coefficient of determination, R^2 , which will be smaller than the correlation coefficient. A simple, non-mathematical interpretation of the PSD is that the magnitude of covariation is limited whenever there are direct and indirect effects operating in opposite directions.

The implications of the PSD criterion are important for macroecology or for any comparative studies relying on analyses of correlation. In a system with three life history or ecological variables, one implication is that the signs of two of the three pairwise relationships may be a weak predictor of the sign of the third. In particular, if two of the three relationships are weak and positive, the PSD criterion allows the third relationship to be positive, but also negative. Another implication is that, if two correlations are expected to be positive and one negative, the predicted relationships may not all be observed. Even though all of the mechanistic processes on which the predictions are based are actually operating, the expected outcomes may be obscured by the constraint on the magnitude of covariation. The implications of the PSD criterion remain for systems with more than three variables. Finally, the existence of the PSD criterion is one reason why, in an analysis containing multiple variables, it is important to consider all meaningful dimensions (Pease and Bull 1988).

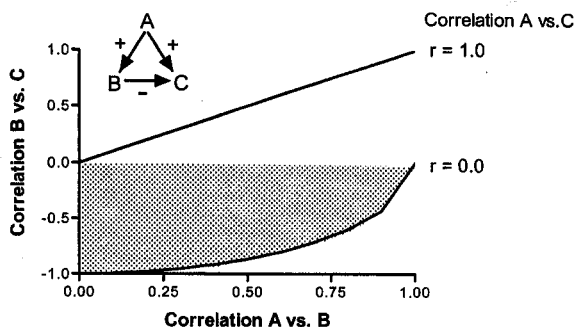


Fig. 1. Constraints on multiple pairwise correlation coefficients due to the positive semi-definite criterion. The area between the lines represents all possible combinations of correlation coefficients for three variables. The lines are defined by the roots of the quadratic: $r_{ab} \times r_{ac} \pm \sqrt{r_{ab}^2 \times r_{ac}^2 + (1 - r_{ab}^2 - r_{ac}^2)}$. Where r_{ab} and r_{ac} are pairwise correlation coefficients. The shaded region indicates those values that are possible when two of the correlations are positive (A vs B and A vs C) and one is negative (B vs C).

We illustrate the implications of the PSD criterion with a case study of covariation among three life history and ecological traits in strigid owls: clutch size, body size, and latitudinal position. A significant finding of comparative and ecological studies has been the repeated occurrence of patterns of variation involving pairwise combinations of these three traits. The first relationship consists of a similar negative allometry for litter or clutch size among mammals and birds (see Rahn and Ar 1974, Western and Ssemakula 1982, Calder 1984). The second is Bergmann's rule, the tendency for body size to increase with increasing latitude, which has been described for mammals, birds, reptiles, and many invertebrates (e.g., Bergmann 1847, Allee et al. 1949, Hess et al. 1951, Krumbiegel 1954, Rensch 1960, Mayr 1963, James 1970, Smith et al. 1995, Van Voorhies 1996). The last pattern of variation, not claimed as an ecogeographic rule but perhaps equally as prevalent as Bergmann's rule, is the increase in clutch or litter size with increasing latitude in both birds and mammals (Rowan and Keith 1956, Burns and Burns 1957, Lord 1960, Cody 1966, Klomp 1970, Conaway et al. 1974, Morton 1976, Murray 1976, Fleming and Rauscher 1978, Innes 1978, Cockburn et al. 1983, Koenig 1984, Millar 1989).

The negative allometry of clutch or litter size, the increase in clutch or litter size with latitude, and the increase in body size with latitude have typically been examined in isolation. These patterns have not always been observed in empirical studies of different taxonomic or functional groups, resulting in considerable debate about their generality and functional basis (e.g., Ashmole 1963, Cody 1966, James 1970, Klomp 1970, Johnston and Selander 1971, McNab 1971, Irving 1972, McMahon 1973, Rahn and Ar 1974, Ricklefs 1980, Calder 1984, Koenig 1984, Geist 1987, Charnov 1993, Hawkins and Lawton 1995, Smith et al. 1995, Hadley 1997). Importantly, the three patterns of variation are necessarily interrelated (Fig. 2). Further, because two of the relationships are positive and the third is negative, collectively they form an apparent evolutionary paradox. If each relationship is only considered separately, then large body sizes and large clutch or litter sizes should generally be expected at high latitudes. Yet, the direct, latitudinal increase in body size and clutch or litter size seems precluded by the fact that latitude also influences these two variables indirectly (i.e., latitude influences body size through clutch or litter size and clutch or litter size through body size) and that indirect and direct effects of latitude have opposite signs.

Where the paradox exists, it represents one example of a complex system with interrelated variables and pairwise relationships exhibiting different signs. The existence of the negative relationship is allowed by the PSD criterion if not all three pairwise relationships are strong. However, the negative relationship places limits on the strength of some of the correlations. Because of

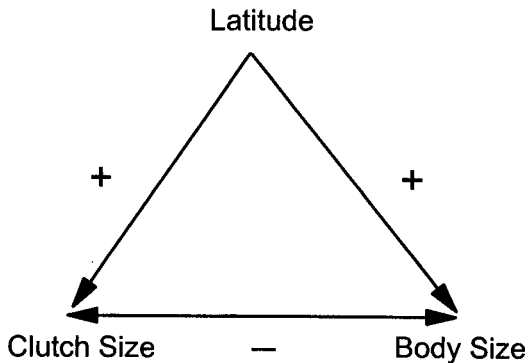


Fig. 2. Diagram of the three-way relationships among latitude, clutch (or litter) size and body size showing the predicted sign of the correlations based on the literature in endotherms. While there is empirical evidence for each of these pairwise correlations, there is a paradox because two of the relationships are positive and the third is negative. Consequently, the expected outcome of the direct influence of latitude on body size and clutch size is contradicted by the indirect pathway: direct and indirect effects of latitude have opposite signs.

these limits, it is possible that one or more of the relationships may not be detected even though the underlying selection processes continue to operate.

Our case study of the patterns of covariation among clutch size, body size, and latitude focuses on strigid owls. The Strigidae is widely recognized as a monophyletic family (e.g., Peters 1940, Burton 1973, Johnsgard 1988, AOU 1998). The member species exhibit substantial variation in body size and clutch size. They are also ecologically diverse, occurring from tropical to polar latitudes, and in habitats ranging from arid deserts to montane forests.

Our main goal is to document the direction and strength of each of the predicted pairwise relationships at the family and genus levels. Our study includes a consideration of phylogeny by comparing patterns of covariation among genera and by controlling for the influence of shared ancestry at the family level. Phylogenetic effects have been shown to influence covariation among life history traits (Stearns 1983, Dunham and Miles 1985) and phenotypic response to environmental conditions (Hawkins and Lawton 1995). If the mechanisms responsible for the three patterns are operating in the Strigidae, then each predicted relationship might be detected in at least one genus, even though the PSD criterion may prevent all three pairwise relationships from being observed in any one genus or in the family as a whole. By statistically controlling for the influence of phylogeny at the family level, one might be better able to detect a relationship which occurs but is weak, in part as a result of the opposing influence of phylogeny (see Harvey and Pagel 1991).

Methods

Data source

We used data in Hume (1991) to derive estimates of: (1) modal clutch size, (2) median latitude, and (3) median body length for 77 (56%) of the 138 strigid owl species described worldwide. All other species could not be used because information on clutch size was not available. Due to the general lack of precise estimates for the mean number of eggs laid by owls, and because the frequency distribution of clutch sizes within many species is not normal (i.e., positively skewed), we recorded modal rather than mean clutch size. However, when modal clutch size could not be inferred, we used the midpoint of the range of clutch sizes reported. Whenever possible, our calculations were based on information gathered near the center of the species' range. When an owl species occurred both in North America and in the Palearctic, we recorded the average between the modal (or mean) clutch sizes observed in those two regions.

From Hume's (1991) maps of geographic distributions, we estimated the median latitude of each species' range. When an owl occurred in one hemisphere only, the median latitude was taken as the midpoint between the northernmost and southernmost latitudes. When a species was found on both sides of the equator, a median latitude was first calculated for each hemisphere and then the mean of those two values was taken. This procedure was used to avoid recording a median latitude near the equator for species showing a wide latitudinal distribution in both hemispheres. We used body length rather than body mass due to the lack of information for many species regarding the latter trait.

Taxonomy and phylogeny

In nearly all instances, we followed Hume's (1991) taxonomic classification. It generally follows the widely used classification of the Strigidae by Peters (1940) with minor modifications by Burton (1973), but it also incorporates recent advances such as vocalization studies to separate cryptic species. We departed from Hume's classification in two cases. As recommended in the most recent AOU checklist (AOU 1998), the striped owl was included in the genus *Pseudoscops* rather than treated as an *Asio* species. Secondly, *Ciccaba* owls were treated as members of the genus *Strix* based on Sibley and Ahlquist's (1990) DNA analyses.

Based on the molecular work of Sibley and Ahlquist (1990) and the classification described above, we constructed a phylogenetic tree for the family Strigidae that included 10 of the 15 genera (70 of the 77 species) originally selected for our study (Fig. 3). Because Sibley and Ahlquist resolve the phylogeny of owls only to the

genus level, we used a polychotomous phylogeny for each genus and assigned a constant arbitrary value to each of the terminal branches of the tree. The burrowing owl was treated as a member of the genus *Athene* (Hume 1991, AOU 1998).

Analyses

We conducted several analyses of the relationships among clutch size, body length, and median latitude. Body length was log-transformed prior to testing the relationships between this variable and the other two. Using SPSS (7.5 version for Windows), linear regressions were run to analyze each pairwise relationship among the three variables.

The relationship between two variables could potentially be affected by the third variable or by phylogeny. First, partial correlation analyses were conducted for all pairwise combinations of the variables for the entire

strigid family treated as one group, and also within each genus. We also conducted a set of independent contrasts analyses (see Felsenstein 1985) using our phylogenetic tree and the PC-based Microsoft DOS PDAP computer program (Garland et al. 1993). Each independent contrasts analysis was conducted for all pairwise combinations of the variables and based on comparisons between each tip species or inferred node and its closest relative in our tree. We tested the relationships between pairwise combinations of the variables for several evolutionary scenarios by manipulating the length of the terminal branches (i.e., branch length was set at 1, 0.1, and 0.01). Tests of the linear relationships between standardized contrasts for any two variables were conducted. Felsenstein's independent contrasts method assumes a gradualistic model of evolution based on Brownian motion.

Results

Linear regressions

At the family level (i.e., when considering all 77 species), there was a significant ($P < 0.05$) positive linear relationship between clutch size and latitude, and a significant ($P < 0.05$) negative linear relationship between clutch size and body length (Fig. 4). The positive linear relationship between latitude and body length was not significant ($P > 0.05$). The positive correlation between latitude and clutch size was stronger than the negative correlation between clutch size and body length. Somewhat different relationships were found at the genus level. Three of the seven genera tested (i.e., *Glaucidium*, *Otus*, and *Strix*) showed a significant positive relationship between clutch size and latitude (Fig. 5A–C). There was a negative correlation between clutch size and body length in the genus *Ninox* (Fig. 5D). Body size increased significantly with latitude in the genera *Strix* and *Ketupa* (Fig. 5E–F). In no genus were all three relationships detected. However, the genus *Strix* showed two of the three relationships predicted in Fig. 2. In that genus, clutch size and body length both increased with latitude.

Partial correlations

When partial correlation analysis was used to control for the third variable, all pairwise combinations of variables showed a highly significant ($P < 0.005$) relationship at the family level (Table 1). Clutch size was strongly positively correlated with latitude and negatively correlated with body length. Body length was positively correlated with latitude. Different subsets of the three pairwise relationships were detected in different genera. Clutch size and latitude were positively

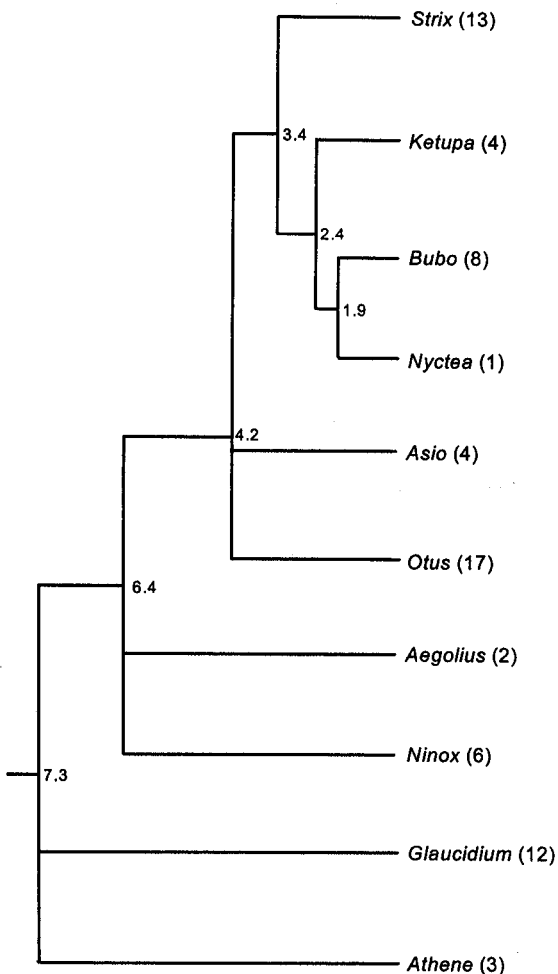


Fig. 3. The phylogeny for ten genera of strigid owls used in the present study.

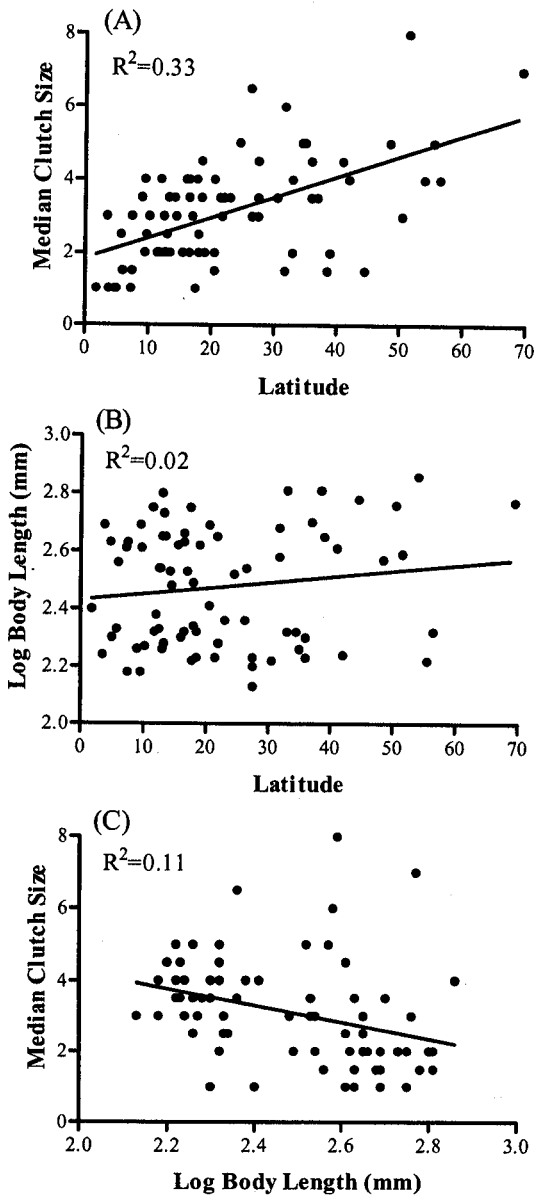


Fig. 4. Pairwise least squares linear regressions among clutch size, body length, and latitude for 77 species of strigid owls. The relationship (A) between clutch size and latitude was significant ($F_{1,76} = 36.6$, $P < 0.001$) as was that (C) between clutch size and body length ($F_{1,76} = 8.9$, $P < 0.005$). The relationship (B) between body length and latitude was not significant ($F_{1,76} = 1.6$, $P = 0.213$).

correlated in three (i.e., *Glaucidium*, *Otus*, *Strix*) of the seven genera tested, while one genus (*Ninox*) showed a negative correlation between body length and clutch size. The relationship between body length and latitude was significant ($P < 0.05$) in the genus *Strix*.

Independent contrasts analyses

When an independent contrast analysis was used to remove phylogenetic effects at the family level, clutch size still increased significantly with latitude (Fig. 6). This relationship was robust, in that it was not affected by changes in the value assigned to the terminal branches of the phylogenetic tree. The increase in body length with latitude, which was not significant when tested by linear regressions but was significant when the influence of clutch size was removed, was again significant ($P < 0.05$) for all the evolutionary scenarios we tested. The significant negative linear relationship between clutch size and body length found when treating all species as independent data points (see linear regressions and partial regressions) was not significant ($P > 0.05$) when using independent contrasts.

Discussion

Although our analyses gave somewhat different results depending on the statistical techniques used (simple regression, partial correlation, or independent contrasts) and on taxon (the family Strigidae or particular genera), overall they provided strong evidence for each of the pairwise relationships among clutch size, body size, and latitude. When the effect of the third variable was held statistically constant in the partial correlation analysis at the family level, all three relationships were strong and highly significant. Additional evidence came from analyzing genera separately. Each of the three relationships was clearly expressed in at least one genus. Finally, using both simple regressions and independent contrasts resulted in each of the three pairwise relationships being detected at the family level. The increase in body size with latitude, a relationship that was not significant when analyzed with simple regressions, became significant after controlling for the influence of phylogeny. The allometry of clutch size, while appearing to be conservative largely due to shared ancestry, was detected using simple regressions.

Where present, each of the three relationships exhibited the direction predicted from life history theory, Bergmann's rule, and allometry (Fig. 2). In no case did we find clutch size to decrease with latitude or increase with body size, and body size never decreased with latitude. Our results not only provide empirical support for the general occurrence of these patterns, but they also show that the paradox (i.e., two of the relationships are positive, the other is negative; the expected outcome of the direct influence of latitude is contradicted by indirect effects) likely occurs in the Strigidae. The existence of the paradox illustrates the first implication of the PSD criterion: when two of three relationships among three interrelated variables are positive, the third may be negative.

Because one of three relationships is negative, not all pairwise relationships can be strong. This second implication of the PSD criterion was also illustrated by the results of our analyses. Although all three relationships appeared to exist overall (see above), within both the Strigidae and individual genera, some of the relationships were not detected in the simple correlation analyses or in the independent contrasts analyses. Patterns detected within genera were also interesting in that regard. In the Strigidae, the relationship between latitude and clutch size appears to be stronger overall than the other two relationships. Although the results for the different genera should be viewed with caution due to small sample sizes, they suggest that the relative strength of each relationship varies among taxa. In general, the increase in clutch size with latitude was strong and consistent, as

it was at the family level. However, our analysis suggests that in some genera, either the negative correlation between body size and clutch size or Bergmann's rule could be the dominant relationship. Altogether, each of the three relationships was detected in at least one genus, but no more than two of them were strong within a single genus.

Our results imply that even when the mechanisms responsible for patterns of variation and covariation are operating, the expected relationships may not always be observed. Many authors have proposed mechanisms for the increase in clutch or litter size with latitude, the increase in body size with latitude, and the negative allometry of clutch or litter size (e.g., Bergmann 1847, Kleiber 1932, Lack 1947, Ashmole 1963, Ricklefs 1980, Lindstedt and Boyce 1985, Charnov 1993). Other authors

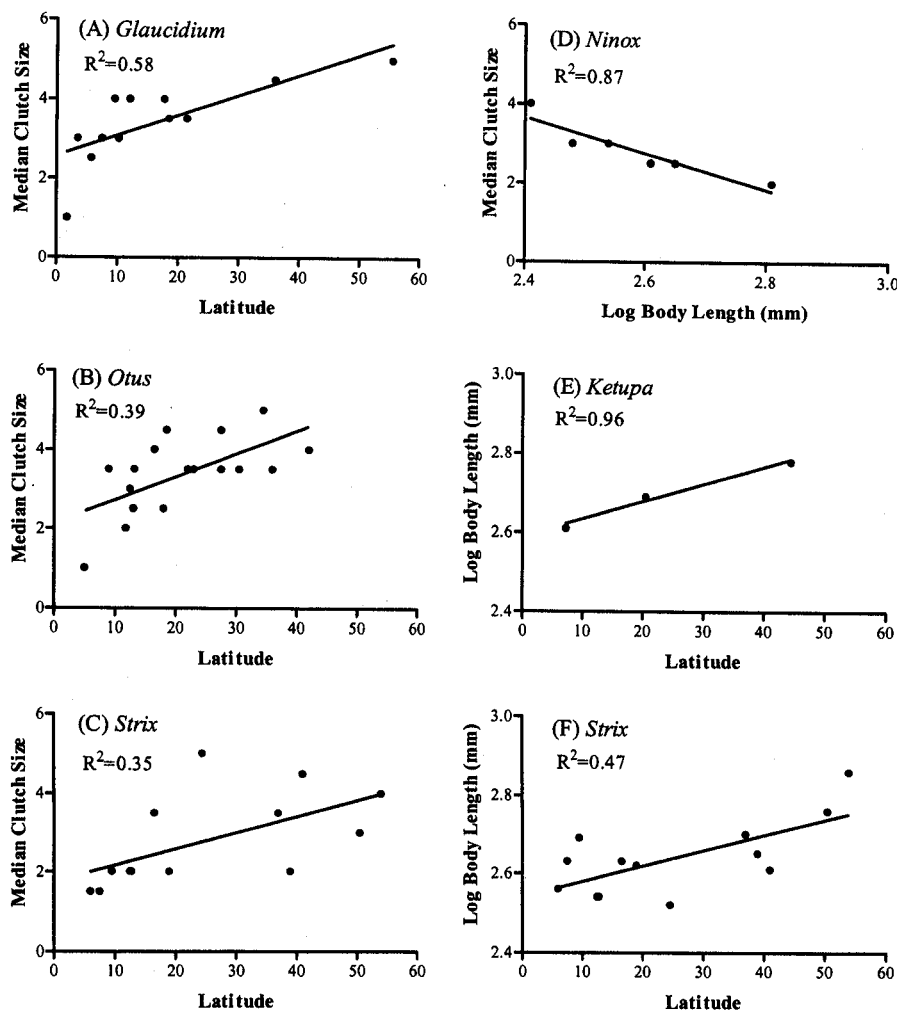


Fig. 5. Significant pairwise least squares linear regressions among clutch size, body length, and latitude within genera of the strigid owls. Clutch size was significantly related to latitude in (A) *Glaucidium* ($F_{1,10} = 13.9$, $P < 0.005$), (B) *Otus* ($F_{1,15} = 9.6$, $P < 0.008$), and (C) *Strix* ($F_{1,11} = 5.9$, $P < 0.04$). Clutch size was significantly related to body length only in (D) *Ninox* ($F_{1,4} = 26.7$, $P < 0.008$). Body length was significantly related to latitude in (E) *Ketupa* ($F_{1,2} = 51.9$, $P < 0.02$), and in (F) *Strix* ($F_{1,11} = 9.8$, $P < 0.01$).

Table 1. Partial correlation coefficients for the relationships among log body length, clutch size, and median latitude for 77 owls in the family Strigidae and six genera within that family. Coefficients reported reflect the relationship between two of the variables when the effect of the third is controlled. * $P < 0.05$.

Group	DF	Clutch size vs latitude		Log body length vs latitude		Log body length vs clutch size	
		<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Strigidae	74	0.67	0.00*	0.43	0.00*	-0.51	0.00*
<i>Asio</i>	1	0.76	0.45	0.12	0.92	-0.27	0.83
<i>Bubo</i>	5	0.14	0.76	0.39	0.39	-0.19	0.68
<i>Glaucidium</i>	9	0.73	0.01*	0.15	0.67	-0.48	0.13
<i>Ketupa</i>	1	-0.82	0.39	0.99	0.07	0.85	0.36
<i>Ninox</i>	3	0.62	0.27	0.68	0.21	-0.96	0.01*
<i>Otus</i>	14	0.61	0.01*	-0.24	0.37	0.01	0.98
<i>Strix</i>	10	0.66	0.02*	0.73	0.01*	-0.39	0.21

have noted that these predicted patterns can be weak or not observed at all in certain groups (e.g., Goldschmidt 1940: 83–89, Scholander 1955, Cody 1971, Calder 1984, Hawkins and Lawton 1995). Neither the limited data for owls nor our statistical analyses allow us to resolve which combination of processes may be responsible for the observed patterns of covariation. Our results do show, however, one reason why there may be apparent exceptions to the patterns. The signs of the relationships prevents them from being strong simultaneously. Which one or two correlations will predominate can be expected to vary from group to group, depending on the strength of selection operating through the underlying mechanisms and the complex assemblage of direct and indirect effects.

A general message of our study is that fundamental mathematical constraints can complicate efforts to detect empirical patterns and to infer the mechanisms responsible for them. Many ecological and evolutionary relationships are expressed as complex patterns of covariation among traits, including potentially opposing direct and indirect effects of certain variables. When some of these relationships are negative, the range of possible values for the correlation coefficients can be limited due to the PSD criterion for correlation matrices.

There are many cases where the PSD criterion may influence ecological and evolutionary inference. One example is another apparent paradox formed by the relationships among body size, area of geographic range, and abundance. There is evidence that range size is positively correlated with body size and abundance, but abundance is negatively related to body size (Hanski 1982, Brown 1984, Brown and Maurer 1987, Damuth 1991, Lawton et al. 1994, Silva and Downing 1995, Gaston 1996, Brown and Lomolino 1998). While all three relationships are observed in at least some cases when sample sizes are very large (Brown and Maurer 1987, 1989, Brown 1995), the correlation coefficients are often small and the substantial variation may be better described by "constraint envelopes" than regression equations. Here again, constraints imposed by the PSD criterion reflect conflicts among direct and

indirect effects. Another example is competition. Competing species are expected to exhibit negative relationships in their population dynamics. In systems of multiple competing species, however, we cannot expect to observe strong negative correlations among all of the species that may actually be competing (see eq. [1]).

A primary focus of our study is the influence of the PSD criterion when one or several of the known relationships is/are negative. However, an important implication of the PSD criterion is the problem of inference if the constraining negative relationships are omitted from the analysis. The existence of limitations in inferring the operation of an underlying process can only be determined if all meaningful dimensions are included, in order to determine whether the PSD criterion limits the magnitude of correlation in any part of the system. Thus, the problem of dimensionality (Pease and Bull 1988) is an important complication that needs to be addressed: hidden or unmeasured variables can powerfully affect the patterns of covariation that can be detected in a statistical analysis.

Although the PSD criterion represents an important difficulty in inferring the operation of underlying mechanisms, it is not the only one. Another difficulty to infer the nature of the underlying process may arise even when the relationships are positive. To illustrate this, we use again the relationships among latitude, body size, and clutch size. Several groups of ectothermic organisms exhibit Bergmann's rule (Ray 1960, Cushman et al. 1993, Hawkins 1995, Van Voorhies 1996). In at least some ectotherms, there are also positive relationships between clutch size and latitude and between clutch size and body size (e.g., in the lizard *Sceloporus undulatus*, Tinkle and Ballinger 1972). Several possible mechanisms relating thermoregulatory performance to environmental temperature that may operate in endotherms cannot apply to ectotherms (McNab 1971). An alternative to a direct selective advantage of large body size at high latitudes is suggested by a three-way analysis. If, in these organisms, selection favors large clutches at higher latitudes and clutch size exhibits a positive allometry, it is possible that the observed Bergmann's rule is an indirect consequence of selection

operating through the other two pathways. This is not, however, the only mechanistic hypothesis which may account for Bergmann's rule in ectotherms (e.g., Cushman et al. 1993, Kaspari and Vargo 1995, Van Voorhies 1996).

The outcome of evolutionary processes that are expressed as patterns of geographic variation reflects not only the influence of the environment in selecting for

particular traits but also phenotypic correlation (Wanntorp et al. 1990). In particular, there are many kinds of trade-offs that can cause negative relationships between life history traits (e.g., Tuttle and Ryan 1981, Clutton-Brock et al. 1982, Stearns 1992), and these can complicate the way that these traits respond to variation both in the environment and in other traits. In such cases, caution should be exercised in drawing inferences about the kinds and consequences of underlying mechanisms.

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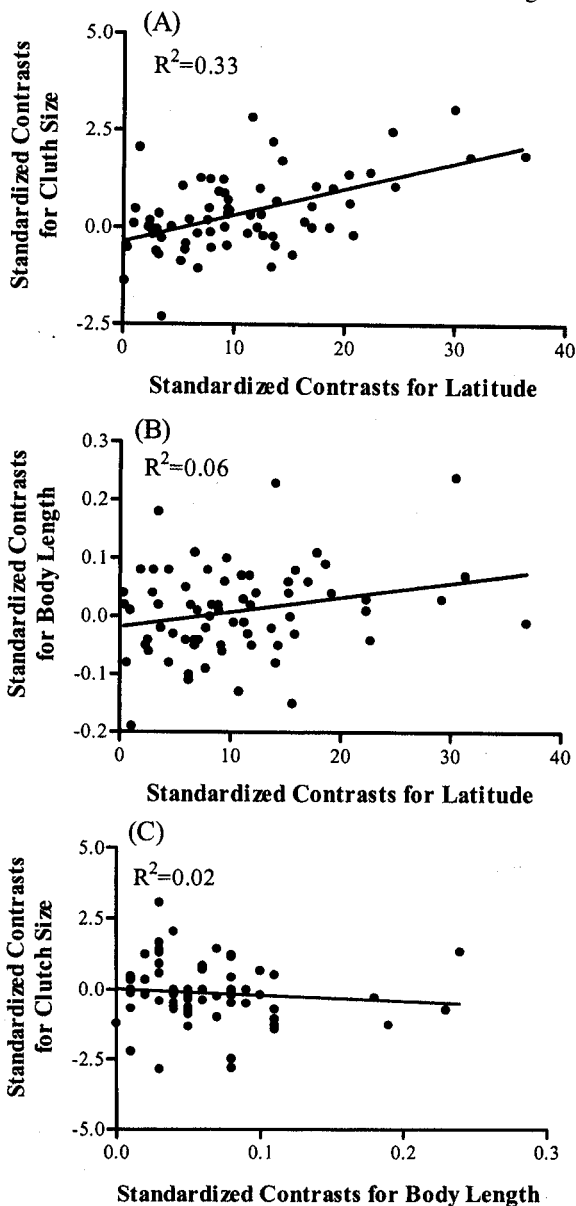


Fig. 6. Pairwise least square linear regressions of standardized independent contrasts among latitude, clutch size, and body size. The relationships between (A) clutch size and latitude ($F_{1,68} = 32.8$, $P < 0.001$) and that between (B) body length and latitude ($F_{1,68} = 4.0$, $P < 0.05$) were significant. The relationship between (C) clutch size and body length was not significant ($F_{1,68} = 1.3$, $P < 0.252$). Results are shown for terminal branch length set at 1 in our phylogenetic tree.

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