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An Interspecific Relationship Between Egg Size and Clutch Size in Birds

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Individual birds should be selected to rear broods that maximize lifetime reproductive success (Lack 1968, Williams 1966). In many species, clutch size may be limited by the number of offspring that parents can feed (Lack 1968, see review *in* Partridge 1990). However, Lack (1967) considered that precocial species laying large clutches should be limited instead by food availability to the laying female. Then, assuming nutrient limitation, any increase in clutch size could be compensated by decreased egg size. Therefore,Lack (1967) considered that such nutrient limited species would likely show trade-offs between clutch size and egg size. Smith and Fretwell (1974) also considered that this trade-off was most likely in species that lay large clutches without parental care. Lack (1967) tested his hypothesis on wildfowl and found that species that laid larger clutches also laid smaller eggs. Although recently called into question (Rohwer 1988), the trade-off among wildfowl has since been confirmed using more appropriate statistical techniques (Blackburn 1991).

Wildfowl show a clutch size/egg size trade-off, but their combination of relatively large clutches and precociality may make them a special case. There has been no detailed attempt to specifically examine this trade-off across a large number of bird species, although data are available. For example, Bennett (1986) reported a partial correlation coefficient of -0.4 for the relationship between clutch size and egg size across 143 bird families, controlling for female body weight and taxonomic relatedness. However, he did not discuss this result, which was simply one of thousands of correlations he performed.

Both clutch size and egg size may respond independently either to variation in other life history traits or to variation in environment. For example, clutch sizes of altricial species inhabiting higher latitudes tend to be larger than those of related tropical species (Arnold 1988, Ashmole 1961, Ricklefs 1980). Similarly, clutch size covaried positively within species with territory quality (Högstedt 1980), and inversely among species with survival rate (Saether 1988). These are potentially confounding variables to any suspected trade-off between clutch size and egg size. Controlling for phylogeny, ecology, behavior, and life history variability, I analyzed the clutch size/egg size trade-off to test whether the trade-off is masked by these variables.

Data for female weight, egg weight (both in grams), and clutch size for 1,530 bird species were extracted from Bennett (1986). All continuous variables were logarithmically transformed before analysis (Harvey 1982). I used standard regression to control for the effects of potentially confounding variables, but all slopes for allometric relationships were calculated using major axis regression (Pagel and Harvey 1988).

Correlation analyses were performed using an evolutionary covariance method developed by Pagel and Harvey (1989), and described fully in Harvey and Pagel (1991), to control for the effects of phylogeny among these species. Closely related species may share adaptations through common ancestry. Analyzing species in comparative studies may thus overestimate the actual number of times a trait or a relationship among traits has evolved. Controlling for the effects of identity by descent is therefore important in comparative studies (see Harvey and Pagel 1991). For example, suppose all species of the infraclass Eoaves (Sibley et al. 1988) have large eggs and lay small clutches, whereas most other species have small eggs and lay large clutches. A relationship between clutch size and egg size based on a comparison across all species could simply be due to the difference between Eoaves and other birds. Large eggs and small clutches may have evolved only once and then have been retained during the radiation of the Eoaves. But in a cross-species comparison the relationship would be falsely represented as having evolved many times.

The best method to control for the effects of phylogenetic similarity is to examine relationships between variables within each pair of taxa below a node in a bifurcating phylogeny. The relationship between the variables is then unaffected by phylogeny because the taxa in each comparison are equally related. This method requires that the true phylogeny be known (Felsenstein 1985). However, a model that applies this method to data sets for which only approximate phylogenies are available was derived by Pagel and Harvey (1989). This method calculates a single value ("contrast") for each variable within each taxon (i.e. for species within each genus, genera within each tribe, etc; Harvey and Pagel 1991). This value represents the magnitude and direction of the change in the variable within the taxon. These independent contrasts will show similar changes within each taxon, if variables are correlated. The set of within-taxa contrasts can then be analyzed using standard regression techniques (Pagel and Harvey 1989; Blackburn 1990, 1991; Harvey and Pagel 1991; Harvey et al. 1991). Species were sorted to family using the taxonomy of Sibley et al. (1988), while assignment below this level was from Howard and Moore (1984).

Egg weight correlated positively with female body weight among taxa (major axis regression slope = -0.79; 95% confidence intervals: -0.76 to -0.82; $r = 0.926$, $n = 515$, $P < 0.0001$; n is the number of independent comparisons calculated by the evolutionary covariance method). Female weight and clutch size were also correlated among taxa; but (inversely) larger-bodied taxa tend to lay smaller clutches ($r = -0.185$, $n = 515$, $P < 0.0001$). Therefore, female body weight was controlled by partial regression for the remainder of the analysis. There was an inverse correlation between egg size and clutch size with female weight controlled (slope = -3.75; 95% C.I.: -5.98 to -2.92; $r = -0.28$, $n = 515$, $P < 0.0001$). However, only 7.8% of the variance in egg size, after removing the effects of female weight, was explained by clutch size.

Historically, comparative analyses of bird data have treated passerines (Order Passeriformes) and nonpasserines (all other orders) separately (e.g. Lack 1968, Bennett 1986), because Passeriformes is a particularly species-rich taxon. This may have caused bias by contributing disproportionately large numbers of species to any analyses. However, I precluded this possibility by the evolutionary covariance method because the contrasts used in the analysis are independent evolutionary events. Nevertheless, the clutch size/egg size relationship was analyzed separately for passerines and nonpasserines, controlling for female weight, and was found to be inverse in both groups (passerines: slope = -3.88; 95% C.I.: -5.96 to -2.85; $r = -0.356$, $n = 216$, $P < 0.0001$; nonpasserines: slope = -3.67; 95% C.I.: -5.97 to -2.61; $r = -0.281$, $n = 298$, $P < 0.0001$).

The clutch size/egg size relationship was recalculated, removing the effects of other potential confounding variables (ecological, behavioral and life history variables). Data on hatchling weight (in grams), incubation time (in days), fledging time (in days), age at independence from parents (in days), age at first breeding (in months), maximum recorded lifespan in the wild (in months), number of broods per year, and the interval (in days) between laying of each egg in a clutch were taken from Bennett (1986). Additionally, I recorded from the literature data (Blackburn 1990) on 12 ecological and behavioral variables for each of the 1,530 species, because Bennett (1986) recorded these variables only at the family level:

Type of development: (1) atricial (chicks hatched naked and helpless and first left the nest late in development), (2) precocial (chicks were able to leave the nest and feed themselves within hours of hatching), or (3) intermediate (such distinctions could not be clearly made).

Breeding latitude: high, low, or tropical, depending on which region contained the largest part of their breeding range.

Degree of migration: mainly or totally migrant, partially migrant, and sedentary or mainly sedentary.

Nest site: ground, arboreal, or hole nesters.

Nest dispersion: solitary, clumped, or colonial.

Activity timing: mainly nocturnal, mainly diurnal, or placed into a third category if active by day or night.

Stratification: aquatic (e.g. grebes), terrestrial (e.g. pheasants), or aerial (e.g. swifts); classification depended on the medium most often associated with a species.

Nesting habitat: aquatic, open land, or scrub/woodland.

Diet: mainly vegetarian (folivorous or frugivorous), omnivorous, or mainly carnivorous (including insectivores, invertebrate feeders).

Mating system: mainly monogamous, polygynous, polyandrous, promiscuous, or communal breeders.

Incubating sex: male, female, or both sexes incubate the clutch.

Caring sex: male, female, or both sexes care for the brood after hatching.

Occasionally, a species' behavior or ecology spanned two or more categories. Where this was the case, the species was placed in the category considered to represent its most frequent behavior or ecological preference.

Correlation coefficients of the clutch size/egg size relationship, controlled for each of the 20 additional variables, were determined (Table 1). Up to 20.25% of the remaining variance in egg size was explained by clutch size. There was always a significant ($P < 0.0001$) inverse correlation between clutch size and egg size, independent of female weight. The extra control variable caused an increase in the strength of the correlation in 16 of 20 cases (Table 1). Therefore, life history and ecology differences across species tend to mask the relationship between egg size and clutch size. As a hypothetical example, imagine that the clutch size/egg size relationship was significantly negative for precocial species but significantly positive for altricial species. A correlation analysis that failed to control for development type might show no relationship between egg size and clutch size, due to including two different groups in one correlation.

TABLE 1. Correlation coefficients (r) for the relationship between clutch size and egg size controlling for phylogeny, female weight, and the variable in the first column. The number of independent comparisons made using evolutionary covariance regression (n) is shown; $P < 0.0001$ in all cases.

	r	n
Development type	−0.389	397
Breeding latitude	−0.254	496
Migration	−0.229	279
Nest dispersion	−0.361	206
Nest site	−0.313	451
Stratification	−0.308	460
Habitat	−0.298	440
Diet	−0.298	430
Activity time	−0.258	264
Mating system	−0.324	187
Incubating sex	−0.312	368
Caring sex	−0.314	339
Inter-egg interval	−0.297	251
No. of broods per year	−0.297	325
Hatchling weight	−0.383	152
Incubation period	−0.276	390
Fledging time	−0.330	327
Age at independence	−0.389	170
Age at first breeding	−0.450	224
Lifespan	−0.365	232

Most, if not all, of the life history variables, and some of the ecological variables, correlated with each other. For example, age at first breeding was significantly related to 15 of the other 19 control variables among birds (Bennett 1986). Hence, simultaneously controlling for 2 of these variables (together with body size and phylogeny) improved the clutch size/egg size relationship in only 16 of 123 possible comparisons (Blackburn 1990: table 2). The average increase in r due to the additional variable in these 16 cases was only 0.033.

My analysis raises a number of points about the relationship between clutch size and egg size in birds. First, a perfect trade-off between egg size and number, in which doubling egg weight causes halving of clutch size, predicts a slope of −1. The slope of the relationship (−3.75) is much greater than a perfect trade-off predicts. A small increase in egg size is balanced by a relatively large decrease in clutch size, or vice

TABLE 2. Correlation coefficients (r) for the relationship between clutch size and egg size controlling for phylogeny, female weight, and the two variables in the first column. The number of independent comparisons made using evolutionary covariance regression (n) is shown; $P < 0.0001$ in all cases.

	r	n
Lifespan, incubation period	−0.37	218
Lifespan, caring sex	−0.42	194
Lifespan, incubating sex	−0.39	197
Lifespan, mating system	−0.47	116
Lifespan, diet	−0.41	202
Lifespan, nest site	−0.39	217
Incubation period, caring sex	−0.32	298
Incubation period, incubating sex	−0.34	317
Incubation period, diet	−0.34	328
Incubation period, stratification	−0.35	359
Incubation period, nest site	−0.35	356
No. broods per year, caring sex	−0.35	265
No. broods per year, incubating sex	−0.32	271
No. broods per year, migration	−0.34	216
Interval between eggs, diet	−0.32	222
Interval between eggs, nest site	−0.32	241

versa. This implies an allocational trade-off (Rohwer 1988). Rohwer (1988) found very similar slopes in his wildfowl analysis, both for this relationship (−3.39) and for the regression of egg weight on female weight (0.72, compared to 0.78 for all bird taxa). The similarity of these two results for female and egg weight, and their similarity to the 0.75 exponent between body weight and metabolic rate (Kleiber 1962, Nagy 1987), neatly demonstrates the assertion that the evolutionary covariance method does not alter the form of allometric relationships (Harvey and Pagel 1991).

Second, limits on clutch size have generally been considered likely to be different in altricial and precocial species. In precocial species it is the ability of the female to produce eggs, whereas for altricial species it is the number of offspring the parents were able to feed (Lack 1968, Klomp 1970, Ricklefs 1977). Rohwer (1991) predicted that the different limits on clutch size should result in a weaker, or at least different, trade-off in altricial species compared with precocial, and that the validity of the egg-production hypothesis would be questioned if no difference was found. In fact there is no evidence that the trade-off is weaker in altricial than precocial species. Controlling for development type increases the strength of the trade-off (Table 1). Altricial passerines actually had a stronger trade-off than the mainly precocial nonpasserines, and the slopes of these two relationships were virtually identical. This finding is on balance against any hypothesis that precocial and altricial species have different limits on clutch size, in particular that precocial species have a special set of problems in egg production (Rohwer 1991). However, it is not definite proof, as it is possible that different constraints on clutch size could produce similar trade-offs in the two groups. Nevertheless, this certainly opens clutch-size theory to further critical study.

Third, these interspecific results do not affect any conclusion that there may be no intraspecific trade-off (Rohwer 1988, 1991). Comparisons within and between species are independent, and the sign of the relationship at one level need not affect that at another. The intraspecific relationship between egg size and clutch size may be positive, negative, or absent (Stearns 1989) (e.g. if there is intraspecific variation in individual quality [van Noordwijk and de Jong 1986]). If good-quality individuals can lay larger clutches of larger eggs than poor-quality individuals within species, the intraspecific relationships between clutch size and egg size will be positive. However, this will not affect interspecific comparisons using these same species, because interspecific comparisons are made between population means. If two species each allocate *on average* the same proportion of resources to reproduction, but one species lays *on average* larger eggs, then it will also *on average* lay smaller clutches. This is independent of whether the intraspecific relationship is negative, positive, or absent.

A problem arises when comparison is between species with greatly differing proportions of resources allocated to reproduction. Then, the high allocation species may produce both larger clutches and larger eggs. However, specific differences in resource allocation to individual clutches will be associated with differences in other life history traits. For example, species with proportionately large clutches tend to mature early, breed often and have short lifespans (Bennett 1986, Read and Harvey 1989). Controlling for these differences will reveal the clutch size/egg size trade-off (e.g. Table 1). The point is not that the clutch size/egg size trade-off is not important, but that in some species other trade-offs may be more so—for example, that between present and future reproduction (Sibly and Calow 1986). Nevertheless, the amount of resource allocated to each reproductive event must still be divided between more small or fewer large offspring.

There is evidence that egg size and clutch size are inversely related across all bird species, independently of female weight and phylogeny. This suggests a trade-off between these traits. This trade-off is partially obscured by differences in species life histories and ecologies. In addition, controlling for potential confounding variables generally strengthens the relationship. The trade-off has important implications for theory on the limitation of clutch size.

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Use of the Relative Frequency of Notes by Veeries in Song Recognition and Production

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The relative frequency of notes is an important feature in the perception of tonal sequences by humans (Deutsch 1982). That is, humans can recognize a tune despite shifts in frequency (for example, a change of octave) so long as the ratio between the frequencies of the notes is preserved. In the music perception literature, the processing of frequency relationships has been subdivided into two categories: frequency contour processing, which uses the direction but not the amount of change, and frequency ratio processing, which uses both the direction and amount of change (Deutsch 1982). In principle, hu-