

each taxon, which represents the magnitude and direction of the change in the variable within the taxon. If variables are correlated, they will show similar changes within each taxon. The set of within-taxon contrasts can then be analyzed using standard regression techniques (Harvey et al. in press).

Using this model, I reanalyzed the data to obtain the relationship between clutch size and egg size, controlling for both phylogeny and female mass. The phylogeny used was the same as that used by Rohwer (Livezey 1986). Using major axis regression, r^2 is 0.28 ($r = -0.529$, n [number of taxa within which comparisons were made] = 37, $P = 0.0008$). Alternatively using standard regression instead of major axis to control for the effects of female size, the relationship from the phylogenetic model was very similar ($r^2 = 0.293$, $r = -0.541$, $n = 37$, $P = 0.0007$). Rohwer claimed that removing the data from the 17 species or subspecies of wildfowl that breed on islands caused the relationship to disappear. Reanalysis without island species (using Madge and Burn 1988, I could define only 16 as such) did weaken the relationship, but only slightly (standard regression, $r^2 = 0.266$, $r = -0.516$, $n = 34$, $P = 0.002$).

Rohwer's conclusion from his interspecific analysis was that, while there was a trade-off between clutch size and egg size in wildfowl, such that species laying relatively large eggs laid relatively small clutches, it was relatively unimportant. Clutch size explained no more than 13% of the variance remaining in egg size after controlling for female mass (Rohwer 1988). However, repeating the analysis on the same data but using more appropriate statistical tests to control for female size and phylogeny, I found that in fact clutch size explained up to 29.3% of the variance in egg size unexplained by female size, a considerable proportion. Therefore I believe that Rohwer's (1988) contention that the trade-off is unimportant was mistaken.

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Response to T. M. Blackburn

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Lack (1967) hypothesized that clutch size in waterfowl and other precocial birds was limited by the cost of producing eggs. Lack tested this hypothesis by examining the interspecific relationship between egg

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mass and clutch size in waterfowl. As predicted, egg mass and clutch size were related inversely (Lack 1967, 1968). My interest in clutch size led me to reexamine the relationship between egg mass and clutch size (Rohwer 1988). My results differed substantially from Lack's results. Some of the difference was attributable to improved data (Rohwer 1988: appendix), but my use of rigorous statistical analyses was the main cause of the different results. I suggested that "... the com-

parative method is robust enough to handle some poor data, but is quite sensitive to analytical technique" (Rohwer 1988: 168). Ironically, Blackburn (1991) has demonstrated that point by reestablishing a trade-off between egg mass and clutch size through the use of new analytical techniques. Blackburn suggests that my analyses were flawed because I used an inappropriate regression technique and because I failed to control for shared inheritance of traits. I will address these two criticisms here and discuss how Blackburn's results influence considerations of clutch size in waterfowl.

Blackburn's first criticism concerns my use of principal axis analysis. Unlike standard least squares regression, principal axis does not assume that the x variable has no error variance. Blackburn argues that the assumption with principal axis that both the y_1 and y_2 variables have equal variance may be incorrect. I agree, but I know that the zero variance assumption of standard regression is incorrect; therefore, the assumption of equal variance for principal axis was palatable.

Aside from the issue of error variance, Blackburn suggests that standard regression is the preferred way to estimate residuals from the relationship between egg mass and body mass. He states that principal axis residuals may not be completely independent of female body mass, so they may bias the egg mass and clutch size relationship. Blackburn and others (Harvey and Mace 1982, Ricker 1984, Pagel and Harvey 1988a: appendix) have suggested that principal axis is the analysis of choice when the focus is on an accurate estimate of the line relating two independent variables. If that is so, then standard regression must produce a less accurate regression for these two variables, which means that residuals will be biased to some degree. Thus, it is not readily apparent that standard regression produces more reliable residuals than does principal axis (see also Pagel and Harvey 1988a: appendix). These points become moot, because Blackburn's technique of controlling for taxonomic variation (see below) largely obliterates the discrepancy caused by using differing regression procedures.

Blackburn's most important criticism concerns my use of species as independent observations. The search for parallel or convergent evolutionary change in traits is the essence of the comparative method, but it can be difficult to separate such adaptive causes of similarity from similarity due to descent (Pagel and Harvey 1988a). In the past few years there has been considerable focus on controlling for the influence of taxonomic association in comparative studies (Ridley 1983; Felsenstein 1985; Pagel and Harvey 1988a, b, 1989). This literature suggests that comparisons based on species can overestimate the extent of adaptive evolutionary change. In my examination of a potential trade-off between egg mass and clutch size, I assumed that using species as independent observations would increase the chance of detecting a trade-off.

Thus, I assumed that the weak association between egg mass and clutch size was a conservative rejection of a major prediction of the "egg production" hypothesis.

Blackburn's results differ substantially from mine because he controlled for taxonomic effects. His analyses are based on a hierarchical set of contrasts within a taxonomic unit. Because each contrast is within a taxon, it is safe to assume that the members in a contrast are about equally related. Two or more subgroups in a taxon allow a contrast and thereby provide one data point for the overall analysis. This technique reduces the data from 151 species to 37 observations. I will use the swans and geese to illustrate the hierarchical nature of Blackburn's analyses. The lowest level contrast involves subspecies within species, so Lesser Snow Geese (*Chen caerulescens caerulescens*) and Greater Snow Geese (*C. c. atlanticus*) provide one data point, as does the contrast of subspecies in Canada Geese (*Branta canadensis*). The next level of contrasts are species within genera, so the *Anser*, *Branta*, and *Chen* groups each provide another unique observation. The four genera within the tribe Anserini provide the next level of contrast (one more data point), and the subsequent contrast between swans and geese provides one unique observation for tribe within subfamily. The final levels of contrast are within family and within order.

Unfortunately, the technique for computation of the contrasts within each taxon is not documented by Blackburn. Brief explanations of the contrasts are available (Harvey et al. in press), but the details of calculation of the contrasts are not yet published, so it is difficult to evaluate the validity of Blackburn's methods. It is likely, however, that Blackburn's hierarchical approach is a good way to control for the taxonomic problem of shared descent.

Blackburn is to be commended for what appears to be a rigorous re-analysis of the data on egg mass and clutch size in waterfowl. Unfortunately, I believe Blackburn ignored the question that prompted the analysis, namely what limits clutch size in waterfowl? When I failed to find a strong relationship between egg mass and clutch size, the interpretation was simple. It called to question the validity of the egg production hypothesis. Blackburn assumes that demonstration of an inverse relationship is strong support for the egg production hypothesis. I believe this interpretation is questionable. The analytical technique that Blackburn used appears to accentuate differences between taxa and thereby increases the strength of associations between traits (see also Harvey et al. in press). I question whether Blackburn's demonstration of a trade-off indicates a nutrient allocation problem faced by waterfowl or is more a reflection of his analytical technique.

To interpret Blackburn's results, it may be necessary to examine data for altricial birds. Avian ecologists generally believe that parental ability to care for young

sets the upper limit on clutch size in altricial birds (Lack 1968, Klomp 1970, Ricklefs 1977, Murphy and Haukioja 1986). If altricial and precocial birds have differing constraints on clutch size, then we would predict a difference in the relationship between egg mass and clutch size for birds with those differing lifestyles (see also Blackburn's second paragraph). The relative strength of the precocial versus altricial trade-off between egg mass and clutch size could be used to evaluate the significance of Blackburn's trade-off in waterfowl. If altricial birds show a weak trade-off, then it would be reasonable to interpret Blackburn's trade-off in waterfowl as evidence of a special set of problems in egg production. If, however, the analytical technique that Blackburn uses also produces a trade-off in altricial birds, then I would suggest that the trade-off in waterfowl is not evidence to support the hypothesis that egg production limits clutch size in waterfowl.

I am also concerned that Blackburn ignores the lack of trade-offs for the individual species of waterfowl (Rohwer 1988: table 2, see also Rohwer and Eisenhauer 1989). Recently, Lessells et al. (1989) looked for such trade-offs in Lesser Snow Geese. Their analyses were based on genetic correlations derived from known relatives in a marked population. As with the earlier studies of phenotypic correlations, there was no significant evidence for a trade-off between clutch size and egg mass (Lessells et al. 1989).

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