that is needed to guide decisions. I believe that we, as an ornithological society and as an ornithological community, need a means both to have what we now know taken into account as decisions are made, and to find out what kinds of knowledge we can and should provide that will be important in future decisions.

I propose the formation of an Ornithological Council to serve as a voice for the science of ornithology wherever and whenever the voice of ornithology should be heard in the making of policy decisions. This Council should be sponsored and supported by the scientific and professional ornithological societies in North America. The Council should be made up of representatives of each participating society and should employ a person who is both knowedgeable in scientific ornithology and able to communicate that knowledge effectively. The Council would serve as a two-way conduit between those who have or can produce, and those who need or should have, important and accurate knowledge about birds as they affect or are affected by environmental and political decisions. The Council should be available—more importantly, should make its presence known—to federal and state agencies at both executive and legislative levels, to corporate organizations, to private or public conservation groups, and to citizens' groups. It should re-

spond when asked, and it should demand to be heard when it has something worth saying. But its actions and input should always have a basis in scientific ornithology.

Adopting this proposal would represent an area of activism that the scientific ornithological societies have traditionally avoided. It might involve a considerable financial outlay. There may always be different interpretations of scientific findings and how they affect environmental decisions. I think that none of these problems is insurmountable. On the other hand, if we do not become actively involved in applying our science in the world we will be relegated to having no effective role in its future.

Postscript.—This essay was drafted in April 1990. An early version was submitted to the executive bodies of the four societies that form OSNA for consideration at their 1990 annual meetings. Each society agreed to appoint two members to a joint committee to study the feasibility of establishing an Ornithological Council and its possible functions. Suggestions or ideas that you would like that committee to consider may be sent to the author.

The Interspecific Relationship Between Egg Size and Clutch Size in Wildfowl

T. M. Blackburn[1]

Individual birds will be selected to rear broods that maximize their lifetime reproductive success (Lack 1954). For most species this optimum clutch size will not be simply the maximum number that an individual is capable of laying. Among other things, there may be a trade-off between the number of offspring produced and the quantity of resources invested in each (Smith and Fretwell 1974, Sibly and Calow 1986). Lack (1968) suggested that the ability of parents to feed offspring should limit the number of offspring in a clutch. Individuals attempting to rear too large a clutch would produce undernourished offspring, which would suffer higher mortality, and hence leave fewer descendants.

If parents do not have to feed their brood (e.g. in highly precocial taxa), then this trade-off will be different. Clutch size will no longer be constrained by the capabilities of the parents to feed the offspring, but instead by the relationship between the availability of resources to the female around the time of

laying and the size of the egg (Lack 1967). Lack hypothesized that individuals could allocate their finite resources to a few relatively large eggs, or to increasing numbers of relatively smaller eggs. He tested this using data from wildfowl (Anatidae), which are highly precocial and lay relatively large clutches for which nutrients are likely to be limiting. He found that there was indeed a trade-off between clutch size and egg size (Lack 1967, 1968).

More recently, this finding has been called into question. Rohwer (1988) argued that Lack had used inappropriate statistical techniques to control for the confounding effects of body size on egg size, had made arbitrary categorizations of egg size, and had used questionable data for some of the wildfowl species. Rohwer repeated the analysis using different statistical tests and more reliable, recently available data. He found that once female size had been controlled for, clutch size accounted for only 11% of the remaining interspecific variance in egg size. Additionally controlling for taxonomy, this proportion rose to 13%. Rohwer considered that this was too small a part of the residual variance in egg size for the trade-off with clutch size to be biologically important.

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Whether 13% is an important proportion of the residual variance is subjective; just because an effect is small, it isn't necessarily unimportant. The egg size/clutch size relationship was always significant when all data were included. However, even leaving aside this argument, I believe that Rohwer's conclusions are flawed, due to the use of questionable techniques in the analysis. Here I present further reanalysis of the interspecific data to demonstrate that the relationship between clutch size and egg size is much stronger than implied by Rohwer. My criticism focuses on two aspects of Rohwer's methodology: the regression technique and the method of controlling for variation due to taxonomy. I will consider the former first.

Three regression models are commonly used in allometric studies: standard (least squares or Model 1), major (principal) axis (Model 2), and reduced major axis. These three models differ in their assumptions about the distribution of error variance. Leaving aside reduced major axis, standard regression assumes that there is no error variance in the x variate, while major axis assumes that the error variances in the x and y variates are equal (Pagel and Harvey 1989). Rohwer used major axis rather than standard regression for his analysis. His justification for this was that neither clutch size nor egg size has logical primacy as the causal agent for variation in the other. Therefore, because standard regression assumes that the y variate is dependent on the x variate, it is an inappropriate method in this case. Since major axis assumes that error variances are equal, and hence that neither variable is dependent on the other, this technique was considered more suitable (Rohwer 1988).

However, there are two problems with the use of major axis regression for this analysis. The first is that the major axis assumption of equal error variances may be no better than the standard regression assumption that there is only error variance in the y variate (Pagel and Harvey 1989). Pagel and Harvey (1988a) showed that none of the three regression models made realistic assumptions about error variances in measurements of brain and body weight in mammals. The situation for clutch and egg size may be no different. There is no *a priori* reason why error variance in egg size should be equal to error variance in clutch size.

The second problem arises from Rohwer's use of major axis residuals to control for female body mass. He first regressed female mass against its major axis slope with egg mass, and calculated the residuals from this slope. He then regressed these residuals against clutch size to obtain the relationship between clutch and egg size, controlling for female mass. However major axis residuals are not independent of the x variate (Pagel and Harvey 1988b), female mass in this instance. Thus there is a correlation between female mass and the residuals, which will potentially bias the clutch size/egg size relationship. In contrast, re-

siduals from standard regression are independent of the x variate, and so do not bias the clutch/egg size relationship. Repeating Rohwer's across-species analysis using standard regression yields an r^2 of 0.216 ($r = -0.465$, $n = 151$, $P < 0.0001$), compared with 0.11 ($r = -0.34$, $n = 151$, $P < 0.0001$) using major axis.

The main advantage of major axis over standard regression when both variables are measured with equal amounts of error is that it provides a more accurate estimate of the slope of the line relating two variables. This is most useful when, for theoretical reasons, it is the precise slope of the relationship that is important. However, if one is looking for the strength of a relationship between two variables, controlling for a confounding variable, standard regression is the better technique (Pagel and Harvey 1988b: appendix).

The second criticism relates to the problem of controlling for the confounding effects of phylogeny on comparative relationships. Closely related species may share characters through descent rather than through their having evolved independently in each case. A comparison across species may therefore overestimate the number of times that certain character combinations have evolved. For example, the genus *Anas* contains 42 of the 151 points in the cross-species comparison (Rohwer 1988: appendix). If a trade-off between egg size and clutch size had evolved in this genus only, an across-species comparison using all the data could possibly show a significant relationship between the two variables, even if there was no trade-off in other taxa. The relationship would only have evolved once, but it would be falsely represented in the analysis as having evolved many times (Pagel and Harvey 1988b).

Rohwer attempts to solve this problem by calculating relative egg mass and clutch mass separately within each tribe, and then correlating these new residuals across all species. While this procedure corrects for differences among major taxa, it is somewhat crude and still suffers from the problem that species within tribes may be similar by descent, and thus not strictly independent (Pagel and Harvey 1988b). Controlling for the differences between tribes, and for the effects of female mass using major axis regression, Rohwer found that $r^2 = 0.13$ ($r = -0.36$, $n = 146$, $P < 0.0001$) for the relationship between clutch and egg size. A more refined method is to examine the relationship between the variables in question within each taxon (e.g. between species within each genus, genera within each tribe, and so on). The relationship between them is then unaffected by phylogeny, since all taxa in the comparison are equally related to each other. This method requires that the true phylogeny be known (Felsenstein 1985). However, a model has recently been derived which applies this method to data sets for which only approximate phylogenies are available (Harvey et al. in press). This method calculates a single value ("contrast") for each variable within

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-taxa 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

Frank C. Rohwer[1]

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-