

Analyzing the Relationship between Clutch Size and Female Body Size in Reptiles

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Ecological studies of reptiles often include linear regression analyses of the relationship between number of eggs or offspring (clutch size) and female body size. Recent issues of *Copeia* (vol. 1997–1998), *Herpetologica* (vol. 53–54) and *Journal of Herpetology* (vol. 31–32) include 19 publications in which the relationship between clutch size and female size in reptiles is reported. Length was used as a measure of female size in 16 analyses and mass was used as a measure of female size in three analyses. In only two cases did authors log transform clutch size and female size prior to analysis. Here, I suggest that analysis of log transformed variables is preferred for meeting the assumptions of linear regression and for facilitating biological interpretation and comparisons among studies. Log transformation of variables such as clutch size and body size is the norm in comparative analyses of reptilian life history for many of the reasons discussed below (e.g., Dunham and Miles, 1985). However, as recent issues of the herpetological journals listed above attest, log transformation has been used infrequently in single species analyses.

One assumption of linear regression is that there is a straight-line (linear) relationship between dependent and independent variables (Zar, 1999, pp. 322). However, principles of allometric scaling suggest that when length is used as a measure of female size, a curvilinear relationship is expected. This is because clutch size is expected to increase as a function of female abdominal volume, whereas female abdominal volume, like mass, is expected to be a cubic function of length. In contrast, when mass is used as a measure of female size or when data are log transformed (using natural logs or \log_{10}), relationships between clutch size and female size are expected to be linear. Visual inspection of clutch size–body size relationships (e.g., in the 19 articles mentioned above) suggests that clutch size–female size relationships are generally linear regardless of how female size is measured. The lack of visual evidence for a curvilinear relationship between clutch size and female length has two likely explanations. First, clutch size is typically quite variable even among females with similar body sizes. As a consequence, female size often explains less than 50% of the variation in clutch size (e.g., Table 8-2 in Seigel and Ford, 1987). Second, body lengths of the smallest and largest female in most studies typically differ by less than a factor of two; and over this small range of body sizes, distinguishing between a linear and a curvilinear relationship may be difficult.

Another assumption of linear regression is that variances are homogeneous (Zar, 1999, pp. 332); i.e., there is no systematic change in the variance of the dependent variable (e.g., clutch size) with changes in the

independent variable (e.g., female size). This assumption is sometimes violated when either length or mass is used as a measure of female body size because variance in clutch size increases with increasing female size (e.g., Fig. 4 in Shine et al., 1998). The reason for this is simple. Suppose that the relationship between clutch size and female size is such that a small female is expected to produce five offspring and a large female is expected to produce 50 offspring. If a small and a large female each produced clutches that were 20% larger than expected, the small female would produce just one additional offspring (six instead of five) whereas the large female would produce ten additional offspring (60 instead of 50). Thus, even if variation in clutch size as a proportion of expected clutch size is constant, absolute variation in clutch size should be greater for larger females.

Log transformation often renders curvilinear relationships linear and reduces or eliminates heteroscedasticity of variances (Zar, 1999, pp. 353–355). More importantly, log transformation facilitates biological interpretation and comparison among studies and taxa. Back transformation of the regression equation $\ln(Y) = a + b(\ln(X))$ yields a power function, $Y = e^{aX^b}$, that describes the allometric relationship between X (body size) and Y (clutch size) (where e is the base of natural logarithms). The exponent b of this power function, also known as the allometric coefficient, provides a scale-independent descriptor of the relationship between clutch size and female size. If clutch size increases as a cubic function of female length, then an allometric coefficient of three is expected; if female mass is used as a measure of female size an allometric coefficient of one is expected. Allometric coefficients that deviate significantly from expected values may indicate a difference in reproductive strategies between smaller and larger females. In some species, larger females produce larger offspring (e.g., Congdon and Gibbons, 1987; King, 1993) and as a consequence may produce fewer offspring than otherwise expected. Alternatively, small and large females may differ in shape and hence, abdominal volume may not be a cubic function of length.

Differences in allometric coefficients among populations or species may reflect ecologically or evolutionarily interesting phenomena that could be overlooked when untransformed variables are analyzed. For example, Seigel and Ford (1987) compiled linear regression statistics relating untransformed clutch size and female length for 49 species or populations of snakes (Table 8-2 in Seigel and Ford, 1987). One of the few generalizations that can be drawn from this compilation is that the proportion of variance in clutch size explained by female length is highly variable. A similar compilation of regression coefficients relating log transformations of clutch size and female size might reveal whether allometric coefficients of three are typical or whether clutch size–female size allometry varies in interesting ways (e.g., between viviparous and oviparous taxa, among taxa differing in mode of locomotion).

To illustrate the potential advantages of using log transformed data, I analyzed the relationship between clutch size and female length in *Iguana iguana* (data from Table 1 in Rand, 1984 and Fig. 6 in Fitch and Henderson, 1977), *Elaphe rufodorsata* (data from Fig. 1

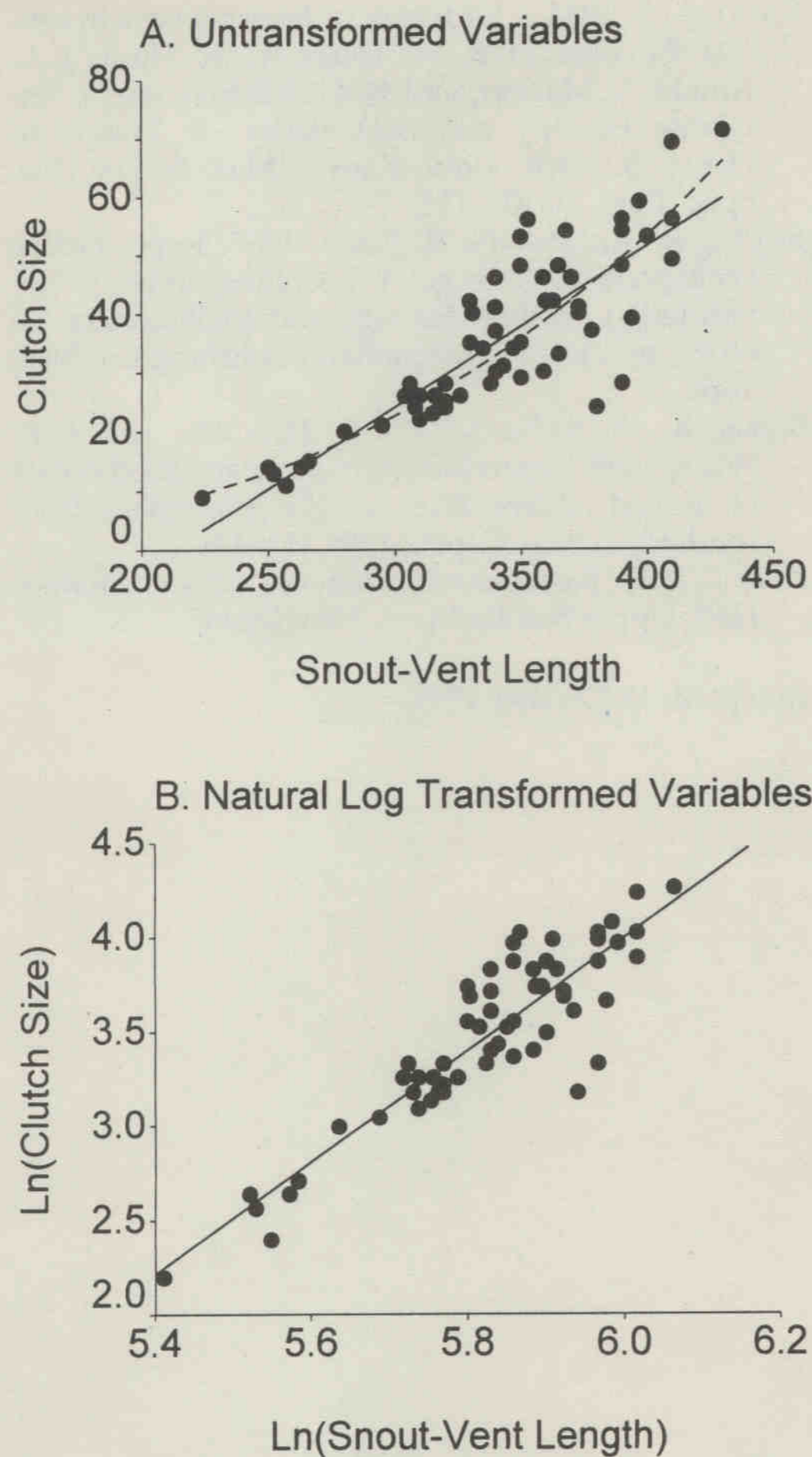


FIG. 1. Relationship between clutch size and female size in *Iguana iguana* based on (A) untransformed variables and (B) log transformed variables. Based on simple linear regression (solid lines), female size explains 71% of the variation in clutch size in (A) and 80% in (B). Linear regression of log transformed data (B) is statistically equivalent to fitting a power function to the untransformed data (dashed line in A).

in Ji et al., 1997), and *Apalone ferox* (data from Fig. 7 in Iverson and Moler, 1997). The lizard (*I. iguana*) data set was selected specifically because the relationship between clutch size and female length appeared at least somewhat curvilinear (Fig. 1A). The *E. rufodorsata* and *A. ferox* data sets were selected because of large sample size and because they represent two other reptilian body forms (a snake and a turtle, respectively).

In addition to appearing somewhat curvilinear, variance in clutch size appeared to increase with increasing female length in *I. iguana* (Fig. 1A). Simple linear regression analysis of these data was highly significant ($P < 0.001$): Clutch Size = $-57.90 + 0.27(\text{SVL})$. Regression analysis fitting a power function to these data was also highly significant ($P < 0.001$): Clutch Size = $0.000001(\text{SVL})^{2.97}$. Although both methods of analysis reveal a highly significant relationship, the

TABLE 1. Relationship between clutch size and female length in *I. iguana*, *E. rufodorsata*, and *A. ferox*. Allometric coefficients are equal to the slopes listed under Natural Log Transformed Data. For *I. iguana* and *E. rufodorsata*, snout-vent length (mm) was used as a measure of female length; for *A. ferox*, plastron length (mm) was used. Errors in estimating clutch size and female size from published figures were small; slopes reported here were within 1% and intercepts within 3% of those reported in the source publications. For *E. rufodorsata*, one outlier (a large female with an unusually small clutch) was omitted.

| Species | N | Untransformed data | | | Natural log transformed data | | |
|---------------------------|----|--------------------|-------------------------|----------------|------------------------------|-------------------------|----------------|
| | | Slope (95% CI) | Intercept (95% CI) | r ² | Slope (95% CI) | Intercept (95% CI) | r ² |
| <i>Iguana iguana</i> | 61 | 0.27 (0.23, 0.32) | -57.90 (-73.61, -42.18) | 0.71 | 2.97 (2.59, 3.26) | -13.83 (-16.07, -11.60) | 0.81 |
| <i>Elathe rufodorsata</i> | 55 | 0.06 (0.05, 0.07) | -22.14 (-29.90, -14.37) | 0.60 | 2.86 (2.24, 3.47) | -15.76 (-19.70, -11.81) | 0.62 |
| <i>Apalone ferox</i> | 46 | 0.12 (0.08, 0.16) | -17.18 (-30.75, -3.61) | 0.41 | 1.61 (0.92, 2.31) | -6.26 (-10.30, -2.28) | 0.33 |

power function explained somewhat more variation in clutch size ($r^2 = 0.80$) than did the linear function ($r^2 = 0.71$). Regression analysis of log transforms of both clutch size and SVL is statistically equivalent to fitting a power function to the untransformed data ($\ln(\text{Clutch Size}) = -13.83 + 2.97(\ln(\text{SVL}))$, $P < 0.001$, $r^2 = 0.80$) and the relationship between $\ln(\text{clutch size})$ and $\ln(\text{SVL})$ appears linear (Fig. 1B).

The improved fit between clutch size and body length seen by using log transformed data for *I. iguana* was not evident for *E. rufodorsata* or *A. ferox* (Table 1). However, examination of the allometric coefficients for these three species illustrates how analysis based on log transformed data facilitates interpretation. First, for *I. iguana* and *E. rufodorsata*, allometric coefficients did not differ significantly from three (95% confidence intervals include three), indicating that clutch size increased as expected with increasing female length in these species. In contrast, the allometric coefficient for *A. ferox* was significantly less than three, indicating that clutch size increased more slowly than expected with increasing body length. Second, allometric coefficients did not differ between *I. iguana* and *E. rufodorsata* (95% confidence intervals overlap) but did differ between *I. iguana* and *A. ferox*. Neither of these patterns is evident from regression coefficients based on untransformed data (Table 1).

The relationship between clutch size and female body size has been documented in a wide variety of reptiles. In this note, I have demonstrated that a simple modification of the way that this relationship is presented, using log transformed measures of clutch size and body size, aids the interpretation of this relationship and facilitates comparisons among populations and species. Certainly situations exist where analysis of untransformed measures is warranted. However, as analyses based on log transformed data accumulate, phylogenetic, morphological, and ecological effects on clutch size–female size relationships may become apparent.

Acknowledgements.—T. Bittner, J. Kerfin, B. King, and an anonymous reviewer provided helpful suggestions.

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Accepted: 13 October 1999.