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CORRESPONDENCE

## Reduced major axis regression and the island rule

The 'island rule' describes a tendency for larger animals to get smaller on islands, and for smaller ones to get larger. The rule has been assessed by comparing matched pairs of species or populations on islands ($Y$) with their presumed continental source ($X$), where $Y$ and $X$ are log-transformed mean body sizes (summarized by Lomolino, 2005). The slope of the least-squares regression of $Y$ on $X$, $b$, measures the extent to which large body sizes tend to decrease and small body sizes to increase. For example, if the mean body size among the island forms is the same as the mean body size among the mainland forms then $b = 0.5$ implies that, on average, species above the mean decrease half-way towards the mean, and species below the mean increase half-way to the mean. $b$ is often significantly $< 1.0$, indicating that taxa of larger body size do tend to decrease, and those of small body size tend to increase (Lomolino, 2005). This result can also be presented in a different way, as the regression of $Y - X$ on $X$, and here the slope ($b'$) is generally negative ($b' = b - 1$).

Two explanations for this finding can be proposed. In the first, the variance in body size among island species ($\sigma^2_Y$) is roughly the same as the variance in body size among continental species ($\sigma^2_X$). Given that large body sizes tend to decrease and small ones to increase when going from mainland to islands (which reduces the variance), some species with more intermediate body sizes on the mainland must increase in body size on the islands, and others with more intermediate body sizes must decrease, in order for the variance to remain constant. The implication is that, if the variances are the same, large-bodied island taxa came from, on average, smaller-bodied source taxa on the mainland; and small-bodied island taxa came from, on average, larger-bodied source taxa on the mainland. This could be shown by the regression of mainland body size on island body size, and implies that the effect is not a special property of islands.

If the variance across island populations and across mainland populations is the same, then $b = r$ and $b' = r - 1$, where $r$ is the correlation between $X$ and $Y$. The decrease of large body sizes and increase of small body sizes on islands is best attributed to those random factors that make the correlation $< 1.0$. For example, consider the possibility that a similar diversity of niches is present on islands and on mainlands. Those taxa of particularly large or small body size in one location occupy extreme niches, and on average one might expect them to occupy a less extreme niche in the second location, and hence to converge towards the mean. Other taxa that experience more intermediate environments in the first location evolve to fill the more extreme niches in the second location.

In the second explanation, there is a general tendency for body sizes to converge on some intermediate value on islands. The decrease of large body sizes and increase in small body sizes is not compensated by corresponding changes in those taxa with intermediate body sizes. This reflects a genuine property of islands and is usually what is described as the 'island rule' (Lomolino, 2005). In addition to the prediction that $b < 1$ and $b' < 0$, this alternative explanation makes the prediction that the variance across island populations is less than that across continental populations. The two alternatives can therefore be distinguished by testing for a lower variance among island populations (Kelly & Price, 2005). The reduced major axis regression provides such a test. The slope of the reduced major axis, $m$, (also known as the standardized major axis; Warton *et al.*, 2006) is the ratio of the standard deviations, $m = \sigma_Y/\sigma_X$ (e.g. Sokal & Rohlf, 1995, p. 544; Warton *et al.*, 2006). The test of the null hypothesis $m = 1$ against the alternative $m \neq 1$ therefore provides a test of equality of variances. The standard error of the slope of the reduced major axis is approximated by that of the least-squares regression (Sokal & Rohlf, 1995; Warton *et al.*, 2006), and the null hypothesis can be tested using a $t$-test, with $n - 2$ degrees of freedom, where n is the number of $(X, Y)$ pairs.

As reviewed by Warton *et al.* (2006), the reduced major axis regression has often been proposed as an appropriate regression model if there is measurement error in $X$, which could be one contributor to a relatively low least-squares regression of $Y$ on $X$. However, the differences in interpretation between the reduced major axis and least-squares regression apply here, even if there is no measurement error in X, that is, the mean values of the populations are known exactly. This, for example, was the case in the hypothetical example of niche filling presented above. In fact, measurement error is likely to make only a small contribution to a low least-squares regression slope based on species means, which is instead a result of real differences between populations (Kelly & Price, 2004). More generally, the choice of reduced major axis based on the presence of measurement error in $X$ does not have much justification, and least-squares regression is the appropriate model for prediction; this applies even if $X$ is measured with error (Warton *et al.*, 2006). Thus, the average body size of an island relative of a mainland population is best predicted by the least-squares regression of island on mainland body size, and the body size of a mainland relative of an island population is best predicted by the regression of mainland on island body size. Reduced major axis regression is used here as a test for equality of variances, to ask if there is an overall tendency for mainland species to converge towards the overall body size mean on islands.

We applied the reduced major axis test to some of the studies analysed by Lomolino (2005), all of which show $b$ values significantly $< 1.0$. Even though $P$-values are increased when the reduced major axis is used, the island rule is generally confirmed.


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**Table 1** Tests of the island rule based on reduced major axis regression.

| | Regression slopes* | | | | | | |
|---|---|---|---|---|---|---|---|
| | Sample size | Correlation*, $r$ | Least squares†, $b$ | Reduced major axis‡, $m$ | S.E.† | Variance ratio‡, $(\sigma^2_Y/\sigma^2_X)$ | $P$§ |
| Mammals | 384 | 0.995 | 0.95 | 0.95 | 0.005 | 0.90 | 0.00 |
| Bats | 90 | 0.996 | 0.96 | 0.97 | 0.010 | 0.93 | 0.00 |
| Birds | 51 | 0.991 | 0.94 | 0.95 | 0.019 | 0.91 | 0.02 |
| Snakes | 30 | 0.705 | 0.53 | 0.75 | 0.100 | 0.56 | 0.02 |
| Non-volant mammals, Denmark | 20 | 0.958 | 0.87 | 0.91 | 0.062 | 0.83 | 0.17 |
| Australian time-dwarfed marsupials | 9 | 0.995 | 0.70 | 0.71 | 0.026 | 0.50 | 0.00 |
| Turtles | 23 | 0.630 | 0.69 | 1.09 | 0.185 | 1.20 | 0.62 |

*Correlation and regressions of log mass (island) on log mass (mainland).

†From Lomolino (2005), who gives the original sources for these data: Table 1 (first row) and Table 2 (other entries).

When only $b'$ (the regression of $Y - X$ vs. $X$), was given, $b$ was calculated as $b' + 1$. The standard error (S.E.) is the same for $b$, $b'$ and the reduced major axis.

‡Calculated using regression and correlation statistics in Lomolino (2005), Tables 1 and 2. $(\sigma^2_Y/\sigma^2_X) = b^2/r^2 = b'^2/r'^2 + 1 + 2b'$, where $r$ is the correlation and $'$ indicates that $Y - X$, rather than $Y$, is the dependent variable.

§From a two-tailed $t$-test of the null hypothesis that the reduced major axis = 1.0.

In most data sets, the correlation between mainland and island is very high ($r > 0.95$), making an explanation for low $b$ values based on regression towards the mean untenable. Variance in body size across islands is often 10–50% lower than the variance across presumed colonization sources (Table 1). However, two data sets, which were marginally significant using least-squares regression, fail to support the island rule when analysed using the reduced major axis.

Meiri *et al.* (2006) presented two additional data sets; one based on mammalian body weights ($n = 91$), and the other based on carnivore skull sizes ($n = 416$). Results differ from the analyses of Lomolino (2005), in that in neither case is $b$ significantly different from 1.0. For mammalian body weights, $b = 0.965 \pm 0.187$ SE, which is close to significantly different from 1.0 ($P = 0.06$), but in the estimate for skull sizes $b = 0.999 \pm 0.005$, which is very close to 1.0 ($P = 0.2$). The correlations are very high ($r = 0.98$ and $r = 0.99$, respectively) and the variance ratios are close to 1.0. In these data, the overwhelming finding is that mammals change very little from mainland to island, at least when compared with the variance in mean body size within each location. The correlation is also very high in Lomolino's large data set (Table 1, first row), but the $b$ value (0.946) is lower than that found by Meiri *et al.* (2006). Possibly the difference between the results of Lomolino (2005) and Meiri *et al.* (2006) stems from Lomolino including more populations at the extremes of the distribution, whose niches are most likely to disappear on islands. The island rule appears to have quite widespread support.

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