

## THE FALLACY OF AVERAGES

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Many questions about organisms require estimation of average values of traits that, for various practical reasons, are difficult to measure directly but that can be decomposed into two or more multiplicative components, each of which can be measured. (Such characteristics are hereafter referred to as product traits.) For instance, although an animal's daily intake of food energy is difficult to measure directly, it can be estimated indirectly using estimates of time spent feeding, food intake per unit of foraging time, and energy content per unit of food mass.

## THE PROBLEM

Many biologists (including two of the authors of this paper) have estimated the population means of product traits by measuring each of the component variables in separate subsamples of the population and then multiplying the component means to produce the desired mean of the product traits. For example, Janson (1985, table 1) and Stacey (1986, eq. 1) both estimated the mean daily energy intake by primates from a given food as the product of the mean daily intake of that food, the mean weight of an item of that food, and the food's mean energy content, in joules per gram. This can be represented by  $\mu(\text{J/day}) = \mu(\text{J/g})\mu(\text{g/item})\mu(\text{items/day})$ . (Here and in what follows,  $\mu(x)$  indicates the mean of  $x$ .) Further examples of this procedure have been presented by Shea and Ricklefs (1985, table 1), Shank (1986, p. 645), Ekman and Askenmo (1986, table 1) and can, indeed, be found in nearly every volume of many biological journals.

A general pattern appears in these calculations. For an individual product trait with multiplicative component variables  $X$  and  $Y$ , the population mean of their product,  $\mu(XY)$ , is commonly assumed to equal  $\mu(X)\mu(Y)$ . Alas, this widespread assumption is not generally correct, although it is if  $X$  and  $Y$  are uncorrelated. The exact relationship between  $\mu(XY)$  and  $\mu(X)\mu(Y)$  is given below. The corresponding assumption is made about division of means, namely, that  $\mu(X/Y)$  equals  $\mu(X)/\mu(Y)$ , and about other functions of means.

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The assumption that  $\mu(XY) = \mu(X)\mu(Y)$  is a special case of what Wagner referred to as *the fallacy of averages*: "Given an arbitrary nonlinear function  $f(x_1, \dots, x_n)$  of random variables  $x_1, \dots, x_n$  it is usually erroneous to assume  $E[f(x_1, \dots, x_n)] = f[E(x_1), \dots, E(x_n)]$ ," where  $E$  indicates an expected value (1969, p. 658).

The fallacy of averages is perhaps the most widespread statistical error in biology. Templeton and Lawlor (1981) gave several examples of this fallacy in the literature on optimization models in ecology, though they did not indicate any of the situations in which the expected value of a function is the same as the function of the expected value; and in only one case, the mean of a reciprocal versus the reciprocal of a mean, did they show how the two are related. Although the particular examples selected by Templeton and Lawlor may be inappropriate (Gilliam et al. 1982; Turelli et al. 1982), the principle is still valid.

A comparable problem arises repeatedly in the study of allometric relationships whenever two or more allometric regression equations are multiplied together or divided by one another, because the estimates of the regression parameters are just weighted averages. For example, in quadrupedal mammals, regression of distance moved per day,  $D$ , against body mass,  $M$  (in kg), yields  $D = 0.875 M^{0.22}$  km/day (Garland 1983), and regression of the increment in energy expended per kilometer walked,  $E$ , against body mass yields  $E = 10700 M^{0.684}$  J/km (Taylor et al. 1982); and on this basis, Altmann (1987) calculated average energy expended on locomotion per day as  $ED$ , that is, at  $10700 M^{0.684} 0.875 M^{0.22}$ . This calculation overlooks possible covariance between distance traveled per day and energy expended per unit of distance.

Similar examples can be found in recent surveys of allometric relationships (Peters 1983; Calder 1984). At the transition from trot to gallop, mammalian stride frequency regressed on body mass yields  $11.8 M^{-0.14}$  strides/s (Heglund et al. 1974), and the regression of stride length on body mass yields  $0.35 M^{0.38}$  m/stride; thus, Calder (1984) estimated the velocity as the product  $11.8 M^{-0.14} 0.35 M^{0.38}$  m/s. This estimate ignores the possible covariance between stride length and stride frequency. As a further example, the regression of the energy content of a full mammalian gut on body mass yields  $757 M^{1.02}$  kJ, and the regression of metabolic demand on body mass yields  $504 M^{0.76}$  kJ/day; therefore, gut turnover time was calculated from the ratio  $757 M^{1.02}/504 M^{0.76}$  days/gutfull (Calder 1984). Again, possible covariance between the component variables is ignored.

In order to demonstrate the potential magnitude of these errors, we used data from Donaldson (1919, table 1) to calculate three quotient traits describing the mass of rat skeletons,  $K$ , as a percentage of body mass,  $M$ . The mean mass of skeleton (i.e.,  $\mu(K/M)$ ) as a percentage of body mass is 6.51%; however,  $\mu(K) = 12.99$  and  $\mu(M) = 222.74$ ; therefore,  $\mu(M)/\mu(K) = 5.83\%$ . Thus, calculating this trait as a quotient of means yields an error of 10.5%. Similar calculations for axial-skeleton mass as a percentage of body mass and appendicular-skeleton mass as a percentage of body mass yield errors of 10.2% and 10.8%, respectively. Using information from papers that correctly calculate product traits but present means of component variables as well, we found that ignoring covariances among com-

ponent variables can introduce errors ranging from near zero (as in estimating sex ratios of hamsters; Labov et al. 1986) to well over 50% (as in estimating aggregation levels in hummingbirds; Tamm 1985).

For regressions, two examples serve to illustrate the potential magnitude of errors caused by combining regression equations without considering covariances. We used data from Greenewalt (1962, table 1, Coleoptera) to estimate the regression of the ratio of wing-beat frequency ( $s^{-1}$ ) to wing length on body mass (mg) in 28 beetles of 12 species. All data were transformed using natural logarithms before analysis. The regression of wing-beat frequency,  $B$ , on body mass,  $M$ , is  $B = 4.942 M^{-0.077}$ ; the regression of wing length,  $L$ , on body mass is  $L = 1.054 M^{0.321}$ . The ratio of these equations is then  $B/L = 4.942 M^{-0.077}/1.054 M^{0.321} = 4.690 M^{-0.398}$ . However, the actual regression of individual values of  $B/L$  on  $M$  is  $B/L = 3.889 M^{-0.398}$ . Thus, although the exponent is correct, the coefficient of  $M$  estimated by the ratio of the regressions is off by 17.1%.

In a second example, we used data from Greenewalt (1962, table 15, Corvidae) to estimate the regression of the ratio of "large" pectoral muscle (= *M. pectoralis*) mass (g) to wing length (cm) on body mass (g) in nine corvids of nine species. All data were transformed using natural logarithms before analysis. The regression of pectoral muscle mass,  $P$ , on body mass  $M$  is  $P = -2.576 M^{1.096}$ ; the regression of wing length  $L$  on body mass is  $L = 0.885 M^{0.404}$ . The ratio of these equations is  $P/L = -2.576 M^{1.096}/0.885 M^{0.404} = -2.910 M^{0.692}$ . However, the actual regression of individual values of  $P/L$  on  $M$  is  $P/L = -3.461 M^{0.692}$ . The error in the estimate of the coefficient of  $M$  is 15.9%.

Our susceptibility to the fallacy of averages stems in part from dimensional analysis, in which we treat our units of measurement algebraically and then ignore the fact that we are using means. So, for example, in a population of birds, the mean lifetime reproductive success (number of chicks fledged) would equal the mean number of chicks fledged per clutch times the mean number of clutches per lifetime if and only if these two characteristics were uncorrelated—which seems unlikely—notwithstanding the fact that chicks/lifetime equals (chicks/clutch)·(clutches/lifetime) for an individual bird. In using means, naive dimensional analysis is likely to be misleading.

Yet another problem arises for traits having additive or subtractive components (e.g., body mass, life span, skeletal elements). Here, although the mean of an additive trait does equal the sum of the component means, that is,  $\mu(X + Y) = \mu(X) + \mu(Y)$ , the variance of the trait is not estimated by the sum or average of the component variances (Lande 1977; Soulé 1982). For example, although the mean age of human females at menopause equals their mean age at menarche plus the mean duration of the reproductive phase between menarche and menopause, the variance of the age at menopause does not equal the variance of age at menarche plus the variance of the length of the reproductive phase if, say, females who reach menarche late tend to reach menopause early. Although Lande (1977) pointed this out with regard to a biological problem, chiropteran wing measurements (Bader and Hall 1960), some biologists continue to base conclusions on the (unstated) assumption of additive variances.

THE SOLUTION

*Products*

Suppose initially that an individual product trait can be decomposed into two multiplicative component variables  $X$  and  $Y$ . Then, provided the moments are finite, it follows from the definition of covariance that

$$\mu(XY) = \mu(X)\mu(Y) + \text{cov}(X, Y),$$

where  $\text{cov}(X, Y)$  denotes the covariance of  $X$  and  $Y$ . Thus,  $\mu(XY) = \mu(X)\mu(Y)$  if and only if  $X$  and  $Y$  are uncorrelated; thus, if  $X$  and  $Y$  are independent,  $\mu(XY) = \mu(X)\mu(Y)$ . (Recall that if  $X$  and  $Y$  are independent, they are uncorrelated, but that the converse need not be true.)

Now, suppose that the component variables can be measured on the same individual; if measurements are made on  $n$  individuals, the data can then be written as  $(X_1, Y_1), (X_2, Y_2), \dots, (X_n, Y_n)$ . It is usual to assume that each pair of measurements is not independent of the other pairs. Consider the estimators

$$\hat{\mu}_{XY} = n^{-1} \sum_{j=1}^n X_j Y_j \quad \text{and} \quad \hat{\mu}_X \hat{\mu}_Y = \left( n^{-1} \sum_{j=1}^n X_j \right) \left( n^{-1} \sum_{j=1}^n Y_j \right).$$

Now,  $\hat{\mu}_{XY}$  is consistent for  $\mu(XY)$  and  $\mu(\hat{\mu}_{XY}) = \mu(XY)$ , but  $\hat{\mu}_X \hat{\mu}_Y$  is consistent for  $\mu(X)\mu(Y)$  and

$$\mu(\hat{\mu}_X \hat{\mu}_Y) = \mu(X)\mu(Y) + \text{cov}(X, Y)/n = \mu(XY) - \text{cov}(X, Y)(n - 1)/n;$$

the product of the component means thus estimates the mean of the product trait if and only if  $X$  and  $Y$  are uncorrelated. Goodman (1960) derived the exact sampling variances of  $\hat{\mu}_{XY}$  and  $\hat{\mu}_X \hat{\mu}_Y$ . In particular, if  $X$  and  $Y$  are independent,

$$\sigma(\hat{\mu}_{XY})^2 = [\mu(X)^2\sigma(Y)^2 + \mu(Y)^2\sigma(X)^2 + \sigma(X)^2\sigma(Y)^2]/n$$

and

$$\sigma(\hat{\mu}_X \hat{\mu}_Y)^2 = [\mu(X)^2\sigma(Y)^2 + \mu(Y)^2\sigma(X)^2 + \sigma(X)^2\sigma(Y)^2/n]/n,$$

where  $\sigma(X)^2$  denotes the variance of  $X$ . If  $X$  and  $Y$  are independent with finite variances and at least one of  $\mu(X), \mu(Y)$  is nonzero, it follows from the central limit theorem that approximately, for large  $n$ ,

$$\hat{\mu}_{XY} \sim N\{\mu(XY), [\mu(X)^2\sigma(Y)^2 + \mu(Y)^2\sigma(X)^2 + \sigma(X)^2\sigma(Y)^2]/n\}$$

and

$$\hat{\mu}_X \hat{\mu}_Y \sim N\{\mu(XY), [\mu(X)^2\sigma(Y)^2 + \mu(Y)^2\sigma(X)^2]/n\},$$

where “ $\sim N(a, b^2)$ ” means “is normally distributed with mean  $a$  and variance  $b^2$ .” If  $X$  and  $Y$  are independent,  $\hat{\mu}_X \hat{\mu}_Y$  has a smaller variance than  $\hat{\mu}_{XY}$  and hence is a more efficient estimator. However, if  $X$  and  $Y$  have nonzero covariance,  $\hat{\mu}_X \hat{\mu}_Y$  is biased and  $\hat{\mu}_{XY}$  is the appropriate estimator.

Analogous results can be derived for products decomposed into several compo-

nent variables. For example, if there are three component variables  $X$ ,  $Y$ , and  $Z$ ,

$$\begin{aligned} \mu(XYZ) &= \mu(X)\mu(Y)\mu(Z) + \mu(Z)\text{cov}(X,Y) + \mu(Y)\text{cov}(X,Z) \\ &+ \mu(X)\text{cov}(Y,Z) + C_{111}(X,Y,Z), \end{aligned}$$

where  $C_{111}(X,Y,Z) = \mu\{[X - \mu(X)][Y - \mu(Y)][Z - \mu(Z)]\}$ . Again, independence ensures that the product of the means equals the mean of the products. The estimators can be analyzed as before, using, for example, results from Goodman (1962), and the same qualitative conclusions obtained.

*Ratios*

The results for multiplicative components can be used to derive results for the ratio of two components. Suppose that  $Y > 0$  and that both  $\sigma(Y)^2$  and  $\sigma(X/Y)^2$  are finite. Then,

$$\mu(X) = \mu(XY/Y) = \mu(Y)\mu(X/Y) + \text{cov}(X/Y,Y),$$

so that

$$\mu(X/Y) = \mu(X)/\mu(Y) - \text{cov}(X/Y,Y)/\mu(Y).$$

Thus,  $\mu(X/Y) = \mu(X)/\mu(Y)$  if and only if  $Y$  and  $X/Y$  are uncorrelated, which is extremely unlikely because of mathematical constraints (Atchley et al. 1976). Since it is usually difficult to think about the dependence between  $Y$  and  $X/Y$ , the situation is complicated. However, provided that  $\sigma(1/Y)^2$  is finite,

$$\mu(X/Y) = \mu(X)\mu(1/Y) + \text{cov}(X,1/Y),$$

so that  $\mu(X/Y) = \mu(X)\mu(1/Y)$  if and only if  $X$  and  $1/Y$  are uncorrelated.

If the component variables can be measured on the same individual, such that the data consist of  $n$  pairs of observations,  $(X_1, Y_1), (X_2, Y_2), \dots, (X_n, Y_n)$ , consider

$$\begin{aligned} \hat{\mu}_{X/Y} &= n^{-1} \sum_{j=1}^n (X_j/Y_j) \\ \hat{\mu}_X \hat{\mu}_{1/Y} &= \left( n^{-1} \sum_{j=1}^n X_j \right) \left( n^{-1} \sum_{j=1}^n 1/Y_j \right) \end{aligned}$$

and

$$\hat{\mu}_X / \hat{\mu}_Y = \left( n^{-1} \sum_{j=1}^n X_j \right) / \left( n^{-1} \sum_{j=1}^n Y_j \right).$$

The last estimator is of interest only if  $X/Y$  and  $Y$  are independent; therefore, it is not discussed further. Now  $\hat{\mu}_{X/Y}$  is consistent for  $\mu(X/Y)$  and  $\mu(\hat{\mu}_{X/Y}) = \mu(X/Y)$ , but  $\hat{\mu}_X \hat{\mu}_{1/Y}$  is consistent for  $\mu(X)\mu(1/Y)$  and

$$\begin{aligned} \mu(\hat{\mu}_X \hat{\mu}_{1/Y}) &= \mu(X)\mu(1/Y) + \text{cov}(X,1/Y)/n \\ &= \mu(X/Y) - \text{cov}(X,1/Y)(n - 1)/n. \end{aligned}$$

Therefore,  $\hat{\mu}_X \hat{\mu}_{1/Y}$  does not estimate  $\mu(X/Y)$  if  $X$  and  $1/Y$  are correlated. By the

results of Goodman (1960), if  $X$  and  $Y$  are independent,

$$\sigma(\hat{\mu}_{X/Y})^2 = [\mu(X)^2\sigma(1/Y)^2 + \mu(1/Y)^2\sigma(X)^2 + \sigma(X)^2\sigma(1/Y)^2]/n$$

and

$$\sigma(\hat{\mu}_X\hat{\mu}_{1/Y})^2 = [\mu(X)^2\sigma(1/Y)^2 + \mu(1/Y)^2\sigma(X)^2 + \sigma(X)^2\sigma(1/Y)^2/n].$$

In large samples, provided that  $X$  and  $Y$  are independent,

$$\hat{\mu}_{X/Y} \sim N[\mu(X/Y), \sigma(\hat{\mu}_{X/Y})^2]$$

and

$$\hat{\mu}_X\hat{\mu}_{1/Y} \sim N\{\mu(X/Y), [\mu(X)^2\sigma(1/Y)^2 + \mu(1/Y)^2\sigma(X)^2]/n\},$$

so that, as before,  $\hat{\mu}_X\hat{\mu}_{1/Y}$  is the preferred estimate as long as  $X$  and  $Y$  are independent.

### *Allometric Relationships*

An alternative approach to a multiplicative decomposition is to take the natural logarithm of the variables to obtain an additive decomposition. Of course, if  $X > 0$ ,  $Y > 0$ , and the moments are finite,

$$\mu(\ln XY) = \mu(\ln X) + \mu(\ln Y)$$

and

$$\sigma(\ln XY)^2 = \sigma(\ln X)^2 + \sigma(\ln Y)^2 + 2 \operatorname{cov}(\ln X, \ln Y),$$

such that the relationship between  $\ln X$  and  $\ln Y$  enters only in the variance calculation. It is usual on an additive scale to assume that the variables  $\ln X$  and  $\ln Y$  are normally distributed. If  $\ln X$  and  $\ln Y$  are normally distributed,

$$\mu(X) = \exp[\mu(\ln X) + \sigma(\ln X)^2/2],$$

$$\mu(Y) = \exp[\mu(\ln Y) + \sigma(\ln Y)^2/2],$$

and

$$\begin{aligned} \mu(XY) &= \exp[\mu(\ln XY) + \sigma(\ln XY)^2/2] \\ &= \mu(X)\mu(Y)\exp[\operatorname{cov}(\ln X, \ln Y)]. \end{aligned}$$

Thus,  $\mu(XY) = \mu(X)\mu(Y)$  if and only if  $\ln X$  and  $\ln Y$  are uncorrelated, so that if  $X$  and  $Y$  are independent,  $\mu(XY) = \mu(X)\mu(Y)$ .

Suppose that  $n$  independent pairs of measurements  $(X_1, Y_1), \dots, (X_n, Y_n)$  have been made, and put

$$\hat{\mu}_{XY} = \exp\left(n^{-1} \sum_{j=1}^n \ln X_j Y_j + \hat{\sigma}^2/2\right)$$

and

$$\hat{\mu}_X\hat{\mu}_Y = \exp\left(n^{-1} \sum_{j=1}^n \ln X_j + \hat{\sigma}_X^2/2\right) \exp\left(n^{-1} \sum_{j=1}^n \ln Y_j + \hat{\sigma}_Y^2/2\right),$$

where

$$\hat{\sigma}^2 = (n - 1)^{-1} \sum_{j=1}^n \left( \ln X_j Y_j - n^{-1} \sum_{i=1}^n \ln X_i Y_i \right)^2,$$

$$\hat{\sigma}_X^2 = (n - 1)^{-1} \sum_{j=1}^n \left( \ln X_j - n^{-1} \sum_{i=1}^n \ln X_i \right)^2,$$

and

$$\hat{\sigma}_Y^2 = (n - 1)^{-1} \sum_{j=1}^n \left( \ln Y_j - n^{-1} \sum_{i=1}^n \ln Y_i \right)^2.$$

If  $\ln X$  and  $\ln Y$  are normally distributed,  $\hat{\mu}_{XY}$  is consistent for  $\mu(XY)$  but  $\exp(n^{-1} \sum_{j=1}^n \ln X_j Y_j)$  is consistent only if  $\ln X$  and  $\ln Y$  have degenerate distributions and otherwise underestimates  $\mu(XY)$ . If  $X$  and  $Y$  are independent and  $\mu[(\ln X)^4]$  and  $\mu[(\ln Y)^4]$  are finite, it follows that approximately, for large  $n$ ,

$$\hat{\mu}_{XY} \sim N \left( m(XY), m(XY)^2 \{ \sigma(\ln X)^2 + \sigma(\ln Y)^2 + \kappa_3(\ln X) + \kappa_3(\ln Y) \right. \\ \left. + [\kappa_4(\ln X) - \sigma(\ln X)^4 + \kappa_4(\ln Y) - \sigma(\ln Y)^4] / 4 + \sigma(\ln X)^2 \sigma(\ln Y)^2 / n \right)$$

and

$$\hat{\mu}_X \hat{\mu}_Y \sim N \left( m(XY), m(XY)^2 \{ \sigma(\ln X)^2 + \sigma(\ln Y)^2 + \kappa_3(\ln X) + \kappa_3(\ln Y) \right. \\ \left. + [\kappa_4(\ln X) - \sigma(\ln X)^4 + \kappa_4(\ln Y) - \sigma(\ln Y)^4] / 4 \right) / n,$$

where  $m(XY) = \exp[\mu(\ln XY) + \sigma(\ln XY)^2 / 2]$  and  $\kappa_c(\ln X) = \mu\{[\ln X - \mu(\ln X)]^c\}$ . (If  $\ln X$  and  $\ln Y$  are normally distributed,  $m(XY) = \mu(XY)$ .) Again, if  $X$  and  $Y$  are independent,  $\hat{\mu}_X \hat{\mu}_Y$  is more efficient than  $\hat{\mu}_{XY}$ , but if  $\ln X$  and  $\ln Y$  are correlated,  $\hat{\mu}_X \hat{\mu}_Y$  is not consistent for  $\mu(XY)$ .

The above results can be extended to the decomposition of allometric relationships. If a product trait can be decomposed into two multiplicative component variables  $X$  and  $Y$ , each of which is related to body mass  $M$  via Huxley's (1932) allometric equation  $X = \alpha_X M^{\beta_X}$  and  $Y = \alpha_Y M^{\beta_Y}$ , then on the additive logarithmic scale it is convenient to suppose that  $\ln X$  given  $M$  is normal with mean  $\mu(\ln X) = \alpha_X + \beta_X \ln M$  and variance  $\sigma(\ln X)^2$  and, similarly, that  $\ln Y$  given  $M$  is normal with mean  $\mu(\ln Y) = \alpha_Y + \beta_Y \ln M$  and variance  $\sigma(\ln Y)^2$ . Of course, on the log scale, the means are additive, though the variances need not be. On the original scale, given  $M$ ,

$$\mu(X) = \exp[\alpha_X + \beta_X \ln M + \sigma(\ln X)^2 / 2],$$

$$\mu(Y) = \exp[\alpha_Y + \beta_Y \ln M + \sigma(\ln Y)^2 / 2],$$

and

$$\mu(XY) = \exp[\alpha_X + \alpha_Y + (\beta_X + \beta_Y) \ln M + \sigma(\ln X)^2 / 2 \\ + \sigma(\ln Y)^2 / 2 + \text{cov}(\ln X, \ln Y)].$$

If  $n$  independent triples of measurements  $(X_1, Y_1, M_1), (X_2, Y_2, M_2), \dots, (X_n, Y_n, M_n)$  have been made, let

$$\hat{\mu}_{XY} = \exp\{\hat{\alpha} + \hat{\beta} \ln M + \hat{\sigma}^2/2\}$$

and

$$\hat{\mu}_X \hat{\mu}_Y = \exp\{\hat{\alpha}_X + \hat{\beta}_X \ln M + \hat{\sigma}_X^2/2\} \exp\{\hat{\alpha}_Y + \hat{\beta}_Y \ln M + \hat{\sigma}_Y^2/2\},$$

where

$$\begin{aligned} \hat{\alpha} &= \hat{\alpha}_X + \hat{\alpha}_Y, \\ \hat{\alpha}_X &= n^{-1} \sum_{j=1}^n \ln X_j - \hat{\beta}_X n^{-1} \sum_{j=1}^n \ln M_j, \\ \hat{\alpha}_Y &= n^{-1} \sum_{j=1}^n \ln Y_j - \hat{\beta}_Y n^{-1} \sum_{j=1}^n \ln M_j, \\ \hat{\beta} &= \hat{\beta}_X + \hat{\beta}_Y, \\ \hat{\beta}_X &= \left[ \sum_{j=1}^n \left( \ln M_j - n^{-1} \sum_{i=1}^n \ln M_i \right) \ln X_j \right] / \sum_{j=1}^n \left( \ln M_j - n^{-1} \sum_{i=1}^n \ln M_i \right)^2, \\ \hat{\beta}_Y &= \left[ \sum_{j=1}^n \left( \ln M_j - n^{-1} \sum_{i=1}^n \ln M_i \right) \ln Y_j \right] / \sum_{j=1}^n \left( \ln M_j - n^{-1} \sum_{i=1}^n \ln M_i \right)^2, \\ \hat{\sigma}^2 &= (n - 2)^{-1} \sum_{j=1}^n (\ln X_j Y_j - \hat{\alpha} - \hat{\beta} \ln M_j)^2, \\ \hat{\sigma}_X^2 &= (n - 2)^{-1} \sum_{j=1}^n (\ln X_j - \hat{\alpha}_X - \hat{\beta}_X \ln M_j)^2, \end{aligned}$$

and

$$\hat{\sigma}_Y^2 = (n - 2)^{-1} \sum_{j=1}^n (\ln Y_j - \hat{\alpha}_Y - \hat{\beta}_Y \ln M_j)^2.$$

As before, notice that if  $\ln X$  and  $\ln Y$  are normally distributed,  $\hat{\mu}_{XY}$  is consistent for  $\mu(XY)$  but  $\exp(\hat{\alpha} + \hat{\beta} \ln M)$  is not. If  $X$  and  $Y$  are independent, then  $\hat{\mu}_{XY}$  and  $\hat{\mu}_X \hat{\mu}_Y$  both estimate  $\mu(XY)$  and it can be shown that asymptotically  $\hat{\mu}_X \hat{\mu}_Y$  is more efficient than  $\hat{\mu}_{XY}$ ; if  $\ln X$  and  $\ln Y$  are correlated,  $\hat{\mu}_X \hat{\mu}_Y$  is not consistent for  $\mu(XY)$ , and  $\hat{\mu}_{XY}$  should be used. Consequently, the problems in taking the product of allometric relationships are the same as those in taking the product of means.

### Summary of Results

We summarize the results relating functions of means to means of functions.

#### A. Functions of a single variable

1. Linear function:  $\mu(aX + b) = a\mu(X) + b.$



2. Reciprocal function:  $\mu(1/X) \neq 1/\mu(X)$ ;  
 $\mu(1/X) \approx 1/\mu(X) + \sigma(X)^2/\mu(X)^3$  (Templeton and Lawlor 1981).
3. Exponential function:  $\mu[\exp(X)] \neq \exp[\mu(X)]$ ;  
 $\mu[\exp(X)] \approx \exp[\mu(X)][1 + \sigma(X)^2/2]$  or  
 $\mu[\exp(X)] = \exp[\mu(X) + \sigma(X)^2/2]$   
 if  $X$  is normal.

**B. Functions of two variables**

1. Product of random variables:  $\mu(XY) = \mu(X)\mu(Y) + \text{cov}(X,Y)$  or  
 $\mu(XY) = \mu[\exp(\ln X + \ln Y)]$   
 $= \exp[\mu(\ln X) + \sigma(\ln X)^2/2]$   
 $+ \mu(\ln Y) + \sigma(\ln Y)^2/2$   
 $+ \text{cov}(\ln X, \ln Y)$ .

If  $X$  and  $Y$  are independent,  $\mu(XY) = \mu(X)\mu(Y)$ .

2. Ratio of random variables:  $\mu(X/Y) = \mu(X)/\mu(Y) - \text{cov}(X/Y, Y)/\mu(Y)$   
 $= \mu(X)\mu(1/Y) + \text{cov}(X, 1/Y)$   
 $\approx \mu(X)/\mu(Y) + \mu(X)\sigma(Y)^2/\mu(Y)^3$ .

If  $Y$  and  $X/Y$  are independent,  $\mu(X/Y) = \mu(X)/\mu(Y)$ . If  $X$  and  $Y$  are independent,  $\mu(X/Y) = \mu(X)\mu(1/Y)$ .

3. Sums of random variables:  $\mu(X + Y) = \mu(X) + \mu(Y)$ ,  
 $\sigma(X + Y)^2 = \sigma(X)^2 + \sigma(Y)^2 + 2\text{cov}(X, Y)$ .

**C. Allometric relationships**

1. Single relationship: If  $X = \alpha M^\beta \exp(Z)$  with  $Z \sim N(0, \sigma^2)$ , then  
 $\mu(X) = \alpha M^\beta \exp(\sigma^2/2)$ .

2. Product of two relationships: If  $X = \alpha_1 M^{\beta_1} \exp(Z_1)$  and  $Y = \alpha_2 M^{\beta_2} \exp(Z_2)$  with  $Z_i \sim N(0, \sigma_i^2)$ , where  $i = 1, 2$ , then

$$\mu(XY) = \alpha_1 \alpha_2 M^{\beta_1 + \beta_2} \exp[\sigma_1^2/2 + \sigma_2^2/2 + \text{cov}(Z_1, Z_2)].$$

If  $Z_1$  and  $Z_2$  are independent, then  $\mu(XY) = \alpha_1 \alpha_2 M^{\beta_1 + \beta_2} \exp(\sigma_1^2/2 + \sigma_2^2/2)$ .

For each of the functions involving two random variables, if the appropriate independence structure is present, combining the component means (on the right side of each equation) yields an estimator with a smaller standard error in the final result than that obtained by combining the components and then averaging them.

## DISCUSSION

From the examples given here and from numerous others in the literature, it is apparent that many results in the biological literature are based on an assumption, one rarely made explicit, of independence of multiplicative components. Yet, the nature of biological systems is such that independence of the traits of individuals is an exception rather than the common situation.

Although the population is a set of individuals in most of the given examples of population means, all of the results presented here apply equally to "populations" in the general statistical sense of the term. Thus, when obtaining mean values for the traits of an individual, the same problem of nonindependence arises if the mean values of traits are to be multiplied or otherwise combined in a nonlinear fashion. For example, in estimating the mean distance that an individual walks per day, the population is the set of distances traveled daily by that individual. The mean daily distance for an individual can be estimated accurately from the product of that individual's mean pace length and mean daily pace frequency only if the covariance between the two is negligible; the covariance would not be negligible if, say, the length of the animal's pace was appreciably longer for days during which it walked more (i.e., took more paces). Similarly, if an animal's food intake rates at different food patches are the population units being sampled, the animal may feed more rapidly in patches containing more food; thus, the mean intake per patch may not be only the product of the mean intake rate and of the mean time per patch.

Although the empirical literature provides numerous examples of the false assumption that the mean of the product of two or more random variables equals the product of their means, theoretical papers are not immune. For example, theorists in optimal foraging (Krebs and McCleery 1984; Lucas 1985, eq. 1) define the expected reward (e.g., energy return)  $E$  from foraging for a given amount of time  $T$  as  $E = TIV$ , where  $I$  is the mean prey-item encounter rate, and  $V$  is the mean reward from a single prey item. This formula, however, ignores potential correlations between encounter rate and value (e.g., foragers may encounter high-yield prey at a lower rate than low-yield prey). In another vein of theorizing, Studd and Robertson (1985) defined a male's expected lifetime reproductive success as the product of (1) the proportion of subadults surviving to breed, (2) the average annual rate of offspring production by adult males, and (3) the expected life span of a breeding male, ignoring any patterns of covariance between (1), (2), and (3), which are expected values. An example of nonindependence of these components was given by Partridge and Farquhar (1981), who demonstrated that fruit fly males that mate frequently have shorter life spans.

For situations in which measurement of component variables on the same individuals is possible, individual product-trait values should be calculated and then averaged. Alternatively, if the covariances are known, the formulas given above can be used, though in such situations the individual values almost invariably are known and the mean of the products can be obtained directly. When measuring component variables on the same individuals is not possible or not feasible, one of several options is available. In some situations, independence of

component variables can reasonably be assumed, and the justification for that assumption can be provided. If so, the product of component means can be used as an estimate of the mean of the products of the components. For situations in which the relationship between the variables is unknown, the product of component means can be presented along with the caveat that the product equals the mean only if the variables are independent. Finally, when the differences between means of product traits in two different populations (e.g., different individuals, groups, or species) are compared, if the covariances between the component variables in the two groups can be assumed equal, they can be ignored because they would cancel out in calculating the differences.

#### SUMMARY

In the biological literature, the mean of the product of two or more random variables is frequently calculated from the product of their means. However, unless the variables are independent, an exceptional occurrence in biological systems, the two are not equivalent. Corresponding false assumptions commonly are made about ratios of means and various other functions of means. These assumptions are examples of perhaps the most common statistical fallacy in the biological literature, the fallacy of averages: the false assumption that the mean of a nonlinear function of several variables equals the function of the means of those variables. We provide the relationship between functions of means and means of functions for common functions of one variable (linear, reciprocal, and exponential functions), for two or more variables (product, ratio, sum), and for the product of allometric relationships.

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