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ACQUISITION AND ALLOCATION OF RESOURCES: THEIR INFLUENCE ON VARIATION IN LIFE HISTORY TACTICS

Attempts to demonstrate trade-offs between alternative life history tactics have been relatively successful at higher taxonomic levels, but often fail at the level of individuals within a population. In this note we propose a simple model that explains this failure. The aim of our model is to understand the observations of positive correlations between life history traits where trade-offs, and hence negative correlations, are expected. It is assumed that the amount of resources that individuals can spend on life history traits varies between individuals. When some individuals spend much on several life history traits and others spend little, positive correlations are observed. Whether the observed correlations between life history traits are negative or positive depends on the relative variation in the acquisition and the variation in the allocation of resources.

HIGHER FITNESS FROM FEWER OFFSPRING

Life history theory is an elaborate answer to the simple question of why having more offspring is not always selected for. There are at least two different answers to this question. First, producing more offspring may result in fewer offspring reaching breeding age. This notion is especially important in theories about optimum clutch size. Kluver (1951) and Lack (1947, 1948) first showed that intermediate-sized clutches produced more offspring at breeding age than the largest-sized clutches in several species of birds.

The second answer was first formulated by Williams (1966), who pointed out that producing more offspring at one time could negatively affect the reproduction of the same individual later in life. If producing one additional offspring reduces the expected future reproduction by more than one individual, it is not selected for.

There is, however, a subtle difference between the theoretical question of why producing more offspring is not advantageous and the empirical question of why some individuals do not produce more offspring. As soon as one analyzes data, one is dealing with the latter question rather than the former, theoretical one. This distinction is important because the empirical question has a third answer, the trivial one that some individuals are "better" than others either through the quality of their microhabitat or through their own quality, for example, a higher metabolic efficiency resulting from genetic variation or an optimal body size. The point of this note is to model the interference between this trivial, but very real, variation in life history traits and the variation caused by alternative strategies.

THE DATA TO BE EXPLAINED

In many case studies, positive correlations are found between life history traits rather than the negative correlations expected from theory. We give a few examples here (birds, beetles, and zooplankton) to indicate the type of results we hope to explain.

In a study of an island population of the song sparrow *Melospiza melodia*, Smith (1981) found the total number of fledglings produced per year to be positively correlated with the subsequent survival of the females to the next breeding season. A similar observation was made for a Dutch population of the great tit, in which the size of first clutches of females that survive until the next breeding season is a little larger than clutches of those that do not survive (van Balen et al. 1986; van Noordwijk, MS). By manipulating clutch size, Perrins and Moss (1975) showed that clutch size is related to the "quality" of the female. Artificially reduced clutches did better, and artificially enlarged clutches did worse, than natural clutches of the same size.

In a study of the life history of two carabid beetles, van Dijk (1979) found no correlation between the reproductive effort and survival of individual females. This was as true for a short-lived autumn breeder (*Calathus melanocephalus* L.) as for a long-lived spring breeder (*Pterostichus coerulescens* L.).

Working with the freshwater copepod *Mesocyclops edax* from two locations, Allan (1983) found that correlations between female body size, egg volume, and clutch size were fairly strong in the pooled data from the two localities and two hybrids, but that the correlations disappeared in some of the individual strains. Overall, there was a strong positive correlation between female body size and the total volume of eggs in the first clutch.

Other similar or dissimilar examples can be found, but the point we want to make is that significant positive correlations are sometimes found when negative correlations would be expected if variation in life history tactics was a major source of variation.

THE MODEL

The aim of our model is to understand the observations of positive correlations between life history traits when trade-offs, and hence negative correlations, are expected. We therefore restrict ourselves to an outline of possible models and to some details of one simple model. We define three quantities: the total amount of resources available to an individual, A , and two life history traits in which these resources can be invested, R and S , which may stand for reproduction and somatic growth or survival. We assume that all three quantities, A , R , and S , can be measured in energy units. It is essential for our model that for each individual

$$A = R + S, \quad (1)$$

representing the basic idea in trade-off models of life history traits. The covariance between R and S determines the sign of the correlation between the measured realizations of R and S .

The basic quantity in life history experiments corresponds to the covariance of R , and $S = A - R$:

$$\begin{aligned} \text{cov}(R, S) &= \text{cov}(R, A - R) = \text{cov}(R, A) - \text{cov}(R, R) = \text{cov}(R, A) - \text{var}(R) \\ &= \text{cov}(A - S, S) = \text{cov}(A, S) - \text{cov}(S, S) = \text{cov}(A, S) - \text{var}(S). \end{aligned} \quad (2)$$

In this covariance of R and S , $\text{var}(R)$ is always greater than 0; the sign of $\text{cov}(R, S)$ depends on the sign of $\text{cov}(R, A)$ and/or the relative magnitude of $\text{cov}(R, A)$ and $\text{var}(R)$.

A negative covariance between A and R means that the energy allocated to reproduction decreases with increasing energy acquisition. A priori, this seems unlikely within a population over a short time; but it might be true in comparisons between populations, or between species over a long time. A negative covariance between R and A certainly results in a negative covariance between R and S . A positive covariance between R and A implies that the energy allocated to R increases with the total amount of acquired energy, which is plausible within a population over a short time. The model below shows how a positive covariance between R and A can result from independent distributions of energy acquirement and energy allocation.

In our more detailed model, the life history strategy is put into effect by a fraction (B) of the total available resources that is used for reproduction (R). The remainder ($1 - B$) is invested in S . Where physiological measurements of reproductive investment are made, the measurement of such a proportion B is quite feasible. An example is the harvest index used in the agricultural literature, defined as the mass of harvested parts per total plant biomass. Most of the increase in crop productivity in annual plants in the last half-century is due to a higher proportion of biomass in the seeds, which are the harvested parts, at a constant total plant biomass (see Gifford et al. 1984).

Two processes govern the investment in life history traits R and S : the total energy A_i acquired by individual i , and the fraction B_i that it allocates to R .

$$R_i = B_i A_i, \quad S_i = (1 - B_i)A_i. \quad (3)$$

$$\begin{aligned} A_i &= \bar{A} + a_i & 0 < A_i \\ B_i &= \bar{B} + b_i & 0 < B_i < 1, \end{aligned} \quad (4)$$

where \bar{A} is the average amount of resources available to an individual and a_i is the deviation of the i th individual in the amount of resources that it can use. Likewise, b_i is the deviation of the i th individual from the average strategy, \bar{B} . The quantities a_i and b_i are assumed to be independently distributed, both with expectation 0 and with variances σ_a^2 and σ_b^2 , respectively. Using equations (3) and (4), the covariance between R and S becomes

$$\begin{aligned} \text{cov}(R, S) &= \text{cov}(A, R) - \text{var}(R) = \bar{B}\sigma_a^2 - (\bar{A}^2\sigma_b^2 + \bar{B}^2\sigma_a^2 + \sigma_a^2\sigma_b^2) \\ &= \bar{B}(1 - \bar{B})\sigma_a^2 - \bar{A}^2\sigma_b^2 - \sigma_a^2\sigma_b^2. \end{aligned} \quad (5)$$

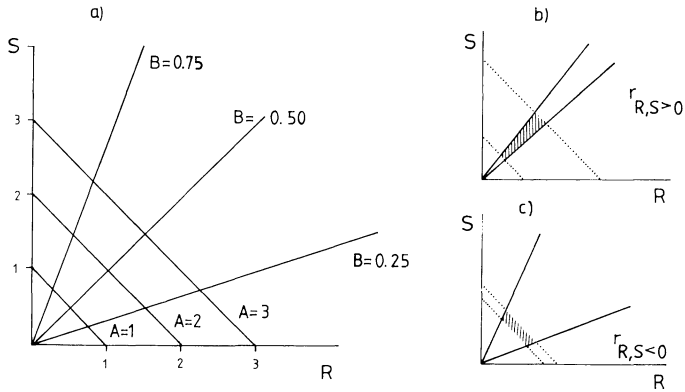


FIG. 1.—An illustration of the model: *a*, the components *A* for the total investment and *B* for the allocation between life history traits *R* and *S*; *b*, the variation in *A* is large and the variation in *B* is small, such that *R* is positively correlated with *S* (observations lie in the hatched area); *c*, the opposite case.

A product formulation of *R* seems likely. Independence between the acquisition of resources and the allocation of these resources to alternative life history traits is modeled as independent distributions of *A* and *B*. Within a population, such independence of acquisition and allocated fraction seems likely. The independence of acquisition and the fraction allocated leads to a positive covariance; the independence of the amount acquired and the amount allocated to each of the alternatives; the independence of *A* and *B* implies that both $\text{cov}(A, R) = \text{cov}(A, AB)$ and $\text{cov}(A, S) = \text{cov}[A, (1 - B)A]$ are necessarily positive. Since the amount of energy allocated to reproduction and that allocated to body mass both increase with the amount of energy acquired, a positive correlation between the two becomes possible, even in the face of the underlying trade-off.

Several relationships follow from expression (5).

1. If $\sigma_b^2 = 0$, such that only the acquirement is variable, $\text{cov}(R, S) = \bar{B}(1 - \bar{B})\sigma_a^2 \geq 0$.
2. If $\sigma_a^2 = 0$, such that only the allocation is variable, $\text{cov}(R, S) = -\bar{A}^2\sigma_b^2 \leq 0$.
3. Given \bar{A} , σ_a^2 , and σ_b^2 , the covariance $\text{cov}(R, S)$ has a maximum at $\bar{B} = 1/2$; that is, the more lopsided the average trade-off ($\bar{B} \approx 0$, $\bar{B} \approx 1$), the more readily a negative $\text{cov}(R, S)$ will be found. At intermediate values of \bar{B} , variance in \bar{B} might be hardest to distinguish because the variance in resource acquisition σ_a^2 has its greatest effect (see fig. 1c).
4. Given \bar{B} , σ_a^2 , and σ_b^2 , the covariance $\text{cov}(R, S)$ decreases with an increasing average amount of food \bar{A} ; at high average food levels, the variance in trade-off ratios plays a more important role (see fig. 1b).

A graphical representation is given in figure 1. One obtains a negative covariance between the resources invested in the different life history traits (fig. 1c) if the variation in the allocation is large and the variation in total available resources is small. Alternatively, if the variation in the allocation of resources is small or absent, the amounts invested in the "alternative" life history traits are positively correlated (fig. 1b). In this model, with two independent processes of acquirement

and allocation, the outcome depends on the relative magnitudes of the expectations and the variances in acquirement and allocation. With due caution, this can, of course, be used the other way around. From the sign of the correlation, inferences can be drawn about these relative magnitudes.

DISCUSSION

Our model explains why positive correlations between life history traits can be observed. There is an analogy in economics: if the budget is fixed, people spending more on housing should spend less on cars. In fact, the amount of expendable income is variable, and in many situations positive correlations are observed between the per-family expenses on housing and on cars. There is little problem in identifying rich and poor families on this basis; neither is there any problem in extending such observations to generalizations about income equalities in societies. Where biologists have observed positive correlations between life history traits, they have often also identified individuals that perform well or poorly. Nevertheless, there seems a residue of wonderment at why negative correlations are not always observed where trade-offs are expected.

In dealing with real data, the crucial question is in what units the quantities should be expressed. There are several alternatives. In many cases each of the three quantities suggests its own natural unit: energy or the amount of the most limiting nutrient for the acquirement, A ; the number of offspring for reproduction, R ; biomass for S . The general idea behind the model is not much affected by the choice of units as long as the transformations from one unit to another are monotonic. If one works with energy units, one may count the number of offspring and use body length, or rather its increase, as a measure of somatic growth as long as investing more energy in offspring never results in fewer offspring or investing more energy in growth never results in smaller body size. These assumptions are likely to hold over short periods and limited ranges of variation.

Our assumption that a_i and b_i are independent is much less realistic at the level of species than at the level of individuals within populations. In higher-level comparisons, the mean values from many individuals are often used. This, of course, also contributes to the visibility of trade-offs, since it eliminates much of the variation in the availability of resources (σ_a^2 in our model).

Our thesis is that the sign of the correlation (and, if it can be interpreted, its magnitude) between alternative investments of energy tells something about the relative magnitude of the expectations of allocation and acquisition and their variances. Relative variances are not easily interpreted. Analogies can be drawn to quantitative genetics, which also deals with proportions of variance. This is not easy because the problem in quantitative genetics is less complicated, since the total phenotypic variance for the characters under consideration can be used as a yardstick, whereas the problems in the conversion of energy units into life history traits prohibit the calculation of a total variance with which the variation and the covariation in the investigated traits can be compared.

Nevertheless, we believe that considering the variation in the amount of resources available to individuals is helpful in explaining why it is difficult to observe trade-offs at the level of individuals within a population. Furthermore,

our model suggests that variation in resource allocation can best be demonstrated when the variation in resource acquisition is relatively small, while the average resource acquisition is high. This has implications for experimental design as well as for the potential effectiveness of natural selection on allocation mechanisms. In both cases one can speak about an acquisition-allocation balance in explaining the covariation between life history traits.

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