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THE OPTIMAL BALANCE BETWEEN
SIZE AND NUMBER OF OFFSPRING

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In searching for patterns of energy expenditure by parents on their offspring, two relationships seem intuitively obvious. (1) As the energy expended on individual offspring is increased, the number of offspring that parents can produce is decreased. (2) As the energy expended on individual offspring increases, the fitness of individual offspring increases. The relationship which is difficult to visualize is the one between the energy expended on individual offspring and the fitness of the parent whose genotype influences how energy is distributed to the young. Here we present a graphical model to represent the relationship between energy expended on individual offspring and the fitness of parents. The validity of the graphical model is then demonstrated by standard analytical procedures.

THE MODEL

The model is based on the one assumption that at any point in an organism's life history there is an optimum percentage of available energy that should be diverted to reproduction to maximize the parents' total contribution to future generations. Energy available for reproduction is thus limited to a set finite amount at any given time. Our model demonstrates how this finite amount can be distributed into different sizes and numbers of offspring. The validity of the basic assumption is discussed later.

The abscissa of the model in figure 1 plots both the size and number of individual offspring. Their relationship on the abscissa is determined by the basic assumption of a set finite amount of energy available for reproduction. The ordinate plots the fitness of individual offspring. Straight lines through the origin are fitness functions or lines of equal fitness for the parent. As we show below, these fitness functions are similar to those of Levins (1968), although their orientation is different. Greater slopes of fitness functions correspond to higher parental fitness. No causal relationship between the abscissa and ordinate is implied in the fitness functions. We do not wish to imply that expected fitness of offspring is linearly proportional to their energy expense over a large range of energy expenses in any real population. Fitness functions are simply a consequence of the values of the ordinate and abscissa.

* Order of authorship was determined by a flip of a coin.

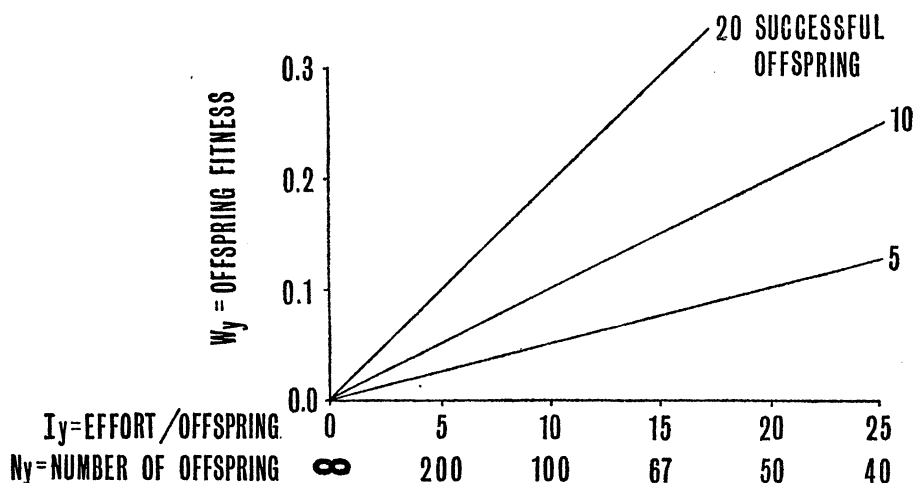


FIG. 1.—Adaptive functions of parental strategies. The vertical axis describes parent types with offspring of a certain fitness, as noted. The horizontal axis describes parent types that put a certain fraction of available energy into each offspring (or equivalently produce a certain number of offspring from the 1,000 units of energy available). The diagonal lines in the two-dimensional space are sets of parental types all of whose members are equally successful in contributing to future generations. Diagonal lines of steeper slope represent more successful parent types.

Real populations have a curve of expected fitness for individual offspring (W_y) in relation to their energy expenses which we assume to be similar in shape to the solid curve in figure 2. The curve leaves the abscissa at some point greater than zero because an offspring must at least have the energy of a complete set of genetic information before it has greater than zero fitness. The curve is defined only for offspring sizes up to that size where all parental investment goes to just one offspring. Beyond that size, expected fitness of the young is irrelevant, since the parent could not produce even one. We consider in detail curves sufficiently convex for the intercept of the derivative to pass through zero for at least one point on the curve. Apparently this case applies to most of nature, as most clutches are greater than one, but we cannot prove this. Such convexity might derive biologically from there being some limit to the fitness of individual offspring that cannot be reached no matter how great the parental investment.

Then, when the clutch is small enough (I_y large enough), a unit decrease in the clutch will produce a relatively large increase in I_y but a relatively small increase in W_y , producing convexity. If such convexity does not obtain, then, assuming a continuous curve, one can prove from the graphical analysis that only a single offspring should be produced per effort.

To determine which energy expense per offspring gives the highest parental fitness, one can draw a series of fitness functions intersecting the curve. The steepest fitness function that intersects the curve is the fitness function tangent to the curve (fig. 2). Therefore the optimum energy expense per offspring is at the point where a fitness function is tangent to the curve

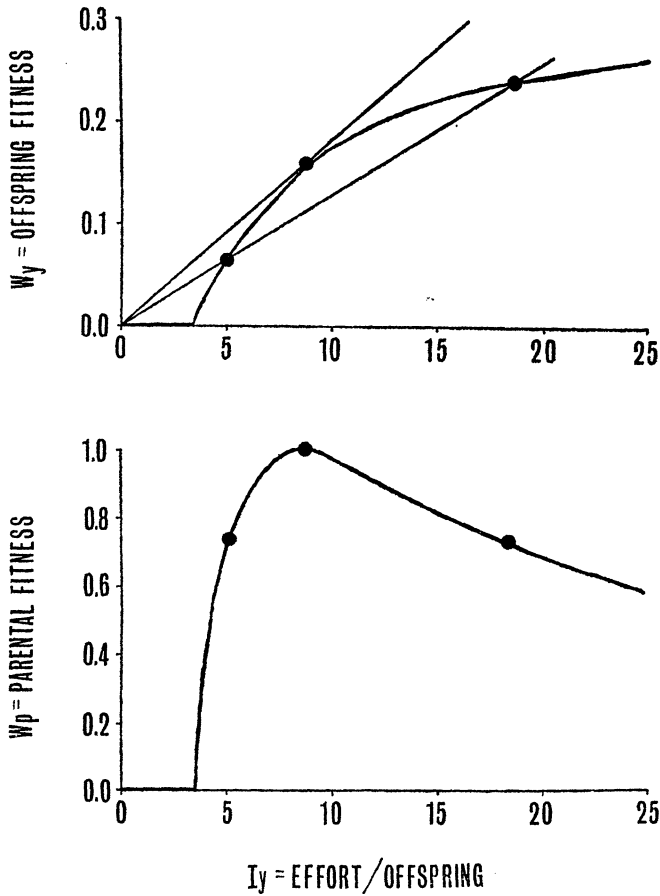


FIG. 2.—Fitness set analysis of parental strategy. The curved line in the upper part of the figure is the set of possible combinations of parental types, each type expending a certain amount of effort per offspring and producing offspring of a certain fitness. The shape of this curve is typical of those that will produce clutches of more than one offspring. The curve can be thought of as a cause-effect relationship (effort per offspring determines the offspring's fitness). Two adaptive functions, drawn as in fig. 1, intersect the curve of possible parental types. The intersection involving the adaptive function of highest slope determines the optimal parental type defined in terms of effort per offspring. Intersections of other adaptive functions determine the relationship between parental fitness and parental type (effort per offspring), plotted in the lower graph. Note that all parental types in a single adaptive function are defined to have equal fitness, so that the two intersections of any lower than optimal adaptive function produce points on the bottom graph with the same value of parental fitness.

of fitness for individual offspring. The ratio of the slope of a fitness function through another point on the curve to the slope of the fitness function tangent to the curve gives the fitness to the parent of expending the amount of energy per offspring represented by that other point (fig. 2). The model, therefore, allows one to visualize in two dimensions the fitness accruing to

both offspring and parent from variation in the energy expended per offspring.

Now, the graphical analysis given above can be presented analytically to prove that the point of contact of the sloping line through the origin with the young's fitness curve is the optimum offspring size for the parent.

Let Wy be the fitness of the young. We assume that energy investment per young (Iy) increases the young's fitness, but that the rate of increase either actually reaches zero or gets close to zero for some high but realistic value of energy investment. This implies a curve of fitness of young on cost of young (fig. 2) that is convex for all Iy greater than some particular value. Let Ny be the number of young produced by the parent, and Ip be the total energy invested by the parent. We assume that

$$Ny = Ip/Iy. \quad (1)$$

This is approximate and simplifying; Ny must in reality have integer values, and yet Ip/Iy can take noninteger values, unless we restrict Iy to certain values (we assume Ip is fixed). Ricklefs (1968) analyzed compromises that might be made at small clutch sizes, when noninteger values of Ny are optimal. We again proceed, recognizing that we will obtain noninteger optimal values for Ny , which require further analysis (see Discussion).

Parental fitness for the clutch is denoted Wp , and that for the young, Wy . We claim that

$$Wp = Wy \cdot Ny = Wy \cdot \frac{Ip}{Iy} \quad (2)$$

for values on the young fitness curve.

We now assume that production of young in the present does not influence the future fitness of parents. Natural selection should then maximize Wp . We find the maximum value of Wp by maximizing Wy/Iy in equation (2) (Ip fixed). But Wy/Iy is the tangent of the angle formed by the sloping line through the origin and by the Iy axis. Since the tangent of an angle and the angle are positively monotonic, maximizing Wy/Iy also maximizes α . This proves that the line with the maximum slope, which intersects the young's fitness curve, also touches that curve at the point that maximizes adult fitness.

These straight lines are analogous to the adaptive or fitness functions of Levins (1968), while the curve of offspring fitness with size is a fitness set. We now establish this correspondence.

In an adaptive function, points on a single line or curve represent alternative parent phenotypes all of which have the same fitness. However, all phenotypes may not be realizable. The statement of an adaptive function is this: if we could find a collection of parental types with certain specified properties, all would have the same fitness. Here, the properties are fitness and size of offspring. Parental fitness is the product of the fitness of each of its offspring times the number of them (eq. [2]).

If all of a group of parents have the same fitness, then $Wp = k$, and from equation (2),

$$Wy = \left(\frac{k}{Ny}\right). \quad (3)$$

From (1),

$$\left(\frac{1}{Ny}\right) = \frac{Iy}{Ip}.$$

So, substituting in (3) we obtain

$$Wy = \frac{k}{Ip} \cdot Iy.$$

Like k , Ip , the total parental investment, is assumed to be constant; and so we have derived an equation for a straight line through the origin, with slope k/Ip . This straight line is made up of points each of which defines a parent with young of a certain size (Iy) and a certain fitness (Wy). All these parents have the same fitness ($Wp = k$), and so the line is an adaptive function. Adaptive functions with higher slopes must have higher Wp (Ip is constant). By Levins' arguments, we know that the optimum phenotype is found on the fitness set (the real possibilities), by taking the point of intersection with the adaptive function of highest fitness (slope).

DISCUSSION

A number of life history phenomena might appear to contradict our basic assumption that at any stage in an organism's life history an optimum fraction of its available energy should be diverted to reproduction to maximize total reproduction during its lifetime. E. R. Pianka and D. H. Feener (personal communication) argue that as an individual's reproductive value declines after the onset of reproductive maturity, it maximizes fitness by diverting a successively higher fraction of its available energy to reproduction with each successive, evenly spaced, reproductive effort. Pianka and Feener's arguments on the effect of changing reproductive value specify what fraction of available energy should be expended on reproduction at given points through a life history, but not how the fraction expended should be divided into numbers of offspring. The fact that the optimum fraction of available energy diverted to reproduction changes throughout a life history in no way negates our model.

For organisms like birds, mammals, and subsocial Hymenoptera (Wilson 1971), where parents progressively provision their offspring as they develop, energy expended per individual offspring is considerably greater than that needed to produce a fertilized egg. Reproductive effort in our model, the fraction of available energy diverted to reproduction, includes all forms of parental care. Energy used to provision progressively or to defend an off-

spring is part of the energy expended upon that individual offspring and also part of the parent's reproductive effort. With progressive provisioning, energy expended per offspring is difficult to measure, but in theory our model still applies.

This model does not hold when the result of one reproductive effort affects fitness of individual offspring in successive reproductive efforts of the same parent. Social Hymenoptera (Wilson 1971) and a few birds (Lack 1968) demonstrate such an interaction of successive reproductive efforts with the parental energy expenditure on individual offspring. In both groups, offspring from early clutches help to provision offspring from later clutches. Feeding of siblings is thought to be an evolutionary consequence of kin selection (Hamilton 1964; Wilson 1971), where the unit under selection is the extended genetic family rather than the individual parent. Our model therefore applies to partitioning of energy by the extended genetic family rather than by an individual parent.

For mammals exhibiting postpartum estrus, one litter may decrease the energy available for another. The same problem may occasionally arise when young from successive litters depend on a parent at the same time, as in beaver (Bourlière 1956), chimpanzees (van Lawick-Goodall 1968), and humans. Overlapping parental care of successive litters generally reduces the total energy available to each litter. It need not affect how the reduced total is divided among individual offspring in any litter. We know of no information that shows that less energy is expended per individual offspring in successive litters.

A parameter not included in our model is the period of time over which energy is collected for a reproductive effort. This parameter is directly related to a significant problem of the model. How does selection respond to a situation in which the energy available for reproduction, when divided by the optimum energy for each offspring, gives a clutch size of 1.5? The problem of fractional offspring is greatest for small clutches (Ricklefs 1968). In optimal clutches of 1.5, 33% of the reproductive effort is unused by a real clutch of one, while for optimum litters of 20.5, less than 3% of the energy is unused by a real clutch of 20. Ricklefs (1968) summarized extensive empirical evidence that birds with smaller clutches (one or two) have a greater between-species variance in their development rates than species with larger clutches (three to five). He argues that this difference in development rates could be explained if clutches which would include fractional young under maximum development rates and maximum feeding rates can be increased to the next largest whole number by evolving reduced rates of development. Adjusting fractions in small litters would lead to a greater slowing of development rates that would occur for larger litters. Empirical evidence from birds indicates that fractional young are adjusted by changes in the time over which energy is gathered. For our model, problems of time of energy accumulation and fractional offspring appear to cancel each other, the first being adjusted to compensate for the second. A flexibility in the time of energy accumulation would give flexibility to

the number of young along the abscissa of our model and make energy cost per young the only significant variable on the abscissa (fig. 2).

Although our model probably applies to all organisms, it is of greatest utility in species with a large clutch size and no parental care. For these species the relative cost of offspring of different sizes is closely estimated by their relative caloric content. If the most common (and presumably optimum) size of offspring such as acorns or salmon eggs contained 10 units of energy, it would be safe to assume, on the basis of our model, that an offspring containing nine units would have a fitness less than nine-tenths that of the 10-unit individual. In most cases fitness will be measured by relative survival. However, in species such as some desert annual plants, competition results in decreased fecundity rather than increased mortality (Went 1955). The competitive advantage during early growth resulting from a larger parental investment (e.g., larger seed size) may not be expressed until a seed has grown up to reproduce itself.

Our model integrates assumptions commonly made by others. Its main advantage is in allowing these ideas, which are usually separated, to be considered together, both graphically and analytically, in only two dimensions. Because the model does not specify how energy is expended, or what advantage is gained from it, effects of competition, predation, and the physical environment can be illustrated simultaneously. The effects of these three environmental factors can also be isolated and treated independently. For example, a 10% decrease in the energy content of a seed might be totally at the expense of endosperm and embryo or totally from seed coats or from some combination of the two. If one could find seeds within a species that expressed all the above alternatives, one could test to see whether the reduction in endosperm and embryo led to reduction of survival in competition with other plants and reduction in seed coats led to increased mortality from seed eaters. This lets one measure the adaptive value of the energy expended in different tissues. Thus, our model can be used to express the effect of competition, predation, or any other aspect of the environment on the fitness of offspring.

SUMMARY

The relationship between the energy expended per offspring, fitness of offspring, and parental fitness is presented in a two-dimensional graphical model. The validity of the model in determining an optimal parental strategy is demonstrated analytically. The model applies under various conditions of parental care and sibling care for the offspring but is most useful for species that produce numerous small offspring which are given no parental care.

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