

Natural Selection and the Evolution of Reproductive Effort

(life history/energy budgets/fitness/reproductive value)

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ABSTRACT Reproductive effort is defined as that proportion of the total energy budget of an organism that is devoted to reproductive processes. Reproductive effort at a given age within a species will be selected to maximize reproductive value at that age. Reproductive effort is not directly affected by changes in juvenile survivorship, nor necessarily reduced by an increase in adult survivorship. Selection for high levels of reproductive effort should occur when extrinsic adult mortality is high, in environments with constant juvenile survivorship, and in good years for juvenile survivorship in a variable environment, provided that the quality of the year is predictable by adults. Data necessary to measure reproductive effort and to understand how selection results in different levels of effort between individuals and species are discussed. We make several predictions about the effect of increased resource availability on reproductive effort. The empirical bases for testing these predictions are presently inadequate, and we consider data on energy budgets of organisms in nature to be essential for such tests. We also conclude that variance in life table parameters must be known in detail to understand the selective bases of levels of reproductive effort.

Reproductive effort has become a central concept in theories of life history evolution. Fisher (1) evidently first called attention to the significance of determining how natural selection adjusts the partitioning of the energy budgets of organisms among reproduction, growth, and maintenance. Theories of how selection effects this adjustment have been developed by Williams (2, 3), Gadgil and Bossert (4), Schaffer (5), and others. Empirical evidence has been variously in accord with, or contradictory to, theoretical predictions (e.g., refs. 6-8).

The difficulties in understanding the evolution of reproductive effort stem from the fact that predictions from theory are, in many cases, results of assumptions in the models which require careful examination before the predictions may be considered relevant to organisms in nature. Difficulties also arise because it is not clear what data constitute adequate measures of reproductive effort. It is impossible at present to decide whether failure of the data to be consistent with theory is due to inappropriate estimators or to inadequate theory.

The purposes of this paper are: (i) to reexamine the theory of the evolution of reproductive effort, cost, and fitness; (ii) to predict those environmental conditions that result in selection for high and low levels of effort; and (iii) to suggest a methodological framework for the study of reproductive effort that will allow unequivocal tests of theoretical predictions.

Relation of reproductive effort to reproductive value and to individual fitness

Reproductive effort is defined as the proportion of total energy, procured over a specified and biologically meaningful

time interval, that an organism devotes to reproduction. To be favorably selected, a phenotype for a given level of reproductive effort must enhance the fitness of the individual exhibiting this phenotype. Each individual at every reproductive opportunity should behave in a way that maximizes its genetic contribution to future generations; this contribution will generally be greatest for those individuals producing the greatest number of offspring that survive and reproduce. Formally, we define expected fitness (w_x) of a female (or male) of age x as:

$$(w_x) = \sum_{y=x}^{\infty} k_y \left[\frac{l_y}{l_x} m_y \cdot \exp(-m(y-x)) \right]$$

in which k_y is the probability of survival from egg or newborn to reproductive maturity, m_y is female offspring per female of age y (or an equivalent measure for males), l_y and l_x are probabilities of survival from age 0 to ages y and x , respectively, and m is Fisher's (1) malthusian parameter measuring rate of increase of a genotype.

That this formulation is equivalent to intuitive ideas of the fitness of a female of age x may be seen by examining the components of the equation. The term l_y/l_x discounts future fecundity by the probability of mortality from age x to any future age, but does take into account that the individual has lived to age x . The exponential term discounts the relative contribution to fitness of offspring born late in life to a female in a growing population, or early in life to a female in a declining one (9). We use k_y because parental fitness does depend on the quality of young produced, and their survivorship to maturity presumably reflects this quality.

The equation above, without k_y , is mathematically identical to Fisher's (1) equation for reproductive value. Since we expect selection to maximize fitness at every age, reproductive value at every age will also be maximized, as many authors have noted (2, 5, 10, 11). Our theoretical viewpoint differs from that of Gadgil and Bossert (4). Their models assume that the life history parameters of organisms are the averages for their respective populations and constitute a life history strategy that is fixed at birth. We feel that the strategies of many organisms allow flexibility of response.

Williams (2) subdivided reproductive value (RV) into that portion attributable to present reproduction (m_x) and that, which he called residual reproductive value (RRV), attributable to later reproduction. Thus:

$$RV = m_x + \left[\sum_{y=x+1}^{\infty} \frac{l_y}{l_x} m_y \cdot \exp(-m(y-x)) \right]$$

That portion of the equation within brackets is the residual reproductive value. At each age an organism is expected to

allocate resources to *present* reproduction in a manner that will maximize reproductive value at that age.

An increase in reproductive effort at a given age should lead to increased m_x at that age or to greater investment per offspring. However, there will often be a direct cost associated with this effort, resulting in lower survival of the adult to subsequent ages or lower fecundity at those ages. Such costs would, in general, reduce the residual reproductive value, but such reduction as a result of higher reproductive effort might be favored under some circumstances. In other circumstances low effort at a given age with a consequently high residual reproductive value might maximize the reproductive value at that age. We formally define cost of a given level of reproductive effort as the difference between residual reproductive value when effort is zero and that residual reproductive value accompanying that particular expenditure of effort. Although high effort at a given age will normally result in a high reproductive value at that age, it does not follow that a high reproductive value at a given age will always result in selection for high effort at that age. In other words, measured reproductive values are not adequate predictors of age-specific reproductive effort.

Schaffer (5) argued that a decrease in juvenile survivorship (equivalent to reducing k_j in our fitness equation) would reduce optimal reproductive effort. Gadgil and Bossert (4) and Taylor *et al.* (11) suggested that a change in survivorship that affected all age classes identically would have no effect on optimal reproductive effort. These statements, while true under certain circumstances prevailing in their models, lack both generality and some biological reality. Specifically, these models overly restrict the possible evolutionary responses of organisms to increased mortality. Shaffer (5), for example, argued that a decline in juvenile survivorship decreases the benefit to the parent of the effort expended in reproduction, and hence selects for lower effort. However, lower effort alone cannot be favored unless those genotypes that result in lower effort also result in increased juvenile survivorship (12). Increased juvenile mortality may select for greater investment by parents in mechanisms that reduce the mortality among their young, but which could result in the same, lower, or higher effort.

Gadgil and Bossert (4) argued that not only juvenile survivorship but also survivorship of offspring to the age of the parent were components of selection on optimal reproductive effort:

"The decrease in the probability of survival to age j as j increases and the reduction in the contribution to fitness by offspring produced at greater age will both tend to reduce P_j (the profit to fitness of offspring produced at age j) with any increase in j ."

Given the assumptions in the model of Gadgil and Bossert, offspring produced late in the life of a female are worth less than those produced early only in growing populations. In stationary populations, because the replacement rate per generation is 1.0, replacement is as likely to come from young produced at any age of the parent and hence the profit from a single offspring is independent of the age of the parent producing it. In a declining population, offspring produced late in a female's life would contribute more to her fitness (9, 13). These conclusions assume that all individuals in the populations are genetically identical. However, in most populations individuals differ genetically. Some may carry a

gene for early and high reproductive effort which increases in frequency at the expense of other alleles at the same locus even though the population may be stable or declining. This increase in frequency may be due solely to the fact that high levels of reproduction at an early age result in a short generation time among individuals carrying that allele and, therefore, an increased frequency of that allele with time. Thus, we agree that alleles producing equivalent offspring early will often be favored by selection, but not because the population as a whole is growing, declining, or stationary.

We disagree with the proposition previously quoted (4) that the decrease in the probability of survival to age j as j increases automatically reduces the value of later offspring. This is because we cast our arguments in terms of individual organisms and not cohorts of them. It is true that the passage of time reduces the numbers of individuals in a cohort, but this fact does not affect the future strategies of the survivors.

The relationship between reproductive effort and cost

If at any age the cost of reproductive effort is near zero, near maximal effort at that age will be favored by selection. Such low cost is expected in species in which adult mortality would be very high even if no reproduction occurred; we will henceforth refer to such species as having high extrinsic adult mortality. Some annual tropical cyprinidontiform fishes or temporary pond invertebrates may exemplify such species. Many annual plants fit this pattern (14).

In iteroparous species, in which costs of reproductive effort at each age are potentially high, we might view cost as declining as the animal's age increases. Such reasoning led Williams (3) and Gadgil and Bossert (4) to argue that reproductive effort should increase with age. Although Gadgil and Bossert (4) arrived at this conclusion by assuming fixed life spans, as Schaffer (5) noted, it is nevertheless true that any age-specific increase in extrinsic adult mortality could result in selection for increasing reproductive effort with age. Similarly, any increase in the efficiency of reproduction with age (e.g., a lower cost associated with obtaining a given amount of energy for reproduction) could also select for an increased effort with age. Some authors have argued that an individual adult organism may have an approximately constant probability of survival at each age. Goodman (10), for example, suggested that long-lived oceanic birds had relatively invariant reproductive effort because of the independence of age and survivorship. However, it could be argued that senescence will occur even though survivorship is relatively constant. One effect of senescence might be an increase in age-specific mortality and, therefore, selection for increased effort. However, such selection might be offset by the deleterious effects of senescence on reproductive efficiency. Therefore, we agree with other authors (5, 10) that senescence will be of minor importance to selection on reproductive effort. However, while we do not think that reproductive effort will necessarily increase with age, we do not wish to imply that it will remain constant.

Environmental determinants of reproductive effort

In an environment (hereafter called constant) in which the variation between years in juvenile survivorship is small, reproductive effort may be high even though the cost in reduced residual reproductive value is also high. Selection in

such an environment could favor alleles that lead to high reproductive effort at the earliest possible age because shortening the generation time would increase the rate at which such alleles are incorporated into the gene pool. Thus, we disagree with Williams (3) that a potentially long adult life necessarily favors low reproductive effort at each age. Selection in a constant environment could result in a short-lived species displaying high reproductive effort and having low measured residual reproductive value, i.e., life history characteristics very similar to those of species with high extrinsic adult mortality. In other words, we expect to find annual species that would die regardless of whether they reproduced and some that die essentially because of high effort. This latter category has been identified among annual plants by Harper and White (14). We recognize that a constant juvenile environment does not *require* semelparity. There will often be cases in which that level of reproductive effort that precludes survival of the adult to another season may result in insufficient increase in parental fitness to offset the advantage of living to reproduce again.

Murphy (15) first suggested that unpredictable juvenile survivorship could select directly for iteroparity. Under natural conditions juvenile survivorship must occasionally be zero to prevent the spread of the semelparous genotype during favorable years if survivorship is truly density independent as Murphy argued. It is clear that a general explanation of the evolution of iteroparity has not yet been developed. Perhaps iteroparity has generally evolved under conditions of competition among adults which render juvenile survivorship variable. Such conditions should favor individual parents exhibiting less than maximal reproductive effort.

Whatever the selective basis for the evolution of iteroparity, the strategy of allocation of energy to reproduction in iteroparous species will depend upon the degree to which adults are able to predict the relative quality of a given year for the growth and survivorship of their young. Such predictability will be difficult (i) if the juvenile period is protracted across several seasons, or (ii) if the adult must make its commitment to reproduction far in advance of the time that young will actually enter the environment, or (iii) if the young develop in the environment that varies differently from that of the adult. We envisage a spectrum of organism from those unable to predict good years to those able to make such predictions reliably. If the parent cannot predict at all, then the best strategy is to hold the probability of its own survival high. Such a strategy should result in low and variable reproductive effort and in long adult life. The variation will result from the fact that in some years the adult may be able to increase its effort without a corresponding increase in cost. Such years might be those with higher resource levels or lower predation levels for adults; nevertheless, the adult may show less than maximal effort because it cannot predict that a good year for it will also be optimal for juvenile survivorship. This situation should be particularly common in organisms, such as amphibians, in which the adults and young occupy separate habitats.

At the other end of the spectrum are species in variable environments which can nevertheless correlate some environmental cue with a favorable prognosis for juvenile survivorship. In such species, high reproductive effort, possibly associated with high cost, should be observed in favorable years, with the result that reproductive effort will vary erratically

with age, as may adult survival. Even suicidal reproductive effort may be observed in an unusually good year, if such a year is unlikely to recur in an individual's lifetime. Century plants of the genus *Agave* might exemplify this strategy. Such plants have wide variability in the age at which particular adults flower, and presumably great variance in germination success between years.

The arguments presented here have direct relevance to the question of the relationship between reproductive effort and increasing age. If we could measure the reproductive effort of an individual each year of its life, we would expect a great deal of variability in effort for reasons previously discussed. We would not expect a monotonic increase of effort with increasing age because we do not believe that age alone is the most important factor affecting selection on reproductive effort. The relative importance of age compared with other factors might best be determined by comparing cohorts of individuals of known age in a single population at a given period in time so that all age classes are exposed to the same environmental regime.

Resource levels and reproductive effort

There are several ways in which an organism might increase its reproductive effort. The one most often considered is the diversion of energy to reproduction and away from growth or maintenance, implying a fixed energy budget. However, an organism could theoretically increase its total budget and allocate the added energy primarily to reproduction. This would increase the total percentage of the energy budget allocated to reproduction. An organism might also reduce its total energy budget, sacrificing primarily growth and maintenance, with a resultant increase in the proportion devoted to reproduction.

Which of these methods of adjusting the effort will be favorably selected may depend on the risk involved in increasing the total energy budget. Whether an organism is primarily resource limited or primarily predator limited there will, in a variable environment, be years in which increased reproductive effort is advantageous. However, in these years resources necessary for increased effort may not be easily obtainable. It is in such instances that diversion of necessary energy for higher effort may come from growth or maintenance energy. For resource limited species this diversion is appropriate because an attempt to increase effort through an increase in the total energy budget would result in increased competition with conspecifics, the cost of which might be high. For predator limited species, diversion of resources is also the appropriate strategy because an attempt to increase the total energy budget could increase the risk of death.

If there are years when resource levels are high relative to population numbers, increased reproductive effort still may or may not be favored. Gadgil and Bossert (4) argued that increasing food levels at all ages and thereby increasing "degree of satisfaction" would result in increased reproductive effort. However, were the degree of satisfaction increased for adults alone, such a largesse might be utilized by adults for growth or maintenance rather than for reproduction, resulting in increased reproductive success in a later and better year. This result would be expected if the resource levels for the adult were not correlated with conditions favorable for juvenile survivorship (see previous arguments), but the de-

gree of favorableness is predictable by the adult. If juvenile survivorship were predicted to be good in the same year, then we would expect the additional energy to be used primarily for producing additional young.

In species regulated primarily by predation, an analogous argument can be made. If resource levels increase, but juvenile survivorship is not concomitantly improved or is unpredictable, then we might expect adults to hold their energy budget and reproductive effort constant, but to reduce the cost associated with obtaining energy through a reduction in search time, resulting in improvement of their own survival. If the year is also a predictably good one for juvenile survivorship, then the same or even higher risk by adults could result in a greater absolute quantity of resources per individual and a diversion of this increased energy to reproduction.

Measurements of reproductive efforts and their interpretation

Williams (2, 3) was not optimistic about the possibility of precisely quantifying reproductive effort. He suggested that species could be ranked as low-effort or high-effort on the basis of phenotypic traits presumably correlated with effort. Among those he suggested were frequent reproduction in one season, a high clutch weight to body weight ratio, aggressive behavior, and strong sexual dimorphism.

Gadgil and Bossert (4) defined reproductive effort as the fraction of the total amount of time and energy available to the individual that is devoted to reproduction. Because both of these quantities can be reduced to the common denominator of energy expenditure, they are, in principle, quantifiable and comparable between species, provided that total energy budgets can be calculated. Unfortunately, these authors concluded that the ratio of clutch weight to body weight was an adequate measure of effort.

It has become common for investigators to measure effort by fecundity, or by clutch or ovary weight in relation to body weight (e.g., 6, 7, 16, 17). Recently, calories have been substituted for weights in this ratio (7, 18), but this does not resolve the fundamental problem of such measures. They may not provide comparable estimates of effort either between species or between age classes within species for at least two reasons:

(i) Individuals of two species could devote the same quantity of energy to reproduction at equivalent body sizes, but differ greatly in the absolute amount of energy gathered or in the time during which it was gathered. In such cases the true proportional allocation to reproduction (reproductive effort) would be unequal, whereas the ratio of clutch weight or calories to body weight or calories would be identical.

(ii) Even if energy budgets were identical for two species, a comparison of clutch weight/body weight ratios might not provide comparable measures of effort if the species differed in the number of clutches produced in a single season.

As an illustration of these two points, consider two species that differ in number of clutches produced in a single season. Species A produces two clutches, each of which contains 10 units of energy. Species B produces a single clutch containing 20 units of energy. Species A contains 75 units of energy in the body, species B contains 100. Species A with a ratio of 10/75 could be considered to have a lower effort than species B

which has a ratio of 20/100. Even if we recognize that species A produced two clutches and, therefore, changed our estimate of reproductive effort to 20/75, we could not legitimately conclude that its true level of effort was higher than that of species B. If we assume that the amount of energy gathered is 200 units for each, then reproductive effort would be identical. Even if the total energy gathered differed in the two species, the ratio of clutch to body calories still might not estimate reproductive effort accurately. This is because, in the absence of data on the total energy budget and time over which body calories are accumulated, there is no way to determine the relationship between the above ratio and reproductive effort as we have defined it.

No theoretical paper thus far has dealt adequately with the difficulty of actually measuring reproductive effort. Schaffer (5), for example, states that:

"Reproductive effort may often be difficult to measure in the field (8). On the other hand it is a helpful guide to our thinking and we will use it in that spirit."

It is precisely our lack of understanding of what constitutes an adequate measure of reproductive effort that has made testing predictions of how selection should affect effort exceedingly difficult. We do not feel that empirical measurement is impossible. Physiologists, in particular, could contribute greatly to our understanding of reproductive effort through detailed study of energy budgets. Fitzpatrick (19), for example, has provided such an estimate of energy compartmentalization in a salamander. Tinkle and Hadley (7) have made similar, but less direct, measurements in lizards. Despite the admittedly great difficulty of determining energy allocations in organisms in nature, we feel that it is possible to estimate the energy allocated to reproduction, growth, and maintenance. Such estimates would provide the information essential to calculate reproductive effort.

We will now summarize those situations in which we expect selection to lead to low or high levels of reproductive effort and discuss how we can recognize relative levels of effort.

Those conditions leading to high reproductive effort include:

- (i) High extrinsic adult mortality.
- (ii) Constant juvenile survivorship.
- (iii) Variable but predictable environments, with high effort in those years favorable for juvenile survivorship.

Those conditions leading to lower reproductive effort include:

- (i) Environments unpredictable for juvenile survivorship.
- (ii) Variable but predictable environments, with low effort in those years unfavorable for juvenile survivorship.

Reproductive effort probably cannot be meaningfully judged as high or low for a single species or age class. We can, however, by measuring energy budgets of a variety of related species of known demography, obtain a range of values for effort between species or age classes. Once such an array of measurements has been made, we can judge what constitutes high effort; however, further study is required to distinguish the selective bases for level of effort. Specifically, it is necessary to know variance in juvenile survivorship, variance of reproductive effort between years, and the cost of reproductive effort. For example, we have predicted that high effort may evolve where extrinsic adult mortality is high and the cost of such effort correspondingly low. We have also predicted high effort in species in which juveniles have constant

survivorship. In the latter instance, however, the cost to the adult of high effort is also high. Presumably this cost could be revealed by reducing experimentally the level of effort in such a species and showing that, compared to the first type of species, such experimental manipulation results in improved adult survivorship and/or growth.

Conclusions

Reproductive effort is a significant concept in the more general theory of life history evolution. Our understanding of the selective bases of differences in effort between age classes or between species will not increase until we obtain real measures of effort as opposed to simple, albeit attractive, measurements of phenotypic characteristics that have a presumed but unknown relationship to reproductive effort. We have identified those aspects of an organism's life history that require examination in any attempt to understand the selective basis for any given level of effort.

At this point several testable predictions can be made.

(i) Experimental reduction in the level of reproductive effort will enhance adult survivorship in those species in which high effort has evolved as an adaptation to environmental constancy. If experiments of this sort on species occupying fairly constant environments consistently result in no alteration of adult survivorship, we would consider this evidence of the falsity of the hypothesis.

(ii) There will be a negative correlation between average reproductive effort and the variance in juvenile survivorship over time in species at similar trophic levels. Such species may live in constant, variable, and unpredictable environments.

(iii) For those species in variable environments with high variance in juvenile survivorship, we expect year to year variation in reproductive effort to increase with increasing predictability of good years for juvenile survivorship.

(iv) For those species living in variable environments and displaying highly variable reproductive effort, a positive correlation between effort and juvenile survivorship should be found.

(v) Semelparous species as a group should show higher efforts than related iteroparous ones.

(vi) We would not expect to find a monotonic increase in reproductive effort during an individual's lifetime because the environmental regimes experienced by the organism at different ages may counterbalance selection for increased effort due to age alone.

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