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NATURAL SELECTION, THE COSTS OF REPRODUCTION,
 AND A REFINEMENT OF LACK'S PRINCIPLE

It would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life-history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction.

R. A. Fisher (1930)

Fisher's work implies that the mass selection of alternative alleles in a population is ordinarily the only force tending to maintain or improve adaptation. If so, the general nature of the solution to the problem outlined above is clear: expenditures on reproductive processes must be in functional harmony with each other and worth the costs, in relation to the long-range reproductive interest; and the use of resources for somatic processes is favored to the extent that somatic survival, and perhaps growth, are important for future reproduction. Here I will formalize this argument with the intent of clarifying discussion on whether reproductive processes serve individual reproductive interest (as advocated by Lack, 1954) or the survival of the species (as envisioned by Wynne-Edwards, 1962). I have distinguished these alternatives as *organic* vs. *biotic* adaptation, respectively (Williams, 1966).

An individual of a certain age and sex has a *reproductive value* (Fisher, 1930, ch. 2), defined as the mean amount of future reproductive success for individuals of that age and sex in the population. Under mass selection the reproductive value (Φ) will be maximized, and deviations from the normal reproductive patterns should reduce its value. A reproducing organism is faced with a series of choices: defend or abandon a threatened mate or litter or territory, make more ovules, more pollen grains, or a vegetative branch, etc. Such issues will normally relate to only a part of Φ and have a less than all-or-none effect on that limited part. When a robin retires for the night instead of foraging once more for its young, its action

has only a limited effect on the nutrition of its current brood, and none on next year's. The part of Φ that is immediately at stake can be designated ϕ . The proportionate increase in ϕ that would result from a positive response (such as "forage once more before retiring") can be a , achieved at cost c , measured as a factor of decrease in the remainder of the reproductive value ($\Phi - \phi$). The loss-factor from a negative response can be b . The positive response would thereby change the reproductive value to

$$\Phi' = (1 + a)\phi + (1 - c)(\Phi - \phi)$$

and a negative response would change it to

$$\Phi'' = (1 - b)\phi + (\Phi - \phi)$$

Selection will favor the positive response, and make it the normal reaction, if $\Phi' > \Phi''$, and will favor the negative if the opposite is true. It is therefore instructive to consider the circumstances that would make the cost just barely justified ($\Phi' = \Phi''$). Solving for c in this equation gives

$$\hat{c} = \frac{(a + b)\phi}{(\Phi - \phi)}$$

The barely justified cost is thus seen to be directly proportional to the magnitude of the threat or opportunity (a or b), or to their sum if both are involved, and also to the size of the investment at stake (ϕ). It is equally significant that the barely justified cost is inversely proportional to $\Phi - \phi$, which may be called the *residual reproductive value* (henceforth RRV).

The theory deals explicitly with yes-or-no decisions, such as whether or not to defend a brood, but quantitative issues must also be resolved, such as how much of a defense should be offered. This sort of problem can be treated as the sum of infinitesimal yes-or-no responses. For any level of expenditure on gonad development or other reproductive process, the question arises "should a slightly greater amount be spent on this activity?" Whatever the normal expenditure is, we can say that positive answers are given up to the observed expenditure, and negative answers are beyond that level. Thus the RRV is important, not only in the selection of such things as flight vs. fight thresholds, but also such quantitative characters as fecundity and development of secondary sex characters.

These conclusions on the role of the RRV in the evolution of reproduction are of broad applicability. With respect to a given reproductive function, however defined, all other simultaneous or future functions contribute to the RRV. The production of pollen and of ovules are, each for the other, an aspect of the RRV; and they both contribute collectively to the RRV with respect to expenditures for petals. The usefulness of foraging for the young tomorrow is a part of the RRV for a robin, with respect to how much it forages today. The cost of a reproductive function is any quantitative decrement in either the effectiveness of another function, or the probability of surviving to perform that function, or both.

Whatever total cost is warranted for a seasonal or other complete reproductive program, the theory developed above means that the allotted resources will be distributed among the component processes in a way that maximizes the rate of reproductive profit on the investment. Reproduction may to some extent represent a mutually interdependent chain of events in which increased strength in one link may be of no value without comparable changes in the others. Perhaps the clearest example is in the relation between fecundity and nestling nutrition in nidicolous birds. As Lack has shown, birds that lay more eggs than the species average may produce fewer than the average number of fledglings, because of the inadequacy of parental food gathering. Even in seemingly additive functions, such as the production of pollen and the production of ovules, there must be some point of diminishing return for each, or at least some nonlinearity in the regression of a on c , which would fix some optimum balance in the division of resources between the two.

In the special case in which ϕ represents the total value of the current breeding season, the RRV would be a simple function of future age-specific natality and mortality. In this special application, the theory can be tested by comparing any series of species with seasonal reproduction and at least approximately known, and widely different, intensities of reproductive effort, annual mortality rates, and perhaps of annual changes in fecundity. The last two are commonly studied demographic parameters, and their measurement presents no theoretical difficulties. The intensity of reproductive effort may be a more elusive entity but could be quantified in a quasi-objective manner. With respect to any aspect of reproduction, such as gonadal mass produced, sex dimorphism, elaborateness of nest architecture, etc., a series of species could be ranked in order from the one with the least to that with the greatest development of the character in question. The sum of its ranks for several aspects of reproduction could serve as the species index of reproductive effort. The theory predicts a negative correlation between this index and an RRV calculated from rates of mortality and natality.

Lastly it should be pointed out that for species with low annual mortality rates, especially those that increase in fecundity from year to year, the parent's lifetime reproductive interest may demand a low reproductive effort in a given season, much lower than that which would maximize reproduction for that season. Thus it may be true, as Cloudsley-Thompson (1955) has argued, that large birds have greater resources and should be able to raise more young than small birds. Nevertheless it is poor strategy for them to do so, because large birds have low mortality rates and, therefore, a high RRV with respect to the ϕ for any one season. When differences in RRV in relation to seasonal expenditures are taken into account, it should be possible to explain phylogenetic variation in reproductive effort. It is not necessary that Lack's principle of the maximization of individual reproductive effectiveness be confined to comparisons within species, as Lack (1955) himself has urged.

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SUFFICIENT CONDITIONS FOR GENETIC POLYMORPHISM

It has been shown by Levene (1953) that if a population is subdivided into n subpopulations each confined to a separate ecological niche when experiencing the effects of selection, stable polymorphism is more readily achieved than if selection were uniform. A population will be called "polymorphic" in this context if there is no tendency for one type to become extinct in the population as a whole; there may well be complete lack of variation in any one or more of the individual niches.

Here we deduce a less restrictive condition on polymorphism than Levene's and show its applicability to a wider variety of cases.

Suppose that two alleles A , a are found in the i th niche in the frequencies p_i , $q_i = 1 - p_i$, respectively, and that the fitnesses of the genotypes AA , Aa , aa are W_i , 1 , V_i , respectively. Let c_i represent the proportion of the population found in the i th niche.

Suppose that due to the effects of interniche migration or interbreeding a proportion k of all gametes may be thought of as leaving their niche and