Natural Selection of Optimal Reproductive Tactics

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SYNOPSIS. Acting through differential reproductive success, natural selection has produced a great diversity of existing reproductive tactics, each of which presumably corresponds to a local optimum that maximizes an individual organism's lifetime reproductive success in its particular environment. A body of theory on so-called reproductive "strategies" has yet to be adequately related to an independent theoretical framework on optimal foraging tactics. Some of the possible interactions and constraints between an animal's input of matter and energy via foraging and its output in offspring using these same materials are briefly considered. For example, storage and utilization of lipids allow an organism to gather and sequester matter and energy during a period that is not suitable for successful reproduction, but enable the organism to expend those materials at a later, more satisfactory time. Such interactions between foraging and reproduction lead to a sort of temporal integration, which greatly complicates estimation of reproductive effort (current investment in seed, eggs, or progeny) in variable environments. An optimal reproductive tactic maximizes an individual's reproductive value (the sum of all present plus the expected probable number of all future offspring) at every age. Reproductive effort should vary inversely with residual reproductive value (expectation of *future* offspring); moreover, the precise form of the trade-off between present offspring versus future progeny, which is itself sensitive to a multitude of environmental influences including resource availability and the immediate environmental conditions for reproduction and survival, dictates the optimal tactic at any given age. Simple graphical models of optimal reproductive tactics are presented and discussed. Finally, some promising directions for future work, as well as certain potential difficulties, are noted.

INTRODUCTION

In presenting the theory of natural selection, Charles Darwin made frequent use of the two phrases "survival of the fittest" and "the struggle for existence." His choice of words was somewhat unfortunate in that it has tended to make many biologists place undue emphasis upon differential mortality and lose sight of the fact that natural selection ultimately operates only by *differential reproductive success.* Differences in survivorship can of course lead to selection, but *only* if they result in a reproductive differential. A fundamental component of the definition of life is self-replication or reproduction and the only currency of natural selection is successful offspring. Yet, even though all living organisms pre-

sumably must maximize their own reproductive success, they vary greatly in their exact modes of reproduction. Some, such as a multitude of insects, certain fish like Pacific salmon, and most annual plants, reproduce only once during their entire lifetime. These "big bang" or semelparous reproducers typically exert a terrific effort in this one and only opportunity to reproduce. (In fact, their exceedingly high investment in reproduction in itself could well contribute substantially to their own demise and consequent failure to reproduce again.) But many other organisms such as most vertebrates and perennial plants reproduce repeatedly during their lifetimes. These organisms have been called "iteroparous" (repeated parenthood). Even within the organisms that use either the big-bang or the iteroparous tactic, individuals and species vary greatly in the numbers of progeny they produce and the exact timing of their reproduction. For example, an individual codfish may produce literally millions of relatively tiny eggs, whereas other fish such as sharks expend

much more on each progeny and hence must produce considerably fewer offspring. The famous "century plant," an *Agave*, devotes years to vegetative growth before suddenly sending up its inflorescence, while certain related plants bloom much sooner. Cicadas typically do not reproduce until they are some 13 or 17 years old, whereas numerous close relatives reproduce at less than one year of age. Delayed reproduction also occurs in many birds, especially among large seabirds. Numerous other examples of the great diversity of existing modes of reproduction could be listed.

How can this overwhelming variety of reproductive tactics be explained? I begin with the working hypothesis that natural selection has molded observed reproductive tactics so that each in some way corresponds to a local optimum that maximizes an individual's lifetime reproductive success in a particular environment. This prompts a variety of questions, such as what environmental factors determine (1) how much to invest in any given act of reproduction? (2) how much to devote to any single seed, egg, or progeny? and (3) when to reproduce? The interaction between the answers to (1) and (2) of course determines the optimal clutch or litter size. Sir Ronald Fisher was among the first to ask such questions, as reflected in the following often quoted and very penetrating statement:

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.

In this early comment, Fisher (1930) clearly anticipated the important concept of *reproductive effort*, which can be loosely defined as an organism's investment in any current act of reproduction. Fisher (1930) also gave the first explicit mathematical definition of *reproductive value*, which is simply an organism's age-specific expectation of all present and future offspring (the latter being discounted back to the present). These two notions have played a central role in the development of an extensive literature on so-called reproductive "strategies." (I prefer to use the term "tactic" as this does not have the teleological implications conjured up by "strategy.") After a ten-year lag following the now classic paper by Cole (1954), publications on life-history tactics have abounded (Lewontin, 1965; Williams, 1957, 1966a, 1966b; Lack, 1966; Cody, 1966, 1971; MacArthur and Wilson, 1967; Cohen, 1967, 1968; Istock, 1967, 1970; Murphy, 1968; Vandermeer, 1968; Tinkle, 1969; Clark, 1970; Tinkle et al., 1970; Harper and Ogden, 1970; Harper et al., 1970; Emlen, 1970; Gadgil and Bossert, 1970; Mertz, 1971; Willson, 1971; Gadgil and Solbrig, 1972; Pianka, 1970, 1972; Trivers, 1972; Ballinger and Clark, 1973; Tinkle and Ballinger, 1972; Tinkle and Hadley, 1973, 1975; Abrahamson and Gadgil, 1973; Charnov and Schaffer, 1973; Goodman, 1974; Taylor et al., 1974; Schaffer, 1974; Wilbur et al., 1974; Constantz, 1974; Demetrius, 1974, 1975a, 1975b; Schaffer and Gadgil, 1975; Pianka and Parker, 1975; Hirshfield and Tinkle, 1975).

Rather than attempt to discuss and review all these dozens of papers in the limited space available here, I instead use this as an opportunity to present my own synthesis and to point out what I perceive to be some promising directions for future work, as well as certain potential difficulties.

TIME AND ENERGY BUDGETS

An organism can be conveniently viewed as a simple input-output system (Fig. 1), with its foraging tactics (or, in the case of plants, photosynthetic capacity) providing an input of materials and energy which are in turn "mapped" into an output consisting of progeny. Fairly extensive bodies of theory now exist both on reproductive tactics (see above references) and on optimal foraging (Emlen, 1966, 1968; MacArthur and Pianka, 1966; MacArthur, 1972; Schoener, 1969a, 1969b, 1971; Royama, 1970; Rapport, 1971; Tullock, 1971; Pulliam, 1974; Charnov, 1973, 1975). In optimal foraging theory, the "goal" that is usually assumed to be maximized is energy
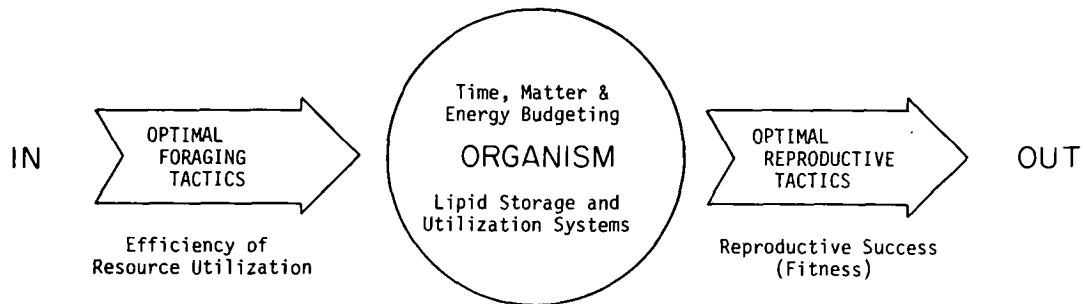
FIG. 1. Diagrammatic view of an organism as a simple input-output system. Optimal foraging theory is concerned with efficiency of resource utilization and input phenomena, whereas theory on optimal reproductive tactics deals largely with output aspects (re- productive success). Constraints and interactions between input and output arise both from lipid storage and utilization systems and through finite time and energy budgets.

uptake per unit time. (Successful offspring produced during an organism's lifetime would be a more realistic measure of its foraging ability, but fitness is exceedingly difficult to measure.) Similarly, among organisms without parental care, reproductive effort has sometimes been estimated by the ratio of calories devoted to eggs or offspring over total female calories at any instant. (Rates of uptake versus expenditure of calories have unfortunately not yet infiltrated empirical studies of reproductive tactics.) To date, empirical studies of resource partitioning and niche structure have been concerned largely with "input" phenomena such as overlap in and efficiency of resource utilization (see Schoener, 1974, 1976, for recent reviews) and have neglected to relate these to "output" aspects. In contrast, empirical studies of reproductive tactics have done the reverse and almost entirely omitted any consideration of foraging. Interactions and constraints between foraging and reproduction have barely begun to be considered (but see Schoener, 1971; Cody, 1974; Pianka and Parker, 1975; and Hirshfield and Tinkle, 1975). A promising area for future work will be to attempt to merge aspects of optimal foraging theory with the theory of optimal reproductive tactics to specify some of the rules by which input is translated into output; moreover, "output" phenomena must surely impose substantial constraints upon "input" possibilities.

An animal's time and energy budget provides a convenient starting point for clarifying some of the ways in which foraging influences reproduction and vice versa. Any animal clearly has only a certain finite period of time available in which to perform all its activities, including foraging and reproduction. This total time budget, which can be considered either on a daily basis or over the animal's entire lifetime, will be determined both by the diurnal rhythm of activity and by the animal's ability to "make time" by performing more than one activity at the same time (such as a male lizard sitting on a perch simultaneously watching for potential prey and predators, while monitoring mates and competing males). Provided that a time period is profitable for foraging with the expected gains in matter and energy exceeding the inevitable losses arising from the energetic costs of foraging, any increase in time devoted to foraging clearly will increase an animal's supply of matter and energy. Necessarily accompanying this increase in matter and energy, however, is a concomitant decrease in time available for non-foraging activities such as mating and reproduction. Thus the profits of time spent foraging are measured in matter and energy, while the costs take on the units of time lost. Conversely, increased time spent on non-foraging activities confers profits in time while costs take the form of decreased energy availability. Hence gains in energy correspond to losses in time, while dividends in time require reductions in energy

availability. (I consider risks of both for-
aging and reproduction below.)

Above arguments suggest that optimal
allocation of a time and energy budget
ultimately depends upon how costs in each
currency vary with profits in the opposite
currency (see also Schoener, 1971, 1973).
However, because the units of costs and
profits in time and energy differ, one would
like to be able to convert them into a
common currency. Costs and profits in time
might be measured empirically in energetic
units by estimation of the net gain in energy
per unit for foraging time (see Wolf, et al.,
1972, for an example). In the very unlikely
event that all potential foraging time is
equivalent, profits would vary linearly with
costs; under such circumstances, the loss in
energy associated with non-foraging ac-
tivities would be directly proportional to
the amount of time devoted to such activity.
Optimal budgeting of time and energy into
foraging versus non-foraging activities will,
of course, often be profoundly influenced
by various circadian and seasonal rhythms
of physical conditions, as well as those of
predators and potential prey. Certain time
periods favorable for foraging clearly re-
turn greater gains in energy gathered per
unit time than other periods. Moreover,
risks of exposure to both harsh physical
conditions and predators must often figure
into how much time is devoted to various
activities. Ideally, one would ultimately like
to measure both an animal's foraging effi-
ciency and its success in budgeting time and
energy by its lifetime reproductive success,
which would reflect all such environmental
"risks."

Foraging and reproductive activities in-
teract in another important way: many
organisms gather and store materials and
energy during time periods that are un-
favorable for successful reproduction but
then expend these same resources on re-
production during a later, more suitable,
time. For example, lipid storage and utiliza-
tion systems obviously facilitate such tem-
poral integration of uptake and expendi-
ture of matter and energy. As discussed
below, this temporal component greatly
complicates the empirical measurement of
reproductive effort.

AGE-SPECIFIC REPRODUCTIVE EFFORT

Given that an animal has optimized the
various trade-offs between foraging and
non-foraging as discussed above, what fac-
tors determine optimal allocation of the
resulting net energy available into repro-
ductive versus non-reproductive (somatic)
tissues, organs, and/or activities? Somatic
tissues are clearly necessary for acquisition
of matter and energy; however, an or-
ganism's soma is of no selective value except
inasmuch as it enhances that organism's
lifelong reproductive success. What is the
present value (in future offspring) of an
organism's body at any particular age? Or,
put another way, how much should the
soma be risked in any given current act of
reproduction? Williams (1966a, 1966b) and
Pianka and Parker (1975) have argued that,
in order to maximize overall lifelong con-
tribution to future generations, an optimal
organism should weigh its immediate pros-
pects of reproductive success against its
long-term future prospects. Thus, an indi-
vidual with a high probability of substantial
future reproductive success should be
more hesitant to risk its soma in present
reproductive activities than another indi-
vidual with a lower expectation of future
reproductive success. The present value of
an organism's soma in terms of its expecta-
tion of future offspring can be quantified
by its residual reproductive value, follow-
ing Fisher (1930), Hamilton (1966), Wil-
liams (1966a, 1966b), Emlen (1970), Taylor
et al. (1974), Schaffer (1974), and Pianka
and Parker (1975). (The following discus-
sion is improved and adapted from Pianka
and Parker, 1975.) Due to negative feed-
back between them, reproductive effort
should generally vary inversely with re-
sidual reproductive value. Allocation of
time and energy to reproduction in itself
doubtlessly often decreases growth and
survivorship and hence expectation of fu-
ture progeny. Moreover, as pointed out
above, successful reproduction often in-
volves taking risks such as exposing oneself
to predators, which by reducing longevity
decreases future reproductive success. The
tradeoff between present progeny versus
expectation of future offspring can be de-

picted graphically by plotting residual reproductive value against current reproductive effort (Fig. 2). Failure to reproduce at a given age maximizes residual reproductive value and future reproductive success but tautologically leads to a current fecundity of zero; conversely, all-out "big bang" reproduction obviously maximizes current fecundity while driving future reproductive success to zero.

Figure 2 depicts several logically possible different forms for the interaction between reproductive effort and residual reproductive value. These curves, which are analogous to fitness sets (Levins, 1962, 1968; Fretwell, 1972), relate profits in present offspring to costs in future offspring. Families of straight lines represent equal lifetime production of offspring (dashed lines) and are analogous to the corresponding "adaptive functions." The point of intersection of the "fitness set" curves with the "adaptive function" line that is farthest from the origin marks the optimal repro-

FIG. 3. During the lifetime of an iteroparous organism, the trade-offs between current reproductive effort and future reproductive success might vary somewhat as illustrated, with the dark solid curve connecting dots tracing the optimal reproductive tactic that maximizes total lifetime reproductive success. The shape of this three-dimensional surface would vary with immediate environmental conditions for foraging, survival, and reproduction, as well as with the actual reproductive tactic taken by the organism concerned. (Figure by Ellen Soderquist.)
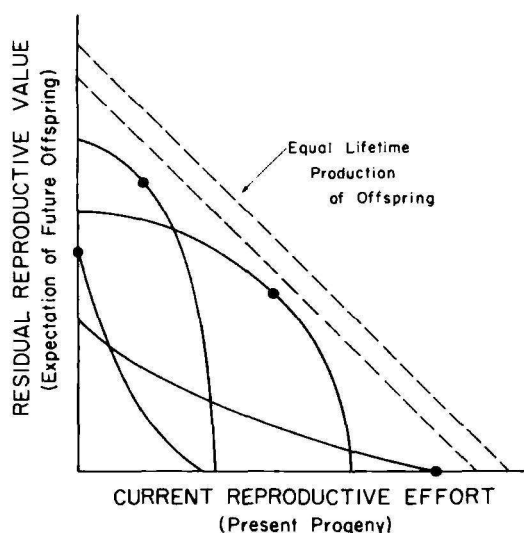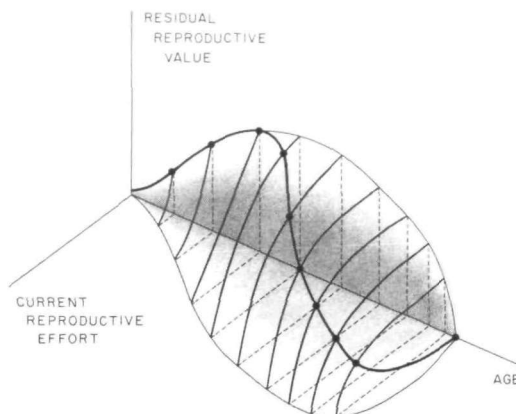

FIG. 2. A fitness set representation of the trade-offs between current reproductive effort and expectation of future offspring at any particular instant (or age). Four hypothetical curves relating costs in future progeny to profits in present offspring (and vice versa) are shown, with a dot marking the reproductive tactic that maximizes total possible lifetime reproductive success. Concave curves lead to all-or-none "big-bang" reproduction, while convex ones result in repeated reproduction (iteroparity). Figures 3 and 4 depict these trade-offs through the lifetime of a typical iteroparous and a semelparous organism, respectively.

ductive tactic that maximizes reproductive value and lifetime production of offspring (dots in Fig. 2). The precise form of the tradeoff between present and future progeny dictates the optimal reproductive tactic at any given age: concave curves lead to all-or-none reproduction, whereas convex ones maximize reproductive value and lifetime reproductive success at an intermediate current level of reproductive effort. Thus concave curves lead to "big-bang" or semelparous reproduction, while convex ones favor repeated reproduction (iteroparity).

Figure 3 attempts to depict the probable trade-offs between current reproduction and future reproductive success during the lifetime of an iteroparous organism. The surface of this three-dimensional solid shows the effects of various non-optimal levels of current fecundity on the organism's future reproductive success, as measured by its residual reproductive value. The dark line traces the optimal tactic that maximizes lifetime reproductive success. As the organism ages, residual reproductive value first rises and then falls; as expectation of future offspring diminishes,

the optimal current level of reproductive effort rises. A semelparous organism would have a similar three-dimensional plot with current fecundity increasing as residual reproductive value falls, but its surface is concave everywhere (Fig. 4). Needless to say, the intercepts and exact shapes of the surfaces depicted in these two figures depend upon the actual reproductive tactic taken by an organism; moreover, immediate environmental conditions for foraging, survival, and reproduction will also influence the precise form of the tradeoffs between present progeny versus future offspring. Thus, various factors such as the availability of resources, abundance of predators, as well as numerous aspects of the physical environment, all interact to determine the shape(s) of the surface(s) at any given instant in time. For example, favorable conditions for immediate reproduction increase the costs of allocating resources to somatic tissues and activities, and therefore result in a higher reproductive effort. (Unfavorable conditions for survivorship, such as harsh physical conditions or an increase in predator abundance, by decreasing returns expected from allocation of resources to soma would have a similar effect.) Conversely, of course,

FIG. 5. Fitness of individual offspring as a function of parental investment under two hypothetical cases. Line A assumes that fitness is directly proportional to expenditure, whereas curve B would obtain if initial outlays upon any given progeny enhanced fitness more than subsequent comparable investment. Curve B is biologically reasonable since the proportional unit contribution to total investment declines as investment increases.

poor conditions for immediate reproduction and/or favorable conditions for survivorship will result in a lower reproductive effort (see also discussions in Gadgil and Bossert, 1970; Pianka, 1970, 1972; Gadgil and Solbrig, 1972; and Hirshfield and Tinkle, 1975).

OPTIMAL EXPENDITURE PER PROGENY

What factors determine optimal investment in any single progeny? Two organisms investing similar total amounts in current reproduction may still differ in how they partition this total investment among their offspring. At one extreme, the entire amount could be invested in a single, very large, progeny. (The other extreme, of course, is to invest the minimal possible amount in each individual progeny and consequently to produce a maximal total number of them.) Often an intermediate tactic maximizes reproductive success: an optimal tactic represents a compromise between conflicting demands for production of offspring with the highest possible individual fitness versus production of the largest possible total number of progeny.
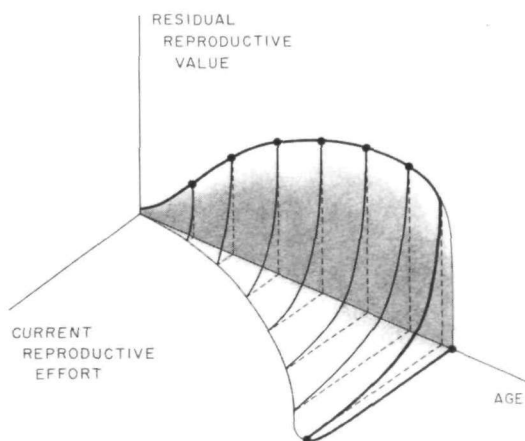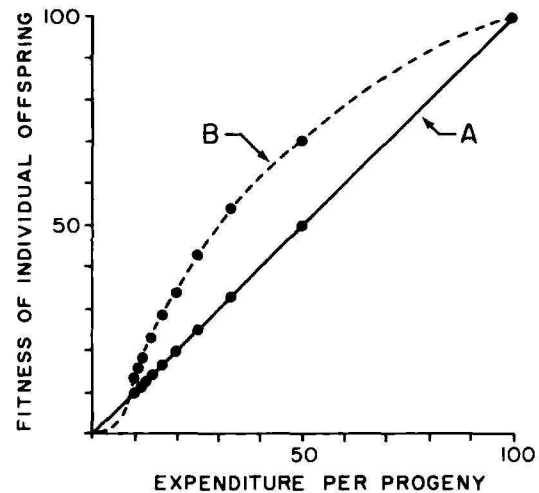

FIG. 4. A plot like Figure 3, but for a typical semelparous or "big-bang" reproducer. The surface relating costs and profits in present versus future offspring is always concave and reproduction is all or none. Again, the actual shape of such a surface would reflect immediate environmental conditions and the organism's actual tactic. (Figure drawn by Ellen Soderquist.)
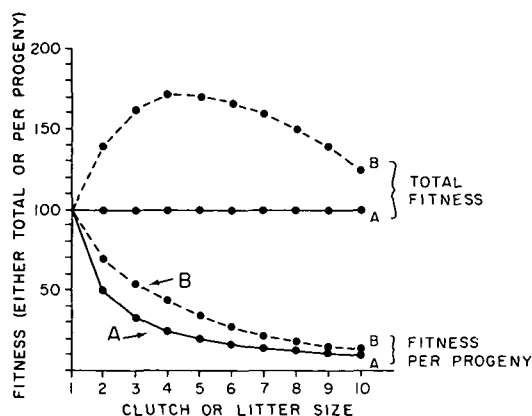
FIG. 6. Per progeny and total parental fitness as a function of clutch or litter size under the two assumptions A and B of Figure 5, assuming a fixed total reproductive effort (investment). Under assumption A, fitness per progeny declines exponentially and total progeny fitness (= parental fitness) is flat with clutch size. However, under assumption B, parental fitness peaks at an intermediate optimal clutch or litter size.

The following very simple graphical model, adapted from Pianka (1974), illustrates this trade-off (for an analogous fitness set model, see Smith and Fretwell, 1974).

All else being equal (genetic background, etc.), expenditure upon an individual offspring should be positively related to that offspring's individual fitness and competitive ability. Given a fixed amount of reproductive effort, there must be an inverse relationship between the total number of progeny produced and their average fitness. In the unlikely event that the fitness of individual offspring is directly proportional to parental investment (Fig. 5, solid line), the fitness of individual progeny declines exponentially with increased clutch or litter size (Fig. 6, lower solid curve). Total fitness, the sum of the fitnesses of all individual offspring, however, remains constant (Fig. 6, upper solid line). Fitness of individual offspring probably does not vary linearly with parental expenditure, but rather gains in progeny fitness per unit of parental investment are likely to be greater at lower expenditures per progeny than at higher ones because the *proportional* increase per unit of allocation is greater at low levels of investment (Fig. 5, dashed line B). Hence total fitness, which should reflect parental fitness, peaks at an

optimal clutch or litter size (Fig. 6, dashed curve B in upper panel). Of course, a virtual plethora of environmental factors must influence the exact shape of the dashed curve B in Figure 5, particularly the competitive environment of immature organisms. Because larger, better endowed, offspring should usually enjoy higher survivorship and generally be better competitors than smaller ones, heightened juvenile competition should often increase the optimal expenditure per progeny.

Note that, since any two parties of the triumvirate determine the third, an optimal clutch or litter size is a direct consequence of an optimum current reproductive effort coupled with an optimum expenditure per progeny. (Indeed, clutch size is equal to reproductive effort divided by expenditure per progeny.) Of course, clutch size can be directly affected by natural selection as well.

PROSPECT: POSSIBILITIES AND DIFFICULTIES

As pointed out above, interactions and constraints between foraging and reproduction constitute a very promising area for future theoretical work. The merger of aspects of optimal foraging theory with the theory of optimal reproductive tactics will be difficult and challenging, but is pregnant with potentially testable non-trivial predictions and seems certain to produce much greater realism.

A multitude of equally significant, but perhaps even more difficult, challenges confront empirically-inclined researchers. Procedures will ultimately have to be worked out to enable costs and profits in time and energy to be converted into common units. Although an extremely powerful conceptual tool, reproductive effort has yet to be adequately quantified. Ratios of reproductive tissues over total body tissue (both weights and calories have been used) are typically exploited as empirical indicators of reproductive effort; however, such measures entirely neglect "risk" phenomena (above) and frequently lack a suitable time dimension. Sometimes calorific ratios are computed over a period of time such as a season or a year, although such lumping often obscures much in-

teresting variation in reproductive tactics in species that reproduce more than once per season. In such multiple-clutched species, reproductive effort defies quantification even with calorific ratios due to seasonal variations in resource availability and temporal integration via lipid storage systems (Pianka and Parker, 1975). Indeed, I cannot identify any even *marginally* adequate operational means of estimating reproductive effort, short of measuring the reduction in lifetime reproductive success resulting from a given current level of reproduction.

Problems associated with estimating residual reproductive value are still more overwhelming. One would ideally like to have such measures for *individual* organisms on an age-specific basis; yet, expectation of life and future reproductive success can only be estimated using a *cohort* of a small population of organisms. Variations between individuals among such an arbitrary cohort in expectation of life and future progeny clearly must often exist. Individuals with lower than average reproductive effort that therefore enjoy below-average mortality and longer lives could still have a lifetime reproductive success comparable to that of individuals with higher than average reproductive effort but consequently shorter lifespans. Such individual variation would lead to considerable variance in residual reproductive value and current reproductive effort among organisms within a given age class. Though it will doubtlessly be tedious to measure, lifetime reproductive success may well prove to be much more useful than residual reproductive value as an operational handle on reproductive tactics.

Unfortunately, models of age-specific reproductive tactics such as those presented in Figures 2, 3, and 4 are exceedingly difficult to test. Merely demonstrating either a concave or convex relationship between current reproductive effort and future reproductive success would be extremely difficult or impossible for most organisms. Nevertheless, substantial progress might be made without establishing this relationship or actually measuring residual reproductive value. Somehow an organism needs to be either tricked or manipulated into adopting a non-optimal tactic, thereby lowering its lifetime reproductive success. (Perhaps natural variation among individuals would be adequate in some species.) Then the future reproductive success of the organism that has expended either more or less (preferably both, using a number of individuals) than the appropriate optimal amount on current reproduction must be monitored against the success of a control organism to measure the corresponding decrease or increase in future reproductive success. (The cost of either suboptimal or superoptimal current reproductive effort could perhaps best be quantified by the concomitant decrease in total lifetime reproductive success arising from that particular non-optimal current level of reproduction.) Of course, such a study should first be made in a relatively constant environment with non-changing conditions for foraging, survivorship, and reproduction. Work on reproductive tactics in variable environments, while much more difficult, might then be possible to design.

Clearly, the theory of reproductive tactics is now fairly sophisticated and well advanced; certainly it is considerably ahead of its data base. A great deal of ingenuity and effort will be required to design and execute research to test this elegant body of theory.

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