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Reproductive tactics

ABSTRACT

Acting through differential reproductive success, natural selection has produced a great diversity of reproductive tactics, each of which presumably must correspond to a local optimum that maximizes an individual's lifetime reproductive success in its particular environment. Such 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 (parental investment in current reproduction) should vary inversely with expectation of future offspring. The precise form of the tradeoff between present progeny and future offspring is itself sensitive to a wide variety of environmental factors, especially resource availability and conditions for survival. A compromise must be reached between producing many small progeny versus fewer large ones: this results in an optimal expenditure per progeny which maximizes parental fitness (the total fitnesses of all progeny). Optimal clutch size is a necessary consequence of reproductive effort and expenditure per progeny. Selection in crowded environments differs from that in uncrowded environments, the former favoring larger more competitive offspring and the latter early reproduction, high reproductive effort, low expenditure per progeny and large clutch size. Early reproduction is advantageous in expanding (opportunistic) populations, whereas reproduction may be delayed without cost in equilibrium populations. Reproductive tactics can be placed on a two dimensional triangular surface in three space with the coordinates: juvenile survivorship, fecundity, and age of first reproduction (or generation time). Reproductive tactics among fishes (and probably all organisms) fall on this two-dimensional triangular surface with three endpoints corresponding to equilibrium (K-strategists), opportunistic, and seasonal species (Winemiller 1992). The r-K selection continuum runs diagonally across this surface from the equilibrium corner to the opportunistic-seasonal edge, and a bet-hedging axis passes across this triangular surface at an angle to the r-K continuum. Sexual selection appears to be weak in seasonal breeders, but may be intense in both opportunistic and equilibrium populations. Sexual reproduction remains an evolutionary enigma because organisms practicing it necessarily dilute their genetic contribution to their own offspring by half, requiring that twice as many progeny be produced for the same reproductive success. In contrast, creatures reproducing asexually replicate only their own genes. Evolutionary advantages of sexual reproduction, such as genetic variability and a consequent ability to track a changing environment, must be substantial in order to outweigh the costs of halved heritability. Several possible advantages to individuals (as opposed to populations) include: (1) the possibility of mating with a very fit member of the opposite sex, thereby associating one's own genes statistically with genes conferring high fitness, (2) reduced competition among siblings, and (3) heterozygosity itself might confer enhanced fitness.

Key words: Sexual reproduction, Sexual selection.

Introduction

A lot of competent people have thought long and hard on the subject of reproductive tactics (a partial list includes Fisher, 1930; Cole, 1954; Williams,

1966; MacArthur & Wilson, 1967; Tinkle, 1969; Gadgil & Bossert, 1970; Mertz, 1971a, b; Stearns, 1976; Grime, 1977; Pianka, 1979, 1976). However, as is so often the case, theory has raced far ahead of data and we still await definitive empirical studies. Unfortunately, my own contribution remains more conceptual than empirical. Although the term «reproductive strategies» is well established in the literature, I prefer the slightly less teleological term «tactics», even though there is a «goal» to reproduction in the sense of maximizing lifetime reproductive success.

An individual's ability to perpetuate its genes in the gene pool of its population, or its reproductive success, represents that individual's Darwinian fitness. Each member of a population has its own relative fitness within its population, which determines in part the fitness of other members of that population; likewise, every individual's fitness is influenced by all other members of its population. Fitness can be defined and understood only in the context of an organism's total environment.

Over evolutionary time, living creatures that passed on their genes in successful reproduction most effectively gradually came to predominate in the world around us. Natural selection is somewhat myopic in that it is incapable of planning ahead, but it operates rather like an short-term efficiency expert, sculpting random variation to maximize the lifetime reproduction of individual organisms, creating quite complex adaptations. Over eons of time, selection has invented and refined sonar (echolocation), celestial navigation (avian migration), hypodermic needles (fangs of spiders and vipers), flight (multiple times), fusiform submarine shapes (fish, dolphins, whales), diving bells (water spiders), one of the best insulators known (feathers), plus innumerable other exquisite mechanisms by which organisms cope with their environments. Natural selection recognizes a common, but only a single, currency: *reproductive success*. Reproduction has primacy even over the almighty dollar. This sweeping generalization is true for all life, from Earth's algae, bacteria, fungi, humans, elephants and redwood trees to protobionts and more advanced forms of life on other planets revolving around distant stars anywhere in the cosmos. Darwin (1859) developed his theory of natural selection without even knowing the precise rules of inheritance, which actually proved to be unnecessary. All that is required in order for selection to operate is some degree of heritability (progeny must resemble their parents).

During the last century, Darwin's theory of natural selection has emerged as a major unifying theme that has revolutionized much biological thought. Unfortunately, however, this powerful central concept in biology is still misunderstood in several different ways, regrettably even among professional biologists. Words used to describe the potent process of selection («struggle for existence» and «survival of the fittest») too often invoke a dog-eat-dog world, overemphasizing death, and diverting attention away from the more subtle and basic mechanism of natural selection, *differential reproductive success*. Differences in survivorship leading to differential mortality can, but need not always, lead to natural selection. A cautious tomcat that seldom crosses noisy streets may live to a ripe old age without leaving as many descendants as another less staid tom killed on a busy road at a much younger age. Unless living longer results in higher reproductive success, long life simply is not favored by selection. Similarly, although we might

wish otherwise, there is no necessary selective premium on beauty, brains or brawn, except inasmuch as such traits are in fact translated into more offspring than average. If ugly, stupid, weak individuals are able to breed faster than pretty, smart, strong ones, the former will prevail.

Again, natural selection recognizes only one currency: successful offspring. Even though all living organisms have presumably been selected to maximize their own lifetime reproductive success, they vary greatly in exact modes of reproduction. Optimality models have borne the brunt of savage attack, but they remain one of the most powerful approaches to adaptation currently available. Our working hypothesis must be that natural selection has shaped observed reproductive tactics and that these represent local optima which maximize an individual's lifetime reproductive success in its particular environment.

Some species, such as most annual plants, a multitude of insects, and certain fish like the Pacific salmon, reproduce only once during their entire lifetime. These «big-bang» or semelparous reproducers typically exert a tremendous effort in this one and only opportunity to reproduce (in fact their exceedingly high investment in reproduction may well contribute substantially to their own demise!).

Many other organisms, including perennial plants and most vertebrates, do not engage in such suicidal bouts of reproduction but reproduce again and again during their lifetime. Such organisms have been called «iteroparous» (repeated parenthood). Even within organisms that use either the big-bang or the iteroparous tactic, individuals and species differ greatly in numbers of progeny produced. Annual seed set of different species of trees ranges from a few hundred or a few thousand in many oaks (which produce acorns, relatively large seeds) to literally millions in the *Sequoia* redwoods. Seed production may vary greatly even among individual plants of the same species grown under different environmental conditions; an individual poppy (*Papaver rhoeas*) produces as few as four seeds under stress conditions, but as many as a third of a million seeds when grown under conditions of high fertility (Harper, 1966). Fecundity is equally variable among fish; a female cod lays millions of relatively small eggs. Perhaps the most fecund vertebrate is the ocean sunfish, *Mola mola*, which lays as many as 200 million tiny eggs. Sharks, skates and rays produce considerably fewer but much larger offspring. Variability of clutch and/or litter size is not nearly so great among other classes of vertebrates, but it is still significant. Among lizards, for example, clutch size varies from a fixed clutch of one in some geckos and *Anolis* to as many as 40 or more in certain horned lizards (*Phrynosoma*) and the large iguanines *Ctenosaura* and *Iguana*.

Timing of reproduction also varies considerably among organisms. Due to the finite chance of death, earlier reproduction is always advantageous, all else being equal. Nevertheless, many organisms postpone reproduction. The century plant, an *Agave*, devotes years to vegetative growth before suddenly sending up its inflorescence (some related monocots bloom much sooner). Delayed reproduction also occurs in most perennial plants, many fish such as salmon, a few insects like cicadas, some lizards, and many mammals and birds, especially among large seabirds.

High fecundity early in life may usually be correlated with decreased fertility later on. For example, in several different strains of white leghorn chickens,

fecundity varies with age and drops off faster in birds that lay many eggs early in life. In strains with lower early fecundity, such fecundity versus age plots are much flatter (this is an excellent example of the principle of allocation). Innumerable other examples of the diversity of existing reproductive tactics could be listed. Of the multitude of environmental factors that impinge on reproductive tactics, the two most important are resource availability and survivorship, both of which vary with the degree of crowding. Major components of reproductive tactics are (1) reproductive effort or parental investment, (2) expenditure per progeny, (3) clutch or litter size, all three of which are intimately interrelated. The timing of reproduction is interfused with all three as well.

Reproductive effort

How much should an organism invest in any given act of reproduction? This question was anticipated over half a century ago by Sir Ronald Fisher:

"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".

Fisher (1930) clearly distinguished between the proximate factor (physiological mechanism) and the ultimate factors (circumstances in the life history and environment) that determine the allocation of resources into reproductive versus nonreproductive tissues and activities. Loosely defined as an organism's investment in any current act of reproduction, reproductive effort has played a central role in thinking about reproductive tactics. Although reproductive effort is conceptually quite useful, it has proven to be difficult to quantify adequately. Ideally, an operational measure of reproductive effort would include not only the direct material and energetic costs of reproduction but also risks associated with a given level of current reproduction. Another difficulty concerns the temporal patterns of collection and expenditure of matter and energy. Many organisms gather and store materials and energy during time periods that are unfavorable for successful reproduction but then expend these same resources on reproduction during a later, more suitable time. The large first clutch of a fat female lizard that has just overwintered may actually represent a smaller investment in reproduction than her subsequent smaller clutches that must be produced with considerably diminished energy reserves. Reproductive effort could perhaps be best measured operationally in terms of the effects of various current levels of reproduction upon future reproductive success.

In spite of such difficulties, instantaneous ratios of reproductive tissues over total body tissue have sometimes been used as a crude first approximation of an organism's reproductive effort (both weights and calories have been used and are termed relative clutch masses). Thus measured, the proportion of the total resources available to an organism that is allocated to reproduction varies widely among organisms. Relative clutch masses among lizards vary from about 4 to

31% of a female's mass (Vitt & Price, 1982; Pianka, 1986). Among different species of plants, energy expenditure on reproduction, integrated over a plant's lifetime, ranges from near zero to as much as 40 percent (Harper *et al.*, 1970). Annual plants tend to expend more energy on reproduction than most perennials (about 14 to 30 percent versus 1 to 24 percent). An experimental study of the annual euphorb *Chamaesyce hirta* showed that calories allocated to reproduction varied directly with nutrient availability and inversely with plant density and competition (Snell & Burch, 1975).

Let us return to Fisher's dichotomy for the apportionment of energy into reproductive versus nonreproductive (somatic) tissues, organs, and activities, and examine optimal reproductive effort. Somatic tissues are clearly necessary for acquisition of matter and energy; at the same time, an organism's soma is of no selective value except inasmuch as it contributes to that organism's lifelong production of successful offspring. Allocation of time, energy, and materials to reproduction in itself usually decreases growth of somatic tissues and often reduces future fecundity. Increased investment in current reproduction may also cost by reducing survivorship of the soma; this is easily seen in the extreme case of big-bang reproduction, in which an organism puts everything available into one suicidal bout of reproduction and then dies. More subtle changes in survivorship with minor alterations in reproductive effort have also been demonstrated.

How great a risk should an organism take with its soma in any given act of reproduction? To explore this question, we need a way to quantify the present value of the soma in terms of expectation of future offspring. Demography has identified such a parameter, known as residual reproductive value, which is simply the age-specific expectation of all future offspring beyond those immediately at stake. To maximize its overall lifetime contribution to future generations, an optimal organism should weigh the profits of its immediate prospects of present reproductive success against the costs to its long-term future prospects (Williams, 1966). An individual with a high probability of future reproductive success should be more hesitant to risk its soma in present reproductive activities than another individual with a lower probability of reproducing successfully in the future. Moreover, to the extent that present reproduction decreases expectation of further life, it may reduce residual reproductive value directly. For both reasons, current investment in reproduction should vary inversely with expectation of future offspring.

Several possible different forms for the inverse interaction between reproductive effort and residual reproductive value are depicted in Figure 1 (Pianka 1986). Curves in this simple graphical model relate costs and profits in future offspring, respectively, to profits and costs associated with various levels of current reproduction, the latter measured in present progeny. Each curve describes all possible tactics available to a given organism at a particular instant, ranging from a current reproductive effort of zero to all-out big-bang reproduction. In a stable population, immediate progeny and offspring in the more distant future are of equivalent value in perpetuation of an organism's genes; here a straight line with a slope of minus 45° represents equal lifetime production of offspring. (In an expanding population, current progeny gain a greater contribution to the gene pool and are therefore worth more than future ones and slopes are steeper; in contrast, in a

declining population with future offspring more valuable than present ones, slopes are gentler than 45 degrees). A family of such lines (dashed) is plotted in Figure 1. An optimal reproductive tactic exists at the point of intersection of any

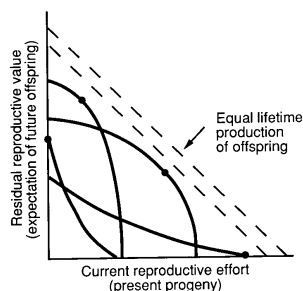


Fig. 1 - Trade offs between current reproductive effort and expectation of future offspring at any particular instant (or age). Four curves relate costs in future progeny to profits in present offspring (and vice versa), with a dot marking the reproductive tactic that maximizes total possible lifetime reproductive success. Concave upwards curves lead to all-or-none "big-bang" reproduction, whereas convex upward curves result in repeated reproduction (iteroparity). Figures 2 and 3 depict these trade offs through the lifetime of a typical iteroparous and a semelparous organism, respectively. (From Pianka, 1976).

given curve of possible tactics with the line of equivalent lifetime reproductive success that is farthest from the origin; this level of current reproduction maximizes both reproductive value at that age and total lifetime production of offspring (dots in Fig. 1). For any given curve of possible tactics, all other tactics yield lower returns in lifetime reproductive success. The precise form of the trade-off between present progeny and expectation of future offspring thus determines the optimal current level of reproductive effort at any given time. Concave-upward curves always lead to big-bang reproduction, whereas convex-upward curves result in iteroparity because reproductive value and lifetime reproductive success are maximized at an intermediate current level of reproduction.

Probable trade-offs between immediate reproduction and future reproductive success over the lifetime of an iteroparous organism are depicted in Figure 2. The surface in this figure shows the effects of different levels of current fecundity on future reproductive success; the dark dots trace the optimal tactic that maximizes overall lifetime reproductive success. The shadow of this line on the age versus current fecundity plane represents the reproductive schedule one would observe in a demographic study. Residual reproductive value first rises and then falls with age in many organisms; the optimal current level of reproduction rises as

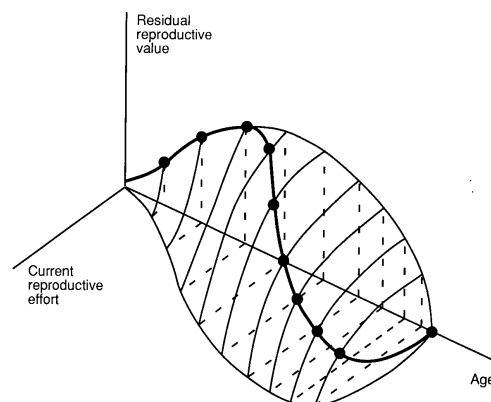


Fig. 2 - During the lifetime of an iteroparous organism, trade offs between current reproductive effort and future reproductive success might vary somewhat as illustrated, with the dark solid curve connecting the dots tracing the optimal reproductive tactic that maximizes total lifetime reproductive success. The shape of this three-dimensional surface would vary with immediate environmental conditions as well as the precise tactic adopted by the organism concerned. (From Pianka, 1976).

expectation of future offspring declines. An analogous plot for a semelparous organism is shown in Figure 3; here current fecundity also increases as residual reproductive value falls, but the surface for a big-bang reproducer is always concave upward. Exact shapes of the surfaces depicted in these two figures depend on the actual reproductive tactic taken by an organism as well as on immediate environmental prospects for foraging, reproduction, and survival. The precise form of the trade-offs between present progeny and expectation of future offspring is, of course, influenced by numerous factors, including predator abundance, resource availability and numerous aspects of the physical environment. Unfavorable conditions for immediate reproduction decrease costs of allocating resources to somatic tissues and activities, resulting in lower reproductive effort. (Improved conditions for survivorship, such as good physical conditions or a decrease in predator abundance, would have a similar effect by increasing returns expected from investment in soma). Conversely, good conditions for reproduction and/or poor conditions for survivorship result in greater current reproductive effort and decreased future reproductive success.

Body shape and escape tactics also influence reproductive tactics (Vitt & Congdon, 1978). Many turtles and horned lizards are long-lived and relatively K-selected as adults, but because of their tank-like body form have a comparatively

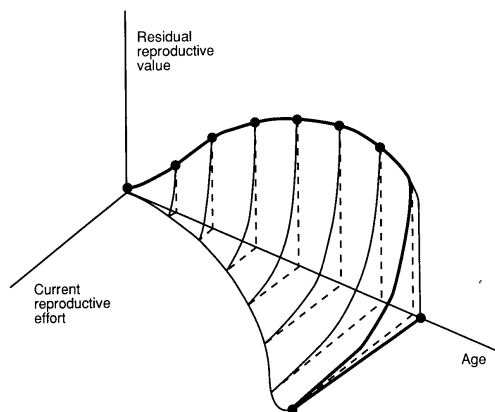


Fig. 3 - A plot like that of Figure 2, but for a typical semelparous or «big-bang» reproducer. The trade off surface relating costs and profits in present versus future offspring is always concave upward, and reproduction is all or none. Again, the actual shape of such a surface would reflect the immediate environmental conditions as well as an organism's actual tactic. (From Pianka, 1976).

large reproductive effort and produce many tiny offspring which suffer very high mortality.

Many birds and some mammals produce larger clutches (or litters) at higher latitudes than they do at lower latitudes, even within the same widely ranging species. Such latitudinal increases in clutch size are widespread. Latitudinal gradients in clutch or litter size could well be influenced by the trade-off between expectation of future offspring and optimal current investment in reproduction. If hazards of migration or overwintering at high latitudes inevitably result in steeper mortality, expectation of further life and residual reproductive value will both be reduced at higher latitudes. This in turn would favor an increased effort in current reproduction and hence the larger clutches observed.

Certain populations fluctuate regularly, such as those of the snowshoe hare, the Canadian lynx, the ruffed grouse, and many microtine rodents (voles and lemmings) as well as their predators, including the arctic fox and the snowy owl. These population fluctuations (sometimes called «cycles», although they should not be) are of two types: voles, lemmings, and their predators display roughly a four-year periodicity; hare, lynx, and grouse have approximately a ten-year interval between peaks. Lemming population eruptions and the fabled, but very rare, suicidal marches of these rodents into the sea have frequently been popularized (and even staged for movie production!) and are therefore all too «well

known» to the lay population. The tantalizing regularity of such fluctuations in population density presents ecologists with a «natural experiment» hopefully one that can provide some general insights into factors influencing population densities. The above ideas about optimal reproductive tactics can be invoked. Current offspring are «worth more» in an expanding population because there is an advantage to early and intense reproduction (high reproductive effort). However, as a population ceases to grow and enters into a decline, the opposite situation arises, favoring little or no current reproduction. Also, if, as seems highly likely, juvenile survivorship diminishes as population density increases, profits to be gained from reproduction would also decrease. Curtailment of present reproduction and total investment in aggressive survival activities could repay an individual that survived the crash with the opportunity for «sweepstakes» reproductive success.

In a declining population such as that of the California condors (Mertz, 1971b), selection favors behavior to postpone reproduction, exacerbating and extending the decline (viewed in this way, the ultimate «winners» are the last pair to reproduce, who thereby capture 100% of the gene pool of the next «generation»).

Expenditure per progeny

Even if we neglect the genetic component (see final section), not all offspring are equivalent. Progeny produced late in a growing season often have lower probabilities of reaching adulthood than those produced earlier — hence, they contribute less to enhancing parental fitness. Likewise, larger offspring may usually cost more to produce, but they are also «worth more». How much should a parent devote to any single progeny? For a fixed amount of reproductive effort, average fitness of individual progeny varies inversely with the total number produced. One extreme would be to invest everything in a single very large but extremely fit progeny. Another extreme would be to maximize the total number of offspring produced by devoting a minimal possible amount to each. Parental fitness is often maximized by producing an intermediate number of offspring of intermediate fitness: Here, the best reproductive tactic is a compromise between conflicting demands for production of the largest possible total number of progeny and production of offspring of the highest possible individual fitness (see also section on *r* and *K* selection).

A simple graphical model illustrates this fundamental tradeoff between quantity and quality of offspring (Figs. 4 and 5). In the unlikely event that progeny fitness increases linearly with parental expenditure (dashed line A in Fig. 4), fitness of individual progeny decreases with increased clutch or litter size (the lowermost dashed curve A in Fig. 5). However, because parental fitness (the total of the fitnesses of all progeny produced) is flat, no optimal clutch size exists from a parental viewpoint (upper dashed line A in Fig. 5). 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; curves level off at higher expenditures due to the law of diminishing returns. If the biologically plausible

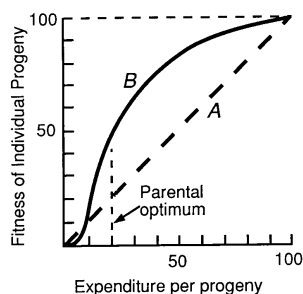


Fig. 4 - Fitness of an individual progeny should generally increase with parental expenditure. Because initial outlays on an offspring usually contribute more to its fitness than subsequent ones, curve B is biologically more realistic than line A. The parental optimum differs from the optimum for individual progeny, setting up a conflict of interests between the parent and its progeny.

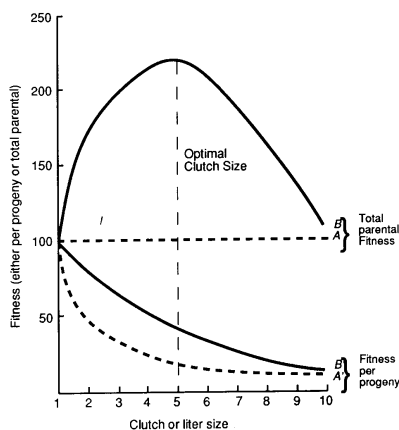


Fig. 5 - Fitness per progeny (A' and B') and total parental fitness, the sum of the fitnesses of all offspring produced (A and B), plotted against clutch and litter size under the assumptions of Figure 4. Total investment in reproduction, or reproductive effort, is assumed to be constant. Parental fitness peaks at an intermediate clutch size under assumption B, marking an optimal clutch size of five in this example.

assumption is made that progeny fitness increases sigmoidally with parental investment (curve B in Fig. 4), there is an optimal parental clutch size (peak of uppermost curve B in Fig. 5). In this hypothetical example, parents that allocate only 20 percent of their reproductive effort to each of five offspring gain a higher total return on their investment than parents opting for any other clutch size (Fig. 5). Such curves have been demonstrated for starlings and swifts (Lack, 1954). Although such a tactic is optimal for parents, it is not the optimum for individual offspring, which would achieve maximal fitness when parents invest everything in a single offspring. Hence, a «parent-offspring conflict» exists (Trivers, 1974). The exact shape of the curve relating progeny fitness to parental expenditure in any real organism is influenced by a virtual plethora of environmental variables, including length of life, body size, survivorship of adults and juveniles, population density, and spatial and temporal patterns of resource availability. The competitive environment of immatures is likely to be of particular importance because larger, better-endowed offspring should usually enjoy higher survivorship and generally be better competitors than smaller ones.

Clutch or litter size

Juveniles and adults are often subjected to very different selective pressures. Reproductive effort should reflect environmental factors operating upon adults, whereas expenditure per progeny will be strongly influenced by juvenile environments. Because 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 optimal 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. For example, it has been suggested that all members of the lizard genus *Anolis* lay but a single egg because the ancestral stock was arboreal and encountered intense selection against being weighted down by a heavy egg load, becoming genetically fixed at a clutch size of one (Andrews & Rand, 1974).

r and K selection

A concept that has proven to be quite useful on which to hang numerous aspects of reproductive tactics is known as r and K selection. Periodic disturbances, including fires, floods, hurricanes, and droughts, often result in catastrophic density-independent mortality, suddenly reducing population densities well below the maximal sustainable level for a particular habitat. Populations of annual plants and insects typically grow rapidly during spring and summer but are greatly reduced at the onset of cold weather. Because populations subjected to such forces grow in erratic or regular bursts, they have been termed opportunistic populations. In contrast, populations such as those of many vertebrates may usually be closer to an equilibrium with their resources and generally exist at much more stable densities (provided that their resources do not fluctuate); such populations deplete their resources and are called equilibrium populations.

Clearly, these two sorts of populations represent end points of a continuum;

however, the dichotomy is useful in comparing different populations. The significance of opportunistic versus equilibrium populations is that density-independent and density-dependent factors and events differ in their effects on natural selection and on populations. In highly variable and/or unpredictable environments, catastrophic mass mortality presumably often has relatively little to do with the genotypes and phenotypes of the organisms concerned or with the size of their populations. (Some degree of selective death and stabilizing selection has been demonstrated in winter kills of certain bird flocks). By way of contrast, under more stable and/or predictable environmental regimes, population densities fluctuate less and much mortality is more directed, favoring individuals that are better able to cope with high densities and strong competition. Organisms in highly rarefied environments seldom deplete their resources to levels as low as do organisms living under less rarefied situations; as a result, the former usually do not encounter such intense competition. In a «competitive vacuum» (or an extensively rarefied environment) the best reproductive strategy is often to put maximal amounts of matter and energy into reproduction and to produce as many total progeny as possible (even small ones) as soon as possible. Because there is little competition, these offspring often can thrive even if they are quite small and therefore energetically inexpensive to produce. There is a premium on early reproduction, because progeny produced sooner can themselves reproduce earlier. (The analogy of interest accruing in a bank account is apt). However, in a «saturated» environment, where density effects are pronounced and competition is keen, the best strategy may often be to put more energy into competition and maintenance and to produce offspring with more substantial competitive abilities. This usually requires larger offspring, and because they are energetically more expensive, it means that fewer can be produced. Reproduction is less urgent in such a crowded situation and reproduction may be postponed until opportunities are particularly good. In a stable population, a baby produced later is worth as much as one produced earlier (unlike the situation in expanding populations).

These two opposing selective forces were designated *r* selection and *K* selection by MacArthur & Wilson (1967), after the two terms in the logistic equation. One should not take these terms too literally, however, as the concepts are independent of the equation. They are also known as density-independent and density-dependent selection. Of course, things are seldom so black and white, but there are usually all shades of gray. No organism is completely *r* selected or completely *K* selected; rather all must reach some compromise between these two extremes. Indeed, one can think of a given organism as an «*r*-strategist» or a «*K*-strategist» only relative to some other organism; thus statements about *r* and *K* selection are invariably comparative. Cats and dogs are *r*-selected compared to humans, but *K*-selected compared to mice and rats. Mice and rats, in turn, are *K*-selected compared to most insects. We can think of an *r*-*K* selection continuum and an organism's position along it in a particular environment at a given instant in time (Pianka, 1970). A variety of correlates of these two kinds of selection are listed in Table 1. Parental care and live bearing (viviparity) constitute a means of increasing expenditure per progeny, and are often a response to crowding and consequent competition as well. In squamate reptiles (lizards and snakes), viviparity has arisen at least 100 times and is associated with cool climates.

TABLE 1 - Some of the correlates of *r* and *K* selection

	<i>r</i> selection	<i>K</i> selection
Climate	Variable and/or unpredictable; uncertain	Fairly constant and/or predictable; more certain
Mortality	Often catastrophic, non-directed, density independent	More directed, density dependent
Survivorship	Often Type III	Usually Types I and II
Population size	Variable in time, non-equilibrium; usually well below carrying capacity of environment; unsaturated communities or portions thereof; ecologic vacuums; recolonization each year	Fairly constant in time, equilibrium, at or near carrying capacity of the environment; saturated communities; no recolonization necessary
Intra- and inter-specific competition	Variable, often lax	Usually keen
Selection favors	1 Rapid development 2 High maximal rate of increase, r_{max} 3 Early reproduction 4 Small body size 5 Single reproduction 6 Many small offspring	1 Slower development 2 Greater competitive ability 3 Delayed reproduction 4 Larger body size 5 Repeated reproduction 6 Fewer larger progeny
Length of life	Short, usually less than a year	Longer, usually more than a year
Leads to	Productivity	Efficiency
Stage in succession	Early	Late, climax

Source: After Pianka (1970).

An interesting special case of an opportunistic species is the fugitive species, envisioned as a predictably inferior competitor always being excluded locally by interspecific competition but which manages to persist in newly disturbed regions by virtue of high fecundity and dispersal ability (Hutchinson, 1951). Such a colonizing species can persist in a continually changing patchy environment in spite of pressures from competitively superior species. Hutchinson (1961) used another argument to explain the apparent «paradox of the plankton», the coexistence of many species in diverse planktonic communities under relatively homogeneous physical conditions, with limited possibilities for ecological separation. He suggested that temporally changing environments may promote diversity by periodically altering relative competitive abilities of component species, thereby allowing their coexistence.

Recently, McLain (1991) suggested that the relative strength of sexual selection depends on the life history strategy, with *r*-strategists being less likely to

be subjected to strong sexual selection than K-strategists. Winemiller (1989, 1992) points out that reproductive tactics among fishes (and probably all organisms) can be placed on a two dimensional triangular surface in three space with the coordinates: juvenile survivorship, fecundity, and age of first reproduction (or generation time). This two-dimensional triangular surface has three vertices corresponding to equilibrium (K-strategists), opportunistic, and seasonal species (Figure 6). The r-K selection continuum runs diagonally across this surface from the equilibrium corner to the opportunistic-seasonal edge. In fish, seasonal breeders exhibit little sexual dimorphism, whereas both opportunistic and equilibrium species display marked sexual dimorphisms (Winemiller, 1992).

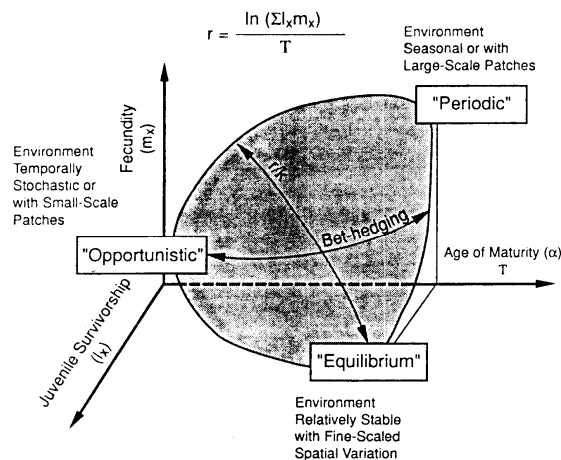


Fig. 6 - Winemiller's 3-D model for a triangular life history continuum (see text). Source: Winemiller (1992).

Bet-hedging

Under situations where survivorship of adults is high but juvenile survival is low and highly unpredictable, there is a selective disadvantage to putting all one's eggs in the same basket, and a consequent advantage to distributing reproduction out over a period of time (Murphy, 1968). This sort of reproductive tactic has become known as «bet hedging» (Stearns, 1976; Seger and Brockmann, 1987) and occurs in both r-strategists and K-strategists. Winemiller (1992) points out that a bet-hedging axis passes across his triangular surface at an angle to the r-K continuum.

Evolution of sexual reproduction

Sexual reproduction itself remains an enigma to students of evolution because organisms engaging in sex perpetuate the genetic materials of another organism. In contrast, an organism that reproduces asexually transmits only its own genes to a clone of its offspring genetically identical to itself, thereby leaving twice as many copies of its genes. In effect, reproducing sexually reduces a reproductive organism's contribution to each of her progeny by a full one half, meaning that to perform as well as an asexual, a sexual form must produce twice as many progeny. Sexual reproduction has arisen at least twice. Presumably, it first came into existence in bacteria billions of years ago in the primeval seas. In bacteria, sex involves exchanging genetic material but does not necessarily result in immediate reproduction. A more elaborate form of sexual reproduction arose later in protists that involved the evolution of diploidy as well as a complex reduction division (meiosis) and production of haploid gametes with only one set of chromosomes. This form of sexual reproduction has persisted to the present day through the evolution of more complex organisms such as ourselves. Diploidy may have evolved as a sort of «fail-safe» mechanism: when there are two copies of the genetic material, if an error is made, a «good» accurate backup copy still exists.

One plausible idea for the origin of sex is a predation hypothesis. Early organisms that consumed others could have simply adopted some of their prey's genetic material and put it to use to their own ends. According to this view, the predator incorporated some of its prey's loci into its own genome, thereby immediately acquiring the ability to synthesize some useful gene products and hence enhancing its own immediate performance and fitness. As an example, evidence is overwhelming that components of the prokaryotes, bacteria and blue-green algae, have been incorporated into eukaryotic higher organisms as cell organelles (chloroplasts and mitochondria).

Once gametes evolved, there was a distinct advantage to producing two distinct types: one large and nutritious, but sedentary, gamete that would support early development (eggs, oocytes, ovules) and another more mobile, but smaller, gamete that carries little more than genetic material (pollen, sperm). Such a specialization of function is superior to the presumed primitive state in which the two gametes are similar in size and function (isogamy). The situation in which gametes adopt different functions is termed anisogamy. Anisogamy gives rise to an asymmetry that results in an interesting fundamental yet inescapable «conflict of interests» between males and females (Trivers, 1972), the basis of sexual selection (Darwin, 1871).

Numerous varieties of sexual reproduction exist. Perhaps the finest of all is facultative sexuality, seen in water fleas (Cladocera): these aquatic micro-crustaceans abandon sex completely during the relatively constant summer months to form all female clones, with each producing only genetically identical daughters (all females possess two full sets of their mother's chromosomes). With the onset of winter, females produce meiotic eggs that develop into haploid males with only one set of their mother's chromosomes. These males inseminate haploid eggs of females in all clones, which then produce a special overwintering resting egg via sexual reproduction. Some organisms are also hermaphroditic, including simul-

taneous hermaphrodites (in which one individual has both male and female gonads at the same time — as in many invertebrates such as earthworms and many plants) and sequential hermaphrodites. Among certain marine fishes, some species are males when young but then change sex to become females as they grow older and larger, whereas other species of coral reef fish are females when small and become males as they get older and larger. Sex change in such fish is under social control. At least one sequentially hermaphroditic plant species may be able to switch back and forth from being either male or female and vice versa. In the most familiar organisms, most vertebrates and some plants, the sexes are separate.

Some have asked «Why have males?» Why are various sex ratios so often near equality? Darwin (1871) speculated that sex ratios of 1:1 might benefit groups by minimizing intrasexual fighting over mates. Other workers have reasoned that since one male can easily serve a number of females, it might «be better for the species» if the population sex ratio were biased in favor of females, because this would increase the total number of offspring produced. Similarly, males are sometimes viewed as supernumerous and therefore «dispensable». Such interpretations invoke naive group selection, and it is preferable to look for an explanation of sex ratio in terms of selection at the level of the individual. This problem was first solved by Fisher (1930), who noted that in sexually reproducing diploid species, exactly half the genes (more precisely, half those on autosomal chromosomes) must come from males and half from females each and every generation. Thus males always contribute as many genes as females to the next generation. In short, one cannot afford not to make males simply because they will sire half the genes in the next generation, making them equivalent to females in terms of their reproductive value.

Most organisms employ sexual reproduction, although many plants and invertebrates use it only infrequently. The evolutionary origin and selective advantage(s) of sexual reproduction remain major unresolved problems in biology (Williams, 1975). Sexual processes allow the genes in a gene pool to be mixed up each generation and recombined in various new combinations; as such, genetic variability is generated by sexual reproduction. The potential rate of evolution of a sexual population is far greater than that of a group of asexual organisms simply because a variety of beneficial mutations are readily combined into the same individual in a sexual species. But a rapid potential rate of evolution is seldom of as much immediate advantage to an individual organism as is a doubly high rate of reproduction. Sexual reproduction is certainly very basic in diploid organisms and is doubtless an ancient and primitive trait. Considered from an individual's perspective, however, sex is expensive because an individual's genes are thereby mixed with those of another organism and hence each of its offspring carries only half of its genes (i.e., heritability is halved). In contrast, a female reproducing asexually (including parthenogenesis) duplicates only her own genome in each of her offspring. Even Fisher (1930) suggested that sex could conceivably have evolved for the benefit of the group by way of some non-Darwinian form of group selection. Strangely enough, although many temporary losses of sexuality have been secondarily evolved, relatively few known organisms seem to have completely lost the capacity to exchange their genes with those of other organisms for any geologically long period of time. All female, unisexual species (known in fish and

lizards), are presumably short-lived on the geological time scale. (See Appendix on «Virgin Birth in Human Females?»)

The fundamental source of variation between individuals is sexual reproduction; reassortment and recombination of genes in each generation assures that new genotypes will arise regularly in any population with genetic variability. In most higher organisms, no two individuals are genetically identical (except identical twins and progeny produced asexually). Factors that create and maintain genetic variability in natural populations include numerous genetic mechanisms, such as linkage, heterosis, and frequency-dependent selection. Phenotypic variation must be distinguished from genotypic variation. The phenotypic component of variability is the total observable variability; the genotypic component is that with a genetic basis. It is often difficult to distinguish genetically induced variation from environmentally induced variation. However, by growing clones of genetically identical individuals (i.e., with the same genotype) under differing environmental conditions, biologists have been able to determine how much interindividual variation is due to the developmental plasticity of a particular genotype in different environments. Pedigree studies show that approximately half the phenotypic variation in height observed in human populations has a genetic basis and the remaining variation is environmentally induced. Because natural selection can act only on heritable traits, many phenotypic variants may have little direct selective value. The degree of developmental flexibility of a given phenotypic trait strongly influences an organism's fitness; such a trait is said to be canalized when the same phenotypic character is produced in a wide range of genetic and environmental backgrounds. Presumably, some genes are rather strongly canalized, such as those that produce «wild-type» individuals, whereas others are less determinant, allowing individuals to adapt and regulate via developmental plasticity. Such environmentally induced phenotypic varieties are common in plants, but they are less common among animals, probably because mobile organisms can more easily select an appropriate environment. Presumably, it is selectively advantageous for certain genetically induced traits to be under tight control, whereas others increase individual fitness by allowing some flexibility of response to differing environmental influences.

A very widespread misconception is that any phenotypic trait can always be assigned to either one of two mutually exclusive categories: genetic or environmental. However, this dichotomy is a gross oversimplification and can be seriously misleading. Because natural selection acts only on heritable phenotypic traits, even environmentally flexible traits must usually have an underlying genetic basis. For example, when fed dry grass, the Texas grasshoppers *Syrphula* and *Chortophaga* become brown, but when fed on moist grasses, these same insects develop green phenotypes — this classic «environmentally induced» polymorphism is presumably highly adaptive since it produces background color-matched green grasshoppers when environments are green but brown ones in brown environments (Otte & Williams, 1972). The capacity for developmental plasticity itself has almost surely evolved in response to the unpredictable environments these grasshoppers must face. If enough were known, much environmentally determined phenotypic variation would presumably have a somewhat comparable basis in natural selection. Truly nongenetic traits are unimportant and uninterest-

ing simply because they cannot evolve and have little or no evolutionary significance,

Genotypic and phenotypic variation between individuals, in itself, is probably seldom selected for directly. But it may often arise and be maintained in a number of more or less indirect ways. Especially important are changing environments; in a temporally varying environment, selective pressures vary from time to time and the phenotype of highest fitness is always changing. There is inevitably some lag in response to selection, and organisms adapted to tolerate a wide range of conditions are frequently at an advantage. (Heterozygotes may often be better able to perform under a wider range of conditions than homozygotes). Indeed, in unpredictably changing environments, reproductive success may usually be maximized by the production of offspring with a broad spectrum of phenotypes (which may well be one of the major advantages of sexual reproduction).

One brave evolutionist has concluded that sex is maladaptive in higher vertebrates (Williams, 1975, p. 109). Evolutionary benefits of genetic recombination and increased variability must more than offset the disadvantage of one organism perpetuating another's genes. In animals with biparental care, two parents can usually raise twice as many progeny as a single parent, offsetting the cost of sex. One possible advantage of an individual could be that by reproducing sexually, an organism can mix its genes with other desirable genes, thereby enhancing the fitness of its progeny (of course, this can work both ways, for by mating with a less fit partner, an organism would tend to diminish its own fitness). Another idea is that competition between siblings is reduced by the formation of a variety of types under sexual reproduction (in contrast, cloned offspring should interfere maximally with one another because they are genetically identical and hence require similar resources). If heterozygosity in itself confers increased fitness, however, sexual reproduction can clearly be advantageous to individuals.

It may be no accident that many parthenoform unisexuals have a biparental origin, arising from the hybridization of two bisexual parental species. Of course, in such a situation, clonal reproduction maintains and perpetuates heterozygosity perfectly, even better than sexual reproduction would.

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