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55. This article has been shaped by helpful suggestions from R. K. Colwell, P. J. DeVries, W. D. Hamilton, A. P. Dobson, H. S. Horn, M. Kreitman, J. H. Lawton, J. May, C. A. Toft, and two anonymous reviewers. Supported in part by NSF grant DMS87-03503.

The Ecological Context of Life History Evolution

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Life histories are the probabilities of survival and the rates of reproduction at each age in the life-span. Reproduction is costly, so that fertility at all ages cannot simultaneously be maximized by natural selection. Allocation of reproductive effort has evolved in response to the demographic impact of different environments but is constrained by genetic variance and evolutionary history.

EVEN THE MOST FAMILIAR ORGANISMS HAVE VERY DIVERSE life histories. Most small birds, such as chickadees or great tits, breed in the spring following their birth, and continue to nest every year until their death. As adults, they have a 50 percent chance of surviving each successive winter. In sharp contrast, most Pacific salmon breed in a suicidal burst as 3-year-olds. Oak trees have high adult survival rates, take more than 3 years before producing even their first few acorns, but then step up production until their acorns are numbered in thousands each year.

Making such diversity intelligible is one reason for studying life history evolution. Another is to predict the ways in which populations will respond to changed environments, including harvesting. Understanding life history diversity means facing fundamental questions about the functioning of organisms: What determines the maximum possible rate of reproduction? What developmental and physiological processes would have to be altered to increase the potential life-span? Why is rapid growth during development often associated with an elevated risk of morality? Answers to these kinds of questions are important in agricultural production and medicine, as well as ecology. Nevertheless, the subject is firmly rooted in ecology because, as we shall see, life histories evolve largely in response to the impact of different environments on the survival and fertility of different age-classes.

Our aim in this article is to evaluate the successes and limitations of the adaptationist approach to understanding life history evolution. It has been claimed that such an approach is doomed (*1*). In contrast, we shall argue that, when appropriately handled, it can have considerable utility for understanding both the diversity of life histories and the mechanisms constraining their form. We do not provide a comprehensive account, for which reviews are already available (*2–4*). We first outline the demographic model underlying most adaptationist interpretations of life history variation before going on to show how optimal life histories might be realized. We

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then discuss constraints on optimization and their implications for empirical work. Finally, we outline recent attempts to place life history evolution into an ecological context using both *r*- and *K*-selection theory and the idea of the "habitat templet" (*5*).

The Demographic Stage

The development of genetic theory for populations with overlapping generations and varying age-specific fertility and survival (*4, 6*) has marked an important advance in our understanding of life history evolution. There is now fairly general agreement that, with certain simplifying assumptions (including stable environments, frequency-independent weak selection, and demographic ergodicity), the optimal life history maximizes the Malthusian parameter or intrinsic rate of increase, r, which is the rate of increase of a population with a stable age distribution in a given environment. The Malthusian parameter is determined by the schedules of age-specific survival and fertility characteristic of individuals in the population (*7*). The most serious omission from the theory is probably frequency dependence, which is necessary to explain some life history patterns (*8*).

Life Histories and Adaptation

An evolutionarily ideal organism, a "Darwinian Demon" (*9*) would simultaneously maximize all aspects of reproductive performance. It would commence breeding at birth and produce copious well-endowed offspring throughout its infinite life-span. The observed diversity of life histories would be incomprehensible if this one were possible, which of course it is not. There are physiological and ecological constraints on the combinations of age-specific fertility and survival schedules that can in practice be realized. The first clear formulation of the central question was made by 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" (*10*). Early insights into life history evolution came from the demographic work of Cole (*11*) and from the models of reproductive effort of Williams (*12*) and of Gadgil and Bossert (*13*). We now outline the basic theory and tests of its applicability.

The Evolution of Repeated Breeding

Why do some organisms die after reproduction, whereas others survive to breed again? This area of life history evolution has been tackled in a series of elegant theoretical studies intiated by Cole (*11, 14*). An annual that adds one offspring to its current brood (size M) is reproductively equivalent to an immortal perennial that produces M offspring at each breeding attempt (assuming equal mortality of parents and offspring, offspring commence breeding at age one, and asexual reproduction): the perennial parent is demographically equivalent to the extra offspring of the annual. It is important to note that this comparison involves an implicit trade-off between fecundity and mortality, because the Darwinian Demon would produce the extra offspring and survive indefinitely. At first sight this argument makes the evolution of repeated breeding seem improbable: surely an extra acorn or two would cost an oak tree less than surviving another winter? However, altering juvenile and adult mortalities can change the picture (*14*). If the probability of parental survival is P and of offspring survival Y, then the annual organism now needs to add P/Y progeny to each brood. If $Y = P$, Cole's original conclusion is unaltered. What matters is the ratio of adult to juvenile survival, not the overall level of mortality. A higher ratio of adult to juvenile survival is expected to lead to the evolution of perennial life histories, which are possible as a result of a reduced brood size in each breeding attempt.

At first sight this apparently simple hypothesis presents no special difficulties for a comparative empirical test, but there are complications. The mortality measure should not include variation in mortality incurred as a result of the organism's own allocation decisions. It may therefore be necessary to make some independent measure of environmental risk factors such as predation, rather than measuring mortality rates directly. In addition, it is essential to standardize the risk of mortality from the environments in which the measurements of tendency to breed repeatedly are made. The great phenotypic plasticity of life history characters (*15, 16*) means that they must be measured under conditions otherwise similar to those in which the life history evolved (including population density, which could of course be affected by the removal of external mortality). Some studies ostensibly testing the model fail to meet one or more of these criteria (*17*).

A fruitful approach to testing the theory has come from studies where environmental risk factors affecting different populations of a species are assessed, and the tendency to breed repeatedly is measured under standard conditions in the field or laboratory (*16, 18–20*). For example, Law (*20*) compared different populations of the annual meadow grass *Poa annua* (despite its name, many individuals of this species live to breed again). Opportunist populations were characterized by low densities and high mortalities of all age classes, whereas pasture populations were characterized by high densities and relatively high juvenile mortality. When grown under standard conditions, adults from the pasture population were more likely to survive to breed again. These results and those of less controlled comparisons (*21*) are so far are in broad agreement with the theory, although there are some anomalies, and more data are sorely needed.

The Evolution of Reproductive Rate

Reproductive effort models of life history evolution, of which Cole's is an example, are based on the assumption of reproductive costs (*4, 10, 12, 13, 22*). Such costs could be physiological if nutrient allocation is involved, or ecological if, for example, reproduction exposes individuals to risks of predation (*23*). The existence of costs of reproduction would constrain the possible combinations of reproduction itself with other costly life history traits, such as growth and somatic maintenance. A general theoretical conclusion from the analysis of reproductive effort models is that organisms are expected to maximize their Fisherian reproductive value at each age, by an appropriate allocation of resources to growth, maintenance, and reproduction (*4, 12, 13, 22, 24*). The model has been used to deduce, for instance, that it will pay to postpone reproduction if allocation of resources to growth produces a sufficient gain in survival or future fertility to compensate for the loss of present offspring, given the change in size of the population in the intervening period. Similarly, intermediate levels of current reproduction may be favored if there is a law of diminishing returns between reproductive effort and the number of offspring thereby produced, or if parental survival or fertility is disproportionately affected by an increase in reproductive effort at higher levels.

Testing these ideas has involved assessing the costs of reproduction, the use of single species studies in attempts to determine whether reproductive rates are indeed optimal, and comparative work examining whether different species or populations vary as predicted by the theory.

Measuring the costs of reproduction. Although the idea of reproductive costs is central to adaptive accounts of life histories, its empirical basis has been contentious (*25–29*). However, the literature does clearly support the idea, and the controversy has sprung from the use of faulty methods. The main problems arise when a correlational approach is used: the organism is allowed to reproduce at its chosen rate, and subsequent survival and fertility are monitored. The difficulty comes from confounding variables: an organism in disadvantageous circumstances (as a result of its own phenotype, the environment it encounters, or an interaction between them) may reproduce at a lower rate and still show poor subsequent performance. For example, poor quality individuals may also be poor competitors, and hence end up in poor quality habitats or territories that depress fecundity and are likely to increase mortality. Spurious negative costs of reproduction are likely to result, and any costs that are found would be underestimated. It is therefore not surprising that this type of study has produced very mixed results (*25, 26, 30*). To investigate costs and measure their magnitude, it is necessary experimentally to manipulate reproductive rates of individuals that have been assigned randomly to groups in comparable environments. This experimental approach does usually reveal costs, both in subsequent survival and fertility (*25–27, 29*), although the occurrence and extent of those costs can depend upon the environment in which the measurements are made (*26, 27*). Ideally, a population with the natural range and frequency of phenotypes and genotypes should be used, and the organisms should be naturally distributed with reference to any environmental heterogeneity. Several recent field studies on birds (*31–36*) are a welcome development in this regard. For example, manipulation of brood size in blue tits (*Parus caeruleus*) showed that female survival decreased with increasing brood size (*31*).

Another unresolved issue in experimental studies is the value of genetic versus purely phenotypic manipulations of reproductive rate. Several investigators have argued that only genetic correlations give valid evidence of costs (*6, 26, 37*). This is true in the important sense that it is possible to predict with certainty the correlated response to selection on one trait by another only by measuring the genetic correlation between them. Genetic correlations can be extracted from correctly designed breeding experiments or directly from correlated responses to selection (*38*). However, there are practical and theoretical difficulties with this kind of approach in empirical studies. Even laboratory estimates of quantitative genetic parameters are often imprecise (*38, 39*). Field conditions would pose extra difficulties. Furthermore, testing optimality models of life histories requires quantitative measurement of the shapes of the curves relating current to potential future reproduction under field conditions. Genetic variation in reproductive rate is often insufficient for this and is usually much lower than can be produced by a phenotypic manipulation (*40, 41*). Finally, both techniques for measuring genetic correlations mainly exploit standing genetic variance. Only if it is assumed that genetic correlations will remain constant during a sustained response to selection, when new mutations are likely to enter, is it legitimate to deduce the form of sustained correlated responses. There is at present no compelling reason to accept this assumption.

There are two ways out of these difficulties. One is to accept that the evolutionarily realistic estimation of a cost function is impossible and to use genetic studies simply to investigate whether costs exist (*42*). The alternative approach, which is to use phenotypic manipulations of reproductive rate to obtain cost functions, would be invalid if the results obtained differed from genetic correlations. At present, it is not clear whether this is a problem. It is clear, however, that phenotypic studies based on naturally occurring variation in reproductive rate with no experimental manipulation can yield correlations between life history components that differ in sign from the genetic correlations between life history components. For example, the genetic correlation between female fertility and longevity is negative in *Drosophila melanogaster* (*40, 43*) whereas the unmanipulated phenotypic correlation is positive (*44*) because females vary in condition, especially body size. However, when reproductive rate is manipulated by varying the availability of food or oviposition site, the phenotypic correlation like the genetic correlation becomes negative (*45*). Quantitative studies comparing costs measured using genetic and a variety of experimental phenotypic manipulations are now needed.

Single species studies. Several empirical studies of the evolution of reproductive rate have tested particular optimality models, which in general imply that breeding organisms should maximize the difference between the number of offspring gained by current reproductive effort and those lost through the death or lowered fertility of the parent. The problem of optimal clutch size in birds has become a classic test case in this context (*29, 31, 32, 36*).

In one such study, Reid (*36*) manipulated the brood size of glaucous gulls (*Larus hyperboreus*), giving them artificial broods of between one and seven chicks (natural range is one to three chicks). Adult survival during the ensuing winter, assessed by resightings at the breeding colony, declined significantly with an increase in brood size above three, while subsequent breeding success appeared to be unaffected. The increase in adult mortality was, however, accompanied by a disproportionate increase in the number of chicks fledged, so that brood sizes greater than those normally found appeared to lead to higher parental fitness.

This kind of optimality approach has given useful insights into the nature and extent of the costs incurred as a result of chick rearing, but it has gone only part of the way to testing the theory. First, not all aspects of reproductive effort are manipulated by varying the number of nestlings; the production of eggs can be costly (*35*). In addition, all costs to the parent must be measured, and those may last into the ensuing breeding season, and perhaps for even longer (*31, 34*). Second, the studies so far have not measured the survival and breeding success of the progeny from manipulated broods. This information is needed to evaluate the optimality of clutch size. Also, as frequently pointed out (*46*), there are many reasons why the optimal solution may not be realized. The best use for optimality models may therefore be to provide an explicit basis for comparative tests.

Some important features of the real world are ignored in current optimality models. For example, trade-off curves may change with age, which could cause the optimal level of reproductive effort to vary. Adult growth, learning, and senescence could alter the optimal reproductive allocation. Experiments in conjunction with longitudinal studies of known individuals are required here, because survivors may not be a random sample or earlier age classes (*47*). Calves of elderly red deer (*Cervus elaphus*) hinds suckle longer, have better body condition, and are more likely to survive their first winter than those produced in the preceding years by the same mother, which suggests that the onset of senescence may discount negative effects on future reproductive prospects (*48*).

Comparative studies. The demographic theory suggests that reproductive effort should increase if the ratio of externally imposed adult to juvenile mortality is high (*14*). An elegant comparative test of this theory was made by Reznick and Endler (*19*) who compared life history characteristics of guppy (*Poecilia reticulata*) populations from locations containing predators that preyed differentially on particular age classes. Sixteen localities were sampled and guppies from those containing *Crenicichla alta*, a predator that prefers to feed on mature fish, exhibited increased reproductive effort compared with those from localities containing predators that preferred smaller age classes or showed no preference. For example, guppies at the sites containing *C. alta* devoted a higher percentage of their body weight to developing offspring, had shorter interbrood intervals, and matured at smaller sizes.

Temporal Variability, Bet-Hedging, and Phenotypic Plasticity

A major feature that has been incorporated into recent optimality models is temporal variability. If an allele has zero fitness in some generations then it will be eventually lost from the population, whatever its arithmetic mean fitness. Long-term fitness is often better measured as geometric mean fitness (*49*), which will be zero when it includes generations with zero fitness. Bet-hedging theory identifies the conditions under which organisms increase their geometric mean fitness at a cost to their arithmetic mean fitness in order to reduce their chances of extinction and depends on a trade-off between the arithmetic mean and variance of fitness (*50, 51*).

When environments tend to vary over a time scale of a few generations, bet-hedging strategies may evolve. A classic suggestion for bet-hedging theory is Cohen's (*52*) model of seed dormancy in plants. In a simple version, one genotype trades the reduced fitness caused by dormant seeds decaying in the ground against the chances of all the seeds germinating in a bad year and dying; surviving seeds have a constant probability each year of germinating. The model demonstrates a characteristic of bet-hedging theory in general: because all phenotypes do not have the same expected fitness at equilibrium, the strategy cannot be realized as a genetic polymorphism (*53*) and the available data for annuals seem to accord with that expectation (*51, 54*).

A more recent application of bet-hedging theory is from Boyce and Perrins' (*55*) analysis of clutch size variation in great tits. These birds lay smaller clutches than they can raise in an average year (8.5 as opposed to 12 eggs). One explanation for these results is that parents trade off smaller clutches against increasing their own chances of surviving to breed again, but brood manipulation experiments indicate that parental survival is not sufficiently increased to account for the observed reduction in clutch sizes. However, years that are poor for survival of young affect individuals laying larger clutches much more than they affect those laying smaller clutches. The observed clutch size is very close to that which maximizes geometric mean fitness.

It seems unlikely that bet-hedging would be a viable strategy to deal with spatially as opposed to temporally heterogeneous environments. As Seger and Brockmann (*51*) point out, if bet-hedgers produced the correct phenotypes at the correct frequencies, they would do no worse than an appropriate genetically polymorphic mixture in a spatial model with complete mixing. But the bet-hedgers would do worse in a model with restricted migration because the genetic variants would tend to be sorted appropriately into differentiated subpopulations.

Environmental variability may favor a varying pattern of resource allocation that could, in theory, be met by an appropriate type of phenotypic plasticity (*56*) in which the phenotypic expression of a genotype varies with the environment in which it occurs. Phenotypic plasticity is character specific, and it can have a genetic basis. The form of phenotypic plasticity, the "norm of reaction," can therefore evolve, and there are now quantitative genetic models of this process (*56–58*). These suggest that evolution toward an appropriate norm is likely to be slow if genetic variance is low or if some environments are rare (*58*). So far there have been few studies of genetic variation for the norm of reaction of life history characters (*59*). At a qualitative level norms of reaction often appear to be adaptive (*60*), but much environmentally induced phenotypic variance may reflect damage or a failure of homeostasis rather than an adaptive response. We need more information about the physiology involved. Does reduced nutrition during development lower adult body sizes because the low food level sets a new adult optimum, or are individuals stunted? What is the nature and cost of machinery for detecting environmental or phenotypic variation and for making an adaptive response?

Constraints

Attempts to account for natural variation in terms of adaptation are valid only when they take proper account of the constraints under which the response to natural selection occurs (*46*). Some constraints, such as costs of reproduction, are made explicit in optimality models. Others are not, yet may have an important effect on the course of evolution.

Phylogenetic history and genetic variance. Stearns (*61*) suggests that various life history traits which are fixed within lineages but vary in closely related lineages that occupy similar habitats may provide good evidence for the absence of (or a lag in the appearance of) appropriate mutational variance. He points out, for example, that the 600 or so lizard species in the family Gekkonidae all appear to lay two eggs per clutch, whereas other lizards with similar habits have more variable clutch sizes, and that all barnacles have six naupliar larval stages, whereas the number of stages in related groups varies considerably. His list could be extended without difficulty. It is, however, important to distinguish between taxonomic association of particular life history traits caused by lack of current genetic variation for alternatives and those caused by adaptive association with some other character not present in the suite under study. In practice, it is difficult to distinguish between these two sources of taxonomic association with life history variation.

Body size. It is frequently argued that life history differences are somehow constrained by body size differences (*62, 63*). In fact, size may be less of a constraint than is often supposed. Lengths and weights of organisms have been shown to be highly correlated with life history measures in cross-taxonomic comparisons (*64, 65*), but it is far from clear what such comparisons actually mean in biological terms. For example, one famous graph, which includes data from 45 species such as sequoia trees, elephants, and bacteria, shows a linear relation between the logarithms of generation time and body length for organisms ranging in size over almost eight orders of magnitude (*65*). The graph is usually interpreted to suggest that, because of the number of cell divisions involved, larger bodied species inevitably take longer to reach full size than smaller bodied species (*66, 67*). Other things being equal, larger bodied species would indeed take longer to grow to adult size. But in practice, this can be only part of the story since larger species sometimes have much shorter generation times. For example, foxes are longer and heavier than horseshoe crabs, but their generation time is almost an order of magnitude shorter (*66*).

Further evidence that life histories have evolved at least partially independently of the constraints of body size comes from the finding that components of life history often correlate more closely with each other than they do with body size. For example, gestation length and age at weaning among mammals are highly and positively correlated with each other when the effects of body size are held constant by partial correlation (*67–70*). Similar patterns between incubation period and fledging time are found across bird species (*71*). Why should different components of life history be correlated with each other if size is not the underlying constraint? Part of the answer may be that, since we are dealing with extant population, birth rates must equal death rates if populations are to persist, and it is not surprising that some components of life history correlate with each other independently of size (*72*). Recent comparative studies of birds and mammals demonstrate that several components of fecundity are highly correlated with mortality rates when body size effects are held constant (*70, 71, 73*).

Size, like metabolic rate or neuronal tissue development, may influence life history evolution through its effect on fertility and mortality schedules (*64*). Rather than viewing size as a fixed constraint that determines life history differences, it is more realistic to view size as a variable that evolves in response to selection on life history. For example, larger weasels may have lower overwinter mortality rates because they can survive longer on stored food reserves, but smaller weasels are more efficient predators because they can chase prey down burrows (*74*). Similarly, larger female insects can carry more eggs, whereas smaller insects may make unprofitable prey for avian predators.

Age, selection intensity, and mutation accumulation. A pervasive feature of plant and animal life histories is an intrinsic drop in biological performance leading to reduced life expectancy and fertility with advancing age (*75*). The process is especially obvious in populations such as the human one and in animals and plants in captivity, where natural hazards are removed, but it can also be detected in natural populations, particularly of long-lived species (*68, 70, 76, 77*).

Senescent decline could simply reflect a constraint on the prevention or repair of somatic wear and tear. This view cannot explain the observed variation in the extent of aging in biologically similar organisms held under optimal conditions, which implies variation in the degree to which the effects of wear and tear are combated (*4, 76, 77*). Medawar proposed that the evolution of aging can be understood as a direct consequence to the extent to which natural selection determines the fate of mutations with age-specific effects on survival or fecundity. Even in populations free of senescence there will be mortality from accidents and the impact of biological enemies. A mutation that influences survival or fertility at the beginning of adult life will therefore affect more of the individuals in which it is present than will a mutation with a similar phenotypic effect with a later age of action, because by then more of the carriers will be dead. As a consequence, selection acts more strongly on mutations which have effects that are apparent early in life (*76*). [The detailed population genetic theory also includes the fertility schedule of the population and its rate of increase (*4, 78*).] Beneficial mutations are therefore more likely to be incorporated by selection if they act early in the adult life-span, and deleterious mutations will achieve a higher frequency under mutation-selection balance if they act late. For both reasons, performance is expected to drop with age after the onset of reproduction in a way that would not be predicted by a gene-free optimality approach. Two recent laboratory tests using *Drosophila* have supported this theory (*79*).

The constraints discussed in this section are real and may be important. What they mean for empirical studies of life histories as with other biological processes (*80*) is that comparative tests may be the most effective way of detecting the effects of natural selection but that optimality models are an essential formalization of the assumptions underlying the tests.

The Ecological Context

Our discussion so far has outlined demographic considerations for life history evolution. But how can this evolutionary structure be placed into an ecological context? We summarize here two rather different approaches to answering that question.

r- *and* K-*selection.* Population density may have a general effect on the way the Malthusian parameter can be maximized (*81, 82*). A theory of density-dependent selection was initially used to compare colonizing with established populations; in the former high logistic r (the potential rate of population increase at low population size) was said to be selected, whereas in the latter high density at K (the carrying capacity) was favored. Subsequent theory has confirmed the idea that selection is likely to have these effects, and that K-selection may often be expected to maximize the numbers in the critical age-group where density-dependence occurs (*4*). The model can accommodate selection on r and K at intermediate population densities or at different life history stages (*82*), but frequency-dependent selection is ignored and its inclusion can lead to different conclusions about the likely course of events where there is intraspecific competition (*82*).

The theory of r- and K-selection has been controversial and has come to have something of a bad name, partly because it has been suggested to invoke group selection, which is not the case (*4, 83*). In addition, based on the assumption that high population densities are necessarily associated with high juvenile mortalities, syndromes of characteristics, including body size, reproductive effort, age of first breeding, and parental care, were said to characterize r- and K-strategies (*84*). The demographic assumption is not necessarily correct and, in addition, has had the effect of mistakenly making r- and K-theory appear to be a subset of the demographic theories. Subsequent empirical tests have therefore sometimes rejected it in their favor (*2, 85*).

The theory has two obvious predictions. The first is that there should be some incompatibility between high r and high K. This prediction has been tested infrequently and with a very restricted range of organisms; some tests have confused logistic r with specific life history characters, and the remainder have produced mixed results (*85–87*). The second prediction is that the growth rate pattern that evolves should reflect the history of population density. Experimental tests have shown that populations of *Drosophila* kept at high densities for many generations do evolve higher equilibrium population sizes (*88*). Despite this confirmatory empirical work, perhaps the main problem with the theory is that selection at high density favors improved competitive ability, which can reduce population size (*82*).

The Influence of Habitat

Southwood (*5*) envisaged habitats as "templets" (a synonym of templates) on which optimal solutions to evolutionary trade-offs are realized [reminiscent of Hutchinson's (*89*) ecological theater and evolutionary play]. He pointed to the importance of habitat stability and adversity axes for the evolution of life history diversity (*5*), an idea that was developed by Greenslade (*90*), who, following Glesner and Tilman's lead (*91*), incorporated biotic unpredictability. Hildrew and Townsend (*92*), studying benthic invertebrates, recognized productivity and disturbance axes as being important; Grime (*93*), working with flowering plants, defined competition, stress, and disturbance axes; and Sibly and Calow (*94*), in a more theoretical vein, suggested that ways in which environments influence offspring growth and offspring survival are critical. Finally, Begon (*95*) found it useful to categorize habitats by the ways in which the size of juvenile and established individuals influenced fitness (*96*). Southwood (*97*) has recently attempted to draw most of these results together by reorienting axes to show how different investigators were describing similar classifications with habitats defined by two basic axes: disturbance and adversity. But, as Southwood stresses, if such classifications are to be of more than ad hoc descriptive value, they must make firm predictions about the relative importance of particular life history tactics and trade-offs in different habitats.

It is not obvious that general trends will emerge. Habitats are not independent of the species that evolve on them. Different sized species or those with different longevities may find the same environment coarse or fine-grained, stable or unstable, predictable or unpredictable, ephemeral or long-lasting. Furthermore, different species will evolve different solutions to similar problems: natural selection works on the material available. However, so long as we are dealing with similar species (usually phylogenetically close relatives occupying similar ecological guilds) and if we are able to scale temporal and spatial features of the habitat to those of the species, we may discover generalizations.

Conclusions

There is now a good theoretical understanding of life history evolution, and detailed explicit optimality models have been constructed. These present a challenge for empirical work examining some of the assumptions, such as the extent and mechanisms of the costs of growth and reproduction. In addition, there is an obvious need for comparative tests of the models. These tests, properly applied, may be particularly informative because they can deal with multiple independent variables, including ecological variables, and can reveal broad trends against a background of constraints on optima and the rate of evolutionary approach to them.

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$$1 = \int_0^w 1_x m_x e^{-rx} dx$$

where x is age, 1_x is survival probability to age x, m_x is fertility at age x, and w is the last age of breeding.
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Genetics and Demography in Biological Conservation

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Predicting the extinction of single populations or species requires ecological and evolutionary information. Primary demographic factors affecting population dynamics include social structure, life history variation caused by environmental fluctuation, dispersal in spatially heterogeneous environments, and local extinction and colonization. In small populations, inbreeding can greatly reduce the average individual fitness, and loss of genetic variability from random genetic drift can diminish future adaptability to a changing environment. Theory and empirical examples suggest that demography is usually of more immediate importance than population genetics in determining the minimum viable sizes of wild populations. The practical need in biological conservation for understanding the interaction of demographic and genetic factors in extinction may provide a focus for fundamental advances at the interface of ecology and evolution.

DESTRUCTION AND FRAGMENTATION OF NATURAL AREAS, especially tropical rain forests with their high species diversity, is now causing extinction of species at a rate that is orders of magnitude as high as normal background rates of extinction (*1*). If there are any paleontologists in the distant future, our "modern age"—the 20th and 21st centuries—will likely be recorded as a period of one of the greatest mass extinctions of all time, comparable to the event 65 million years ago in which it can be estimated that the majority of species then living on Earth perished (*1, 2*). In addition to the ethical problem of extirpating life forms that evolved over millions of years, there are practical reasons for conserving wild areas containing species of potential medical, agricultural, recreational, and industrial value (*3*). Ultimately, sufficient alteration of natural ecosystems may destabilize regional and global climate and biogeochemical cycles, with potentially disastrous effects (*4*).

Awareness of the benefits of conserving biological diversity is growing rapidly in many countries, but it remains to be seen whether conservation efforts will increase fast enough in relation to the rate of destruction to preserve much of the natural diversity that existed in the last century. As the remaining natural areas become smaller and more fragmented, it is increasingly important to understand the ecological and evolutionary dynamics of small populations in order to effectively manage and preserve them for a time when future restoration of natural areas may allow expansion of their ranges. Propagation of endangered species in captivity, for example, in zoos and arboreta, can contribute significantly to global conservation efforts; this alone, however, is not a viable alternative because limited facilities are available and because inevitable genetic changes from random genetic drift and selection in artificial environments

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