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ENVIRONMENTAL CERTAINTY, TROPHIC LEVEL, AND  
RESOURCE AVAILABILITY IN LIFE HISTORY  
EVOLUTION

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In recent years a growing appreciation for the organism as an adapted complex has increased awareness of adaptation not only at the biochemical, physiological, and anatomical level, but also at the life history level (Svardson 1949; Lack 1948, 1954; Cole 1954; Williams 1966*a*). The rapid development of this holistic approach to the biology of organisms has resulted in several largely theoretical papers (MacArthur and Wilson 1967; Lewontin 1965; Gadgil and Bossert 1970; Emlen 1970; Murphy 1968; Schaffer 1974) as well as papers which synthesize data available for a particular group of organisms (Tinkle 1969; Tinkle et al. 1970; Salthe 1969; Lack 1966, 1968). These studies have common objectives: (1) to explain the diversity of observable life history patterns in terms of a minimum number of selective pressures; (2) to identify those areas in need of more detailed examination and experimentation.

The life history of organisms, like all other phenotypic attributes, represents a series of selective compromises to a suite of environmental variables. Components of any life history, such as clutch size, age at maturity, and body size, constitute a life history "strategy," implying a suite of adaptive responses accumulated over evolutionary time, without any teleological implications.

Discussions of the evolution of life histories attempt to specify a minimum number of selective pressures required to explain common components of life history strategies such as egg size, clutch size, or age at first reproduction. For example, some authors (MacArthur and Wilson 1967; Pianka 1970, 1972; Gadgil and Solbrig 1972) have identified the density of a species with respect to resources as one such selective pressure capable of explaining many life history differences within and between species. Species which exist near  $K$ , the carrying capacity of the environment with respect to resources, are under a suite of selection pressures ( $K$ -selection) different

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from those of species which frequently experience periods of population expansion (*r*-selection). Williams (1966*a*, 1966*b*) argued that the demographic structure of populations is a strong selective component molding life histories; selection should have different results in long-lived and short-lived species.

A life history strategy will usually consist of at least the following components: (1) juvenile and adult mortality schedules; (2) age at first reproduction; (3) reproductive life-span; (4) fecundity, including number of eggs which, in turn, depends upon egg size and nutritional quality and on frequency of clutches, and fertility, that proportion of females actually reproducing at a particular time; (5) the fecundity-age regression; (6) the degree of parental care which includes any parental activity increasing survival of eggs or young; and (7) reproductive effort, which is the allocation of resources to any reproductive activity as opposed to growth, tissue maintenance, escape from predators, manufacture of poisons, and metabolic heat production.

Natural selection will modify each of these components to produce a life history strategy that results in the highest individual fitness and reflects a compromise between many selection pressures. However, the fact that the components of life history strategies can be correlated with certain environmental parameters that can be shown theoretically to play a strong role in selection on life history characters does not demonstrate that these parameters have *actually* been responsible for the evolution of those characters. For example, Cody (1966, 1971) argued that the smaller clutch sizes of tropical birds compared with temperate relatives was due to a large extent to density of birds in relation to resources. Tropical birds, presumably near their carrying capacity much of the time and exposed to many close competitors, lay smaller clutches than temperate-zone birds whose resources are usually relatively high compared with population numbers in the breeding season. Although this argument is consistent with evolutionary theory, the data themselves are explicable in other ways. Lack (1968) argued that longer day lengths in the temperate zone allow longer periods for adult food gathering and, therefore, for raising larger clutches. Others (Skutch 1961, 1967) argued that smaller clutches are an adaptation to high predation in tropical areas.

We are convinced that attempts to explain life histories as outcomes of single selective pressures, however simple and appealing, have obscured rather than elucidated the evolution of life histories. Our purpose here is partly to amplify reasons for this conviction, but mostly to offer suggestions of those selective regimes which seem to us necessary to explain and understand the evolution of life history strategies.

#### DENSITY OF POPULATION IN RELATION TO RESOURCES

That crowding in populations has an important selective effect on life histories was formalized by the concepts of *r*- and *K*-selection (MacArthur and

Wilson 1967). MacArthur and Wilson stated that at least one kind of environmental change to which populations are exposed is predictable, the change caused by expansion of the population. They used  $K$ , the carrying capacity of the environment, as an ecological measure of genotypic fitness. Under crowded conditions genotypes of individuals that are relatively unaffected by high density will increase at the expense of other genotypes. This selection is clearly density dependent, unless one genotype has the advantage at all densities. This concept of selection in a usually crowded environment that is presumably resource limiting has become known as  $K$ -selection. At the opposite extreme is selection in an environment that is less resource limiting to the organism, such as in the initial stages of population growth subsequent to a catastrophe or following the founding of a new population. In this case the rate of change in population size will be relatively density independent and genotypes will be favored which have the effect of maximizing  $r$ , the intrinsic rate of increase. This process has been called  $r$ -selection. As Pianka (1970) has clearly stated, species may exist in populations that are at all possible densities in relation to resources and, therefore, a continuum exists between  $r$ -selection and  $K$ -selection.

If the position of a population with respect to resources were the primary determinant of the evolution of life history characters, then it is logical to predict, as have many authors, how certain life history characters will be shaped by the population numbers relative to the carrying capacity of its environment. For example, we would agree that in a relatively nonlimiting environment such life history components as early maturity, large clutches, and minimal parental care should maximize individual fitness and therefore be incorporated into the life history phenotype. In contrast, delayed maturity, which allows time for learning to exploit resources, and smaller clutches with larger young or hatchlings with better competitive advantage might be expected in more limiting environments.

Because neither the carrying capacity nor the mechanism of population regulation is known for most natural populations, data on life history parameters are often consistent with more than a single hypothesis. As we have already pointed out, clutch-size evolution in tropical birds has been explained in three different ways by three different investigators. This problem of correlation versus causation comes into focus when considering the details of some life history studies from the literature.

*Sceloporus olivaceus*, a large, highly arboreal, iguanid lizard, has been studied over a 5-year period in Texas by Blair (1960). Despite its large size, it matures in 1 year or less and lays both large (about 20 eggs) and frequent (up to four times per season) clutches which hatch into young that are small in relation to the size of the mother. The young grow rapidly, have high mortality rates and have a short generation time of about 2 years. These are precisely those life history characteristics expected in expanding populations, but in the absence of any data on carrying capacity of the environment for this species, or any evidence that population expansion is frequent, we can only state that the life history components are consistent

with those we would expect selection to favor in frequently expanding populations. However, this correlation of data with hypothetical deductions from theory in no way demonstrates that frequent population expansion has been the primary selective pressure for these life history characteristics. Blair (1960) has argued that because adult males are aggressive and rarely occur more than one per tree, the adult population is regulated by the number of territories. Consequently, the populations are not frequently expanding, a fact that argues against frequent population expansion as the primary selective factor in the evolution of the life history of this species.

This species must return to the ground to lay its eggs, and Blair has shown that egg predation by snakes is extremely high, accounting for at least 80% of the prereproductive mortality. Because there is little that the female can do to reduce this mortality, the strategy of laying frequent large clutches of eggs scattered in space and time might have evolved as a mechanism for reducing this mortality.

The green sea turtle *Chelonia mydas* is widely distributed in all the world's oceans and apparently migrates long distances to reach a limited number of beaches favorable for reproduction. At the beaches, females deposit several clutches during a single breeding season, each containing about 100 eggs (Carr and Ogren 1960). At hatching, the young are very small relative to the adults and are subject to high mortality. The large herbivorous adults have among the longest life expectancies of any vertebrates. Factors responsible for regulating adult numbers prior to human exploitation are unknown, but it seems unlikely, given the long adult life expectancy, that they existed in frequently expanding populations. Therefore, the extremely high fecundity and small young, although consistent with life history attributes expected to evolve in expanding populations (*r*-selection), must be explained on the basis of some other selective pressure. In this instance, the long adult life (expected in *K*-selected species) and high fecundity might well have evolved in response to juvenile mortality which had a high mean and high annual variation. These examples demonstrate the internal inconsistency of the simplistic *r-K* selection explanation.

The manx shearwater *Puffinus puffinus* is a pelagic seabird of the North Atlantic (Perrins 1965*b*; Perrins et al. 1973; Harris 1966*a*, 1966*b*). Like nearly all Procellariiformes it lays a single egg which is about 14% of the adult weight. There are prolonged incubation and fledging periods. Age of first breeding is about 5 years, and the adults have an annual survivorship near 90%. They are specialized predators on an uncertain food supply usually found long distances from the breeding colony. Fledging success is high so that postfledging deaths before first reproduction must account for most mortality in the life cycle.

Clearly, these seabirds possess every life history characteristic expected from evolution in a resource limited environment (i.e., *K*-selected). However, in interpreting such a life history, the virtual absence of predators and the long distances traveled to obtain an uncertain food supply must be considered. These birds may require a long period of learning to exploit

such a food supply. Therefore, early reproduction would probably be unsuccessful and yet entail a cost in adult survivorship without a compensating reproductive profit. The absence of nest predation allows the expenditure of resources on a single offspring each year. The prolonged developmental time of eggs and nestlings allows exploitation of an uncertain food supply. To call this bird a *K*-selected species on the basis of its life history characteristics probably obscures the selective factors responsible for these characteristics.

#### TROPHIC POSITION AND SELECTION ON LIFE HISTORY CHARACTERS

Whether a species is limited by its resources is related to its trophic position in the community. Predators high in the food web would often be limited primarily by food supply, whereas lower-order predators and herbivores might be limited by predation to densities below those set by food resources. Both types of species may exist in stable nonexpanding populations, and yet the consequences of trophic position on selection of life history characteristics can be quite different.

In species limited by food resources, such as generalized predators, population growth proceeds to a point of relative stability around a density determined by resource levels. A prey species may also reach a stable equilibrium, but one that results from the action of predators that begin to exploit it at a certain density. Although the prey population is not expanding, it occupies a similar position with regard to resources as a species that is frequently expanding. However, its life history characteristics, unlike those of a predator, are not precisely predictable from this fact alone, as discussed below.

Prey strategies should evolve to reduce mortality from predation. If the mortality affects primarily adults, then there are alternate adaptations to predation. First, if prey can evolve defense mechanisms such as armor, poisons, or large body size, then they may have such life history characteristics as long adult life, delayed maturity, and even large eggs and young. Clearly, these are the same sorts of life history parameters that we have associated with learning predators. Second, if these defense mechanisms are ineffective, then short adult life expectancy will result from predation. This will favor early maturity and very high reproductive efforts soon after reaching adulthood.

If mortality falls primarily on juveniles, a diversity of solutions is also possible. Selection may favor growth through the stage most susceptible to predation, resulting in a delay in maturity. Another set of solutions involves modification of parental behavior. Eggs may be laid singly and scattered in time or space, encapsulated, actively protected, or developed internally. The strategy of replacing lost clutches or young may also evolve.

The strategy of satiation (Lloyd and Dybas 1966; Janzen 1969) has been suggested as another adaptation to predation. The population reproduces synchronously and floods the environment with large numbers of young. If

these brief periods of synchronous reproductions are unpredictable in time and space, it may be difficult for a predator to consume more than a small fraction of the available prey.

*Uta stansburiana* is a small (45–50 mm), ground-dwelling predatory lizard, widespread and abundant in the southwestern United States and Mexico (Tinkle 1967; Turner et al. 1970). Wherever studied, adults show nearly annual population turnover. They lay as many as five clutches (three to five eggs each) per season, mature in less than 1 year, and have high mortality rates throughout their life. It exists in relatively stable population numbers; mortality, presumably from predation, is relatively high and constant, resulting in predictable juvenile survivorship. Because juvenile survivorship is predictable, selection favors individuals that invest their reproductive effort maximally and early in life. This is true because offspring produced late in life have no higher probability of survivorship than those produced at the first breeding opportunity. Thus, genotypes for early maturity and high fecundity prevail because of the advantage of a short generation time in increasing the frequency of these genotypes over some finite time.

*Sceloporus graciosus* is a relatively small, predatory lizard that usually occurs at higher elevations (Tinkle 1973) than *Uta*. Because there are fewer predators in these areas, this species is more nearly a top-order predator in its ecosystem than is *Uta* and presumably much more limited by food resources. Compared with *Uta*, this species has delayed maturity, low fecundity, small clutch size, with no more than two clutches per year. Where studied, it is long lived and occurs at stationary high densities; juvenile mortality is high but predictable. The average generation time is 3 years. All of these facts about its life history predict that it should be resource limited.

The Red Grouse, *Lagopus scoticus*, is a large nidifugous upland game bird of the British Isles (Jenkins et al. 1963). This herbivorous species has a single brood of seven to eight large eggs, which may be postponed or reduced in size in years with low food levels. Prehatching mortality and predation on adults during winter are both high. Females breed their first year and have a high annual mortality of about 70%, but this estimate may be biased by hunting on the study area. Renesting typically occurs after nests are destroyed by predators. These relationships between fecundity, timing of reproduction, and food supply suggest that populations of this bird are resource limited. However, such characteristics as high juvenile mortality, early maturity, short generation time, high fecundity, and rapid growth seem to be characteristics atypical of a resource-limited species. Such characteristics, as well as the high degree of parental care and the renesting, may be adaptations to a high and constant level of predation, in short, to the grouses' trophic position.

Janzen (1967, 1971a, 1971b) has discussed the coevolution of tropical trees and their seed predators. *Cassia grandis* is a common legume in the

highly seasonal deciduous forests at low elevation in Central America. It is 10–12 m high and is found in all stages of woody succession. Two bruchid beetles and several species of moths destroy almost all of the seed crop unless vertebrate dispersal agents scatter the seeds. Individual trees bloom about every 2 years during the early part of the dry season. Seeds remain on the tree for 11–12 months. During this time, they are attacked by insect predators which bore into the seed pods. Mature seeds are encased in a sweet, odoriferous material that attracts deer, squirrels, agoutis, and pacas. Seeds require scarification, as occurs during their passage through the gut of these mammals, to germinate. Unless these dispersal agents remove the seeds from the vicinity of the parent tree, all seeds are killed by insects. While some characteristics, such as high fecundity, could be explained as adaptations in expanding populations, others, such as large seeds, widely spaced reproduction, and parental care, suggest adaptation to resource limitation. However, all of them can be satisfactorily explained by the trophic relations argued by Janzen between this plant and its insect and mammalian predators.

#### ENVIRONMENTAL PREDICTABILITY

Many components in the organism's environment, such as its food supply, the degree of predation, and weather conditions, vary through time and space in amplitude, frequency, and in degree of predictability of both. In this section, egg or seed size, semelparity versus iteroparity, and early versus delayed maturity will be related to the uncertainty of juvenile and adult survivorship.

If, in a changing environment, juvenile survivorship can be predicted by the parent, the life history tactic should be to postpone or minimize reproduction until a favorable period is anticipated and then to expend a high amount of effort in reproduction, even if maximizing reproductive effort results in a short adult life span. The loss of reproductive potential incurred by reduced adult survivorship is outweighed by the selective advantage of early and maximal reproduction because juvenile survivorship is, in this case, predictably high. In this sort of species, considerable variability in life expectancy might be expected from year to year, but reproduction should be synchronized in local populations.

If, as Murphy (1968) has argued, juvenile survivorship is low and unpredictable, there should be strong selection for long adult life, delayed maturity, and iteroparity. A female at the onset of a particular reproductive season may have no environmental cues which correlate with prospects of high reproductive success. In such cases selection should favor a relatively fixed clutch size which would be a compromise between the advantage of producing large numbers of offspring and the advantage of high annual female survivorship and, hence, several opportunities to reproduce. Thus, one might expect annual and other semelparous species to have higher repro-

ductive efforts than iteroparous ones. Once long adult life expectancy is characteristic of a species, then other adaptive modifications of life history are more easily evolved.

Reproductive strategies of plants of different successional stages (Salisbury 1942) illustrate these points. Species occupying early successional stages are exploiting newly opened habitats that may be widely spaced. Once the offspring of such organisms find a new habitat, there is often low competition during their juvenile period. Consequently, these offspring can be small because they do not have to compete with a lot of other individuals. The premium instead is on dispersal to newly opening habitats, the position of which in time and space is unpredictable to the parent. The parents will be outcompeted by other species during the next growing season (Keever 1950). Such parents should have very high reproductive efforts; many of them will be annual, and the high effort will be manifested as high fecundity, with low expenditure per progeny.

At the other extreme are species that occupy climax associations. To these species it is important to be able to become established within the community, even if establishment entails the cost of delayed reproduction. Young individuals of climax species can only enter the community following the death of older individuals. Opportunities for recruitment created by such deaths are unpredictable. Annual reproductive effort in such species is relatively low and characterized by large eggs, young or seeds, or parental care so that juveniles are good competitors when they occupy new spaces. Large seeds of some climax plants (e.g., *Quercus*, *Carya* in temperate forests and various legumes in tropical forests [Janzen 1969]) have relatively low passive dispersal rates, and parents must invest considerable effort in making the seeds attractive or adherent to animals which serve as dispersal agents, or by providing specialized structures that facilitate wind dispersal.

Life histories of many amphibians can be interpreted in relation to the permanence of the breeding habitat (Wilbur and Collins 1973). Bullfrogs, *Rana catesbeiana*, breed in stable pond habitats, have delayed maturity (at least 3 years in Michigan), have a long adult life expectancy, and yet produce large numbers of small eggs each summer, probably because predators are equally effective against large and small tadpoles. The delayed maturity probably is related to the highly territorial behavior of adult males (Emlen 1968) in which large animals should have a mating advantage and to the dramatic increase of clutch size with increased body size in females (Collins, unpublished).

Ambystomatid salamanders of the eastern United States breed in temporary ponds. These species as a group have delayed maturity, large clutch sizes, small eggs, no parental care, long adult life span, long generation time, and high reproductive effort compared with other salamanders. Adult populations remain stable from year to year (Husting 1965; Wilbur 1972, unpublished). Evolution of this life history strategy can be explained by the unpredictability of juvenile survivorship (Wilbur and Collins 1973). The evolution of iteroparity is, in part, an adaptation to the uncertainty that any

year class will successfully leave the pond in which the adults deposit their eggs. The long adult life makes possible the delay of maturity until optimum body size and fecundity are achieved.

The great tit, *Parus major*, is a generalized predator, which occurs at high densities in oak forests of Europe (Lack 1950, 1954; Perrins 1965a; Kluyver 1951, 1963). Compared with most birds, it has a large clutch of nine to 10 eggs, which are replaced if lost early in the season. True second broods are rare, but when they are laid the female begins incubating before the clutch is completed. This mechanism produces a range in body size of the nestlings so that if food becomes scarce only the larger nestlings are fed, resulting in adjustment of brood size to food availability. Tits mature their first year and have a mean annual adult survivorship approaching 50%. Lack (1966) implies that plasticity in the timing of reproduction and in the clutch size is in response to availability of oak moth caterpillars, an important food of the adults and young (see Feeny 1970). This species is able to adjust its effort to the food supply and thus incurs less negative feedback on adult life expectancy than if it were putting forth maximal effort each season. This presumably results in longer adult life and iteroparity. We have found it instructive to consider environmental uncertainty rather than merely the position of this species with respect to carrying capacity of its environment in attempting to explain some of its life history characteristics.

There are several species of migratory locusts in Africa. *Schistocerca gregaria*, the best known species (Kennedy 1956; 1961), has two life history phases, *solitaria* and *gregaria*. The *solitaria* phase is relatively sedentary, although it migrates in response to seasonal changes in the habitat, such as increasing aridity. Migration of the *solitaria* phase is an individual phenomenon, but migration by *gregaria* is massive, daily, erratic, and covers wide areas. The *gregaria* phase is produced primarily as a response to high densities associated with long periods of favorable environment in the *solitaria* habitat. Phases of the locust are clearly facultative life history changes occurring within a single species. Differences in life history are profound, involving female size, larval size, larval survivorship and growth, age at maturity, life expectancy, fertility, behavior, and ecology. The *solitaria* foci are in the most favorable habitat, and populations soon reach the carrying capacity of the environment, at which point phase shift to *gregaria* occurs. Thus the *solitaria* phase might be considered an adaptation to expanding populations, the *gregaria* phase to resource limitation. The larger eggs and larvae, greater survivorship of larvae when food is limited, and lower fecundity all might be interpreted as characteristics of *gregaria* evolved in response to resource limitation. However, earlier maturity at a smaller size and shorter life expectancy than *solitaria* are not easily explained on this basis. Such characteristics may be explained by considering *gregaria* specialized to exploit an unpredictable habitat in space that persists for only a short period.

*Senecio vulgaris* is an annual typical of many composites (Harper and Ogden 1970). It has early maturity, short reproductive life span, rapid

growth, and a high reproductive effort that is quite insensitive to density. It occurs at high densities, has a high fecundity, and a short generation time. Because of its successional position, this species maximizes the probability that some seeds will fall in a site suitable for growth by producing large numbers of small seeds. Experiments show that these plants have consistently high reproductive effort irrespective of density (Harper and Ogden 1970). If reproduction at high density, and probably with strong intraspecific competition, had not been a consistent feature in the evolution of this plant, such an adaptive response to high density would be unexpected. In summary, the reproductive strategy of this weed seems best explained by the unpredictability of both the adult and juvenile environment.

#### DISCUSSION

Although the concepts of  $r$ - and  $K$ -selection were formulated in terms of selection in expanding versus crowded populations, they may be (and have been) somewhat broadened. For example, a population may be stable, but still below  $K$ , if it is regulated by predators. However, if we call such a species an  $r$ -strategist, such an appellation has little predictive value for its life history evolution because there are several possible strategies for such an organism. On the other hand, there is also no greater explanatory value in calling it a  $K$ -strategist (the population size in this case being set by predators rather than resources). In either case we gain facile simplification at the expense of genuine understanding of the selective pressures responsible for the evolution of a particular suite of life history characteristics.

Life history characteristics, such as early maturity, high fecundity, and short generation time, would certainly result in high values of  $r$  for species with these characteristics if they lived in unlimited environments. Such reasoning underlies the rationale for calling them  $r$ -characteristics. However, it is at best meretricious to reverse the logic and argue that relatively nonlimiting environments are the primary selective pressures responsible for such life history characters. And yet, Pianka (1972) and Gadgil and Solbrig (1972) have argued that the position of a species on a so-called  $r$ - $K$  continuum can be predicted from selected life history parameters. This is certainly a useful way to correlate life history characters with the presumed underlying selective mechanism responsible for them, but we emphasize that the exact causal relationship may be obscured by such a practice. For example, viewing delayed maturity as a  $K$ -characteristic, without in fact demonstrating that resource limitation was significant in the evolution of delayed maturity, can be very misleading. As our examples illustrate, delayed maturity can evolve in contexts other than resource limitation.

In a similar vein, we offer one caveat to casual interpretation of life history characteristics as being due to resource limitation. Diversion of available resources to reproduction, for example clutch size, might have been selected in a context which maximized fitness across the lifetime of the indi-

vidual parent. Consequently, small clutches might reflect a compromise between resource availability and parental risk involved in making that resource available to offspring. In some environments, regardless of resource level, parental risk involved in producing larger clutches may be unacceptably costly in terms of lifetime reproductive success.

This simple *r-K* dichotomy is not easily replaced with an equally simple concept with greater explanatory value. Instead of coining new terms, we suggest additional ecological dimensions, such as environmental predictability and relative trophic position of species, that also seem important in the evolution of life histories. It remains a challenge to evolutionary theory to specify the number of dimensions that are necessary and sufficient to explain the evolutionary processes that have generated the observed diversity of life histories in plants and animals.

#### SUMMARY

Evolutionary theory has not yet determined the necessary and sufficient environmental factors that can be used to explain the observed diversity of life history patterns in plants and animals. Although recent theoretical treatments of the evolution of life history rely heavily on the concepts of *r*- and *K*-selection, we find this framework inadequate to explain life histories of many well-known organisms. Instead, using well-studied examples from the literature, we attempt to identify causal mechanisms in the evolution of their life histories. The density of the population in relation to resources, the trophic and successional position of the population, and predictability of mortality patterns all appear to be important determinants of adaptive strategies. Therefore, consideration of many environmental dimensions seems essential to provide complete understanding of the evolution of life histories.

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