PREDATION, SUBMERGENT BEHAVIOR, AND TROPICAL DIVERSITY

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ABSTRACT: Life-history traits of organisms influence many aspects of community structure and a species' position in its community influences its life-history traits. A joint consideration of two traditionally separate disciplines provides a new focus for the comparison of tropical and temperate communities.

I propose that evolutionary explanations of life-history patterns require broad, integrative studies of a species' biology and comparative studies of diverse taxonomic groups. Life-history traits are as much a product of other aspects of a species' biology as they are of the external environment. Though the interactions among different aspects may produce a unique life-history response to a given set of environmental conditions, ecologically important aspects such as body size or trophic level produce patterns in the life-history adaptations of species. Describing and explaining the selective influence of the external environment on life-history patterns necessitates the study of diverse taxonomic groups with similar ecological traits. A comparative review of latitudinal gradients in reproductive patterns of terrestrial vertebrates and benthic marine invertebrates exemplify these arguments.

Life-history adaptations are shown to influence several aspects of community structure including niche specialization, rate of energy turnover in communities, the evolution of increased body size within lineages (Cope's Rule), and the species diversity of a community. The strategy of submergent behavior (the avoidance of predation by reducing foraging activity and hence food intake) seems to be an important aspect of large-scale ecological patterns.

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I. INTRODUCTION

Both the study of life-history patterns and the study of community structure (resource-partitioning patterns) as a function of the physical environment have been popular in recent years but have largely been treated separately at both theoretical and empirical levels. Yet there is good reason to suspect strong interactions between life histories of species and their organization into communities. Community structure in part reflects the competition among species for the available energy, and life-history features determine the amount of energy a species demands or can get in that community. Life-history changes, induced by the physical and biotic environments, are constrained within an evolving phylogenetic lineage, but the evolving lineages in a community give structure to that community.

In this paper I argue that the study of life history or of community structure is incomplete without an implicit treatment of the other. I focus on patterns of latitudinal variation in life history and in species diversity to illustrate my arguments, but touch on a number of other topics as they illustrate the central argument.

II. COMMUNITY INFLUENCES ON LIFE-HISTORY PATTERNS

Consider the following actual case: Individuals of the plethodontid salamander Batrachoseps attenuatus are distributed within a habitat in such a way

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that individuals found from one to a few meters apart (a distance over which an individual can move on a moist night) show significant differences in size-specific fatness and thus probably in fecundity (Maiorana, 1974). Salamanders at the ends of a 100 m stretch of continuous habitat show a 2 mm difference in mean age-specific trunk length or a 19% difference in mean age-specific fecundity. A salamander can probably move through the length of this area in a few days at most, as shown by observations on movement (Maiorana, 1974; J. Hanken, pers. comm.). Other habitats show the same pattern of local age-specific variation in body size and fatness, both of which are positively correlated with fecundity (Maiorana, 1974).

The local variation in body size and fatness is associated with a difference in the physical environment. Larger and fatter salamanders are found in areas that remain moist over longer periods of time. After a rain, when all areas are wet, salamanders feed with equal success in all areas; at least the amount of food in the stomachs shows little variation from place to place. A long drought results in greater variance in the amount of food found in the salamanders. At one such time the salamanders having greater amounts of food were observed to be the ones having fatter tails (Maiorana, 1974). Actual densities of salamanders are difficult to estimate but collecting densities did not vary significantly between wet and dry areas. Both the activity of salamanders and that of their prey are positively correlated with moisture (Maiorana, 1974). Thus, a salamander in a wetter area can grow larger, store more fat, or both, because it can feed for longer periods during the year than can a salamander in a dry area.

A difference in the physical environment can explain the observed difference in fecundity, but it is an insufficient explanation. Salamanders are not plants; they are capable of moving about to locate suitable habitats. Fretwell and Lucas (1970) proposed that under such circumstances animals distribute themselves in such a way as to equalize the fitness of each individual. Why then don't the salamanders aggregate more densely in the wet areas and less densely in the dry? One explanation is that some spatial resource such as the abundance of logs or the number of underground burrows regulates the density in an area. Since shelter is as important as food some salamanders are forced by intraspecific competitive pressures to live in drier areas or not live at all. Another viable hypothesis, compatible with the first, is that predation makes both dry and wet areas equally suitable with respect to overall fitness. There is some evidence for both hypotheses; an explanation of the second hypothesis follows.

Both the salamanders and their prey are active for longer periods in wet patches than in dry ones. This implies that the prey suffer seasonally a greater numerical loss from salamander predation in wet patches than in dry even though the daily loss rate is the same. Any advantage the prey may have from an increased period available for feeding is countered to some degree by increased mortality from predation by salamanders, also feeding longer in the wet patches. Extending the argument to a higher trophic level, the predators of salamanders (larger salamanders, snakes, large predaceous invertebrates, and birds) may also be more active in wet patches or they may preferentially locate and feed in the wet patches during dry periods. Some available data suggest that the salamanders suffer greater predation in the wetter areas. Thus increased numerical loss from predation may cancel the increased fecundity of salamanders in the wet patches, rendering both wet and dry areas equally suitable with respect to overall fitness.

The second hypothesis presented above to account for local variation in fecundity of a salamander implies that predation, as a function of environmental moisture, may exert a similar selective force on species that belong to a

number of trophic levels and that are of different sizes. Local and latitudinal gradients in physical parameters of the environment may create gradients in the competitive and predatory pressures that will, in turn, exert potentially similar selective pressures on each species in a community. Though the exact response of each species may be unique in detail, it is generally hypothesized that there are patterns to how the species respond (MacArthur, 1972). For example, with respect to life-history patterns, it can be hypothesized that the type of response to a given change in the physical environment may be largely determined by the species' trophic position in the community and its body size, both of which reflect to some extent the number and kinds of predators or competitors the species will have. To test this one can examine the fecundity of centipedes, spiders, scorpions, Gryllotalpa, millipedes, snails, collembolans, and oribatid mites in the same wet and dry areas of the habitat in which Batrachoseps is found and analyze the results with respect to differences in trophic position and body size. But such a procedure has complications, since life-history traits of a species are not simply a function of the external physical and biotic environments. Complications derive from the selective influence exerted by the species' morphology, physiology and behavior, some traits of which may be constrained by developmental interactions and thus invariant under changing environmental conditions.

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Current studies on the evolution of life-history patterns have two types of limitations. The first is that single environmental factors, such as climatic stability or the degree of environmental saturation with competing organisms, are chosen as the important selective force and used to predict geographic or habitat variation in certain life-history traits or suites of traits. Empirical studies usually focus on one or a few of these traits with which to test a particular model. Difficulties arise in that different environmental factors can often explain the same pattern of variation in life-history traits. Choosing among models may require information additional to the pattern of variation in life-history traits. For example, there are at least two hypotheses that explain local variation in fecundity of the salamander discussed above. Examining other factors such as predation rates, dispersal patterns or the regulating resource can help test each of the hypotheses in this case. However, such factors usually fall outside the scope of life-history studies and thus knowledge of them is generally unavailable for sorting out possible causal mechanisms. More complete studies of life-history traits than those typically done now may improve the testing and formation of general models but full understanding will probably necessitate broadening the scope of life-history analyses.

Secondly, since life-history traits of a species are influenced by other aspects of its biology, animals with different morphologies or behaviors may have totally different life-history patterns in response to the same external environment or they may have the same pattern. To what extent does a theory on latitudinal gradients in clutch size in birds have predictive accuracy for clutch-size gradients of lizards, mammals, insects or marine invertebrates? This problem has barely been touched upon in the work on life-history evolution. Though many studies have focused on geographic variation within a species or among related species, none has asked how much variation in life-history patterns exists among taxonomically diverse species in the same community, how much of this variation is attributable to ecological characteristics of the species, such as body size or trophic level, or how much to developmental or more broadly adaptive constraints, such as being sessile or homeothermic.

The above criticisms have centered on the scope of the empirical base from which models are generated and tested. Explaining the diversity of life-history

patterns will ultimately require knowing much more about the animals than their life-history traits. In the next two sections I amplify the basis for the above criticisms. I outline briefly in the next section the types of life-history changes that have been postulated to result from changes in single environmental factors and discuss the difficulties in studying variation of a few life-history traits in order to reveal the selective factors responsible for their evolution. I then review comparatively latitudinal gradients in life-history traits to illustrate the need for a broader comparative approach to the evolutionary study of life-history patterns.

Environmental Influences on Reproductive Patterns

The following brief survey of environmental influences on life-history patterns is based in part on the theoretical work of Cole (1954), Lewontin (1965), Williams (1966), Murdoch (1966), MacArthur and Wilson (1967), Murphy (1968), Emlen (1970), Gadgil and Bossert (1970), Schaffer (1974), and Wilbur, Tinkle, and Collins (1974), and in part on the literature of natural history and on personal observations.

Abiotic Factors: When physical conditions are most favorable for sustaining life, organisms can attain a maximum rate of growth. Energy expenditures related to survival through inclement periods are reduced. The benign physical environment imposes no age-specific pattern of mortality on a species which is important for predicting directions of change in a life-history pattern. So a benign physical environment, in itself, only favors a maximization of the intrinsic rate of increase. As a species moves into unfavorable environments, where the duration and stress of inclement periods are unpredictable, two opposite changes in life history may occur depending on whether the adult or the juvenile stage is more susceptible to mortality. If the adult stage has a greater probability of survival an iteroparous life history with delayed maturity and reduced reproductive output may characterize the species. Parental care of the offspring and viviparity may also be favored in this case. If survival of the adult stage is uncertain, early maturity and high reproductive output may be favored, especially if the egg (or some stage shortly thereafter) is a resistant, dormant stage.

Competition: When physical conditions are most favorable for sustaining life, rapid reproduction may soon lead to a saturated community in which food is limited. The benign physical environment does not act to keep the densities of animals low. Competition can produce a variety of changes in the life-history pattern of a species. Selection for competitive ability may involve increased longevity of the adult, delayed maturity, reduced reproductive output, and parental care. Such traits allow either the adult or the offspring to allocate more energy for competitive interactions. But such traits are likely selected when competition involves interference. Exploitative competition probably favors rapid reproduction which then selects for early maturity and high reproductive output. Competition may cause a species to shift its habitat, which, in turn, may have a direct effect on its life-history pattern. For example, competition in the aquatic larval zone may have selected for direct terrestrial development in some tropical frogs (see the next section).

Predation: As the periods of favorable conditions increase in length over the year, an increased production results in both predator and prey being able to increase their energy intake. A prey species can adapt to increase in predation in one of two ways: reproduce more or avoid predation, which may entail reproducing less.

Increased reproductive output as a response to predation can change the life history of a species in a number of ways. A strategy of increased reproductive

output requires that the increase in predation be accompanied by an increase in the productivity of the environment. Since so little is known about what actually regulates the density of predators, it is not possible to specify yet exactly how a change in the physical environment alters predation pressures. Under some conditions it is possible that the prey cannot hope to increase their reproductive output enough. For example, when the density of predators is regulated by the density of prey, increasing reproductive output becomes self-defeating unless the prey can reach a density where other factors regulate the predator. However, if increasing reproductive output is great enough this may be a viable alternative. It is often possible to outreproduce a predator's consumption if a very large number of offspring are produced at unpredictable intervals and temporally spaced so that the predator cannot wait them out. This strategy is mainly available to plant individuals, since the mobility of animals generally precludes the production of very large broods at any one time. However, animals which synchronoze their breeding attempts, such as colonial birds or the periodic cicadas have been successful with this strategy. In cases where the density of predators is regulated by a factor other than the density of prey, increasing reproductive output may be a viable strategy.

A change in life history that increases reproductive output in response to predation is likely to be a function of the age class on which predation is most intense, which in turn is largely a function of body size. The young of a large animal are generally more susceptible to predation than is the adult. Life-history changes for large animals in a community may include an increase in the number of young produced per season (larger clutch size, more broods), an increase in the longevity of the adults (e.g., by the evolution of antipredatory behaviors and morphologies), or both. An initially high growth rate might lead to attainment of large size relatively early and the escape of some predation. Strong selection for reaching a large size rapidly might lead to reproduction being delayed until large size is reached. Small species in the community are often susceptible to predation at all sizes, so that no one stage represents a refuge from predation. A high probability of mortality from predation as an adult often favors a reduction in age at maturity, rapid growth and high reproductive output. Antipredatory features (toxins,unpleasant projections or other morphological structures or behavior to increase size), which protects an individual against a predator of nearly the same size, are not usually effective against a much larger predator. Such features may not be common in small species whose important predators are much larger (but toxicity may be effective in small species if it is very potent or if the predator typically eats a large number of individuals at one time). An example is that of the coiling behavior of the isopod *Armadillidium vulgare*. A coiled isopod is nearly twice the thickness of an uncoiled isopod and effectively twice its size to a salamander which swallows its food whole. An isopod of all but the smallest sizes can increase its effective size by this simple behavioral act and render itself immune to predation by a small salamander species (*Batrachoseps attenuatus*) but not to the much larger sympatric species *Aneides lugubris*, which frequently eats the largest isopods (personal observation).

Another means of coping with an increased predation pressure is to hide from predators and escape mortality. This alternative decreases feeding time for the individual and thus reduces its growth rate, fecundity, or both. But it increases the expected longevity of the adult and may favor delayed maturity because of a slower growth rate. As a consequence of its increased longevity an individual can spread its reproductive output over a long time and thus reduce the risk that all its offspring will be preyed upon. It is a behavioral equivalent to toxicity or antipredatory morphologies and may generally be more effective against a wider spectrum of predators than either toxicity or morphology

against which some predators can evolve an immunity. This mechanism of escaping predation has been proposed for birds in the tropics (see the next section) as well as for Batrachoseps (Maiorana, 1974). To facilitate later discussion I will call this alternative submergent behavior, which can be defined as a reduction in the foraging activity of an individual in order to make it less susceptible to predation.

Another way for a species to avoid predation is to change its habitat. A change in habitat may lead to a change in reproductive pattern. For example, high egg predation in the aquatic zone may have selected for some tropical frogs to lay their eggs on emergent vegetation (see the next section).

Discussion: Each environmental factor discussed above converges with one or both of the other factors with respect to predicted life-history traits. For example, in a benign physical environment interference competition and predation (selecting for submergent behavior) may select for decreased reproductive output, increased longevity, and delayed maturity. A benign physical environment, predation on the adult, and exploitative competition may favor early maturity, fast growth rates, and high reproductive output. Both predation and competition may lead to a shift in habitat utilization. A broader analysis of an animal's biology is needed to discriminate which environmental factor(s) is (are) most important.

Take for instance large body size. Competition for food implies that energy (or possibly a chemical) regulates the density of a species. A bird may produce a smaller clutch to gain greater competitive advantage by attaining a larger size, which allows it to hold a territory and to reproduce at all. If predation is high so that food is not regulatory, individuals may attain a large body size as a protection against predators but do not have to reduce their reproductive output as a consequence. Thus, seasonal egg production may discriminate between competition and predation, but not always. Attaining a larger body size may enable individuals to fare better in competition so that they can obtain more food and produce more eggs. Alternatively, a bird, reducing its feeding activity and consequently its clutch size, may avoid detection of itself or its eggs by a predator and, thus, have a reproductive advantage over more active individuals. However, experiments controlling the intensity of predation or the degree of food limitation may distinguish which force is important.

Compromise solutions to the action of these selective forces may be more difficult to analyze. To the extent that effective predation reduces competition among conspecifics and among species for food (though not for refuges), compromise solutions between these two forces may not be a frequent occurrence. If, however, predation intensifies competition for refuges, then selection for submergent behavior and for increasing competitive ability may enhance one another. Competition for refuges may result in one species adopting a new habitat but the shift in habitat is also a response to predation pressure. In these cases predation produces the limiting resource over which species compete.

These general comments on how convergent responses to different environmental selective factors complicate the analysis of life-history patterns are illustrated in the next section with a comparative review of latitudinal gradients in life-history traits. Since comparative studies of diverse taxa have not been done the information available is not parallel among taxa. Unfortunately, analyses of latitudinal trends have been largely confined to terrestrial vertebrates. Considerable insight can be gained by study of a wider variety of organisms, but this information is not readily available.

Latitudinal Trends in Life-History Patterns

Birds: A major latitudinal trend in the life history of birds is that of increased clutch size in temperate birds relative to their tropical relatives.

Many hypotheses have been proposed to explain this increase. These are: (1) An increase in the daylight hours at high latitudes during the breeding season results in increased opportunity for feeding the young (Lack, 1948, 1968). (2) In the tropics an increase in nest predation results in selection for reduced activity to avoid detection by predators (Skutch, 1947, 1967). The reduced foraging activity results in a reduction in clutch size or the number of offspring which must be fed. It is a possible example of submergent behavior. (3) An increase in nest predation in the tropics selects for a lower reproductive effort in any one attempt so that more nesting attempts can be made through a longer breeding season (Foster, 1974). A greater number of nesting attempts through the breeding season increases the probability of one attempt being successful. By reducing reproductive output in any one nesting attempt a bird can prolong the breeding season by having it overlap with the molting season. For temperate birds the molting and breeding seasons are non-overlapping. (4) A reduction in food availability in the tropics is a result of a continual coevolution of predator and prey (Ricklefs, 1970). (5) A model combining the effect of predation and competition and stressing the importance of compromise can be used to explain most clutch size variation in tropical and temperate birds (Cody, 1966).

It is well documented that nesting success is low in the tropics compared to temperate regions as a result of high nest predation (e.g., Skutch, 1949; Ricklefs, 1969). There is no positive evidence that energy limits the number of young raised by tropical birds. Skutch (1949, 1967) provides some evidence that birds can raise more young than they do. Foster (1974) notes a temporal overlap in molting and nesting in tropical birds, which suggests that they have more energy available to them than they put into a given nesting attempt. These facts support hypotheses 2 and 3 listed above better than the other three. Predation may be the primary selective force resulting in small clutch size in tropical birds. Abiotic factors and competition for energy have little support from actual data.

Lizards: Tropical lizards, in contrast to temperate lizards, are characterized by early maturity, multiple but smaller clutches, and reduced life expectancy (Inger and Greenberg, 1966; Tinkle, 1969; Tinkle *et al.*, 1970), Fitch, 1973). Like temperate lizards, tropical lizards in seasonal habitats tend to confine their reproduction to the season of high food availability.

Tinkle (1969) postulates that a long favorable season selects for laying clutches frequently. Producing frequent clutches, however, reduces the life expectancy of the lizard, because of the high risk involved in reproduction. The reduced life expectancy of reproductive animals favors early maturity. The adaptive significance for multiple clutches can be explained by either the benign physical environment or by high predation on adult lizards, both of which favor a high rate of increase. Data support that predation rates are high in tropical lizards (e.g., Fitch, 1973), but whether the high predation is a result of high risk activities or these high risk features have been selected to enhance breeding in an environment where time is at a premium because of a high predation pressure cannot be determined with available evidence.

The above explanation for the tropical life-history pattern does not account for a smaller clutch size. Competition for food seems unlikely, at least in Borneo, where food seems to be abundant all year. Apparently, the lizards in Borneo are turning food into yolk immediately and are unable to build up accumulations of fat that are necessary for yolking large clutches (Inger and Greenberg, 1966). The significance of frequent, small clutches can be explained by predation. If predation is a constant threat, laying fewer eggs as rapidly as they can be produced results in a larger probable yield for two reasons. (1) Producing few eggs at a time reduces predation on the eggs

or young by not having them concentrated in time and space (Fitch, 1973). Concentrations of young may attract specialized attention from predators. (2) Alternatively, a lizard accumulating fat reserves to produce a larger clutch may be caught before it can produce its eggs.

A seasonal environment selects for breeding only at the most favorable time for juvenile survival. Tropical lizards in seasonal habitats show early maturity, multiple clutches, and short life expectancy as do nonseasonal tropical lizards (Fitch, 1973), but in contrast to temperate lizards. This suggests that the seasonal fluctuations in tropical environments are not as adverse to juvenile survival as they are in temperate regions. The uncertainty of juvenile survivorship in temperate areas favors a long adult life: clutches dispersed through many seasons will increase the probability that some clutches will coincide with favorable conditions for juvenile survival. Delayed maturity and the reduction to one or two clutches per season may enhance adult longevity (Tinkle, 1969).

In conclusion abiotic factors may be important in shaping the reproductive patterns of temperate lizards (length of favorable season and uncertainty in the quality of that season). Predation is probably an important selective force in the life-history patterns of tropical lizards but in seasonal tropical environments abiotic factors also seem to influence the timing of reproduction. There is no good evidence that competition is an important selective force in the life-history patterns discussed above.

Mammals: Among small, nonhibernating mammals, litter size increases with latitude, parallel to clutch size in birds. Lord (1960) suggests that a greater mortality among nonhibernating small mammals during winter at higher latitudes selects for an increase in litter size. The mortality may be largely from increased predation during the winter months. Supporting this interpretation is the absence of a significant latitudinal trend in litter size in predatory species (*Vulpes*, *Felis*, *Mustela*) and a lower increase in hibernating mammals than in nonhibernating ones.

Alternatively, Spencer and Steinhoff (1968) and Smith and McGinnis (1968) postulate that the shorter activity season at higher latitudes reduces the number of times a female can reproduce and this selects for larger litter size each time. Larger litters may reduce the life expectancy of these animals, reinforcing selection for early, large litters.

Fleming (1974) compared the demographic characteristics of two tropical heteromyid rodents, one of which inhabits a seasonal forest and the other a relatively nonseasonal forest. The species in the seasonal forest appears to have a higher mortality, earlier maturity and larger litter size than the species in the nonseasonal forest. The higher mortality in the seasonal forest may be a result of the environmental fluctuations. This result supports Lord's suggestion that increased mortality as a direct or indirect result of environmental fluctuations can result in early maturity and large litter size in mammals.

Amphibians: The most notable distinction in life-history features between tropical and temperate species of anurans is the increased diversity of reproductive modes in tropical communities (Salthe and Duellman, 1972). One factor initiating differences in reproductive modes is competition for food resources (Dixon and Heyer, 1968; Heyer, 1969, 1973; Van Dijk, 1971). In the ancestral larval environment, that of ponds, competition among the different species of tadpoles may have initiated a temporal division of the pond. This pattern has also been observed in temperate salamander species (Worthington, 1968, 1969). Heyer (1973) found that in seasonal tropical environments egg laying by anurans is more concentrated in time than in less seasonal tropical habitats and that it coincides with the pattern of rainfall. The shorter is the length of the

favorable season, the fewer are the species which can coexist by this means of niche partitioning.

Other reproductive patterns (e.g., deposition of eggs on emergent vegetation so that the newly hatched tadpoles drop into the pond and develop simultaneously with other species; construction of foam nests) are not easily explained by competiton for food resources. Predation on the eggs, however, may initiate the use of emergent vegetation or foam nests. Predation pressure, competition for food resources in the pond, or both may have initiated the terrestrial development of larvae and evolution of direct development (Heyer, 1969; Van Dijk, 1971; Wilbur and Collins, 1973).

Changes in the mode of reproduction as a result of predation may also be important in the evolution and diversification of salamanders. Hairston (1949), Organ (1961) and Sweet (1973), in studies on the evolution and radiation of the plethodontid salamander genus Desmognathus, argue that predation on the stream-dwelling larval stage led to a shortening of the larval period with a consequent reduction of maximum adult size. These smaller species became increasingly more terrestrial. Since the smaller adults are also more susceptible to predation by the large salamander species in the genus, predation may be an important component in the spatial separation of these species. Potential competition for food or space among salamanders of equal size probably maintains size differences in this genus, thus allowing coexistence of several congeners.

Thus, both predation and competition appear to have been important factors leading to an alteration of life-history parameters of amphibians that in turn has led to an increase in species diversity in the community.

The life histories of very few tropical salamanders are known (Vial, 1968; McDiarmid and Worthington, 1970; Houck, 1975) and are restricted mainly to montane species. These studies suggest that many tropical species have delayed maturity as great as or well beyond that of temperate species in the same family. They may grow relatively more slowly, but live for a long time. The frequency of reproduction may be less or the same as temperate species. This apparent slowing down of growth and reproduction in tropical species combined with a prolonged life span suggests relatively little mortality on the adults. A low mortality on adults is tentatively supported by data on tail breaks. Since the frequency of tail breaks is probably correlated with the frequency of encounters with predators, a species with a high proportion of individuals with tail breaks suffers a high mortality from predation relative to a species with few tail breaks. Vial (1968) noted that Bolitoglossa subpalmata showed fewer tail breaks than a similar temperate species, Ensatina eschscholtzii. Wake and Dresner (1967) present data supporting the above observation. They have other data which suggest that several tropical species have a low percentage of tail breaks, but others are in the same range as Ensatina.

Geographic variation in life history of temperate species of plethodontid salamanders suggest that the life history of tropical montane species may be influenced in part by the physical environment. Temperate species show a trend of delayed maturity with larger body size at maturity and prolonged life spans in cooler environments with a shorter season for activity (Highton, 1962; Tilley, 1973). Some tropical salamanders live in environments as cool as many temperate areas during periods of activity but these cool tropical environments are characterized by longer periods favorable for activity. Delayed maturity in some tropical areas may proximately be a result of cool temperatures slowing maturation. The longer season, however, is predicted to shorten the time to maturity, based on patterns in temperate species. Thus, the large delay in maturity and slow growth that appear to characterize some species seem to require an explanation beyond that of the physical environment. Insufficient data are available at present to sort out biotic pressures that may be molding life-history patterns of tropical salamanders.

Marine Invertebrates: Latitudinal variation in life-history features of benthic marine invertebrates parallels that of lizards, but not that which has been described for birds, mammals and salamanders (Thorson, 1950; Mileikovsky, 1971). Direct modes of development, which require the production of larger (hence, fewer) eggs than for planktotrophic development, are characteristic of high latitudes; at low latitudes, planktotrophic development predominates. Coastal fish at high latitudes produce fewer, larger eggs and the young hatch at a more advanced stage than do related species at lower latitudes (Marshall, 1953). The patterns of larval development and egg size with increasing water depth parallels that with increasing latitude.

Explanations for these patterns have stressed the importance of the physical environment and nutrition (Thorson, 1950; Mileikovsky, 1971; Marshall, 1953) or the interaction of larval predation and nutrition (Vance, 1973a, b). These studies have accounted for the selective advantage of direct developmental modes [but see Ghiselin (1974) and Underwood (1974) for some difficulties in their explanations]; they have not, however, adequately explained the significance of planktotrophic development. A consideration of community dynamics suggests factors that may be important, but these factors have not been studied extensively with respect to the evolution of reproductive modes (but see Menge, 1975).

In the intertidal space is a limiting factor for sessile organisms and competition for space is potentially important (Connell, 1961a, b; Paine, 1966; Dayton, 1972). A large number of dispersal units that can be disseminated over large areas may be important to sessile species in order to locate small areas of suitable living space that become available in unpredictable patterns as a result of predation or physical disruptions (cf. also Strathmann, 1974). This is analogous to the seeding strategy of many forest trees (Stebbins, 1971). Thus, predation and physical disruptions produce competition at a level different from fighting directly for space--they produce competition over finding space. Predation and physical disruptions can also completely eliminate local populations of a sessile species. Producing many widely dispersing larvae increases the probability that an individual will replace itself despite frequent, unpredictable population extinctions (see Van Valen, 1971, Spight, 1974, and Strathmann, 1974, for a discussion of this problem).

At low latitudes where physical factors are more favorable, predation is more continuous than at high latitudes (Paine, 1966). It is unclear whether predation is less effective on many dispersed larvae than on fewer but faster developing larvae. However, an increased loss is incurred if the female is killed by a predator while brooding rather than after releasing her eggs.

Recently, Menge (1975) has hypothesized that a difference in body size, produced by interspecific competition, has been a major selective factor on the mode of larval development. Menge argues that for sluggish benthic predators as starfish, dispersal may be too slow for finding rich patches of food that become available in unpredictable patterns in space and time. Broadcasting many small planktotrophic larvae is more effective for widespread dispersal than producing fewer, more advanced larvae. However, broadcasting many small larvae each with a high probability of mortality may not often be a viable strategy for small species because of their typically shorter life expectancies as adults.

In conclusion, a variety of interacting biotic factors, the intensity of which may be influenced by the physical environment, seem important for explaining the observed latitudinal gradient of developmental modes in benthic marine invertebrates.

Comparisons: Some interesting differences and similarities emerge from this brief review of life-history modifications of tropical animals. The first

is that birds and lizards, both typically active animals, may take alternative routes in coping with tropical environments or rather similar ones, depending on the reason for the small clutch size observed in tropical birds.

Predation pressures appear to be an important selective force to both, but birds (if Skutch's hypothesis is correct) may reduce their activity and consequently their clutch size to avoid predation, whereas lizards may be as active as their temperate relatives and reproduce as soon and as often as possible. The following aspects of their biologies may explain this difference in strategy. Birds brood their eggs and typically feed their young for some time. If a predator locates a nest, the entire clutch or all of the nestlings will likely be eaten. If the bird is killed at any time during the period of parental care, the brood will perish unless more than one bird is tending the nest. Thus, attracting the attention of a predator presents a greater potential loss to a bird over a longer period than it does to a lizard, most of which do not tend their eggs or young. After hatching the young lizards disperse and then will not represent as high a loss to the parent since dispersion makes it improbable that a predator will find all of the young of a particular lizard. Once a lizard has laid its eggs, it does not lose as much if killed by a predator as does a bird which is caring for its young.

If Foster's hypothesis is correct, tropical birds may use a strategy rather similar to that of lizards. This strategy involves distributing a few eggs through time to increase the chance of some nesting attempts escaping predation or to avoid attracting a predator by a large concentration of potential prey.

A second feature of comparison is that there is little temporal separation of breeding among most of the groups discussed above. Such separation can help reduce competition among similar species by separating the time period during the activity season when each species makes its largest demands on the environment. Ricklefs (1966) for birds and Fleming (1973) for mammals noted that tropical species timed breeding to coincide with the period of highest food availability. As a consequence, species using the same food resource are still in direct competition. McDiarmid and Worthington (1970) noted that many tropical plethodontid salamanders in seasonal habitats timed egg deposition so that the juveniles hatched at the beginning of the wet season (a time when the environment is most favorable for feeding); other species in nonseasonal habitats had acyclic patterns of egg deposition. Fitch (1973) and Inger and Greenberg (1966) also noted a lack of temporal partitioning among tropical lizards, even though this partitioning occurs to some extent in temperate areas. If tropical birds and lizards and perhaps mammals tend to reproduce at low levels throughout a prolonged season of favorable conditions as an adaptation for escaping predation, then temporal partitioning of resources cannot occur. The Anura is the only taxon which tends to partition a resource temporally in tropical environments. With a longer season of favorable activity this temporal division of ponds may account for some of the unusually large increase in tropical frog diversity.

Lizards and benthic marine invertebrates show parallel trends with latitude in their life-history features. At least in part, this may be due to a similar response to predation. A greater risk of predation on adults in the tropics selects against the retention of eggs in the mother, and so against brooding of the eggs or viviparity. Dispersal of the eggs in time (lizards) and wide dispersal in space (benthic marine invertebrates) may be adaptations to high predation pressures on the young.

Examining these latitudinal patterns of life-history variations in the context of the widely cited *r*- and *K*- selection model does not show that one mode of selection is operating in the tropics (*K*-selection) and another in the temperate regions (r-selection), as predicted from a consideration of climatic

stability and its influence on the degree of environmental saturation (MacArthur and Wilson, 1967). Benthic marine invertebrates and lizards show characteristics expected of r-selection in tropical environments. Populations of both groups may be kept below saturation by effective predation. Conversely, by being a more frequent cause of death than competition, predation may be more important in the modifications of life-history patterns even if the environment is saturated (cf. the discussion of proximal vs. ultimate regulatory factors, and dominant controlling factors, by Van Valen,1973). Moreover, if competition for space is important in tropical sessile marine invertebrates, it may select for a different strategy than does competition among birds or other mobile animals. But birds, which show characteristics expected of K-selection, appear to be adapted to avoiding predation rather than to increasing competitive ability. Thus, the complex of traits associated with life-history modifications are not in themselves sufficient for understanding the selective forces that have produced the modifications.

This review of latitudinal gradients in reproductive patterns suggests that constraints of broad adaptations may indeed complicate models of life-history evolution based solely on external environmental factors but that they do not obscure all patterns derived from strictly ecological traits of species. Broad adaptations appear to constrain a group in the options it can take in response to a particular environmental pressure. For example, parental care in birds and a lack of such in most lizards may be the most important factor leading to a difference in the life-history modifications of these two groups.

To reiterate my earlier claim, in-depth comparative studies of diverse phylogenetic groups within a community promise to provide insights into how environmental factors influence the evolution of life-history patterns of species. General models cannot be constructed from the knowledge base of one well-studied group, or, once constructed, they cannot be accepted without testing from a diverse set of phylogenetic groups. Yet studies of latitudinal gradients of life-history patterns have been slow in accumulating information on taxonomically diverse species.

Some General Conclusions

I have argued above that evolutionary explanations of life-history patterns must be based on broad, integrative studies of an animal's biology and on comparative studies of diverse phylogenetic groups. Wilbur, Tinkle, and Collins (1974) have also suggested new procedures for the study of life-history patterns. They argue, as I have done, that simple models need to incorporate more selective parameters in order to explain the observed diversity of life-history patterns among species. However, in their enumeration of what they consider to be important dimensions to a general model they compound environmental factors (e.g., competition or climatic predictability) and the animal's own traits (e.g., body size, trophic level) that I will call organismal factors. Lumping these environmental and organismal factors obscures how they interact to produce diversity in life-history patterns.

As I mentioned earlier, the physical environment may act directly on an animal or indirectly through influencing the animal's biotic (competitive, trophic and predatory) environment. These environmental factors influence all aspects of the animal's biology. Changes in one aspect influence changes in other aspects. Thus, since every species is unique the resulting organismal selective vectors may cause unique life-history responses to a given set of environmental conditions. But I have suggested that certain ecologically important organismal traits of an animal, such as trophic level, body size or activity pattern, influence in a predictable manner the type of life-history response a species

makes to a given set of environmental conditions. Thus, studying how a few environmental forces influence the life-history adaptations of a species with respect to its important organismal traits seems necessary. Such a procedure involves comparative studies of taxonomically diverse species that nevertheless have certain similar organismal traits. Thus the life-history traits of an animal cannot be studied productively in isolation from the rest of its biology and of its position or influence in its community.

III. LIFE-HISTORY INFLUENCES ON COMMUNITY STRUCTURE

Life-history features are basic to the impact a species makes on its community and thus they are essential to our understanding of community structure and function. How a species responds reproductively to a change in the physical, competitive or predatory environment, influences the amount of energy that species can demand from the community and influences the pattern of availability of its energy to its predators and the pattern of interactions that it exerts on its competitors. For example, a species that uses its energy for defense mechanisms and thereby reduces the number of young produced, influences the number and kinds of potential predators differently from a species that puts its acquired energy into producing many young. In this section I indicate some of the ways in which life-history features influence the evolution of ecologically important aspects of species, such as body size and niche specialization, and thereby indicate how reproductive patterns can influence community structure and function. In particular I emphasize the strategy of submergent behavior.

Evolution of Increased Body Size (Cope's Rule)

Community dynamics acting on demographic features of species may in part explain Cope's Rule, the tendency for species within higher taxa to evolve toward larger size. Stanley (1973) presents a stochastic model to explain this phenomenon: Higher taxa evolve toward a larger mean size only because they originate at a size smaller than the mean optimum for the group and through sporadic changes in size diverge in both directions. Such changes in size cluster most species in the taxon away from the relatively small size at which the taxon originated. Why do taxa originate at relatively small size? Stanley argues that for any type of body plan the larger and smaller limits in size require structural specializations. The large species in a higher taxon, structurally specialized for the adaptive zone the taxon is occupying, are unlikely to break into a new adaptive zone, since such a breakthrough typically requires structural modifications. Stanley claims that as a consequence of structural specialization large species are less apt to be able to change in response to an environmental change and may be more susceptible to extinction than would a smaller, structurally less specialized species in the same taxon.

Demographic considerations within the framework of community dynamics complement Stanley's morphological arguments. Both competitive and predatory pressures can increase the variance in body size of species in a taxon. Competition frequently results in a separation of species along a size axis (cf. Schoener, 1970). Predation can favor either an increase or a decrease in body size depending on the initial size relations between predator and prey. For example, consider a case where the species in a taxon are loosely clustered around a certain body size. The major predators of this taxon are somewhat larger than all species but within the same order of magnitude. Predation on the larger species in the taxon may often favor a size increase in the species for one of two reasons. An increase in body size of an adult may render it more difficult to attack. Also, when a large species is so large that it is

relatively immune from the predator when mature, the juveniles may bear the brunt of predatory attacks. This predation on juveniles may continue to select for an increase in body size of adults when such an increase results in a higher fecundity or enables the adult to defend its young from attacks more successfully. Predation on the smaller species in the taxon may often select for smaller body size. For a small species to achieve the same immunity from the predators requires it to increase proportionately greater in size relative to a large species. With this disadvantage a small species is more likely to mature and reproduce rapidly since the adults are not immune from predation (and may be more susceptible depending on the size relationships between major predators and the prey). This demographic change of early maturity and rapid reproduction is associated with a decrease in body size.

Community pressures may help explain the phenomenon that a taxon typically originates at a smaller size than the mean for that group. Predation or competitive pressures acting on the various sized species within a community are not as likely to select for a change in adaptive zone for larger species as for smaller species, given the following assumptions. Large species tend to be dominant components in the community. Such species typically possess superior competitive ability in commanding limited resources. For example, size can be important in the defense of a resource with the larger species having the advantage in a contest. Social dominance between species has been correlated with large size (Miller, 1967; Morse, 1974). For many general predators, a large individual has a competitive advantage over a smaller one in the range of prey it can take. A larger individual can eat as small a prey item as a smaller individual, but also can take prey of sizes beyond the range of the small individuals (e.g., Schoener, 1968; Lynch, 1974). Thus any response of large species to an increase in predation or competition pressure is likely to be quantitative by the command of more resources to compensate for the energy loss that these pressures may incur. Small species may often respond qualitatively to these pressures by shifting their way of life, since they have less competitive advantage in the same zone. Also, small species do not have as many ways as large species to escape predation, since defensive morphologies and toxicity are often not effective against very much larger predators. One escape may be to reproduce more if sufficient resources are available, but competition may often exclude this option. Thus with more disadvantages in a particular adaptive zone than large species, small species may be more likely to break away from it and enter a new adaptive zone.

Demographic features of large species may also explain why they are more vulnerable to extinction. This permits another explanation for Cope's Rule (Van Valen, 1975). Large species are characterized by increased longevity and relatively low recruitment of juveniles. A relatively sudden environmental change that increases the mortality of the adults may reduce the population size to such an extent that it cannot recover reproductively and thus the species may become extinct. (This would not be the case if the adults, via competition, caused the low recuirtment rate of young.) Mertz (1971) observed this pattern in the California condor, which is at present on the verge of extinction. The large, long-lived condors have an extremely low rate of juvenile recruitment. In recent times human activity has caused an increase in mortality of the adults. The low recruitment is insufficient to compensate for this mortality and the populations have been gradually declining. Small species, in contrast, generally have high rates of juvenile recruitment, because of low probability of adult survival. A change in the intensity of mortality on these species, resulting from a change in environment, may often be compensated, because new adaptations have a chance to become rapidly incorporated into a population with a high rate of turnover of its members. A small species may be better able to

survive a period of rapid environmental change than large ones. However, within a community during stable periods, small species may be more rapidly excluded and replaced than large ones, because of the advantages of the large species in competitive and predatory interactions.

Niche Specialization and Rate of Energy Turnover in Communities

In a community a species can adapt to an increase in predation pressure by either compensating reproductively or defensively via poison, morphology, crypsi and/or submergent behavior. The adoption of one of these alternatives by some species in a community may influence the choice of other species. For example, if one species of prey shows submergent behavior and thereby avoids detection by a predator, a second species of prey may suffer an increase in predation, because it is now proportionately more available to the predator than is the first species. In a community with a high level of predation already, an additional increase in predation pressure as a result of the submergent behavior of another prey species may be difficult to compensate by increasing reproductive output. Thus, individuals of the second species may also show submergent behavior. An entire community of animals may so evolve to use the alternative of reduced foraging activity to avoid predation. This type of community resembles a tropical rainforest described by Elton (1973).

The fact that predators can influence the level of foraging activity in their prey implies that predation may be an important determinant in the rate of energy turnover for specific trophic categories of a community and that reduced activity may lead to niche specialization in species.

If predation influences the rate of energy transfer between trophic levels, different communities in the same general area may evolve different equilibrium rates. The physical environment sets certain rates of primary productivity. It also sets a certain range to the activity levels of the herbivores and their predators. The actual level at which herbivores exploit the producers may additionally be influenced by predation pressure. If the herbivores respond to predation by increasing reproductive output, there will be a high rate of energy turnover by the consumers of living organisms in the community. If the herbivores reduce their foraging activity to avoid predation but the availability of refuges maintains the same equilibrium density of herbivores, there will be a low rate of energy turnover by consumers and a correspondingly greater rate by decomposers. The level of energy turnover in a community may vary in time if the adaptations of its members to predation change. If one species either breaks from this equilibrium level or enters from outside once it is set, it would likely be selected against. A successful breakthrough by one or several species may allow the attainment of a new equilibrium. These considerations focus on the question of what determines the levels of regulation among trophic levels in different communities (Hairston, Smith, Slobodkin, 1960; Van Valen, 1973; May, 1973). More comparative studies of community dynamics are required to answer this question.

Submergent behavior may either increase or decrease the degree of feeding specialization, depending on the size of the animal relative to its food. If submergent behavior does not increase the equilibrium density of a species because some resource other than food is limiting, food will increase in relative abundance to the individual, but time spent feeding will be at a premium. Under these circumstances, the more efficient a species is at harvesting and processing food, the more it can gain in reproductive output relative to the probability of loss through being eaten by a predator while obtaining food (Schoener, 1971). Whether increased feeding efficiency will be accompanied by increased or decreased specialization may be largely a function of the size of

the animal relative to its food. For consumers that are small relative to their food, e.g., many herbivores, finding a particular type of food does not require much activity since the food is spatially concentrated for the individual. In such cases, feeding efficiency can be improved by increasing harvesting and metabolic specialization on a particular food resource. For consumers that are large relative to their food, e.g., vertebrate insectivores, a particular prey species is generally not spatially concentrated for the individual. Thus, if searching for food exposes the consumer to predation, harvesting efficiency can be improved by increasing the ability to catch all types of species available and to digest and assimilate a wide spectrum of species.

If prey species respond to increased predation by increasing reproductive output, trophic resources will likely be limited in abundance--individuals are being selected to obtain as much energy as possible in order to reproduce more. This leads to intra- and interspecific competition over trophic resources. Increased specialization or generalization with trophic resources in short supply is a function of the distribution of the resources in space and time (cf. MacArthur and Levins, 1964).

In summary, predation may influence the degree of trophic specialization observed in species and thereby influence the species diversity of communities. Does predation help explain the difference in species diversity in temperate and tropical communities? This question is pursued in the next section.

Species Diversity

The fact that the period of favorable activity is increased in the tropics and thus the amount of energy flowing through the community is increased does not in itself explain an increase in the number of species. With pressure from intraspecific competition populations are initially likely to expand to use the energy available to them. An increase in species diversity requires that some species decrease the proportion of energy they control in the community or evolve to use currently unused resources. Evolutionary changes that may decrease the amount of energy a species controls in the community or enhance its ability to use unexploited resources are (1) a change in way of life as a response to either competition or predation and (2) a decrease in foraging activity to avoid predation.

A change in way of life may not decrease the amount of energy a species controls in the community but it potentially can do so. Such a change may often reallocate number of species found in various higher taxa, but may not add to the total number of species. If a shift in way of life depresses the abundance of other species but does not eliminate those species or if such a shift taps unused energy resources, then this shift may increase species diversity.

Submergent behavior decreases the energy intake of an individual and consequently may decrease the total amount of energy that the species' population controls in the community. This is true only when a resource other than energy is regulating so that the equilibrium density of the species does not increase as a result of submergent behavior. As a consequence of submergent behavior refuges rather than energy may become the regulating resource. Dispersion can be considered a type of refuge from predation that leads to the coexistence of more species, since the density of any one species is limited by the minimum safe distance between individuals. Dispersion as an escape from predation is thought to be one of the main factors explaining high tropical diversity (Janzen, 1970; Connell, 1971). In addition to dispersion, a greater number of species can coexist if there are more ways to partition refuges than to partition energy resources.

For generalist predators (such as lizards, salamanders, frogs, birds) it seems likely that competition for refuges, territories or feeding perches that

are size-dependent allows for coexistence of more species than does competition for trophic resources (Maiorana, MSb). Both spatial and food resources are potentially partitioned by size in these predators, with large animals eating large prey and using large burrows or branches in a tree. Large animals can typically use the entire trophic resource range of small animals but have an exclusive range above that of small animals (e.g., Schoener, 1968; Lynch, 1974; Maiorana, MSb). In contrast, small animals can typically use the entire spatial resource range of large animals but have an exclusive range below that of large animals. Since large animals are typically dominant competitors, they can usually exclude small animals if trophic resources are regulating their density; small animals have no exclusive resource unless the large predators are very inefficient at using small prey (which may become the case as the difference in size of the competitors increases). However, if spatial resources are regulating, small predators can contract into their exclusive resource range. In a survey of resource partitioning, Schoener (1974) found that habitat partitioning was most common among sets of related species. However, more extensive studies using experimental techniques such as those of R. Jaeger (pers. comm.) and Fraser (1974) for plethodontid salamanders, are crucial for analyzing how effective in maintaining species coexistence is the partitioning of different resource dimensions. Since partitioning of one resource may be a byproduct of partitioning another, strictly observational techniques are of limited value in analyzing the dynamics of the system. I suspect that the commonly observed phenomenon of different diets among coexisting species is often caused by a primary adaptation to different ways in which spatial factors regulate their population densities.

Thus, I propose that more species can coexist as a result of predation, as does Paine (1966), Janzen (1970), and Connell (1971), but in the case of submergent behavior the intensity of competition remains the same but the resource over which competition occurs is changed.

Competitive pressures are often unlikely to result in a decrease in energy intake by a species. Competition may shift the way of life of species and thereby result in a decrease in energy control as mentioned above. But competition as often as not results in dominance of a relatively few species. Why is not more dominance observed in tropical environments? In this paper I have suggested, as have others, that predation can reduce the dominant competitors by several mechanisms. One is just keeping their abundance low (Paine, 1966; Janzen, 1970; Connell, 1971). Another is by selecting for reduced foraging activity which in changing the regulating resource, reduces the incidence of exclusion of subordinate competitors. But why does predation reduce the dominant competitors to a greater extent in tropical than in temperate environments?

Connell (1971) suggests that predators are more susceptible to fluctuations in temperate areas than are their prey and thus the prey can more often increase beyond control of their predators. I suggest two possibilities with respect to submergent behavior, the first not depending on any difference in the intensity of predation between temperate and tropical regions and the second assuming that there is greater predation in the tropics.

Fluctuations in the severity of the physical environment, producing uncertainty in survival at any given time, probably select for increasing the amount of energy converted into offspring at the expense of elaborate predator defenses. In such environments there will be large populations of both long- and short-lived species. For this reason submergent behavior is unlikely to be as extreme in temperate as in tropical areas. Hence, species in temperate areas would not have the low population densities or the low rates of growth and reproduction typical of many tropical species, and fewer species could coexist there. Climatically stable environments may be necessary for the extreme

expression of submergent behavior, as for the extreme expressions of many other specializations that lead to rarity in species. Secondly, a higher intensity of predation in the tropics may produce a greater frequency of submergent behavior there or other predator defenses that increase the rarity of species and allow more to coexist.

There are many species in the tropics, but generally individuals of any one of them are rare. There is evidence that this rarity is partly due to the high intensity of predation in the tropics. I propose that each species of potential prey may be forced into inconspicuousness by the inconspicuousness of all other potential prey species. Competition for inconspicuousness can lead to the wide dispersion of conspecifics and thus to the rarity of species, or it can lead to the partitioning of spatial rather than trophic resources and thus give the subordinate competitor a refuge from exclusion by the dominant competitor. Spatial refuges may be, therefore, of greater importance in the control of tropical diversity than is food, even though diversity in feeding results as a byproduct. To submerge is to survive, but the cost of submergence is the loss of a greater domain.

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LITERATURE CITED

Cody, M.L. 1966. A general theory of clutch size. Evolution, 20:174-184.

Cole, L.C. 1954. The population consequences of life history phenomena. Quart. Rev. Biol., 29:103-137.

Connell, J.H. 1961a. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecol. Monogr., 31:61-104.

_____. 1961b. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology, 42:710-723.

_____. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In P.J. den Boer and G.R. Gradwell (eds.), Proc. Adv. Study Inst. Dynamics Numbers Popul., pp. 298-312. Wageningen.

Dayton, P.K. 1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr., 41:351-389.

Dixon, J.R., and W.R. Heyer. 1968. Anuran succession in a temporary pond in Colima, Mexico. Bull. So. Calif. Acad., 67:129-137.

Elton, C.S. 1973. The structure of invertebrate populations inside Neotropical rainforest. J. Anim. Ecol., 42:55-104.

Emlen, J.M. 1970. Age specificity and ecological theory. Ecology, 51:588-601.

Fitch, H.S. 1973. Population structure and survivorship in some Costa Rican lizards. Occ. Paper. Mus. Nat. Hist. Kansas, 18:1-41.

Fleming, T.H. 1973. The reproductive cycles of three species of opposums and other mammals in the Panama Canal Zone. J. Mammal., 54:439-455.

_____. 1974. The population ecology of two species of Costa Rican heteromyid rodents. Ecology, 55:493-510.

Foster, M.S. 1974. A model to explain molt-breeding overlap and clutch size in some tropical birds. Evolution, 28:182-190.

Fraser, D.F. 1974. Interactions between salamanders of the genus Plethodon in the Central Appalachians: Studies of coexistence and competition. Ph.D. Dissertation, University of Maryland, College Park.

Fretwell, S.D., and H.L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica, 19:16-36.

Gadgil, M., and W.H. Bossert. 1970. Life historical consequences of natural selection. Am. Natur., 104:1-24.

Ghiselin, M.T. 1974. The Economy of Nature and the Evolution of Sex. University of California Press, Berkeley.

Hairston, N.G. The local distribution and ecology of the plethodontid salamanders of the southern Appalachians. Ecol. Monogr., 19:47-73.

_____, F.E. Smith, and L.B. Slobodkin. 1960. Community structure, population control, and competition. Am. Natur., 94:421-425.

Heyer, W.R. 1969. The adaptive ecology of the species groups of the genus Leptodactylus (Amphibia, Leptodactylidae). Evolution, 23:421-428.

_____. 1973. Ecological interactions of frog larvae at a seasonal tropical location in Thailand. J. Herpetology, 7:337-361.

Highton, R. 1962. Geographical variation in the life history of the Slimy Salamander. Copeia, 1962:597-613.

Houck, L.D. 1975. Reproductive biology of a Neotropical salamander, Bolitoglossa rostrata. M.A. Thesis, University of California, Berkeley.

Inger, R.F., and B. Greenberg. 1966. Annual reproductive patterns of lizards from a Bornean rainforest. Ecology, 47:1007-1021.

Janzen, D.H. 1970. Herbivores and the number of tree species in tropical forests. Am. Natur., 104:501-528.

Lack, D. 1948. The significance of clutch size. Part III. Some interspecific comparisons. Ibis, 90:25-45.

_____. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.

Lewontin, R.C. 1965. Selection for colonizing species. In H.G. Baker and G.L. Stebbins (eds.). The Genetics of Colonizing Species, pp. 77-94. Academic Press, New York.

Lord, R.D. 1960. Litter size and latitude in North American mammals. Am. Midl. Nat., 64:488-499.

Lynch, J.F. 1974. Ontogenetic and geographic variation in the morphology and ecology of the Black Salamander (Aneides flavipunctatus). Ph.D. Dissertation, University of California, Berkeley.

MacArthur, R.H. 1972. Geographical Ecology. Harper and Row, New York.

_____, and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy habitat. Proc. Natl. Acad. Sci., 51:1207-1210.

_____, and E.O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Maiorana, V.C. 1974. Studies in the behavioral ecology of the plethodontid salamander Batrachoseps attenuatus. Ph.D. Dissertation, University of California, Berkeley.

_____. MSa. Size and environmental predictability for salamanders.

_____. MSb. Space as a regulating factor for salamanders.

Marshall, N.B. 1953. Egg size in Arctic, Antarctic and deep-sea fishes. Evolution, 7:328-341.

May, R.M. 1973. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton.

McDiarmid, R.W., and R.D. Worthington. 1970. Concerning the reproductive habits of tropical plethodontid salamanders. Herpetologica, 26:47-70.

Menge, B.A. 1975. Brood or broadcast? The adaptive significance of different reproductive strategies in the two intertidal sea stars Leptasterias hexactis and Pisaster ochraceus. Marine Biology, 31:87-100.

Mertz, D.B. 1971. The mathematical demography of the California condor population. Am. Natur., 105:437-453.

Mileikovsky, S.A. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a reevaluation. Marine Biology, 10:193-213.

Miller, R.S. 1967. Pattern and process in competition. Adv. Ecol. Res., 4:1-74.

Morse, D.H. 1974. Niche breadth and social dominance. Am. Natur., 108:818-830.

Murdoch, W.W. 1966. Population stability and life history phenomena. Am. Natur., 100:5-11.

Murphy, G.I. 1968. Pattern in life history and the environment. Am. Natur., 102:391-403.

Organ, J.A. 1961. Studies of the local distribution, life history, and population dynamics of the salamander genus Desmognathus in Virginia. Ecol. Monogr., 31:189-220.

Paine, R.T. 1966. Food web complexity and species diversity. Am. Natur., 100:65-75.

Ricklefs, R.E. 1966. The temporal component of diversity among species of birds. Evolution, 20:235-242.

_____. 1969. An analysis of nesting mortality in birds. Smithson. Contrib. Zool., 9:1-48.

_____. 1970. Clutch size in birds: outcome of opposing predator and prey adaptations. Science, 168:599-600.

Salthe, S.N., and W.E. Duellman. 1972. Quantitative constraints associated with reproductive mode in anurans. In J.L. Vial (ed.), Evolutionary Biology of the Anurans, pp. 229-249. University of Missouri Press, Columbia.

Schaffer, W.M. 1974. Optimal reproductive effort in fluctuating environments. Am. Natur., 108:783-790.

Schoener, T.W. 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology, 49:704-726.

_____. 1970. Size patterns in West Indian Anolis lizards. II. Correlations with the sizes of particular sympatric species--displacement and convergence. Am. Natur., 104:155-174.

_____. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst., 2:369-404.

_____. 1974. Resource partitioning in ecological communities. Science, 185:27-39.

Skutch, A.F. 1949. Do tropical birds rear as many young as they can nourish? Ibis, 91:430-455.

_____. 1967. Adaptive limitation of the reproductive rate of birds. Ibis, 109:579-599.

Smith, M.H., and J.T. McGinnis. 1968. Relationships of latitude, altitude, and body size to litter size and mean annual production of offspring of Peromyscus. Res. Popul. Ecol., 10:115-126.

Spencer, A.W., and H.W. Steinhoff. 1968. An explanation of geographic variation in litter size. J. Mammal., 49:281-286.

Spight, T.M. 1974. Sizes of populations of a marine snail. Ecology, 55:712-729.

Stanley, S.M. 1973. An explanation for Cope's Rule. Evolution, 27:1-26.

Stebbins, G.L. 1971. Adaptive radiation of reproductive characteristics in Angiosperms. II. Seeds and seedlings. Ann. Rev. Ecol. Syst., 2:237-260.
Strathmann, R. 1974. The spread of sibling larvae of sedentary marine invertebrates. Am. Natur., 108:29-44.
Sweet, S.S. 1973. Allometry, life history, and the evolution of the desmognathine salamanders. M.A. Thesis, University of California, Berkeley.
Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev., 25:1-45.
Tilley, S.G. 1973. Life histories and natural selection in populations of the salamander Desmognathus ochrophaeus. Ecology, 54:3-17.
Tinkle, D.W. 1969. The concept of reproductive effort and its relation to the evolution of life histories of lizards. Am. Natur., 103:501-516.
_____, H.M. Wilbur, and S.G. Tilley. 1970. Evolutionary strategies in lizard reproduction. Evolution, 24:55-74.
Underwood, A.J. 1974. On models for reproductive strategy in marine benthic invertebrates. Am. Natur., 108:874-878.
Vance, R.R. 1973a. On reproductive strategies in marine benthic invertebrates. Am. Natur., 107:339-352.
_____. 1973b. More on reproductive strategies in marine benthic invertebrates. Am. Natur., 107:353-361.
Van Dijk, D.E. 1971. Anuran ecology in relation particularly to oviposition and development out of water. Zoologica Africana, 6:119-132.
Van Valen, L. 1971. Group selection and the evolution of dispersal. Evolution, 25:591-598.
_____. 1973. Pattern and the balance of nature. Evol. Theory, 1:31-49.
_____. 1975. Group selection, sex, and fossils. Evolution, 29:87-94.
Vial, J.L. 1968. The ecology of the tropical salamander, Bolitoglossa subpalmata, in Costa Rica. Revista Biologia Tropical, 15:13-115.
Wake, D.B., and I.G. Dresner. 1967. Functional morphology and evolution of tail autotomy in salamanders. J. Morph., 122:265-306.
Wilbur, H.M., and J.P. Collins. 1973. Ecological aspects of amphibian metamorphosis. Science, 182:1305-1314.
_____, D.W. Tinkle, and J.P. Collins. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. Am. Natur., 108:805-817.
Williams, G.C. 1966. Adaptation and Natural Selection. Princeton University Press, Princeton.
Worthington, R.D. 1968. Observations on the relative sizes of three species of salamander larvae in a Maryland pond. Herpetologica, 24:242-246.
_____. 1969. Additional observations on sympatric species of salamander larvae in a Maryland pond. Herpetologica, 25:227-229.