RESTITUTION OF *r*- AND *K*-SELECTION AS A MODEL OF DENSITY-DEPENDENT NATURAL SELECTION

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INTRODUCTION

Dawkins (36, p. 293) observes that "ecologists enjoy a curious love/hate relationship with the r/K concept, often pretending to disapprove of it while finding it indispensable." Others have suggested that the model of *r*- and *K*-selection is inadequate and outmoded and does not further our understanding of life history phenomena (105, 120, 123). These views unfortunately result from frequent misuse and overgeneralization of the model. I contend that *r*- and *K*-selection may have important ramifications for our understanding of life history evolution, but for the model to be useful, it must be interpreted strictly as it was originally formulated: as a model of density-dependent natural selection.

To minimize confusion, I begin this review with an outline of *r*- and *K*-selection explicitly as a model of density-dependent natural selection. I then attempt to place this model within a historical context with other life history theory. As with recent criticisms of competition theory (109), I find that *r*- and *K*-selection suffers from a lack of true tests of its hypotheses. Although it may play a significant role in the evolution of life histories, there are few empirical studies that can identify density dependence that is independent of other potential selective forces.

427

THE MODEL

In the simplest case, consider a population consisting of 2 genotypes, $i = 1,2$, reproducing clonally according to logistic dynamics. The Malthusian parameter of fitness, m_i, for each genotype is a decreasing linear function of the total population size, N, where each genotype has different values of r_i, the potential rate of increase when $N = 0$, and of K_i, the carrying capacity or population size when $dN_i/dt = 0$. Thus, $m_i = dN_i/N_i dt = r_i - (r_i/K_i)N$. When N is small, the genotype with the highest r_i possesses superior Malthusian fitness, irrespective of K_i. Conversely, individuals of the genotype with highest K_i have highest fitness at large N, irrespective of r_i. [Graphical illustration of this model is presented in MacArthur's *Geographical Ecology* (73, Figure 8-15).]

Such a continuous-time model is inadequate for monitoring diploid populations because changes in allelic frequency cannot reflect corresponding changes in genotypic frequency (68). This problem is avoided in a discrete-time version of the logistic model, commonly written as a function of absolute fitness, W_{ij} (given $W_{ij} > 0$) for the ith and jth alleles segregating at a single locus (68, 80, 101): $W_{ij} = 1 + r_{ij} - (r_{ij}/K_{ij})N$. For small to moderate values of r_{ij} (41), this version has properties similar to the original differential equation model, although it potentially allows for a heterozygote advantage at any density and consequent maintenance of polymorphism (68, 99, 101).

A frequently voiced interpretation of this model is that natural selection operates on K at high densities (29, 72). This extension of the model is trivial because although natural selection still maximizes the Malthusian parameter of fitness, genotypes with maximum K possess superior fitness at large N.

Considerable confusion exists because r is frequently used to denote dN/Ndt in exponential growth models. In the logistic model, however, r is not equal to dN/Ndt except at the imaginary point where $N = 0$. Logistic r is a constant that quantifies the rate at which a population will grow in a particular environment given the absence of *any* density-dependent effects. Kozlowski (63) misunderstood this and suggested that r is a density-dependent variable. In their appendix demonstrating that maximizing K is equivalent to maximizing realized r (which equals dN/Ndt), Sibly & Calow's (107) argument is similar to the preceding paragraph, but they are not clear about the distinction between realized r and logistic r.

Logistic r is also distinct from the abstraction called r_{max}. r_{max} is the potential growth rate in a totally unlimited environment, that is, the maximum growth rate attainable under ideal conditions—e.g. in the laboratory. Logistic r, on the other hand is the growth rate that may be achieved *in a particular environment* if there are no density effects (contra 42). Evolutionarily, this value may be maximized by either increasing the birth rate or decreasing the death rate, depending upon the particular demographic environment (105). Therefore, a

high *r* does not necessarily mean a high birth rate, and it certainly cannot be equated with the birth rate (as in 89).

The structure of the model does not imply that *K* should necessarily decrease as *r* increases or visa versa. Mutants with higher *r* and *K* will clearly have superior fitness at all densities. It still holds that at high density forms with higher *K* should be favored irrespective of *r*, and similarly, at low *N* natural selection favors individuals with high *r* irrespective of *K*. Thus, it does not seem at all contradictory that Luckinbill (69) should find that genotypes of *Escherichia coli* with high *r* and *K* did best and that there was no necessary trade-off between *r* and *K*. Still such a trade-off may occur for some organisms. Various characters correlated with fitness may maintain additive genetic variance through the evolution of antagonistic pleiotropism (40). Consequently, within a population we may see that characters correlated with high *K* will be inversely correlated genetically with characters associated with high *r*. Pleiotropic genes for a positive association between *r* and *K* would become genetically fixed, and the only variability that would remain would be that for antagonistic pleiotropy.

Heckel & Roughgarden (58) presented a stochastic *r*- and *K*-model where selection for increased *K* leads to a reduction in *r*. They argued that genotypes with high *r*-values would realize greater variance in fitness; therefore, long-term geometric mean fitness would select for reduced *r*. Turelli & Petry (130) argued that this result was not robust, that it depended critically on the specific manner in which stochasticity was incorporated, and that it could also be modified for nonlinear generalizations of the logistic (e.g. 49).

Robustness of the r and K Model

The logistic model is obviously too simplistic to be realistic, and *r*- and *K*-selection is consequently dismissed by some authors (78). Specific criticisms of logistic constraints are not justified because the *r*- and *K*-model is readily written in generalized forms (29, 100)—the logistic version just happens to be the simplest case. Except for the case of frequency-dependent selection, the maximization of population size under *K*-selection and of potential *r* at low *N* appears to be a robust prediction.

Although the logistic model is only valid if mortality and fertility rates are independent of age (29), Charlesworth (28, 29) claimed that *r*- and *K*-selection is generally valid for both discrete and overlapping generations, even when density-dependence occurs age specifically. Dingle (37) and Blau (12) argued, in contrast, that *r*- and *K*-selection is not always valid because natural populations often violate the implicit assumption of a stable age-distribution. Templeton (126) pointed out that fluctuating populations may not maximize $m = dN/Ndt$ because growth in populations that do not have a stable age-distribution is determined by all of the eigenvalues of a population projection matrix.

Nevertheless, long-term mean population growth is approximated reasonably well by mean fertility and survivorship parameters in stochastic projection matrices (34; but see 14, 129). Therefore, deviations from a stable age-distribution do not invalidate long-term growth rates as one measure of fitness (129).

Relaxing the linearity assumption does not influence the basic structure of the model (72; see also 15, 29, 45, 90, 100); indeed, selection may operate directly on the concavity of $m(N)$ (termed θ-selection) (43, 49). For example, in populations maintained at intermediate N (i.e. $< K$), genotypes able to sustain high rates of increase—in spite of N—may possess a selective advantage irrespective of r_{ij} or K_{ij}, potentially leading to a more concave $m(N)$ function. Indeed, $m(N)$ is concave for many populations of vertebrates (43).

Stochastic extensions of the deterministic model of r- and K-selection complicate the mathematics and convert outcomes to probabilistic functions, but in the case of a linear $m(N)$, they do not drastically alter the structure of the model or its interpretation (29, 58). For non-linear $m(N)$'s, however, the stochastic model's results can be influenced by the degree of concavity of $m(N)$ for each genotype (15, 130).

Complex life cycles complicate the theory because although selection for increased K may occur in one environment or stage of the life cycle, totally different selective pressures may dominate another (133). Still, r- and K-selection is valid within the relevant life cycle stages. Charlesworth (29) noted that K-selection in age-structured populations tends to maximize the number of individuals in a critical age group. But of course the critical age group or life cycle stage may vary considerably among taxa. In blowfly *(Lucilia cuprina)* experiments, the critical stage under K-selection was female fecundity (84), whereas in *Drosophila birchi* K-selection enhanced adult survivorship (6; F. Ayala, personal communication).

The r- and K-model suffers most seriously with the incorporation of frequency-dependent natural selection (68); indeed, mean fitness may decrease under these conditions (29, 68, 82, 86). This complication is perhaps best illustrated by the evolution of competitive ability (termed α-selection; 24, 47, 48)—either interspecific or intergenotypic. Here, a superior competitor may possess a selective advantage in a genetically variable population, even at the cost of lower K. Although K-selection is not the only evolutionary response possible at high density, there is considerable empirical evidence that K-selection occurs (6, 29, 62, 69, 70, 80, 84). But by definition, K-selection only occurs when selection at high density results in an increase in equilibrium population size. Thus, K-selection is not necessarily synonymous with selection for competitive ability (contra 87), and selection at high densities need not result in K-selection (47, 51).

Single-species population models with continuous, density-dependent functions (e.g. the logistic and age-structured or nonlinear extensions) may be most

applicable to taxa with a constant rate of resource renewal (27). Many species, however, interact with other species that constitute their resources. The result is an interactive set of equations with much more complex dynamics than the logistic ones—e.g. predator-prey models and plant-herbivore models (27). These interactive models reveal frequency-dependent influences on evolution, and consequently, density-dependent natural selection may not always maximize population size (1).

Density-dependence is only one of a multitude of factors that can shape the evolution of life histories (8). Furthermore, density-independent selection can occur at any density (93). For example demographic selection can alter life history parameters irrespective of density. Thus clearly *r*- and *K*-selection is limited in scope. Yet, some authors have attributed virtually all life history variation to this simple model (118, 119, 123). To place these works in perspective, I review the historical context of *r*- and *K*-selection.

THE HISTORY OF *r–K* THEORY

The basic rudiments of *r*- and *K*-selection appear as early as MacArthur's 1958 *Ecology* paper (71), where he attempted to understand variation in clutch size among 5 species of parulid warblers. He noted that "in a population which has reached an equilibrium size, abundance is independent of birth and death rates. For species in equilibrium, then, a study of birth and death rates is not necessary to understand the control of the equilibrium abundance" (71, p. 610). In the same context, MacArthur quotes Darwin (35): "A large number of eggs is of some importance to those species which depend upon a fluctuating amount of food, for it allows them rapidly to increase in numbers" (71, p. 610). This paper was followed by MacArthur's genetic formalization of how natural selection maximizes *K* (72), which was heralded as one of the early efforts to integrate population genetics and ecology.

The first explicit reference to *r*- and *K*-selection appears to have been by MacArthur's student, M. Cody (33), who credits the idea to MacArthur. Cody (33) used *r* and *K* in his attempt to explain patterns of geographic variation in avian clutch size. He argued that in seasonal environments, density-independent mortality lowers the mean population size, thus reducing competition among survivors. Therefore, birds in seasonal environments have more resources to allocate to reproductive functions, including clutch size. In contrast, in less seasonal environments, populations are nearer to carrying capacity, and more resources are consequently allocated to competitive activities. Although characterizing environmental seasonality as simply imposing density-independent mortality is a gross oversimplification (15), Cody's loose interpretation of *r*- and *K*-selection may have some merit here (95). When resources are abundant, individuals with large clutch sizes may leave more offspring. But in resource-limited populations, birds with smaller clutches may

have lower energetic demands—and thus a higher K. Slagsvold (111) challenged the latitudinal pattern of avian density dependence, however, so references to r- and K-selection may be invalid. Ashmole's (5, 15, 96) hypothesis, which explicitly defines the role of environmental seasonality in clutch size evolution, is greatly preferable.

MacArthur & Wilson (74, p. 149ff) described r- and K-selection as a model of density-dependent natural selection. They noted that in an initially colonized population, r-selection would predominate for a time, but ultimately the population would come under K-selection. Under r-selection, they argued, evolution promotes productivity, high rates of resource exploitation, and high reproductive output. Under K-selection, "genotypes which can at least replace themselves with a small family at the lowest food level will win, the food density being lowered so that large families cannot be fed. Evolution here favors efficiency of conversion of food into offspring" (74, p. 149). Nothing in this discussion is inconsistent with a strict interpretation of r and K as a model of density-dependent natural selection.

MacArthur & Wilson went on to suggest, however, that in seasonal environments with highly density-independent mortality, we might expect r-selection for large productivity. Unfortunately, this argument is a very loose interpretation of the consequences of seasonality (15) and implies that density-independent mortality falls evenly on all age classes. This implication certainly may not be true, and it has led to much confusion about the consequences of density-independent vs density-dependent sources of mortality. Also, many authors appear to have equated r-selection with selection in fluctuating environments, overextending the original model (87, 98). Additionally, MacArthur & Wilson were confused about the mechanism for K-selection, suggesting that it may require group selection. Roughgarden (99) clearly showed that group selection was not necessary, a point MacArthur (73) later recognized.

Pianka's (89) short note published in 1970 had a long lasting impact on the interpretation of r–K theory. Pianka implicitly assumed that increased population density will result in decreased juvenile survivorship, and consequently the optimal reproductive effort should decrease with increasing population size (60a, 90, 106). Based upon this overgeneralization, he generated a table that lists what he claims are life history correlates of r- and K-selection, e.g. r-selected taxa mature early, exhibit high levels of reproductive effort, and do not have parental care; K-selected forms should somehow have the opposite traits, such as delayed breeding, low levels of reproductive effort, and parental care. No such conclusions can be drawn from density-dependent natural selection, and it is not true that r- and K-selection collapses into demographic theory, even if one accepts Pianka's assumption of age specificity [contra Horn (60a)].

Since the appearance of Pianka's table, r-selection has been equated with high reproductive potential and K-selection with low reproductive potential

(87, 119). Why?—because r-selection should clearly select for high reproductive potential; and K-selection, for the forms with highest fitness in a competitive environment. It is easy to envisage a "good competitor" as a large, aggressive individual with a large territory (despite the consequences for K). Critical evaluations of the concept or explicit definitions of the model were quickly ignored. It was convenient to have a label for species with high vs low r; indeed, there are many useful distinctions among taxa with variable potential rates of increase (122, 123). The origin of the concepts no longer mattered; "r-strategists" and "K-strategists" became jargon that everyone could understand: small species that could reproduce quickly vs large species that could not.

Pianka's table was reproduced in many introductory ecology texts (39, 64, 91, 94); misuse of the concept became rampant. People working on life history evolution quickly recognized that Pianka's interpretation was not a general one (104, 134). MacArthur (73) apparently recognized the problem and presented an explicit model of r- and K-selection in his last work, *Geographical Ecology*. At the same time, population geneticists began to examine density-dependent natural selection (3, 28, 31, 99), but these authors were usually cautious about extrapolating their results to life histories. Life history theory became a demographic theory with a focus on schedules of reproductive effort and life table prediction (105), perhaps even avoiding density-dependence and resource-based models.

Southwood (116) developed a very different interpretation of r- and K-selection. According to it, the permanence of habitats or "habitat durational stability" can clearly influence maximum longevity and the potential for density dependence. Obviously different life histories are associated with temporary vs permanent habitats, but the association with r- and K-selection is not always a clear one. As Parry (87) argued, to imply exact synonymy between habitat durational stability and r- and K-selection can only obscure the actual selective forces that operate in different habitats. Similar difficulties arise with attempts to collapse a wide variety of stress phenomena into a single factor (52, 76a), as in Grime's (54, 55) triangular classification of life histories.

Many of the authors purporting to provide evidence in support of r- and K-selection interpreted the model very loosely or as Pianka (89) proposed in his table. For example, Solbrig's (46, 115) study of dandelions *(Taraxacum officianale)* is frequently championed as a rigorous test of r- and K-selection (101, 106). Solbrig compared the reproductive effort, size, and survivorship of three populations of dandelions, presumably of different genotypes. The so-called r-selected population was frequently trampled and mowed and thus thought to be experiencing high, density-independent mortality. The population claimed to be K-selected was in a less disturbed site with high *interspecific* competition. But the population density on the trampled and mowed site was higher than on the undisturbed site! The higher reproductive effort on the

trampled and mowed site may have been a consequence of selective trampling and mowing, and the large biomass of individuals in the low density population may have been a product of interspecific competition and the resulting α-selection. Consequently, Solbrig's dandelion study is not clearly a test of r- and K-selection.

The most recent phase in studies of r and K has been prompted by Stearns (118, 119), who proposed to test life history theory by comparing Pianka's predictions of r- and K-selection and those of bet-hedging and demographic theory with results from empirical studies. Several similar "tests" of r and K have subsequently appeared (7a, 38, 125). Since Pianka (89) made rather stringent assumptions and overgeneralized, r and K does not usually fare well under such "tests." In this case, r and K is rejected in favor of demographic theory. Thus, misinterpretations of theory can lead to spurious hypotheses that have little or no bearing on the model. Since density is only one of many environmental forces shaping life histories, we cannot expect life history patterns to reflect the consequences of r-

cases. The only appropriate solution is to study the original model of r- and K-selection as formulated in MacArthur's (72) original paper and to consider carefully the possible life history consequences of natural selection as it is affected by density dependence.

THE IMPLICATIONS FOR LIFE HISTORIES

Demographic approaches to life history evolution attempt to predict the optimal schedule of reproductive effort, E_x, that maximizes the average m in a particular demographic environment (26, 29, 79, 104). There is no reason that such a theory should not be valid at any density; similarly, any form of density-independent selection can occur irrespective of density (93).

As Schaffer (105) emphasizes, neither r nor K can be clearly expressed as explicit life table parameters (105). Stearns (119) stated that K is not a simple population parameter but a composite of a population, its resources, and their interaction. This statement is not necessarily true, since the density-dependent mechanism determining K need not be resource based, but his point is valid. K is not linked in any predictable way either to the life table or to the schedule of reproductive effort.

Which life history traits determine variation in K? Our ability to answer this question is obscured by the fact that a variety of density-dependent mechanisms may be responsible for setting K. Even in generalized models with age structure included (29), whether density-dependence occurs via competition, predation, or dispersal is not specified. I will proceed by reviewing the possible life history consequences of each density-dependent mechanism separately.

Density–Dependent Resource Availability

We know that the relationship between dN/Ndt and resource availability is generally concave, often following Michaelis-Menton, Monod (127) or von Bertalanffy functions (15). In the last instance, we see $dN/Ndt = r^*\{1-\exp[-Z(X-D)]\}$, where r^* is the potential rate of increase given unlimited resource availability, X; D is the resource demand ($D=X$ when $dN/Ndt = 0$); and Z is the initial slope of the function $dN/Ndt(X)$. We may easily envisage an analog to the model of r- and K-selection (illustrated in 15, Figure 1). Here natural selection favors genotypes with high r^* when resources are abundant, but genotypes with low resource demands, D, have a selective advantage when resources are scarce (see 15 for a density-dependent extension of this model). MacArthur (73) explicitly interpreted r- and K-selection with a focus on density-dependent resource availability (see his Figures 8–15) and with good justification. The ecological constraints of resource availability on reproduction and growth have been extensively documented for many groups of organisms, including plants (136, 137), mammals (102), and birds (66).

Critical to understanding r- and K-selection under density-dependent resource availability is a knowledge of the correlations between life history and K or D. As Roughgarden (99a) noted, K-selection occurs when a genotype is able to continue reproduction and sustain a positive growth rate when all other genotypes have reached carrying capacity. MacArthur (73) pointed out that one mechanism resulting in higher K is increased efficiency of resource conversion. Calder (18) showed that the efficiency of resource conversion is size independent, at least among birds and mammals, but a variety of physiological adaptations can improve this efficiency. MacArthur (73), Smith (112), and Odum & Pinkerton (85) have suggested that high reproductive output is inconsistent with high efficiency, and conversely, individuals with low reproductive output should have higher efficiency and higher K. I am unaware of the existence of adequate biological evidence to support this hypothesis. The issue is complicated by the fact that the energy conversion efficiencies involved in the production of gametes are often higher than for the production of somatic tissues—but they differ among taxa (22).

In resource-limited populations, carrying capacity is higher for genotypes with lower total-resource budgets. Therefore, K-selection should favor individuals with lower total resource or energy demands (51, 72). Conversely, when resources are abundant, increased resource acquisition can be used selfishly to enhance both fecundity and survivorship via larger size and/or increased reproductive output (19, 21). Thus, total resource budgets should increase under r-selection and decrease under K-selection.

Abrams (1) came to a similar conclusion noting that less foraging effort and thus less total resource acquisition results in a larger equilibrium population size. He assumed that an increase in foraging effort and the concomitant

increase in the total resource budget is funneled to reproductive effort, but this assumption is unnecessary. Increasing foraging effort may result in greater somatic allocation with the same consequences, i.e. a larger total resource budget and a smaller equilibrium population size.

Smaller body size is an example of a life history response that may occur as a consequence of K-selection (contra 89). Merritt & Merritt (77) argued that the lower food requirements of small individuals of lower mass enhance the probability of survival for voles in restricted subnivean environments. Larger individuals appear to be less able to tolerate the long periods of acute food shortage associated with high density; Clutton-Brock & Harvey reviewed the evidence for mammals (32). Lower mass and the concomitant lower food requirements increase the probability that individuals can meet their basic metabolic requirements during food shortages and still acquire energy to allocate to reproduction. Conversely, the allocation of resources to large body size or tap roots can *enhance* survival, particularly in seasonal environments (15). Thus, when resources are abundant r-selection may favor increased growth rates and larger size. Size may also be correlated with age-specific fecundity in some taxa (118), but not all. When size is positively correlated with age at first reproduction, large size may still offer a selective advantage through enhanced survivorship (15) if adequate resources are available.

Although not a life history character, reduced metabolic rate is a physiological response that may be expected to occur as a consequence of K-selection. Paraphrasing Bennett (10), "the low metabolic rate of ectothermic vertebrates has obvious advantages in permitting survival on very little food and conversion of a large fraction of ingested food into biomass." The consequence of variation in metabolic rates is greater than was previously thought. Nagy (81) noted that if food supply limits density, lizards could maintain a population 50 times as dense as a population of mammals of the same size and diet! I am unaware of direct evidence suggesting that density-dependent natural selection has resulted in reduced metabolic rates, although the indirect evidence from lizards is tantalizing (30, 81).

DEMOGRAPHIC RESPONSE   Michod (79) evaluated the consequences of variation in resource levels for optimal reproductive effort as Charlesworth (29) did for age-structured density-dependence. Basically, increased resources may result in either an increase or a decrease in optimal reproductive effort, depending upon the relative "rewards" to increased fecundity or increased survivorship. If increased reproductive allocation does not increase fitness substantially, increased somatic allocation may be able to enhance fitness more through increased survivorship. In populations where survival is hardly affected by somatic allocation, fitness may be enhanced more by increasing reproductive effort.

Such a demographic approach has proven to be useful for interpretating many instances of phenotypic variation in life histories. For example, decreasing food supplies stimulate a greater reproductive effort in triclad flatworms because young individuals may have a better chance than adults of surviving starvation conditions (23). Decreased food results in decreased reproductive effort in *Tribolium,* in contrast, because adult mortality is affected less than juvenile mortality by food shortages (78, 121). Among fish, reduced food availability typically leads to delayed breeding at a smaller size, and the delay in breeding decreases with increasing adult mortality (121). High densities in red deer *(Cervus elaphus)* populations (2), however, result in delayed breeding at a larger body size, probably because of the seasonal constraint on breeding.

The basic premise of much life history theory is that increased reproductive effort at a particular age results in decreased survivorship and residual reproductive value (20, 105) known as the "cost of reproduction". But along a resource or density gradient, this hypothesis need not be true. Soule & Werner (115a) proposed that along an environmental gradient, there may be an optimum at which reproductive effort is maximal. Deviations from this optimum may increase the relative maintenance costs and reduce the resources available for reproduction, thus decreasing the reproductive effort. Independent of demography, allometric constraints may also shape resource allocation patterns, e.g. more massive supportive structures may be necessary to ensure reproduction and survival at large sizes (75).

Calow (20) observed that if resources were adequate to ensure all maintenance requirements, increased reproductive allocation need not entail survival costs. Because such patterns might be viewed as contradictions of demographic theory that assumes reproductive effort is inversely correlated with residual reproductive value (104, 107), Calow proposed to redefine reproductive effort as the extent to which nutrients are allocated to reproduction when they are also required "to support other aspects of metabolism" (20, p. 36). Although Calow's approach helps us understand some apparent exceptions to demographic life history theory, reproductive effort becomes even more elusive and difficult to quantify. As a consequence, it is harder to use the theory to understand the life history parameters we observe in nature. As discussed in the previous section, resources can influence the evolution of life history patterns irrespective of trade-offs between reproductive effort and residual reproductive value. Therefore, I do not find Calow's redefinition of reproductive effort necessary; but furthermore, such redefinition implies excessive focus on the cost of reproduction for determining life history optima (9a).

SEX AND GENETIC VARIABILITY   The most direct evidence for *K*-selection would appear to come from *Drosophila* spp., where *K* becomes progressively larger over many generations in laboratory populations raised at high densities,

and the rate of evolution of K is highest in populations with high genetic variability (6, 17, 62). These observations, however, have been shown to be a consequence of both frequency-dependent and density-dependent natural selection (128). When resources are limiting, competition is greatest among individuals of the same genotype, whereas the fitness of other genotypes exploiting the environment differently is inversely correlated with frequency (7, 128). As in models of competitive ability (24, 47), genotypic carrying capacities may actually decrease, even if population size increases. Interestingly, positive frequency-dependent selection occurs at low densities, and negative frequency-dependent selection only occurs at high densities (114, 128).

Nevertheless, this process may still occur under K-selection when genes control genetic variability and thereby the collective niche breadth of the offspring. Genes that confer high rates of recombination or other mechanisms resulting in high genetic variability among offspring will be favored under K-selection. Note that precisely this rationale has been used in the "Tangled Bank" hypothesis to explain the evolution of sex (9). Even though asexual forms are able to achieve higher genotypic rates of increase in unlimiting environments (i.e. r-selection), in populations at K sexual forms can continue to increase because their offspring exploit the environment in a variety of ways, and therefore they possess higher K.

Williams (134a) proposed that the ratio of sexual to vegetative reproductive effort should increase with density. However, Schaffer & Gadgil (106) have proposed exactly the opposite—i.e. that vegetative reproduction should become more important at high densities [contrary to Pitelka et al's reading (92) of 106]. Empirical observations are inconsistent as well (92) and are probably confounded by varying opportunities for dispersal, density-dependent pollinator abundance, and density-dependent seed predation. The same problems complicate investigations of the optimal balance between seed size and number as a function of density (106, 113). More theoretical and empirical work is clearly needed on these problems (136, 137).

Density–Dependent Predation

Predation can be either density dependent or density independent. Although predation can clearly play a major role in shaping the evolution of life histories, in most cases it is not clear why it should make any difference whether predation is density-dependent or density-independent. Therefore, I will not attempt to review the possible consequences of predation for life histories.

One situation does seem particularly relevant, however. It has been shown that weasels *(Mustela nivalis)* develop a search image on great tit *(Parus major)* nests and thus impose density-dependent mortality (65). The probability of predation on great tit nests is a function of brood size because parent birds have difficulty keeping large broods fed, and therefore large broods make more

noise and are more likely to be found by weasels (88). In other words, the predation rate is positively correlated with clutch size, resulting in selection against large clutch size.

As noted above, predator-prey (or plant-herbivore) interactions may be inadequately modeled by the logistic equation. If dynamics can be characterized by an interactive system such as Caughley & Lawton's (27) plant-herbivore system, a decreased foraging rate increases the equilibrium density for the herbivore (i.e. the predator). Holding all else constant, an increase in the potential growth rate of the predator will ultimately result in a larger equilibrium population size, as it would for the logistic if the rate of density-dependence (which equals $-r/K$) were maintained constant. Nevertheless, frequency-dependent selection will sometimes (but not always) confound predator-prey interactions (1, 68). Predator-prey models can become quite complex, and the mechanisms of density-dependent selection may vary according to the parameters that are incorporated into the system. Regardless, it should be quite apparent that the life history responses to density-dependent predation may be quite different from those imposed by density-dependent resource availability (134).

Density–Dependent Migration

The population growth rate may vary in a density-dependent fashion owing to differential rates of dispersal or immigration. The genotypic growth rate is maximized under r-selection by low dispersal rates. As population density increases, individuals presumably maximize their own fitness by dispersing rather than facing low fitness opportunities in a crowded environment, particularly if crowding is localized (44, 53, 61). Hamilton & May (56) argued that even in stable habitats, parents should ensure some dispersal among their offspring, even when dispersal results in considerable mortality, because of competition with relatives or other conspecifics. The dispersal of prereproductives can also reduce the disadvantages of inbreeding depression, yet among animals, parents can maintain the advantage of familiarity with the area which they acquired through learning (53).

But how does K-selection operate under density-dependent dispersal, and what implications does this have for life histories? The fact that philopatry may be favored under r-selection does not mean that it will not be favored under K-selection. As Greenwood & Harvey (53) pointed out, it is not clear which life history characteristics correlate with dispersal patterns or density-dependent dispersal.

The spatial and temporal patterns of resources do offer some interesting correlates with dispersal and life history. For example, Andersson (3a) showed that autocorrelated periodic environments can favor nomadism and large clutch size. Similarly, Southwood (116) noted that ephemeral habitats offer a selec-

tive advantage for high reproductive effort and dispersal ability, since opportunities for future survival may be low. But neither of these examples have any necessary relation with r- and K-selection.

Similarly, dispersal ability or propensity need not be tied to r- and K-selection (37, 108), contrary to the loose interpretations by MacArthur & Wilson (74). Dingle (37) presented data on migratory forms within species, noting that r is actually higher among low migratory populations. He argued that this is a consequence of deteriorating habitats that stimulate dispersal—where selection favors movement even if it results in delayed reproduction—and reduced fecundity. Likewise, density-intolerant rodents possess lower reproductive rates, have larger body sizes and are highly aggressive (4, 13). These dispersal genotypes certainly are not a consequence of K-selection since they can not survive at high densities—rather, these forms may be selected for dispersal ability.

Although colonizing ability is another issue often correlated with r and K-selection, there seems no justification for doing so. Simberloff (108) showed that good island colonists may be either adept at reaching the islands and/or able to persist once colonized. MacArthur & Wilson (74, Chap. 4) suggested that colonists should be at the maximal reproductive ages, postulating that the probability of founding new populations would be highest at this point. Using branching process theory, Williamson & Charlesworth (135), however, found no particular relation between the age-specific reproductive value and the probability of survival of a population founded by individuals of a particular age.

More theoretical and empirical work is clearly needed in order to ascertain whether density-dependent migration or dispersal has any consistent consequences for life history evolution. Yet, as argued above in the case of density-dependent predation, the life history consequences of migration or dispersal are probably much different from those of density-dependent resource availability.

FLUCTUATING ENVIRONMENTS

Most organisms live in fluctuating environments, and the degree and effect of these environmental fluctuations can have important consequences for life histories (15, 25, 57, 103, 106). Contrary to frequent interpretation, the original model of r- and K-selection is a deterministic one providing no direct insight into the consequences of environmental variability. Yet, if population size is not perturbed, r-selection will be a fleeting experience with populations typically undergoing K-selection. The most common view is that fluctuating environments impose density-independent mortality, which reduces population size (33, 74). One may incorporate a density-independent mortality effect into the r- and K-model, yielding $W_{ij} = 1 + r_{ij} - (r_{ij}/K_{ij})N - y$, where y is the density-independent mortality rate, independent of genotype. As y increases,

equilibrium N^* decreases. With this model, we have the frequently cited situation where high, density-independent mortality results in selection for genotypes with high r; whereas low, density-independent mortality means that populations will be near K, where selection usually results in fixation of the mutants possessing high K.

The nature of density-independent mortality is critical. MacArthur & Wilson (74) and Pianka (89, 90) implicitly assumed that y is a pure rarefaction term that imposes no selection itself, i.e. y must be age-independent, resource-independent, and independent of any life history characters. This assumption is usually unrealistic. For example, Sinclair (110) showed that drought related density-independent mortality among African buffalo *(Syncerus cafer)* is much higher among juveniles than adults. Therefore, the greater the intensity of density-independent mortality, the greater the selection for the low, age-specific reproductive effort predicted by demographic approaches (e.g. 107).

Similarly, density-independent mortality can directly select for particular life history traits. For example, high overwinter mortality may fall more heavily on small individuals than on larger ones because large individuals are able to survive longer food shortage periods (15). Likewise, density-independent mortality imposed by wave action on intertidal molluscs may select for thick-shelled individuals that are able to withstand the heavy force of waves (8, 131, 132).

In reality, the effects of environmental fluctuations are much more complex than simply imposing density-independent mortality. One may envisage seasonally fluctuating carrying capacity or resource availability (15, 16), fluctuating age-specific mortality rates (29, 57, 103), or spatial patchiness where different patches vary temporally in resource abundance (3a). The precise nature of environmental variability is critical to understanding its potential impact on life history evolution; to collapse all environmental variability into one model of r- and K-selection is naive.

Caswell (25) recently proposed that the proportion of time that a population spends increasing or decreasing will have important effects on life history. Populations that are usually increasing should experience selection for high reproductive effort, early age at first breeding, semelparity, fast development, short lifespans, and little investment in individual offspring; in decreasing populations, in contrast, a premium is placed upon long lifespans, slow development, delayed breeding, iteroparity, and high investments in individual offspring. These predictions depend entirely upon explicit assumptions about the demographic environment during population growth and decline. Caswell presumed that the change in population size during population increase equals that of population decrease, irrespective of the time spent decreasing or increasing. Therefore, the magnitude of selection is potentially equal during population increase or decrease. As with density-independent mortality, the precise selective forces operating during population growth or decline determine the

life history consequences of fluctuating environments, and these are potentially independent of the proportion of time a population is increasing or decreasing. For example, "catastrophic mortality" may occur in an age-specific fashion that could reverse Caswell's predictions for populations spending a majority of time increasing.

The phenotypic plasticity of life history traits in fluctuating environments may be considerable (83). Phenotypic responses to environmental change are typically expected to occur in the same direction as that favored by natural selection (16, 50, 59). But such an approach should be viewed cautiously because phenotypic responses to environmental influences can mask genetic variation (11), and virtually nothing is known about the genetic control of phenotypic plasticity.

CONCLUSIONS

To be useful, r- and K-selection must be interpreted consistently (87). Although ecological theory does not subscribe to a law of priority like that prevalent in taxonomy, historical precedence commands that r- and K-selection be viewed strictly as a model of density-dependent natural selection (72).

Generalizations of the original model of r- and K-selection to allow for discrete time intervals and to incorporate age-structures, stochasticity, and nonlinearity show it to be reasonably robust (29, 100). The model is based on the assumption, however, that natural selection maximizes mean fitness, so extensions to frequency dependence may invalidate it (68). At high densities, K-selection can only increase K, but the evolution of competitive ability via frequency-dependent natural selection (α-selection) can actually reduce genotypic K (24, 47, 76). Therefore, evolution of competitive ability is not synonymous with K-selection.

Density-dependence is only one of many environmental factors that may shape the evolution of life histories. This evolution can occur with decidedly different consequences via density-dependent competition, predation, or migration. Even so, Prout (93) demonstrated that density-independent selection can occur at any density. Additionally, frequency-dependent natural selection may also be a function of density (128). Therefore, it may be difficult to demonstrate that any particular example of life history evolution is the consequence of density-dependent natural selection, especially in field studies.

This statement does not imply that density-dependent natural selection is not an important force in the evolution of life histories. Indeed, in resource limited populations K-selection increases the efficiency of resource utilization or favors a decrease in total resource use per individual. It may be associated with decreased reproductive output or decreased somatic allocation, e.g. smaller body size. In contrast, r-selection results in the use of as many resources as can possibly enhance fitness—through increased reproductive output to enhance

fecundity and/or increased growth and somatic allocation for improved survivorship (21). Additionally, when linked with frequency-dependence, r- and K-selection offers a relevant framework for the fixation of genes that promote genetic variability or niche breadth, including sexual reproduction via Ghiselin's "Tangled Bank" hypothesis (9).

Much confusion exists over the role of environmental variability in the interpretation of r- and K-selection. Although density-independent mortality can reduce N and thus promote r-selection, it may also impose selective mortality, which may shape the evolution of life histories. The precise nature of environmental variability can be extremely important in shaping life history evolution (15, 57, 103, 130), but this effect may be totally independent of r- and K-selection.

Law (67) criticized Charlesworth (29) for developing theory on K-selection, claiming that there is little evidence that K-selection in natural populations is significant. I insist that the existing tests of the theory have not been adequate to justify such a criticism, although granted that the scope of the model is narrow, i.e. restricted to density effects. Schaffer (105) implied that life history evolution entails the prediction of life tables and age-specific schedules of reproductive effort. But such an approach obscures life history parameters that may be correlated with an organism's total resource budget, e.g. reproductive output and the size of the organism (60). Life history theory will remain rudimentary until predictions can encompass variation in the original life history characters that stimulated the development of the theory initially, including clutch size, litter size, total reproductive output, body size, and plant biomass.

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CONTENTS

vii

viii   CONTENTS   *(Continued)*