r- AND *K*-SELECTION REVISITED: THE ROLE OF POPULATION REGULATION IN LIFE-HISTORY EVOLUTION

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Abstract. The theory of *r*- and *K*-selection was one of the first predictive models for life-history evolution. It helped to galvanize the empirical field of comparative life-history and dominated thinking on the subject from the late 1960s through the 1970s. Large quantities of field data were collected that claimed to test predictions of the theory. By the early 1980s, sentiment about the theory had changed so completely that a proposal to test it or the use of it to interpret empirical results would likely be viewed as archaic and naïve. The theory was displaced by demographic models that concentrated on mortality patterns as the cause of life-history evolution. Although demographic models are known for their density-independent approach and focus on extrinsic mortality, these models can incorporate many ecological features captured by *r*- and *K*-selection, such as density-dependent population regulation, resource availability, and environmental fluctuations. We highlight the incorporation of these factors in recent theory, then show how they are manifest in our research on life-history evolution in Trinidadian guppies (*Poecilia reticulata*). Explanations of the repeatable suites of life-history differences across populations of guppies originate from demographic models of predator-driven age-specific mortality. Recently, careful examination of guppy demography and habitat has revealed that density-dependent regulation and resource availability may have influenced the evolution of guppy life histories. In the field, these factors covary with predation risk; however, they can be uncoupled experimentally, providing insight into how they may have synergistically driven guppy life-history evolution. Although life-history theory has shifted away from a focus on *r*- and *K*-selection, the themes of density-dependent regulation, resource availability, and environmental fluctuations are integral to current demographic theory and are potentially important in any natural system.

Key words: adaptation; demography; density dependence; environmental variability; life-history evolution; Poecilia reticulata; r- *and* K-*selection; resource availability.*

INTRODUCTION

This explanation was suggestive and influential but incorrect.

—Stearns (1992:206)
(commenting on *r*- and *K*-selection)

Physics has frictionless hockey pucks, thermodynamics has Carnot engines, and evolutionary ecology has r- and K-selection.

—Mueller (1997:270)

These two quotes represent alternative opinions about a concept that played a major role in motivating empirical researchers to study the evolution of life histories. Stearns' sentiment is more representative of current feelings than Mueller's, but Mueller's point is important. First, both authors accord *r*- and *K*-selection its due credit for motivating interest in this subdiscipline. Second, Mueller points out that, while *r*- and *K*-selection may not represent the real world, it contains an element of reality worth retaining in current re-

search. This caricature of reality and the popularity of the model contributed to *r*- and *K*-selection's development as an important paradigm in evolutionary ecology.

Our goals are to (1) review the historical context in which *r*- and *K*-selection was proposed, (2) explain reasons why it was influential in the field of life-history evolution, but later criticized, (3) present some modern manifestations in life-history theory of important elements of *r*- and *K*-selection, and finally, (4) illustrate how these elements appear to be playing a role in our own study system.

THE DEVELOPMENT OF *r*- AND *K*-SELECTION AS A PARADIGM OF LIFE-HISTORY EVOLUTION

When the theory of *r*- and *K*-selection was proposed, the field of life-history evolution was a nascent discipline (Korfiatis and Stamou 1994). Seminal papers by Cole (1954) and Lack (1954) laid the foundations of the field years earlier, but critical mass had not yet been attained. Both workers addressed the problem of why organisms show reduced or delayed reproduction and argued that life-history traits should be studied as adaptations (Real and Levin 1991). Their approach reflected the wider interest in adaptation that followed

SPECIAL FEATURE

TABLE 1. Pianka's correlates of *r*-selection and *K*-selection (adapted from Pianka 1970).

Feature	*r*-selection	*K*-selection
Climate	variable and/or unpredictable	fairly constant and/or predictable
Mortality	often catastrophic, nondirected, density independent	more directed, density dependent
Surivorship	often Type III Deevey survivorship curves	usually Type I or II Deevey survivorship curves
Population size	variable in time, nonequilibrium	fairly constant, equilibrium
Intra- and interspecific competition	variable, often lax	usually keen
Relative abundance	often does not fit broken stick model	usually fits broken stick model
Favored by selection	1) rapid development	1) slow development, greater competitive ability
	2) high r_{max}	2) lower resource thresholds
	3) early reproduction	3) delayed reproduction
	4) small body size	4) larger body size
	5) semelparity	5) iteroparity
Length of life	short	long
Leads to	productivity	efficiency

the modern synthesis and the engineering focus of the postwar years (Kingsland 1985). Moreover, by that time, the tools of population ecology (Lotka 1925, Pearl 1925, Leslie 1945) had advanced enough to allow for quantitative analyses of adaptations (Cole 1954, Brown 1991). Despite contributions of these authors and the empirical work they stimulated, the field of life-history evolution would require development of the concept of *r*- and *K*-selection before it truly blossomed.

The theory of *r*- and *K*-selection was proposed and popularized by MacArthur and his colleagues in the 1960s and early 1970s (MacArthur 1962, 1972, Cody 1966, MacArthur and Wilson 1967, Pianka 1970). MacArthur and Wilson (1967) envisioned an island, when first colonized, as having abundant resources. As the environment became fully occupied, resources would become limiting. They therefore felt that the kind of selection that organisms experienced would change over time and would be associated with the amount of density-dependent regulation or resource limitation experienced by a population.

These basic ideas could also be applied to mainland populations. All organisms experience fluctuations in population size to varying degrees. Frequent declines in population size, caused by factors such as regular or irregular fluctuations in climate (e.g., seasons or storms) will cause populations to experience density-independent mortality, followed by abundant resources and high population growth rates as they recover from declines. In expanding populations, selection would favor individuals with a high capacity for increase in population size. MacArthur and Wilson referred to this scenario as ''*r*-selection,'' invoking the parameter from the logistic equation for per capita population growth when population size is near zero. Alternatively, organisms in more stable environments tend to remain close to their carrying capacity. These organisms would experience density-dependent mortality and would be consistently exposed to intense intraspecific competition. This regime of selection was termed ''*K*-selec-

tion'' after the parameter for carrying capacity. The term *K* implies selection for traits that favor individual persistence in the face of scarce resources and high intraspecific competition, the kinds of conditions believed to prevail when populations remain close to their carrying capacity. These ideas had been expressed earlier (e.g., Dobzhansky 1950), but the *Island Biogeography* monograph was most responsible for popularizing them. Even though MacArthur and Wilson (1967) popularized this concept, it is surprising to see how sparse their predictions were for the way organisms would evolve in response to *r*- or *K*-selection. The substance of their predictions is limited to a single paragraph (p. 149) in which they suggest that *r*-selection will favor a capacity to rapidly acquire resources and convert them into offspring, while *K*-selection will favor the evolution of efficiency in resource utilization.

Pianka (1970) applied *r*- and *K*-selection to the evolution of life histories by making explicit predictions for how individual life-history traits would evolve in response to differences between *r*- and *K*-environments (Table 1). For example, a resource-rich, noncompetitive, *r* environment selects for traits that enhance population growth rate, including early maturity, small body size, high reproductive effort, high fecundity, and semelparity. Conversely, resource-limited, competitive, *K*-environments select for traits that enhance persistence of individuals, including delayed maturity, large body size, high investment in individual maintenance at the cost of low reproductive effort, low fecundity with a large investment in each offspring, and longer life span. These alternative constellations of life-history traits became known as life-history strategies (Pianka 1974). Pianka envisioned environments that might fluctuate in the extent to which they exerted *r*- or *K*-selection and organisms as falling on a continuum from pure *r*- to pure *K*-selection, depending on the extent to which they experienced either of these two alternatives. The discovery and description of such alternative life-history strategies quickly became a
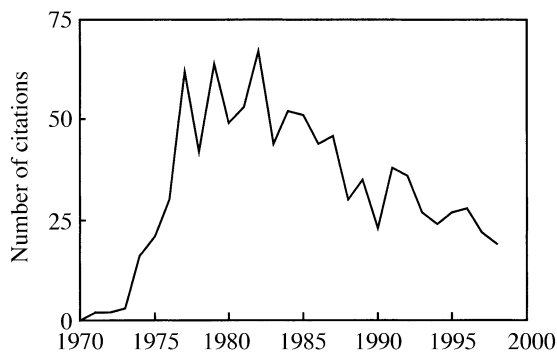
FIG. 1. The number of citations per year of Pianka's (1970) application of the concept of r- and K-selection to life-history evolution. Data gathered from Science Citation Index, 1970–2001.

leading endeavor in the empirical study of life histories. One measure of Pianka's influence is the frequency with which his paper was cited (Fig. 1). While the citation rate peaked in the early 1980s, this paper remains widely cited today. The nature of citations shifted over time, since citations originally emphasized the positive aspect of his predictions, but later became more critical of their oversimplification of life-history evolution (Pianka 1979).

The influence of Pianka's work can also be gauged by the quantity and quality of data that were generated. Review papers provide one measure of the growth of the discipline. For example, Tinkle et al. (1970) included data from 88 species in their comparative study of lizard life histories. A full suite of variables was available for only 37 species. When Dunham et al. (1988) updated this review, they were able to marshal data from 185 populations and 149 species, with a full suite of variables for 122 species.

Popular textbooks reveal how r- and K-selection became a part of general ecology education. All four editions of Ricklefs' *Ecology* textbook (Ricklefs 1973 to Ricklefs and Miller 2000) include r- and K-selection as one model of life-history evolution. The *Ecology* text by Krebs (five editions from 1972 to 2001) places r- and K-selection in a section on competition with only limited discussion of life-history evolution. The focus of Pianka's *Evolutionary Ecology* text (six editions from 1974 to 2000) shifted over time. The first edition (1974) has extensive reference to the concept, including a whole subsection entitled ''r and K selection''. By the sixth edition, Pianka presents a multifaceted categorization of life-history traits (adapted from Winemiller 1992) with r- and K-selection as one axis of variation and ''bet hedging'' as another. As a concept, r- and K-selection appears to be a standard part of ecology texts, but the emphasis on its importance to life-history evolution has diminished somewhat over the past 30 yr.

Why was r- and K-selection influential? One reason is that MacArthur and Wilson (1967) proposed a relationship between density-dependent regulation and evolution. They focused attention on the truism that traits that confer high fitness in one environment (e.g., low-density environment) are not necessarily those that do so in another environment (e.g., high-density environment). Boyce (1984) and Mueller (1997) argue convincingly that this hypothesis had merit. In fact, it is MacArthur and Wilson's correct inference about the importance of density-dependent selection that allowed for Pianka's extension of the theory to become accepted.

The second reason for the influence of r- and K-selection is the intuitive appeal of Pianka's (1970) table (Table 1). Pianka extended MacArthur and Wilson's theory to the evolution of life histories. Specifically, he predicted how life-history traits would evolve in response to selection for high population growth rates vs. high population densities. Although Pianka's predictions do not follow directly from MacArthur and Wilson's presentation of r- and K-selection, they make sense in terms of population dynamics. In fact, Pianka developed his table for presenting r- and K-selection to his elementary population biology class at the University of Texas at Austin (Pianka 1979). Many criticisms of r- and K-selection were inspired by the uncritical application of these predictions to empirical studies.

Williams' (1966*a, b*) contemporaneous model acted synergistically with r- and K-selection to stimulate the development of the field of life-history evolution. Williams focused on the trade-off between current investment in reproduction and future prospects of reproductive success. His subdivision of reproductive value into reproductive effort and residual reproductive value was important for its emphasis on the role of costs and benefits in shaping life-history evolution. Williams neither invoked a mathematical constraint nor attempted to dichotomize a continuum of life histories, but simply emphasized the balance between current and future investment. We are not concerned with the relative importance of Williams' vs. MacArthur and Wilson's contributions in the development of life-history research, in part because they overlap. For example, the notion of trade-offs, such as between maintenance and reproduction, is present in both models. Empiricists were more inclined to cite r- and K-selection as the cause of observed patterns, yet the same papers (e.g., Derickson 1976) often invoked the sort of cost–benefit approach proposed by Williams.

Finally, the theory of r- and K-selection was influential to the field of life-history evolution because it appealed to a desire to enumerate laws of nature. One goal of science that was championed by MacArthur was to find generalizations that allow us to understand the world. By focusing on differences in the degree of density dependence as the major selective difference between populations, it becomes possible to distribute organisms on an axis of density dependence and predict

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the optimal phenotypes. Moreover, the potential to classify life histories as strategies simplified the otherwise complex morass of individual life-history traits.

The theory of *r*- and *K*-selection as presented by MacArthur and Wilson (1967) and extended by Pianka (1970) fits Kuhn's (1970:10–11) definition of a paradigm. First, it was sufficiently unprecedented to draw biologists to the study of life-history evolution. Second, it was sufficiently open ended to create a diversity of questions for future investigators to resolve. Pianka's (1970) citation history (Fig. 1) reflects the new paradigm's development. The advent of the *r–K* paradigm created the critical mass that initiated the growth of life-history evolution into a subdiscipline of evolutionary biology. Its status as a paradigm was short lived, yet the subdiscipline of life-history evolution continues to grow.

CRITIQUE OF THE *r*- AND *K*-SELECTION PARADIGM IN THE FIELD OF LIFE-HISTORY EVOLUTION

Derickson's (1976) comparison of the life histories of the lizards *Sceloporus undulatus* and *S. graciousus* serves well as an example of both positive and negative aspects of some of the empirical research that was stimulated by the theory of *r*- and *K*-selection. Prior research had shown that *S. undulatus* matures at an earlier age and produces more clutches of eggs per season than *S. graciousus*. On this basis, *S. undulatus* was classified as *r*-selected and *S. graciousus* was classified as *K*-selected, at least relative to each other. Derickson then made predictions about fat metabolism, efficiency of resource utilization, reproduction, and the nature of the environment (e.g., productivity) based upon their *r*- or *K*-selected life histories. For example, he predicted that food availability would be greater for *S. undulatus* and that, as a result, they should have higher levels of lipid reserves. He also predicted that *S. undulatus* should have a higher rate of lipid utilization when food is scarce and that they should be less efficient at extracting energy from food. Finally, this species should produce more offspring per season and expend fewer resources per offspring. These predictions were mostly upheld by Derickson's results.

What is wrong with this approach? Rather than building an argument for life histories as an adaptation to the environment, life histories were categorized on the basis of a cursory description, then used as a basis for further predictions about the metabolism and environment of the organism. All the features of the environment that we now think of as being important in selecting for life-history adaptations were never evaluated. For example, Derickson's hypotheses rested primarily on the assumption that food was more abundant for the *r*-selected species; however, evaluation of this assumption was quite superficial. Moreover, nothing was known about population dynamics, the degree to which population sizes fluctuated over time, density-dependent regulation, or the degree to which either

species was subject to density-dependent selection. Other possible mechanisms of selection that could be equally effective in selecting for these life histories, such as predation, were not considered. Theory had already demonstrated that an adaptive response could be a function of the age specificity of mortality (Gadgil and Bossert 1970), but the age structure and the degree to which mortality factors might be age specific in their action were not known for these populations.

On the positive side, Derickson's study of metabolism and fat storage represented a focus on physiological mechanisms that can mediate life-history evolution; he was ahead of his time in evaluating these factors on a comparative basis. More generally, investigators were now interested in life histories, resulting in a huge increase in effort devoted to describing organisms' life histories and a broader view of how life histories might evolve.

Criticisms of the application of *r*- and *K*-selection to life-history evolution focused on a lack of scientific rigor and an oversimplified view of the process of natural selection (Stearns 1976, 1977). As exemplified by Derickson (1976), correlation between a rough description of an environment and life-history traits was often seen as sufficient to classify organisms without an evaluation of population regulation or any test of causation (Parry 1981, Stearns 1992). Moreover, the focus on density-dependent vs. density-independent selection neglected other important agents of selection. As early as 1974, Wilbur et al. voiced this opinion: "we are convinced that attempts to explain life histories as outcomes of single selective pressures, however simple and appealing, have obscured rather than elucidated the evolution of life histories" (p. 806). These authors argued that other factors, such as environmental variability and predation, must play a role in life-history evolution.

It is important to distinguish between MacArthur and Wilson's (1967) original presentation of the model vs. Pianka's (1970) application to life-history evolution. The original theory correctly indicated that fitness would be associated with different traits under density-dependent vs. density-independent selection (Boyce 1984, Mueller 1997). Unfortunately, the life-history differences proposed by Pianka (Table 1), while appealing, do not necessarily follow logically from MacArthur and Wilson's original theory. Specifically, the traits attributed to *K*-selection are not readily justifiable on their own, but instead represent a contrast to traits attributed to *r*-selection. The lack of concordance between *r*- and *K*-selection and life-history differences postulated by Pianka has been borne out by both experimental and observational studies. For example, Mueller and his colleagues derived *r*- and *K*-selected lines by rearing replicate populations of fruit flies (*Drosophila melanogaster*) at persistently high or low densities. The *r*-selected lines evolved a higher capacity to increase in population size at low densities, but a

lower capacity for increase at high densities (Mueller and Ayala 1981, Mueller et al. 1991). *K*-selected lines evolved more competitive larvae (Mueller 1988). The important attributes of the *K*-lines are that they feed at a higher rate (Joshi and Mueller 1988) and pupate at a greater height above the medium than do *r*-lines (Mueller and Sweet 1986). These attributes are consistent with Pianka's (1970) and MacArthur and Wilson's (1967) prediction for the evolution of competitive ability under *K*-selection, but not with Pianka's prediction for the evolution of specific life-history strategies. Similarly, Bradshaw and Holzapfel's (1989) experimental work on natural populations of pitcher-plant mosquitoes (*Wyeomyia smithii*) that experienced consistent differences in population density showed differences in competitive ability, but no differences in life-history traits. These studies thus vindicate MacArthur and Wilson's proposal that density dependence can act as an agent of selection. They do not support Pianka's extension of this theory to the evolution of life-history strategies.

The evolution of specific life-history traits can be more fully explained by age-specific demographic models that provide a mechanistic link between a selective pressure and the optimal life histories. Below, we briefly review these models. Specifically, we demonstrate how life-history theory rose to the challenge of including multiple selective factors and how themes associated with *r*- and *K*-selection are viewed in the context of current theory.

SHIFTING PARADIGMS: THE RISE OF DEMOGRAPHIC THEORY

The primary alternative to *r*- and *K*-selection is labeled as ''demographic theory'' (Stearns 1992) because of its emphasis on age-structured populations and frequent use of the Euler equation and the Leslie matrix as a basis for modeling life-history evolution. Influential early examples of this approach include Gadgil and Bossert (1970), Schaffer (1974*b*), Law (1979), Michod (1979), and Charlesworth (1980). An important feature of such demographic models is that the pattern of life-history evolution depends strongly on which age groups are influenced by selection (Fig. 2). All models cited here envisioned extrinsic mortality, rather than resource availability or other sources of density-dependent regulation, as the major agent of selection. Models were developed to predict how individual aspects of the life history, such as age at maturity or age-specific reproductive effort, would evolve in response to selection. For example, increased adult mortality rates were predicted to favor genotypes that mature earlier and had higher reproductive effort (Fig. 2B). If, instead, juvenile mortality is increased, then selection was predicted to favor genotypes associated with delayed maturity and decreased reproductive effort (Fig. 2C).

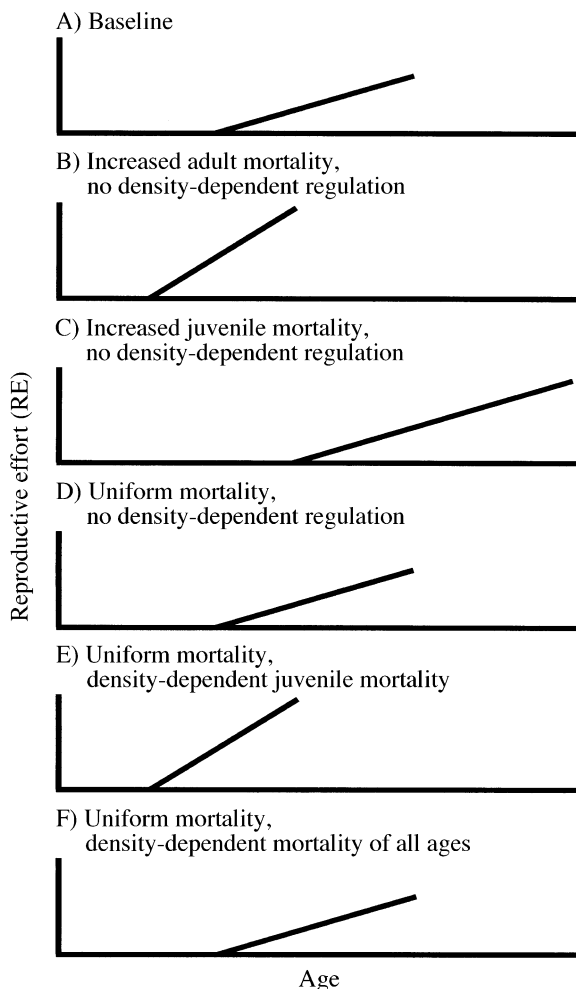Early demographic theories tended to assume that

FIG. 2. Graphical representation of predicted changes in optimal reproductive effort (RE) of a generalized life history as outlined in Charlesworth (1980). RE is defined as the proportion of resources allocated to reproduction as opposed to investment in growth or survival. The age at which RE increases from zero indicates age at maturity. The linearly increasing depiction of RE with age is arbitrary, and plot A is the baseline iteroparous life history. Plots B–D give predictions for unregulated populations growing exponentially (see Gadgil and Bossert 1970) after: (B) mortality increases only for older age classes (earlier age at maturity and higher RE at each age), (C) mortality increases only for younger age classes (later age at maturity and lower RE at each age), and (D) mortality increases uniformly across all ages (no change from baseline). Plots E and F give predictions for regulated populations subjected to density dependence (see Michod 1970): the effect of a uniform increase in mortality when density dependence affects (E) only juveniles (note the increase in RE over baseline and earlier age at maturity) vs. (F) all ages (no change from baseline).

populations were not subject to density-dependent selection, the agent of selection assumed by MacArthur and Wilson (1967). The most fit genotype, and hence the one favored by natural selection, had the highest rate of increase in population size. Such models were modified in a variety of ways in an effort to make them

more biologically realistic. One early effort at such a modification was to incorporate density-dependent population regulation (Michod 1979, Charlesworth 1980), or to assume that resources could be limiting, so that the intrinsic rate of increase might not be an appropriate index of fitness. A second approach was to directly incorporate the effects of resource availability on growth or fecundity (e.g., Kozlowski and Wiegert 1987). A third alternative was to incorporate indirect effects of mortality agents, such as predation. Predator-induced mortality can reduce density, and hence increase resource availability (Abrams and Rowe 1996). Finally, models have incorporated either temporal or spatial variation in environmental conditions (e.g., Kawecki and Stearns 1993).

When density-dependent population regulation is incorporated in demographic models, the predicted optimal life history often becomes a function of how density dependence is modeled. For example, Charlesworth (1980) found that an increase in mortality rate uniformly distributed across all age classes will not select for a change in optimal reproductive effort or age at maturity in the absence of density-dependent regulation (Fig. 2D). However, if increased density causes a selective increase in juvenile mortality rate, the same uniform increase in mortality is predicted to select for earlier maturity (Fig. 2E). If increased density instead causes a uniform increase in the mortality rate of all age classes, then adding density dependence does not change the predictions from a model that assumes no density-dependent regulation (Fig. 2F). It thus appears that some form of heterogeneity among age classes must exist for there to be a change in the optimal life history, but that this heterogeneity may be due either to mortality caused by external factors or to density-dependent population regulation.

Incorporating effects of density through density-dependent population regulation is subtly different from invoking density-dependent selection (Prout 1980). Density-dependent population regulation refers to phenotypic changes in the life history in response to density that cause negative feedback on population growth rates (cf. Hixon et al. 2002). For example, increased density could cause reduced individual growth rate, delayed maturity, reduced fecundity, or increased mortality rates. Density-dependent selection refers to differential fitness of genotypes as a function of population density. MacArthur and Wilson (1967) saw consistent differences in population density as being a key type of selection causing evolutionary differences between populations.

Including density-dependent regulation in models of life-history evolution can change the way fitness is evaluated and requires assumptions concerning the way density dependence is represented. The maximum rate of population increase is the index of fitness in models without density-dependent regulation, but may no longer be an appropriate index of fitness in models with density-dependent regulation because populations are no longer free to grow exponentially. Some authors have adopted lifetime reproductive success (R_0) or K as indices of fitness, meaning that natural selection might maximize either of these quantities, rather than r, in response to selection under density limitation (cf. Roff 1992, Brommer 2000). In addition, density-dependent regulation can be achieved by manipulating vital rates in a diversity of ways. The mechanism of density regulation can determine which index of fitness is appropriate. For example, r is a valid fitness criterion under density regulation if the population is regulated by density-dependent effects that affect each individual (or age class) identically (Pasztor et al. 1996). R_0 is appropriate as an index of fitness if the population is regulated by density-dependent juvenile mortality (Mylius and Diekmann 1995). A different approach to defining fitness is to use the invasibility criterion. In this case, the fittest phenotype is one that cannot be invaded (an evolutionarily stable strategy, Maynard Smith 1972). While more complicated to use, this criterion has the advantage that it is robust in scenarios where density dependence, frequency dependence, or environmental stochasticity are important (Metz et al. 1992, Mylius and Diekmann 1995, Benton and Grant 1999).

An alternative way of incorporating environmental influences into life-history models is to include the effects of resource availability. MacArthur and Wilson (1967) predicted that resource limitation (K-selection) favors individuals that are more efficient at resource utilization. Subsequent theory does not yield a general prediction for how changes in resource availability affect the evolution of life-history traits. For example, while Gadgil and Bossert (1970) argued that reduced resource availability would select for a later age at maturity and lower reproductive effort, Kozlowski and colleagues (Kozlowski and Uchmanski 1987, Kozlowski and Wiegert 1987) predict the opposite change in life history in response to reduced resource availability. The discrepancy between these predictions is due to the use of a different fitness criterion and different assumed relationships between resource availability and age-specific survival and fecundity.

A different way of improving the match between models and the real world is to consider indirect effects of predation (e.g., Abrams and Rowe 1996). One possible indirect effect is that increased mortality will reduce density and, as a consequence, increase resource availability to the surviving individuals. Under density-independent assumptions, high predation will generally select for a decrease in the age and size at maturity. However, if high predation causes a substantial increase in individual growth rate as an indirect effect, then it can select for an increase in the size at maturity. The important feature of the model is that it makes explicit how there can be an interaction among factors that cause life-history evolution, in this case between extrinsic mortality and resource availability. Such indi-

rect effects have already been investigated in ecological contexts, but their evolutionary consequences have not yet been fully considered (Wootton 1994).

A fourth way of making models more realistic is to include the effects of temporal variation in resource availability, in part to address one of the presumed mechanisms that underlie r- and K-selection. In an environment that fluctuates during the lifetime of the organisms, the appropriate fitness measure relates to the variance in r (Roff 1992). Early examinations of fluctuating environments showed that variability in juvenile survival or fecundity leads to iteroparous life histories, while variation in adult mortality leads to semelparous life histories (Murphy 1968, Schaffer 1974a). However, later analyses showed these results to be a special case, and that predicting the direction of life-history evolution requires knowing the absolute amount of environmental variability and the temporal correlation of vital rates (Orzack and Tuljapurkar 1989, Tuljapurkar 1990). Nevertheless, a variable environment can select for dramatically different life histories from a constant environment (Benton and Grant 1996). The selective effect of a variable environment is likely to be most significant when (1) there is a high cost of reproduction on adult survival or (2) life histories are extreme (very high or low reproductive effort) in a deterministic setting.

Environmental variation in vital rates (e.g., mortality or birth rate) can influence the way density-dependent selection affects the evolution of life histories (Benton and Grant 1999, Grant and Benton 2000). Benton and Grant (1999) simulated the effects of stochasticity and density dependence in vital rates on the evolution of reproductive effort and found that density dependence and stochasticity interact, leading to either increased or decreased reproductive effort. A generalization of this result is that when density dependence and stochasticity affect the same vital rate, the amount of effort channeled to that rate increases to insulate the organism from the negative effects of density dependence and environmental variability. Thus, reproductive effort can decrease if survivorship is affected by both density dependence and stochasticity, whereas it will increase if fecundity is affected.

A universal feature of all these models is that environmental effects operate through age- or stage-specific effects. Thus, density-dependent regulation or stochastic effects interact with demographic selection, so that the predicted optimal life history is a function of both demographic selection and the way these additional environmental effects are manifested. A common theme in all these models is that changing the mode of density-dependent regulation (e.g., reduced fecundity vs. increased mortality) can change the predicted optimal life history. Furthermore, predictions from most of these models depend upon the shape of the relationship between environmental effects (e.g., resource availability, stochasticity) and vital rates. Predicted

outcomes are no longer the simple alternatives proposed by early modeling efforts. Pianka's (1970) simple attractive paradigm that was so appealing to empiricists has thus been replaced by a complexity of alternatives that can only be correctly applied if a great deal is known about an organism and its environment.

LIFE-HISTORY EVOLUTION IN GUPPIES: THE POTENTIAL ROLE OF MULTIPLE SELECTIVE PRESSURES

Our own work involves experimental studies of life-history evolution in guppies (*Poecilia reticulata*). Our work was initially motivated by the apparent fit between models that focused on the impact of age-specific mortality and differences in mortality rates among natural populations of guppies. However, as we learn more about the system, density dependence, resource availability, and environmental fluctuations have arisen as factors that could be playing an important role in the evolution of guppy life histories. Before explaining why, we will summarize some earlier work, which makes a strong case for predator-mediated mortality being an important agent of selection.

We have focused on natural populations from the Northern Range Mountains of Trinidad and the contrast between high- and low-predation sites that was first described by Haskins and colleagues (1961), then examined by Endler (1978, 1980) in his study of effects of predators on evolution of color patterns in male guppies. High-predation environments are those in which guppies co-occur with larger species of fish, such as the pike cichlid (*Crenicichla alta*), that frequently feed on guppies. Low-predation environments are found in the same drainages, but upstream of rapids or waterfalls that exclude the larger species of predators. At these sites, guppies co-occur with just the killifish (*Rivulus hartii*). *Crenicichla* is a more efficient forager on adult guppies, while *Rivulus* is limited to feeding on juvenile guppies (Seghers 1973, Liley and Seghers 1975). This difference in age-specific mortality risk formed the basis for our initial hypothesis about the evolution of life-history traits in guppies: guppies from high-predation locales should mature at an earlier age and have a higher reproductive effort (Fig. 2B) than their counterparts from low-predation environments (Fig. 2C; following demographic models such as Gadgil and Bossert 1970 and Law 1979).

Several lines of evidence support these predictions, including:

1) Comparative studies of the life-history phenotypes of wild-caught guppies from a large number of natural populations (Reznick and Endler 1982, Reznick 1989).

2) Laboratory comparisons of the genetic basis of these life-history patterns, again from a series of high- and low-predation environments (Reznick 1982).

3) Convergence of these same life-history patterns in a series of localities on the northern slope of the

Northern Range Mountains in Trinidad, where guppies are again found in high- vs. low-predation environments, but where species of predators differ almost entirely from those on the south slope (Reznick and Bryga 1996, Reznick et al. 1996*b*).

4) Statistical analyses that demonstrate that predation is the dominant factor associated with differences among localities in life-history phenotypes in spite of environmental covariates (Strauss 1990).

5) Replicated introduction experiments that demonstrate that a change in mortality rate is associated with the rapid evolution of life-history patterns in the predicted direction (Reznick and Bryga 1987, Reznick et al. 1990, 1997).

In spite of this strong case for age-specific mortality, we have also found a potential role for density dependence, resource availability, and environmental fluctuations. We will examine each of these potential effects in turn.

Role of density dependence

In our analysis of age-specific mortality as the mechanism of selection on guppy life histories, we found an overall difference in mortality rates between *Crenicichla* and *Rivulus* locales, but no difference in size-specific mortality (Reznick et al. 1996*a*). One interpretation of this result is that there are also no differences among high- and low-predation sites in age-specific mortality, or that guppies of all age classes in high-predation sites suffer a uniform increase in mortality rate in comparison to low-predation sites. Classic demographic theory predicts that in density-independent populations or in populations where density-dependent regulation affects all ages equally, a uniform change in mortality rate will not select for any change in reproductive effort or age at maturity (Gadgil and Bossert 1970). However, if density dependence acts by affecting juvenile survivorship, then a uniform increase in mortality will select for early maturity and higher reproductive effort (Charlesworth 1980; Fig. 2E). Thus, although we have established that guppies have evolved in response to the different predation regimes, the original mechanism of selection we assumed may not be correct unless there is also a specific form of density-dependent population regulation.

A different argument for the potential role of density dependence in the evolution of guppy life histories comes from our simulations of the introduction of guppies from high-to-low vs. low-to-high-predation environments. We used our data from mark–recapture studies to characterize the life histories and environments of guppies (Reznick et al., *in press*). We assumed that growth and mortality rates characterize the environment and that age/size at maturity and fecundity characterize the life history. While this division between genotype and phenotype is not precise, it serves well as a first estimate in modeling guppy population biology. Our simulations (Table 2) consider first how

TABLE 2. Results of simulated introductions of guppies between low- and high-predation environments.

| From | To | Probability of extinction after | | | |
		1 yr	2 yr	3 yr	Survivors
High	high	0/20	1/20	4/20	97
High	low	0/9	—	—	1000
Low	low	0/20	0/20	0/20	320
Low	high	0/20	4/20	15/20	11

Notes: Each population was initiated with 150 individuals. Twenty populations were initiated for all combinations except the introduction of guppies from a high- to a low-predation environment, which contained only nine populations. These were individually based simulations in which each individual was assigned a growth increment, probability of survival, probability of reproduction, and fecundity based upon data collected in mark–recapture studies of natural populations. Listed are the probabilities of extinction 1, 2, and 3 yr after the initiation of the population, and the mean population size after 3 yr, not including populations that have gone extinct. Results are recorded differently for the "High to Low" combination because all nine populations exceeded 1000 individuals within 1 yr (after Reznick et al., *in press*).

well each type of guppy population survives in its own environment, and then how each would do if introduced into the other environment. Simulated populations of guppies from high-predation environments are predicted to have higher population growth rates than those from low-predation environments in either high- or low-predation localities. If this prediction is true, then why does the low-predation life history evolve? We have shown in replicated introduction experiments that the low-predation life history does evolve when guppies are transplanted from high-predation localities to previously guppy-free low-predation localities (Reznick and Bryga 1987, Reznick et al. 1990, 1997). One possible reason for the discrepancy between these simulations and the real world is that density dependence is not taken into account. In fact, a recent demographic analysis (Bronikowski et al. 2002) has shown that when incorporating density-dependent effects both high- and low-predation life histories have equal fitness in their own environment.

We are using laboratory and field experiments to better understand the role of density dependence in guppy populations. In the field, we have manipulated density in natural populations to characterize how density-dependent regulation is manifested. Our dependent variables are size (age)-specific mortality rate, growth, and fecundity (D. Reznick and F. H. Rood, *unpublished manuscript*). In the lab, we have explored the effects of density on growth and life-history traits in both single stock and interpopulation competition experiments (M. Bryant and D. Reznick, *unpublished manuscript*). These studies will provide information not only about how density-dependent regulation acts, but also with regard to whether populations have experienced differential degrees of density-dependent selection.

Role of resource availability

We have also found a potential role of resource availability, either as a consequence of environmental factors that are correlated with, but otherwise independent of predators, or as a consequence of indirect effects of predation (Reznick et al. 2001). Many of these conclusions are derived from an intensive study of 14 pools, seven each in high- and low-predation localities, distributed among three different high- and low-predation streams. Our work revealed that, on average, high-predation localities had higher light levels and higher levels of primary productivity than low-predation localities. These differences were present because high-predation localities tend to be higher order streams, which means that they are wider and have larger light gaps in the forest canopy. Such differences are correlated with, but independent of, predation. We also found that the size distribution of guppies from high-predation sites was smaller, on average, than low-predation sites. Rodd and Reznick (1997) found the same difference in a different series of guppy collections, mostly from a different series of localities. This difference in population structure is an indirect consequence of predation, since predators cause higher mortality rates and higher birth rates. This difference in size distribution results in high-predation streams having only one quarter of the guppy biomass per unit area of stream, which should in turn lower demand for resources. This indirect consequence of predation will have the same impact on resource availability as the correlated environmental effects, so that guppies from high-predation environments should have higher levels of resource availability than those from low-predation environments.

If guppies from high-predation environments indeed have higher levels of resource availability, then we would predict evidence for this in elevated growth rates. In the field, we found that high-predation guppies tended to grow faster and to have larger asymptotic body sizes (Reznick et al. 2001). Both of these differences parallel what happens in the laboratory when guppies are fed more food. Other aspects of our laboratory studies indicate that these differences in growth rate and asymptotic body size do not have a genetic basis and are hence likely to be attributable to environmental effects, with resource availability being a likely cause.

Grether et al. (2001) demonstrate that resource availability can be evaluated independently of predation. They evaluated guppies from a series of low-predation environments that differ in stream size and canopy cover. Larger streams have more open canopies and higher levels of primary productivity. The guppies from these streams have significantly higher growth rates. Increased stream size without increased predation can thus cause increased resource availability, increased growth rates, and perhaps the evolution of life-history traits in response to resource availability independently of predation.

In summary, guppies from high-predation environments experience higher resource availability for two reasons. First, differences in the physical environment result in high-predation pools having higher levels of primary productivity. Second, indirect effects of predators influence guppy size distribution and density. We have begun to develop a dynamic optimization model of resource allocation specific to guppies (F. Bashey, U. Dieckmann, and D. Reznick, *unpublished manuscript*) to determine the effects these resource differences are likely to have on the evolution of guppy life-history traits. Our aim with this model is to identify the assumptions and functional relationships critical in selecting for differences in life histories, so that we can more effectively test the predictions of this model in the field.

Role of environmental fluctuations

Guppies exist in a seasonal environment characterized by temporal cycles in rainfall. In the dry season, resources for guppies are relatively plentiful, whereas in the rainy season resources are scarce (Reznick 1989). What effect does this predictable source of environmental fluctuation have on guppy life histories? One possible effect is the evolution of adaptive phenotypic plasticity (Boyce 1979, Orzack 1985). Female guppies respond to low food or fluctuations in food availability by producing larger offspring that have a higher fat content and that potentially grow and survive better in a low-food environment than smaller offspring (Reznick and Yang 1993; F. Bashey, *unpublished manuscript*). Moreover, the level of plasticity can differ between guppy populations (F. Bashey, *unpublished manuscript*). It is possible that the degree of environmental variability or the effects of this variation on demographic rates has selected for interpopulational differences in plasticity. Our current understanding about the influence of environmental stochasticity in the guppy system is limited. However, we have recently undertaken a mark–recapture study to quantify both temporal and spatial fluctuations across two low-predation and two high-predation locales. Although this study is still in progress, we have found that populations differ in their propensity to fluctuate in density or suffer local extinctions (M. Bryant, *unpublished manuscript*).

In conclusion, while there is a strong case for predation as the agent of selection for the evolution of guppy life-history patterns, circumstantial evidence suggests that density-dependent regulation, resource availability, and environmental variability also play an important role. We consider such compounded effects of different selective factors to be inevitable in natural systems. A greater challenge is evaluating the relative importance of these different factors in shaping the evolution of life histories. A more general challenge is reconciling the possibility of multiple causes with our

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preconceived notion that the simplistic application of the scientific method, or evaluation of alternative hypotheses, is the key to establishing causality. A too rigid interpretation of this approach leads one to expect that there really are single explanations for all phenomena. In fact, a more universal lesson from empirical studies of adaptation is that causal analyses reveal multiple, potentially interacting factors as contributing to the shaping of any feature of an organism, be it the ADH polymorphism in *Drosophila* (Chambers 1988), shell banding in *Cepea* snails (Jones et al. 1977), industrial melanism in *Biston betularia* (Kettelwell 1973, Majerus 1998), or life-history patterns of guppies.

CONCLUSIONS

r- and *K*-selection played a key role in stimulating empirical and theoretical work on life-history evolution. The theory as presented by MacArthur and Wilson (1967) and extended by Pianka (1970) was sufficiently compelling to draw biologists to the study of life histories. In fact, the acquisition of the *r*–*K* paradigm can be viewed as the sign that the study of life-history evolution had advanced enough to be considered its own subdiscipline (Kuhn 1970). The distinguishing feature of the *r*- and *K*-selection paradigm was the focus on density-dependent selection as the important agent of selection on organisms' life histories. This paradigm was challenged as it became clear that other factors, such as age-specific mortality, could provide a more mechanistic causative link between an environment and an optimal life history (Wilbur et al. 1974, Stearns 1976, 1977). The *r*- and *K*-selection paradigm was replaced by new paradigm that focused on age-specific mortality (Stearns 1976, Charlesworth 1980). This new life-history paradigm has matured into one that uses age-structured models as a framework to incorporate many of the themes important to the *r*–*K* paradigm. The controversy surrounding the *r*–*K* paradigm did temporarily overshadow the potential importance of density dependence, resource limitation, and environmental fluctuations as components of selection. More current theory views these factors as interacting with each other as well as with density-independent factors or extrinsic mortality to shape the evolution of life histories.

If the field of life-history evolution is now working under a new paradigm, how far have we come? Clearly the idea that several factors interact to shape life histories was recognized early on (Ashmole 1963). However, by focusing on a continuum of density dependence and dichotomizing suites of life-history traits, the *r*–*K* paradigm brought a lot of excitement to the empirical study of life histories. As empirical studies progressed, it became clear that the predictions of *r*- and *K*-selection were not always upheld and that the underlying assumptions (density regulation) were not easily evaluated. This dose of reality helped the field develop a more rigorous theory to approach the evolution of life histories. The predictions of more heavily derived models are often dependent on describing the specific functional form of density regulation or the magnitude of an environmental effect—factors that are hard to measure in natural populations. It is this disparity between theoretical concepts and empirical realities that continues to create a "muddle in life-history thinking" (Ricklefs 2000:13). The challenge now for the current paradigm is to overcome this disparity so that our understanding of life histories continues to progress.

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