

1995. In: *Population Dynamics: New Approaches and Synthesis* (N. Cappuccino and P. Price, eds.), Academic Press, New York.

## *The Dominance of Different Regulating Factors for Rangeland Grasshoppers*

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### I. Introduction

Developing a unified, conceptual framework that explains population fluctuations presents a fundamental and critical challenge to ecologists. Empirically and theoretically, this is a formidable undertaking since so many mechanisms can potentially contribute to population fluctuations, including predation, intraspecific competition, and abiotic-induced mortality. This complexity has largely stifled progress as well as interest in the problem. Yet, these issues underlie all of population ecology and cannot be left unresolved. Though our perspective on each population mechanism is not new, we believe that our integration of these processes, using grasshoppers as model organisms, offers some important resolutions to the general problem of population fluctuations.

Previously, rather than viewing these mechanisms in an integrated fashion, ecologists have viewed one or another of them to be *generally dominant* in controlling most populations in nature and this has led to considerable debate for more than 50 years. However, an approach that integrates these mechanisms does not eliminate the issue of which mechanism dominates in limiting a *particular* population. Given our emphasis on integrating mechanisms, it may seem contradictory to refer to a dominant mechanism; however, we will demonstrate that even when a number of mechanisms are operating together, only one density-dependent mechanism can exert a regulating influence at a time in a population. This does not mean that other mechanisms are unimportant in controlling population size, for they help define which mechanism assumes a dominant regulating influence. For example, holding predation and food availability constant, a population experiencing high abiotic-induced mortality may be regulated by predation, whereas another population with lower abiotic-induced mortality may be food-limited.

Within this integrated approach, it is possible for mechanisms to change in

importance under different environmental conditions, and our approach shifts the focus away from determining which mechanism is *generally* limiting for all populations to defining the environmental and biotic conditions where different mechanisms come to dominate the regulation of a species' population. For example, what conditions lead to a population being limited by predators versus being limited by food resources? Insights gained under this perspective will help to identify which data are most important for assessing population dynamics. Finally, our integrated approach indicates that it is possible to observe alternative stable states for a population that emerge when different conditions (e.g., historical effects) arise in a homogeneous environment or as a heterogeneous environment varies over time.

To evaluate our integrated perspective, we argue that an experimental approach combined with field observations is necessary. Given the environmental variation occurring over time for each population of a species and over space by different populations of the same species, we do not see how the issue of population limitation can be clearly and easily resolved by statistically analyzing large data sets composed of population numbers obtained over time and space in nature (Royama, 1993; Strong, 1984, 1986a,b). Likewise, though experimental population studies can demonstrate how a particular mechanism operates, these results have to be combined with observational studies of field populations to demonstrate whether the experiments provide insights into nature.

In this chapter, we first review data from our studies on grasshoppers that led to our integrated perspective. Second, we develop graphical representations for the operation of different ecological mechanisms. Third, we develop a graphical model of population dynamics that integrates the proposed mechanisms. Fourth, we describe the experimental and observational methods and review representative results from our continuing long-term studies with grasshoppers that are designed to evaluate the model. Finally, we contrast the insights gained by our approach with those provided by others, placing our findings into a general ecological context.

## II. Grasshoppers, a First Visit

We evaluated our integrated perspective using grasshoppers in western U.S. grasslands. Grasshoppers (Orthoptera, Acrididae) and grasslands are well suited for this. Grasshoppers are hemimetabolous so they do not dramatically change their behavior during ontogeny; grasshoppers are easy to observe and enumerate given their body size and high activity; most grasshoppers are not highly specialized herbivores, which ensures that their population dynamics do not rely on changes in the availability of a few plant species; many grasshoppers are regularly abundant, even though their population densities can vary dramatically over

time and space; grasshoppers are important primary consumers; and grasshoppers are a major source of food to many predators, parasitoids, and parasites. Grasslands are structurally simple terrestrial environments compared to forests, making observations of grasshoppers relatively simple, and grasslands vary dramatically in productivity within sites among years and between sites within a year, making evaluation of environmental differences straightforward.

Although the standard notion is that grasshopper densities are related to annual weather (Andrewartha and Birch, 1954, 1984), the population mechanisms associated with weather have not been established. Furthermore, anomalous patterns emerge between weather conditions and grasshopper densities in northern and southern regions. In the south, densities tend to decrease with hot and dry conditions, whereas in the north they tend to increase (Capinera, 1987; Capinera and Thompson, 1987; Capinera and Horton, 1989; Lockwood and Lockwood, 1991). Therefore, our understanding of grasshopper population dynamics may not be as firm as commonly thought.

Background data for assessing the importance of different mechanisms that might be important to grasshopper populations in grasslands come from more than 15 years of experience gained independently by each of the authors at two different sites (Belovsky at the National Bison Range in Montana, a Palouse prairie, and Joern at Arapaho Prairie in Nebraska, a Sandhill mixed-grass prairie). Each of us initially chose a research approach based on the supposition that a single mechanism would dominate the regulation of grasshopper populations at our study sites, but each of us thought that a different mechanism would be important (for Belovsky, food, and for Joern, predation). Eight years ago, we began to discuss our separate studies, because we were coming to disparate conclusions (Belovsky in Montana was observing food limitation and Joern in Nebraska was observing predator, especially avian, limitation). Rather than arguing over who was correct, we wondered what differences between our study sites might explain our diverging conclusions or what each of us might have overlooked.

Our willingness to seek a unifying explanation was obviated because each of us had employed experimental methods that provided unambiguous results. However, we had each employed different experimental manipulations in the different systems. Belovsky in Montana eliminated all predators and varied initial grasshopper density (nymphs) and plant availability in the field to observe how these factors affected adult grasshopper density and reproduction; these values were compared with unmanipulated field populations. Joern in Nebraska eliminated avian predation and compared grasshopper population densities in the presence and absence of birds. Therefore, it was obvious that each of us needed to conduct the other's experiments at our own study sites.

Comparative results on intraspecific competition for food, predation, and abiotic factors that were obtained from common experiments with the most abun-

dant grasshoppers at each site (*Melanoplus sanguinipes*, *M. femurrubrum*, and *Ageneotettix deorum* in Montana and *A. deorum* in Nebraska) are summarized in the following. Other factors (e.g., parasitoids) could be important at some times and places, but our goal was to examine a manageable set of mechanisms that we already suspected to be important, and then use these to construct a general framework for the integration of mechanisms that are simultaneously operating.

#### A. Predators Eliminated and the Initial Grasshopper Density and Plant Availability Varied

These experiments were conducted in small cages (0.1–1.0 m<sup>2</sup>) placed over field vegetation that maintained abiotic conditions for the grasshoppers and plants (Belovsky and Slade, 1993, 1995; Joern and Klucas, 1993). The cages were stocked with grasshopper nymphs at densities comparable to the range of values observed in the field at hatching time. Though the use of small enclosed populations is sometimes criticized as being too artificial, we believe that they provide an important experimental tool for identifying the presence of particular population mechanisms and describing how they operate, because the necessary manipulations cannot be maintained outside of enclosures. The important caveat is that enclosed populations must be contrasted with unmanipulated field populations to ensure that the observations are pertinent.

We obtained many similar results at both sites. First, adult grasshopper density at a given plant availability stabilized at a single constant density, if the initial density of nymphs was sufficiently large (see Fig. 3d). Second, the adult density increased with increasing plant availability in Montana (Fig. 1a), where availability was increased by providing vegetation with supplemental water (Fig. 1b) and/or nitrogen (Schmitz, 1993). *Ageneotettix deorum* densities also increased with supplemental water and nitrogen (J. Moorehead, personal communication). In Nebraska, *A. deorum* densities did not change with supplemental water and/or nitrogen in most years, but decreased in abundance with supplemental water and/or nitrogen in another year (Fig. 1c). However, *M. sanguinipes* increased in abundance with supplemental water and nitrogen (Fig. 1c).

The different responses for *A. deorum* at the two sites may reflect generally lower plant quality in Nebraska. This is supported by measures of plant solubility in HCl + pepsin, which are correlated with digestibility to grasshoppers (Belovsky and Slade, 1995) and plant protein content (Heidorn and Joern, 1987): 20–30% soluble in Nebraska versus 32–41% in Montana in July. The smaller-bodied *A. deorum* needs plants of higher nutritional value than *M. sanguinipes* (Belovsky, 1986; Belovsky and Slade, 1996a), and supplemental water and nitrogen tend to increase plant biomass while diminishing its nutrient content (Belovsky and Slade, 1995; Joern, 1989b, 1990). Therefore, many of the plants in Nebraska, which are nutritionally poorer than in Montana, may become too poor

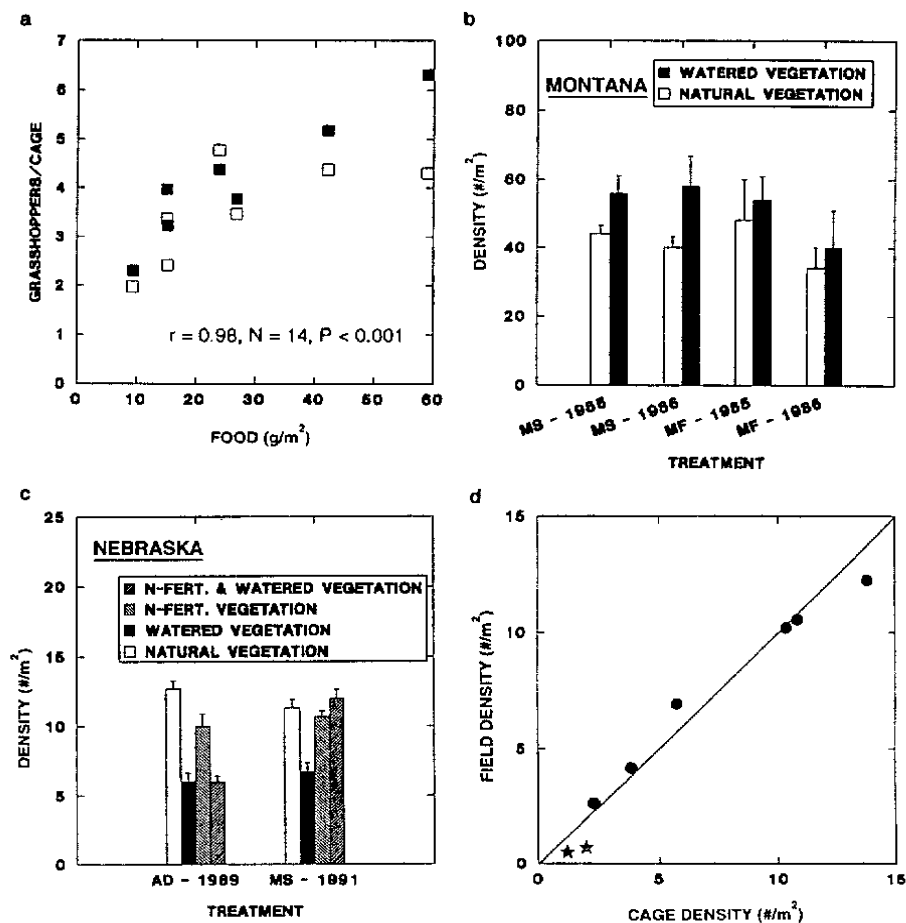


Figure 1. A summary of experimental results using caged populations of grasshoppers. (a) The relationship between grasshopper density and food abundance (product of plant biomass and its solubility in HCl + pepsin, see text) for *M. sanguinipes* (solid squares) and *M. femurrubrum* (open squares) in Montana (Belovsky and Slade, 1995). (b) The effect of supplemental water for vegetation on the survival to the adult stage for *M. sanguinipes* (MS) and *M. femurrubrum* (MF) in Montana (Belovsky and Slade, 1995). (c) The effect of supplemental water and/or nitrogen fertilizer for vegetation on survival to the adult stage for *A. deorum* (AD) and *M. sanguinipes* (MS) in Nebraska (Joern, 1989b, 1990). (d) Comparison of densities attained in cages by *M. sanguinipes* in Montana (circles) (Belovsky and Slade, 1995) and *A. deorum* in Nebraska (stars) (Joern and Klucas, 1993) with field densities. All error bars represent the standard error with sample size equal to 6.

for *A. deorum* to feed upon when they receive supplemental water and nitrogen; whereas the higher-quality plants in Montana may still be of sufficient quality after supplementation.

When constant grasshopper densities obtained in cages were compared with unmanipulated field densities, differences emerged. In Montana, field and experimental population densities were similar (Fig. 1d), indicating that field populations were food-limited (i.e., bottom-up control, *sensu* Hunter and Price, 1992). In Nebraska, the field population densities were lower than experimental densities, indicating that food was not limiting (Fig. 1c). Because the cages did not appreciably modify abiotic conditions (Belovsky and Slade, 1993), differences in density-independent mechanisms cannot explain discrepancies or concordance between cage and field densities.

### B. Elimination of Avian Predators

Avian predation was examined in other experiments (100-m<sup>2</sup> areas covered with netting to exclude birds and not covered) (Joern, 1986, 1992; Belovsky and Slade, 1993). Different average results were obtained at the two sites, but infrequent annual variation was observed. In Nebraska, the densities of all grasshopper species tended to be lower in the presence of birds (7 of 9 years and locations), indicating that birds generally exert a limit on grasshopper densities (Fig. 2a) (top-down control, *sensu* Hunter and Price, 1992). In Montana, the densities of some large-bodied grasshopper species declined in the presence of birds, but the smaller-bodied common grasshoppers increased in abundance with birds (Fig. 2b), indicating that birds did not limit (16 of 18 years and locations), but enhanced the abundance of common species, which is expected if food (bottom-up control) limits their abundance and the larger-bodied species are superior competitors for food (Belovsky, 1986; Belovsky and Slade, 1993).

### C. Our Observations and Support from Elsewhere in the Western United States

The foregoing results indicate the importance of long-term experiments, because our original identification of disparities between the sites was based on neither of us having observed the other's results at our sites (e.g., predator limitation in Montana). However, in recent years we have each observed periodic changes in the dominance of population-limiting mechanisms in particular years and locations. This has led us to ask under what conditions the grasshopper populations might shift between predator- and food-limited regulation.

To assess whether patterns exist between grasshopper populations that were predator-limited versus food-limited, we reviewed literature on grasshoppers from the western United States. We restricted our review to studies that employed field experiments (Fowler *et al.*, 1991; Evans, 1989; Brusven and Fielding, 1990; Wang and Walgenbach, 1989, 1990; Thompson *et al.*, 1989; E. Evans, personal communication; M. Ritchie, personal communication; Bock

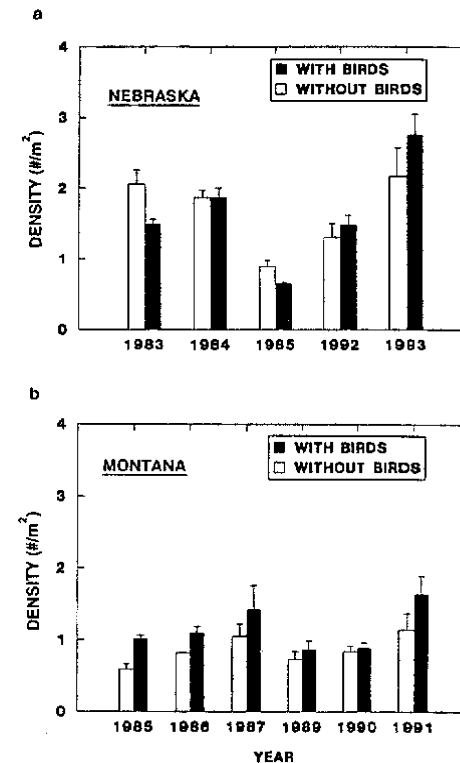


Figure 2. A summary of experimental results using avian exclosures. (a) In most years at one location in Nebraska, in the presence of birds grasshopper numbers decreased or did not change, but in 1993 numbers increased. (b) In most years at one location in Montana, in the presence of birds grasshopper numbers increased (also see Fig. 8d), but in 1992 numbers decreased (Fig. 8c). All error bars represent the standard error with sample size equal to 3.

*et al.*, 1992), and where the data indicated food- or predator-limited populations. Because different methods were often used in these studies, we employed only qualitative comparisons (e.g., density classes, body size classes, evidence for interspecific competition, mainly C<sub>3</sub> or C<sub>4</sub> grasses). The literature review reinforced our emerging conclusions that populations could be either predator- or food-limited and predictable patterns were associated with one or the other mode of limitation. Sites exhibiting predator-limited populations tended to be dominated by small-bodied grasshoppers that have low densities and where C<sub>4</sub> grasses dominate. Sites exhibiting food-limited populations tend to be dominated by large-bodied grasshoppers that have high densities and compete interspecifically and where C<sub>3</sub> grasses dominate.

These patterns translate geographically and taxonomically, because  $C_4$  grasses dominate in the south (Teeri and Stowe, 1976), and Gomphocerine grasshoppers, which generally are small, tend to be more abundant with  $C_4$  grasses (Otte, 1984). Furthermore, these patterns have well-established ecological explanations. Grasshoppers tend to harvest less, and less thoroughly assimilate,  $C_4$  grasses as compared with  $C_3$  grasses (Caswell *et al.*, 1973; Caswell and Reed, 1976), and Gomphocerine species compete less (Joern and Klucas, 1993; Chase and Belovsky, 1994) and have narrower feeding niches than Melanopline or Oedopodine grasshoppers (Joern, 1979a,b, 1989a; Joern and Lawlor, 1980; Otte and Joern, 1977; Chapman, 1990).

Results from our studies, as well as from the literature review, confirmed our earlier conclusions that grasshopper populations may be limited differently. We know that a similar array of mechanisms existed at our sites and presumably most western U.S. sites, but a different mechanism appears to emerge as dominant (i.e., limiting) at each site. Why might the same mechanisms operating at our sites, and presumably at other sites, differ in magnitude and consequently lead to differences in grasshopper population limitation? Furthermore, why will annual shifts in how populations are limited emerge and how frequently might these shifts be observed?

### III. Graphical Depictions of Population Mechanisms Identified in Our Studies

To develop an integrated perspective, we focused on demographic responses most likely to exhibit significant density-dependent and -independent effects. The density-dependent responses are particularly important since these are necessary for populations to be regulated (Sinclair, 1989). We considered three responses: (1) survival of hatchlings to the adult stage in the absence of predators, which assesses the impacts of food competition and density-independent mortality; (2) the production of hatchlings per female for the next generation, which assesses the impacts of food competition and density-independent processes; and (3) predatory mortality. To date, data addressing the mechanisms underlying each of the responses (competition for food, avian predation, and density-independent processes) come from the studies in Montana with *M. sanguinipes*.

#### A. Probability of Surviving from Hatching to the Adult Stage in the Absence of Predators

An individual's probability of surviving (proportion of all individuals surviving) should be a function of initial hatchling density. This probability will be constant (density independent) over a range of low hatchling densities and then

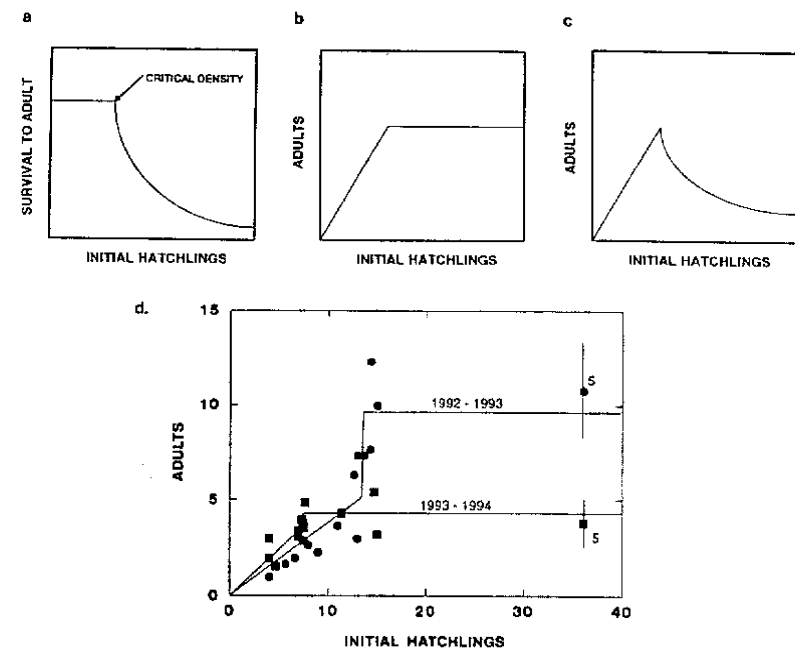


Figure 3. A mechanistic view of survival probability from hatching to the adult stage in the absence of predators. (a) Survival probability is density independent until a critical density is attained and food competition reduces survival. The relationship between survival and initial density in (a) can lead to a constant density of adults, if individuals do not compete equally (b), or to a declining density of adults, if all individuals compete equally (c). (d) Survival observed in experimental Montana populations of *M. sanguinipes* over two generations.

will decrease hyperbolically after hatchling density reaches a critical value. Density-independent survival depends on abiotic conditions and nutrition before per capita food intake begins to decline due to competition (Fig. 3a). After the critical density is attained, survival will decline hyperbolically as per capita food intake (available food/hatchlings) declines (Schoener, 1973; Lomnicki, 1988).

The decline in survival with food competition can result in two patterns: a constant density of adults or a decreasing density of adults as hatchling density continues to increase. The constant adult density reflects exploitative competition where some individuals are more capable of acquiring resources (e.g., different stages of development or genetic differences), so that the less capable individuals die (Fig. 3b) (Lomnicki, 1988). The declining adult density reflects exploitative competition where all individuals are relatively similar in their capabilities for acquiring food, so they all experience reduced survival (Fig. 3c). The Montana data indicate that survival of hatchlings to the adult stage in experimental cages

leads to constant, but different annual, adult densities as hatchling density increases (Fig. 3d). The two years were very different (1992 was warm and dry and the food plants were more digestible; 1993 was very cool and wet, and the food plants were less digestible) (Belovsky and Slade, 1996b). Therefore, annual differences in food resources and abiotic conditions are important, especially because abiotic conditions strongly impact food resource quality and quantity (Belovsky and Slade, 1995).

### B. Production of Hatchlings per Adult Female

Hatchlings produced per adult female should exhibit a pattern like that observed for survival: until a critical initial hatchling density is attained, per capita production should remain constant (density independent), and then should decline as per capita food intake declines with increasing initial hatchling density (density dependent) (Fig. 4a). The density-independent production is set by a female's ability to process food and convert it into young, given food quality and the abiotic environment. This is equivalent to White's (1978, 1984, 1993) claim that insect reproduction can change in a density-independent fashion as food quality changes.

The Montana data for reproduction were obtained in two ways. First, adult females reared in field cages at different initial hatchling densities were dissected to count ovariole relicts that remain after each egg is produced (Joern and Klucas, 1993). These data (Fig. 4b) indicate that egg production/adult female followed the pattern hypothesized in Fig. 4a. Second, hatchling production/adult female cannot be directly measured because the hatchlings observed in the cages at the start of the next year cannot be attributed to a particular adult female. Consequently, the density of hatchlings was divided by the density of adult females in the cage during the previous year to estimate the hatchlings produced/adult female; this also led to the hypothesized pattern (Fig. 4c).

As observed for the survival function, the reproduction functions also varied between years: egg and hatchling production/adult female were lower in 1993 than 1992. These differences are consistent with the previous described annual variations in abiotic conditions and food quality. Therefore, annual differences in food quantity and quality are critical in setting reproductive output.

### C. Probability That an Individual Grasshopper Is Killed by Predators

An individual's probability of being killed by predators (proportion of the population killed by predators) should be a function of initial hatchling density. This function will be a combination of the functional and numerical responses for the array of predators in the environment (Holling, 1966). The combined func-

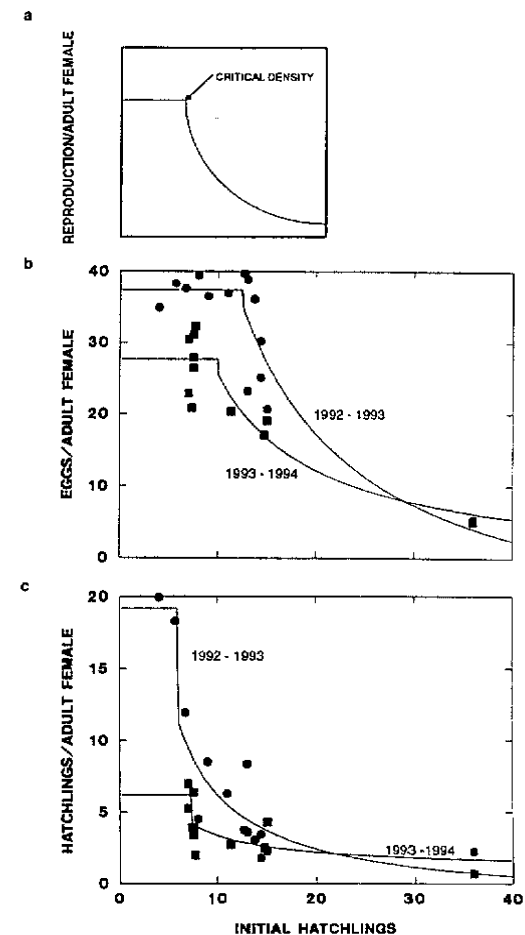


Figure 4. A mechanistic view of per capita reproduction by adult females. (a) Per capita reproduction should be density independent until a critical density is attained and food competition reduces reproduction. The relationship between per capita reproduction and initial density based on ovariole relicts (b) and hatchling production (c) for *M. sanguinipes* in experimental populations over two generations in Montana.

tions should show the probability increasing as initial prey density increases, but at some critical initial density the probability will begin to decline as initial density increases and the predators become "saturated" with prey, unable to kill any more.

The combined functional and numerical responses or the responses for individual predator species are difficult to obtain in the field. However, grasshoppers

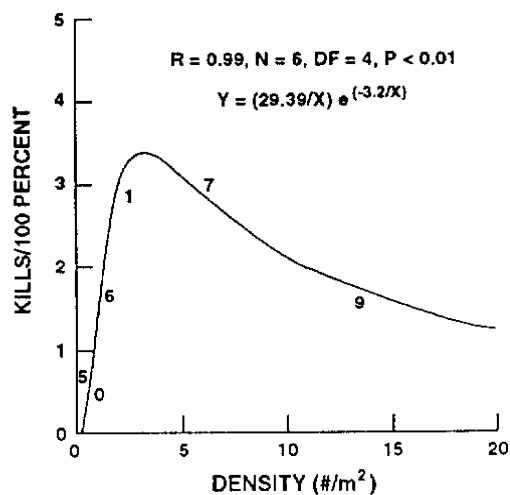


Figure 5. The probability of a grasshopper being killed (kills/100 individuals present/day) by avian, mammalian, spider, and ant predators at different grasshopper densities. Data are for *M. sanguinipes* in Montana that were tethered in the field over 6 years (Belovsky *et al.*, 1990); each year is labeled by the year's last digit (1985, 1986, 1987, 1989, 1990, 1991). The line and equation are the best-fit function to these observations.

can be tethered on nylon monofilament in the field and monitored for predator removal. In most cases, the predator can be identified (Belovsky *et al.*, 1990). This was done in different years to obtain predation probabilities at different grasshopper densities. As hypothesized, the predation function initially increases as hatchling density increases and then declines (Fig. 5). Although spiders, ants, and mammals killed grasshoppers, birds were the major predator creating this function (Belovsky *et al.*, 1990), and this response was independently verified with experimental studies of optimal foraging behavior in cowbirds (*Molothrus ater*), one of the principal avian predators at the site (Belovsky, 1990, 1993). A similar response has been observed for parasitoids that attack grasshoppers (Smith, 1965; M. Lietti de Guibert, J. B. Slade, and G. E. Belovsky, unpublished).

#### IV. An Integrated Model of Population Limitation

We developed a theoretical framework to integrate the population responses and their underlying mechanisms described earlier. We then determined whether food and predator limitation can both be accommodated by this framework, as

well as the contribution played by variable abiotic conditions. With a theoretical framework, field experiments can be performed that manipulate the mechanisms presumed to be operating within populations and then observing whether changes in population responses (survival and reproduction) agree with expectations.

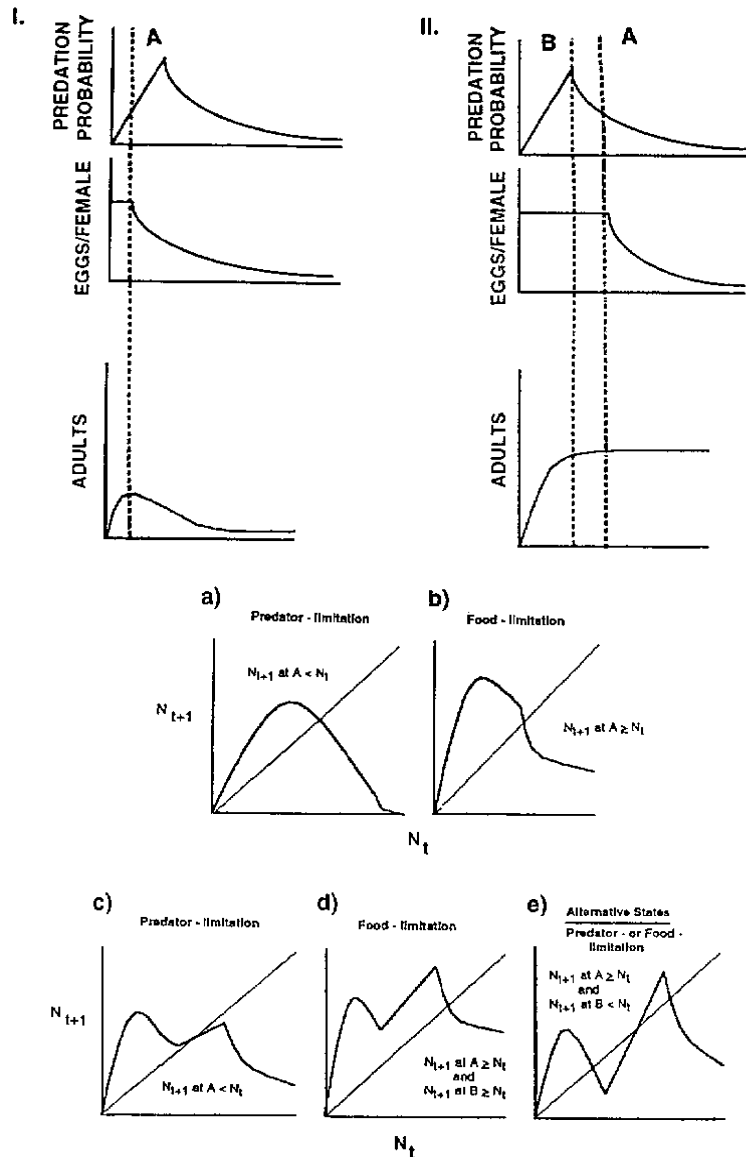
#### A. Basic Modeling Strategy

A model that captures the three population processes is Ricker Curve (sometimes referred to as recruitment curve) analysis, which is particularly suited for univoltine (i.e., nonoverlapping generations that are produced annually) species like our grasshoppers (Varley *et al.*, 1973). This analysis plots the density of offspring initiating one generation ( $N_t$ ) against the density of offspring produced by that generation to initiate the next generation ( $N_{t+1}$ ), given constant environmental conditions (Fig. 6; Ricker, 1954, 1958). The curve (Ricker Curve) represents the entire range of population responses ( $N_t$  and  $N_{t+1}$ ) for the environmental conditions; however, a population at a given site and time will exhibit only a single pair of  $N_t$  and  $N_{t+1}$  values. When environmental (abiotic and biotic) conditions vary between sites or over time (a likely situation), it is not proper to empirically construct a Ricker Curve by plotting observed  $N_t$  and  $N_{t+1}$  values, because each observed pair of values resides on a different Ricker Curve. Therefore, an experiment must be used to reconstruct the Ricker Curve (i.e., range of  $N_t$  and  $N_{t+1}$  values) when environmental conditions are constant; this is what the experiments described earlier allowed us to do.

A reference line ( $N_t = N_{t+1}$ ) can be added to the Ricker Curve plot (Fig. 6). An intersection between the line and the Ricker Curve denotes an equilibrium population (self-sustaining condition), because the density of hatchlings initiating the population at time  $t$  equals the density of hatchlings produced by them to initiate the next generation. We do not expect the population to be at equilibrium given the annual variability in environmental conditions; however, the equilibrium still has importance, because it defines a state that is attracting the population, and this state defines the mechanism that is dominant over others in terms of regulating the population. Because there are two graphical representations of the function relating adult density to the initial density of hatchlings (see the foregoing), a Ricker Curve analysis must be developed for each (Fig. 6).

#### B. Scenario 1: Adult Density without Predators Declines as Initial Hatchling Density Increases

In this case the Ricker Curve is unimodal (Fig. 6.I), which means that the reference line, if it intersects the Ricker Curve, can only intersect it at a single point.



**Figure 6.** Possibilities for Ricker Curves (a–e) are developed given different relationships for survival, reproduction, and predation; straight lines are reference lines that denote equilibria at the intersection with the Ricker Curve. (I) Ricker Curves (a) or (b) can be observed when the critical density for the predation function (A) is greater than the critical densities for survival and reproduction (B), and either survival function (Figs. 3b and 3c) is observed. (II) Ricker Curves (c–e) can be observed when the critical density for the predation function (A) is less than the critical density for reproduction and the survival function attains a constant value (Fig. 3b).

### C. Scenario 2: Adult Density without Predators Is Constant as Initial Hatchling Density Increases

In this case the Ricker Curve can be unimodal or bimodal (Fig. 6.II). To be unimodal the critical density at which reproduction becomes density dependent (point A in Fig. 6.II) must be less than the density at which the predation function peaks (point B in Fig. 6.II). A unimodal Ricker Curve can only be intersected by the reference line once. If the critical density at which reproduction becomes density dependent (point A in Fig. 6.II) is greater than the density at which the predation function peaks (point B in Fig. 6.II), then the Ricker Curve is bimodal. A bimodal Ricker Curve, if it is intersected by the reference line, can be intersected once or three times.

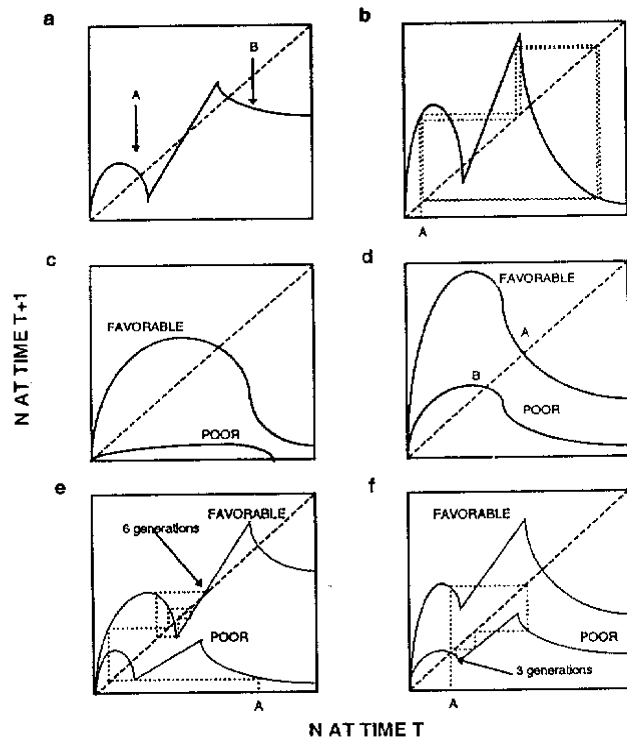
### D. Operation of the Ricker Curve Model

If the reference line intersects the Ricker Curve once (unimodal or bimodal curve), two modes of population limitation are possible. If the intersection occurs at an  $N_t$  value greater than or equal to the critical density where density dependence is observed for either survival in the absence of predation or reproduction, whichever is smaller, then the population is food-limited (Figs. 6b and 6d: bottom-up control). If the intersection occurs at an  $N_t$  value less than the critical value where density dependence is observed for either survival in the absence of predation or reproduction, whichever is smaller, then the population is predator-limited (Figs. 6a and 6c: top-down control). Either of these outcomes is typical of the classic density-dependent perspective argued by some ecologists (e.g., Lack, 1954).

If the reference line intersects the bimodal Ricker Curve three times, possibilities for population limitation are diversified, because this denotes the existence of multiple stable equilibria (Fig. 7a). The intersection closest to the origin is a predator-limited equilibrium, the intersection farthest from the origin is a food-limited equilibrium, and the intermediate intersection is an unstable equilibrium (saddle point). The saddle point delimits regions where the population at lower  $N_t$  values moves toward the predator-limited equilibrium and the population at higher  $N_t$  values moves toward the food-limited equilibrium. Therefore, even though the population is limited by density-dependent processes (food and predation), it is possible for the population depending on the density of individuals founding it to be attracted to either the predator- or food-limited equilibrium; this is not classic density dependence (e.g., Lack, 1954). Furthermore, given the proper shape of the Ricker Curve (Fig. 7b), the population might switch chaotically over time between predator and food limitation (Hastings *et al.*, 1993).

If there is no intersection between the reference line and Ricker Curve, then the population cannot persist unless the environment varies between years, and





**Figure 7.** Various Ricker Curve outcomes are portrayed, where the dashed line is the reference line that denotes equilibria where it intersects the Ricker Curve. (a) A bimodal Ricker Curve can provide multiple stable equilibria depending on initial densities in the population: (A) represents an initial density leading to predator limitation and (B) represents food limitation. (b) A bimodal Ricker Curve can produce a population that varies between predator- and food-limited generations (dotted line trajectory), if the population is initiated with (A) individuals (c). If environmental conditions generally produce a low Ricker Curve (poor) that is not intersected by the reference line, the population must occasionally experience better environmental conditions that produce a higher Ricker Curve (favorable) that intersects the reference line, if the population is to persist. (d) If environmental conditions vary between generations, favorable conditions will tend to produce a food-limited population (A) and poor conditions will tend to produce a predator-limited population (B). (e) When environmental conditions generally are favorable and populations tend to be food-limited, an occasional poor year can produce a number of generations (dotted line trajectory) that are predator-limited in subsequent favorable years (six generations in this example). (f) The opposite can emerge when poor years are common and occasional favorable years emerge.

some years provide a favorable environment so the Ricker Curves in those years lie above the reference line and are intersected (Fig. 7c). This case does not imply density-independent population limitation, because density dependence (food or predator limitation) is occurring at all  $N_t$  values, even if the Ricker

Curve does not intersect the reference line. However, it does imply that the population is not attracted (regulated) toward an equilibrium except in occasional favorable years. This is equivalent to the classic density-independent perspective of some population ecologists (e.g., Andrewartha and Birch, 1954, 1984), but the population growth trajectories still result from density-dependent mechanisms (Sinclair, 1989).

*Environmental variation between years* not only can create the classic density-independent view, but can result in a different Ricker Curve for each year. The existence of different Ricker Curves in different years indicates that a population can be limited by predation and food in different years; that is, as the reference line intersects each year's Ricker Curve at a different  $N_t$ , the population can be attracted to an equilibrium that is defined by a different dominant density-dependent process (Fig. 7d). The Ricker Curve changes shape as annual variations in food quantity and quality affect survival and reproduction and abiotic-induced mortality varies.

Annual shifts in observed modes of population limitation can occur in several ways, but they are most likely for bimodal Ricker Curves, because less variation is needed to create curves that produce either predator or food limitation, or both.

1. As the Ricker Curve is lowered (reduce  $N_{t+1}$  for a given  $N_t$ ), predator limitation is more likely, and as the curve is raised, food limitation is more likely (Fig. 7d). The effects of each population process on the Ricker Curve must be considered. Increased abiotic mortality and predator efficiency (greater proportion killed at a density and greater critical density at which the proportion killed begins to decline) decrease the Ricker Curve, making predator limitation more likely. Food quality and quantity have diverging effects. Increased food quality increases density-independent survival and reproduction and allows a larger population to be supported, possibly permitting an escape from the effects of predation. This raises the Ricker Curve and fosters food limitation. However, increased food quality and quantity increase the critical density at which food competition occurs, decreasing the likelihood of food competition. The net effect is that increased food quality and quantity increase the likelihood of food limitation.

2. As annual environmental conditions shift between being generally favorable (higher Ricker Curves) to being occasionally unfavorable (lower Ricker Curve), or the reverse, the occasional year can have a profound effect on the mode of limitation observed. This requires that the conditions generally observed produce bimodal Ricker Curves that are intersected three times by the reference line. For example, when favorable environmental conditions are generally observed and food limitation is expected, an occasional unfavorable year would have a population initiated with a large density of hatchlings (Fig. 7e). The unfavorable year with a large initial density would experience food competition,

even though predator limitation is expected, and produce very few hatchlings for the next year, which is once again favorable (Fig. 7e). This creates a series of years with favorable conditions that are predator-limited, even though food limitation is expected (Fig. 7e). If unfavorable conditions are generally expected and favorable conditions appear only occasionally, the opposite effect (i.e., food limitation when predator limitation is expected) can be produced (Fig. 7f). Therefore, varying environmental conditions can create historical effects so that population dynamics, though deterministic and predictable, cannot be discerned without examining variations in the Ricker Curve over time.

Although the conclusions about population limitation are apparent when the Ricker Curves are examined, they are not intuitive when the mechanisms are considered in isolation, as is typical of classic density-dependent and -independent views. Furthermore, these conclusions may be counterintuitive (e.g., food competition is fostered as food quantity and quality increase). A variety of possibilities for population dynamics does not imply lack of understanding, because this variety can emerge from a simple model. The simple model also illustrates the need to view population dynamics in a broader and more long-term perspective (Belovsky and Joern, 1996).

## V. Grasshoppers Revisited: Ricker Curves

The precautions that must be taken in measuring a Ricker Curve were discussed in the preceding section, that is, the range of  $N_t$  and  $N_{t+1}$  values must be acquired from a single set of environmental conditions (abiotic and biotic). Our experimental system meets these criteria, where replicate populations (9-m<sup>2</sup> field enclosures) at a given site and year are initiated with a range of hatchling densities ( $N_t$ ) and the production of hatchlings in the next year is measured ( $N_{t+1}$ ). In this way, a Ricker Curve can be constructed for each site and year. The experiments can also be used to assess whether a predator- or food-limited equilibrium is attracting the field population by predicting its mode of limitation given its initial hatchling density and the Ricker Curve, and comparing it with the observed mode in the experiment.

### A. Observed Ricker Curves

To date, we have the information to construct two Ricker Curves for *M. sanguinipes*, a single site over 2 years in Montana. In both years (generations), the Ricker Curves were bimodal and intersected the reference line at three points (Figs. 8a and 8b). This was expected because the observed functions for survival, reproduction, and predation (Figs. 3c, 5c, and 5d) met the conditions for this type of Ricker Curve (Fig. 6). Finally, the higher Ricker Curve in 1992–1993 compared to 1993–1994 (as well as greater survival and reproduction: Figs. 3c,

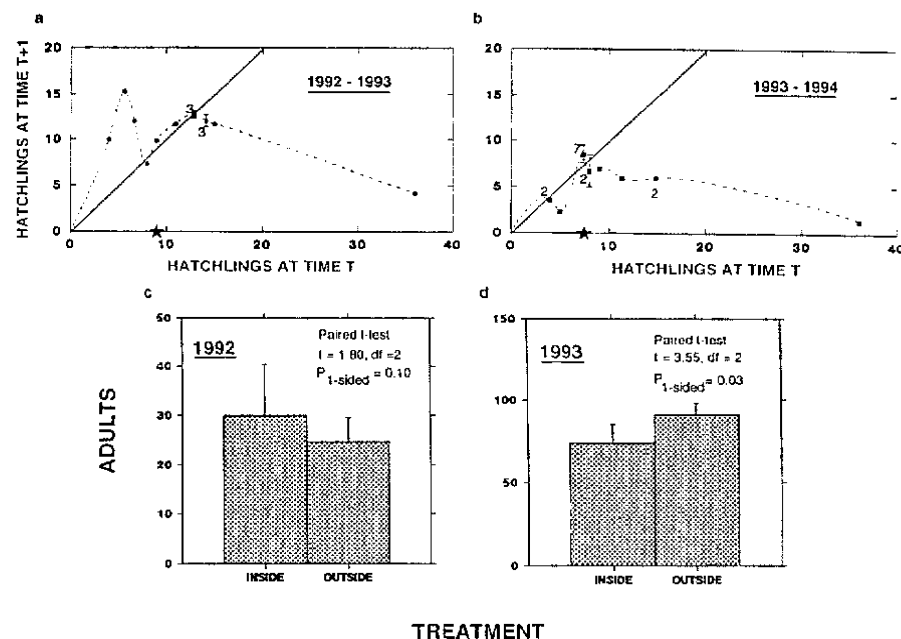


Figure 8. Experimentally determined Ricker Curves (dashed lines) for *M. sanguinipes* over two generations in Montana are presented in (a) and (b). Ricker Curves were fit to data from experimental populations using a Spline-smoothing algorithm, and standard deviations are presented for populations that had the same initial densities (numbers refer to the sample size), indicating the confidence in generated curves. The reference line is a solid line. The initial density of hatchlings observed in the field in each year is marked by a star. (c) and (d) present the results from avian enclosure experiments (total number in enclosure or control area). Error bars represent standard errors (sample size = 3); statistical tests are one-sided, because birds are expected to decrease grasshopper numbers.

5c, and 5d) appears to be due to food plants having higher quality and quantity in 1992 (Belovsky and Slade, 1996b).

The Ricker Curves predicted shifting modes of population limitation between these two generations:

1. In 1992–1993, field initial hatchling densities produced predator limitation of adults, but food limitation of reproduction (Fig. 8a), because the densities fell between the saddle point (intermediate intersection) and the food-limited equilibrium (intersection farthest from origin). This was observed (Fig. 8c) and agrees with the idea that predator limitation is more likely as years vary from unfavorable to favorable conditions (food quality was lower in 1991 than 1992; Belovsky and Slade, 1996b).

2. In 1993–1994, initial hatchling density produced food limitation of adults and reproduction (Fig. 8b), because densities fell above the food-limited

equilibrium (intersection farthest from origin). This was observed (Fig. 8d) and, as pointed out earlier, a shift from predator to food limitation may be more likely as years vary from favorable to unfavorable (food quality was higher in 1993 than 1994; Belovsky and Slade, 1996b).

An interesting additional property emerges: the populations within each generation (year) were at equilibrium with the food resource (i.e., utilized all available food so that food was competed for), because reproduction was food-limited in 1992–1993 even though survival was predator-limited, and survival and reproduction were food-limited in 1993–1994. However, in neither of the generations was the population at an equilibrium ( $N_t = N_{t+1}$ ) based on density. This poses wide-ranging implications for traditional perspectives in population ecology and food web theory that we discuss later.

### B. Implications for Our Grasshopper Populations

Results from Montana indicate that the conditions that enhance the likelihood for modes of population limitation to shift between sites and years are exhibited, because the Ricker Curves vary with year and bimodal Ricker Curves, especially if they intersect the reference line at three points, can most easily be shifted between food (bottom-up control) and predator limitation (top-down control). Combining the observed Ricker Curves with the Ricker Curve scenarios developed earlier provides possible explanations why some western U.S. grasshopper populations, like those at the Montana site, tend to be bottom-up controlled and others, like those at the Nebraska site, tend to be top-down controlled. For top-down control to be expected, the Ricker Curves at the Nebraska site, which are yet unmeasured, and at other predator-limited sites must be lower than, and the density at which food competition begins must be higher than, observed at the Montana site. These conditions can arise when:

1. *Food is of lower quality in Nebraska than Montana.* This is supported by the data presented earlier on plant solubility in HCl + pepsin. In addition, Nebraska grasses tend to be coarser, tend to be represented by more C<sub>4</sub> species that are less digestible than C<sub>3</sub> species, and tend to grow in tufts, which is related to lower quality and cropping rates.

2. *Food is of greater quantity in Nebraska than in Montana.* Plant biomass measures at the two sites ( $\approx 250$  g-dry/m<sup>2</sup> in Nebraska versus  $\approx 190$  g-dry/m<sup>2</sup> in Montana) support this. However, we believe that the observed differences in food quantity cannot account for the different modes of limitation observed in Montana and Nebraska, whereas this may not be the case for the entire western United States, such as the shortgrass steppe.

3. *Abiotic-induced mortality and predator efficiency are greater in Nebraska than in Montana.* At present, we have no evidence to suggest that abiotic conditions reduce survival in Nebraska more than in Montana. However, there is

evidence that avian predators, although of comparable abundance at both sites, may be more successful at capturing grasshoppers in Nebraska (85%: Joern, 1988) than in Montana (22–28%: Belovsky *et al.*, 1990); this may be due to greater cover in Montana (fewer tuft-forming grasses).

## VI. Insights for Population Ecology

Our integrated approach resembles population models developed by others for a variety of species (e.g., insects: Southwood and Comins, 1976; Berryman, 1987; insects and fish: Peterman *et al.*, 1979; mammals: Sinclair *et al.*, 1990; Haber and Walters, 1980). These earlier models were phenomenological (i.e., relying on the general shapes of population growth functions) rather than mechanistic (i.e., relying on explicit functions defining the operation of mechanisms that impact the population). Therefore, our approach has implications for an array of other organisms and general ecological issues. These are summarized in the following.

### A. Study Design

There are no shortcuts for assessing population dynamics. Our results indicate the need for long-term data sets, which are based on experimental manipulations coupled with careful descriptions of populations. The need for experimental populations arises because different Ricker Curves emerge in different habitats for a given year and between years in the same habitat. This seriously handicaps the ability to statistically unravel population dynamics from large data sets composed of field population censuses made at the same site or different sites over time (Royama, 1993). It further questions the utility of existing data sets for addressing issues like density vagueness, density veiled, and density dependence (*sensu* Strong, 1984, 1986a,b; Stiling, 1988).

### B. Fallacy of Searching for Single Explanations

Much of the 50-year debate over population limitation arises in part from weaknesses in the available data sets, but largely stems from the desire of ecologists to attribute limitation to a single mechanism (e.g., predation, food, and so on). Our Ricker Curve approach integrates the operation of a number of potentially limiting mechanisms and indicates that one density-dependent mechanism *must* limit a population at a given site and time, but the limiting density-dependent mechanism can change over time and between sites. Consider two populations of a species with identical density-dependent responses produced by food competition and predation. One population has lower density-independent survival and reproduction; this population may be predator-limited, whereas the

other is food-limited. Even though the populations are respectively predator- and food-limited, is it correct to view density-independent effects as unimportant? We need to consider all the mechanisms together.

Our findings with the Ricker Curve model have similarities to Sinclair's (1989) distinction that density-independent mechanisms (e.g., abiotic-induced mortality) cannot regulate populations; regulation requires density-dependent processes. For example, density-independent processes can depress populations to densities where food competition may not occur. However, for density-independent processes to be limiting, they must reduce the population to such a low density that its predators cannot persist in the environment; otherwise, predation, a density-dependent process, will limit the population. Therefore, density-independent processes are very important in determining which density-dependent processes regulate (attract toward an equilibrium) the population, but the density-independent processes are not limiting in themselves. This is one of the attributes that emerges when all population mechanisms are considered to be operating simultaneously.

### C. Misconception of Invariant Density Dependence and Equilibrium

Ecologists often consider the mechanism limiting a population to be constant over time, even though occasional divergences during periods of exceptional environmental conditions (e.g., drought) occur. This has been taken to the extreme by considering that populations not fluctuating greatly over time are largely limited by density-dependent mechanisms, whereas widely fluctuating populations are limited by density-independent mechanisms (Horn, 1966). As pointed out in the foregoing, density-independent mechanisms cannot regulate a population, but variation in the intensity of their operation, as the environment varies over time, can change which density-dependent mechanism limits a population. Therefore, the mode of population regulation for a population is not constant.

As discussed earlier, there are additional ways that the mode of population regulation can change over time for a population or be different for populations in similar environments. When the population can exhibit multiple stable equilibria (bimodal Ricker Curve that intersects the reference line at three points), historical factors can produce different modes of limitation given different densities of founder individuals or different chronologies of favorable and unfavorable time periods. A population with multiple stable equilibria can exhibit chaotic shifts in its mode of limitation over time, even in a constant environment.

The issue of equilibria in population ecology must also be reexamined given our model. The classical notion of population equilibrium as a constant density, where  $N_t = N_{t+1}$ , is unlikely to be attained in our population model. However, this equilibrium is still very important for ecologists to consider and estimate, because the equilibrium acts as an attractor as environmental conditions vary

over time and defines the mode of limitation operating on the population. Therefore, the unlikely event of observing a population at equilibrium does not mean that an understanding of population dynamics based on equilibrium models is invalid.

Our model and experiments with grasshopper populations indicate the potential for a different type of equilibrium, even if the population does not attain the equilibrium densities. It is possible that food resources are fully utilized (consumptive equilibrium), even at population densities below the equilibrium density ( $N_t = N_{t+1}$ ). This arises because the equilibrium density in a food-limited population is set at a point where per capita food intake permits an individual to replace only itself reproductively (Schoener, 1973). However, if the population is food-limited, but not at the equilibrium density, there exists a range of population densities at which individuals still consume the same total quantity of food but have more or less on a per capita basis, so that reproduction is greater or less than a replacement level. Therefore, populations do not have to be at equilibrium densities to "track" changing food resources (Roughgarden, 1979).

The distinction between an equilibrium based on density and consumption has important implications for food web theory. Observing that a predator reduces the density of prey does not imply top-down dynamics with the expectation of trophic cascades (Hairston *et al.*, 1960; Slobodkin *et al.*, 1967; Hairston, 1989; Fretwell, 1977; Oksanen, 1990, 1991; Oksanen *et al.*, 1981; Carpenter and Kitchell, 1984, 1987, 1988), if the reduced density of prey still maintains the equilibrium consumption. This was theoretically argued by Schmitz (1992).

### D. Multiple Stable Equilibria

The importance of multiple stable equilibria in population dynamics has been downplayed after Connell and Sousa (1983) reviewed the evidence. Their argument that little, if any, evidence supports the existence of multiple stable equilibria was appropriate given the types of long-term data available. Nonetheless, the issue of populations with multiple stable equilibria has continued to be raised, even though data neither support nor refute their existence (e.g., Berryman, 1987; Sinclair *et al.*, 1990; Messier, 1994; Knowlton, 1992; Leonardsson, 1994). However, we believe that the Ricker Curves measured by us for a grasshopper population in two different years clearly demonstrate for the first time the existence of the necessary dynamics to produce multiple stable states.

## VII. Conclusions

Our findings support the need for long-term studies of population dynamics that combine experimental manipulations and field observations to decipher how ecological mechanisms (e.g., predation, food competition, and biotic-induced

mortality) operate in concert on the population over time. This is necessary because these mechanisms can have different effects over time and between habitats.

Our studies indicate that one of the key mechanisms that changes over time and between sites for herbivore populations is the influence of plant quality and quantity. Plant quality and quantity impact density-independent survival and reproduction and determine the strength of food competition. For example, given two populations of the same herbivore with identical functions relating predatory mortality to prey density and abiotic-induced mortality, the population with better food resources will more likely be food-limited, whereas a population with poorer food resources will more likely be predator-limited. Therefore, studies of population dynamics must consider food resources and how they vary over time and space (Price, 1984, 1992), especially if we are to resolve issues like population limitation and top-down versus bottom-up control.

## Acknowledgments

We wish to thank J. B. Slade and Jon Chase for commenting on this manuscript. The work was funded by The Grasshopper Integrated Pest Management Program (USDA/APHIS), the National Science Foundation (DEB-9317984), and the Utah State University Agricultural Experiment Station.

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