VII.14 Grasshopper Population Regulation

G. E. Belovsky

Factors controlling the dynamics of a population are often referred to as either limiting or regulating a population (Sinclair 1989). Limiting factors operate to depress a population without regard to its number; limiting factors are density independent. Regulating factors are special depressing factors that tend to bring the population to a specific number; to reach the specific number, the depressing effect must be great when the population is much larger than the specific number and less when the population is below or near the specific number. Regulating factors are density dependent.

Population ecologists have demonstrated that, although there may be a correlation between weather and population numbers, this correlation does not mean that weather is the causal factor determining population dynamics or even the most important factor—even if it is a limiting factor (Horn 1968). In fact, it is well established that the density-independent effects of weather on survival and reproduction cannot regulate populations. The effects can only interact with regulating mechanisms to set population numbers because regulation requires the negative feedback of density dependent processes.

Science's understanding of grasshopper population dynamics has been largely built on long-standing observations that grasshopper numbers in a given year are correlated with temperature and precipitation (Joern and Gaines 1990). While these correlations provide convenient forecasting tools for pest managers, the correlations do not imply that weather is the causal mechanism limiting or regulating populations, nor that scientists understand grasshopper population dynamics. Furthermore, correlations between grasshopper numbers and weather, while statistically significant, are weak and are not consistent between different western rangelands with grasshopper numbers sometimes being greater in hot–dry years and sometimes greater in cool–wet years (see chapter IV.8).

Variability in the response to weather suggests that grasshopper populations may respond to other factors that are correlated with weather and not to the weather directly (for example, the abundance and nutritional value of food, the cover providing protection from predators, diseases, etc.). Consequently, the value of weather as a forecasting tool for particular western regions and the concept of weather as the driving factor in grasshopper population dynamics should not be confused.

A number of general models have been developed to portray insect population dynamics (Southwood and Comins 1976, Berryman 1987). These models are generic and are not based upon specific mechanisms that operate upon the insect's population but attempt to depict the insect's population dynamics in terms of the shape of a Ricker curve. A Ricker curve (fig. VII.14–1) is a plot of a species' number (N) at time t (N_t) against its number at a later time, t+1 (N_{t+1}). This type of population analysis is appropriate for insects that have a single generation each year, which includes nearly all western rangeland grasshoppers (Varley et al. 1973). Ricker curves are depictions of population dynamics because their intersection with a reference line ($N_t = N_{t+1}$) defines the number to which the population is being drawn by regulating factors (fig. VII.14–1).

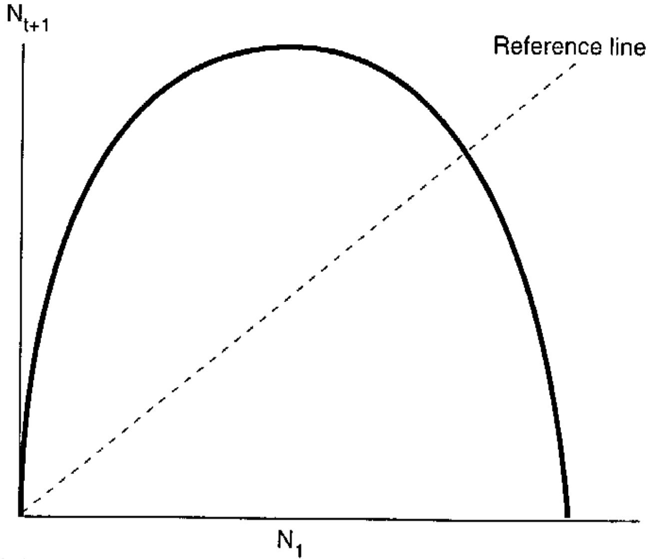

Figure VII.14–1—A simple Ricker curve relating the number of individuals starting the population in generation t (N_t) to the number of individuals produced by them to start the next generation (N_{t+1}). The point where the reference line ($N_t = N_{t+1}$) intersects the Ricker curve is an equilibrium point that the population may approach.

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Three Relationships Important in Grasshopper Population Dynamics

The shape of the Ricker curve depends upon the ecological mechanisms that operate on the population and how they change in intensity with density. Three mechanisms may be particularly important for grasshoppers: (1) the relationship between density and the probability of surviving to the adult stage in the absence of natural enemies, (2) the relationship between density and the probability that an individual is killed by a natural enemy, and (3) the relationship between the current year's density and the number of hatchlings produced for the next year by each current female. In each case, density refers to the number of hatchlings per area that initiates the year's population. I will review each of these functions.

Density and Survival.—In the absence of natural enemies, the relationship between initial grasshopper hatchling density and survival determines the density of adult females that can produce hatchlings. First, at low densities, survival should be a constant proportion of the population set by weather and the nutritional value of foods because the individuals consume as much food as they can potentially process. This survival is **density independent** because it does not vary with the density of grasshoppers present. Second, at higher densities, survival becomes **density dependent,** as competition reduces the food available per individual, and the mortality rate increases.

This survival relationship leads to a pattern where the density of adults increases as hatchling density increases and then becomes a constant set by the maximum adult density that the available food can support. This relationship can be seen at a Palouse prairie site in western Montana for *Melanoplus sanguinipes* where the addition of food increases survival to the adult stage (fig. VII.14–2A) (Belovsky and Slade 1995). Weather can increase or decrease food: cool–moist conditions tend to increase plant production, but tend to decrease the nutritional quality of the plants.

Density and Predation.—The relationship between the initial density of hatchling grasshoppers and an individual's probability of being killed by natural enemies depends upon the rate at which an individual enemy can kill grasshoppers (functional response) and the number of enemies present (numerical response). The functional and the numerical responses for a natural enemy frequently increase to constant values as the density of prey increases; this phenomenon is observed in predator–prey systems ranging from insects and spiders to wolves and deer.

The implication is that as density of the grasshoppers increases, the proportion killed (probability of an individual being killed) will first increase with density and then decrease. An example can be seen at a Palouse prairie site in western Montana for the grasshopper *M. sanguinipes* where vertebrate predators, especially birds, are the principal natural enemies (fig. VII.14–2B) (Belovsky and Slade 1993). Weather can modify the effects of these natural enemies. For example, cool–moist conditions can increase plant production, and increased plant biomass enables grasshoppers to conceal themselves from predators. But cool–wet conditions do not always enhance grasshopper survival: they can increase the virulence of some diseases.

Density and Reproduction.—The relationship between the current year's density of hatchlings and the hatchlings produced for the next year's generation by each current female reflects two conditions. First, at low densities, hatchling production per female should be constant because each female has all of the food that she can utilize for egg production. This level of reproduction is **density independent** because it does not vary with the density of hatchlings present. Second, at higher densities, hatchling production per female should decline as the density of current hatchlings increases because each female acquires less and less of the available food. This level of reproduction is **density dependent** because it declines with the current density of hatchlings present. This decline emerges as females acquire less and less food because the increasing number of grasshoppers depletes the available food. The above pattern in reproduction can be seen at a Palouse prairie site in western Montana for *M. sanguinipes* where the addition of food increases reproduction (fig. VII.14–2C) (Belovsky and Slade 1995). Weather can increase or decrease food availability. For example, cool–moist conditions tend to increase plant production but tend to decrease the nutritional quality of the plants.

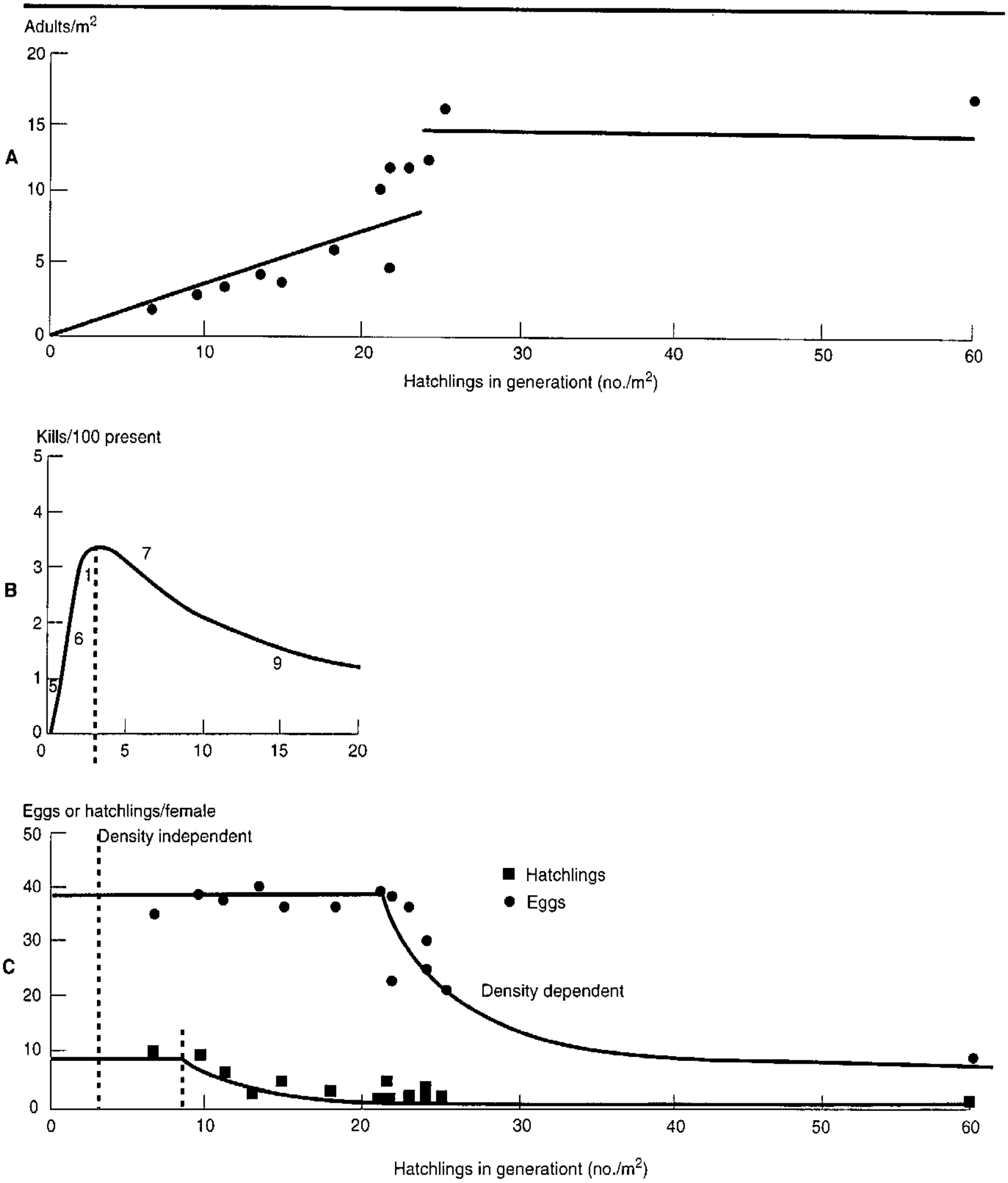

Figure VII.14–2—The relationships between hatchling density of *Melanoplus sanguinipes* and (A) adult density, (B) the probability of an individual being killed by a predator, and (C) the production of eggs and hatchlings per adult female, as observed at a Palouse prairie site in western Montana. The vertical dashed lines relate the points where the probability of predation and reproduction per adult female begin to decline with hatchling density. (*A* and *C* are adapted from Belovsky and Slade [1995]. *B* is adapted from Belovsky and Slade [1993].)

Using the Ricker Curve

The above three relationships can be combined to construct a Ricker curve, which enables scientists to integrate the effects of weather-induced density-independent mortality, natural enemy-caused mortality, and food resources. This integration produces three possible Ricker curve shapes, each reflecting a different dominant form of population regulation.

Population Regulated Only by Natural Enemies.—This type of regulation occurs when the peak of the function relating the probability of being killed by a natural enemy occurs at a grasshopper density that is greater than the density at which hatchling production begins to decline and/or adult densities attain their maximum level. In this case, a Ricker curve emerges with a single peak or two peaks, where the reference line intersects the Ricker curve only on the first peak (fig. VII.14–3A). This case emerges if the actions of the natural enemies (a) are so strong that grasshopper density cannot attain a level at which competition for food occurs or (b) continue to increase as competition for food increases.

Population Regulated Only by Food Availability.—This type of regulation occurs when the peak of the function relating the probability of being killed by a natural enemy occurs at a grasshopper density that is much less than the density at which hatchling production begins to decline and/or adult densities attain their maximum level. The Ricker curve emerges with two peaks, where the reference line intersects the Ricker curve only on the second peak (fig. VII.14–3B). In this case, the population is capable of "escaping" the effects of natural enemies, because (a) the natural enemies are not very effective and/or (b) the impact of the natural enemies rapidly diminishes as grasshopper density increases.

Population Regulated by Either Natural Enemies or Food Availability Depending Upon the Density of Hatchlings Initiating the Population.—This type of regulation occurs when the peak of the function relating the probability of being killed by a natural enemy occurs at a grasshopper density that is less, but not much less, than the density at which hatchling production begins to decline and/or adult densities attain their maximum level. In this case, a Ricker curve emerges with two peaks,

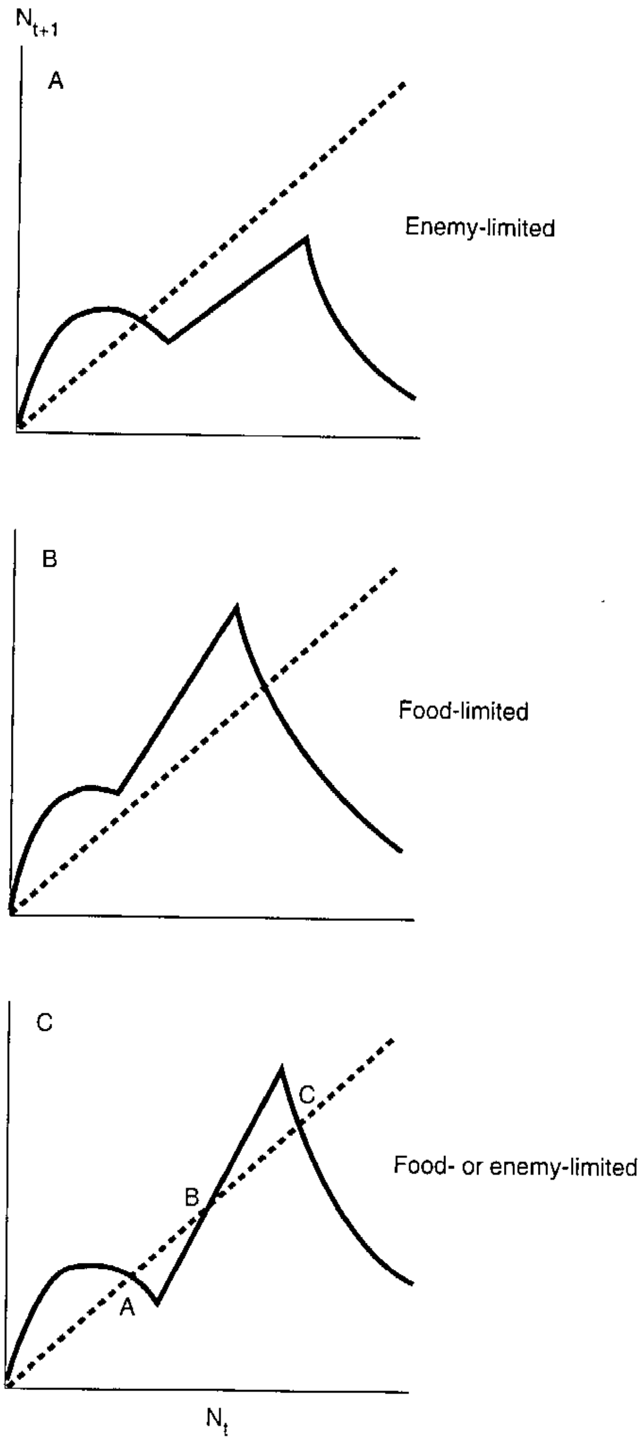

Figure VII.14–3—The three Ricker curve shapes that emerge (see text).

where the reference line intersects the Ricker curve at three points (fig. VII.14–3C).

The intersection with the first peak represents a population state regulated by natural enemies. The intersection with the second peak represents a population state regulated by food availability. The intersection lying between the above two intersections defines the "watershed," where populations initiated with densities less than this point become limited by natural enemies and with densities greater than this point become limited by food availability. In this case, the population can "jump" from one mode of regulation to the other depending upon the densities of hatchlings initiating a population from year to year.

The picture of grasshopper population regulation described above can be validated experimentally. From experimental (enclosed) populations established at different densities of *M. sanguinipes* at the Palouse prairie site in western Montana, the Ricker curve has been measured (fig. VII.14–4). The curve has two peaks and is intersected by the reference line at three points, indicating a population that can be regulated by either natural enemies or food availability depending on initial hatchling densities.

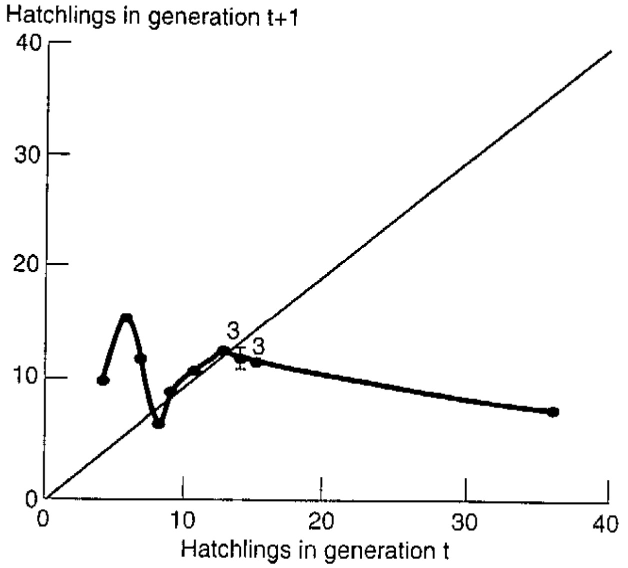

Figure VII.14–4—The Ricker curve for a *M. sanguinipes* population during a single year at a Palouse prairie site in western Montana. Error bars and sample sizes are presented for populations initiated at the same hatchling density.

More than 12 years of observation of this population disclosed that it has consistently been regulated by food availability, not by natural enemies (Belovsky and Slade 1993, 1995). This fact suggests that the population is near the intersection with the second peak of the Ricker curve. Furthermore, this conclusion was expected given the three underlying functions measured at this site and presented in figure VII.14–2.

What Weather Can Do

A new perspective toward weather and grasshopper population regulation can be gained from the Ricker curve model by appreciating that weather can affect both density-independent mortality and food availability.

Weather-induced density-independent mortality can operate in conjunction with natural enemy mortality to prevent populations from attaining levels where food availability becomes regulating. For the density-independent mortality to be important, it would have to accomplish at least one of three things. First, inclement spring weather can kill a high proportion of hatchlings, most likely through cold-induced starvation. Second, weather might be sufficiently severe over the entire life cycle of the grasshoppers so that few individuals can survive to become adults. Third, weather might shorten the period of time that adults have to live so that the number of hatchlings produced is dramatically diminished.

On the other hand, weather exerts a far more pervasive influence by altering food availability from year to year (see chapters IV.4 and IV.5). This variation in food abundance can be as great as sixfold between years and more than twofold within a summer (Belovsky and Slade 1995). The variation in food abundance could easily shift the shape of the Ricker curve from producing a population regulated by natural enemies in years with low food abundance to a population regulated by food abundance in years with high food abundance, and vice versa.

Weather Interacts With Enemies and Food Availability

The weather-induced shifts in food abundance, and perhaps to a lesser extent, changes in density-independent mortality result in domains of attraction (shaded regions in fig. VII.14–5), where the grasshopper population fluctuates with weather, but is regulated by either natural enemies or food availability at any one time. This is the point made by Horn (1968) that weather can create population fluctuations by varying density-independent or density-dependent (such as food availability) factors, but the density-dependent factor(s) must still regulate the population (attract it to particular levels).

In some environments, the points of attraction may be set by population levels created by natural enemies in different years (fig. VII.14–5A). In other environments, the points of attraction may be set by population levels created by food availability in different years (fig. VII.14–5B). In still other environments, the points of attraction may vary between levels set by natural enemies in some years and food availability in other years (fig. VII.14–5C).

Unique spatial relationships for population regulation emerge when several populations are placed in juxtaposition. The above discussion considers that each population is isolated from other populations. The conclusions concerning the regulation of a single population may have to be modified when adjacent populations are considered. For example, consider two adjacent or near populations. One population is regulated by natural enemies (fig. VII.14–3A) and the other population, by food availability (fig. VII.14–3B). It is possible that the food-regulated population will produce individuals that migrate rather than die. Therefore, if the two populations are close enough in relation to the dispersal ability of the grasshopper, the population that would otherwise be regulated by natural enemies may be able to increase in density with the addition of immigrants and, thereby, become food regulated. The immigrants permit the population to escape the effects of natural enemies.

The above simple scenario says that in some situations pest managers need to understand not only how individual populations are regulated but also the juxtaposition (landscape) of populations to determine the potential for population regulation to be complicated by dispersal. For example, the population receiving dispersers and thereby escaping regulation by natural enemies might be causing economic damage, and pest managers might decide to control it. However, control of this population

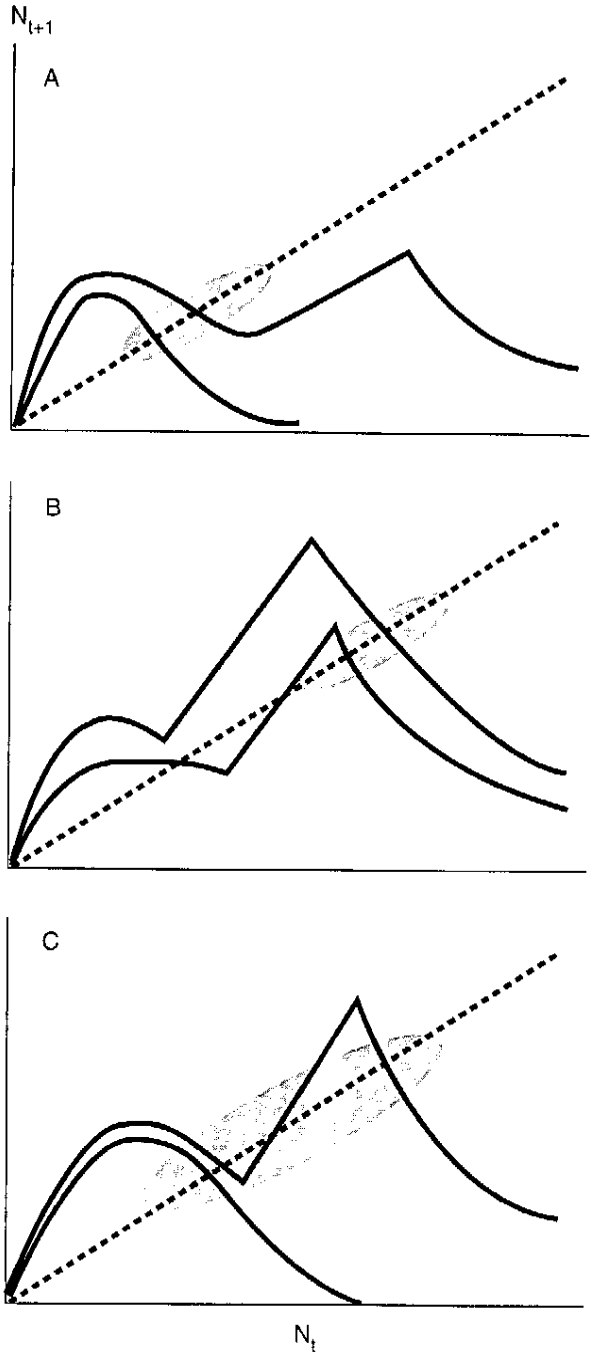

Figure VII.14–5—Domains of attraction might emerge for grasshopper population regulation, where natural enemies along with weather—which primarily affects density-independent survival and reproduction—sets the bounds of population fluctuations *(A)*; competition for food along with weather–which primarily affects food abundance–sets the bounds of population fluctuations *(B)*; or natural enemies and food competition in different years with weather set the bounds of population fluctuations *(C)*.

might be largely ineffective unless the nearby population providing dispersers is controlled, too. In this scenario, the population causing damage is not the population that should be controlled because the dynamics of the former are dependent on the latter.

The implications of population regulation for grasshopper management may seem of little importance to managers entrusted with reducing the economic damage caused by pest grasshoppers. However, understanding how particular populations entrusted to a manager are regulated can provide critical insights that could make monitoring and control more cost effective.

General Conclusions

In terms of monitoring, the following generalizations might be reached:

1. Populations consistently within a domain that is regulated by natural enemies seldom reach densities at which economic damage is sufficient to warrant control; therefore, these populations may not warrant monitoring.

2. Populations consistently within a domain that is regulated by food availability often reach densities that cause economic damage and regularly warrant control; therefore, these populations may not warrant monitoring.

3. Populations in a domain where regulation can frequently "jump" between natural enemy limitation and food limitation will only periodically cause economic damage and warrant control; therefore, these populations may warrant monitoring.

If a manager knows the mode of regulation operating on a specific grasshopper population, monitoring efforts can be more effectively carried out, and that will save time and money.

In terms of control strategies, with the knowledge of how a population is regulated, a manager may be able to enhance efficiency by creating strategies that are tailored to the particular population. For example, I found (1992 unpubl.) that an insecticide application that killed less than 20 percent of the grasshopper nymphs—an application level much less than commonly employed—could shift a population from being regulated by food availability to being regulated by natural enemies. Switching to such a spray regimen would lessen control costs directly and also indirectly, by taking advantage of the more effective actions of natural enemies. Low-mortality spraying also would lead to less future management activity, with further cost reductions, because natural enemies would help to suppress future population increases.

Understanding how grasshopper populations are regulated and how regulation differs between regions of the western rangelands is essential for the development of new control strategies that involve reduced insecticide use, biocontrol agents, and grazing and habitat manipulation.

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