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Small Rodent Fluctuations in Arid Ecosystems: Natural Laboratories for Testing Population Dynamic Theory

Mauricio Lima

Center for Advanced Studies in Ecology and Biodiversity (CASEB), Pontificia Universidad Catolica de Chile, Casilla 114-D, Santiago CP 6513677, Chile

Abstract: The dramatic responses of primary productivity to rainfall variability in deserts represent a unique opportunity for testing basic principles of population dynamic theory. In particular, these ecosystems are natural laboratories for studying the relative importance of the feedback structure (intrinsic processes) and exogenous (climatic or environmental) factors in determining population dynamics, in particular because the interaction between density-dependence and climate is a major question in population ecology. In this article, I review the findings from two different deserts about the role of rainfall in determining population dynamics of small rodents. Previous studies using long-term data from small rodent monitoring in northern Chile and southwestern USA have applied simple theoretically based population dynamics models for understanding small rodent fluctuations. The findings show that simple models can be useful in explaining and predicting the dynamics of natural populations, particularly when they are based on a sound theoretical framework. In particular, Royama's classification of exogenous perturbation effects has been extremely useful in population modeling. Using these models together with Royama's paradigm for classifying exogenous (climate) perturbations, it is possible to distinguish how rainfall influences the limiting factors (food) in small rodent populations. The remarkable simplicity and generality of the models used appear to be very successful in explaining rodent fluctuations at different arid ecosystems such as southwestern North America and western South America, suggesting that this is a strong and useful approach for incorporating the role of exogenous factors such as climate into population models.

Key words: Desert rodents, intra-specific competition, limiting factors, rainfall, theoretical models.

Water supply is the ultimate limiting factor of life in the desert. The pattern of rainfall variability directly limits plant growth and primary production (Jaksic, 2001; Brown and Ernest, 2002; De la Maza *et al.*, 2009). Years of exceptionally heavy and frequent rains produce the spectacular desert blooms observed in many arid and semi-arid ecosystems. This particular link between climate variability and primary production, so tightly related in deserts, makes them unique natural laboratories for studying how to include climate in population dynamic models and to clarify the concepts of population limitation and regulation (Berryman, 2004; White, 2004). Therefore, rodents inhabiting deserts represent excellent systems for studying the effects of climate on population dynamics. In desert ecosystems, years with unusually high rainfall can produce a cascade of ecological events characterized

by increases in plant cover, seeds, insects, and finally, small-mammal consumers (Jaksic *et al.*, 1997; Lima *et al.*, 1999, 2002, 2006; Jaksic, 2001). As a result, most small mammal species exhibit striking population irruptions during and immediately after years of high rainfall (Jaksic *et al.*, 1997; Lima *et al.*, 1999; Jaksic, 2001; Meserve *et al.*, 2003).

Deserts represent natural laboratories for testing population dynamic theory predictions. For example, because of the over- whelming influence of rainfall on food resources for small rodents, a clear simple prediction is that rainfall will determine the equilibrium numbers (carrying capacity of the environment), but not the maximum per capita growth rates (Royama, 1992). Because rainfall influences the limiting resource in deserts, its effects can only be evaluated jointly with the effect of population density (Royama, 1992). Therefore, for this scenario, rainfall represents a non-additive force, because the ratio (i.e., population density/rainfall) will characterize the per capita share of the resources and the competition strength; this case represents what Royama (1992) calls 'lateral perturbation effects'.

Otherwise, these pulses of resources related to rainfall represent a unique opportunity to deduce how population limitation and regulation are part of the same fundamental population process. This argument had been clearly elaborated using laboratory experiments with *Tribolium* (Berryman, 2004), but empirical support from natural population data is scarce (but see Lima *et al.*, 2006, Lima and Berryman, 2006; Berryman and Lima, 2006; Lima *et al.*, 2008).

In this article I will review how the empirical pattern of population fluctuations of small rodents in South and North American deserts can be used as natural laboratories for testing population dynamic and logistic theory and for clarifying the concepts of population limitation and regulation.

Theoretical Models of Population Dynamics

Population dynamics of small rodents are the result of intra-population processes that cause a first-order feedback structure in rodent fluctuations. To understand how these processes determine rodent dynamics, I used a simple model of intra-specific competition, the exponential form of the discrete logistic model (Ricker, 1954; Royama, 1992), and we used its generalized version (Royama, 1992):

$$N_t = N_{t-1} \cdot r_m \cdot e^{(-c \cdot N_{t-1}{}^{a})} \quad .....(1)$$

In this model N_t represents the rodent abundance at time t, r_m is a positive constant representing the maximum finite reproductive rate, c is a constant representing competition and resource depletion and a indicates the effect of interference on each individual as density increases (Royama, 1992); $a>1$ indicates that interference intensifies with density and $a<1$ indicates habituation to interference. By defining the above equation in terms of the R-function, by defining $R_t = \log_e (N_t/N_{t-1})$, log transforming equation (3) and defining the population density in logarithm $X_t = log_e (N_t)$, we obtain:

$$R_t = R_m - e^{(a \cdot X_{t-1} + C)} \quad .....(2)$$

where,
R_t is the realized per capita growth rate $R_t = \log(N_t/N_{t-1})$, $R_m = \log(r_m)$, a is the same parameter as in equation (4), $C = \log(c)$, and $X = \log(N)$. This model represents the basic feedback structure determined by intra-population processes.

Because in this model the three parameters R_m, a and C have an explicit biological interpretation climatic perturbations can be included in each parameter using the framework of Royama (1992). In this manner, it is possible to build mechanistic hypotheses about the effects of climate in these two rodent populations. For example, simple additive rainfall perturbation effects can be represented as "vertical" effects, which shift the relative position of the R-function by changing R_m on the y axis (Royama 1992). This can be expressed as:

$$R'_m = R_m + g(Rain_{t-d}) \quad .....(3)$$

where, g is a simple linear function (+ or -) of the rainfall level with different lags. Another kind of climatic perturbation is when the equilibrium point of the population is influenced by the climate. This is the case when climate influences a limiting factor or resource (food, shelter). The correct model structure in this scenario is that the carrying capacity (equilibrium point) is affected by the rainfall. In this case the climatic factor shifts the R-function curve along the x-axis without changing the slope at the equilibrium, that represents a "lateral" perturbation in the Royama (1992) framework:

$$C' = C + g(Rain_{t-d}) \quad .....(4)$$

Finally, a climatic factor may change the intra-population processes by changing the intensity of competition between individuals because of the effect on a resource that is depleted during a season or year. In such a case it is expected that climate influences parameter a in equation (2). This kind of climatic effect is called the "non-linear" perturbation because changes in climate can change the relative shape of the R-function by changing the slope of the function at equilibrium ($R_t = 0$):

$$a' = a + g(Rain_{t-d}) \quad .....(5)$$

Arid Ecosystems and Small Rodent Fluctuations

Evidence of the influence of rainfall perturbations in small rodent fluctuations is clearly observable in western South America, but the pattern appears to be less clear in the Chihuahuan Desert in North America (Lima *et al.*, 2006, 2008; Previtali *et al.*, 2009). Long-term data of population densities of small rodents in both the continents represent a unique opportunity for comparative studies of population dynamics in order to gain an in-depth understanding of the processes regulating small rodent populations in both arid ecosystems. For example, the fluctuations of small rodents in western South America are characterized by the overwhelming role of rainfall pulses in determining rodent outbreaks (Lima *et al.*, 1999, 2006; Previtali *et al.*, 2009). Alternately, this strong coupling between rainfall and small rodent fluctuations has not been observed in semi-arid ecosystems of southwestern North America (Brown and Ernest, 2002) because of the apparent complexity and nonlinearity of the relationship between rainfall and rodent dynamics (Brown and Ernest, 2002).

In fact, the population dynamics of the small mammals in response to rainfall variability at one study site in the Chihuahuan Desert do not appear to follow this pattern.

However, using population dynamic and logistic theory it is possible to deduce the combined effects of population density and rainfall in the numerical fluctuations of South and North American small rodents (Lima *et al.*, 2006, 2008; Previtali *et al.*, 2009). In fact, the model structure is the same in both systems; it seems that rodent fluctuations in these two arid ecosystems are the result of the non-additive ("lateral" perturbations sensu Royama 1992) effect of rainfall on demographic rates. This result is consistent with the idea that these small rodent populations are strongly food-limited and rainfall represents a proxy for food availability. The ratio of density/rainfall is a proxy for the per capita shared resources. In consequence, the dominant force influencing the dynamics of these small rodent populations in arid ecosystems appears to be the limitation by food (represented by the non-additive effects of rainfall) and intra-specific competition. Very simple models appear to capture the essential features of the observed fluctuations and also suggest a mechanistic explanation for these fluctuations. In addition, the models support the contention that rainfall acts as a lateral perturbation through food availability, and that small rodents are limited by this indirect relationship. The analysis does not contradict previous results in these two systems; however, it provides a much more parsimonious and theoretically pleasing interpretation. It supports the view that analyses of population data done within the framework of credible theoretical models may be useful for improving our understanding of complex population systems. Finally, the non-additive effect of rainfall on rodent dynamics suggests that we can not evaluate the effects of rainfall on population dynamics of rodents independently of rodent population size. Logistic models expressed in terms of ecological demand/offer ratios represent a very plausible theoretical model structure for representing these ecological populations.

Finally, these results from long-term data of small rodent fluctuations in arid ecosystems represent one of the best empirical evidence for seeing the connection between population limitation and regulation. While limitation is focused on the environmental factor (rainfall) that determine the limit to population growth and the equilibrium density, regulation is the process that keeps the population at or close to this point (Berryman *et al.*, 2002; Berryman, 2004). Therefore, data from small rodent fluctuations in these arid ecosystems are the natural counterpart of the Chapman's laboratory experiments using *Tribolium* populations in different flour concentrations (Chapman, 1928; see Berryman, 2004).

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