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Plant productivity, predation, and the abundance of black-tailed jackrabbits in the Chihuahuan Desert of Mexico

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ABSTRACT

The abundance of black-tailed jackrabbits (*Lepus californicus*) can fluctuate dramatically. We used data from the Chihuahuan Desert to test the relative strength of top-down (predation) or bottom-up (food availability) limiting forces. Predictions for the top-down hypothesis were, 1) a positive relationship between coyote (*Canis latrans)* and jackrabbit abundance (numerical response) and 2) a positive relationship between percent occurrence of jackrabbits in coyote scats and jackrabbit abundance (functional response). Predictions for the bottom-up hypothesis were, 1) plant productivity is directly related to precipitation, 2) jackrabbit abundance is positively related to precipitation and plant productivity, and 3) changes in abundance of jackrabbits over the reproductive season will be directly related to precipitation and plant productivity. We found a limited numerical response but no functional response of coyotes to jackrabbit abundance. Forb productivity was significantly related to annual precipitation levels ($r^2 = 0.69$, $p = 0.002$). Grass productivity was related to annual precipitation ($r^2 = 0.34$, $p = 0.028$). Jackrabbit abundance ($r^2 = 0.38$, $p = 0.002$) and changes in abundance ($r^2 = 0.73$, $p < 0.001$) were significantly related to precipitation and forb and grass productivity. We conclude that precipitation levels and plant productivity affect jackrabbit abundance more than predation levels.

1. Introduction

The role of predation in the dynamics of prey populations is important not only for the prey but for community dynamics and structure (Kotler, 1984; Sih et al., 1985). However, since the inception of the original Lotka-Volterra predator-prey models, the extent of this "top-down" influence has been highly debated (Ale and Whelan, 2008; Laundré et al., 2007, 2006; Smuts, 1978). It remains unclear as to whether predators are limiting prey or prey are limiting predators (Clark, 1972; Krebs et al., 2001; Tanner, 1975; Wagner and Stoddart, 1972). Added to the debate is the role of bottom-up forces on prey populations such as precipitation and plant productivity (Ernest et al., 2000; Hunter and Price, 1992). The extent of these bottom-up forces in humid environments is often not very clear because plant productivity appears not to be as directly associated with precipitation levels (Krebs et al., 2001). However, these factors seem to have more prominent roles in the harsh desert environments where precipitation and thus primary productivity is more limiting (Hernández et al., 2005; Ogle and Reynolds, 2004). Still, the respective roles of plant productivity and predation in limiting prey populations in these environments are not well defined. Here we examine the respective top-down and bottom-up roles of predation and plant productivity on the black-tailed jackrabbit (*Lepus californicus*) in the Chihuahuan Desert of Mexico.

Black-tailed jackrabbits are common midsized herbivores that inhabit an extensive part of the arid and semi-arid regions of northern Mexico and western United States (Best, 1996). Jackrabbits are principal prey of various predator species including coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) (Delibes and Hiraldo, 1987; Hernández et al., 2002). In many areas of their range, their populations are cyclic and can reach densities of >120 individuals/km^2 (Bartel and Knowlton, 2005; Gross et al., 1974). At high densities,

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they can modify shrub cover and architecture, especially in desert environments (Anderson and Shumar, 1986; Hernández et al., 2002; Martínez and López-Portillo, 2003). Their high abundance, often followed by a rapid decline, can also impact predator populations (Knick, 1990). Because of this prominent ecological role of jackrabbits, investigating the relative strengths of top-down and bottom-up factors that influence their abundance can be helpful in understanding the community dynamics of the desert systems where they occur.

Regarding top-down factors, predation by coyotes is considered the main source of proximate mortality in jackrabbits (Bartel and Knowlton, 2005; Wagner and Stoddart, 1972). Although all mortality sources by definition are limiting factors, whether coyote predation is a regulating factor depends if their impact is density dependent (Messier, 1991). For predation to be density dependent, predators either have to increase in number (numerical response) or increase their harvest rate (functional response) in response to increases in prey numbers. To determine if coyotes potentially can be a regulating factor of jackrabbit populations, we tested the predictions that they will show 1) numerical and 2) functional responses to changes in jackrabbit abundance.

For bottom-up limits on jackrabbit populations, we first tested the prediction that plant productivity in the Chihuahuan Desert was related to precipitation levels. Next we tested the prediction that jackrabbit abundance at the end of the plant growing season in the fall and toward the end of the dry season in the spring are related to plant productivity levels in the fall. These two predictions relate to the impact plant productivity may have on summer survival (fall) and on survival over the dry season (spring). Finally, we tested the prediction that changes in jackrabbit abundance from the beginning to the end of the reproductive season (Feb–Sept; Portales et al., 2004) was directly related to precipitation and plant productivity over that time period. This prediction relates to the impact of plant productivity on survival of individuals over the summer.

To test the various predictions, we used data sets from 1997 to 2007 on spring and fall jackrabbit and coyote abundances, coyote diets, annual precipitation, and vegetation cover at the end of the growing season (November) from the Chihuahuan Desert in Northern Mexico. The results of these tests should provide further insights into relative strengths of top-down or bottom-up factors affecting jackrabbit abundance in the Chihuahuan Desert.

2. Methods

2.1. Study site and data collection

We conducted the study from 1997 to 2007 in the Mapimi Biosphere Reserve (MBR) in the Chihuahuan Desert of Northern Mexico (26°40'N, 103° 40'W). Our field efforts were in two distinct habitat types, a grassland dominated by tobosa grass (*Pleurophis mutica*) and a shrubland dominated by mesquite (*Prosopis glandulosa*), creosotebush (*Larrea tridentata*), and prickly pear cacti (*Opuntia rastrera*). The average mean temperature of the coldest month (January) was 11.8 °C. The highest average summer temperature (28 °C) occurred in June (Cornet, 1988). The 28 year average Jan–Dec rainfall was 280.4 ± 19.4 mm with a large amount of year-to-year variation (Range, 122–510 mm). Approximately 71% of the total yearly rainfall amount is in the rainy season from June to September. Because the calendar year does not correspond to the more biologically relevant annual dry and rainy seasons, we used precipitation amounts from the previous 12 months relative to the particular parameters we analyzed. For example, for November analyses, we used precipitation amounts from the previous December–October.

We estimated relative coyote abundance with standard scent stations (Linhart and Knowlton, 1975) each consisting of a 1.0 m diameter circle of sifted soil with a commercial scent tab in the center (U.S. Department of Agriculture Supply Depot, Pocatello, Idaho). Thirty-one stations each were set at 0.5 km intervals along two 15 km dirt roads, one in each of the two habitats. Over the length of the study we conducted the scent station surveys in March and in November. In each month, we activated the stations for 2 consecutive nights and expressed coyote abundance as the # tracks/100 scent station nights.

In each March and November of 2000–2007, we collected coyote feces along the two 15 km routes in the two habitats used for the scent station surveys. Collection of feces was normally over a one week period within each of these months and concurred with the time of the station surveys. However, we did not start collecting feces until the 4th year of the study. After air drying the fecal samples we hand analyzed the samples to identify animal and plant contents. For mammals we used reference collections to aid in identification of hair and bones we found. We expressed identified jackrabbit remains as percent occurrence (# of feces with jackrabbit remains/total # of feces collected *100; Hernández et al., 2002) and used this as an estimate of the level of consumption of jackrabbits by coyotes for the different years.

We conducted abundance counts of jackrabbits in March and November of each year of the study (1997–2007). Counts were along the same two 15 km roads where we conducted the scent stations. In each of the sample months (March and November) we counted jackrabbits over one night between 20:00 to 22:00 h. Sample nights were between the last and first quarters of the moon phase. From the back of a pickup truck driven approximately 10 km/h along the roads (Smith and Nydegger, 1985), two persons scanned for jackrabbits with two 1 000 000 candle power Brinkman Q-Beam® spotting lamps. We standardized the abundance counts to number of jackrabbits/10 km and used these as relative abundance indices for the various analyses.

For the vegetation analyses, we established 4 randomly placed 36 × 36 m quadrants in each of the two study habitats. Each quadrant had 36 (6 × 6) sample points spaced 6 m apart. At each point, we measured percent cover of shrubs, cacti, forbs and grasses within a 1 × 1 m point intercept frame (Floyd and Anderson, 1982). Vegetation measurements were made in November of each year of this study (1997–2007).

2.2. Testing predictions

To test the prediction of a numerical response in coyotes to jackrabbit abundance, we regressed the March and November coyote abundance indices (# tracks/100 scent station nights) against November jackrabbit abundance indices (# sighted/10 km).We used only the November jackrabbit abundance indices in this analysis because these indices reflect annual reproduction. Because jackrabbits rarely reproduce between November and March (Portales et al., 2004), the March indices would only reflect survival of animals over that time. For the prediction of a functional response in diets of coyotes, we regressed estimates of percent occurrence of jackrabbit in coyote scats against jackrabbit abundance indices.

To test the predictions regarding bottom-up forces, we used percent plant cover as a measure of plant productivity (Ernest et al., 2000; Flombaum and Sala, 2007). We first tested with a simple regression analysis whether the dependent variable of arc-sine transformed percent plant cover in November was related to precipitation from the previous 12 months (Nov–Oct). We conducted separate analyses for the 4 groups of plants (shrubs, cacti, forbs and grasses) and for the two habitat types. If a significant