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## The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance?

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**Abstract.** Identifying factors that may be responsible for regulating the size of animal populations is a cornerstone in understanding population ecology. The main factors that are thought to influence population size are either resources (bottom-up), or predation (top-down), or interspecific competition (parallel). However, there are highly variable and often contradictory results regarding their relative strengths and influence. These varied results are often interpreted as indicating “shifting control” among the three main factors, or a complex, nonlinear relationship among environmental variables, resource availability, predation, and competition. We argue here that there is a “missing link” in our understanding of predator–prey dynamics. We explore whether the landscape-of-fear model can help us clarify the inconsistencies and increase our understanding of the roles, extent, and possible interactions of top-down, bottom-up, and parallel factors on prey population abundance. We propose two main predictions derived from the landscape-of-fear model: (1) for a single species, we suggest that as the makeup of the landscape of fear changes from relatively safe to relatively risky, bottom-up impacts switch from strong to weak as top-down impacts go from weak to strong; (2) for two or more species, interspecific competitive interactions produce various combinations of bottom-up, top-down, and parallel impacts depending on the dominant competing species and whether the landscapes of fear are shared or distinctive among competing species. We contend that these predictions could successfully explain many of the complex and contradictory results of current research. We test some of these predictions based on long-term data for small mammals from the Chihuahuan Desert in the United States and Mexico. We conclude that the landscape-of-fear model does provide reasonable explanations for many of the reported studies and should be tested further to better understand the effects of bottom-up, top-down, and parallel factors on population dynamics.

**Key words:** *bottom-up control; Chihuahuan Desert, United States and Mexico; fox abundance; Jornada Experimental Range, New Mexico, USA; landscape of fear; Mapimi Biosphere Reserve, Durango, Mexico; Merriami kangaroo rat, Dipodomys merriami; parallel control effects; population density; predation risk; species conservation and management; top-down control.*

### INTRODUCTION

The main influences on population size are thought to be either resources, e.g., bottom-up, predation, e.g., top-down, or interspecific competition, what we call here parallel, factors (Brown and Heske 1990, Meserve et al. 1993, Brown and Ernest 2002, Ernest et al. 2008). The extent to which any one of these factors influences

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primarily herbivore populations has been extensively studied (Ernest et al. 2000, Denno et al. 2003, Meserve et al. 2003, Vucetich and Peterson 2004, Hernández et al. 2005, 2011a, Ale and Whelan 2008, just to list a few)

Regarding impacts of bottom-up factors, it is assumed that climate (primarily precipitation and evapotranspiration) directly affects food supplies (plant productivity), which in turn, have direct effects on the population size of primary consumers. There is ample support for the climate–productivity–population density relationship (Brown and Heske 1990, Dickman et al. 1999, Meserve et al. 1999, Ernest et al. 2000, Hernández et al. 2005, 2011a, Previtalli et al. 2009). However, this relationship varies in strength across and even within studies and species, and some studies have failed to find support for bottom-up impacts on density of some areas (Ernest et al. 2000).

For top-down predation control of prey populations the assumption is that lethal removal of individuals by the predator, or consumptive effects, directly affect population abundance of the prey (Sih et al. 1985, Estes 1996). However, the impact of consumptive effects on the population is still unclear (Kittlein 1997, Denno et al. 2003, Vucetich and Peterson 2004, Bishop et al. 2005, Laundré et al. 2006). Reviews of vertebrate predator–prey systems (Connolly 1978, Jaksic et al. 1997, Kittlein 1997, Ballard et al. 2001, Meserve et al. 2003, Previtalli et al. 2009) failed to demonstrate conclusive top-down CE control by predators on their prey. However, others have noted strong top-down effects (Erlinge et al. 1983, Hanski et al. 2001, Terborgh et al. 2001) or show evidence that top-down effects varied among species and even within the same species over time (Meserve et al. 2003, Previtalli et al. 2009).

With regard to interspecific competition or parallel effects, the assumption involves relative competitive advantages (Pimm et al. 1985, Sih et al. 1985), with the better competitor keeping the poorer competitor(s) at lower population levels than would otherwise be predicted. Though this competitive mechanism seems realistic, again, field evidence of competitive interactions affecting population densities is mixed (Sih et al. 1985, Brown and Heske 1990, Meserve et al. 2003).

The general interpretation of all these studies is that the results are too varied and often contradictory to make definite conclusions regarding the relative influence of bottom-up, top-down, and parallel factors. These varied results are interpreted as indicating “shifting control” between the various forces (Meserve et al. 2003) or the existence of a complex, nonlinear relationship among climate, resource availability, predation, and competition (Ernest et al. 2000, Brown and Ernest 2002).

It can be argued that if there is shifting control, some factor or factors should cause that shift to occur. Likewise, if the relationship is complex and nonlinear, could there be a factor or factors that might transform it into a simpler, more direct, predictable relationship? In

both cases an argument can be made for an unconsidered factor, a “missing link,” that will help us better understand the relationships among bottom-up, top-down, and parallel effects and how they impact population abundance. To that end, we explore whether the relatively recent ecological model of the landscape of fear (Laundré et al. 2001, 2010) can help clarify the inconsistencies found and to explain the roles, extent, and possible interactions among top-down, bottom-up, and parallel impacts on prey population abundance.

Under the landscape-of-fear model, the area used by a prey consists of high- to low-risk microhabitat patches as determined by the lethality and ubiquity of the predator within those patches (Shrader et al. 2008, van der Merwe and Brown 2008). These microhabitat patches are imbedded within landscapes sufficiently large to contain local populations of a species (Olsson and Molokwu 2007). The sizes, shapes, and juxtaposition of these patches in an area define the structural makeup of the landscape of fear. Another important property of these landscapes is the proportion of risky vs. safe microhabitat patches making up that landscape, as it can affect the overall risk to individuals living there, e.g., landscapes with higher proportions of risky patches will have higher overall risk.

Others have shown that changes in predation risk can impact absolute population density and even community structure of prey species (Kotler 1984, Eggers et al. 2006, Creel et al. 2007, Zanette et al. 2011). Consequently, with regard to population density, we propose that the proportion of risky to safe microhabitat patches of an area (the makeup of the landscape of fear) can affect the absolute population density of a species living there. We further propose the hypothesis that the relative contributions of bottom-up, top-down, and parallel factors to changes in that absolute density over time will also depend on the makeup of the landscape of fear that a species lives in.

Based on our proposed hypothesis, we develop various predictions regarding the impacts of differing proportions of risky and safe microhabitat patches on absolute population density and bottom-up, top-down, and parallel effects on that density. We then test some of these predictions with long-term data from small-mammal populations in the Chihuahuan Desert. We discuss whether it is worth pursuing further tests of the landscape-of-fear model in other predator–prey systems regarding its possible role in the relative impact of bottom-up, top-down, and parallel influences on population dynamics.

#### PREDICTIONS

##### *Impacts of the landscape of fear on population abundance*

Under our hypothesis, differences in absolute prey population abundances are dependent on the makeup of the landscape of fear. For the initial example, we consider two hypothetical areas large enough to contain enough safe and risky patches (Olsson and Molokwu

2007) to maintain local populations of a given species. It is understood that local densities of the safe and risky patches will differ but that the sum of these patch densities produce the absolute abundance of the area. In fact, we propose that this is the mechanism by which the landscape of fear impacts the absolute population abundance of an area. By altering the amount of safe vs. risky patches within that area we change their relative contributions to the absolute abundance of prey in the area.

We first consider an area consisting of 75% safe patches for a particular species. Assuming an area of 75% safe patches may appear to be an extreme case. The proportion of risky and safe patches in an area can range reciprocally from total risky to total safe patches, assuming, in this case, no “neutral” risk patches. However, it is probably rare that the amounts of safe and risky patches will be exactly equal (50:50), either one or the other patch type will be dominant on the landscape and occur between 51% to 100%. Consequently, 75% occurrence of the dominant type, in this case safe patches, actually represents a medium value between 50% and 100%.

With this amount of safe patches, regardless of patch size, configuration, or juxtaposition, overall predation risk is low and prey can have relatively safe access to most of the food resources across the landscape. Consequently, the absolute population abundance will be close to predicted carrying capacity of the area based on overall food resource levels.

In contrast, in an equal-sized area with 75% risky patches, overall predation risk will be high regardless of the configuration of safe patches, and prey will have to traverse more risky patches. Prey will concentrate in the limited safe patches (Sih 1984, 2005, Laundré 2010) where increased intraspecific competition for the limited food resources will force animals, especially younger ones, to seek food in riskier patches in an ideal despotic or preemptive distribution (China et al. 2008). Higher predation rates in the abundant risky patches will reduce the population and produce a behavioral carrying capacity of prey density lower than in the first example. Our first prediction, then, is that areas with higher proportions of risky patches—and thus predation risk—will inherently have lower absolute population abundances than areas of lower predation risk, even under similar overall food-resource levels.

#### *Impacts on top-down, bottom-up, and parallel effects*

In the above two examples we analyzed impacts of the proportion of risky and safe patches on absolute population abundance of an area, under a given food-resource level. We consider here the annual variations in resource levels to explore how top-down, bottom-up, and parallel effects will impact absolute prey population abundance in a landscape of fear. We first predict how the makeup of the landscape of fear affects the response of a single-species population to either top-down or

bottom-up forces, in the absence of interspecific competition (Table 1). We then add interspecific competition or parallel effects and predict how they might affect dominant and subordinate competing species (Table 1). Here we only show the predictions for the single species but include detailed explanations for competing species in Appendix A.

Using our example of an area of 75% safe patches, if plant productivity increases in a subsequent year, we predict an increase in the absolute prey population abundance, with a year lag response (Ernest et al. 2000, Hernández et al. 2005, Lightfoot et al. 2012), because most of the increased productivity is available at a relatively low predation cost. Conversely, in a year of declining productivity, the overall resource base is reduced and the population size will decline. As a result, we will expect high correlations among precipitation, plant productivity, and population density and would then conclude there are strong bottom-up impacts (Table 1).

Because predators only have easy access to a small proportion of the prey base, as prey increase, predators cannot capitalize on that increase and the response of the predator numbers to prey changes will be weak. We also predict that predator-removal experiments will result in minimal increases in prey populations because the predator had limited impact on the prey initially. Thus, in this example, top-down impacts on prey population change will appear relatively weak (Table 1).

In an area of 75% risky patches for a single species (Table 1), based on the previous discussion the prey species will be less abundant on the landscape. If plant productivity increases in a subsequent year, we will still expect an increase in the population. However, this response will not follow increases in resource availability because most resource increases will be in risky patches. Animals trying to use these highly attractive but risky patches become more susceptible to predation and removal (Rohner and Krebs 1996). Thus, we would predict in this case low correlations between the changes in plant productivity and the numerical response of herbivores, i.e., weak bottom-up effects.

On the other hand, in an area of 75% risky patches, predators will have access to prey, albeit at a lower prey density (Sih 1984, Marín et al. 2003, Laundré 2010). In this case, increases in prey abundance in high-resource years will lead to increased prey availability and greater predator numbers. As prey decline in low-resource years, predator numbers will also decline, with what appears to be also a one-year lag (Laundré et al. 2007). Because predator populations will respond to changes in prey numbers, there will be a significant correlation between prey and predator numbers. We also predict that predator-removal experiments can show positive effects for prey as they will safely expand to the large previously risky areas. Overall, the data will provide evidence for stronger top-down impacts (Table 1).

TABLE 1. Predicted strengths of bottom-up, top-down, and parallel effects on population abundance relative to proportions of risky vs. safe habitat.

Scenario	Bottom-up effects	Top-down effects†		Parallel effects
		Population	Removal	
Dominant competitor: 75% safe habitat	strong	weak	weak	
Subordinate competitor: 75% safe habitat	weak	weak	weak	strong
Subordinate competitor: 75% risky habitat	weak	weak	inverse	weak
Dominant competitor: 75% risky habitat	weak	strong	strong	
Subordinate competitor: 75% risky habitat	weak	weak	moderate	weak
Subordinate competitor: 75% safe habitat	strong	weak	inverse	weak

Notes: For this example, we use relatively high (75%) amounts of first safe and then risky habitat for a dominant competing species. Under each scenario, we add a subordinate competitor whose landscape of fear first overlaps with and then is opposite to the dominant species.

† Under the top-down category we make predictions relative to the predator's population response to prey changes (Population) and then the predator's response to removal of the predator (Removal).

In a similar manner, in Appendix A we develop the predictions for when we add a subordinate competitor to the mix and show that as the proportions of shared and distinctive risky and safe patches change for competing species, bottom-up, top-down, and parallel effects will vary from weak, to moderate, to strong (Table 1). In one case, i.e., dominant species with 75% safe patches, subordinate species with 75% risky patches, we even predict inverse top-down impacts (Table 1, Appendix A).

Under the proposed hypothesis, bottom-up, top-down, and parallel effects will always contribute to a species' population dynamics as a function of the specific landscape-of-fear mosaic for a given prey and its specific predator(s) and competitors (Kotler et al. 2002). Although the outlined interactions can become complex, they can be predictable if the landscape of fear for the species of interest is characterized. If this hypothesis is supported, the landscape-of-fear model can be considered the "shifting control" factor to explain why the extent of bottom-up, top-down, and parallel regulation varies among and within studies for different species.

#### METHODS

To test the hypothesis that the makeup of the landscape of fear will directly affect absolute population abundance of a species and the relative impacts of top-down and bottom-up forces, we use data on Merriam's kangaroo rat (*Dipodomys merriami*) abundances and population dynamics from two study sites in the Chihuahuan Desert of Mexico (Fig. 1; Appendix B).

##### *Absolute prey abundance and risk levels*

To test for a relationship between absolute prey abundance and risk levels, we used data for eight sample areas in the Mexico site and four sample areas in the United States site (Appendix B). Each area was >1 ha and consisted of mixtures of microhabitat patches that varied in predation risk (López Medina 2005, Burke 2006). At both sites we estimated absolute prey abundance on the areas and relative levels of predation risk (giving-up distances, GUDs; Appendix B). In using

GUDs we assumed that predation risk was the main component of foraging costs, more than metabolic and missed-opportunity costs, that may differ among sample areas (Kotler et al. 2004a, Olsson and Molokwu 2007, Rieucau et al. 2009), as explained in Appendix B.

Our first prediction was that prey densities within sample areas will be inversely related to predation-risk levels, and we tested it by regressing kangaroo rat densities against GUD estimates independently at both study sites. Additionally, for the Jornada site we regressed the percentage of GUD estimates within plots that were 2 SDs above the cross-plot mean against



FIG. 1. Location of the Jornada and Mapimí LTER study sites within the Chihuahuan Desert of North America.

kangaroo rat density (see Appendix B for details). As food-resource levels affect population density on an annual basis (Hernández et al. 2005, 2011a) and can affect GUDs as a missed-opportunity cost (Brown 1988, Rieucan et al. 2009), we tested for their possible effects on our results by regressing the normalized difference vegetation index (NDVI) from satellite images of the Jornada plots against kangaroo rat densities (see Appendix B for method details). We did not have similar data from Mapimí to do this analysis.

*Impact of predation risk on bottom-up, top-down, and parallel effects*

To test for impacts of predation risk on the strength of bottom-up effects on rodent densities, we used long-term (12 years) data sets from the Mapimí site on kangaroo rat densities and plant productivity estimates (Hernández et al. 2005, 2011b; Appendix B). These data came from two distinct areas, shrubland and grassland, that differed in the proportion of closed shrub and open sparse grass/bare ground microhabitats (J. López-Portillo, L. Hernández, and A. González-Romero, unpublished data). Predation risk for desert rodents is higher in open microhabitat patches, especially during the full moon (Kotler et al. 2004b, López Medina 2005, Burke 2006); thus the grassland area will have higher overall predation risk (Burke 2006). If the strength of bottom-up forces is greater in low-risk areas, we predict that in the area with the lower predation risk, the shrubland, there will be a stronger relation between kangaroo rat densities and grass and forb cover when compared to the high-risk grassland. To test this prediction, we regressed yearly November estimates of Merriam's kangaroo rat densities against annual November estimates of percent cover of forb and grasses separately for the grassland and shrubland areas (Appendix B).

Finally, we also estimated the relative abundance of kit fox (*Vulpes macrotis*) and gray fox (*Urocyon cinereoargenteus*) in the grassland and shrubland areas in Mapimí (Appendix B). The main diet of these two fox species is kangaroo rats (L. Hernández and M. Delibes, unpublished data). If the level of predation risk directly influences the strength of top-down forces, then, as in Table 1, we predict that fox abundance should be higher and strongly related to changes in kangaroo rat densities in the high-risk grassland areas. To test the predictions regarding fox abundance, we first compared annual fox track numbers between grassland and shrubland. We then regressed the annual November number of fox tracks per 100 scent-station nights (for details see Appendix B: Estimates of abundance) against corresponding kangaroo rat densities separately for the shrubland and grassland areas. Though there are coyotes (*Canis latrans*) in the area, their main diet is black-tailed jackrabbits (*Lepus californicus*) (Hernández and Delibes 1994, Martínez Calderas 2005, Laundré et al. 2009), so we did not consider them in this analysis.

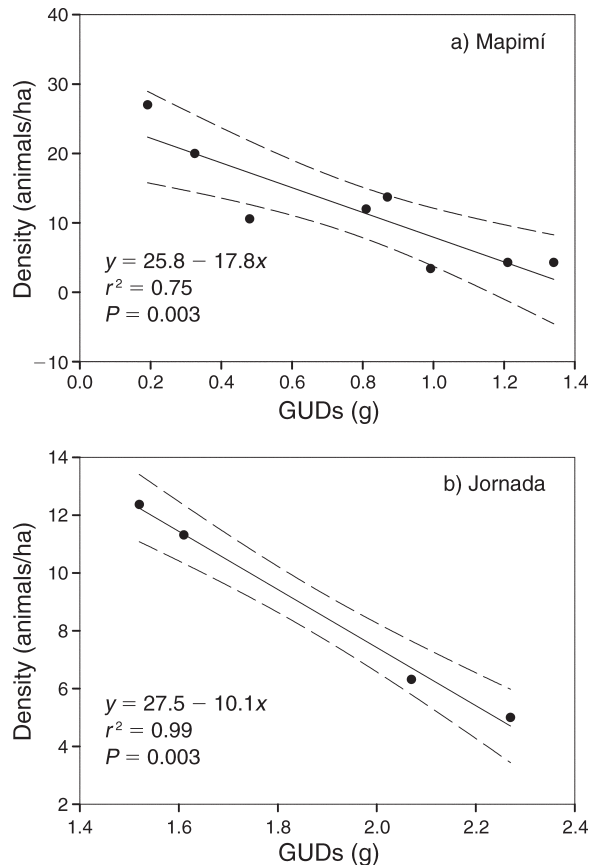


FIG. 2. Relationships between rodent density vs. giving-up densities (GUDs) for the (a) Mapimí and (b) Jornada sites. Solid lines are the regression lines. The dashed lines show 95% confidence intervals. (Note: GUD is presented in grams because the millet seed used in the boxes was measured in grams.)

## RESULTS

### *Kangaroo rat densities and GUDs*

There was a significant inverse relationship between GUDs (giving-up densities) and kangaroo rat density for Mapimí (Fig. 2a) and the Jornada (Fig. 2b) sites. The linear regression accounted for 75% and 99% of the data variability for Mapimí and Jornada, respectively. When we compared the estimate of the percent of GUDs  $>2$  SD from the overall mean to the density of kangaroo rats at the Jornada site, this relationship was also significant (Fig. 3a) and accounted for 92% of the data variability. There was no significant relation between the density of kangaroo rats and the mean NDVI (normalized difference vegetation index) estimates at the Jornada site (Fig. 3b).

### *Bottom-up and predation risk*

Over the 12 years of the study in Mapimí, percent cover of grass and forbs was significantly higher in the grassland area ( $12.5\% \pm 1.8\%$  [mean  $\pm$  SE]) compared to the shrubland area ( $1.6\% \pm 0.48\%$ ; paired  $t = 7.5$ ,  $P <$

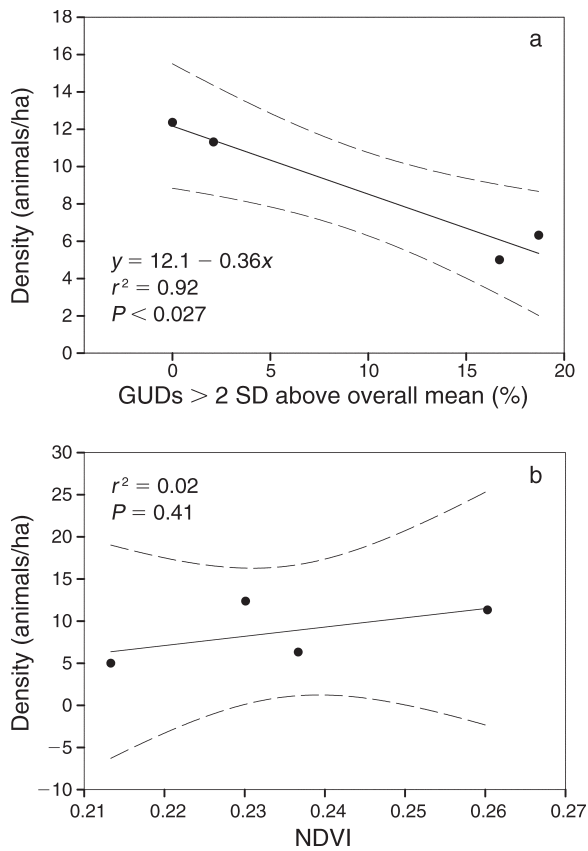


FIG. 3. (a) Relationship between density of kangaroo rats and the percentage of GUD measurements that were  $>2$  SDs above the overall mean GUD for the four sample plots at the Jornada site. (b) Kangaroo rat densities on the four sample plots at the Jornada site vs. the normalized difference vegetation index (NDVI) measurements as an estimator of primary productivity. Solid lines are the regression lines. The dashed lines show 95% confidence intervals.

0.001). Moreover, the slope of the linear regressions, which indicates the increase of plant cover per millimeter of precipitation, was also significantly greater in the grassland than in the shrubland ( $P > 0.01$ , Fig. 4a).

As with other studies (Ernest et al. 2000, Meserve et al. 2003, Hernández et al. 2005), when we regressed annual estimates of kangaroo rat densities against the corresponding plant cover for the same year, there was no significant relationship for either site. Since a one-year lag response in rodent densities is well established in the literature (Ernest et al. 2000, Hernández et al. 2005), we regressed kangaroo rat densities against the previous year's plant cover and found significant relationships (Fig. 4b). However, the coefficient of determination was higher in the shrubland than in the grassland ( $R^2 = 0.66$  vs. 0.45, respectively), indicating, as we predicted, stronger bottom-up effects in the shrubland.

As with precipitation vs. plant cover (Fig. 4a), the slopes of the two regression lines differed significantly ( $P < 0.001$ ) between communities. However, in this case the slope was one order of magnitude higher in the

shrubland than in the grassland (1.2 vs. 0.15; Fig. 4b). Thus, as predicted, the population size of kangaroo rats increased faster in the shrubland as grass and forb cover increased, even if plant cover gain in relation to precipitation was lower in the shrubland than in the grassland.

#### Top-down impacts and predation risk

Over the 12-year period there were significantly higher fox track counts (per 100 scent-station nights) in the higher risk grassland ( $17.0 \pm 3.8$  fox tracks) than in the shrubland ( $10.0 \pm 1.8$  fox tracks) (signed rank test,  $P = 0.04$ ), and consistently higher kangaroo rat densities in the shrubland ( $7.6 \pm 0.74$  animals/ha vs.  $2.6 \pm 0.4$  animals/ha; paired  $t = 8.2$ ,  $P < 0.001$ ). In addition to higher fox abundance in the higher risk grassland, the regression of the number of fox tracks against kangaroo rat densities was significant at  $P = 0.07$  (Fig. 5a) in the higher risk grassland but not significant for the lower risk shrubland ( $P = 0.48$ , Fig. 5a). Likewise, the coefficient of determination was one order magnitude greater in the higher risk grassland ( $R^2 = 0.24$ ) than in the lower risk shrubland ( $R^2 = 0.01$ ; Fig. 5a). When we combined the densities of all the rodent species (see Hernández et al. 2011a for species list), the regression was highly significant for grasslands ( $P = 0.003$ ,  $R^2 = 0.61$ ) and again, not significant for the shrubland ( $P = 0.27$ ,  $R^2 = 0.04$ ; Fig. 5b and c).

#### DISCUSSION

Our purpose in the present study was to explore the hypothesis that the proportions of safe and risky habitats making up a landscape of fear can affect (1) the absolute abundance of a prey species in an area and (2) the relative impacts of bottom-up, top-down, and parallel factors on annual changes in that absolute abundance in areas. We developed various predictions associated with this hypothesis and used long-term data from two sites to test some of these predictions. The results of our analyses lend support to those predictions, warranting further investigation.

#### Implications of the landscape of fear for prey abundance

Our analyses of data from the Jornada and Mapimi sites were used to test the prediction that predation-risk levels affect the absolute population of prey in an area, and the results indicated that further work is in order. Future studies could include manipulative designs, such as artificially altering the predation risk or perceived risk over time on plots. For example, in our system, after obtaining preliminary estimates of prey density and GUDs (giving-up densities) in study plots, some plots could be fenced to exclude terrestrial and aerial predators. The prediction would be that in the fenced areas rodent densities would increase and there would be lower GUDs compared to the open controls. Perceived predation risk could also be altered in areas as done by Schmitz et al. (1997) with grasshoppers (*Melanoplus*

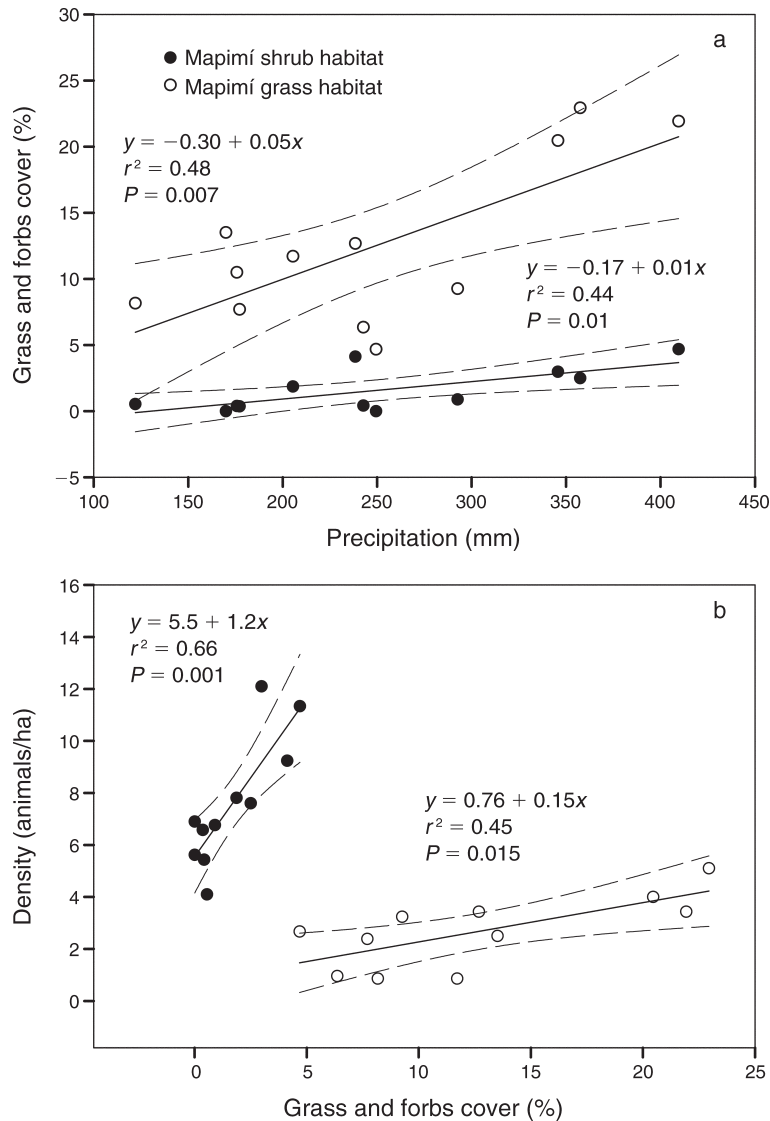


FIG. 4. (a) Relationship between percent cover of grass and forbs vs. precipitation levels at the Mapimí study site for the grassland and shrubland habitats. (b) Fall densities of kangaroo rats over 12 years vs. percent cover of grass and forbs of the previous year in grassland and shrubland habitats. The dashed lines show 95% confidence intervals.

*femurrubrum*) and spiders (*Pisurina mira*) or by Zanette et al. (2011) with songbirds. In such studies, designs as used by Rieucou et al. (2009), should be employed to better identify changes in GUDs due to predation risk vs. the marginal value of energy (China et al. 2008). Alternatively, other methods of assessing risk, e.g., vigilance, could be employed.

#### *Implications for bottom-up, top-down, and parallel control*

Besides possibly explaining differences in prey absolute abundance across landscapes, an additional outcome of this work is in potentially helping understand the roles of bottom-up, top-down, and parallel forces on population dynamics over time. One of the perplexing aspects of these factors is the high variability in results

(Jaksic et al. 1997, Kittlein 1997, Erlinge et al. 1983, Hanski et al. 2001, Meserve et al. 2003, Previtali et al. 2009, Gutiérrez et al. 2010). These often-conflicting results make it difficult to discern which factor is more important. As others have observed, one could find results to support whatever position is desired (Connolly 1978, Ballard et al. 2001). Our results were similar in that in two adjacent habitats separated by less than 2 km, top-down forces appear stronger in one site while bottom-up forces seem to be more prevalent in the other. Thus, like other studies, we also have the dilemma of a complex system where apparent “shifting control” occurs over a relatively small spatial scale for seemingly complex reasons.

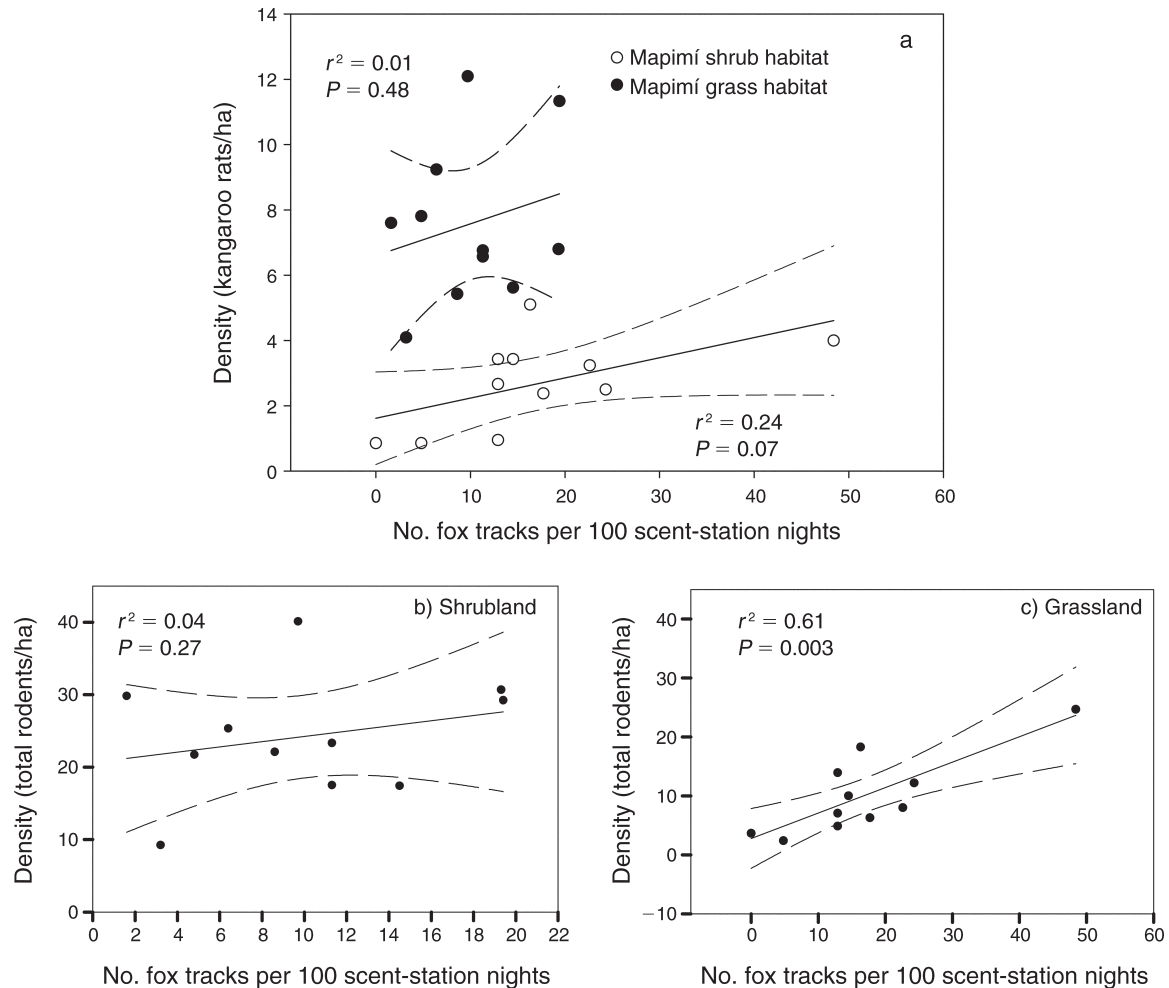


FIG. 5. (a) Number of fox tracks per 100 track nights vs. annual fall kangaroo rat density estimates for grassland and shrubland in the Mapimí study site. (b and c) Number of fox tracks per 100 track nights vs. annual fall total rodent density estimates for the (b) shrubland and (c) grassland and in the Mapimí study site. Solid lines are the regression lines. The dashed lines show 95% confidence intervals. "Track nights" refers to sets of tracks at the scent stations: (no. tracks per station-night)  $\times$  100; for details see Appendix B: Estimates for abundance.

In this context, the landscape-of-fear model provides a possible solution since it allows us to predict that as the proportion of risky patches increases, the lethal and non-lethal impacts of predators on prey will increase. This results not only in lower prey abundance but predictable change in the level of bottom-up, top-down, and parallel impacts on prey population dynamics. Specifically, the model predicts, as we found, that bottom-up forces will be weaker and top-down ones stronger as the level of predation risk increases, and vice versa.

In the perusal of the extensive literature on just small-mammal species, every combination we predicted in Table 1 was found. For example, data from Chile lent support to the prediction associated with lower levels of predation risk because in the predator-exclusion areas of low risk, *Octodon degus*, responded more to increased resources than in the high-risk controls, (Meserve et al.

2003; Fig. 7), suggesting a stronger bottom-up effect. Conversely, the greater declines of *O. degus* in controls compared to exclusions (Meserve et al. 2003; Fig. 7) indicate a possible stronger top-down effect due to predation risk. In southern Arizona (USA) J. H. Brown and his team had several results that could be explained by the landscape-of-fear model. For example, when they removed the numerically and competitively dominant kangaroo rat species (*Dipodomys merriami* and *D. spectabilis*), they did not find the strong response by subordinate species that they predicted (Ernest et al. 2008). This result fits the prediction of weak parallel effects, if the dominant species has a high amount of safe patches while the subordinate ones have mainly higher amounts of risky patches (Table 1). By collecting data on levels of predation risk, critical tests of the model could be done at these sites.



### *Application to other ecosystems*

Although we used a small-mammal–medium-predator system to provide preliminary tests of some of our predictions, the implications of the landscape-of-fear model extend to larger and smaller predator–prey systems as well as to terrestrial and aquatic systems. Our initial study of habitat shifts by elk in response to wolves (Hernández and Laundré 2005) demonstrated that elk under predation risk by wolves had poorer diets than elk in areas without wolves. We predicted that this would lead to lower survival and reproductive success. This prediction has been supported by the fact that poorer diet and increased stress from fear had direct effects on reproduction and recruitment (Creel et al. 2007). Ongoing studies of snowshoe hare (*Lepus americanus*) extend such stress responses to fear to medium-sized mammalian systems and potentially help explain temporal population changes in this species (Sheriff et al. 2009). The previously cited works with song birds not only demonstrated that the risk of predation alone affects nest-site selection and clutch size in birds (Eggers et al. 2006) but reduced the number of offspring produced per year by up to 40% (Zanette et al. 2011). Schmitz et al. (1997) and others (Denno et al. 2003) demonstrated that the impact of predation risk extends the possible application of our predictions to insect predator–prey systems.

In marine systems, researchers are also investigating predation risk on a seascape scale, i.e., the “seascapes of fear” and its impact on habitat use (Wirsing et al. 2008, Wirsing and Heithaus 2009). Of particular interest are the developments in foraging-arena models in marine environments (Walters and Juanes 1993, Walters and Christensen 2009). Foraging-arena and landscape-of-fear models are similar in that the landscape or seascape can be divided into safe (refuges) and risky (foraging arenas) patches. However, foraging-arena theory emphasizes more exchange rates of individuals between refuges and feeding arenas and the implications of changing those rates on population stability. As the proportion of risky and safe patches in our model directly affects these exchange rates, applying foraging-arena theory, especially the Ecopath with Ecosim model (Walters and Christensen 2009), can provide functional insights as to why the makeup of the landscape of fear matters. Wirsing and Ripple (2011) noted that the response to predation risk in aquatic and terrestrial systems appears to be highly similar and that cross-exchanging ideas could be beneficial to both. Combining landscape-of-fear and foraging-arena models is an example of how just such an interchange could prove to be highly productive.

### *Summary and conclusions*

We have presented a novel hypothesis that predicts how the changes in the level of predation risk over the

landscape can influence the population dynamics of a species. We propose that such changes over space and time can alter the relative impacts of bottom-up, top-down, and parallel effects on population abundance. We offered innovative predictions to test this hypothesis and present data to support some of the predictions made. Our results indicate that this hypothesis is worth further investigation, especially in other predator–prey systems, where estimating species specific predation risk becomes as essential as estimating species-specific population densities. If future research supports our hypothesis, then the landscape-of-fear model could provide the “missing link” in understanding the population dynamics of species across a wide variety of taxa and ecosystems.

Additionally, we have noted impacts that the makeup of the landscape of fear might have on the predators, e.g., lower absolute predator abundance with high percentage of safe patches. However, we did not consider in detail the impact the makeup of the landscape of opportunity (the flipside of the landscape of fear; Laundré et al. 2010), has on the population dynamics of the predator. It is anticipated that similar predictions can be made regarding predators and could even further help our understanding of both sides of the predator–prey relationship.

Last, besides the scientific value of further understanding predator–prey relationships, the implications of a landscape-of-fear model for conservation and management should be noted. If the absolute population abundance of the prey, and likely the predator, is dependent on the physical makeup of the landscape of fear, microhabitat composition of an area relative to predation risk becomes an important factor in determining the baseline population abundance in an area. It also affects how that population will respond to annual food-resource changes relative to predation and competition. Manipulation of the microhabitat patches, the building blocks of the landscape of fear, could then be a powerful conservation and management tool for prey and predator (Yong 2013). For example, the current standard management practice to reduce the lethal impact of predators on desired prey species is to lethally reduce the predator population. Under the landscape-of-fear model, increasing the proportion of safe patches within an area would increase prey population levels, reducing the need for lethal control of the predators. Conversely, increasing the amount of risky patches for prey could aid in the conservation of declining predator populations. Conservation then, could rely on balancing the proportions of risky and safe patches for the desired species, which would in turn modify structure and composition of the community. Further investigating the magnitude of the landscape of fear on prey and predator dynamics may hold great potential when incorporating this ecological process into conservation and management practices.



PLATE 1. Lucina Hernández (1960–2013), waiting for a puma (*Puma concolor*) to wake up after radio tagging it for a study on puma behavior and ecology . . . a previous research study that helped lead to the ideas explored in the current paper, for which she was instrumental in conducting the field work. Lucina truly enjoyed working in the field and was as comfortable hiking in snow as under the intense heat of the Chihuahuan Desert of her native country, Mexico. Her indomitable spirit and joy for life buoyed her throughout her all too short time with us. She will be fondly remembered by her husband, John Laundré, her daughter Cecile, and the many colleagues and students she touched in her life. Photo by J. W. Laundré.

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This paper is heartfully dedicated to our co-author Lucina Hernández, who died shortly before manuscript completion. Lucina devoted her professional career to working and teaching mainly in the southern Chihuahuan Desert. It is through her steadfast devotion and discipline that the data sets used in this manuscript were possible. She was considered by her peers as one of the top mammal ecologists in Mexico, and received many accolades for her promotion of desert ecology among scientists and lay people alike. She worked diligently and tirelessly alongside co-workers and students, and recently was quite dedicated to the development of the Rice Creek Field Station at the State University of New York at Oswego. Lucina was also a loving and caring mother and wife to Cecile and John Laundré. We will miss the indomitable spirit that kept her smiling and happy. We will never forget her enthusiasm, happiness, and joy for life.

This paper is also dedicated to the memory of our local parataxonomist, tracker, guide, and field assistant, Adalberto “Chuca” Herrera, who also passed away a few months before Lucina. Chuca helped Lucina and her co-workers over many years in the Mapimí Biosphere Reserve, which he knew by hand. His stories, natural history knowledge, and wit will be deeply missed.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Development of predictions for the impact of the landscape of fear for parallel effects between competing species ([Ecological Archives E095-098-A1](#)).

### Appendix B

Detailed description of study areas and methods used to test predictions ([Ecological Archives E095-098-A2](#)).