



Original investigation

Apprehension affecting foraging patterns and landscape use of mule deer in arid environments

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ABSTRACT

Foraging animals make trade-offs between food and predation risk. To avoid predation, animals will seek out safe habitats for foraging, often at the sacrifice of food resources. Habitat structure and specific predators prey face determine the risk level of specific habitat types. In northern forested areas, forest edges have been shown to be high risk habitat for mule deer (*Odocoileus hemionius*) foraging under predation risk from pumas (*Puma concolor*). In more open habitats, e.g. deserts, *a priori* knowledge of what characteristics might contribute to predation risk levels for this species complex is lacking. Our objective was to evaluate the potential predation risk faced by mule deer from pumas under different habitat characteristics in the open habitat of the Chihuahuan Desert. We measured apprehension levels in mule deer with Giving Up Densities (GUDs) to evaluate predation risk levels of different habitat variables. We used supplemental (experimental) GUDs and natural GUDs: browse of candelilla (*Euphorbia antisiphylitica*). Supplemental GUDs were best modeled with macro-habitat variables: they were negatively associated variables, with the interaction between distance to hills and bush height being the strongest predictor, indicating possible predation risk by stalking pumas. Also natural GUDs (candelillas) indicated that mule deer perceived the proximity to hills as riskier. Identification of habitat characteristics that may contribute to predation risk in the Chihuahuan desert will enable further investigation into how habitat characteristics in the Chihuahuan Desert contribute to predator-prey dynamics of mule deer and pumas.

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Introduction

It is now well established that while foraging, prey species need to incorporate both the levels of food resources and predation risk in their decisions of habitat use (Brown et al., 1999; Lima and Dill, 1990). There is also growing evidence that prey live in a landscape of fear (Kuijper et al., 2013; Laundré et al., 2001) where the level of predation risk varies over the landscape dependent on the predator they face and how the habitat influences the efficiency of predation, predator lethality (Laundré, 2010). Preys become more apprehen-

sive, fearful, when faced with increased predation risk (Altendorf et al., 2001; Hernández et al., 2005). It is well documented that prey respond to this risk by either changes in time allocation, avoiding risky areas, or in behavior, increased vigilance (Brown et al., 1999; Kotler et al., 1994; Laundré et al., 2001) and these responses can be used to identify risky habitats (Iribarren and Kotler, 2012; Shrader et al., 2008). Although it will vary with the particular predator, habitat characteristic and how they contribute to the lethality of predation are the main mediators of risk levels (Laundré et al., 2001; Laundré, 2010). For example, wolves (*Canis lupus*) are more adapt at running down their prey and so open habitats have a higher predation risk for their prey than closed forests (Laundré et al., 2001). Conversely, pumas (*Puma concolor*) primarily stalk their prey and so open areas are of low predation risk while forest edges appear to be high risk areas (Altendorf et al., 2001; Hernández et al., 2005).

Identifying what habitat characteristics contribute to predation risk becomes an important first step in characterizing the makeup of the landscape of fear for a particular prey and its predator(s). Once the link between predation risk and apprehension levels is well established, prey species can enable us to identify risk levels

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though their behavior, either in changes in their spatial foraging patterns or behavioral levels of vigilance (Kotler et al., 1994; Kuijper et al., 2013; Hernández and Laundré, 2005). These changes can often be easily observed visually or measured through standardized GUD techniques (Brown, 1988). The latter method involves offering boxes with fixed limited quantities of food mixed in with an inedible substrate. This offers a diminishing return on foraging efforts and eventually the animal will stop foraging. The amount (density) of food left is the GUD. These GUDs have been shown to be directly related to apprehension levels (Brown, 1988; Kotler et al., 1994).

With these techniques, investigators have been able to identify relative levels of risk of different habitat characteristics over a landscape (Iribarren and Kotler, 2012; Shrader et al., 2008). This is the case for mule deer (*Odocoileus hemionius*) in forested habitats foraging under predation risk from pumas (*Puma concolor*) (Altendorf et al., 2001; Hernández et al., 2005). A majority of mule deer are killed by pumas along forest edges (Laundré and Hernández, 2003) and pumas were found to spend more time hunting in these areas (Holmes and Laundré, 2006). Subsequently, through the use of GUDs and fecal group distributions, it was demonstrated that mule deer perceived these areas as being risky and avoided using them (Altendorf et al., 2001; Hernández et al., 2005).

Although we have been able to identify risky habitat for mule deer faced with predation by pumas in forested area, mule deer and pumas coexist over large expanses of relatively open desert habitat. In these areas, such as the Chihuahuan Desert, habitat characteristics change more subtly and clear distinctions, such as open vs. edge in forested areas, can rarely be made. Then, it can be asked what habitat characteristics in the Chihuahuan Desert landscape might contribute to risk levels that mule deer face under puma predation? Identifying these habitat characteristics becomes a first step in understanding the spatial and behavioral aspects of the predator-prey relationship between pumas and mule deer in this vast ecosystem. Given that levels of apprehension (fear) exhibited by prey in feeding trials (supplemental and natural GUDs) are known to be related to risk levels, we postulate that foraging intensity of mule deer is strongly influenced by habitat characteristics in order to avoid predation and, to a lesser degree, for habitat variables related to food resources. Specifically, we postulate that foraging is influenced by vegetation structure associated with stalking pumas: tall bushes, less visibility, high bush density, steeper slopes, and nearness to hills. Also, we postulate that foraging would be positively related to food abundance. We evaluated the perceived risk levels of various habitat characteristics across a Chihuahuan Desert landscape through the use of a combination of mule deer pellets distribution (spatial use) and GUDs (apprehension levels). Results of this study will help to determine if variables known to be sources of apprehension influence foraging decisions of mule deer in the Chihuahuan Desert, similar to behaviors observed in northern regions. Natural GUD's measurements were based on foraging intensity of candelilla (*Euphorbia antisiphylitica*), a known principle food in mule deer diet in the area (Guth, 1987). Based on *a priori* knowledge from other studies of what might constitute risky habitat, e.g. possible stalking cover, we identified a variety of habitat characteristics on the macro and micro habitat scales as possible contributors to predation risk. We then used linear multiple regression to investigate the relationship between GUD measurements (apprehension) and each identified characteristic.

Material and methods

Study area

The work was conducted in the Laboratorio del Desierto (LD-INECOL), located at 26°41'10"N and 103°44'42"W, in Mapimí

Biosphere Reserve (MBR), in the State of Durango, Mexico. The MBR is a closed basin, characterized by extended flat zones, small hills, and isolated mountains. The climate is arid; annual average temperature is 21 °C, winters are cool and summers are warm, with 15 °C and 26 °C mean temperature respectively. Annual average precipitation is 287 mm, with summer rains (data from weather station, LD-INECOL). In the first year of our study (Jun 2004–May 2005), it rained 10 months for a total of 417 mm and mean temperature was 20 °C; in the second year (Jun 2005–May 2006), it rained 10 months for total of 205 mm and mean temperature was 18 °C. Finally, during the third year (Jun 2006–May 2007) it rained 9 months for total of 374 mm, with a mean temperature of 16 °C.

The study was conducted at altitudes between 1150 and 1200 masl, in a relatively flat area called the Bajadas, next to hills of igneous and sedimentary origins. This landscape element comprises 37% of the region, and is where mule deer are primarily found (Sánchez-Rojas and Gallina, 2000). Specifically, the study was conducted in the upper Bajadas (closer to the foothills and the base of the San Ignacio Mountain) because it is where mule deer principally forage. In the lower Bajadas there are patches of dense vegetation (mesquite trees-*Prosopis glandulosa*- and associated bushes) called mogotes, which provide horizontal and vertical cover, and where mule deer do rest and start foraging every day (pers. obs.). In upper Bajadas, the few sites where occasionally mule deer occasionally did rest (under isolated big bushes), were excluded from analysis.

The vegetation in the upper Bajadas is homogeneous in composition, dominated by creosote (*Larrea tridentata*), ocotillo (*Fouquieria splendens*), prickly pear (*Opuntia rastrera*), yucca (*Yucca rigida*), and agaves (*Agave scabra* and *A. lechuguilla*) (Montaña and Bremier, 1988). The diet of mule deer in the area is primarily bushes (43% of annual diet), forbs (34%, principally in summer), succulents (13%), and grasses (10%). The candelilla bush is an important food item in the Chihuahuan Desert, especially in dry years (Urness, 1981; Esparza-Carlos et al., 2011), contributing 14% of the annual diet (range 10–24% between seasons) (Guth, 1987). Wildlife in the area includes the black-tailed jack rabbit (*Lepus californicus*), one of the few species defecating in pellets; however, the shape and size, as well as the number of pellets, make them clearly distinct from those of the mule deer. The only animals in the area that could interfere with the habitat use or activity patterns of mule deer is the collared peccary (*Dicotyles angulatus*); however, the region is in the edge of its potential distribution. Historically peccaries did not occur in the study area, but there are about 6–8 individuals found there, remnants of a group that was released in 2000 (approximately 30 individuals). Therefore, we consider that the effect of interactions between species is minimal. Cattle could potentially have impacted the movements and distribution of mule deer. However, they do not consume candelilla and were located outside the study area during the supplemental GUD experiments.

In this work we consider predation risk to mule deer only by pumas. Besides pumas, the coyote (*Canis latrans*) is the only other potential predator in the area. However, diet and habitat studies of coyotes in the area have shown that they are not a threat for mule deer (Hernández and Delibes, 1994). During our experiments period, we registered puma occurrence by tracks, scats, trail camera records, visual observations and five kill sites in the study area. Thus, it was assumed that predation risk by pumas was sufficient to influence foraging behavior of mule deer. Human disturbance in the area is low, hunting is prohibited and human activities are centered in cattle management on water catchments (3.5–6 km far).

Mule deer habitat use during foraging and candelilla abundance estimation

We initially plotted the distribution of mule deer fecal groups in a 74 ha study site. We used the previously established relationship

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