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Non-trophic interactions in deserts: Facilitation, interference, and an endangered lizard species

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Abstract

Research on plant–animal interactions has been focused on direct consumer interactions (*i.e.* plants as resources), but non-trophic interactions including providing shelter or interference with movement can also affect the fine-scale distribution of animals. In particular, non-trophic interactions that are positive could support threatened animal populations. Positive interactions have been used in the restoration of plant communities, but have not yet been extended to the management of animal habitat. In this study, we tested the hypothesis that non-trophic interactions influence the occurrence of an endangered lizard species in an arid shrub-annual system. At a location known to have a population of blunt-nosed leopard lizards (*Gambelia sila*), we geotagged 700 shrubs, measured shrub morphometric traits, collected biomass samples, and surveyed for lizard presence using scat detection dogs over two years. Relative to 2014, in 2013 plant productivity was high and lizard scats were found more frequently in areas with low invasive grass cover (*i.e.* residual dry matter, RDM). In 2014, plant productivity was low because of an extreme drought year, and lizard scats were more frequently observed under shrub canopies, particularly those with relatively dense cover. These findings support the novel theory that positive non-trophic interactions are a critical form of plant–animal interactions in addition to consumption. Dominant shrubs can act as a foundation species by functioning as a basal node in structuring both plant and animal communities through a network of interactions. Managing dominant plants, in addition to habitat, is therefore important for conserving animal species in arid ecosystems.

Keywords: *Gambelia sila*; Shrubs; Facilitation; Non-trophic interactions; Lizard habitat; Scat; Scat detection dogs

Introduction

Positive interactions are important in resource-limited ecosystems. In deserts, dominant shrubs are a common benefactor to many other species, particularly plant species within their canopy (Flores & Jurado 2003). Positive shrub interactions in these systems have been shown to directly and indirectly influence animals at nearly an equivalent rate (Lortie, Filazzola, & Sotomayor 2015). Shrubs can positively influence animals directly by providing food resources, such as seeds (Hansen, Kiesbüy, Jones, & Müller 2007; Valido & Nogales 1994), or indirectly by facilitating a prey species (Parmenter & MacMahon 1983). Desert shrubs can

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also influence animals by providing thermal shelters for thermoregulation (Bauwens, Hertz, & Castilla 1996; Parmenter & MacMahon 1983) or by acting as a refuge from predators (Milchunas & Noy-Meir 2002). In addition, shrubs can play a more passive role by acting as a physical designation of territory (Muller 1998) or as a perching site for birds (Aukema & Martínez del Rio 2002). Consequently, animal species associate with shrubs more than open spaces because the shrub fulfils a critical functional role (Lortie et al. 2015). Plants are a form of habitat, but their effects on animals can extend much further through indirect pathways. It is thus reasonable to propose that explicitly examining the positive effects of shrubs on animals in deserts will inform our understanding of ecosystem structure and provide an estimate of plant–animal interactions. Moreover, examination of positive non-trophic interactions of shrubs on animals could have management implications in support of species that are threatened.

Non-trophic interactions are any non-consumptive interactions between two species that are characterised by their mechanism, sign (positive, neutral or negative), and strength. Non-trophic interactions between shrubs and lizards in deserts are novel and advances ecological theory because these interactions are described as a habitat requirement. Deserts are high-stress ecosystems and positive interactions are more frequent in these systems (Filazzola & Lortie 2014). However, trophic interactions, such as herbivory, can be less important or infrequent given the relatively low productivity of arid systems (Crain 2008; Howard, Eldridge, & Soliveres 2012). Research has explored lizard adaptations to environmental extremes that include altered behaviour in favour of specific habitat characteristics (Kearney, Shine, & Porter 2009; Sunday et al. 2014). For example, the habitat of desert lizards is commonly characterised by a combination of vegetation composition, availability of animal burrows for refuges, and food resources (Grillet et al. 2010; Souter, Bull, Lethbridge, & Hutchinson 2007). Burrows and shrubs are also important shelters for lizards (Milne, Bull, & Hutchinson 2003; Sunday et al. 2014) because they provide refuges from predators and relief from extreme temperatures for ectotherms (Milne & Bull 2000; Milne et al. 2003). There can also be negative non-trophic interactions of plants on lizards in desert systems. For example, dense annual cover has been shown to increase predation risk (Vásquez, Ebensperger, & Bozinovic 2002), inhibit movement (Newbold 2005) and reduce foraging ability for animals (Castellano & Valone 2006). Therefore, the distribution of a desert animal species within a landscape is not only determined by vegetation composition, burrow availability, and food resources but also the interaction among these factors. Identifying these non-trophic interactions will provide more realistic descriptions of lizard habitat with which to inform conservation (Barrows, Preston, Rotenberry, & Allen 2008). Positive non-trophic interactions mediated by dominant, 'nurse' plants can provide the means to couple plant–animal theory with practice in deserts.

Herein, we measured the fine-scale association patterns of an endangered species, *Gambelia sila,* with the dominant shrub *Ephedra californica* and invasive annual grasses. We used highly trained dogs to survey for lizard scat as a proxy for *G. sila* occurrence because this technique rapidly detects animal presence and accounts for biases in visual surveys (Woollett (Smith), Hurt, & Richards 2014). The hypothesis that non-trophic interactions influence the occurrence of an endangered lizard species in an arid shrub-annual system was tested. Shrubs potentially provide benefits to lizards directly by ameliorating the microclimate, increasing visual cover from predators, and indirectly by increasing habitat availability through burrows (Prugh & Brashares 2012). Conversely, shrubs can indirectly impact lizards negatively by increasing invasive grass cover that interferes with movement increasing susceptibility to predation. These predictions were tested to examine the following mechanisms:

1. Shrubs reduce temperature and relative humidity under their canopy (direct benefit), increase relative plant cover (indirect benefit from reduced potential predation), and support higher burrow densities (indirect benefit) relative to paired open microsites.
2. Lizard scat is more frequently observed under shrubs (proxy to estimate plant–animal facilitation).
3. Lizard scat is more frequently observed with relatively lower cover of annual grasses (indirect cost via interference effects).

Materials and methods

Study site

All surveys were conducted at the Panoche Hills Management Area located on the western margin of the San Joaquin Valley, California (Bureau of Land Management; 36°41.78′N, 120°47.89′W at 650 m. a.s.l.). The region has an arid climate with the majority of precipitation in the late fall and winter months (October–March). The average annual precipitation is 22.9 cm with mean monthly temperatures of 7.6 °C in January and 25.8 °C in July as recorded at Los Banos weather station, CA (37°03.30′N, 120°51.00′W; http://www.usclimatedata.com/). During 2013 and 2014, Panoche Hills experienced below-average rainfall levels receiving 18.35 cm and 12.65 cm respectively (http://www.usclimatedata.com/).

The vegetation at Panoche Hills is characterised by an *Ephedra californica* scrubland that is heavily invaded by Mediterranean annual grasses and forbs including red brome (*Bromus madritensis* ssp. *rubens*, hereafter *B. madritensis*), *Bromus hordeaceus*, *Erodium cicutarium* and *Schismus barbatus*. The native community is significantly underrepresented but nonetheless includes *Phacelia tanacetifolia*, *Amsinckia grandiflora* and *Monolopia congdonii*. The shrub *E. californica* is dominant (>80% cover) (Hawbecker 1951).