Effects of habitat complexity on the abundance, species richness and size of darkling beetles (Tenebrionidae) in artificial vegetation

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ABSTRACT

We deployed artificial vegetation with 4 different interstructural space widths (complexities): 6, 10, 14 and 27 mm. At the high levels of habitat complexity used in this study, the main effect of increasing complexity was excluding beetles from higher complexity treatments, particularly larger beetle species. The 6 mm (highest complexity) treatment had significantly lower abundance than the other three treatments. The treatments also had significantly different beetle widths (sizes), and the 27 mm (lowest complexity) treatment appeared to have slightly wider beetles than the other three treatments. Increasing complexity appeared to lead to decreasing beetle widths. 9 beetle species were relatively rare in, or absent from, the higher complexity treatments, including 5 of the 6 largest species. 2 rare, small beetle species were only found in higher complexity treatments. There were no apparent differences in beetle species richness between treatments, due to these conflicting results. This experiment highlights the importance of using complexity indices that measure interstructural space sizes, and scale the complexity measurement to the size of the organism, in order to better understand how habitat complexity can affect faunal abundance, average size and species richness.

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1. Introduction

Numerous studies have shown that habitat complexity can have very important effects on both faunal abundance and community diversity (Kovalenko et al., 2012). Note that "habitat complexity" in this paper refers to the total amount of structures within a given area, such that "increasing habitat complexity" means an increase in structure density. This is different than "habitat heterogeneity", which refers to the relative abundances of different habitat structural components (McCoy and Bell, 1991).

Increasing habitat complexity can increase faunal abundance in several ways. Higher structure density may create more livable surfaces or attachment sites for fauna (Hall and Bell, 1988; Nett and Rypstra, 2000), more favorable microclimates (Stapp, 1997; Grimbacher et al., 2006) and may increase food availability (Bologna and Heck, 1999; Laegdsgaard and Johnson, 2001). Increasing habitat complexity provides better refuge for prey from

their predators. Generally prey abundance is higher in more complex habitats due to higher survivorship (Beukers and Jones, 1997; Scharf et al., 2006) or prey preference (Bell and Westoby, 1986).

It should be noted, however, that habitats with higher complexity also tend to have higher predator densities (Langellotto and Denno, 2004), and so any survivorship benefits that prey receive from decreased predator foraging efficiency may be nullified by higher predator densities in more complex habitats (Canion and Heck, 2009). In some cases, increased habitat complexity may actually enhance predator foraging efficiency (Horinouchi et al., 2009), and may also provide predators with better access to their prey (Denno et al., 2002; Klecka and Boukal, 2014).

Bartholomew et al. (2000) developed an index of habitat complexity, Sp/Py, which is calculated as average interstructural space size divided by the width of a prey organism. Bartholomew (2012) predicts that prey survivorship should be maximized at intermediate complexity levels with Sp/Py just greater than 1, such that prey can move through the spaces in the habitat, but predators that are wider than the prey cannot. Less complex habitats may have lower refuge value because more predators would be able to move more easily through the wider spaces in the habitat. Higher complexity habitats may exclude prey from using the habitat as refuge. If predation is an important factor determining the

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abundance of a prey species in an area, then that prey species should have the highest densities in intermediate-complexity habitats. This index scales the complexity measurement to organisms' body size, which is important since animals with different sizes will perceive a given habitat differently, in terms of its refuge value and how easily they can move through the habitat spaces. Fractal indices of habitat complexity can also be used in order to scale the complexity measurement to organisms' sizes (Warfe et al., 2008).

Increasing habitat heterogeneity may provide a greater variety of niches in a habitat, and may therefore lead to increased faunal diversity (Greenstone, 1984; Dennis et al., 1998; Benton et al., 2003). Increasing habitat complexity may also increase faunal diversity, by providing various species with refuges from predators, superior competitors and unfavorable abiotic conditions (Hauser et al., 2006; Meager and Schlacher, 2013). Increasing habitat complexity may create stabilizing, Type III functional responses (Toscano and Griffen, 2013; Barrios-O'Neill et al., 2015) allowing coexistence between predators and prey (Diehl, 1992), and thus increasing species richness. Certain smaller species may not choose to inhabit, or may not survive in, lower complexity habitats with wider spaces, and may only be found in higher complexity habitats with narrow spaces. However, increasing complexity may also reduce faunal diversity by excluding certain larger species from using the habitat spaces (Kelaher, 2003; Ferreiro et al., 2014). Certain fauna may also prefer less complex habitats as they can move through the habitat more efficiently (Lassau and Hochuli, 2004).

Increasing complexity may also reduce the average size of organisms in the habitat (Hacker and Steneck, 1990; MacAbendroth et al., 2005, Gibb and Parr, 2010) because larger individuals may be at least partially excluded from higher complexity habitats, and/or smaller individuals survive better in, or prefer, higher complexity habitats. In this way, increasing habitat complexity can change faunal community composition. Camp et al. (2014) compared the fish and macrofaunal communities in different rivers with submerged aquatic vegetation and higher complexity filamentous algae, and found that two larger species were less prevalent, and smaller species were more numerous, in areas with more filamentous algae.

We deployed pit traps surrounded by artificial vegetation of four different complexity levels in a Sharjah, United Arab Emirates desert habitat, and counted and identified the darkling beetles (Tenebrionidae) we collected. We hypothesized that beetle abundance would be the highest in intermediate complexity treatments (Bartholomew, 2012). This is different from the results of many other studies, which often find increasing faunal abundance with increasing complexity. Bartholomew and Ebeid (2011) conducted research in the same region, and found that smaller beetles were not more abundant in higher complexity treatments. Based on this result, we hypothesized that beetle species richness should decline with increasing complexity, since high complexity treatments could exclude certain larger beetle species, but also not attract smaller species. We also hypothesized that average beetle size would decrease with increasing complexity, as larger individuals would be at least partially excluded from higher complexity treatments. The purpose of this experiment was to test specific hypotheses related to prey faunal responses to habitat complexity, using desert beetles as model organisms. The results from this experiment may be useful in understanding and predicting faunal responses to habitat complexity in very different habitats as well.

2. Materials and methods

2.1. Field site

We randomly deployed artificial vegetation treatments in a 150 m × 65 m patch of Sharjah, United Arab Emirates (UAE) desert. The center of the deployment area was approximately 25.313671 N, 55.500416 E in decimal degrees. Deployments occurred between mid-September 2014 and early April 2015. Historically, the average high temperature between September and March in Sharjah ranges from 24 to 39 °C and the average low temperature ranges from 15 to 28 °C. Historically, average monthly rainfall between September and March varies between approximately 1 mm/month in Sep to approximately 8 mm/month in December and January. We did not measure weather data during our deployments.

The deployment area contained a variety of microhabitats, including a 3 m dune with northeast and southwest facing slopes, flat areas, disturbed and undisturbed areas, areas with relatively high and very low natural vegetation densities, and areas with sandy, mixed sand/gravel and solid sandstone soils. The vegetation was mostly low-lying shrubs, approximately 30—100 cm in height. The plant with the highest percent coverage was *Hammada elegans*, which is a short shrub with numerous, dense branches emerging from the base of the plant. The study area is surrounded by roads and residential areas, and seems to have higher plant percent coverage than other "open desert" habitats that are further away from residential areas (pers. obs.). This may be because it has been isolated from large mammalian grazers for more than ten years (pers. obs.). Note that this study was performed in a limited area, in a habitat that is not necessarily representative of UAE deserts as a whole. Different results may or may not have been obtained if this study was performed in a different desert habitat.

Possible predators of darkling beetles that have been directly or indirectly observed in the study area include foxes (unknown species), grey francolins *Francolinus pondicerianus*, several species of geckos, fringe-toed lizards *Acanthodactylus* sp., sand skinks *Scincus mitranus*, scorpions (unknown species) and camel spiders *Galeodes arabs* (pers. obs.).

2.2. Model organisms

Darkling beetles (Tenebrionidae) are common in arid and semi-arid environments. For our experiments, "beetles" refers to Tenebrionid beetles only. Adult and larval darkling beetles generally feed on dead and decaying plant matter, although the larvae of some species feed on plant roots (Saji and Al Dhaheri, 2011). They may play important ecological roles in desert detritus cycling and as potential prey for a variety of predators. Ayal and Merkl (1994) and Bartholomew and Ebeid (2011) found higher beetle densities, for certain species, in vegetated areas. Vegetation may benefit beetles by providing refuges from predation, creating favorable microhabitats, containing more animal burrows and having more food resources (Stapp, 1997). Beetle species in the UAE vary in size: *Prionotheca coronata* are more than 30 mm long, while *Mesostena puncticolis* are approximately 7 mm long, as examples. We chose to use these beetles as model organisms for several reasons. They are locally fairly diverse and common, and they are potentially an important part of the local desert food web. Past studies have shown that predation can influence Tenebrionid beetle abundance, and that vegetation can provide them with refuges from predators (Groner and Ayal, 2001). Furthermore, these beetles cannot fly, and therefore could not escape our pit traps. We followed applicable guidelines for the treatment of animals in this study.