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Cascading ecological effects from local extirpation of an ecosystem engineer in the Arava desert

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Abstract

The extinction of a single species from a local community may carry little cost in terms of species diversity, yet its loss eliminates its biotic and abiotic interactions. We describe such a scenario in the Arava desert, where different cultural and law enforcement practices exclude gazelles from the Jordanian side of the border while protecting their populations on the Israeli side. We found that gazelles break the soil crust, formed in desert systems after annual flooding, thereby creating patches of loose and cooler sand that are used by pit-building antlions. When we artificially broke the soil crust on both sides of the border we found a significant increase in antlion density in these patches, but only on the Israeli side. On the Jordanian side, where no gazelles have been observed since the early 1980s, no antlions colonized either the control or manipulated plots. Additional choice/no-choice feeding experiments, in which we offered antlions to lizards and birds, revealed that the effect of humans on gazelles cascades further, as antlions serve as a palatable food source for both groups. Thus the human-mediated loss of non-trophic interactions between gazelles and antlions cascades to the loss of trophic interactions between antlions and their predators.

Keyword: ecological engineer, food web, Dorcas gazelle (Gazella dorcas L., 1758), antlion, desert

Introduction

The progression of species extinction draws considerable attention from the scientific world (Dirzo et al. 2014; Ceballos et al. 2015; Urban 2015; Jordano 2016; Tracewski et al. 2016) and has become one of the major challenges for humanity (Pereira et al. 2010; Seddon et al. 2014; Hautier et al. 2015). Yet, alongside species extinction, a parallel process—ecological interaction extinction—often goes unnoticed but should nonetheless act as a warning sign (Jordano 2016). Understanding that ecological interactions encompass both trophic and non-trophic interfaces extends the simplistic perception of food webs. While the importance of trophic interactions has gained considerable attention (e.g. Estes et al. 2011), owing to the abundance of data and the more straightforward observations they require, losses of non-trophic interactions are less documented and studied.

Interestingly most evidence to date on the importance of trophic and non-trophic interactions are found when the species excluded from the ecosystem is a keystone species or an ecosystem engineer. Keystone species are usually recognized as species that exert a large effect on biodiversity, disproportionate to their abundance (Paine 1995). An ecosystem engineer is best described as a species that significantly modifies its habitat, resulting in direct and indirect consequences for other species (Jones et al. 1994; Jones et al. 1997; Olff et al. 2009; Thébault and Fontaine 2010). Identifying ecosystem engineers often helps to explain natural processes (Kéfi et al. 2012; Romero et al. 2015) and solve practical problems (Byers et al. 2006; Sanders et al. 2014).

Unfortunately, many human societies degrade the surrounding ecosystems on which they rely for multiple ecosystem services by excluding ecosystem engineers from or introducing them to the local food web. Since experimentally excluding a single species from a large area is methodologically unachievable and morally questionable, these rare and unintended cases of species exclusion provide unique opportunities to explore the cascading trophic and non-trophic effects of losing an ecosystem engineer. In the Arava Valley, an arid ecosystem shared by Israel and Jordan, such an "experiment" has already taken place: the desert gazelle (*Gazella dorcas* L. 1758), which used to prevail on both sides of the political border, is now present only on the Israeli side. In Jordan, desert gazelles have been heavily poached, and were last observed in the early 1980s (Amr et al. 2000; Namrouqa 2011). By contrast, gazelles are protected by law on the Israeli side of the border and enjoy an iconic cultural status. Recent surveys of gazelles on the Israeli side of the Arava Valley estimate a population of 366 individuals (Talbi, 2015).

We hypothesize that the desert gazelle acts as an ecosystem engineer in the Arava Valley by breaking the soil crust with their hoofs. In areas of high gazelle activity, gazelles may prevent soil crust formation altogether, yet even in areas of relatively low activity, gazelles can generate small patches of loose soil. These small patches may be crucial for sand-dwelling arthropods. The effect of gazelles in the ecosystem may cascade to higher trophic levels, such as lizards and birds, which may consume sand-dwelling arthropods as part of their natural diet (Fig. 1).

Amongst the various arthropods that inhabit the desert salt flats of the southern Arava Valley, pit-building antlions (Neuroptera, Myrmeleontidae) can potentially serve as good indicators of human impact on the land. Pit-building antlions are obligatory sessile and generalist predators (Griffiths 1980; Farji-Brener 2003), and thus local conditions can strongly affect their survival and distribution. Indeed, the increased abundance of gazelles on the Israeli side of the border may be the main reason for the significantly higher density of antlions in Israeli salt-marsh sites compared to environmentally similar sites on the Jordanian side of the border (average 32.7 vs. 0.3 per 2.25 hectares, $Z=1.98$, $p<0.05$) (Mittler 2007).

We explored the role of gazelles as a keystone species and ecosystem engineer. First, by manipulating the soil crust cover on both sides of the border, we asked whether increased coverage of loose soil affects antlion abundance (Fig 1, a?). Second, to further examine the role of the desert gazelle as an ecosystem engineer, we monitored the number of antlion pitfalls within and outside gazelles' footprints (Fig 1, a?). Third, we explored if antlions were a palatable and preferred food source for several lizard species and one bird species, using no-choice/choice feeding experiments (Fig 1, b?, c?).

Material and methods

The southern Arava Valley encompasses four salt flats, of which two served as sites for this study: the Yotvata salt flat, shared by Israel and Jordan (named the Taba salt flat in Jordan), and Ein Evrona. The Yotvata salt flat is located 30 km north of the Red Sea and spans about 50 km^2, most of it within the boundaries of

Jordan. The Ein Evrona salt flat is 8 km north of the Red Sea, spans about 15 km^2, and is located primarily within the boundaries of Israel. The salt flats are typified by silt and clay and evaporative deposits (Abed and Barth 2002; Makhlouf et al. 2010), which form a hard clay crust when the soil dries out after floods or rain. Common bushes in the salt flats are *Nitraria retusa* (Forssk. Asch.), *Alhagi graecorum* (Boiss.) and *Zygophyllum* spp. *Acacia* spp. trees are common on the edges of the salt flats, where alluvial fans drain into the flats during seasonal floods. Monthly average temperatures in this region range from 10.4–12.1°C to 27.3–40.4°C during the coldest (January) and hottest (July) months respectively (data for the years 1995-2009, Israel Central Bureau of Statistics). Precipitation averages 22 mm (data for the years 1981-2010, Israel Central Bureau of Statistics).

Artificial crust-breaking manipulation

We set a total of 20, 44 and 20 plots at Evrona (Israel, UTM: E285000, N693800), Yotvata (Israel, UTM: E700016, N3306386) and Taba (Jordan, UTM: E703000, N30600) salt flats, respectively. Each 1×1 m plot was gazelle proofed by a 1 cm wide plastic brown ribbon attached to four corner poles, measuring 50 cm high above ground (preliminary tests showed that gazelles tend to avoid plots that are surrounded by ribbon). In each location, we manipulated about half of the plots (10, 26 and 10 in Evrona, Yotvata and Taba, respectively) by artificially breaking 80% of the soil crust in each plot using the hoof of a stuffed gazelle leg. The other half remained intact with their crust unbroken as controls. We continued to break the manipulation plots every 3–4 weeks during the winter, after which antlion pits were counted. We used a Mann-Whitney test to compare the density of antlions in manipulated and control plots.

Ground temperatures in a gazelle hoof print

Ground temperatures in the Arava valley can reach extremely high values. Yet, evaporating water from the relatively high underground water of the salt flats can potentially cool the ground and thus provide a more habitable micro niche for ground dwelling organisms. To examine this hypothesis we randomly chose 10 gazelle hoof prints in Evrona salt flat during mid day (13:00-15:00) in April. Air temperatures 5 cm above ground at the time we began measurements were 40.9°C. We measured the ground temperatures 4cm below ground in the gazelle hoof prints and simultaneously in a random location under the salt flat crust, 50 cm away. All measurements were performed using a TES Dual data logger 1316 Thermometer, K thermocouple, with two probes. We used a paired t-test to compare the temperatures under the two different setups.

Antlions in a gazelle hoof print

The fenced Hai Bar Yotvata Nature Reserve is located within the Yotvata salt flat. It is generally used for rearing reintroduced animals, however it also contains a herd of desert gazelles (*Gazella dorcas*), comprising 15–17 individuals at the time of the study. We randomly chose 38 bushes in the reserve and examined a metre-long strip surrounding each bush for antlion pits. The pits were scored as either located within or outside a clear gazelle hoof print. In these strips loose sand could only be found where the soil crust had been broken by gazelles or, occasionally, by bush branches swaying in the wind. We used a Mann-Whitney test to compare the frequency of antlions inside and outside the hoof prints.

Antlions as prey for lizards

Antlion larvae contain digestive fluids and toxins (Matsuda et al. 1995; Yoshida et al. 1999), therefore we questioned their palatability for predators. We first examined the potential for lizards to prey upon antlion larvae. Although antlions can be found in a wide range of habitats, our focus in this study was the antlions of the Arava Valley and potential local lizard predators. We did not try to identify the antlions to the species level but used the pit-building antlion larvae as a functional group. We used two methods to capture lizards: active diurnal and nocturnal searches near bushes; and trapping. Trapping was accomplished using a combination of a pitfall trap, made of a bucket (18 L) submerged in the ground, and a plastic drift fence (20 cm high) that surrounded the bush where lizards' burrows or hideouts were found, ending at both ends above the bucket's edge. The pitfall trap was shaded from above and cardboard hiding places at the bottom provided temporary shelters for the lizards.

Captured individuals were transferred to the rearing room in the laboratory and placed in individual rearing containers (49 x 37 x 25 cm) with a layer of 3–4 cm of sieved sand and cardboard hiding shelters at the bottom, and a fine mesh net above. The containers were heated by circulating warm water (30–35°C) through a pipe that was submerged in the sand. Room temperature was kept at 20–25°C with a 14:10 L/D regime. The lizards were fed every 2–3 days with speckled feeder roach nymphs (*Nauphoeta cinerea* Oliver, 1789), common house fly maggots (*Musca domestica* L. 1758), house crickets (*Acheta domestica* L. 1758) and Yellow Mealworm beetle larvae (*Tenebrio molitor* L. 1758).

To explore whether any of the lizards preys upon antlion larvae under natural circumstances, the lizards' faeces were sifted daily from the sand for 20 days after capture. The faeces were dissolved in water and scanned for antlion larvae remains using a Zeiss Stereomicroscope, model Stemi 2000 – C (Fig. A1). Thereafter we determined the willingness of the lizards to prey on antlions by offering the five lizard species (Table 1) exposed (out of the sand) antlion larvae. The lizards were placed on one side of an open container (49 x 37 x 25 cm) that was divided at its centre by a piece of cardboard. They were provided with sand and food ad-lib. Three days before the experiment we stopped feeding them. On the day of the experiment, we lifted the divider and the lizards were free to move to the other side of the container where we placed five antlion larvae. We watched the lizards' consumption behaviour and counted how many larvae were left after 24 hours.

The skink *Sphenops sepsoides* (Audouin 1829) dwells underground in the salt flats, therefore we hypothesized that, of all species, *S. sepsoides* was most likely to take advantage of submerged antlions. A rearing container was filled with sand to a height of 6–7 cm and a barrier was placed in the middle of the container dividing it into skink and antlion compartments. Five pit-building antlion larvae were placed on the sand in their compartment and allowed to construct a pit. Sessions did not start before at least three antlion pits were constructed. In cases where less than three pits were built, more larvae were added (up to eight). After all larvae were submerged, the barrier was removed and the skinks were free to forage in the entire container. At the end of the session, after 24 hours, the larvae were filtered out from the sand and counted, and a faecal analysis was conducted for the next two weeks to ensure that the missing larvae had been consumed as prey. The lizards were released at their capture location after the experiments terminated.

Antlions as prey for birds

We also studied the attractiveness of antlion larvae for desert birds in the Shezaf Nature Reserve (northern Arava Valley, Israel, 100 km north of the Yotvata site) by presenting antlion larvae to habituated (Zahavi and Zahavi 1997) Arabian babbler (*Turdoides squamiceps* Cretzschmar 1827) groups. The advantage of using these habituated birds is the ease of close observations, especially experiments involving feeding behaviour. The individuals residing in the Shezaf Nature Reserve are not dependent on human feedings, making them ideal objects for studying food preferences.

We first offered the birds mealworms in Petri dishes to ensure that the plates were not obstacles to feeding (mealworms are regularly used as food bait when studying Arabian babblers in the Shezaf Nature Reserve). We then offered two antlion larvae in a Petri dish to each of the 15 birds studied in this experiment, and scored the number of larvae consumed. We predicted that if the larvae were palatable, the birds would continue to eat the second larvae as well. We next sought to clarify whether antlions constitute a preferred food source for the Arabian babbler. We followed three different groups of Arabian babbler in the nature reserve. Upon approach we offered the groups petri dishes with both a third instar antlion larva and a fly maggot, which was similar in size to the larva. In many cases several birds approached concomitantly, requiring the provision of multiple petri dishes (Fig. A2). We examined whether there was a preference for antlion larvae or fly maggots using a chi-square test.

Results

Artificial crust-breaking manipulation

We compared the effect of breaking the soil crust on antlion density on both sides of the border. In the two salt flats located on the Israeli side of the border, significantly more antlions were found in the broken crust plots (Yotvata: 0.9 ± 0.5SE; Ein Evrona: 0.2±0.1SE) than in intact plots (Yotvata: 0 ± 0SE; Ein Evrona: 0±0SE) (Mann-Whitney test, Yotvata, Z=2.097, $p<0.05$; Evrona, Z=3.78, $p<0.001$). In the Jordanian site (Taba), neither manipulated nor control plots contained antlion pits.

Ground temperatures in a gazelle hoof print

Ground temperatures 4cm below surface was significantly lower (paired two-tailed t-test, $p<0.001$) in gazelle hoof prints (35.2°C±0.8SE) than under the surface crust in the salt flat (39.7°C±0.69SE).

Antlions in gazelle hoof prints

A comparison of antlion pits within (Fig. A3) and outside gazelle hoof tracks showed a significant trend (Mann-Whitney test, Z=2.6, $p<0.01$) for antlions to construct their pits within gazelle tracks (1.3±0.4SE vs 0.9±0.1SE).

Antlions as prey for lizards

Of the 25 lizard individuals, representing six species, collected in the Arava Valley, four individuals arrived from the field with antlion mandibles in their faeces: Bosk's fringe-toed lizard (*Acanthodactylus boskianus* Daudin 1802, 1 out of 3), Wedge-snouted skink (*Sphenops sepsoides* Audouin 1829, 1 out of 4), Middle eastern short-fingered gecko (*Stenodactuylus doriae* Blanford 1874, 1 out of 11), and Lichtenstein's short-fingered gecko (*Stenodactylus sthenodactylus* Lichtenstein 1823, 1 out of 2). Two non-native gecko species *Hemidactylus turcicus* (L. 1758) and *Cryptodion scabrum* (Heyden 1827) had no antlion remains in their faeces.

All individuals of the five species (except for one *S. sepsoides*) were observed to consume at least two of the five presented larvae (Table 1). Of the four *S. sepsoides* maintained under laboratory conditions, three consumed antlions in their pits (Table 2).

Antlions as prey for birds

We found that decisions made by the Arabian babblers regarding the number of antlion larvae consumed were not random (Chi^2=10.8, $p<0.01$). Most continued to eat the second larvae after consuming the first (Fig. 2). When given a choice between an antlion larva and a fly maggot of the same size, the birds preferred to prey on the antlion larva first (5.6±1.7SE vs 2.6±0.9SE) (one-tailed t-test, t=1.922, df=9, p=0.043).

Discussion

Our results suggest that unless gazelles are present to break the soil crust, the antlions will have insufficient amounts of loose sand to construct their pit traps. Our results further suggest that in the absence of gazelles, lizards and birds lose a potentially valuable source of food. Furthermore, pit-building antlions also serve as main hosts to several species of flying parasitoids, specifically bee flies (Matsura et al. 1998). Interestingly bee flies from the Bombyliidae family are pollinators of acacia trees (Tybirk 1993; Greathead et al. 2006). It is possible, therefore, that acacia trees, gazelles, bee flies and antlions form a complex interaction web along with birds and lizards (Fig. 1). Moreover, it has been demonstrated that gazelles have an important role in the distribution of acacia trees, which are considered keystone flora species in the Arava Valley (Munzbergova and Ward 2002) and in other desert lands (Hobbs et al. 2014). It would seem that by eco-engineering the soil for antlions, gazelles also indirectly help in the pollination of acacia trees, and thus help themselves in a two-step non-trophic/trophic fashion (Fig. 1).

Density differences of an ecological engineer across a political border may have profound effects on biodiversity patterns. Gazelles, abundant only on one side of the border, are known as a keystone species in the Arava Valley ecosystem (Rohner and Ward 1999; Or and Ward 2003). We have shown that only after the gazelle hoofs break the soil crusts, which form on top of the salt flats' soil, can antlion larvae construct their pit traps (Gotelli 1993), allowing them to assume a meaningful ecological role in this system. Thus, gazelles provide pit-building antlions with the patches of loose sand required to complete their life cycle. This effect, evident only in some of the sites due to human interference, cascades to other species.

Our experiments further showed that artificially breaking the soil crust resulted in antlion establishment only on the Israeli side of the border. Thus the Jordanian Taba salt flat was probably devoid of antlions population reservoirs. Yet pit-building antlions were observed in Jordan in some specific small salt flat areas outside the experimental region that were visited by herds of goats—but not camels (camels' hoofs usually do not break soil crust). Thus, to a certain degree, domesticated goats may take the place of gazelles as ecosystem engineers for pit-building antlions.

The salt flats of the Arava Valley are mostly made of clay (Abed and Barth 2002), which hardens after becoming wet, forming a crust of few millimetres. We assume that this crust is formed physically by raindrops, which break up the soil aggregates to form smaller particles. These small particles are then washed into the open spaces between the larger particles, sealing the soil from further infiltration. When the soil dries, the surface tension causes the expansion of the particles, thus forming a hard layer (Belnap 2003). This cohesion dynamic of the soil crust may have important consequences for biodiversity in desert ecosystems. A study in the northern Arava Valley (Israel) showed that crust formation affects the distribution of lizards. Three sand dwelling lizards showed a significant preference for fragile crusts over loose sand and hard crust soils (Zaady and Bouskila 2002). Under such intermediate hard soils, lizards are able to dig burrows without the roof collapsing on them. Zaady and Bouskila (2002) suggested that unless trampled by an external agent, soil crust becomes too hard for digging and thus unavailable for these desert lizards. They offered a range of vectors that can break the crust, including gazelles. Similar to lizards, antlions also build structures in the sand. However, unlike lizards, antlions rely on the collapse of the sand in their pitfall traps to capture their prey, thus preferring loose sand over fragile crust.

In fact, antlions require loose sand not only to capture prey, but also to thermoregulate in the extreme arid conditions of desert ecosystems. In the southern Arava Valley, surface soil temperatures can increase above 60°C. Therefore antlions will rarely occupy exposed desert soils, except those of salt flats (Mittler, 2007). The Arava Valley salt flats are characterized by a high level of underground water, which filtrate up to the soil surface by the force of capillarity (Danin, 1984), thereby moisturizing the soil surface. The relatively high soil humidity can promote the settlement of antlion larvae since a cooling effect is created by the encounter of extremely dry, desert air with water vapour rising from the humid soil. We show here that by breaking the soil crust, the gazelle not only provides loose sand for desert organisms, but also significantly lower the ground temperatures. In the middle of the day in the hottest months, as the surface temperature exceeded 60°C, antlion larvae were observed digging deep into the sand (up to 13 cm below the surface)(Mittler 2007), a well-known behaviour of pit-building antlions (Marsh 1987; Gotelli 1993). On the other hand, when temperatures in the desert become cold at night and in the first hours in the morning, antlions may again prefer to submerge themselves deeper in the soil, seeking the accumulated heat.

At other times, when temperatures are within antlions' tolerable active range, most will remain at the bottom of the pit in an ambush position (Gotelli 1993), playing an important role in the food web. While antions most commonly prey on ants, these sedentary predators also eat other species including isopods, spiders, caterpillars, flies and wasps (Lucas and Brockmann 1981). Ants can also potentially prey on antlions (Gatti and Farji-Brener 2002), and antlions may cannibalize their conspecific neighbours (Barkae et al. 2014). In the oligotrophic desert ecosystem, pit-building antlions can also assume the role of a prey. They may provide a reliable, easy to locate (Ruxton and Hansell 2009) source of protein. To date, the predation of antlions by birds has been mostly anecdotal (Hauber 1999), however we have shown here that antlions can actually be a preferable source of food for desert birds (Fig. 2). Indeed, we have also observed naturally occurring Arabian babblers digging into antlion pits.

In addition, we provide evidence that antlions are also a food source for several desert lizards, both under natural conditions and in controlled feeding experiments (Table 1). Furthermore, we showed that the Wedge-snouted skink (*S. sepsoides*), with its similar preference for under-sand dwelling as antlions, can locate and consume antlions in their pits (Table 2). While we cannot rule out that antlion larvae engaged in cannibalism (Barkae et al. 2014) in some of the experiments, the open space experiment where lizards were observed to prey on antlions as well as the discovery of antlion remains in the faeces of laboratory-kept skinks provide reliable evidence for the role of antlions as prey for lizards. Moreover, we have observed *S. doriae* geckos catching adult flying antlions in the field. Similarly, Best and Gennaro (1985) found that antlions were a consistent dietary item in the stomach of the western whiptail lizard (*Cnemidophorus tigris* Baird & Girard 1852). Therefore it appears that pit-building antlions may constitute an important factor in the desert food web.

Shanas et al. previously showed that arthropod and reptile diversity across the Israeli-Jordanian border was not even, with reptiles demonstrating significantly lower values on the Israeli side (Shanas et al. 2006; Shanas et al. 2011). In recent years, studies have increasingly examined the social aspects that shape ecological processes (Bradshaw and Bekoff 2001; Folke 2006). Differences across human societies usually result from contrasting land management practices, which can be attributed to socioeconomic factors, policies and management approaches, as well as the oversight capacities of both governmental and non-governmental institutions (Kuemmerle et al. 2007). One of the social practices observed only on the Jordanian side of the border is hunting (Sagie et al. 2013). Accordingly, whereas in Jordan, the desert gazelle has become a rare sight (Mallon and Kingswood, 2001), in Israel, gazelles are protected by a meticulously enforced law (Wildlife Protection Law, 1955) and have formed two healthy herds that roam the southern Arava Valley (238 and 128 individuals in the Ein Evrona and the Yotvata salt flats respectively, Talbi, 2015).

Hunting is often correlated with poverty (Shively 1997; Barbier 2012). In addition to profound cultural differences, the two societies on the opposite sides of the border have significantly different standards of living (Sagie et al. 2013). Opening the border to tourism, trade and mutual cultural exchange may contribute to improved livelihoods in the Jordanian Bedouin villages and thus reduce existing incentives for hunting gazelles. Given the gazelle's role as an ecosystem engineer, such a change could quickly cascade, affecting the complex, local food web and increasing the diversity and ecological stability of the region.

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Table 1. Exposed antlion larvae consumed by lizards (average). Except for one *S. sepsoides* all individuals consumed at least one antlion larvae.

Species	No. of individuals	Average number of consumed larvae (out of 5)
Stenodactylus doriae	9	4.6
Acanthodactylus boskianus	2	5
Sphenops sepsoides	2	2
Stenodactylus sthenodactylus	1	2
Cryptodion scabrum	1	2

Table 2. Antlion consumption by *S. sepsoides* under laboratory conditions.

Individual	Number of served larvae	Number of built pitfalls	Number of consumed larvae
1	9	5	0
2	5	3	4
3	5	5	1
4	5	5	4

Figure Legends

Fig. 1: Some of the trophic and non-trophic interactions across the Israeli-Jordanian border in southern Arava valley. Humans in Jordan hunt gazelles and use Acacia trees as fuel woods (Sagie et al. 2013). The Acacia trees provides shade and food for gazelles which in return save seed from infestation, help the spread and germination of the Acacia seeds (Or and Ward 2003). Gazelles provide ecosystem engineering for pit building antlions (postulated hypothesis “a?”) which consume arthropods such as ants and provide prey for reptiles (“b?”), birds (“c?”) and bee flies (as parasitoids, Matsura et al. 1998). Bee flies may help Acacia trees by providing pollination services. The hunting of gazelles may have cascading effects on the ecosystem.

Fig. 2: Number of times Arabian babbler individuals (N=15) consumed none, one or two antlion larvae (out of two offered antlions).

Figure 1:

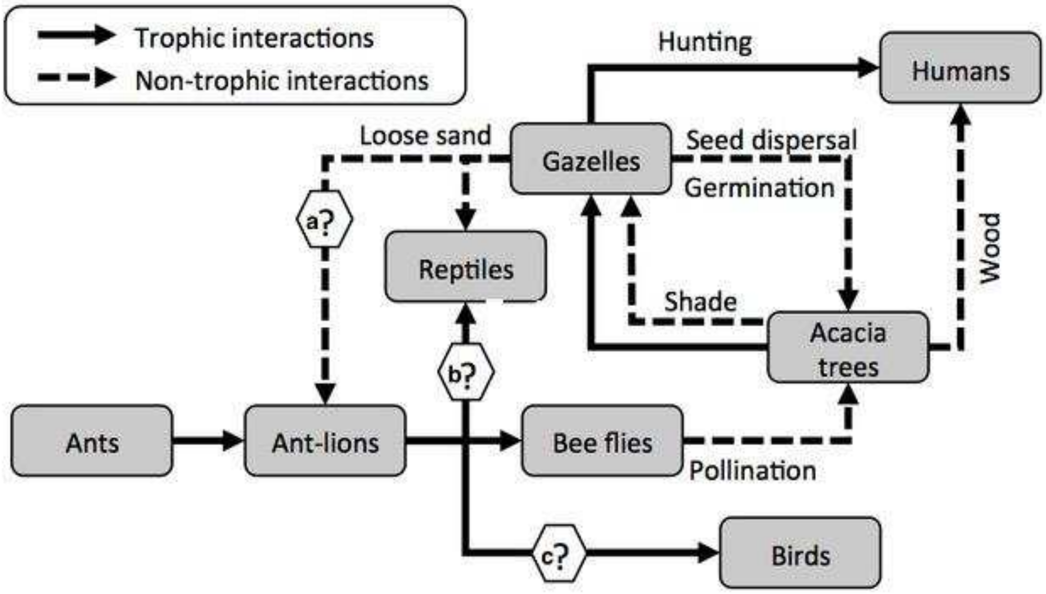
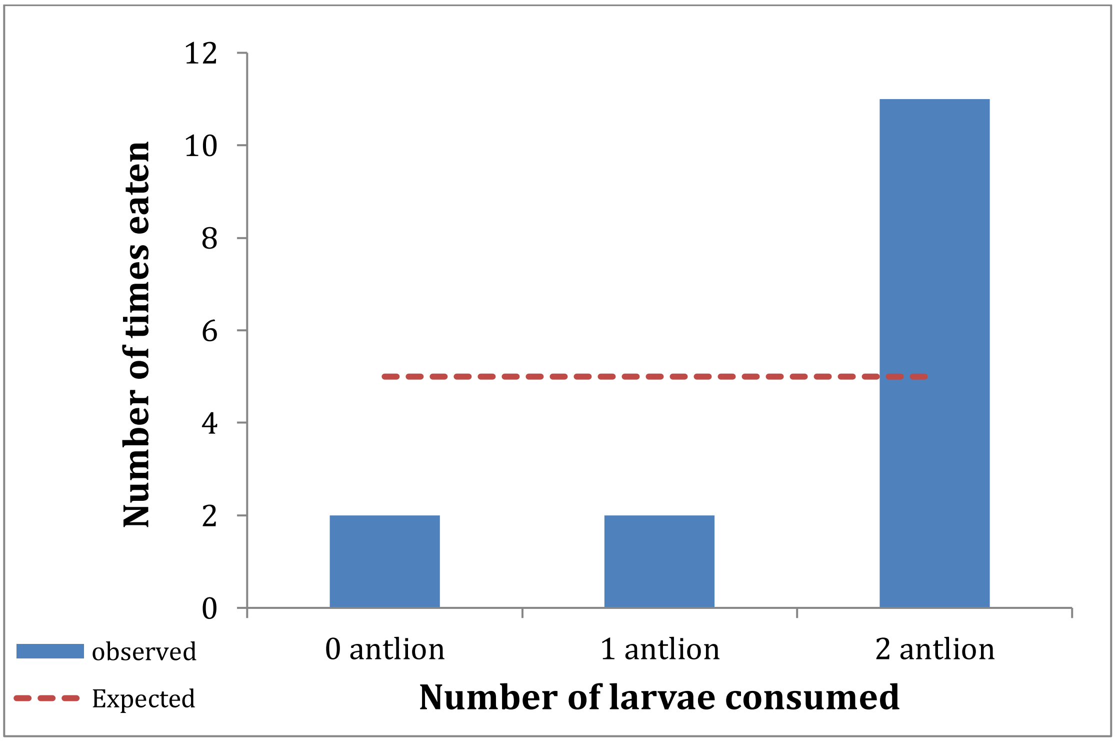

Trophic interactions
Non-trophic interactions
Hunting
Humans
Loose sand
Gazelles
Seed dispersal
Germination
a?
Reptiles
Wood
Shade
Acacia trees
b?
Ants
Ant-lions
Bee flies
Pollination
c?
Birds

Figure 2:



12
10
8
6
4
2
0
Number of times eaten
observed
Expected
0 antlion
1 antlion
2 antlion
Number of larvae consumed