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Factors Influencing Site Abandonment and Site Selection in a Sit-and-Wait Predator: A Review of Pit-Building Antlion Larvae

Inon Scharf[1,2] **and Ofer Ovadia**[1]

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There is a large body of evidence indicating that predator behavior may strongly influence patterns and processes at the population and community level. Site selection is a major component of fitness in sit-and-wait predators, especially when relocation is rare. Although several review articles dealt with these issues in web-building spiders, this is the first attempt to summarize the effects of biotic and abiotic factors on site selection and relocation in another group of sit-and-wait predators, the pit-building antlions (Neuroptera: Myrmeleontidae). Our synthesis shows that prey abundance may have relatively little effect on pit relocation and that physical properties of the habitat or competition often override its effect. We suggest that owing to a variety of constraints such as physiological constraints or difficulties in assessing site quality, site selection and relocation are not necessarily optimal and thus food intake rate is not maximized. We call for a multi-factorial study on a single species in order to pinpoint the dominant factors and to assess to what extent they influence site selection and relocation. We conclude by proposing new research directions, such as studying whether pit relocation is an adaptive response, when controlling for possible phylogenetic effects.

KEY WORDS: antlions; spiders; sit-and-wait predators; habitat selection; optimal foraging; foraging mode.

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[1] Department of Life Sciences, Ben-Gurion University of the Negev, 84105, Beer Sheva, Israel.
[2] To whom correspondence should be addressed at Department of Life Sciences, Ben-Gurion University of the Negev,POB 653, 84105, Beer Sheva, Israel; e-mail: schari@bgu.ac.il.

INTRODUCTION

Ecologists have long recognized that individual behavior (e.g., habitat selection and foraging mode) can strongly influence higher levels of organization (e.g., population dynamics, Pulliam 1988, strength of intraguild competitive effects, Rosenzweig and Abramsky, 1997). Moreover, recent studies have illustrated that the foraging mode of top predators can influence the strength of cascading effects in food webs (Schmitz and Suttle, 2001; Schmitz *et al.*, 2004). Therefore, individual behavior and specifically foraging should be thoroughly studied. This review article examines the effects of biotic and abiotic conditions on foraging behavior and site selection in a classical sit-and-wait predator, the pit-building antlion. Each topic is followed by a brief comparison with spiders, as an example of a well-studied and reviewed sit-and-wait predator. We conclude by proposing future research directions which may enable us to better understand the behavior of pit-building antlions.

The family Myrmeleontidae (Neuroptera) consists of about 2,000 insect species distributed globally. All species undergo complete metamorphosis (holometaboly). Larvae develop through three instar stages and may live between one to three years; their large mandibles make them efficient predators of small arthropods. Adults are short-lived and weak-flying insects (Mansell, 1986; Daly *et al.*, 1998). Antlion species can be classified according to their hunting tactics during the larval period, namely, sit-and-wait or sit-and-pursue predators. Sit-and-wait predators, the subject of most studies on antlions (Lucas, 1989a; Simon, 1989), dig conical pits in the dry sand and feed on prey entering these traps. In contrast, sit-and-pursue predators bury themselves backwards in the sand and ambush prey on the surface (Wheeler, 1930; Youthed and Moran, 1969a; Mansell, 1986).

Classical theories in behavioral ecology (e.g., optimal foraging, habitat selection) suggest that individuals respond to their biotic and abiotic environment optimally to maximize their fitness. Site selection in an arthropod sit-and-wait predator may be affected by the physical properties of the environment, and by ecological components such as physiology, food abundance, the type and strength of competitive interactions and predation risk (Janetos, 1986). According to the "marginal value theorem," a forager should quit a patch once its net energy gain equals the average rate of energy gain over all patches in the habitat (Charnov, 1976). A sit-and-wait predator, however, usually does not deplete food resources significantly in its ambush site (Janetos, 1986; Crowley and Linton, 1999). Rather, an optimal sit-and-wait predator should relocate its ambush site when the benefit gained at a particular site falls below the environmental average gain.

Previous studies have investigated the function and importance of pit construction in antlions (e.g., Mansell, 1988; Lucas, 1989b; Devetak, 2005). These studies showed that the hunting success of pit-building antlions without a pit was very low (e.g., Griffiths, 1992). These findings are also supported indirectly by other studies demonstrating a positive correlation between pit size and prey capture success (e.g., Wilson, 1974; Griffiths, 1980). Furthermore, although little is known about antlion predators, antlions on the soil surface are exposed to predation. Specifically, by constructing pits and staying beneath the surface antlions can reduce possible predation pressure by small reptiles (Simon, 1989, p. 122), birds (Hauber, 1999), ants foraging in groups (Lucas, 1986; Gatti and Farji-Brener, 2002), hymenopterous parasites, (Wheeler, 1930) or conspecifics (i.e., cannibalism or intraguild predation) (e.g., Simberloff *et al.*, 1978; Matsura and Takano, 1989). To this end, owing to the risk and possible costs associated with lack of a pit, antlions which are disturbed or removed from their pits are expected to construct new traps soon afterwards. Indeed, several studies have indicated that pit reconstruction after disturbance is usually done on the same or the next day (Boake *et al.*, 1984; Eltz, 1997; Botz *et al.*, 2003).

Pit reconstruction also depends on other factors, such as satiation, which may cause a delay in pit reconstruction after disturbance (Matsura, 1987), a phenomenon similar to the delay in web-building exhibited by satiated spiders (Pasquet *et al.*, 1994). In addition, differences in pit construction and reconstruction rates between field and lab experiments are also common (Heinrich and Heinrich, 1984; Griffiths, 1986; Lucas, 1989b; Crowley and Linton, 1999). Frequent relocations are rare in pit-building antlions, probably due to the high risk of intra- and interspecific predation and possibly due to the metabolic cost associated with relocation. For instance, Lucas, (1985) showed that metabolic rates were about 10 times higher during pit construction than while resting.

Most experiments investigating pit relocation in antlions were done using a single species while focusing on one or a few factors. Thus, it is difficult to determine the relative importance of the different forces influencing relocation in antlions. Sorting out this type of complexity requires examining the influence of prey abundance on pit relocation using a fully factorial experimental design incorporating several other biotic and abiotic factors. We summarize the different factors that have been found to influence site selection and stimulate pit relocation in antlions (Table I). Next we discuss the effects of biotic and abiotic factors in more detail.

Table I. Factors Influencing Habitat Selection in Antlions After Selected Studies

Species	Origin	Hunger	Interference competition & disturbance	Exploitation competition	Temperature & shade	Rain and humidity	Sand particle size	Reference
Myrmeleon acer Walker	Queensland, Australia	–	+	–				Day and Zalucki (2000)
Myrmeleon pictifrons	Queensland & N. S. W, Australia	+					+	Allen and Croft (1985), Jenkins (1994)
Myrmeleon immaculatus	Connecticut & Rhode Island, Georgia & S. Carolina	+			–			Arnett and Gotelli (2001)
Myrmeleon immaculatus	Vermont	+			+			Heinrich and Heinrich (1984)
Myrmeleon immaculatus	Kentucky			+	+			Linton *et al.* (1991)
Myrmeleon immculatus & M. crudelis	Oklahoma	– ?	+	+				Gotelli (1997), Gotelli (1993)
Myrmeleon crudelis	Costa Rica Florida	– ?					+	Gatti and Farji-Brener (2002), Farji-Brener (2003), Botz *et al.* (2003)
Myrmeleon sp.	Costa Rica			+				Wilson (1974)
Myrmeleon sp.	Costa Rica		+			+		McClure (1976)
Myrmeleon sp.	Costa Rica & Florida	+	+	– ?			+	Simberloff *et al.* (1978)
Myrmeleon carolinus	Florida	+	– ?		–		–	Hauber (1999), Rosenberg (1987)
Brachynemurus	Florida				+			Cain (1987)

Myrmeleon mobilis	N. Carolina	+	–					Eltz (1997)
Myrmeleon uniformis	Minas Gerais, Brazil		+	+		+		Prado *et al.* (1993)
Macroleon quinquemaculatus Hagen	Dar es-Salaam, Tanzania	– ?	+	+				Griffiths (1993), Griffiths (1992), Griffiths (1991)
Myrmeleon obscurus	Grahamstown, S. Africa		+	+	+		+	Youthed and Moran (1969a, 1969b)
Myrmeleon bore	Kyoto, Japan	–	+					Matsura (1987), Matsura and Murao (1994), Matsura and Takano (1989)
Myrmeleon formicarius & Hagenomiya micans	Kyoto, Japan	+						Matsura and Murao (1994)

‘ + ’ indicates that the factor stimulates pit relocation or influences habitat selection.

‘ – ’ indicates that the factor do not influence pit relocation or habitat selection.

‘?’ indicates a suggestion by the author.

INFLUENCE OF PREY ABUNDANCE

An optimal sit-and-wait predator should relocate its ambush site when the benefit gained at a particular site falls below the environmental average gain. Indeed, spiders tend to relocate their nests in response to low rate of prey arrivals (e.g., Vollrath, 1985; Riechert, 1992; Nakata and Ushimaru, 1999; but see Vollrath and Houston, 1986), and so do other sit-and-wait predators (e.g., mantis, Inoue and Matsura, 1983). Spiders, however, cannot reduce their basal metabolic costs to such an extent as antlions, and thus may be more sensitive to longer periods of starvation (Lucas, 1985). Antlions, on the other hand, display a continuous range of responses to changes in prey abundance. For example, pit relocations in response to starvation were very frequent in some studies (Rosenberg, 1987; Hauber, 1999) but rare in some others (Matsura, 1987; Prado *et al.*, 1993). Moreover, because of differences in the testing period among studies it is difficult to pinpoint the effect of prey abundance on pit relocation. Specifically, the testing period in some studies was probably too short for observing pit relocation. For example, Day and Zalucki (2000) reported almost no movement of *Myrmelon acer* during the 15 days of their laboratory experiment, and indeed in long term experiments conducted, antlions began to move only after 15–20 days (Heinrich and Heinrich, 1984; Eltz, 1997). Results of starvation experiments are summarized in Table II. Note that antlion species vary in their ability to resist starvation.

Understanding the effect of prey abundance on pit relocation requires an examination of the following factors: (1) natural prey availability, (2) temporal and spatial variation in prey abundance, and (3) the rate of feeding just before entering a starvation period. The natural habitat of an individual antlion may greatly influence its ability to cope with a starvation period. It seems that antlions from a relatively prey-rich environment have a higher metabolic rate and starvation mortality and are more likely to relocate compared with antlions from a relatively prey-poor environment (Lucas, 1989a; Matsura and Murao, 1994; Crowley and Linton, 1999). Similar tendencies occur in spiders. Desert spiders relocate their nests rarely compared with tropical spiders (see for example rates of web relocation in Vollrath (1985), compared with Ward and Lubin (1993)). Moreover, spiders (and other sit-and-wait predators) occupying a rich habitat may experience significant stochastic variations in prey abundance and, since this can alter their ability to evaluate site quality, they should relocate more frequently. In this case relocation can reduce the chances of staying in a poor site by mistake (Nakata and Ushimaru, 1999). In other words, if it is difficult to assess the habitat quality, food is highly abundant, and the cost of relocation is relatively small, an individual should relocate frequently in order to avoid

Table II. Results of Starvation Experiments

Species	Origin	Habitat characteristics	Starvation degree	Duration	Influence on relocation rate	Reference
Myrmeleon acer	Queensland, Australia	Not mentioned	Complete	15 days	Very few relocations, very little influence	Day and Zalucki (2000)
Myrmeleon mobilis	North Carolina	Sheltered & shaded areas	Partial	48 days	Hunger influences greatly, but only after 2 weeks	Eltz (1997)
Myrmeleon carolinus	Florida	Open areas (a sandy fire lane)	Complete	6 days	Hunger influences greatly, even in a short duration	Hauber (1999)
Myrmeleon carolinus	Florida	Open areas (a sandy fire lane)	Complete	12 days	Hunger influences greatly, even in a short duration	Rosenberg (1987)
Myrmeleon immcaulatus	Vermont	Open areas and shaded areas	Complete	About 3 months	Hunger influences, but only after 20 days	Heinrich and Heinrich (1984)
Hagenomiya micans & Myrmeleon formicarius	Kyoto, Japan	H. micans — shaded areas, M. formicarius — open areas	Complete	Till death, about 120 days	H. micans usually relocates after fasting 20–40 days. M. formicarius relocates less, with no obvious peak	Matsura and Murao (1994)
Myrmeleon Bore	Kyoto, Japan	Open areas (sea side dunes)	Complete	Till death, about 110 days	Hunger has almost no influence, very few relocations	Matsura (1987)
Morter obscurus	Sierra Leone	Open areas	Complete	9 days	Hunger influences greatly, even in a short duration	Griffiths (1980)
Myrmeleon sp.	Costa Rica & Florida	Mostly sheltered & shaded areas (e.g. under overhanging cliffs)	Complete	Not mentioned	Hunger may trigger relocations, but it may have only minor influence	Simberloff *et al.* (1978)

a local spatial shortage. Clearly, this might be another important reason for the more frequent relocations observed in richer environments.

Another source of variation in pit relocation rate may be the different types of environmental variability that an individual experiences. In a spatially variable environment it should be more profitable to relocate when the prey is scarce, since a reduction in prey abundance is probably the result of an inferior location. However, the adaptive response of antlions experiencing temporal variation in prey abundance might be different. Studies have suggested that an alternative adaptive response to temporal shortage in prey abundance would be to consume greater proportions of the prey (Loiterton and Magrath, 1996), to reduce metabolic costs or to improve the pit by making it deeper or larger (Hauber, 1999; Lomascolo and Farji-Brener, 2001). Indeed, starvation in the short term may result in an increase in pit diameter and size. However, in the long term, pits become smaller, probably due to exhaustion (Heinrich and Heinrich, 1984; Matsura, 1987, Lomascolo and Farji-Brener, 2001). Similarly, studies on spiders have shown that an individual experiencing spatio-temporal variation in prey abundance rarely relocates its nest. Desert widow spiders experiencing strong temporal variation in prey abundance rarely relocate their webs to improve prey availability (Lubin *et al.*, 1993). In such cases, when relocation is unprofitable, spiders, like antlions, can modify their traps to improve their chances of catching prey (Olive, 1982).

Rosenberg (1987) hypothesized that *Myrmeleon carolinus* from Florida tends to move more than *Myrmeleon immaculatus* from Vermont (Heinrich and Heinrich, 1984) because a tropical environment is richer in prey items than a temperate one, thus making relocation more profitable. This hypothesis has not been tested. An additional explanation for the increased pit relocation rate observed in tropical regions may be the relatively low temporal variation in prey abundance characterizing such stable environments, which means that most changes in food abundance experienced by antlions are related to spatial variation.

Matsura and Murao (1994) compared site relocation in three species of pit-building antlions, *Hagenomyia micans*, *Myrmeleon formicarius* and *Myrmeleon bore.* They showed that the daily relocation rate of *M. formicarius* is 3.3 times higher than that of *H. micans*, while *M. bore* almost never moves (also based on Matsura, 1987). *H. micans* occupies shaded areas, while *M. formicarius* and *M. bore* occupy open sands and costal dunes, respectively. We interpret this to mean that the open sand areas are less stable temporally, and thus relocation rate in this habitat is lower. An opposite pattern, however, was found in Hauber's and Rosenberg's experiments, where *M. carolinus*, which like *M. bore* occupies open areas, relocates often, and is greatly influenced by starvation pressure (Rosenberg, 1987; Hauber, 1999). Crowley and Linton (1999) used a simulation model to explain several behavioral characteristics observed in the field, such as low rate of relocation. Their simulation results indicated that the most important factor depressing high relocation rate is the cost of moving, and that increasing the variance of prey availability resulted in an increase in the relocation rate, as suggested earlier. These suggestions and the inconsistency between different studies suggest that further empirical research is needed to better understand the relationship between variability in prey abundance and pit relocation rate.

Lucas (1989a) studied the physiology and ecology of two antlion species, *Myrmeleon crudelis* and *Myrmeleon carolinus*, in Florida. The former occupies shaded/sheltered habitats and the latter open habitats (Lucas and Stange, 1981). Lucas found that pit relocation was more common in the shaded areas and that the species occupying this habitat has a higher metabolic rate. This pattern of higher metabolic rates in the shaded habitat is consistent with the findings of Matsura and Murao (1994). In spite of minor differences in prey availability between the two habitats, prey capture rates during the summer were more variable in the open habitats.

Several studies suggested that relocation occurs only when there is no other way to avoid starvation mortality. Eltz (1997) suggested that antlions move rarely because they mainly track temporal changes by adjusting their pits and reducing basal metabolism costs. Griffiths (1986) suggested that relocation should occur following local food shortage but not general or temporal shortage. He hypothesized that antlions have probably no way to distinguish between these two types of environmental variability, and therefore rarely move. There is no direct evidence indicating that antlions can differentiate between spatial and temporal variability in prey abundance, and thus further research is needed. Griffiths (1986), however, could not detect relocation after a moderate decrease in food supply, while an abrupt decline brought about an increase in relocation rate. A moderate decrease may be perceived by the antlions as a temporal change, and in response they may reduce their metabolic rates, preparing themselves for the coming shortage. Jenkins (1994) conducted starvation experiments, manipulating food abundance and feeding frequency before starting the starvation period. He showed that the propensity of antlions to relocate was significantly higher when they were fed more or more often before the starvation period. Similar results were found by Vollrath (1985), who tested the influence of prey abundance on web relocation in an orb spider. Spiders were kept in two cages, and food was given only in one cage. Abruptly, the feeding ceased and rates of web relocation were compared to the relocation rates in the constantly unfed cage. As in Jenkins' experiment, an immediate cessation of feeding resulted in a higher rate of relocations than that measured in a poor but constant environment. We suggest that an abrupt change is perceived by a sit-and-wait forager as spatial change, while a moderate decrease is interpreted as a temporal change.

Most experiments testing antlions' response to changes in prey abundance can be classified as starvation experiments, while few examined the effect of increasing prey abundance on pit relocation. In a field experiment, Heinrich and Heinrich (1984) observed that *M. immaculatus* did not locate its pits in vicinity to ant colonies, and thus concluded that prey presence is not a necessary stimulus for pit construction. Furhtermore, entrances to ant-nests were more abundant outside the antlion zone than inside and ants were observed to avoid entering the antlion zone (Gotelli, 1996; Day and Zalucki, 2000). Matsura (1987) kept *M. bore* antlions in a container and manipulated the food abundance by providing food only in one half of the container. There was no movement from the unfed to the fed part of the container. Other studies that aimed to understand why antlions are not more abundant in prey-rich areas, reached the conclusion that other factors may override the effect of prey surplus (Gotelli, 1993; Eltz, 1997; Gatti and Farji-Brener, 2002). Spiders, in contrast, strongly respond to prey abundance by choosing sites with high prey availability (e.g., Olive, 1982; Rypstra, 1985; Chmiel *et al.*, 2000). Experiments showed that prey existence could stimulate web construction (Pasquet *et al.*, 1994). Moreover, in contrast to antlions, widow spiders were observed locating their webs near ant nest entrances and abandoning them when ants stopped foraging (MacKay, 1982). These differences between antlions and spiders may result from the stronger dependence of antlions on abiotic factors or from antlions' ability to reduce their metabolic rate to a greater extent than spiders.

When relocating, starved antlions move longer distances than fed larvae. After relocation takes place, the larvae build initially small pits and over the next several days enlarge them, if they capture enough prey (Heinrich and Heinrich, 1984). Spiders exhibit the same behavior: an orb-web spider was observed increasing its total length of web thread on the second day at a new site. This supports the idea that the investment of sit-and-wait predators in constructing a trap occurs gradually; they initially invest little and only after making some evaluations do they decide whether to increase their investment or not (Nakata and Ushimaru, 1999).

In conclusion, low prey abundance usually triggers pit relocation, even if the effect is not immediately noticeable. Species may respond differently according to their natural habitat characteristics and according to their ability to resist starvation for a considerable period of time.

INFLUENCE OF DIRECT AND INDIRECT COMPETITION

Previous research has shown that in response to increased conspecific density, antlions increase their relocation rate (Simberloff *et al.*, 1978; Griffiths, 1992; Day and Zalucki, 2000), decrease their rates of pit establishment (McClure, 1976; Matsura and Takano, 1989; Griffiths, 1991) and reduce pit size (Youthed and Moran, 1969a; Day and Zalucki, 2000; but see McClure, 1976). However, due to inconsistency among studies, it is difficult to arrive at further generalizations with respect to the effect of competition on antlion behavior. Several types of competitive interactions (e.g., exploitation, interference) were tested empirically, but it is still not clear which type of competition has the greater influence on antlion spatial distribution pattern, on pit relocation and on some other pit characteristics.

Several studies examined the consequences of exploitation competition (i.e., indirect interaction via depletion of limited shared resources) on antlion spacing, location and relocation (e.g., Wilson, 1974; McClure, 1976). Wilson (1974) suggested that 'shadow competition,' a type of exploitation competition, is the major factor influencing pit spatial arrangement, and consequently an antlion's decision when and where to relocate. Shadow competition occurs when one sit-and-wait predator can catch the moving prey before it encounters other predators (Linton *et al.*, 1991), and this has also been documented in spiders (Lubin *et al.*, 2001). Wilson (1974) suggested that this type of competition should cause antlions to form a 'doughnut' configuration, i.e., the antlions occupy the periphery of their patch. Others have criticized this theory claiming that: (1) prey may also land directly into the pit; (2) prey might not approach in equal numbers from all directions; (3) prey might not move across the antlion's area in a straight line; (4) simple removal of antlions at the center of the patch (by cannibalism, for example) could also form this spatial arrangement; and (5) there are no statistical methods to measure this spatial distribution (McClure, 1976; Simberloff *et al.*, 1978). More recent studies suggest that at high population densities antlions should be distributed uniformly, while at low densities they should be distributed randomly (e.g., Matsura and Takano, 1989).

Linton *et al.* (1991) tested the hypothesis of 'shadow competition' and its influence on spacing and pit relocation. They used a model simulating a group of randomly distributed antlions, and prey items that moved and crossed the arena from random points along its edges in straight lines. Antlions relocated when feeding rate was less than an arbitrary hunger threshold. The results showed that shadow competition affects pit relocation when densities are high and prey abundance is intermediate. When prey abundance is high there is enough for everyone and when there is too little, according to the relocation rule, antlions keep relocating over and over again. The design of the laboratory experiment was similar: Points along the arena edge were selected randomly, and the prey items were given to the first individual antlion which encountered the straight line plotted from the edge into the arena. The results of both the simulation model and the laboratory experiment demonstrated that antlions concentrated on the arena edges, as predicted by the 'shadow competition' theory. However, it seems to us that the assumptions of the model and the experimental design are problematic. For example, the model assumes that antlions have a fixed hunger threshold, and consequently in low prey abundance they are expected to relocate over and over again. This pattern is rarely observed in nature, possibly because of the high cost of relocation (e.g., Griffiths, 1980). Moreover, the experimental design assumes that prey behaves in a very particular way: it has the same probability to arrive from all directions; it moves in straight lines and always falls into the first pit encountered. These two components of the experimental design and the fact that prey can sometimes escape the first pit encountered are some of the basis for the criticism against 'shadow competition' and thus should be tested before being incorporated in such an experimental design.

Contrary to Wilson (1974), McClure (1976) suggested that the major factor influencing pit spatial arrangement and pit relocation is direct competition, i.e., interference. Simberloff *et al.* (1978) suggested that interference by sand throwing during pit maintenance is the most important cause of relocation, while food limitation appears to be only a minor cause (see also Youthed and Moran, 1969b for a description of sand-throwing interference and its implications on the antlion distribution and relocation tendency). Indeed, manifestations of intra- and interspecific interference competition were conducted afterwards (Matsura and Takano, 1989; Griffiths, 1991, respectively). Griffiths (1993) suggested that the antlion densities used in several laboratory experiments were too high compared with field densities, meaning that interference competition cannot be the only component shaping antlions' spatial distribution, and that its relative importance may vary among habitats and species. Moreover, since behavioral patterns of interference are much easier to observe than exploitation, this may bias the results.

A field experiment by Boake *et al.* (1984), in which antlion densities did not reach high peaks, detected very little interference by sand-throwing, suggesting that sand-throwing is not a major component of interference competition. Griffiths (1991) suggested that interference competition may be driven by other factors, such as displays (movements of the forelegs up to 5 cm away) and challenges (one larva entering another's pit usually while being built). Rosenberg (1987) conducted a laboratory experiment, rejecting the hypothesis of Simberloff *et al.*, about sand-throwing. Rosenberg hypothesized that antlions kept in different soil types should influence each other differently, depending on the soil type. The rationale behind this hypothesis was taken from observations made by Lucas (1982), indicating that larger sand particles are thrown to greater distances. Thus, antlions kept in coarser sand would experience stronger sand-throwing interference competition, resulting in a sparser arrangement. However, this hypothesis was not supported by the results of this experiment.

Interference is documented to cause web relocations in colonial spiders, when larger spiders usually take over webs of weaker ones, and it may result in regular spatial patterns (Riechert and Gillespie, 1986; Rayor and Uetz, 2000). Interference is probably related to prey abundance since it can increase in lower prey levels (Rypstra, 1985). Smallwood (1993) claimed that agonistic interactions among spiders are a dominant factor causing web relocations (and to a lesser extent—cannibalism). He partially supported his hypothesis by reducing spider densities and showing a decrease in web relocations. Exploitation is also common in colonial spiders, especially in large groups (Riechert, 1992). However, some studies suggest that grouping actually contributes to the individual foraging success by the ‘ricochet effect’ (Uetz, 1989; Lubin *et al.*, 2001): the capture of prey items after they were slowed and weakened by several webs in succession. As far as we know, a possible ‘ricochet effect’ has not been studied in antlions.

In summary, exploitation and interference competition may influence both relocation rate and spatial arrangement of antlion larvae. The influence of competition intensifies with density, but there is no agreement regarding which factor is dominant, and the relative importance of each factor can change as a function of the species tested and the environmental conditions.

INFLUENCE OF DISTURBANCE

Disturbance to pits, whether it results in partial or total pit destruction, may influence decisions regarding pit location and size. Disturbed antlions built smaller pits than undisturbed ones (Youthed and Moran, 1969a; Griffiths, 1986; Eltz, 1997). Eltz observed no reduction in the proportion of antlions building pits while Youthed and Moran reported a decreasing proportion of antlions building pits as disturbance continued.

Similarly, damage to the web is reported to be an important factor determining web relocation in orb-web spiders. The interaction between low feeding rate and frequent disturbance resulted in moving the greatest distances before reestablishing a web compared to each factor separately (Chmiel *et al.*, 2000). Moreover, the movement direction is decided according to which side of the web was damaged. Movement following disturbance is also dependent in the expected life span of the web damaged, since some species rebuild there webs every day (Riechert and Gillespie, 1986).

INFLUENCE OF BODY SIZE

Pit size is highly correlated with larva size (e.g., Youthed and Moran, 1969a; Wilson, 1974; Allen and Croft, 1985). Larger pits enable the larvae to cope with a larger variety of prey items, since their ability to handle the larger prey types does not reduce their ability to handle small prey types (Youthed and Moran, 1969b; Wilson, 1974; Heinrich and Heinrich, 1984). Thus, it is not surprising that larger larvae are usually less hungry and suffer less from exploitation competition than small larvae. Moreover, due to interference competition, which is also determined by the contestants' relative size or mandible size (Griffiths, 1991), large larvae occupy the more favorable areas and tend to move less compared to small larvae (Prado *et al.*, 1993; Griffiths, 1993). Larger larvae were also found to be more resistant to high temperatures (Lucas, 1989a). Other studies, however, have found different results. For example, Griffiths (1986) found that medium-sized larvae were the most likely to relocate in a starvation experiment. There is also a disagreement with respect to which are the least favorable areas. Griffiths (1992) showed that larger larvae inhabited the edges of the antlion zone, as predicted by Wilson, while McClure (1976) reported that larger larvae built their pits in the central area of the experiment plot, forcing the smaller ones to move to the edges.

In experiments with orb-weaving colonial spiders, quite similar results were obtained. Large spiders were more likely to win in contests (Rayor and Uetz, 2000) and were the first to choose where to establish their web. Smaller spiders were reported to build their webs more slowly in order to avoid conflicts with larger ones and were susceptible to disturbance by large spiders (Jakob *et al.*, 2001). The preferred sites were those in the colony core (possibly due to protection and the 'ricochet effect'), while smaller spiders were forced to move to the periphery. The periphery area may be richer in prey but it is also riskier due to high predation levels. A similar hypothesis regarding an environmental trade-off has been suggested by Eltz (1997) and Gotelli (1997). More exposed pits may have a higher encounter rate but are more likely to be disturbed. Indeed, Gotelli (1997) showed that larvae near the edges of the antlion zone grew faster, probably due to greater food availability, but experienced higher chances of mortality during pupation.

POSSIBLE INFLUENCE OF PREDATION AND CANNIBALISM

Predation and cannibalism may influence antlion site location, propensity to relocate and spacing, but the possible influence of such biotic factors on antlion foraging behavior has not been thoroughly studied. Several reports observed cannibalism and intra-guild predation (i.e., predation on other antlion species), mainly at high population densities (e.g., Matsura and Takano, 1989; Griffiths, 1991; Day and Zalucki, 2000). Griffiths (1991, 1992) detected density-dependent cannibalism in a laboratory experiment, and suggested that the victims are usually the smaller larvae, i.e., earlier instar. He also observed that cannibalism is much more likely when there is a greater size difference between two antlions and when antlions are hungry. In addition, Gotelli (1997) suggested that cannibalism is triggered more by competition than by hunger. Day and Zalucki (2000) suggested that cannibalism is an artifact of laboratory experiments, because antlions do not reach such high densities in nature. This claim may be supported by antlion behavior when encountering other pits—they immediately retreat backwards (Heinrich and Heinrich, 1984).

In comparison, non-sexual cannibalism in spiders is quite common, and found to be dependent on similar factors: the spider's hunger level and the relative size of the attacker and the victim, as shown in two experiments conducted with wolf spiders (Samu *et al.*, 1999; Buddle *et al.*, 2003). It has not yet been tested in antlions whether kinship affects cannibalism (but see the negative effect of kinship on cannibalism in spiders, Bilde and Lubin, 2001) or whether there are possible additional costs, such as transmission of parasites. Li and Lee (2004) showed that web-building spiders responded to cues from their predators by reducing the net size or by adjusting it to be less remarkable and visible to predators. By doing so, spiders trade off safety and prey arrivals. No similar trend of reducing the pit size has been reported in antlions.

INFLUENCE OF MICROCLIMATOLOGICAL FACTORS

Antlions are restricted to specific habitats and therefore selective pressures on choosing the appropriate habitat should be strong. Various factors which limit antlion dispersion and influence pit location and relocation have been suggested, such as shade (Topoff, 1977), soil temperature (Marsh, 1987; Cain, 1987) soil particles (e.g., Allen and Croft, 1985; Farji-Brener, 2003), rain and soil moisture (e.g., Gotelli, 1993; Morrison, 2004), and other factors, such as moon phase (Youthed and Moran, 1969b). In general, there is disagreement over the relative importance of the various factors. Topoff (1977) suggested that soil particle size is less important, because antlions can build pits in a wide range of soil particle sizes. He therefore proposed shade as the major factor, since *M. immaculatus*, the subject of his research, inhabits shaded areas. Shade was also suggested as an important factor by Crowley and Linton (1999), who observed antlions tracking sources of shade or cover. However, there are many known species which inhabit open habitats and do not need shade, such as *M. formicarius* and *M. bore* (Matsura and Murao, 1994). The tendency to prefer shaded areas may depend on the average soil temperature. In hotter environments antlions may need shade in order to avoid desiccation, but in colder environments they may prefer sunnier habitats (Heinrich and Heinrich, 1984). Another influence of temperature has been suggested by Arnett and Gotelli (2001), who found that antlions tend to neglect their pits in high temperatures. An interesting report by Marsh (1987) concluded that antlions are adapted to be active at almost the same temperature range of their prey. Their ability to cope with high temperatures is thus important for prey capture, and there might be a trade-off between maintaining low metabolic rates and capturing prey (as suggested for desert spiders by Henschel *et al.*, 1992). Some other studies have examined the influence of soil particle size on antlion site selection. Studies conducted on different antlion species during which individuals could choose between different sites characterized by varying levels of soil particle size, showed that antlions prefer building pits in finer soil (Youthed and Moran, 1969a; Allen and Croft, 1985; Lucas 1986; Gatti and Farji-Brener, 2002; Farji-Brener, 2003). Botz *et al.* (2003) and Farji-Brener (2003) observed trails crossing different soil types, suggesting that antlions decided where to build pits in accordance with particle size. When antlions are given no other choice, they construct pits even in coarser sand fractions. Antlions actively choose the finer particles because it is easier and faster to build pits there and because finer particles allow them to build larger pits (Gatti and Farji-Brener, 2002; Farji-Brener, 2003). Moreover, pits built in finer soils serve as a better refuge of thermally stressful conditions, ease the mandible grasp in prey items and enable pits to support steeper walls which make it more difficult for ants to escape after falling into the pit (Allen and Croft, 1985; Marsh, 1987; Loiterton and Magrath, 1996; Botz *et al.*, 2003). In conclusion, constructing pits in fine-grained soil is a good example of habitat selection (Farji-Brener, 2003), and it is not always driven by physical constraints (Botz *et al.*, 2003).

Rainfall and soil moisture are considered in several studies to be the dominant factors influencing location and dispersion. Antlions were observed not to build pits when it rains (Youthed and Moran, 1969b) and to prefer areas sheltered from rain (Gotelli, 1993). Cain (1987) observed that as soon as rain started, *Brachynemurus* would dig themselves few centimeters below surface, and thus concluded that antlion larvae avoid wet sand. Gotelli (1993) suggested that the combined effect of temperature and rainfall restricts antlions to specific zones, since they cannot dig in wet soil and they desiccate when exposed to high temperatures. Morrison (2004) partially supported Gotelli's conclusions and suggested that antlions can cope with high temperatures in different ways, such as changing their location inside the pit (Allen and Croft, 1985). Thus, Morrison (2004) rejected the temperature hypothesis, while accepting the rainfall hypothesis. The difference between Gotelli and Morrison may result from differences between the study species. Gotelli studied two *Myrmeleon* species, which occupy sheltered microhabitats, and thus are likely to be sensitive to direct sun and high temperatures. A similar avoidance behavior of high temperature was found in desert spiders. Desert spiders respond to temperature and sunlight by orientating their webs to the extent that the direct exposure to sunlight is minimal (Riechert, 1992).

Microclimatological factors are known to have an effect on habitat selection in other sit-and-wait arthropod predators, especially in extreme environments such as deserts (spiders: Henschel *et al.*, 1992; scorpions: Shachak and Brand, 1983). However, we believe that antlions, due to their dependence on the physical properties of their environment, are more influenced by these factors than other sit-and-wait predators.

CONCLUSIONS AND FUTURE RESEARCH

Animal decision-making is rarely optimal, owing to a variety of constraints. Here we show that site selection and foraging in antlions are occasionally not optimal and may be constrained by biotic and abiotic factors. Therefore, Eltz's (1997) suggestion, that antlion larvae are an ideal subject for testing theories of optimal foraging, owing to the fact that they are not yet in a reproductive stage, should be followed with caution. We are aware of constraints being an integral part of every biological system and we do not claim that antlions are not adapted as a result of their constraints (Parker and Maynard-Smith, 1990). However, this paper emphasizes some deviations from classical optimal foraging in antlions, which require special attention.

According to classical optimal foraging theory, the majority of pit relocations should be related to prey abundance and site quality. This classical view ignores important aspects, such as physiological constraints, and sit-and-wait predators in particular might not always follow this rule. This statement can be supported by the following three explanations:

1. Physiological constraints—antlions are highly dependent on microclimatological factors, and cannot survive unless a specific combination of environmental factors (such as temperature and soil particles) exists. Such conditions are not necessarily correlated with prey abundance and thus antlions may not forage optimally in this sense. More recent derivatives of foraging theory incorporate physiological constraints (Brown, 1988) and therefore are more adequate in describing antlion behavior.
2. Difficulties in assessing site quality—in highly variable environments it might be almost impossible for an antlion to evaluate patch quality. Evaluation in this case mainly depends on the individual's ability to follow temporal variation in food abundance (Nakata and Ushimaru, 1999). Several laboratory studies have concluded that prey abundance does not influence relocation rate. However, the subject animals in these studies could have been evolutionary adapted to habitats with large temporal variability in prey abundance or to habitats in which changing sites has little chance of improving site quality
3. Maternal effects—habitat selection in antlions may be dependent on the females and may be influenced by their preferred sites for oviposition (Lucas, 1989a; Gotelli, 1997). Hence, high densities of antlions may be attributed at least partially to maternal effects, in spite of the larvae ability to move. The behavior of the ovipositing female has rarely been investigated.

Our study emphasizes the need for a better understanding of adult behavior, as well as other aspects of antlion behavioral ecology. First, it would be important to investigate the cues used by antlions to assess site quality, before they start to sample their environment by constructing pits. Laboratory studies on wolf spiders showed that their tendency to stay in a particular site was higher when exposed to vibratory or visual signals of prey, and assess site quality in advance (Persons and Uetz, 1996). This capability may be very valuable when the cost of relocation is high. We suggest that it may also exist in antlions, since they are capable of sensing vibrations in the soil from a distance of a few centimeters (Devetak, 2005) and may use them to assess site quality as well. Exploring if and how antlions can distinguish between spatial and temporal variation in prey abundance and site quality may have important implications for their adaptive response, because the response to each type of variation should be different (stay, if the scarcity of food is temporal; leave, if it is spatial). As far as we know, this interesting direction has never been tested empirically, either in antlions or in other sit-and-wait predators. We propose that the habitat of origin would determine how frequent the antlions relocate in response to food shortage.

We also propose that there is a necessity to conduct phylogenetic research in relation to pit relocation rate. In order to test whether low rates of pit relocation are an adaptation, one should control for possible phylogenetic effects. Only if the same trait has evolved in independent lineages can we conclude that the traits evolved in correlated fashion and explanations associated with phylogenetic history are not applicable (Perry, 1999). Finally, in order to understand how commonly cannibalism occurs in nature, one should explore the cannibalistic behavior of antlions in field experiments, and later investigate how cannibalistic behavior is affected by different factors, such as hunger level, size differences and kinship.

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