The Energetic Determination, Spatial Dispersion and Density Dependence of *Myrmeleon* Ant Lion Pits in Las Cruces, Costa Rica

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ABSTRACT

The amount of space used by an organism is energetically determined. We utilized a population of ant lion larvae in Costa Rica to test allometric theories concerning the use of space by organisms and how different densities of individuals affect the use of space. The area of ant lion trapping pits scaled with mass to the three-quarters power, supporting allometric theory for sessile organisms. Our analyses also show that larger ant lion larvae show spatial repulsion and facultative density dependent pit-building strategies.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: allometry; competition; home range; overdispersion; scaling; tropical moist forest.

ANT LIONS ARE IMMATURE INSECTS IN THE FAMILY MYRMELEONTI-DAE (NEUROPTERA), and species in the subfamily Myrmeleontinae have particular interest because they build conical pits in fine sandy substrate to capture passing arthropods (Triplehorn & Johnson 2005). Pit-making ant lions are generally sit-and-wait predators that minimize movement unless stressed (Matsura & Takano 1989, Linton *et al.* 1991, Crowley & Linton 1999). The individual, positioned at the bottom of its constructed pit, subdues fallen prey (largely ants) with its long jaws, feeds on the hemolymph and extra-orally digested organs, and discards the carcass (Triplehorn & Johnson 2005). As abundant, sessile, terrestrial predators, ant lions have frequently been the subject of ecological investigation, especially in studies of optimal foraging and spatial arrangement (*e.g.*, Wilson 1974, McClure 1976, Griffiths 1980, Heinrich & Heinrich 1984, Gotelli 1997, Crowley & Linton 1999, Day & Zalucki 2000, Arnett & Gotelli 2001).

Ant lions pose an interesting allometric problem: as they are sessile, sit-and-wait predators, they may still compete with neighbors during pit territory establishment and pit maintenance. Ant lions construct trapping pits during the first larval stage, and exhibit strong site fidelity, as pit relocation is energetically costly (Lucas 1985, Crowley & Linton 1999). Ant lions acquire all of their resources within the trapping pit, which leads to the hypothesis that

overall pit size should be proportional to the size of the ant lion occupant (Wilson 1974, Kitching 1984, Day & Zalucki 2000). Ant lions can interact with conspecific neighbors in two ways that may influence pit size. First, during pit maintenance, ant lions use their mandibles to toss sand from their pit (McClure 1976, Day & Zalucki 2000). Ant lions may therefore expel sand into the pits of neighbors, exacting an energetic maintenance cost (Simberloff *et al.* 1978, Day & Zalucki 2000). Second, ant lions may compete spatially for passing prey, as the pit of one ant lion may block prey flow to a neighboring ant lion pit (Wilson 1974, McClure 1976, Linton *et al.* 1991, Griffiths 1993, Gotelli 1997). Other factors being equal, an ant lion whose pit is surrounded by neighboring pits may trap fewer prey than an ant lion whose pit is placed in the open. The role of neighbor competition in driving the spatial arrangement of ant lion pits has been previously explored (Wilson 1974; McClure 1976; Simberloff *et al.* 1978; Griffiths 1991, 1993; Linton *et al.* 1991; Day & Zalucki 2000), yet none of these studies have tested predictions made by allometric theory.

Classical allometric theory (McNab 1963, Calder 1984, Mace & Harvey 1983) has posited that the space required by an organism to capture resources, home range size, should scale as:

$$H \propto M^{3/4}$$

Where, H is home range size and M is mass. The framework for this argument is simple in that the amount of prey captured (P)

should be directly proportional to space utilized by the organism (*i.e.*, home range) and should scale isometrically with the metabolic rate of the organism (R), which scales to the 3/4 power with mass:

$$H \propto P \propto R \propto M^{3/4}.$$

Simplified, home range scales with mass to the 3/4 power. Yet, despite McNab's original findings (McNab 1963), empirical evidence from nonsessile vertebrate organisms generally does not support a three-quarters scaling relationship between home range size and mass. Rather, a scaling exponent of one or greater is observed for vertebrates (Schoener 1968, Turner *et al.* 1969, Harestad & Bunnell 1979, Mace & Harvey 1983, Peters 1983), and invertebrates such as *Solenopsis* ants (although the value of this exponent varies seasonally; Tschinkel *et al.* 1995). Recently Jetz *et al.* (2004) have incorporated species interactions in space into allometric theory as a solution to this incongruence of theory and observation. Specifically, if one incorporates the amount of home range space that overlaps with a conspecific individual and the amount of energy required to maintain home range boundaries through interactions with other individuals, the total amount of space required to fulfill an individual's metabolic requirements increases. This increase in home range size due to competitive interactions predicts an allometric relationship in which home range scales with body mass with an exponent of one.

Although ant lions have been shown to competitively interact during pit establishment (Day & Zalucki 2000), the competitive mechanism proposed in the Jetz *et al.* (2004) model may not apply to them. Their model predicts a scaling exponent of one due to territory overlap or persistent competition involved in maintaining territory boundaries. Once they have constructed pits, ant lions reside in exclusive territories, and do not compete within their territory boundaries for resources; as such, a scaling exponent of three-quarters may be expected in ant lions.

This prediction is consistent with studies of space use for resource acquisition in other sessile organisms, including plants (Niklas & Enquist 2001, 2002; Enquist & Niklas 2002) and purse-web spiders (Anderson 1987). For vascular plants, Niklas and Enquist (2001, 2002; Enquist & Niklas 2002) have predicted a three-quarters power relationship relating resource acquisition area (whole plant leaf area) to body mass. Because carbon resource acquisition rate (C) should scale with whole plant mass (M) as:

$$C \propto M^{3/4},$$

and because whole plant mass scales with whole plant leaf mass (M_L) to the 3/4 power, and whole plant leaf mass is expected to scale isometrically with whole plant leaf area (L), we get the following by substitution:

$$M^{3/4} \propto M_L \propto L.$$

This prediction has been supported with empirical evidence from plants with body sizes covering 20 orders of magnitude (Niklas & Enquist 2001, Enquist & Niklas 2002). The area a plant requires for resource capture scales differently than the resource capturing area (*i.e.*, a home range) for a nonsessile organism. As mentioned

above this prediction is upheld for plant data, but may also prove to be a general principle for sessile animals as well. In particular, the resource capturing device of spiders, their web, has been shown to scale with an exponent of 0.65 rather than 1 (Anderson 1987). Using the analogy that the resource capturing area for ant lions is pit area, rather than leaf area in plants or web area in spiders, gives the alternative hypothesis to the Jetz *et al.* (2004) model that pit area should scale with body mass to the 3/4 power in ant lions.

A large population of ant lions (immature *Myrmeleon* sp.) located at 8°47'9′ N 82°57'51′ W in Las Cruces Biological Station, Costa Rica was utilized for the present research. Five sample quadrats 0.25 m² in size were randomly placed in the population of *Myrmeleon*. After the sample quadrat was in place, a photograph was taken directly overhead of each quadrat. Each photograph was then manipulated using imagery software in order to assign coordinates and individual numbers to each pit in each quadrat. Thus relative distances between all pits could be obtained.

The diameter of each ant lion pit was measured to a resolution of 0.1 cm using a caliper. The diameter was then used to estimate the area of each pit assuming that they were circular. After the diameter of each pit was measured, the resident ant lion was extracted and placed into a container. The mass of each individual ant lion was later recorded.

Three distinct ant lion size classes were identified from field observations. Classes were determined by plotting the distribution of the body masses of all individuals collected from the observational study. When plotted, there were three distinct groupings of body mass indicating three larval instars, which is consistent with other *Myrmeleon* populations observed in Costa Rica (Wilson 1974).

To understand the effects of larval density on pit size and number, a manipulative experiment was conducted where medium-sized ant lions were placed into plastic arenas (300 cm²) at densities of 2, 5, 10, and 20 (ant lions were placed in the center of the arena and allowed to spatially segregate on their own, following McClure [1976]). Earlier field observations showed that approximately five ant lions resided in areas the size of the plastic arenas. Thus, we chose to use experimental densities that were higher and lower than those generally observed in nature to adequately determine whether density dependence could occur in ant lion populations under certain conditions. Each treatment was replicated three times and placed on a covered outdoor porch near our observational study site. After 12 h the number of pits and the diameter of pits were recorded.

Ant lion mass and pit area were tightly correlated. When pit size was regressed onto mass from natural populations, the slope of the regression was indistinguishable from 0.75, yet it was distinguishable from 1 using a 95% CI around the slope (Fig. 1A). Next, a Mantel test was performed on body size and spatial distance dissimilarity matrices to assess the level of correlation in each quadrat. Specifically, the two dissimilarity matrices were characterized as the pairwise difference in mass between all individuals in a quadrat and the pairwise Euclidean distance between all individuals in a quadrat. There was no correlation between these two variables for any of the five quadrats as a whole. To understand the spatial relationship between cohorts of ant lions through time the quadrat data were parsed into the three size classes (instars). The mean Euclidean distance between pits of all similarly sized individuals in a quadrat was
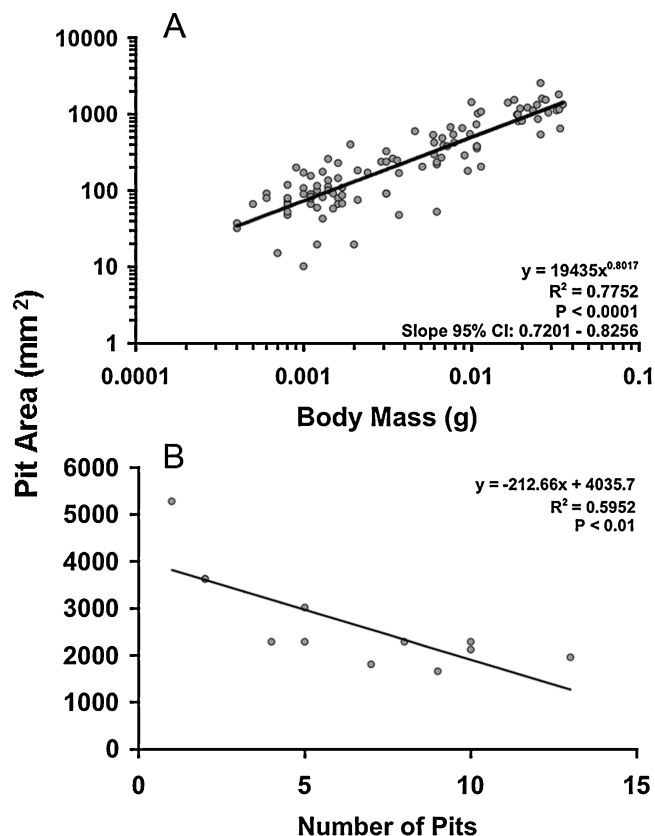
FIGURE 1.   (A) Log-log plot of pit area versus body mass from natural populations. (B) The area of ant lion pits as a function of the number of pits formed during the experiment.

$Q_t = 3.86$, $P = 0.10$). The number of pits in each treatment was negatively correlated with the size of the pits in that treatment (Fig. 1B).

The ant lion population studied in Las Cruces exhibits pit areas that scale with mass with a scaling exponent indistinguishable from 3/4. Therefore allometrically, and energetically, ant lions conform to patterns expected for sessile organisms. The results do not support the allometric home range model of Jetz et al. (2004), which predicts a scaling exponent of one to accommodate competitive interactions during resource acquisition. Energetic expenditure due to overlapping home ranges and defense of boundaries are explicit parameters in the Jetz et al. (2004) model and both are common in mobile organisms in nature, but signatures of such expenditure were not evident in our study of ant lions. While ant lions may indeed interact with neighbors during pit establishment, these interactions are not compensated by a proportional increase in pit area after establishment and may have negligible energetic consequences on ant lion life history.

Ant lion populations that span multiple size classes (instars) are not spatially structured as a whole, yet larger-sized individuals are spaced more evenly than expected by chance. Although there are likely interactions between larvae from different body size classes, this result suggests that surviving individual ant lions from a cohort become more evenly spaced. These results are in accord with the finding of Gotelli (1997) that ant lion larvae suffered density dependent mortality in the second and third instars, but not in the first.

An experimental quadrupling of natural ant lion densities significantly reduced the size of pits formed as well as inducing a slight trend toward fewer pits constructed. This suggests that just prior to, and during, pit establishment ant lions experience moderate density dependent interactions in space. A decrease in pit size was observed as a response to crowding across all treatment densities, but abandonment of pit construction became somewhat evident at extreme densities. We infer that the latter behavioral shift is unfavorable and perhaps utilized as a last resort under extreme competition for space and that the former may be the result of ant lions repeatedly being displaced by other individuals, thereby reducing the amount of undisturbed time necessary to construct larger pits.

Our experimental results describe a small role for competition in ant lion pit establishment. At the same time the allometric results based solely on first principles metabolic theory suggest that the most parsimonious conclusion is that ant lion pits sizes are energetically determined, and that it is not immediately necessary to invoke competition to explain the vast majority of the variance in pit sizes found in natural populations. This finding is consistent with the scaling relationship between resource capturing area and body mass, predicted and observed in plants, and observed in other sessile invertebrates such as spiders (Anderson 1987, Niklas & Enquist 2001, Enquist & Niklas 2002). Plausible alternatives to this energetic conclusion are that smaller pits constructed by smaller individuals are merely the result of constant displacement by other individuals in the population, as observed in artificially manipulated high densities, or that competitive processes occur during different portions of ant lion life history that were not examined in the present study. Future experimentation that uses natural densities

measured and then compared to 1000 randomly generated communities. Each random community had individual numbers that were constrained to match the observed data and coordinates that could not extend outside the quadrat. The random placement of ant lion pits was done using circular two-dimensional areas using the same distribution of areas as those observed. Thus zero-dimensional point representations of ant lion pits were not used. This was done to protect against unrealistically overlapping ant lion pits in the null populations (Simberloff et al. 1978, Simberloff 1979). The spatial distribution of the smallest size class for each quadrat was random (Quantiles > 25 and < 975). Two of the five quadrats had medium size class individuals that were evenly dispersed in space (Quantiles = 981 and 978). The spatial distribution of the largest individuals in each of the five quadrats was even (Quantiles > 983).

An ANOVA followed by Tukey Tests was used to quantify which density treatments differed from one another in the experimental manipulations of population density. The ANOVA result showed that there was a noticeable difference between two of the treatments ($F_{3,8} = 10.26$, $P < 0.05$). The number of pits formed per number of individuals was not different between the two, five, and ten density treatments. The 20-individual treatment tended to have fewer pits formed than the five and 10-individual treatments yet this trend was not significant ($Q_t = 3.99$, $P = 0.09$;

and longer time periods for observation will be required to test these less parsimonious possibilities.

Ultimately our evidence corroborates the above studies, suggesting that sessile organisms do indeed exhibit a different scaling relationship for resource capture and body size than mobile organisms (Schoener 1968, Turner *et al.* 1969, Harestad & Bunnell 1979, Peters 1983, Tschinkel *et al.* 1995). Future research concerning the use of space to capture resources across multiple taxa of sessile organisms is necessary to more fully understand the generality of these scaling relationships. Further, experiments that alter the frequency and intensity of resource availability are needed to more explicitly test the mechanism proposed by Jetz *et al.* (2004).

ACKNOWLEDGMENTS

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