Pit-Building Decisions of Larval Ant Lions: Effects of Larval Age, Temperature, Food, and Population Source

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Foraging decisions are an integral component of growth and maintenance and may reflect both environmental and genetic effects. We used a common garden experiment to evaluate the effects of food, temperature, and population source on pit-building decisions of the larval ant lion Myrmeleon immaculatus. *In a laboratory common garden experiment, first-instar larvae from two southern (Georgia, South Carolina) and two northern (Connecticut, Rhode Island) populations were reared for 14 months in incubators under high- and low-food and high- and low-temperature regimes. For all populations, there was no effect of larval age on pit-building behavior. All larvae built and maintained pits more frequently at high temperatures than at low temperatures, and larvae in the low-food treatments built and maintained pits more frequently than larvae in the high-food treatments. Larvae from the southern populations built and maintained pits more frequently than larvae from northern populations. These results suggest that regional differences in foraging behavior may contribute to latitudinal gradients in life history strategies seen in this insect.*

KEY WORDS: ant lion; *Myrmeleon immaculatus*; common garden; foraging behavior; latitude; temperature.

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INTRODUCTION

Although prey capture is essential for successful growth and reproduction, foraging takes time and energy away from other activities, entails metabolic costs, and may increase the risk of mortality to foragers (Kamil and Sargent, 1981; McNamara and Houston, 1997). Thus, foragers may respond predictably to changes in the biotic environment, including food availability (Lubin and Henschel, 1996; Bautista *et al.*, 1998; Gilchrist *et al.*, 1998), conspecific density (Norris and Johnstone, 1998; Mappes, 1998), and predation risk (Lima and Dill, 1990; Skelly and Werner, 1990; Gotelli, 1996; Pravosudov and Grubb, 1998). Foraging decisions may also depend on abiotic factors such as temperature and moisture (Machmer and Ydenberg, 1990; Gilchrist *et al.*, 1998; Rotenberry and Wiens, 1998; Weetman *et al.*, 1998).

An individual's foraging strategy may also change as it ages, either because of predictable ontogenetic shifts in morphology and feeding structures (Galis, 1990) or because of dynamic foraging decisions that maximize the probability of achieving a certain weight or developmental stage after a fixed amount of time (Mangel and Clark, 1988; McEdward, 1997).

Larval ant lions capture arthropod prey with a steep-walled sand trap, an example of tool use among the invertebrates. From an engineering perspective, the pit is constructed in a way that maximizes prey capture (Lucas, 1986). The placement of the pit is an important component of the ant lion's foraging strategy, and pit construction sites may be selected on the basis of habitat suitability (Lucas, 1986), particle size (Lucas, 1986), prey availability (Griffiths, 1980), disturbance regime (Gotelli, 1993), and conspecific density (Matsura and Takano, 1989; Linton *et al.*, 1991).

We recently discovered that the choice of whether or not to build a pit is also an important component of an ant lion's foraging strategy. During a large common garden experiment on ant lion growth and development, we noticed consistent differences among larvae in their decisions to build pits. In this paper, we analyze the effects of larval age, population source, temperature, and food availability on pit-building behavior in larval ant lions.

METHODS

Ant Lion Life History

Ant lion larvae are sit-and-wait predators that capture arthropod prey in conical sand pits. Larvae pass through three instars and may persist for 2 years, so that overlapping generations occur in natural populations (Furunichi and Masaki, 1981, 1982; Gotelli, 1997). Third-instar larvae form sand cocoons and exist as pupae for approximately 28 days (A. Arnett, unpublished data).

After emergence, adult females oviposit eggs in the sand. Adults live about 1 month. In eastern and central North America, the ant lion *Myrmeleon immaculatus* is common in sheltered, sandy microhabitats, which support dense larval aggregations (Gotelli, 1993).

Common Garden Experiment

In 1996, we collected first-instar *M. immaculatus* larvae from two adjacent populations in Connecticut and Rhode Island (Washington County, RI, $n = 96$; Tolland County, CT, $n = 40$) and simultaneously from two adjacent populations in Georgia and South Carolina (Pickens County, SC, $n = 71$; Lumpkin County, GA, $n = 68$). At each site, first-instar larvae were collected randomly, placed individually in 1.5-ml cryotubes, and mailed overnight to Burlington, Vermont. Upon arrival, each larva was placed by itself in a plastic drinking cup, 90.5 cm in diameter, three-quarters full of sterilized sand. The cups were wide enough that sand throwing by the larvae did not influence pit building. Each cup was assigned randomly to either a "high-food" treatment or a "low-food" treatment and assigned randomly to one of two Percival incubators, a shelf within the incubator, and a position on the shelf. One incubator was the high-temperature incubator, which was maintained at a constant day temperature of 29.4°C and a night temperature of 23.9°C. The second incubator was the low-temperature incubator, which was maintained at a constant day temperature of 23.9°C and a night temperature of 21.0°C. At temperatures lower than 21.0°C, *M. immaculatus* larvae will stop constructing and maintaining their pits (A. Arnett, unpublished data). Humidity was maintained at 60% in both incubators, and photoperiod at 12 h light/12 h dark from April to November. From December to March, winter photoperiods were mimicked in both incubators by changing the light schedule to 10 h light/14 h dark. Treatments were maintained for 14 months, until all larvae had pupated or died.

Larvae in the high-food treatment initially were fed five live adult *Drosophila* per week and the larvae in the low-food treatment were fed one live adult *Drosophila* per week. Larvae in the low-food treatment did not gain weight after 30 days, so we increased the food to 15 live adult *Drosophila* per week for the high-food treatment and 6 live adult *Drosophila* per week for the low-food treatment. The flies were briefly placed on ice prior to feeding so they would not fly away.

Behavioral Observations

Once a month, before we weighed each larva, we recorded whether or not it had constructed a pit. Quantification of larval growth rates from the

monthly weighing is documented by Arnett and Gotelli (1999a). When the larvae were weighed, their pits were destroyed, forcing them to decide each month whether to build a new pit. Thus, every month, we recorded whether or not each larva had a pit, had no pit, or was in the process of constructing a pit. A pit was defined as a discrete conical structure. If there was merely an indentation in the sand and no discrete structure, we scored the observation as no pit. Larvae constructing pits threw sand with their mandibles and created a characteristic corkscrew trail.

All analyses were conducted twice, first classifying larvae in the process of building pits as having pits and then as not having pits. There was no difference between these results. Thus, we report only results from classifying pit builders as having pits. Analyses were conducted using JMP statistical software, version 3.0 (SAS Institute Inc., 1994).

Shifts in Pit-Building with Larval Age

The data for each larva consist of an ordered sequence of observations on the presence or absence of a pit taken each month just before the animal was weighed. The null hypothesis is that the absences and presences are randomly interspersed, with no clustering of pit-building activity at particular times. The alternative hypothesis is that an animal's decision to build a pit or not changes as it ages, so that the occurrence of pit-building is clustered in time.

We tested the null hypothesis of random pit-building occurrence by fitting the data to a logistic regression, in which the nominal response variable was the presence or absence of a pit, and the continuous predictor variable was the number of months since the start of the study (1–14). We fit the logistic regression to pit-building sequences for each of the 270 individuals in the study and recorded whether the fitted shape parameter differed significantly from zero ($P < 0.05$).

Effects of Population Source, Temperature, and Food Availability

For each larva, we calculated the proportion of observations in which a pit was maintained. Proportions were arcsine square transformed prior to analysis. To analyze differences among treatments in pit maintenance, we used a nested three-way analysis of covariance. Populations were nested within regions (southern, northern). Regions were crossed with temperature (high, low) and food (high, low). Populations were treated as a random factor, and regions, temperature, and food level were treated as fixed factors.

Initial body mass differed significantly among the populations ($F_{3,232} = 67.7$, $P < 0.0001$): southern larvae were significantly larger than northern larvae ($F_{1,234} = 182.9$, $P < 0.0001$). Because of this initial size discrepancy, log initial body mass was used as a covariate in all analyses.

RESULTS

Shifts in Pit-Building with Larval Age

Of the 270 larval pit-building sequences we analyzed, only 19 sequences rejected the null hypothesis of random pit maintenance with respect to age. These 19 observations were scattered among the eight experimental treatments, so we did not perform any additional analyses of these data.

Effects of Population Source, Temperature, and Food Availability

The analysis of variance revealed significant main effects of region, population within region, temperature, and food availability on the proportion of time that larvae maintained pits (Table I). The proportion of time that larvae maintained pits differed significantly among the populations ($F_{3,264} = 4.4773$, $P = 0.0044$): Washington County, RI, 0.8798; Tolland County, CT, 0.9327; Lumpkin County, GA, 0.9464; and Pickens County, SC, 0.9330. Although there were differences in initial body size among populations, initial body size was not a significant covariate in the model.

Table I. Summary of the ANCOVA of the Proportion of Time a Pit Was Maintained by *M. immaculatus* Larvae from Two Northern and Two Southern Populations Reared in a Common Garden Experiment

Source[a]	df	SS	F	P
Initial weight	1	0.1037	2.6063	0.1077
R	1	0.2837	7.1304	0.0081
P(R)	2	0.2656	3.3364	0.0371
T	1	2.5231	63.3985	<0.0001
F	1	1.3727	34.4905	<0.0001
R × T	1	0.0880	2.2107	0.1383
R × F	1	0.0302	0.7596	0.3843
T × F	1	0.3076	7.7300	0.0058
R × T × F	1	0.0031	0.0789	0.7791
Error	257	10.2283		
Total	267			

[a]R, region (north, south); P(R), Populations nested within regions; T, temperature (high, low); F, food (high, low).
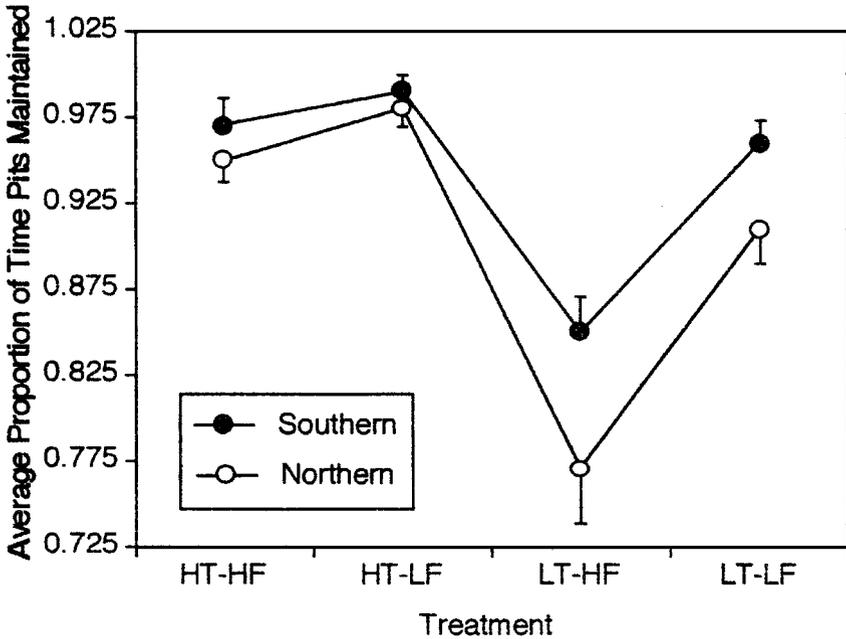
Fig. 1. Average proportion of observations in which *M. immaculatus* larvae, reared in a common garden experiment, maintained feeding pits. Each point is the average proportion calculated from pooled data from two populations in a region ±1 SD. HT, high-temperature treatment; HF, high-food treatment; LT, low-temperature treatment; LF, low-food treatment.

Although there was variation among populations within a region, southern larvae, on average, maintained pits more often than northern larvae. Larvae maintained pits more frequently at high temperatures than at low temperatures, and larvae in the low-food treatments maintained pits more frequently than larvae in the high-food treatments (Fig. 1). There was also a significant interaction between temperature and food level: the difference in pit maintenance between high- and low-food treatments was more pronounced at low temperatures than at high temperatures.

DISCUSSION

Although most of the ant lion larvae in the experiment built pits throughout their larval lives, there were consistent differences due to latitudinal population source and environmental conditions. As would be expected for an ectotherm, pit-building activity was reduced at low temperatures. In the

low-temperature treatments in this experiment (23.9°C), the larvae maintained pits, but not as frequently as did larvae in the high-temperature treatments. Larvae in low-food treatments maintained pits more often than did larvae in the high-food treatments. We noticed that larvae in the low-food treatment consistently had deep, well-maintained pits, whereas larvae in the high-food treatment often had shallow, poorly maintained pits. In the field, larvae should spend more time and energy maintaining pits when prey is sparse. Although there is a large energetic cost of pit-building (Lucas, 1985), prey capture is profitable because food resources can be stored as metabolic fat reserves (Griffiths, 1991). Our results suggest that if food is abundant, ant lions will conserve energy by reducing pit maintenance.

Matsura and Takano (1989) have shown that larval ant lions will stop making pits when the larvae become crowded. Our study shows that solitary larvae also make decisions about when to build pits. Although our experimental design does not control strictly for maternal effects (Mousseau, 1991), it appears that these decisions have an environmental component (temperature and food abundance) plus a genetic component (northern versus southern populations).

Because pit-building is energetically expensive (Lucas, 1985), it is not surprising that food availability influences foraging strategies. Variation in foraging strategies, based on abundance or certainty of food, has been shown in many other taxa including birds (Bautista *et al.*, 1998), mammals (Mappes, 1998), fish (Lokkeborg, 1998), and arthropods (Lubin and Henschel, 1996). For example, burrowing spiders reduce their foraging activity and web dimensions when they are provided with supplemental food (Lubin and Henschel, 1996). This strategy, similar to that employed by *M. immaculatus*, suggests that foraging effort decreases due to increased costs or risks (Abrams, 1991).

Pit-building decisions should greatly affect the energy associated with other life history traits, and, like other life-history traits, the propensity for larvae to build pits appears to have a genetic component. Southern ant lions build and maintain pits more frequently than do northern ant lions. In previous studies, we found a latitudinal gradient in body size, with northern *M. immaculatus* being larger than southern (Arnett and Gotelli, 1999b). We also found that northern larvae grow faster and reach a larger final body size than southern larvae in both a reciprocal transplant experiment and a common garden experiment (Arnett and Gotelli, 1999a). From these experiments, we concluded that the southern environment is more appropriate for fast growth but that northern ant lions genetically grow faster and reach a larger body size. These studies, combined with the current result, suggest that northern ant lion larvae may grow faster and reach a larger body size, despite being in a "lesser" environment for growth, in part because they invest less energy into pit-building activities than do southern larvae.

Behavioral differences are not often considered in the study of life-history traits. The basis of life-history theory assumes that fitness will be maximized (Roff, 1992); the basis of optimizing foraging strategies is also to maximize fitness (Dukas, 1998). Thus, behavioral decisions in foraging are tightly linked to the optimization of life-history traits. Our results illustrate this: latitudinal variation in ant lion pit-building behavior, based on abiotic and genotypic cues, may contribute to the latitudinal gradient in ant lion body size and growth rate (Arnett and Gotelli, 1999a).

Two points emerge from this study. The first is that temperature, food, and latitudinal population source (north vs south) play an important role in an ant lion's decision to build a pit. Second, geographic variation in foraging decisions between northern and southern populations may be a mechanism contributing to latitudinal variation in growth and body size previously documented in this insect (Arnett and Gotelli, 1999a).

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