Bergmann's rule in larval ant lions: testing the starvation resistance hypothesis

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Abstract. 1. Body size of the ant lion *Myrmeleon immaculatus* follows Bergmann's rule – an increase in body size towards higher latitudes. The hypothesis that ant lion body size is larger in the north as an adaptation for starvation resistance was tested.

2. In a laboratory experiment testing starvation resistance, survivorship curves differed among 10 ant lion populations for both a *starved* and a *fed* treatment.

3. The average number of months survived by each population was correlated positively with latitude for both treatments. Across both treatments and all populations, large individuals survived longer than small individuals; however individuals from high latitudes had higher survivorship, even after factoring out variation due to initial body size.

4. These results suggest that starvation resistance may be an adaptation for coping with reduced prey availability in high latitudes. Starvation resistance may contribute to latitudinal gradients in body size of ant lions and other ectotherms.

Key words. Ant lion, Bergmann's rule, body size, latitudinal gradients, *Myrmeleon immaculatus*, starvation resistance.

Introduction

Bergmann's rule – an increase in body size with latitude – is a common geographic pattern that has been described for many taxa including birds (James, 1970; Graves, 1991), mammals (Boyce, 1978; Sand *et al.*, 1995; Sharples *et al.*, 1996), fish (L'Abée-Lund *et al.*, 1989; Taylor & Gotelli, 1994), insects (Cushman *et al.*, 1993; James *et al.*, 1995; Arnett & Gotelli, 1999a), aquatic ectotherms (Atkinson, 1994), and ectothermic vertebrates (Ray, 1960; Lindsey, 1966).

What causes Bergmann's rule? The original explanation, heat conservation (Bergmann, 1847), has largely been discarded (Scholander, 1955; McNab, 1971) and is not usually relevant for ectotherms. One current hypothesis to explain increasing body size with latitude is based on the risks of starvation in seasonal or unpredictable environments. Because energy stores increase with size faster than metabolic rate, resistance to starvation should increase with

body size (Cushman *et al.*, 1993). If food availability decreases at high latitudes, starvation resistance may be genetically based and promote large body size at high latitudes. Size-dependent resistance to starvation is supported by many studies of both endotherms and ectotherms (Brodie, 1975; Kondoh, 1977; Boyce, 1978; Lindstedt & Boyce, 1985; Murphy, 1985; Cushman *et al.*, 1993).

On the other hand, for many ectotherms final body size may depend on food availability. Food availability often limits body size and growth in ectotherms (Reznick, 1990; Niewiarowski, 1995). For example, in controlled laboratory experiments, growth rates and size at maturity of guppies (Reznick, 1990) and ant lions (Arnett & Gotelli, 1999b) increased at higher food levels. Thus, phenotypic gradients in body size may reflect a compromise: genetic differences among populations may promote large body size at high latitudes, but environmental gradients in seasonality and food availability may also limit growth at high latitudes. This pattern of counter-gradient variation (Conover & Schultz, 1995) may arise in seasonal food-limited environments (Conover, 1990; Conover & Present, 1990).

In eastern North America, larval and adult body size of the ant lion *Myrmeleon immaculatus* (DeGeer) increases weakly with latitude (Arnett & Gotelli, 1999a). In a

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common garden laboratory experiment, ant lion larvae were collected from southern (Georgia, South Carolina) and northern (Connecticut, Rhode Island) populations and reared under different environmental conditions. Larvae reared with increased food levels grew faster and achieved a larger body size, regardless of temperature or population source (Arnett & Gotelli, 1999b). In a controlled field experiment, larvae in an Oklahoma population also grew faster and reached a larger adult body size with food supplements (Gotelli, 1996). These studies established that food availability can influence larval and adult body size in ant lions.

In the work reported here, the hypothesis for Bergmann's rule in *M. immaculatus*, that large body size, and presumably greater energy stores, is an adaptation for starvation resistance in seasonal, northern latitudes, was tested. Ant lion larvae collected from 10 populations were reared under starved and fed treatments, the time to death or pupation was measured, and these times were correlated with initial body mass and latitude of the source populations. If the starvation resistance hypothesis is correct, larger larvae should survive longer than smaller larvae, regardless of latitude, and larvae from high-latitude populations should survive longer than larvae from low-latitude populations, regardless of initial body size.

Methods

Ant lion life history

Ant lion larvae are sit-and-wait predators that capture arthropod prey in sand pits. Larvae pass through three instars and may persist for 2 years, so that overlapping generations occur in natural populations (Furunishi & Masaki, 1981, 1982; Gotelli, 1997). Third-instar larvae form sand cocoons and exist as pupae for ≈ 28 days (A. Arnett, unpubl. data). After emergence, adult females oviposit eggs in the sand. Adults are feeble fliers, nocturnal, and live for ≈ 1 month. In eastern and central North America, the ant lion *M. immaculatus* is common in sheltered, sandy microhabitats, which support dense larval aggregations (Gotelli, 1993).

Starvation resistance experiment

In 1995, third-instar *M. immaculatus* larvae were collected from 10 populations ranging from Mississippi to New York (Fig. 1). Collecting began in Mississippi on 14 July and finished in New York on 7 August (Table 1). The latitude and longitude of each site were measured using a Magellan Global Positioning System Instrument (Thales Navigation, Santa Clara, California). Elevation was calculated with United States Geological Survey topographic maps. The habitat at each site consisted of sandy, loose soil located under a shelter such as a cliff edge or bridge. At each site, ≈ 30 third-instar larvae were collected randomly, placed individually in

Fig. 1. Locations of the 10 *Myrmeleon immaculatus* populations used in the starvation resistance experiment.

1.5 ml cryotubes, and mailed overnight to the laboratory. Each larva was then assigned randomly to either a *fed* or *starved* treatment. Ant lion larvae in the *fed* treatment were fed one *Tribolium* larva every day. Larvae in the *starved* treatment were not fed. Each larva was placed in a plastic drinking cup, three-quarters full of sterilised playground sand. Each cup was assigned randomly to a location on a laboratory bench. Temperature and humidity were ambient but all larvae were reared simultaneously at the same temperature. A LD 12:12 h photoperiod was maintained from April to November. A winter photoperiod (December to March) was mimicked by changing to a LD 10:14 h photoperiod. To minimise desiccation stress (Karan *et al.*, 1998), all larvae were misted lightly twice a week. Weight, measured to the nearest 0.1 mg, was recorded for each ant lion initially and once a month thereafter until the last individual had pupated or died. All weights were logarithm (base 10) transformed prior to analysis. All statistical analyses were conducted using JMP statistical software, version 3.0 (SAS, 1994).

Analysis of starvation resistance experiment. All larvae in both treatments had either pupated or died by month 11 (fed: 121 died, 30 pupated; starved: 128 died, 25 pupated). For each larva, the number of months until death or pupation, called larval persistence, was measured. Differences in $\log_{10}$ initial body mass among the populations were analysed using a one-way ANOVA.

Significant variation of survivorship was tested among the 10 populations within each of the two treatments by

Table 1. Location, number of third instars collected, latitude, longitude, and elevation of the 10 *Myrmeleon immaculatus* populations used in the starvation resistance experiment.

Site	n	Latitude (N)	Longitude (W)	Elevation (m)
New York	18	43°35′29″	73°38′30″	121.91
Connecticut	30	41°53′00″	72°15′00″	219.51
Connecticut	30	41°32′49″	72°27′06″	76.21
North Carolina	31	35°55′36″	76°08′49″	45.73
North Carolina	32	34°38′01″	78°36′06″	9.14
South Carolina	31	33°40′49″	82°51′20″	158.53
Mississippi	33	33°34′53″	88°28′56″	54.87
Alabama	31	33°06′20″	86°45′11″	170.73
South Carolina	38	32°43′59″	80°35′35″	4.57
Georgia	31	31°23′10″	83°11′31″	88.41

fitting survivorship curves to each population and calculating product-limit survival estimates (Hutchings *et al.*, 1991). To analyse larval persistence among populations, the average of $\log_{10}$ initial body size, and the average number of months of larval persistence were calculated. The fed and starved populations were compared using ANCOVA, with latitude and average initial body mass as the covariates. Interactions between the covariates and the treatment were not significant and were not included in the final model.

A similar analysis was conducted at the level of individuals, using initial body mass and latitude as the covariates, and the persistence time of each larva as the response variable. The two analyses produced similar results but the individual-level analysis allowed the effects of body size on larval persistence to be examined in more detail. In the individual-level analyses, interactions between initial body mass and feeding treatment were significant and were included in the final model.

Results

Third-instar $\log_{10}$ initial body mass differed significantly among the populations ($F_{9,294} = 5.64$, $P < 0.001$). There was a weak positive correlation between $\log_{10}$ initial body mass and latitude ($F_{1,302} = 18.6$, $P < 0.001$; Fig. 2a) and a negative correlation between $\log_{10}$ initial body mass and longitude ($F_{1,302} = 23.4$, $P < 0.001$; Fig. 2b). There was no correlation between initial body mass and elevation ($F_{1,302} = 0.29$, $P = $ NS).

Survivorship curves differed significantly among the populations within both treatments (starved: $\chi^2_{10} = 52.70$, $P < 0.001$; fed: $\chi^2_{10} = 74.43$, $P < 0.001$). The number of months survived by each population also differed among populations for both treatments (starved: $F_{9,142} = 7.75$, $P < 0.001$; fed: $F_{9,139} = 14.3$, $P < 0.001$).
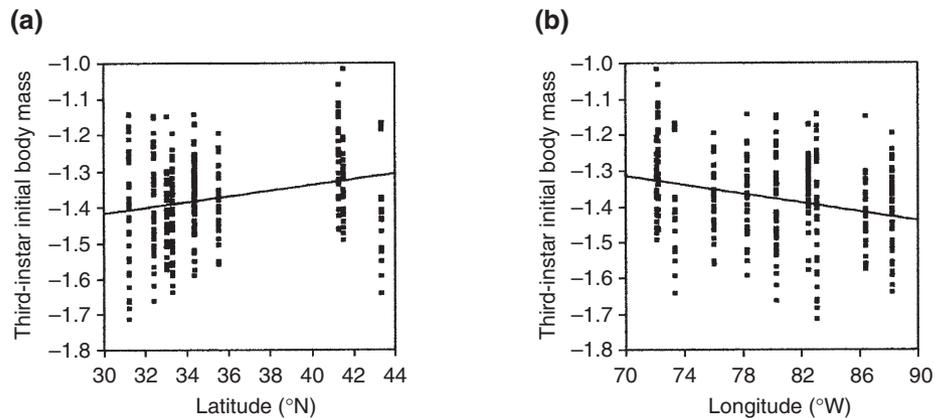
At the level of whole populations, persistence time was greater for fed than for starved larvae (6.49 months vs. 4.71 months; $F_{1,16} = 6.45$, $P = 0.01$) and was greater at high latitudes than at low latitudes ($F_{1,16} = 31.7$, $P < 0.001$; Fig. 3). Longitude ($F_{1,14} = 0.50$, $P = $ NS), elevation ($F_{1,14} = 0.0012$, $P = $ NS), and average initial body mass ($F_{1,14} = 0.08$, $P = $ NS) did not contribute to persistence time.

At the level of individual larvae, there were also significant effects of treatment ($F_{1,298} = 5.09$, $P < 0.05$) and latitude ($F_{1,298} = 145.5$, $P < 0.001$) on larval persistence. In this analysis, initial body mass was also a significant predictor ($F_{1,298} = 14.35$, $P < 0.001$) and there was a significant interaction between treatment and initial body mass ($F_{1,298} = 7.97$, $P < 0.01$). In the fed treatment, initial body mass was correlated negatively with time to pupation or death (slope $= -4.71$), whereas in the starved treatment, initial body mass was correlated positively with time to pupation or death (slope $= 2.58$).

Discussion

The results presented above are consistent with the hypothesis that large body size in larval ant lions is an adaptation to cope with starvation resistance in seasonal, northern latitudes. In the laboratory experiment, survivorship varied among populations collected on a latitudinal gradient, and average survivorship was correlated with latitude (Fig. 3). At the level of the individual larva, body size is tied closely to survivorship time, as individuals deplete fat reserves during starvation (Griffiths, 1991). At the population level, however, average initial body mass is less important than the latitude from which the population originated. The correlation between survival times and latitude is actually stronger than the correlation between body size and latitude, which is statistically significant, but accounts for less than half of the variation between populations in body size (Arnett & Gotelli, 1999a). Statistically, latitude contributes to survivorship beyond the correlated effects of large body size. This finding is consistent with the results of both laboratory common garden experiments and reciprocal field transplant experiments, in which northern larvae had higher survivorship than southern larvae under a variety of environmental conditions (Arnett & Gotelli, 1999b). The slope of survivorship time versus initial body size was found to be opposite in the two treatments. In the fed treatment, the slope was negative because larvae that were initially large took less time to reach a size for pupation. In

(a)

(b)

Fig. 2. (a) Initial body mass of third instars in the starvation resistance experiment increased with latitude ($F_{1,302} = 18.6$, $P < 0.001$) and (b) decreased with longitude ($F_{1,302} = 23.4$, $P < 0.001$). Each point represents the initial body mass of individual third instars from each population in the starvation resistance experiment.

the starved treatment, the slope was positive because larvae that were initially large took a longer time to deplete their stored food reserves before death.
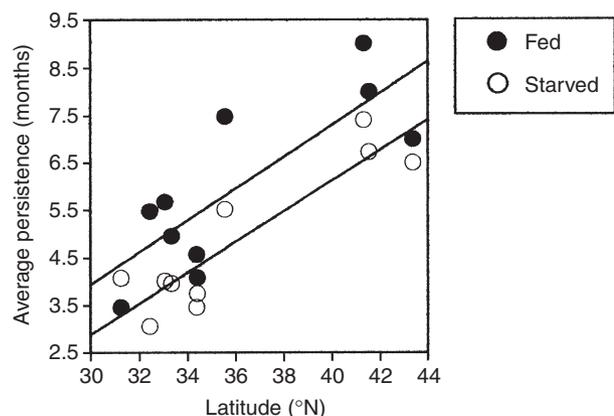
If starvation resistance is indeed an adaptation for coping with seasonal environments, selection should favour genotypes that produce larger individuals in northern vs. southern populations. Common garden experiments confirm that northern larvae have faster growth rates and reach a larger asymptotic body mass, regardless of environmental conditions (Arnett & Gotelli, 1999b). Moreover, ant lion survivorship is tied closely to fat storage, which increases at large body size in some species (Griffiths, 1991).

An alternative perspective for ectotherms is that environmental effects of food and temperature largely determine body size and other life-history traits (Lutz, 1974; Bizer, 1978; Berven *et al*., 1979; Roltsch *et al*., 1990). In particular, cool temperatures often slow down the growth of ectotherms and lead to a larger body size at maturity (Ray, 1960; Atkinson, 1994; Berrigan & Charnov, 1994; Atkinson & Sibly, 1997; Partridge & Coyne, 1997). In this experiment, southern and northern larvae had been exposed to different temperatures and food regimes prior to collection. Based on previous work on larval ant lions, however, there was no effect of temperature on development or asymptotic body size, whereas increased food reduced development time and increased asymptotic body size (Arnett & Gotelli, 1999b).

Thus, if environment were largely controlling geographic gradients in ant lion body size, food availability would necessarily be greater in the north than in the south. Rabenold (1993) speculated that there is a seasonal pulse of insect abundance in northern latitudes that may increase prey availability greatly, at least for some insectivorous birds; however animal abundance is usually correlated negatively with latitude (Damuth, 1991; Brown, 1995). Moreover, pitfall trap data (Gotelli, 1993) and observations at baits suggest that ant lion prey is more abundant in the south at all times of year. Even more important than the

standing crop of insect abundance is the time period available for feeding. In laboratory experiments, ant lions stopped constructing pits at temperatures below 21.0 °C (Arnett & Gotelli, 2001) so the seasonal window during which ant lions can feed in the north is relatively brief.

Thus, the results from this study on survival rates in ant lions are consistent with the starvation resistance hypothesis. Other studies have also accumulated evidence in favour of this hypothesis. In ectotherms, Kondoh (1977) examined survival of worker ants under starvation conditions and found that mortality was correlated with body size, with smaller individuals dying first. Thus, average body size of the surviving colony was larger. Kaspari and Vargo (1995) documented clines in ant colony size that may reflect starvation resistance. Clines in starvation resistance have also been documented in four species of *Drosophila* in India

Fig. 3. Average number of months survived for populations in the starvation resistance experiment increased with latitude (starved: $P < 0.001$, $r = 0.91$; fed: $P < 0.01$, $r = 0.80$). Each point represents the average number of months for which third-instar larvae from each population in the starvation resistance experiment survived.

(Karan *et al.*, 1998; Karan & Parkash, 1998), and latitudinal gradients in *Drosophila* body size in South America appear to evolve very rapidly (Huey *et al.*, 2000).

Other hypotheses for Bergmann's rule in ectotherms include latitudinal gradients in voltinism (Mousseau & Roff, 1989; Roff, 1995) and gradients in environmental factors such as desiccation stress (Levins, 1969; Karan *et al.*, 1998). Gradients in voltinism can be discounted for *M. immaculatus* because the latitudinal gradient in body size is seen for all three instars (Arnett, 1998), and both southern and northern larvae typically live for at least two growing seasons (A. E. Arnett and N. J. Gotelli, pers. obs.). Desiccation stress can also be discounted because, assuming that south-western sites are drier, body size would be expected to be larger in the south-west than in the north-east, which is opposite to the observed pattern (Arnett & Gotelli, 1999a). Finally, the results could be accounted for by a simple scenario of acclimatisation: under conditions of food stress, high latitude populations that have experienced chronic food shortages may survive the starvation treatments for longer than populations that have not experienced food shortages; however differences between northern and southern populations that were reared from tiny first instars persisted across a variety of temperature and food regimes (Arnett & Gotelli, 1999b).

Experiments conducted to test the influence of food, temperature, and population source on growth and body size of *M. immaculatus* showed that larvae in high food treatments grew faster and reached a larger body size, regardless of temperature or population source (Arnett & Gotelli, 1999b). Moreover, for all treatments, northern larvae grew faster than southern larvae. These results suggest that latitudinal gradients in food, not temperature, are driving Bergmann's rule in this insect, and that northern larvae may have adapted to seasonal climates by evolving a larger body size.

Acknowledgements

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