

Bergmann's rule, ant lion body size, and starvation resistance

AMY E. ARNETT and NICHOLAS J. GOTELLI Department of Biology, University of Vermont, U.S.A.

Abstract. 1. Body size of the ant lion *Stegomyia* 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 high and a low food 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, 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; Sanderson, 1995; Sharples, 1996), fish (L'Abée-Lund, 1989; Taylor & Gotelli, 1994), insects (Cushman, 1993; James, 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, 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, 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 *Stegomyia* (DeGeer) increases weakly with latitude (Arnett & Gotelli, 1999a). In a

Correspondence: Amy E. Arnett, Department of Environmental Programs, Unity College, 90 Quaker Hill Road, Unity, ME 04988, U.S.A. E-mail: aarnett@unity.edu

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.

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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 ($F_{1,302} = 0.29$, $p = \text{NS}$).

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 differed significantly among populations (starved: $F_{9,294} = 5.64$, $p < 0.001$; fed: $F_{9,294} = 5.64$, $p < 0.001$).

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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,

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