GEOGRAPHIC VARIATION IN LIFE-HISTORY TRAITS OF THE ANT LION, *MYRMELEON IMMACULATUS*: EVOLUTIONARY IMPLICATIONS OF BERGMANN'S RULE

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Abstract.—In eastern North America, body size of the larval ant lion *Myrmeleon immaculatus* increases from south to north, following Bergmann's rule. We used a common-garden experiment and a reciprocal-transplant experiment to evaluate the effects of food and temperature on ant lion growth, body size, and survivorship. In the laboratory common-garden experiment, first-instar larvae from two southern (Georgia, South Carolina) and two northern (Connecticut, Rhode Island) populations were reared in incubators under high- and low-food and high- and low-temperature regimes. For all populations, high food increased final body mass and growth rate and decreased development time. Growth rates were higher at low temperatures, but temperature did not affect larval or adult body mass. Survivorship was highest in high-food and low-temperature treatments. Across all food and temperature treatments, northern populations exhibited a larger final body mass, shorter development time, faster growth rate, and greater survivorship than did southern populations. Results were similar for a field reciprocal-transplant experiment of third-instar larvae between populations in Connecticut and Oklahoma: Connecticut larvae grew faster than Oklahoma larvae, regardless of transplant site. Conversely, larvae transplanted to Oklahoma grew faster than larvae transplanted to Connecticut, regardless of population source. These results suggest that variation in food availability, not temperature, may account for differences in growth and body size of northern and southern ant lions. Although northern larvae grew faster and reached a larger body size in both experiments, northern environments should suppress growth because of reduced food availability and a limited growing season. This study provides the first example of countergradient selection causing Bergmann's rule in an ectotherm.

Key words.—Ant lion, Bergmann's rule, body size, common garden, countergradient selection, latitude, reciprocal transplant.

The causes of latitudinal variation in body size have long interested evolutionary ecologists (Bergmann 1847; Ray 1960; Lindsey 1966; James 1970; McNab 1971; Van Voorhies 1996; Worthen 1996). Historically, researchers have focused on Bergmann's rule—a latitudinal increase in homeotherm body size within or among closely related species (Bergmann 1847; Mayr 1963). More recently, latitudinal gradients in ectotherm body size have been documented (Cushman *et al.* 1993; Barlow 1994), and a controversy has arisen over the generality of the pattern and mechanisms responsible for it (Atkinson and Sibly 1997; Mousseau 1997; Partridge and Coyne 1997; Van Voorhies 1997).

The controversy centers around whether body size gradients are genetically driven (David et al. 1977; Coyne and Beecham 1987; Mousseau 1997; Partridge and Coyne 1997) or the result of passive phenotypic responses to local temperatures (Cavicchi et al. 1985; Partridge et al. 1994; James et al. 1995; Van Voorhies 1996). For ectotherms, temperature is an important correlate of development time, growth rate, and final body size (reviewed in Ray 1960; Atkinson 1994). Cool temperatures tend to delay maturation, thus causing adults to emerge at a larger body size (Ray 1960; Atkinson 1994; Berrigan and Charnov 1994; Atkinson and Sibly 1997; Partridge and Coyne 1997). For example, Van Voorhies (1996) showed that adult body size in nematodes increased when they were raised in cool temperatures. He suggested that a simple developmental process caused cells to grow to

a larger size in cool temperatures, which may explain latitudinal gradients in ectotherm body size.

However, temperature is not the only environmental factor that varies with latitude. Latitudinal gradients in productivity (Brodie 1975; Cushing 1975; Conover and Present 1990) and seasonality (Murphy 1985; Dingle et al. 1990) may reduce food availability for northern populations. Decreased food availability often reduces growth rate and size at maturity (Berrigan and Charnov 1994; Scott and Fore 1995). Thus, the interaction between food and temperature may be an important environmental determinant of latitudinal gradients in body size.

How important is the local genotype in determining body size? Researchers have focused on the extent to which the environment or the genotype influences phenotypic differences (Berven and Gill 1983; James 1983; Lonsdale and Levinton 1985; Leroi et al. 1994; Yampolsky and Scheiner 1996). More recently, the evolution of phenotypic plasticity itself as an adaptive response to environmental heterogeneity has been debated (Via and Lande 1985; Schlichting 1986; Via et al. 1995). Whether phenotypic plasticity is adaptive or nonadaptive, latitudinal gradients in food and temperature may either reinforce or weaken underlying genotypic gradients in body size and growth (Conover and Schultz 1995).

In eastern North America, larval and adult body size of the ant lion, *Myrmeleon immaculatus*, exhibits a weak positive correlation with latitude (Arnett and Gotelli 1999). In this paper, we describe the results of a laboratory common-garden experiment, carried out under controlled temperature and photoperiod conditions and a field reciprocal-transplant experiment with larval ant lions. These experiments test the

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hypothesis that latitudinal variation in body size of *M. immaculatus* is caused by variation in food, temperature, and population source. The results provide insight into selective pressures that may explain latitudinal differences or similarities in body size of ectotherms.

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 two 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, unpubl. data). After emergence, adult females oviposit eggs in the sand. Adults live about one month. In eastern North America, the ant lion *M. 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, $n = 96$, average body mass $= 0.009$ g; Tolland County, CT, $n = 40$, average body mass $= 0.010$ g) and two adjacent populations in Georgia and South Carolina (Pickens County, SC, $n = 71$, average body mass $= 0.003$ g; Lumpkin County, GA, $n = 68$, average body mass $= 0.004$ g). Because the increase in body size with latitude for *M. immaculatus* is weak (Arnett and Gotelli 1999), we chose two geographic locations that represent the extremes. Intermediate sites would most likely reveal no differences. 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 in a plastic drinking cup that was three-quarters full of sterilized sand. 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 an incubator, and a position on the shelf. One incubator was the high-temperature incubator and 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 and 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, larvae stopped constructing and maintaining their pits. Humidity was maintained at 60% in both incubators, and photoperiod at 12:12 L:D from April to November. From December to March, winter photoperiods were mimicked in both incubators by changing the light schedule to 10:14 L:D.

Larvae in the high-food treatment were initially fed five *Drosophila* per week and the larvae in the low-food treatment were fed one *Drosophila* per week. Larvae in the low-food treatment did not gain weight after 30 days, so we increased the food to 15 *Drosophila* per week for the high-food treatment and six *Drosophila* per week for the low-food treatment. Weight, measured to the 0.1 mg, was recorded for each larva
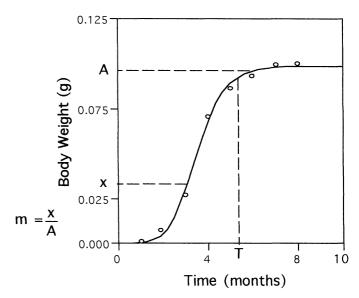

FIG. 1. Parameters estimated for each individual in the common-garden experiment using a modified form of the Richards growth equation (see text). Each point represents the body mass of a single larvae measured at different times. A is the asymptotic (maximum) mass; T is the inverse of the proportional weighted mean growth rate, which represents the time period during which approximately 90% of growth occurs; m is a curve-shape parameter that measures the proportion of final mass at which the inflection point of the growth curve occurs.

initially and once per month thereafter for 19 months. All weights were log-transformed prior to analysis. In analyses of growth and body size, we used the $\log_{10}$ of initial body mass as a covariate. Unless otherwise noted, analyses were conducted using JMP statistical software, version 3.0 (SAS Institute 1994).

Analysis of Common Garden Growth Data

Using nonlinear optimization techniques (PROC NLIN, SAS 1990), we fit the Richards growth equation (Richards 1959) to growth data of each individual. This growth curve is commonly used to study growth in birds (White and Brisbin 1980; Brisbin et al. 1986; Rhymer 1992) and is a better descriptor of growth than simply measuring adult body size. We used a modification of the Richards growth equation that reduces autocorrelation of the residuals (Rhymer 1992):

$$\frac{W_{(i+1)} - W_{(i)}}{t_{(i+1)} - t_{(i)}} = \frac{2(m + 1)}{T(1 - m)}[A^{1-m}W_{(i)}^m - W_{(i)}], \quad (1)$$

where $W_{(i)}$ is the weight at time $t_{(i)}$. Three parameters were estimated by iterative least squares: T (the inverse of the proportional weighted mean growth rate) is the time period during which approximately 90% of growth occurs; A is the asymptotic (maximum) body mass; m is a curve shape parameter that determines the proportion of final size at which the inflection point (maximum rate of growth) of the sigmoid growth curve occurs (Fig. 1). In the Richards growth equation, the curve shape parameter (m) provides a better fit to the data than do standard growth models such as the Gompertz, logistic, and Van Bertalanffy equations (Richards 1959; Rhymer 1992). Only data collected from larvae that com-
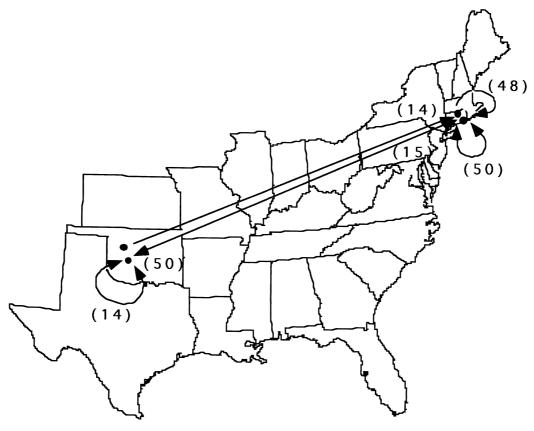
FIG. 2. Design of the reciprocal transplant experiment using third-instar *Myrmeleon immaculatus* larvae. Two populations in each region were used to quantify local variation. Sample sizes are in parentheses.

pleted 19 months of growth were fit with the Richards function. Of the original 276 larvae, 236 were used in the analyses.

From these analyses, the three growth parameters (A, T, and m) were estimated for each larva from the growth records. We analyzed these parameters with 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).

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, $\log_{10}$ initial body mass was used as a covariate in all growth analyses.

Analysis of Common-Garden Survivorship Data

The fate of each individual was categorized as live or dead by month 10. Pupated individuals were categorized as live. Nominal-logistic multiple regressions were conducted with fate as the response variable and $\log_{10}$ initial body mass, population, food, and temperature as the predictor variables.

Analysis of Common-Garden Adult Body Size Data

For the 66 larvae that successfully emerged in the common-garden experiment, we measured interorbital distance with an ocular micrometer. Interorbital distance is a common mea-

sure of insect body size (Hogue and Hawkins 1991). Sex was determined by the presence of oviposition setae in females and the presence of the pilula axillaris at the base of the hind wing in males (Stange 1980).

Because relatively few adults emerged from the Georgia populations, analyses of adult body size were conducted only with Connecticut larvae. An ANOVA was conducted using $\log_{10}$ adult body size as the response variable and population, food, and temperature as the predictor variables. Linear contrasts among populations were used to detect regional differences in adult body size.

Reciprocal-Transplant Experiment

In June 1996, we reciprocally transplanted third-instar ant lion larvae between Tolland County, Connecticut, and Caddo County, Oklahoma (Fig. 2). Reciprocal-transplant experiments are often constrained by a lack of replication at the population level (Via 1991; Niewiarowski and Roosenburg 1993). If only one population from each region is used, it is impossible to say whether the results are characteristic of the region or whether they reflect idiosyncratic local conditions. However, the number of treatment combinations necessary for a fully crossed reciprocal-transplant experiment with n populations is n^2. Thus, in our case, replication of two populations within each region would require 16 treatment combinations, which is not feasible. Our solution was to select two populations in each region, establish four treatments for

the complete transplant between two of the sites, and establish two additional treatments to assess within-site variation.

Larvae from two populations from each state were collected on 15 June and assigned randomly to treatments. All larvae were mailed to their new location in 1.5-ml cryotubes, even if they were assigned to their native site. Upon arrival, each larva was weighed to the nearest 0.1 mg and placed in a 16-ounce plastic cup partially filled with sand. Each cup was assigned a random location at the site and buried in the sand to the rim so that prey could enter but ant lion larvae could not escape. Larvae built pits and actively fed and gained weight in these transplant cups (Gotelli 1997). At both sites, larvae were transplanted into habitats with ant lions. In Connecticut, larvae were transplanted to a sandy hillside sheltered by maples and brush in Salmon River State Forest (Arnett 1998). In Oklahoma, larvae were transplanted to beneath a sheltered cliff ledge in Pugh Canyon (Gotelli 1993).

Larvae were collected and weighed again on 20 July and 21 August. All measurements and manipulations were synchronized between the Oklahoma and Connecticut sites. Missing larvae were categorized as dead. Cocoons were raised to adults in the laboratory. Of the 22 cocoons from all the populations, six were parasitized by Bombyliidae flies and one did not emerge properly. Of the 15 adults obtained, nine were female and six were male. Sample sizes were not large enough to justify an analysis of adult body size.

Analysis of Reciprocal-Transplant Growth Data

We first used an ANCOVA with $\log_{10}$ initial mass as the covariate to compare ant lion growth among the six treatments of the third-instar experiment. Next, we used linear orthogonal contrasts to test for source and site effects. We then used an ANCOVA to test for differences in ant lion growth among populations within a region. Finding none, we pooled the data for populations within a region and conducted a two-way ANCOVA with population source and transplant site as fixed effects, $\log_{10}$ initial mass as a covariate, and final body mass as the response variable.

Analysis of Reciprocal-Transplant Survivorship Data

Differences in fate (live, pupated, dead) among the six treatments were analyzed using a nominal logistic regression with $\log_{10}$ initial body mass as the covariate. A nominal logistic regression was also conducted with the pooled dataset, with source and transplant site as independent variables and $\log_{10}$ initial body mass as the covariate.

RESULTS

Common-Garden Experiment

Asymptotic Mass (A)

Asymptotic mass did not differ among populations within regions ($F_{2,225} = 2.65$, $P = 0.07$), but differed between regions ($F_{1,2} = 12.17$, $P = 0.03$). There was also a significant effect of food ($F_{1,225} = 24.82$, $P < 0.0001$), and an interaction between food and region ($F_{1,225} = 6.52$, $P = 0.01$). There were no significant main effects or interactions with temperature (Table 1). Northern larvae had a greater asymptotic

TABLE 1. Summary of ANCOVAs of asymptotic body mass (A), development time (T), and growth rate (m) and summary of a nominal logistic regression of fate (categorized as dead or live) by month 15 of *Myrmeleon immaculatus* larvae from two northern and two southern populations reared in a common-garden experiment. Each entry is the probability level for a given effect in the model. ns, $P > 0.05$; R, region (north, south); T, temperature (high, low); F, food (high, low).

Source	A	T	m	Fate
Initial Weight	ns	ns	ns	0.003
R	0.033	ns	ns	< 0.0001
T	ns	ns	0.045	0.035
F	< 0.0001	< 0.0001	< 0.0001	ns
R × T	ns	ns	ns	ns
R × F	0.011	0.007	0.003	ns
T × F	ns	ns	ns	ns
R × T × F	ns	ns	ns	ns

mass than southern larvae, and high-food larvae had a greater asymptotic mass than low-food larvae. The effect of food was greater for southern larvae than for northern larvae (Fig. 3a).

Growing Time (T)

T differed among populations within regions ($F_{2,225} = 4.64$, $P = 0.01$). There was a significant main effect of food ($F_{1,225} = 30.11$, $P < 0.0001$) and an interaction between food and region ($F_{1,225} = 7.38$, $P < 0.01$). The main effect of region was marginally nonsignificant ($F_{1,2} = 7.04$, $P = 0.09$) and main effects and interactions with temperature were nonsignificant (Table 1). High-food treatments had a shorter development time (T) than did low-food treatments, and northern larvae developed faster than southern larvae. Effects of the food treatment were greater for southern larvae than for northern larvae (Fig. 3b).

Growth Rate (m)

Average growth rate, m, differed among populations within regions ($F_{2,225} = 11.73$, $P < 0.0001$), but the main effect of region was not significant ($F_{1,2} = 0.61$, $P = 0.50$). There were significant main effects of temperature ($F_{1,225} = 4.07$, $P = 0.05$) and food ($F_{1,225} = 26.12$, $P < 0.0001$) and an interaction between food and region ($F_{1,225} = 9.32$, $P < 0.01$). Growth rate was faster in northern populations, high-food treatments, and low-temperature treatments. The effects of food and temperature were greater for southern than for northern populations (Fig. 3c).

Survivorship

Survivorship curves differed significantly among the populations ($\chi^2_4 = 28.6$, $P < 0.0001$) and among treatments ($\chi^2_4 = 43.6$, $P < 0.0001$). Fate of individuals (live, dead) differed among populations within regions ($\chi^2_2 = 28.34$, $P < 0.0001$). The main effects of temperature and region were significant (temp: $\chi^2_1 = 4.95$, $P = 0.03$; region: $\chi^2_1 = 14.84$, $P = 0.0001$) and the main effect of food was marginally nonsignificant ($\chi^2_1 = 2.97$, $P = 0.08$). The interactions with temperature, food, and region were nonsignificant (Table 1). Low-temperature treatments had lower mortality than did
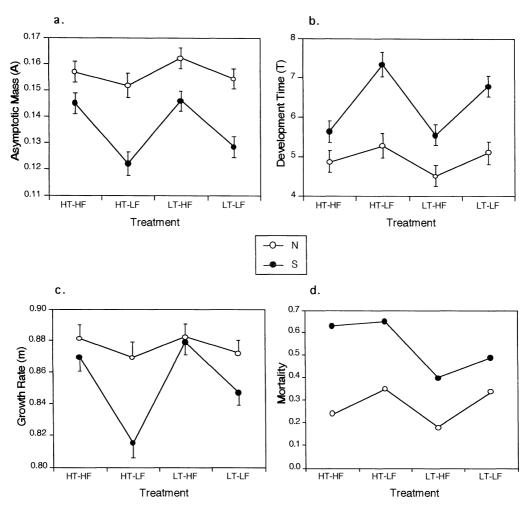
FIG. 3. (A) Asymptotic weight (A); (B) development time (T); and (C) growth rate (m) for first-instar larvae reared in a common-garden experiment. Each point is the mean of two populations in a region, adjusted for initial body mass (± 1 SD). (D) Percent mortality for first-instar larvae reared in a common-garden experiment. Each point is the combined percent mortality in a region, adjusted for initial body mass. N, northern populations; S, southern populations. HT, high-temperature treatment; HF, high-food treatment; LT, low-temperature treatment; LF, low-food treatment.

high-temperature treatments. High-food treatments had lower mortality than low-food treatments, and northern larvae had lower mortality than southern larvae (Fig. 3d).

Adult Body Size

Of the 66 adults that pupated from this experiment, 32 were female and 33 were male. Females were significantly larger than males ($F_{1,63}$ = 8.65, P = 0.0046). Sex ratio was approximately 50:50 in all the populations, even though sample size differed. Because 51 of the 66 adults that emerged were from Connecticut populations, we used only the Connecticut adults in an ANOVA to address effects of food and temperature on adult body size.

Adult body size did not differ between the Connecticut populations ($F_{1,45}$ = 2.21, P = 0.14). There was a significant main effect of food: Adults from high-food treatments were significantly larger than adults from low-food treatments ($F_{1,45}$ = 6.58, P = 0.01). The main effects and interactions with temperature were nonsignificant (temperature: $F_{1,45}$ = 0.91, P = 0.34; temperature × food: $F_{1,45}$ = 0.15, P = 0.71).

The results of a linear contrast conducted from a one-way ANOVA with adult body size as the response variable revealed no difference in body size between Connecticut and Georgia individuals ($F_{1,62}$ = 1.46, P = 0.23). Linear contrasts showed that adults from the high-food treatment were larger than adults from low-food treatments ($F_{1,59}$ = 8.7, P = 0.0045). There was no significant difference in adult body size between temperature treatments ($F_{1,59}$ = 2.96, P = 0.09).

Reciprocal-Transplant Experiment

Growth

There were significant differences in $\log_{10}$ final body mass (adjusted for initial mass) among the six transplant treatments ($F_{5,65}$ = 6.33, P = 0.0001; Fig. 4). Larvae transplanted to Oklahoma were significantly larger at the end of the experiment than larvae transplanted to Connecticut (linear contrast: $F_{1,65}$ = 5.20, P = 0.02). Population source effects were marginally nonsignificant (linear contrast: $F_{1,65}$ = 3.05, P = 0.08). Because there was no significant difference between
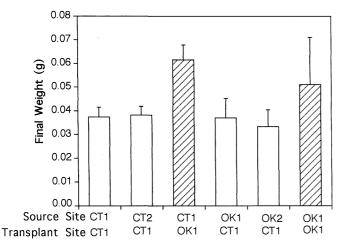
FIG. 4. Third-instar body mass for six reciprocal-transplant treatments. Each bar is the mean body mass at the end of the experiment, adjusted for initial body mass ($\pm$ 1 SE). Shaded bars represent Oklahoma transplant sites. Open bars represent Connecticut transplant sites. CT1, CT2, Connecticut populations; OK1, OK2, Oklahoma populations.

the final mass of larvae originating from populations within a region (Connecticut: $F_{1,45} = 0.024$, $P = 0.87$; Oklahoma: $F_{1,10} = 0.23$, $P = 0.63$), data were pooled. The two-way ANCOVA of transplant and source effects (using the pooled data) on third-instar final mass was significant for transplant site and nearly significant for source site (Table 2). Individuals from Connecticut grew somewhat more than individuals from Oklahoma, but all larvae raised in Oklahoma grew significantly more than those raised in Connecticut (Fig. 5). There was no difference in initial body mass among populations ($F_{3,187} = 1.25$, $P = 0.29$) and treatments ($F_{5,185} = 0.97$, $P = 0.43$) in this experiment.

Survivorship

There was a significant difference among the six transplant treatments in the fate of individuals at the end of the experiment (live, pupated, dead; $\chi^2_{10} = 20.43$, $P = 0.02$). This effect was marginally nonsignificant if pupated larvae were classified as living ($\chi^2_5 = 10.92$, $P = 0.053$). There were significant effects of transplant site on fate (live, pupated, dead; $\chi^2_2 = 16.4$, $P = 0.0003$): fewer larvae persisted in Oklahoma than in Connecticut (Fig. 6). The source effect was not significant. Transplant site was significant and source site was marginally nonsignificant when the pupae were clas-
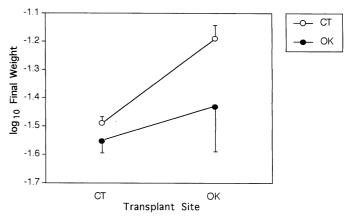
FIG. 5. Third-instar body mass of larvae reciprocally transplanted between Oklahoma and Connecticut. Data from separate populations (Fig. 4) are pooled. Each point is the mean, adjusted for initial body mass ($\pm$ 1 SE).

sified as living (transplant: $\chi^2_1 = 5.7$, $P = 0.02$; source: $\chi^2_1 = 3.7$, $P = 0.053$). Larvae transplanted to Oklahoma pupated at a greater frequency than did larvae transplanted to Connecticut ($\chi^2_1 = 4.22$, $P = 0.03$). There was no significant effect of population source on pupation frequency. Our results probably reflect mortality rates similar to those typically found in nature because the technique used to raise ant lion larvae in the field has been used successfully in other studies (Gotelli 1997).

DISCUSSION

The results of this study suggest that prey availability, not temperature, may be responsible for differences in growth and body size of southern and northern ant lion populations. Temperature had negligible effects on ant lion development compared to the effects of food and population source (Fig. 3a,b,c). Traditionally, temperature has been considered the primary influence on body size in ectotherms (Ray 1960; Lindsey 1966; Atkinson 1994; Atkinson and Sibly 1997). Our results suggest that gradients in food availability may be more important and should be investigated along with temperature effects.

TABLE 2. ANCOVA of final mass of *Myrmeleon immaculatus* larvae from a reciprocal-transplant field experiment between Oklahoma and Connecticut populations. T, transplant site; S, source site.

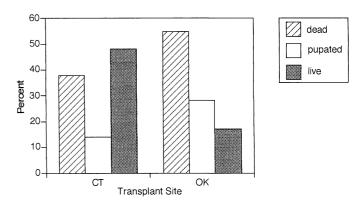| Source	df	SS	F	P
Initial Weight	1	2.8688292	106.5542	< 0.0001
T	1	0.1453534	5.3987	0.0232
S	1	0.0747959	2.7781	0.1002
T × S	1	0.0266120	0.9884	0.3237
Error	67	1.8038860		
Total	71			

FIG. 6. Effects of transplant site on third-instar fate (dead, pupated, live) for larvae reared in Oklahoma and Connecticut ($\chi^2_1 = 20.31$, $P < 0.0001$). The effect of population source was not significant ($\chi^2_6 = 5.30$, $P = 0.50$).

Both the common-garden and the reciprocal-transplant experiment revealed latitudinal differences in growth, with northern larvae growing more rapidly and achieving a larger body size than southern larvae (Figs. 3a,b,c, 5). In contrast, the reciprocal transplant revealed that northern environments suppress growth relative to southern environments (Fig. 4). This is directly opposite to the relative growth rates of larvae from the two geographic regions. This phenomenon in which geographic variation in genotypes opposes environmental influences is termed "countergradient variation" (Levins 1968; Conover and Present 1990). Environmental variation suppresses phenotypic variation in a trait and is probably responsible for the weak correlation between latitude and body size in *M. immaculatus* (Arnett and Gotelli 1999). The relative strength of selection at different latitudes determines whether differences in phenotypes are seen (Conover and Schultz 1995). Although much of the controversy has focused on body size, this variable itself depends on the interaction between development time and growth rate, both of which have genetic and environmental components (Roff 1992). Thus, variation in selection gradients could explain why some organisms do not demonstrate latitudinal variation in body size (Hawkins 1995; Hawkins and Lawton 1995) and why some demonstrate the converse to Bergmann's rule (Masaki 1967; Scott and Dingle 1990; Mousseau 1997).

Because larvae were field collected, maternal effects (e.g., egg size) or other residual effects of parental environment (e.g., growth history) may have affected our findings. Therefore, our "source" effect may reflect not only genetic differences among populations, but also a combination of maternal genetic and environmental effects (Mousseau 1991). We used a covariance approach (ANCOVA) to adjust response variables for residual environmental and maternal effects. This technique works only to the extent that such effects are due to differences in initial size, including egg size (Brown 1985). However, a covariance analysis may not account for maternal genetic effects. The best design to assess maternal genetic effects is to simultaneously transplant both the F_1 and parental stock (Berven 1982). This is impossible with ant lions and difficult to achieve in most organisms (Bernardo 1994). Although variation in growth and body size of *M. immaculatus* could be due to maternal effects, traits are very plastic and can be modified by food or microhabitat even in late third-instar larvae (Gotelli 1997). Our results cannot be explained by early environment effects because the pattern of countergradient variation is one in which the genotypic effects on the phenotype are opposite the environmental effects at the site of origin.

What is causing the dichotomy in growth rates between northern and southern populations? Because energy stores increase with size faster than metabolic rate (Peters 1983; Calder 1984; Cushman et al. 1993), resistance to starvation should increase with body size. Because food availability in northern latitudes is seasonal, strong selective pressure for larger body size may exist (Lindstedt and Boyce 1985). Starvation resistance has been documented or implicated in many organisms (Brodie 1975; Kondoh 1977; Boyce 1978; Lindstedt and Boyce 1985; Murphy 1985; Cushman *et al.* 1993; Chippindale et al. 1996; Karan et al. 1998) and may explain latitudinal variation in *M. immaculatus* (Arnett 1998).

Life-history theory suggests that a trade-off between increased growth and survivorship or fecundity would prevent the spread of a single optimal genotype. For example, somatic growth in the juvenile stage may be negatively correlated with an ability to withstand environmental challenges, such as disease or desiccation (Roff 1992; Stearns 1992). However, there were no differences in survivorship of Oklahoma and Connecticut larvae in the reciprocal-transplant experiment, and in the common-garden experiment, northern larvae had a faster growth rate and higher survivorship than did southern larvae (Fig. 3c,d).

Another explanation is that there are different constraints on body size at different latitudes. Large size may be beneficial at high latitudes for winter survival, but at low latitudes other factors may favor smaller body sizes, such as size-selective predation or crowding effects (Roff 1981; Conover and Schultz 1995; Santos 1996). In the reciprocal-transplant experiment, we found increased growth (Figs. 4, 5) and decreased survivorship (Fig. 6) of larvae transplanted to Oklahoma versus Connecticut, suggesting that selective regimes are different in southern versus northern environments.

In summary, two important conclusions emerge from these experiments. The first is that countergradient variation may be responsible for the disparate correlations of size and latitude that have been documented in ectotherms (Masaki 1967; Cushman et al. 1993; Barlow 1994; Hawkins 1995; Hawkins and Lawton 1995; Kaspari and Vargo 1995; Van Voorhies 1996; Mousseau 1997). The second is that geographic gradients in food availability may be as important as geographic gradients in temperature, which have traditionally been thought to control ectotherm growth and body size.

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