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Thamnophis elegans

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Source: *Evolution*, Vol. 54, No. 5 (Oct., 2000), pp. 1760-1767

Published by: Society for the Study of Evolution

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EXPERIMENTAL EVIDENCE FOR THE ADAPTIVE EVOLUTION OF GROWTH RATE IN THE GARTER SNAKE *THAMNOPHIS ELEGANS*

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Abstract.—The western terrestrial garter snake (*Thamnophis elegans*) varies significantly in individual growth rates and life-history traits (maturation, reproduction, and survival) among adjacent populations in nature. This study focuses on assessing the genetic and environmental components of the substantial among-population variation in growth rates. Litters of neonates from nine populations inhabiting either mountain meadow or lakeshore habitat were reared for one year in a common-garden experiment with two temperature treatments. Diet, frequency of feeding, light exposure, and daytime temperatures were identical for all individuals. The two different nighttime temperatures (20°C and 25°C) were chosen to mirror field differences in nighttime thermoregulatory constraints for mountain-meadow and lakeshore snakes, respectively. Temperature and source habitat interacted to affect first-year growth rate. Neonates from meadow dams grew fastest in the cooler treatment, whereas those from lakeshore dams grew fastest in the warmer treatment. The observation that naive neonates, which were gestated and raised under identical conditions, grew fastest in environments characteristic of their natal population is evidence both that there are genetic differences among populations for growth and that these differences reflect adaptation to local habitats at a very small geographic scale. In addition, significant directional selection for large birthweight was measured for neonates from all populations. These results are considered in the context of population colonization history, migration and selection, and competing models for growth rate variation.

Key words.—Adaptation, common-garden experiment, garter snake, genotype × environment interaction, growth rate, temperature variation, *Thamnophis elegans*.

Received August 4, 1999. Accepted March 9, 2000.

An individual's growth rate can affect many of its life-history traits, such as age and size of maturation, reproductive output, and longevity (Case 1978; Andrews 1982). The question of how growth affects these life-history traits continues to motivate much debate and empirical work, particularly for long-lived organisms with indeterminate growth (reviewed in Roff 1992; Stearns 1992; Charlesworth 1994). If no costs are associated with fast growth, individuals are expected to grow as quickly as possible to begin reproducing. However, if fast growth entails costs to reproduction, longevity, or maturation, then individuals should balance these costs with the benefits of larger body size (Charlesworth 1990, 1994). Indeed, the persistence of many examples of intraspecific variation in growth and maturation in nature suggests that there may be costs associated with fast growth (e.g., Stamps et al. 1998; Bronikowski and Arnold 1999; reviewed in Arendt 1997). These studies suggest that growth rate variation is common in nature.

Controlled laboratory or field experiments that have documented the causes of growth rate variation among populations of long-lived organisms with well-characterized natural histories have lagged behind their field-observation counterparts. Notable exceptions are experiments that documented the sources of variation in growth among populations of sceloporine lizards (Sinervo and Adolph 1989, 1994; Sinervo 1990; Niewiarowski and Roosenburg 1993; Smith et al. 1994; Niewiarowski 1995). These studies reported that growth rate variation can be caused by all of genotype, environment, and/or maternal effects. Furthermore, the role of evolutionary and colonization history among local popula-

tions can be an important source of variation among populations (e.g., Patton and Smith 1992).

A 20-year field study documented variation in individual growth and life histories in a long-lived vertebrate, the western terrestrial garter snake (*Thamnophis elegans*) (Bronikowski and Arnold 1999). The emphasis of that study was on multiple adjacent populations that occurred in two primary habitats with two associated life-history patterns. Lakeshore snakes grew quickly to large adult body sizes and had early reproduction, increased fecundity with larger body size, and high annual mortality. In contrast, mountain meadow snakes grew slowly to smaller adult body sizes, began reproducing late, had no change in fecundity with body size, and had low annual mortality. Whether these habitat-specific life histories have a genetic basis and represent adaptations to lakeshore versus meadow living could not be addressed with the field data.

Here, I present common-garden growth experiments of this long-lived squamate from the lakeshore/meadow complex to identify the causes of variation in first-year growth rates. The common gardens were embedded within two temperature treatments designed to reflect field variation in temperature. Additional outgroup populations of *T. elegans* were included to assess intraspecific variation in growth outside of this complex. This experiment, when combined with a study of *T. elegans* DNA sequence variability (Bronikowski 1997; Bronikowski and Arnold 2001), identifies whether the individual growth rate variation observed in the field is due to colonization history, genotype, environment, or size-related maternal effects. The results of these laboratory studies are considered in the context of two competing hypotheses for growth rate variation (maximize vs. optimize: Case 1978; Charlesworth 1990; Stearns 1992; Bronikowski and Arnold 1999) with evidence presented that the observed growth rates are adaptive.

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TABLE 1. Study sites and sample sizes.

Population	Habitat (elevation, m)	Litters (neonates)			Neonate mortality
		Start	Hibernation	End	
Eagle Lake, California:					
L1	lakeshore (1555)	3 (20)	3 (17)	3 (16)	20%
L2	lakeshore (1555)	13 (144)	12 (94)	10 (66)	54%
L3	lakeshore (1555)	9 (62)	9 (54)	9 (43)	31%
M1	mountain meadow (1630)	18 (94)	16 (66)	14 (41)	56%
M2	mountain meadow (1910)	9 (30)	7 (16)	6 (9)	70%
M3	mountain meadow (2055)	4 (19)	4 (18)	3 (8)	58%
M4	mountain meadow (1695)	2 (11)	2 (4)	2 (2)	82%
Eagle Lake Total		58 (380)	53 (269)	47 (185)	51%
Other:					
GB (Idaho)	Great Basin (550)	8 (51)	7 (24)	7 (19)	63%
S (California)	mountain meadow (1830)	2 (17)	2 (14)	2 (7)	59%
Grand total		68 (448)	62 (307)	56 (211)	53%

METHODS

Study Populations

I collected pregnant females from nine populations of the western terrestrial garter snake (*T. elegans*) (Table 1). Seven of these populations were from the vicinity of Eagle Lake, Lassen County, California, and were in close proximity to each other (5–20 km). The thermal ecology and the evolution of feeding behavior and morphology have been intensely studied in a subset of these populations (Arnold 1981a,b,c, 1988, 1992; Kephart 1982; Kephart and Arnold 1982; Huey et al. 1989; Peterson et al. 1993; Kelley et al. 1997). Three of the Eagle Lake populations lived along the lakeshore (L1–L3) and four were from surrounding mountain meadows (M1–M4). Pregnant females from two distant populations were gathered to compare neonate growth to the Eagle Lake complex. “S” is a mountain meadow population of *T. e. elegans* located in the Tahoe National Forest (Sierra Co., CA), approximately 100 km south of Eagle Lake in the Sierra Nevada range (White and Kolb 1974). “GB” is a Great Basin population (*T. e. vagrans*) from Blackfoot Reservoir (Caribou County, ID) located 800 km to the northeast of Eagle Lake. The subspecific status of the Eagle Lake garter snakes is equivocal: they are either considered to be *T. e. elegans* (Fitch 1983; Bronikowski and Arnold 2001) or *T. e. vagrans* (Rossman et al. 1996).

Laboratory Procedures

I caught pregnant females in June and July 1996 and brought them to the laboratory, where they were housed individually in ventilated plastic boxes (32 × 18 × 18 cm) lined with corn cob bedding. Females were provided a thermal gradient such that one end of the box was 32°C and the other end was 27°C for 12 h of light, followed by 12 h of dark at 25°C. I provided fresh water and twice weekly ad libitum feedings of live minnows. Female feeding was monitored to ensure that more fish were offered than were eaten. Each pregnant female gave birth on a single day between August 20 and September 24. Beginning in mid-August, I examined the females twice a day (early morning and late afternoon). If a female had given birth, the neonates were

left in her box until the following day. If a female gave birth overnight, the neonates were not removed until the second day. I sexed, weighed (g), and measured (mm from snout-vent, SVL) each neonate, and weighed and measured (SVL) the dam at the same time. Each neonate was placed in an individual plastic box, with water and paper towel bedding.

Three days postbirth, I divided each litter randomly among four environmental chambers with one of two different temperature regimes, 14 h of light at 28°C and 10 h of dark at either 25°C or 20°C, which corresponded to the natural thermal regimes of Eagle Lake snakes. These two temperature treatments were based on field and laboratory studies that reported thermal choice, thermal optima, and field constraints for Eagle Lake snakes (Huey et al. 1989; Peterson et al. 1993; Arnold et al. 1995; C. R. Peterson, unpubl. data). A total of 448 neonates were divided between the two temperature treatments, representing 68 litters from nine populations.

I fed the neonate snakes twice a week a 2-g mixture of tadpoles (*Hyla regilla*), earthworms, and cooked, ground minnows. Diet composition was based on reported field observations of snake diets (Kephart and Arnold 1982; Arnold 1992). Food was provided in the afternoon and uneaten food was removed on the following morning, when feeding data were recorded. For each snake, I recorded whether the snake ate at each (*i*th) feeding. Uneaten food was not weighed, rather I assigned a proportion eaten, n_i , to each snake (e.g., $n_i = 1$ if a snake ate all food, $n_i = 0.5$ if a snake ate half of its food, $n_i = 0$ if a snake did not eat, etc.). I summarized these behavioral data to create an index of each snake's propensity to feed to use as a covariate in analyzing growth (propensity to feed = $\sum n_i/N$, where N is the total number of times that food was offered during the experiment). I changed the drinking water at each feeding and changed the bedding once a week. Dead snakes were removed at feeding times and preserved. I weighed the neonates and measured SVL once a month, at which time their boxes were washed.

Snakes were maintained on this twice-a-week feeding schedule from birth (August 20 to September 24, 1996) until December 8, 1996. Then temperatures were decreased over one week to a constant 5°C with continuous dark. Snakes

TABLE 2. Analysis of variance of first-year growth in Eagle Lake *Thamnophis elegans*. Litter(habitat) was a random effect, thus the main effect of Habitat was tested over a synthesized mean square (Kirk 1982). All possible covariates (birth size, feeding propensity, age, and dam size) were not significant in analyses of covariance and were subsequently excluded.

Source of variation	df	Increase in length			Increase in weight		
		Type III MS	F	P	Type III MS	F	P
Habitat	1	8347	6.57	0.01	60.2	8.77	0.004
Temperature	1	278	0.43	0.51	0.8	0.22	0.64
Sex	1	321	0.50	0.48	2.6	0.75	0.39
Habitat × temperature	1	2248	3.48	0.06	17.1	4.81	0.03
Litter(habitat)	45	1672	2.59	< 0.0001	9.0	2.53	< 0.0001
Error	135	651			3.6		
Total	184						

were kept in this laboratory hibernation until mid-February, at which time I programmed the chambers to resume their previous temperature treatments. I weighed and measured the neonates for the final time on June 16, 1997.

Statistical Analysis

I analyzed both change in SVL and change in weight from birth to the end of the experiment with mixed model analysis of variance (ANOVA) (JMP3.1.5, SAS Institute, Cary, NC). Only Eagle Lake snakes that survived the duration of the experiment were included in these analyses (i.e., 185 of the initial 380 Eagle Lake neonates, see Table 1). The main effects included in the ANOVAs were sex, habitat (lakeshore vs. meadow), and temperature (28/25°C vs. 28/20°C). The effect of source habitat was analyzed rather than source population directly because neonate mortality precluded the use of source population as an effect. Litter within habitat was also included as a random effect. In a secondary analysis, data on the birth sizes and final body sizes of neonates for all nine populations were compared in a mixed model ANOVA with source population as the main effect and litter (within population) as a random effect.

Several possible covariates could have impacted neonate growth. Specifically, I examined propensity to feed, age (date of final measurement minus date of birth), maternal body size, and neonate birthweight for how they affected growth. None of these covariates were significant when included in an analysis of covariance of growth; thus, only the ANOVA results (without covariates) are presented. However, because both birthweight and propensity to feed affected neonate survival, they indirectly affected growth (i.e., growth was only analyzed for snakes that survived the experiment). Therefore, the relationships among birthweight, propensity to feed, and survival are considered in detail. I analyzed the impact of birthweight on survival for all 448 neonates to compute the standardized coefficient of selection on birthweight (β' of Lande and Arnold 1983) and its significance level via logistic regression (Janzen and Stern 1998) in SAS version 6.11 (SAS Institute Inc., Cary, NC). Finally, I analyzed whether habitat, temperature, sex, and litter affected survival during the first year for Eagle Lake snakes with multifactor logistic analysis. For these survival analyses, the logit function of survival was the dependent variable, but, for ease of interpretation, results are discussed in terms of the probability of survival.

RESULTS

First-Year Growth

Source habitat directly affected first-year growth, but temperature did not (Table 2). Lakeshore neonates grew faster than meadow neonates at both temperature treatments for both increase in length (least-squares mean \pm SE: lakeshore = 78 ± 3.5 mm, meadow = 61 ± 4.7 mm) and increase in weight (least-squares mean \pm SE: lakeshore = 5.02 ± 0.26 g, meadow = 3.54 ± 0.40 g). However, the primary result of interest for both dependent variables was that habitat and temperature interacted to affect growth (Table 2). Within habitat type, snakes from lakeshore sites grew fastest at the warmer treatment and snakes from meadow sites grew fastest at the cooler treatment (Fig. 1).

When the beginning and ending body sizes of the two outgroup populations were analyzed with the Eagle Lake populations, significant variation was evident. Final body size varied significantly among populations ($F_{8,47} = 5.04$, $P < 0.0001$) as did birth size ($F_{8,58} = 4.92$, $P < 0.0001$) (see Fig. 2). Within Eagle Lake populations, larger birth sizes and faster growth rates in lakeshore snakes resulted in larger first-year body size than meadow snakes. Furthermore, snakes from the outgroup Sierran population (S) had similar body sizes and growth rates as lakeshore snakes, and the outgroup Great Basin population (GB) had the fastest individual growth rates of all populations, despite starting out at similar body sizes as the Eagle Lake snakes (Fig. 2).

Birth Size, Feeding Behavior, and Survival

Although neither birth size nor feeding behavior were significant predictors of first-year growth, both variables strongly affected which snakes survived the experiment (and thus which snakes were ultimately included in the analysis of growth). Snakes that died during the experiment did so during one of two intervals: either from birth to hibernation or during hibernation. Snakes that died during the three months preceding hibernation weighed significantly less at birth than snakes that survived the experiment ($F_{2,445} = 12.97$, $P < 0.0001$, see Table 3). Furthermore, the snakes that died before hibernation either never ate or ate irregularly (mean propensity to feed \pm SE = 0.10 ± 0.05). A second group of snakes survived until hibernation, but died during hibernation. Snakes that died during hibernation had lower prehibernation

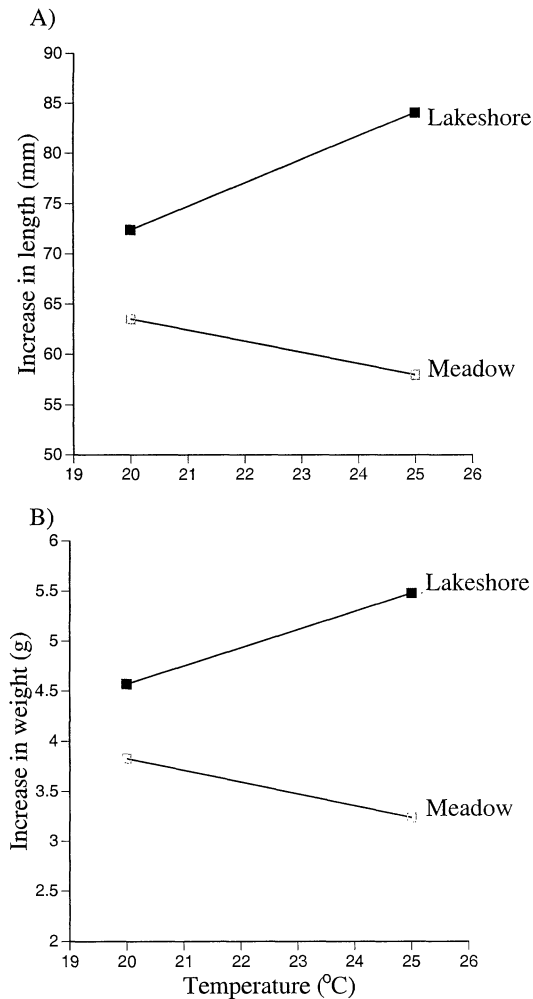


FIG. 1. Interaction between habitat- and temperature-affected growth measured as either change in length or change in weight (see Table 2). (A) Lakeshore snakes had greater increases in length in the warm treatment than in the cool treatment (least-squares mean = 84.1 mm and 72.4 mm, respectively). In contrast, meadow snakes increased in length faster in the cool treatment than in the warm treatment (least-squares mean = 63.6 mm and 58.0 mm, respectively). (B) Lakeshore snakes gained weight faster in the warm treatment than in the cool treatment (least squares mean = 5.48 g and 4.57 g, respectively). In contrast, meadow snakes gained weight faster in the cool treatment versus the warm treatment (least-square mean = 3.83 g and 3.24 g, respectively).

feeding propensities than snakes that survived hibernation (Table 3) and therefore lower prehibernation weight (mean weight at hibernation \pm SE = 2.85 \pm 0.13 g vs. 4.54 \pm 0.09 g for those that lived). Thus the high prehibernation feeding propensities for surviving snakes translated into greater weight gain and higher probability of survival. Snakes that survived the experiment both weighed more at birth and ate almost all food at all feedings. Together, these feeding and birth size patterns resulted in size-related survival (Logit [survival] = $-2.24 + 0.80$ [birthweight]; see Fig. 3). The standardized selection coefficient on birthweight ($\beta' \pm$ SE) was 0.23 \pm 0.04, $P = 0.001$ (Lande and Arnold 1983; Janzen and Stern 1998), indicating significant directional selection for large birthweight.

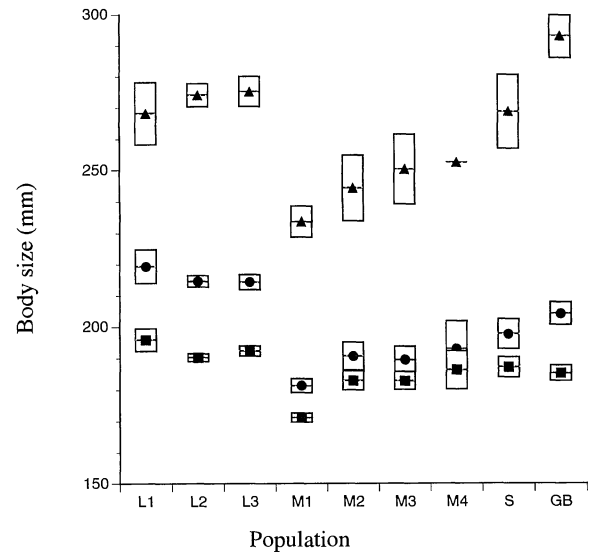


FIG. 2. Mean body size (mm \pm 2 SE) at birth (squares), at hibernation (circles), and at the end of the experiment (triangles) of snakes for each population. Sample sizes are in Table 1. L1–L3 are Eagle lakeshore populations, M1–M4 are mountain meadow populations surrounding Eagle Lake, S is an outgroup Sierran population, GB is a Great Basin population. Mean final body size (mm): GB = 293, S = 269, L1 = 268, L2 = 274, L3 = 275, M1 = 234, M2 = 244, M3 = 250, M4 = 252.

In addition to birthweight, source habitat and temperature treatment interacted significantly to determine which snakes survived the experiment ($\chi^2 = 13.2$, $P = 0.0003$; Table 4). Within habitat type, meadow neonates in the warm treatment were less likely to survive the experiment than meadow neonates in the cool treatment (probability of survival = 0.31 and 0.51, respectively; see Fig. 4). In contrast, lakeshore neonates in the cool treatment were less likely to survive than were lakeshore neonates in the warm treatment (probability of survival = 0.55 and 0.69, respectively; see Fig. 4).

DISCUSSION

In the field, lakeshore snakes grow almost twice as fast as meadow snakes (Bronikowski and Arnold 1999). The results of this laboratory study show that this field variation in growth has a genetic basis: lakeshore neonates grew significantly faster than meadow neonates under identical laboratory conditions. Birthweight and feeding behavior were important in determining growth rate in that small birthweight neonates and those that did not feed 90% of the time that

TABLE 3. Mean (SE) for birthweight and feeding propensity of neonates that died before hibernation, died during hibernation, and lived until the end of the experiment.

Timing of death	<i>n</i>	Mean birthweight (g)	Mean feeding propensity
Before hibernation	143	2.43 (0.05)	0.10 (0.05)
During hibernation	94	2.59 (0.06)	0.45 (0.03)
Survived entire experiment	211	2.74 (0.04)	0.90 (0.04)

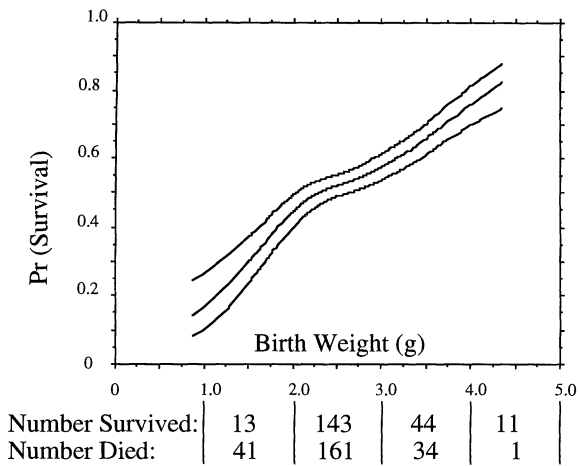


FIG. 3. Snakes that were heavier at birth had a higher probability of surviving the experiment. Visualized with cubic spline (Schluter 1988) and 95% confidence interval of the probability of survival versus birthweight. The number of individuals that survived and died in 1 g size intervals are given below the x-axis.

food was offered did not survive the experiment. In addition, despite the prevalence of size-related maternal effects on birthweight (Bronikowski and Arnold 1999), size-related maternal effects were not important in neonate growth (although this does not preclude the possibility that environmental maternal effects are important to growth). Source habitat and temperature interacted to affect growth rate and survival such that neonates from dams collected in warm lakeshore habitats grew fastest and had increased survival in the warm treatment, whereas neonates from dams collected from cooler mountain-meadow habitats grew fastest and had increased survival in the cool treatment. This habitat × temperature interaction is evidence that growth rate may be adapted to habitat-specific differences at this extremely small geographic scale.

Source Habitat, Temperature, and Growth

Laboratory and field experiments on squamates that have reported significant population differences in individual growth rates have tested populations separated by distances greater than 100 km (like Eagle Lake vs. S and GB in this study). These reports are mainly on *Sceloporus* lizards, including *S. occidentalis* (Sinervo 1990; Sinervo and Adolph 1994) and *S. undulatus* (Niewiarowski and Roosenburg 1993; Niewiarowski 1995), and chuckwallas (*Sauromalus obesus*) from the southwestern United States (Tracy 1999). In all of these studies, laboratory or reciprocal-transplant growth rate mirrored naturally occurring between-population growth rate variation. Unlike the present study, however, reports of laboratory growth rates among populations in close proximity (like those in the Eagle Lake complex) have not found significant population differences in growth (California populations of *S. occidentalis* and of *S. graciosus*: Sinervo and Adolph 1994; Arizona populations of *S. jarrovi*: Smith et al. 1994; French populations of *Lacerta vivipara*: Sorci et al. 1996). Therefore, the present study is unique because genetic differences for growth rate were found for this vertebrate at a very small geographic scale.

TABLE 4. Logistic analysis of first-year survival in Eagle Lake *Thamnophis elegans*. Total sample size for this analysis was 341 rather than 380 because 39 Eagle Lake neonates died in the first few days of life and were not assigned to a temperature treatment.

Source of variation	df	χ^2	P
Habitat	1	0.02	0.89
Temperature	1	0.93	0.33
Sex	1	1.50	0.22
Habitat × temperature	1	13.2	0.0003
Litter(habitat)	53	40.8	0.89

Although temperature did not affect growth overall, it interacted with source habitat to influence growth. This result is in contrast to the above studies, all of which reported that individuals grew faster at warmer temperatures and with longer exposure to radiant heat, regardless of source population and regardless of whether growth differed among populations. In addition to these multipopulation reports, studies conducted on single populations of squamates also reported that first-year growth is faster at warmer temperatures (e.g., snakes: *Thamnophis sirtalis*: Peterson et al. 1993; lizards: *S. occidentalis* and *S. graciosus*: Sinervo and Adolph 1989; *Cyclura nubila*: Alberts et al. 1997).

In the laboratory, meadow snakes did not respond to continuous prey availability and warmer temperatures to grow as fast as lakeshore snakes. Because all snakes surviving the experiment ate the same type and amount of food (Table 3), this slow growth phenotype of meadow must have a physiological basis (reviewed in Garland and Adolph 1991). This physiological differentiation may derive from predictably low food availability (e.g., Forsman and Lindell 1996), variable energy assimilation of different prey organisms (e.g., Scudder-Davis and Burghardt 1987), or natural thermal constraints (sensu Bashey and Dunham 1997). The speculation that physiological differentiation has occurred between snakes living in these two habitats is bolstered when climate

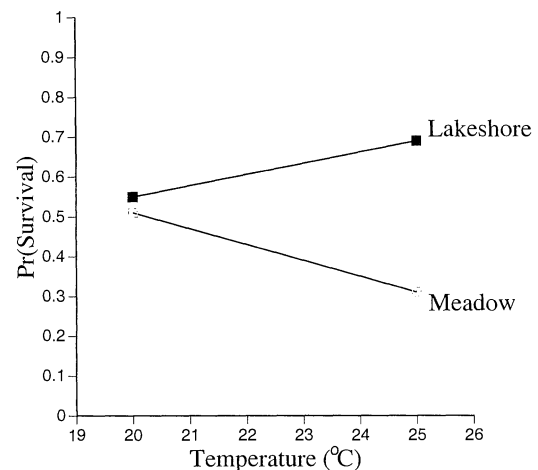


FIG. 4. Within habitat type, lakeshore neonates had a greater probability of surviving their first year of life in the warm treatment than in the cool treatment (Pr[survival] = 0.69 and 0.55, respectively). In contrast, meadow neonates had greater probability of surviving in the cool treatment than in the warm treatment (Pr[survival] = 0.51 and 0.31, respectively).

and prey availability data are considered. In this system, the probability of a "good" year for a meadow snake (a year with enough precipitation for anurans to breed) is about 0.50 versus a probability of 1.0 that lakeshore snakes will have a good year (a year with bountiful fish prey) (Bronikowski and Arnold 1999). Thus, if meadow snakes took advantage of a year with high prey availability by increasing their growth beyond typical rates, these large bodies would require more maintenance food in subsequent years. Survival rates would be expected to decline to levels seen in lakeshore habitats (Bronikowski and Arnold 1999). Large body size may be too costly in meadow habitats based on the reality of low food availability. This proposition is supported by two recent studies on the ecological energetics of growth in a closely related species of garter snake living in the same mountain meadows (Peterson et al. 1998, 1999). Peterson et al. measured a significant metabolic cost of growth in the field (minimally 2 kJ per gram of net growth), which incorporates both physiological (constant) and size-related ecological costs of growth such that the cost of growth increases with body size. Furthermore, they reported significant effects of body size on both resting ("maintenance") and field metabolic rates. In addition, snakes with high growth rates for their body size also had high field metabolic rates for their body size.

Birthweight, Survival, and Growth

Birthweight was not correlated with first-year growth rate in this study. Gregory and Prelypchan (1994) reported a similar finding that larger neonate *T. elegans* from a single British Columbia population ate more food and attained larger yearling body size, but did not grow faster. Interestingly, in utero growth rates for thamnophiine snakes are correlated with birth size (Velhagen and Savitzky 1998), so one might expect a priori that larger neonates would continue growing faster than smaller neonates. In fact, Andrews (1982) compared data on 17 species of snakes and found that species with larger young at birth had higher individual growth rates during the first year of life.

Although birthweight was not a good predictor of growth rate, it predicted which snakes survived the experiment (Fig. 3). Overall, survival in the laboratory was greater than in the field (laboratory first-year survival: meadow = 39%, lakeshore = 55%; field first-year survival: meadow = 23%, lakeshore = 15%, A. M. Bronikowski and S. J. Arnold, unpubl. data). In this study, the two intervals with high mortality were from birth to hibernation and during hibernation. From birth to hibernation, neonates that died weighed significantly less at birth and ate significantly less often while alive than those that survived until hibernation (Table 3). The observation that hibernation was a time of high mortality is consistent with the general phenomenon that hibernation is a period of high mortality for all life stages (reviewed in Parker and Plummer 1987; Rossman et al. 1996). The difference in prehibernation weight gain between snakes that lived (65%) and snakes that died (10%) suggests that neonates had to gain a certain amount of weight to survive hibernation (see also Völkl 1989).

Given the strong and significant directional selection favoring larger birthweight ($\beta' \pm SE = 0.23 \pm 0.04$), it is

surprising that females produced small offspring because of the apparent survival risks. Possible constraints on the evolution of larger birthweight in these snakes include nongenetic maternal effects that influence birthweight (such as maternal condition), or selection for litter size rather than offspring size. Bronikowski and Arnold (1999) reported laboratory repeatability estimates (within dams) for both litter size and offspring birthweight. Repeatability (which places an upper bound on heritability) for litter size was 0.20, while that for offspring birthweight was 0.43. Thus, heritability for litter size may be lower than that for offspring birthweight, which would imply stronger selection on litter size (sensu Mousseau and Roff 1987). Jayne and Bennett (1990) found that larger neonate *Thamnophis sirtalis* were more likely to survive after release into their natal population. Thus, the result that larger neonates had a higher probability of survival in the laboratory may be relevant in the field (e.g., Janzen 1993; Janzen et al. 2000).

Evolutionary History

This study documented that the life-history phenotypes observed in lakeshore versus meadow populations of garter snakes are based in part on genetic differences among populations. However, this genetic difference could result from different ancestry of lakeshore and meadow populations rather than from adaptive evolution to habitat differences. The populations of snakes along the lakeshore resemble Great Basin garter snakes (Stebbins 1985: *T. e. vagrans*) in color and stripe patterns. In particular, they have olive, gray, or black dorsal backgrounds, which are often checkered, with lateral stripes of muted yellow, orange, olive, or beige. In contrast, snakes from meadow populations resemble other Sierra Nevada garter snakes (Stebbins 1985: *T. e. elegans*) in dorsal background (black) and stripe color (bright yellow). These population differences in color pattern are congenital and persist in laboratory bred hybrids (S. J. Arnold, unpubl. data). Therefore, an alternative explanation for these habitat-specific life histories is that these populations were colonized by two different subspecies. However, in a separate study examining the subspecific status of these Eagle Lake populations with cytochrome *b* DNA sequence data (Bronikowski and Arnold 2000), all Eagle Lake populations formed a monophyletic group (methods of Swofford et al. 1996) with other *T. e. elegans*. Thus, it does not appear that snakes inhabiting meadow sites have a separate evolutionary history from lakeshore snakes.

Migration and Selection

Given that genetic differentiation has occurred for growth rate among these populations of garter snakes, the role of migration in mitigating differential selection is important to consider. For example, King and Lawson (1995, 1997) and Lawson and King (1996) have shown that a small rate of migration among populations of Lake Erie water snakes (0.08–1.0% per generation) is sufficient to maintain color variation within populations that experience selection coefficients ranging from 0.1 to 0.2 for population-specific color pattern variants. In the 20 years that these Eagle Lake populations have been followed, 16 migration events (of over

1700 recaptures) were observed: 12 between meadow sites, two between lakeshore sites, one from a meadow to a lakeshore site, and one from a lakeshore to a meadow site. The majority of movement occurred between populations that share the same life history and the number of migrants between lakeshore and meadow sites was too small to estimate number of migrants (Nichols et al. 1993). Nevertheless, the actual number of migrants (Nm) and thus migration rate (m) is undoubtedly higher than observed. Therefore, selection must be acting against the force of migration to maintain the genetic differences between lakeshore and meadow snakes.

Competing Models for Growth Rate Variation

Arguments concerning the relationship between an individual's growth rate and its other life-history traits can be summarized by the maximization versus optimization paradigm for organisms with indeterminate growth (Case 1978; Stearns 1992; Charlesworth 1994; Bronikowski and Arnold 1999). The maximization hypothesis predicts that individuals that grow fast do not incur costs, but benefit through either earlier reproductive maturation, higher survival, or higher reproductive success than those that grow more slowly. Growth is limited by the environment and, in a common environment, individuals should grow at the same rate. Alternatively, under the optimization hypothesis, life-history traits, including an individual's growth rate, are genetically coupled such that an increase in growth involves fitness costs or trade-offs with other life-history components due to negative genetic correlations. The genetic basis of growth variation reported in this study supports the optimization hypothesis. Further evidence was observed in the field, where both a trade-off between growth and survival for all snakes and between growth and reproduction for meadow snakes also support the optimization hypothesis (Bronikowski and Arnold 1999). Thus, by coupling long-term observational field data with short-term experimentation, this study examined the genetic and environmental causes of naturally occurring growth rate variation.

ACKNOWLEDGMENTS

I thank S. Arnold, L. Arnold, F. Janzen, L. Houck, and S. Rollmann for help collecting pregnant snakes. J. Gladstone's years of captive snake care experience enabled me to conduct this experiment. Iowa State University allowed me the use of several controlled-environment chambers with the particular help of P. Lelonek. Several undergraduates helped take care of the snakes and record data: thanks to J. McRoberts, B. Wooldridge, L. Bush, and L. Harmon. H. Stern provided the SAS code to calculate selection coefficients. Previous versions of the manuscript benefited from comments by S. Arnold (SJA), B. Charlesworth (BC), S. Hackett, F. Janzen, J. Voight, and M. Wade. This research was supported in part by a grant to S. Arnold from the National Science Foundation (BSR-9119588); a National Science Foundation Doctoral Dissertation Improvement Grant to AMB, SJA, and BC (DEB-9520694), a Sigma Xi research grant, a grant from the Hinds Fund of the University of Chicago, and a Howard Hughes Medical Institute Predoctoral Fellowship in mathematical biology to AMB.

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Corresponding Editor: E. Brodie III