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THE EVOLUTIONARY ECOLOGY OF LIFE HISTORY VARIATION IN THE GARTER SNAKE *THAMNOPHIS ELEGANS*

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Abstract. The purpose of this study was to document the extent of variation in individual growth rates and its fitness consequences among several populations of an indeterminate grower, the western terrestrial garter snake *Thamnophis elegans*. Twenty years of mark–recapture data and six years of laboratory breeding data provided evidence of large differences among six populations in individual growth rates and subsequent reproductive maturation, fecundity, and survival. Weather, diet composition, and prey availability were examined for their effects on individual growth. Two ecotypes were revealed whose distribution coincided with differences in prey availability. Individuals from populations that had continuous access to prey and water across years exhibited fast growth, early maturation, high fecundity, and low adult survival. In contrast, individuals from populations that experienced variable prey availability exhibited slow growth, late maturation, low fecundity, and high adult survival. This growth rate variation was examined in the context of two competing explanations: the maximization and optimization hypotheses. Food availability may be a primary limiting factor to growth and subsequent life history traits, which is consistent with the maximization hypothesis. However, negative phenotypic correlations between growth and survival and between growth and reproduction may indicate an underlying negative genetic correlation, consistent with the trade-off hypothesis. Field studies such as this one are useful for documenting the patterns of life history variation that occur in nature, identifying possible causes of such variation, and generating testable hypotheses for controlled experiments.

Key words: fecundity; garter snake; growth, maximized vs. optimized; growth rate, individual; life history variation, spatial; migration; phenotypic plasticity; reproductive maturation; survival; *Thamnophis elegans*.

INTRODUCTION

In the study of life history evolution, a long-debated question is how individual growth rates affect the life histories of long-lived organisms (Case 1978, Arendt 1997). Understanding this relationship is particularly important for organisms with continuous growth over their life-span (Roff 1992: Chapters 6 and 7, Stearns 1992: Chapter 6, Charlesworth 1994: Chapter 5). Two competing hypotheses have been put forth (Ricklefs 1969, Case 1978, Charlesworth 1990, Shine 1992, Stearns 1992). The maximization hypothesis identifies the environment as the limiting factor for growth and fitness, rather than inherent organismal constraints. In increasing populations, this hypothesis predicts that individuals who grow fast benefit through increased fitness as a consequence of early reproductive maturation, increased longevity, or a positive correlation between

body size and reproductive output (e.g., size of neonates, survivorship of neonates, or litter size). Limits to this fitness premium are set by the environment (e.g., food availability, temperature). In contrast, the optimization or trade-off hypothesis views growth as one of a suite of genetically coupled fitness traits that have coevolved. Due to negative genetic correlations, higher growth rates are expected to be costly because of the channeling of energy into growth (e.g., decreased longevity, delayed reproductive maturation, or maturity at a smaller size).

To test between these two hypotheses for long-lived organisms, long-term data on multiple populations must be collected (Sibly 1996). This is because temporal and/or spatial intraspecific variation in life histories has been shown to be widespread (Seigel and Fitch 1985, Gibbons 1990, Brown 1991, Frazer et al. 1993, Janzen 1993, Tinkle et al. 1993, Bernardo 1994, Congdon et al. 1994, Baron et al. 1996, Plummer 1997). In particular, the study of multiple populations of a species reveals the spatial scale over which life history traits are variable, i.e., the degree of potential plasticity of these traits. The knowledge of whether life histories are constant or whether they change as a function of geography is key to understanding the benefits and costs associated with individual traits.

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TABLE 1. Study site characteristics and sample sizes.

Population	Number	Elevation (m)	Habitat	Years studied	Total no. animals marked	No. animals recaptured among years	No. wild-bred litters
Main sites							
L1	19	1555	Lakeshore	1980–1987, 1994–1997	1112	169	29
L2	1	1555	Lakeshore	1978–1988, 1992, 1994–1997	1143	487	130
M1	22	1630	Meadow	1979–1989, 1992, 1994–1997	1944	659	46
M2	20	1910	Meadow	1980–1988, 1994–1997	757	99	37
M3	2	2055	Meadow	1978–1989, 1993–1997	1000	300	54
Additional sites							
L3	11	1555	Lakeshore	1979–1980, 1982–1988, 1995–1996	684	26	98
M4	10	1695	Meadow	1979–1981, 1983–1988, 1994–1996	239	29	25
Total					6879	1769	419

Notes: Population number is from Kephart (1982). Years studied are years that effort was expended recapturing animals.

We use the framework of maximization vs. optimization to examine spatial variation in individual growth rates, and subsequent life history traits. We present 20 years of data for multiple populations of the western terrestrial garter snake *Thamnophis elegans*, a long-lived species with indeterminate growth. These snakes often continue growing over their reproductive lifespan and exhibit considerable intraspecific variation in the relationship between growth rate, reproductive maturation, and reproductive output (Case 1978, Seigel and Ford 1987, Rossman et al. 1996). From a previous report, female *T. elegans* in the study area of northeastern California mature at ~400 mm snout-to-vent length, and larger females often have larger litters than smaller mature females (Kephart 1981). Thus, in the maximization vs. optimization context, if early maturation did not result in decreased longevity or decreased reproductive output, then large fitness gains would exist for individuals that matured at a younger age (i.e., that attained 400 mm earlier). However, if these fast-growing females incurred a cost of decreased fecundity or longevity, early maturation would not necessarily be advantageous.

We report the consequences of spatial variation in individual growth rates for age of maturity, survival, and reproduction with field and laboratory data. We examine key predictions of the maximization and optimization hypotheses that are testable with these data. We then ask whether variation in precipitation and corresponding food availability can explain the documented spatial variation in life history traits. We end by using these field and laboratory data sets to explore the issues of the optimal age for maturation and the degree of plasticity of life histories.

METHODS

Study sites

Our study populations were located near Eagle Lake in Lassen County, California. These populations have been the subject of numerous reports on snake diets,

thermal ecology, and the evolution of behavior and morphology (Arnold 1981a–c, 1988, 1992, Kephart 1981, 1982, Kephart and Arnold 1982, Huey et al. 1989, Kelly et al. 1997). We monitored five main populations, separated by 5–15 km, during most summers from 1978–1993 and all summers from 1994–1997 (see “Years studied” in Table 1). In some years, we monitored two additional populations on an ad hoc basis, and we include data on these populations where relevant. Three of the five main populations occurred in mountain meadow habitats and two in lower elevation lakeshore habitats (Table 1). Mountain meadow habitats were characterized by variable prey and water availability, and cool temperatures (Table 2). In contrast, lakeshore habitats had continuous availability of water and prey, and air temperatures that averaged 5°–10°C warmer than meadows (C. R. Peterson, unpublished data). In addition, diet composition varied between the two habitat types. Snakes in meadow habitats fed primarily on anuran tadpoles and metamorphs (*Hyla regilla*, *Bufo boreas*), whereas snakes in lakeshore habitats primarily ate fish (Table 2). The average adult female garter snake had the following annual cycle in both habitats: emerge from hibernation and mate after the spring thaw (approximately mid-April), forage until mid-August, give birth on a single day between mid-August and the end of September, and hibernate from October to March.

Mark–recapture data

We processed captured snakes in one of two ways. All nonpregnant snakes were forced to regurgitate (as in Carpenter 1952), sexed, weighed (nearest g), measured (snout-to-vent length [SVL]), and marked with a unique identifier. In years prior to 1994, the unique identifier was a numerical pattern clipped into the ventral scales, which when healed, left a readable scar. After 1993, we injected a transponder (Avid Corporation, Norco, California) into the body cavity (Camper and Dixon 1988, Keck 1994). These transponders had

TABLE 2. Environmental and dietary differences between lakeshore and meadow habitats.

Variable	Lakeshore	Meadow
Presence of standing water	constant	varies annually with precipitation
Daytime summer temperature†	20–34°C	5–10°C cooler than at lakeshore
Prey type‡		
Primary	fish	anuran
Secondary	leech	leech
Tertiary	anuran	fish
Availability of primary prey	constant	varies annually with presence of standing water
Empty stomachs (%)§	constant 60%	either 50 or 90%

† Air temperature taken at approximately ground level (C. R. Peterson and S. Arnold, *unpublished data*).

‡ Fish, *Rhinichthys osculus*; leech, *Erpobdella punctata*; anuran, *Bufo boreas*, *Hyla regilla* (from Kephart [1982]).

§ The percentage of empty stomachs for meadow snakes varies directly with the availability of their primary prey.

a unique nine digit number identifying the snake. Pregnant females were not forced to regurgitate, but were instead maintained in the laboratory until parturition and then were uniquely marked and released in the following spring, or were kept in captivity for breeding studies. Total numbers of snakes marked at each site, as well as among-year recaptures (for survival estimates) and number of litters (for fecundity estimates) are reported in Table 1.

Growth

We calculated growth for each recaptured snake as the change in snout-to-vent length (SVL) between captures. We used two covariates in the analysis of growth: number of growth days in the interval between captures and average SVL during the interval. Number of growth days was calculated as the number of growth season days (15 April–15 August) that had elapsed since the animal was last measured. For example, a snake caught and marked on 1 September and recaptured on 1 May of the following year would have a covariate of 16 growth days, as would a snake caught on 1 June and again on 17 June in the same year. Average SVL during the growth interval was used as a covariate because as snakes get larger, instantaneous growth rate decreases (Andrews 1982).

We computed von Bertalanffy (1957) growth curves for the females of each population by regressing change in SVL on average SVL for snakes captured in consecutive years (Kephart 1981, Andrews 1982). The x -intercept of the regression line is the asymptotic maximum length (L_{\max}), and the slope of the regression line (β) is the rate of closure on the asymptotic length. Curves were generated with L_0 = average size at birth:

$$L_{t+1} = L_t + \beta(L_{\max} - L_t). \quad (1)$$

Curves were compared for significant heterogeneity by comparing the regression slopes (growth rates) and x -intercepts (asymptotic lengths).

Female reproductive maturation

We used two lines of evidence to deduce the age of reproductive maturation for females. First, a subset of recaptured females had been marked as newborns.

These known-age individuals were used to correlate growth rates and body size with age. Then, we established a minimum size for reproduction from the pregnant-female size data, and assigned a population-specific age from the known-age data to this threshold size. Second, some newborns were not released, but were maintained in the laboratory for breeding experiments. We used these data to estimate a size-independent minimum age of reproduction (see *Discussion*).

Survival

The calculation of survival rates from mark–recapture data is a complex process that involves choosing an underlying population model, testing for goodness-of-fit to the underlying model, and calculating simultaneously recapture and survival probabilities (Burnham et al. 1987, Pollock et al. 1990, Lebreton et al. 1992). For this report, we confined our analyses to annual survival during two stages: the adult stage (“adult survival”) and the juvenile-to-adult transition (“juvenile survival”). Rates were pooled over time for each population.

We chose the Cormack-Jolly-Seber (CJS) underlying population model (Cormack 1964, Jolly 1965, Seber 1965) because this model allows births, deaths, and migration. (Migration is reflected in decreased recapture probabilities.) We used program RELEASE (Burnham et al. 1987) in the package CR (Praxème, Incorporated, Montpellier, France) to test the goodness-of-fit of the snake mark–recapture data to the assumptions of the CJS model (specifically, for the computation of Tests 2 and 3 from Burnham et al. 1987). Test 2 tests the null hypothesis that the survival and recapture probabilities for a group of animals are specific to sampling occasion and sampling site. Behavioral differences between marked and unmarked animals would lead to the rejection of this hypothesis. Test 3 tests the null hypothesis that the survival and recapture probabilities for a group of animals are independent of their capture histories (Burnham et al. 1987).

We estimated population-specific annual survival rates using program MARK⁵ (G. C. White, Colorado

⁵ URL: (<http://www.cnr.colostate.edu/~gwhite/mark/mark.htm>)

TABLE 3. Analysis of covariance of growth measured as change in snout-to-vent (SVL) length (mm).

Source	df	Type III ms	F	P
AvgSVL	1	274 591	188.1	<0.0001
Growth Days	1	1 764 888	1209.0	<0.0001
Sex	1	2619	1.8	0.18
Population	4	10 712	7.3	<0.0001
Population × AvgSVL	4	10 991	7.5	<0.0001
Population × Growth Days	4	188 900	129.4	<0.0001
Population × Sex	4	1678	1.1	0.33
Sex × AvgSVL	1	6139	4.2	0.0404
Sex × Growth Days	1	35 315	24.2	<0.0001
Population × Sex × AvgSVL	4	1831	1.2	0.29
Population × Sex × Growth Days	4	21 610	14.8	<0.0001
Error	1684	1460		

Notes: The main effects are sex and population; the covariates are average length during the growth interval (AvgSVL) and number of elapsed days during growth seasons (Growth Days). Type III mean squares correct for the effects of other factors in the statistical model.

State University, Fort Collins, unpublished program). MARK relies on Fisher's likelihood principle, and uses profile likelihood methods for the computation of confidence intervals. Differences in survival rates among populations were determined using 95% confidence intervals calculated in MARK.

Fecundity

We shipped pregnant snakes to the University of Chicago to determine the number and size of newborn snakes. We maintained these pregnant females in individual glass tanks (60 × 30 × 30 cm) with corncob bedding ~1 mo prior to parturition. Dams were provided with a shelter, a light/dark cycle that matched their natural photoperiod, continuous availability of water, and twice a week ad lib feedings of live minnows. One end of each tank was placed on a heating element, producing a tank temperature gradient of 26°–32°C. During the night, the heating elements were turned off and the tank temperature was kept at 21°C.

On the day following birth, we counted, sexed, and weighed the neonates. All stillborns and undeveloped yolk masses were also weighed. In this report, we used only live-and stillborn neonates to compute average offspring mass and litter size. Some authors have suggested including undeveloped yolks in these estimates (e.g., Farr and Gregory 1991, Gregory et al. 1992). However, in our study, the inclusion of yolks would result in the underestimation of average offspring mass. Population differences in litter size and average offspring mass were evaluated with analysis of covariance, with dam size (SVL) as a covariate, litter-within-population as a random effect, and source population as a fixed effect.

From 1982 through 1987, 32 wild-captured pregnant females were bred repeatedly in the laboratory. Litters from laboratory-bred mothers were not included in the above analyses of fecundity in nature. Instead, we compared a female's wild-bred litter with her first laboratory-bred litter, and we compared her repeated laboratory litters. For females that had more than one lab-

oratory litter, estimates of repeatability (Falconer 1989) for litter size and average offspring mass were calculated. Females were bred in April of each year with a new male and produced from two to four laboratory-bred litters.

Meteorological data and anuran breeding

We obtained daily records of precipitation and minimum/maximum temperature at Eagle Lake for the entire study period from the California Department of Water Resources. From these daily records, we computed annual precipitation, average temperature, and annual precipitation evenness (Shannon diversity index, Magurran 1988, e.g., Bronikowski and Webb 1996). In addition, we noted the presence or absence of tadpoles each year at the meadow sites. We examined these data to see if patterns could be found between the meteorological variables and anuran breeding.

RESULTS

Growth

Both average SVL and number of growth days had significant effects on growth (Table 3). In addition, several interactions were significant. Of interest to this study, the interaction between population and average body size indicates that the rate of growth decline with increasing body size varied among populations. Population-specific von Bertalanffy growth curves help to visualize this interaction (Fig. 1). The slopes of the regression of growth on average SVL were significantly heterogeneous among populations (Table 4). Individuals from populations L1 and L2 grew faster than those from M1 and M3. Individuals from population M2 grew the slowest. In addition, the asymptotic adult sizes (x -intercepts) were different between the two habitat types (Table 4). These different growth rates and asymptotes produced curves for the two lakeshore populations that were significantly different from those for the meadow populations (Fig. 1).

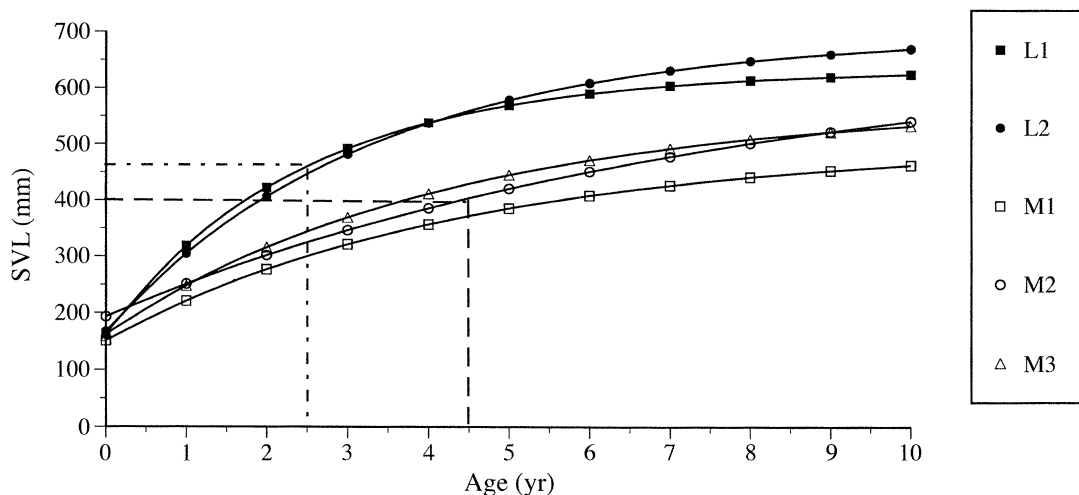


FIG. 1. Von Bertalanffy growth curves for each of the five main study populations. SVL is snout-to-vent length in mm. See the *Discussion* for the relevance of the dashed lines. The curves were generated with the Bertalanffy growth equation, which uses the x -intercept and slope from a regression of change-in-length on average length for each population (Table 4).

Female reproductive maturation

Of 394 wild-caught pregnant females from lakeshore and meadow populations (including population L3), none were <400 mm in length and 40 g in mass. Using the subset of known-age recaptures, lakeshore females were estimated to attain this size during their second summer. Meadow females were more variable in the age at which they attained this threshold size: from their fourth through sixth summer (plotted with dashed lines in Fig. 1). Thus, the average lakeshore female would have its first litter the following summer at 3 yr of age, and an average meadow female would first reproduce from 5 to 7 yr of age. Furthermore, when laboratory-reared females attained this minimum size by the end of their 1st yr of life, they still did not reproduce until they were 3 yr of age. This suggests a more accurate reproduction threshold definition to be 400 mm/40 g and at least 3 yr of age.

Survival

The Cormack-Jolly-Seber (CJS) model was never rejected in goodness-of-fit tests (tests 2 and 3 of Burnham et al. 1987). (For example, for population L2 adults, test 3 $\chi^2 = 16.24$, $df = 16$, $P = 0.44$, test 2 $\chi^2 = 12.03$, $df = 10$, $P = 0.28$.) In situations when data were too sparse for overall goodness-of-fit testing, the compo-

TABLE 4. Regression slopes and x -intercepts of growth on average SVL (see Fig. 1).

Population	Slope \pm SE	x -intercept (mm)
L1	0.33 \pm 0.04	632
L2	0.30 \pm 0.03	690
M3	0.21 \pm 0.03	550
M1	0.20 \pm 0.01	503
M2	0.12 \pm 0.04	559

nents of test 2 and test 3 were examined for rejection of the CJS model (as in Lebreton et al. 1992). Using the above criteria, the CJS model was not rejected when data were sufficient for computation of overall tests (populations L2 and M1), nor was it rejected when data were only sufficient to calculate certain components of the overall test statistics (populations L1, M2, and M3). Thus, survival rates could be computed legitimately from the CJS model.

For both adults and juveniles, annual survival rates did not differ between males and females. Adults from the two lakeshore populations, L1 and L2, had lower probabilities of year-to-year survival than those from the three meadow populations (Table 5). Within the lakeshore habitat type, population L1 adults had significantly lower annual survival than those from L2. Adult survival was equivalent in all three meadow sites. In all populations, adults had higher survival rates than juveniles. Like adults, juveniles from the two lakeshore sites had lower annual survival than juveniles from the three meadow populations (Table 5).

TABLE 5. The 95% confidence intervals for adult and juvenile annual rates of survival.

Population	95% CI	
	Adult	Juvenile
L1	0.34, 0.40	0.14, 0.21
L2	0.55, 0.57	0.19, 0.19
M3	0.71, 0.76	0.27, 0.50
M1	0.74, 0.78	0.23, 0.33
M2	0.76, 0.86	0.22, 0.44

Notes: Rates were estimated using the among year recapture samples shown in Table 1 and are pooled for males and females. Juvenile rates are for the juvenile-to-adult transition. The lines separate populations that are significantly different in individual per annum survival rates.

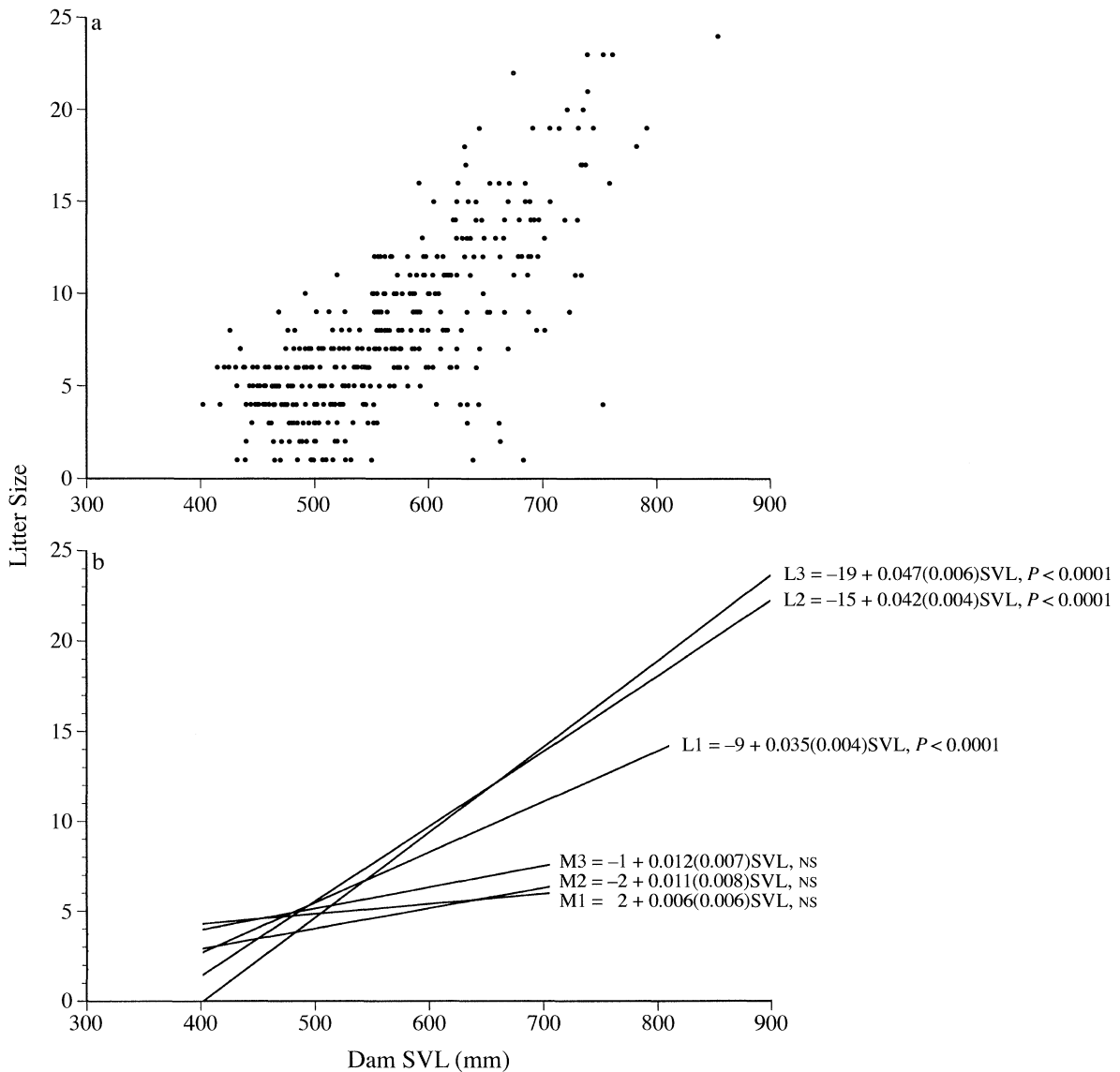


FIG. 2. Litter size and maternal body size. (a) Pooled scatter plot of litter size by maternal size (dam SVL). Dam SVL is snout-to-vent length (mm). Data are pooled for six populations. (b) Regression of litter size on maternal body size (dam SVL) by population. The numbers in parentheses are the standard errors associated with each regression slope.

Fecundity

Larger females tended to produce larger litters (Fig. 2a), but this relationship varied among populations (significant interaction in Table 6). Populations L1, L2, and L3 had significantly steeper slopes than the three meadow populations for the regression of litter size on dam SVL (Fig. 2b). Thus, in lakeshore females, litter size increased with body size faster than in meadow females. The regression slopes for meadow females were not significantly different than zero, which indicates that body size was not a good predictor of litter size for meadow females.

Larger females tended to produce larger offspring, but populations did not differ in this relationship (Table

6). Furthermore, there was no evidence for a trade-off between litter size and offspring size in the combined-years data set. When dam size was held constant, the partial correlation coefficients for litter size and offspring size ranged from -0.1 to $+0.1$, but were never statistically significant.

The question of whether size or age affects fecundity could also be addressed. An analysis of known-age dams indicated that age per se was not a consistent predictor of reproductive effort. Dam age predicted litter size for meadow, but not lakeshore females (Pearson correlation: meadow, $r = 0.710$, $n = 9$, $P = 0.03$; lakeshore, $r = 0.002$, $n = 27$, $P = 0.98$). However, dam age did not predict average offspring mass in either

TABLE 6. Analysis of covariance of litter size and average offspring mass.

Source	df	Litter size			Average offspring mass (g)		
		Type III MS	F	P	Type III MS	F	P
Dam SVL	1	279.0	33.6	0.0001	5.32	17.2	0.0001
Population	5	37.3	4.5	0.0006	0.03	0.1	0.99
Population × Dam SVL	5	41.6	5.0	0.0002	0.06	0.1	0.96
Error	382	8.3			0.31		

Notes: A female's litter consisted of live + stillborn snakes but excluded undeveloped yolks. The main effect is population (L1, L2, L3, M1, M2, M3). The covariate is the mother's snout-to-vent length one day post-birth (Dam SVL). Type III mean squares correct for the effects of other factors in the statistical model.

habitat (meadow, $r = -0.280$, $P = 0.46$; lakeshore, $r = 0.230$, $P = 0.24$). These results suggest that age and body size are decoupled in meadow populations, i.e., old females were not necessarily larger than young adult females. Thus, one component of reproductive effort (litter size) increased with age rather than body size for meadow females.

From 1982 through 1987, 32 pregnant wild-bred females were captured and were bred in the laboratory the following year. These females produced smaller litters of larger young in their first laboratory-bred litter relative to their wild-bred litter of the previous year (litter size, $F = 14.35_{1,575}$, $P = 0.0004$; average offspring mass, $F = 6.26_{1,53}$, $P = 0.0155$). Dam growth was accounted for with body size covariates and did not explain the change. There was no change in overall litter mass (after correcting for dam growth), but rather a female's allocation to number vs. size of offspring was plastic, regardless of source population. Average corrected litter size decreased from 8.62 to 5.23 offspring, and average offspring mass increased from 3.11 to 3.80 g. Of the 32 dams, 13 produced at least one additional laboratory litter in a later year. In these subsequent laboratory breedings, there was low repeatability for both litter size and offspring mass (intraclass correlations calculated from Table 7 and harmonic mean of 2.38; litter size, $r = 0.20$, average offspring mass, $r = 0.43$).

Meteorological data and anuran breeding

Total annual precipitation was the only weather variable that corresponded to the presence of breeding anu-

TABLE 7. Analysis of variance for the estimation of repeatability of litter size and average offspring mass within dams.

Source	df	Litter size			Average offspring mass (g)		
		Type III MS	F	P	Type III MS	F	P
Dam	12	13.80	1.61	0.17	1.14	2.80	0.02
Error	18	8.55			0.41		

Notes: Both litter size and average offspring mass include live and stillborn neonates but exclude undeveloped yolks. The mother's size (SVL) was not significant and therefore was not separated from the error mean square.

rans. At least 500 mm precipitation per year was required for anurans to breed at meadow sites (based on the direct observation of standing water and anuran breeding in these years). During this study, 10 of the 20 yr had precipitation >500 mm. Thus, the main food item for meadow snakes was only available in 50% of the studied years.

DISCUSSION

Life history ecotypes: growth, maturation, survival, and fecundity

The results of this study suggest two life history ecotypes for *T. elegans* in the Eagle Lake region. Snakes from the two lakeshore sites, L1 and L2, were characterized by fast growth, early maturation, large adult body size, increasing litter and offspring size with larger body size in females, and low annual adult survival. An additional lakeshore population, L3, was consistent with this lakeshore ecotype in terms of reproduction (Fig. 2) and average adult female body size (700 mm). In contrast, snakes from the meadow populations had slow growth, late maturation, small adult body size, little reproductive premium to larger body size in females, and high annual adult survival.

These two ecotypes might reflect environmental differences (maximization hypothesis) or genetic differences (optimization hypothesis) between lakeshore and meadow sites. Two findings provide evidence for the optimization hypothesis. First, lakeshore populations characterized by individuals that grew fast and continued growing over their life-spans, were also characterized by low adult survival. This apparent cost is consistent with the optimization hypothesis, suggesting a trade-off between growth and survival. Second, meadow populations characterized by individuals that grew slow and matured late, were also characterized by little or no growth after maturation. In meadow populations, years with plentiful food were followed by years with a high incidence of pregnant snakes (>70% of adult females were pregnant vs. 0% in years following low-food summers), none of whom had invested in growth. This observation that meadow adult females reproduced rather than grew is consistent with a trade-off between growth and reproduction.

The existence of an anomalous meadow population

allows a further test of the maximize/optimize question. Population M4 occupied a typical meadow with a small creek running through it in wet years (see Table 1). However, during road construction just prior to this study, a culvert was built that restricted the movement of fish (*Rhinichthys osculus*) in the stream. As a consequence, fish became an abundant and reliable source of food throughout the summers. Thus, these meadow snakes were recently introduced to lakeshore food conditions (see Table 2). Their life history attributes appear to reflect their current food supply rather than their meadow ancestry. During this study period, individuals from M4 exhibited mean growth (corrected for covariates) of 50 ± 2 mm/yr and a mean litter size of 7.8 ± 0.6 individuals (regression of litter size on dam SVL: $-20 + 0.05(\text{SVL})$, $P < 0.0001$). These values group M4 with lakeshore populations rather than with meadow populations (see Fig. 2). Thus, the lakeshore vs. meadow dichotomy of life histories might be explained by differences in food type or availability.

Further examination of these dietary differences between habitats may help to clarify the roles of prey type and prey availability in affecting the life histories of these snakes. During the time period of this study, lakeshore snakes ate fish almost exclusively. In all years, the frequency of empty stomachs for lakeshore snakes averaged 60%. At meadow sites, in years that anurans bred (i.e., precipitation > 500 mm), meadow snakes had lower frequencies of empty stomachs (50%) than lakeshore snakes. However, when anurans did not breed at meadow sites, the frequency of empty stomachs in meadow snakes was $>90\%$. During these low-food years, the small percentage of stomachs with prey items contained fish or leeches in M1 and leeches in M3. Snakes from M2 were inactive in years when anurans did not breed; the few snakes that were observed were detected in damp cracks in the drying meadow floor and had empty stomachs. Thus, the presence of continuously available prey across years for lakeshore snakes (judged by the invariant frequency of empty stomachs) coincided with the fast growth ecotype. In contrast, the variable availability of prey across years for meadow snakes coincided with the slow growth ecotype. Other studies that have examined environmental influences on the growth and life histories of snakes have also provided evidence that food enhancement, either direct or indirect through longer foraging days or growth seasons, can result in faster growth, larger adult sizes, larger maturation sizes, or higher fecundity (reviewed in Parker and Plummer 1987, see also Ford and Seigel 1989a, 1994a, b, Seigel and Ford 1991, Beaupré 1995, 1996, Lindell 1997, Luiselli et al. 1997, Plummer 1997).

The observation that food quality and quantity can cause ectotherms to mature earlier at a larger size has received much recent attention (Berrigan and Charnov 1994, Ernsting 1995, Perrin 1995, Atkinson and Sibly 1996). In particular, discussion has focused on the di-

chotomy between maturing earlier at *larger* sizes with food enhancement vs. maturing earlier at *smaller* sizes with warmer temperature. The result that lakeshore snakes mature both earlier and larger than meadow snakes suggests that food enhancement has occurred relative to meadow snakes and that temperature differences (Table 2) may not be as important.

Thus, both genetic and environmental effects may be important in the different life histories of lakeshore and meadow snakes. The apparent trade-offs between survival and growth, and reproduction and growth are consistent with the optimization hypothesis. In addition, the examination of prey availability, particularly in the anomalous meadow population, lends support to the maximization hypothesis. A laboratory common-garden growth experiment would be required to truly test whether genetic differences exist between the two ecotypes for growth (Bronikowski, 1997). Field observations, such as those in this report, can suggest which environmental variables to manipulate in such a laboratory experiment. In this case, prey type and availability appear to be important.

Reproductive maturation

Whether resulting from proximate ecological causes or genetic differences among populations, the growth rate differences between lakeshore and meadow snakes produced two different ages of reproductive maturation (α). The average lakeshore snake could reproduce at 3 yr of age, while the average meadow snake could reproduce as soon as it attained 400 mm SVL (5–7 yr of age). The presence of this twofold maturation threshold (minimum age and mass) probably indicates complex relationships among life history traits that together determine first reproduction (Bernardo 1993).

Competing models for the optimal age of first reproduction can be divided into two classes. The first model assumes that a conflict exists between growth and reproduction, and that reproductive success increases with body size. Under this model, the optimal age for beginning reproduction (α) depends on the mortality probabilities around the potential ages of maturation (i.e., 3–7 yr of age in these snakes) and on the timing of growth completion (Charlesworth 1994). For example, early growth completion combined with high mortality during these critical ages would result in the evolution of earlier maturation. The alternate model assumes that adult mortality is constant across populations. Then, α depends on the reproductive value at age α (i.e., the present value of future offspring, Fisher 1958), and the probability of surviving to α . This results in a trade-off between maximizing both post- α reproduction and pre- α survival (Charnov 1990, Charnov and Berrigan 1991a, b). How growth completion and mortality related to reproduction is considered below.

Concerning growth completion, meadow snakes reached adult sizes (>400 mm) much later than lake-

shore snakes, and their asymptotic adult body sizes were less than that of lakeshore snakes (Fig. 1). Data on the size distributions of reproductive females suggest that on average, meadow snakes reproduced at smaller sizes than lakeshore snakes as a result of their late growth completion. The body size range of wild-captured pregnant females from lakeshore populations was 460–850 mm (mean, 600 mm). Pregnant females from meadow populations were significantly smaller (range, excluding M4, 400–634 mm; mean, 491 mm; $F = 254_{1,392}$, $P = 0.0001$). (Pregnant females from M4, the lakeshore-like meadow population were similar to lakeshore snakes, mean, 566 mm; range, 463–640 mm.) The fact that females from meadow sites reproduced at smaller sizes suggests that their late maturation results from a trade-off between growth and reproduction. After their first reproduction, their subsequent reproductive bouts entail a cost to future growth, despite the possibility of increased fecundity with larger body size (see also Brown and Weatherhead 1997).

Both adult and juvenile mortality differed among populations ($1 - \text{Pr}[\text{survive}]$ from Table 5). At all sites, the annual mortality rates of juveniles were higher than those for adults. The annual mortality probability for juveniles was ~82% for lakeshore juveniles and 67% for meadow juveniles (Table 5). This pattern of earlier growth completion and higher juvenile mortality at lakeshore sites suggests selection for earlier maturation in lakeshore sites relative to meadow sites (Charlesworth 1994), a pattern that is realized. Thus, this system appears to support the first model for reproductive maturation.

Studies that have attempted to dissect the causes underlying intraspecific variation in maturation have found many different explanations. Bernardo (1994) performed a common garden study on multiple populations of the salamander *Desmognathus ochrophaeus* and found that food enhancement increased growth rates, but unlike this study, the age of maturation was fixed. Ford and Seigel (1994a) found that neither age nor size of first reproduction was fixed in the oviparous corn snake *Elaphe guttata*: food enhancement resulted in either earlier maturation, or larger size at maturation. Gregory and Larsen (1993, 1996) found an east-west cline in maturation size in Canadian *T. sirtalis*, but no environmental variable correlated with this trend, including food availability, temperature, elevation, or subspecies. Perhaps the most insightful studies have been done on the guppy *Poecilia reticulata*. Like this study, Reznick (1990) found that fast growth resulted in larger maturation sizes. Further reports (Reznick et al. 1992, 1996) showed that by experimentally increasing mortality rates around the potential ages of reproduction, earlier maturation evolved.

Phenotypic plasticity of reproductive traits

Published reports on snakes have consistently shown increasing litter sizes with larger body size (reviewed

in Seigel and Ford 1987; see also Brodie and Ducey 1989, Ford and Seigel 1989a, Plummer 1992, King 1993, Baron et al. 1996, Luiselli et al. 1996). In this study, larger lakeshore females had larger litters, but this was not the case for meadow females for whom age was a better predictor of litter size. Other studies that have separated age from size effects found that body size, not age predicted litter size (Madsen and Shine 1992, Olsson and Shine 1996). Furthermore, in this study, for all populations, larger females had larger offspring. As a result, lakeshore females had larger total litter mass per unit body size than did meadow snakes.

Much empirical work has focused on documenting trade-offs between litter size and offspring size (citations in Roff 1992: Chapter 10, Stearns 1992: Chapter 7). Although snakes would seem to be ideal organisms to test for this trade-off because of their large litters, the literature is equivocal. Some reports have found a trade-off (Ford and Seigel 1989b, Madsen and Shine 1992, 1996, King 1993), but others have not (reviewed in Ford and Seigel 1989b, see also Plummer 1992). In this study, with substantial sample sizes, there was no evidence for a trade-off between litter size and offspring mass when maternal size was held constant through partial correlation analysis. However, the trade-off between number and size of offspring can vary with resources (Ford and Seigel 1989b), and resources varied among years in this study. Thus, the lack of support for a trade-off may simply reflect changing resources across years.

Despite the lack of a negative correlation between litter size and offspring mass in this study, the laboratory breeding experiment revealed that the relationship between these two variables was not fixed. All females, regardless of source population, exhibited plasticity in the investment for both number and size of offspring. All had smaller litters of larger young. This plasticity was documented in the comparison of wild- vs. lab-bred litters and in the analysis of repeated laboratory breedings. King (1993) also found plasticity in reproductive traits for laboratory-bred female brown snakes (*Storeria dekayi*). These females had smaller young relative to their previous wild-bred litters.

Plasticity of reproductive investment arising from food or temperature effects can be considered a physiological constraint, uninteresting from an adaptive point of view (Gotthard and Nylin 1995, Via et al. 1995). However, plasticity in allocation to number and/or size of offspring could be adaptive in the sense that it may lead to increased fitness under varying environments. Lab-bred females maintained a total litter mass consistent with predictions based on source population and body size. But the components of total litter mass (litter size and average offspring mass) were different from predictions based on dam growth and previous wild-bred litter. Thus, whether the laboratory is viewed as beneficial, in terms of food availability and

protection from predators, or detrimental, in terms of the stress of handling and confinement, the laboratory acted as a stimulus for the plasticity response. Litter size was decreased and offspring size was increased relative to natural litters. In subsequent lab-bred litters, the repeatability measurement for litter size was $r = 0.20$, while that for offspring size was $r = 0.43$. Thus, at least 64% of the variation in litter size and at least 32% of the variation in average offspring size was due to environmental effects. Ongoing demographic perturbation analyses of our populations will address the question of whether this plasticity is adaptive.

Concluding remarks

This study provided evidence that suites of life history traits (growth, maturation, survival, and fecundity) can differ among local populations. If these differences represent genetic variation among populations, then migration is relevant to the question of whether the ecotypes are currently maintained by selection. During this study, 12 snakes were observed to migrate between meadow sites, two among lakeshore sites, one from a meadow to a lakeshore site, and one from a lakeshore to a meadow site. The majority of this movement occurred between meadow sites that share the same life history. The number of migrants between lakeshore and meadow sites is negligible for estimating certain population parameters (Nichols et al. 1993). Nonetheless, the number of migrants (N_m), and thus migration rates (m) are probably higher than those observed. A better understanding of the role of genetic contributions to growth rate variation between ecotypes through laboratory experimentation will help to elucidate the importance of migration in this system.

A number of observations suggested that variation in individual growth rates was the key to understanding the different life history ecotypes. Several possible causes of this growth rate variation were highlighted. Food and temperature differences correlated with the two ecotypes, which supported the maximization hypothesis. However, the negative phenotypic correlations between survival and growth, and between reproduction and growth suggest that genetic effects on growth, either historical or current, may exist, and are the subjects of laboratory experiments.

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