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THE INFLUENCE OF FOOD AVAILABILITY ON LIFE-HISTORY TRAJECTORIES

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Ecology

by
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Abstract

Variation in environments, particularly in food availability, can strongly influence life-history traits, and these effects may be immediate or delayed. In order to maximize fitness, organisms must differentially allocate energy among multiple life-history traits such as growth, survival and reproduction, and decisions regarding trade-offs may differ between males and females. Body size is a fundamental component of an organism's life-history, and for indeterminately growing species, lifelong trade-offs may occur between increasing body size or nutrient storage, survival and reproduction. For most reptiles, little is known about actual demographic rates and life-history variation, despite geographically and taxonomically widespread declines in these species over recent decades. Using 17 years of capture-mark-recapture data, we investigate the relationship between demographic parameters and environmental variation to quantify patterns in life-history traits for multiple populations of garter snakes. We evaluated the effect of food availability on key traits including somatic growth, survival, reproduction and body condition, which ultimately drive population demography. We analyzed data on growth in snout-vent length (SVL) and body condition (measured as the residual of the regression of log-transformed mass on SVL) for two species: the western terrestrial garter snake, *Thamnophis elegans*, and the common garter snake, *Thamnophis sirtalis* from five sites surrounding Eagle Lake in Lassen County California. We found that the impact of food availability on structural growth and nutritional reserves is largely context dependent, and patterns of energy allocation may shift with resource availability. Crucially, we found that the influence of food availability early in life is a critical determinant of lifetime patterns of growth. For both *T. elegans* and *T. sirtalis*, individuals from nutritionally deficient early-life cohorts increased structural body size more rapidly than individuals from high nutrition cohorts when food was abundant later in life. The results of our study suggest that spatial and temporal variation in traits such as growth and body condition are a result of the complex integration of food availability throughout the lifetime of animals within wild populations. This study highlights the importance of assessing the long-term response in life-history traits to differing environmental conditions using multiple populations to ensure robust estimates for predicting future shifts in population demographic processes.

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Chapter 1: Direct and delayed effects of food availability on acquisition of nutrient reserves and structural growth in garter snakes

Abstract

In environments where conditions vary significantly from year-to-year, the rate of growth and maximum body size constitutes a link between resource acquisition and allocation. Additionally, nutritional conditions experienced during development or early life can have pronounced influence on lifetime patterns of growth, and thereby, significant impacts on reproductive success and survival. We analyzed 17 years of mark-recapture data for population from two ecotypes of the western terrestrial garter snake (*Thamnophis elegans*). Our objective was to determine how snake responses in growth rate and maximum body size to prey availability varied within and among populations. Ecotypes of *T. elegans* differ in key life-history traits, where fast-living lakeshore ecotype snakes reproduce younger, have larger litters, and experience lower survival than their slow-living mountain meadow counterparts. Using a novel Bayesian von Bertalanffy growth model to estimate temporal variation in structural growth rates and body condition index to assess variation in nutrient reserves, we found slow-growing meadow snakes exhibit more sensitivity to annual variation in prey availability than the faster growing lakeshore ecotype. Males reach smaller asymptotic sizes than females in both ecotypes, and both males and females grow at similar rates. The magnitude of the difference in size varies by population, suggesting an ecological effect on the expression of sexual size dimorphism. When early-life conditions were considered, our results indicate compensatory growth—accelerated growth following unfavorable conditions—which was most pronounced in the meadow ecotype. The lakeshore ecotype, because of its faster pace-of-life, is likely unable to achieve the same degree of compensatory growth because allocation of energy to reproduction is more constant. This study highlights how we can use spatial and temporal variability in the environment to predict population level responses in growth parameters of reptiles. Furthermore, our results indicate that slow growth and starvation endurance may improve an animals' ability to compensate for a poor start, which has important implications for individual and population level demographic processes in increasingly stochastic climactic conditions. In addition, the approach we use to estimate structural growth from mark-recapture data has the potential to provide important demographic and life-history insights for other indeterminately growing species.

Keywords: Cohort, condition, body size, growth, reptiles, von Bertalanffy

The magnitude and rate of growth in overall body size (i.e. somatic growth) is a fundamental component of an organism's life-history. The trajectory of an individual's growth will depend on variability in environmental conditions such as habitat quality, temperature and food abundance, particularly in ectotherms (Caley and Schwarzkopf 2004, Bjorndal et al. 2016, Muñoz et al. 2016). Organisms can modulate their growth rate to compensate for environmental variation, and early-life nutrition plays an important role in determining lifetime patterns of growth (Radder et al. 2007, Miller 2010). Dietary restriction early in life may result in growth that is

ontogenetically static, as in the ‘silver spoon’ effect, where early life sets a growth trajectory that is maintained later in life. Alternately, individuals may ‘catch-up’ if growth can be accelerated later in life to compensate for a poor start (Grafen 1988, Larsson et al. 1998, Radder et al. 2007). Growth rate plasticity can have important implications for not only growth and size, but also affect survival and fecundity (Van De Pol et al. 2006). Understanding growth is key to understanding population persistence and the consequences of environmental variation for individuals, populations and communities (Roff 1992, Fox and Kendall 2002, Caley and Schwarzkopf 2004, Bolnick et al. 2011).

Trait variation among individuals is common within natural populations, especially in labile traits like growth and body size (Ghalambor et al. 2007, Kinnison and Hairston 2007). Such plasticity can allow populations to cope with changing conditions, resulting in population-level shifts in mean trait values. Importantly, changes in individual fitness-related traits may precede changes in population level dynamics that lead to changes abundance (Germano and Bury 2009). Global climate change, habitat fragmentation, and habitat loss are driving forces behind the unprecedented rate of contemporary biodiversity decline (Sala et al. 2000, Barnosky et al. 2011). Accordingly, understanding spatial and temporal variation in traits like growth is a crucial element to predicting persistence of populations in a globally changing climate (Fahrig 2001, Fox and Kendall 2002, Ramos and González-Solís 2012). Understanding the evolution of growth-related life-history traits necessitates long-term data on temporal growth variation at the individual level and between the sexes in order to better understand population patterns. Long-lived iteroparous species with indeterminate growth, allowing for lifelong trade-offs between growth and other life-history traits. In addition, for many squamate reptiles, female reproductive success which scales with body size are ideal study organisms for appraising trade-offs between energy apportioned for growth—invested in future reproduction and survival, and energy devoted to storage, which buffers survival against starvation. The ability of organism to modulate their growth, either within-individuals of the same population or among individuals of populations in different locations is important for allowing organisms to cope with unfavorable and unpredictable environmental conditions (Nussey et al. 2007, Bolnick et al. 2011).

Body size, and therefore growth, has direct implications for an organism’s survival, longevity, reproductive capacity, and competitive ability (Calder 1984, Ferguson and Fox 1984, Reiss 1989). Differences in overall rate of growth among species and populations of the same species have been associated with resource availability (Dunham 1978, Sebens 1987, Madsen and Shine 2000a). Similarly, differences in growth trajectory between males and females, or sexual size dimorphism (SSD) is shaped by forces such as resource availability, which spur distinctly differing and adaptive responses between the sexes (Andrews and Stamps 1994, Fairbairn et al. 2009, Stillwell and Davidowitz 2010). Somatic growth, particularly in reptiles and other animals where the period of growth is extended, represents an integrated response of individuals to environmental conditions. Thus, somatic growth depends on an individual’s environmental-matching decisions regarding energy allocation to a given environment. Within-individual trade-

offs can occur between two general types of growth and among other life-history traits. Energy allocated for somatic growth is partitioned between increases in skeletal or structural size (i.e. increasing length) and deposition in easily metabolized nutrient reserves (i.e. increasing fat reserves). Allocating resources to structural growth or nutrient reserves reflects trade-offs between immediate increases in fecundity and competitive ability through increased size versus investment in future reproductions and survival through nutrient storage (Tveiten et al. 1996, Heino and Kaitala 1999). During unfavorable conditions, when resources demands are not met, organisms may depress skeletal growth or deplete energetic reserves (Metcalf et al. 2002). The ability to endure periods of prolonged food scarcity should be strongly linked with how fast individuals of that species or population grow. Fast-growing individuals, which must sustain higher metabolic rates, are more likely to be sensitive to prey shortages (Scharf et al. 2009, Rotkopf et al. 2013). Given the complexity of these interactions and the influence of growth on other life-history traits, adequately describing patterns of growth and the factors influencing growth for a species requires long-term studies of multiple populations (English et al. 2012, Laver et al. 2012).

Much of what we know about plasticity in growth is based on studies of captive animals and of endothermic vertebrates. Measuring within individual variation in growth requires the ability to repeatedly measure animals across their lifetime and complementary statistical methods that can 1) account for missing observations when animals could not be captured, and 2) partial information about age and cohort. Previous studies have shown that many species respond to resource fluctuations by depressing growth when conditions are unfavorable and accelerating growth when conditions improve (Wilson and Osbourn 1960, Weatherley and Gill 1981, Arendt 1997, Ali et al. 2003, Hirose et al. 2012). Compensatory or catch-up growth will be favored by selection if key functions (e.g. reproductive and neurologic function) can be safeguarded, and those traits bearing the expense are either less important to fitness or where the expense can be paid over a longer timeframe (Metcalf and Monaghan 2001, Mangel and Munch 2005). For example, individuals may forgo reproduction in years where resources are scarce in order to buffer other traits (Cubaynes et al. 2011, Rideout and Tomkiewicz 2011). A shortage of nutritional resources during development or early-life may have disproportionate effects on lifetime patterns of growth which may not manifest until later in life (Lindström 1999, Madsen and Shine 2000a, Botterill-James et al. 2019). The effects of maternal and early-life environment may result in common shifts on growth and body size and thereby buttress or weaken cohort-level responses to environmental stressors experienced later in life. Robust modeling practices which account for uncertainty and missing observations using long-term data are essential to evaluating how patterns of growth are altered by changes in the environment in wild populations, which have important consequences for the capacity of whole populations to adapt to changing environments (Nussey et al. 2007, Lee et al. 2012, Auer et al. 2015). Accurate estimates of growth parameters like maximum size, growth rate and body condition indices across wild populations under differing environmental conditions provides important insight into how populations can respond to changing environments.

Variation in traits like growth reflects underlying trade-offs which allow organisms to cope with fluctuating or unfavorable conditions. The fast-to-slow life continuum results from disparate strategies for prioritizing resources (e.g. for reproduction, growth and survival) (Roff 1992, Ricklefs and Wikelski 2002). Briefly, “fast-living” organisms are defined by rapid growth leading to early maturation, high reproductive rate, and comparatively shorter life span, while “slow-living” organisms are characterized by slow growth, delayed maturation, lower reproductive rate and relatively long life span (Promislow and Harvey 1990, Ricklefs and Wikelski 2002). The optimal strategy for coping with fluctuations in the environment differs across the pace-of-life continuum (Stearns 1989, 1992, Roff 2002). Such within species differentiation is well illustrated by the metapopulation of western terrestrial garter snakes (*Thamnophis elegans*) around Eagle Lake in Lassen Co. California, USA (Palacios et al. 2012). Spatially distinct populations occur along the rocky shoreline of the lake as well as in nearby high elevation mountain meadows. Lakeshore snakes are characterized by fast growth and early maturation, high reproductive output and lower adult survival, while meadow snakes exhibit slow growth, late maturation, subdued reproduction and higher adult survival (Bronikowski and Arnold 1999, Sparkman et al. 2007, Miller et al. 2011). Previous studies of Eagle Lake *T. elegans* suggest that stochastic variation in annual precipitation influences the length of water inundation within meadows, in turn affecting prey availability for snakes (i.e. abundance of larval and metamorph frogs and toads) (Bronikowski and Arnold 1999, Miller et al. 2011). This hydrologic dynamic leads to a boom and bust cycle for snakes occupying meadow sites such that in years when anurans bred (i.e. precipitation > 500 mm), meadow snakes had lower frequencies of empty stomachs (50%), while in drought years > 90% of observed meadow snakes had empty stomachs (Bronikowski and Arnold 1999). Previous work has demonstrated year-to-year variation in environmental conditions has significant influence on demographic processes including survival and reproduction probabilities (Bronikowski and Arnold 1999, Miller et al. 2014).

Given the fitness implications of nutritional stress and the highly plastic physiology and life-history of squamate reptiles, populations of *T. elegans* present an optimal system for investigating the evolution of plastic traits that buffer individuals and populations from global change. In this study, we examine variation in growth, maximum body size and body condition for garter snakes in response to fluctuating levels of food availability across 17 years of capture-recapture data. Our primary goal was to determine how growth varies in response to 1) annual variation in the availability of prey, 2) differences between males and females and 3) differences between the two ecotypes, and 4) interactions between environmental conditions and sex across the two ecotypes. We test two sets of predictions: First, that growth will be most sensitive to prey abundance in the slow-living meadow ecotype, as these populations have evolved in habitats experiencing greater annual variation in resource abundance. Following the condition-dependence hypothesis, we expect that increases in prey abundance will induce more rapid growth in female *T. elegans* than their male conspecifics, thereby maximizing size-based reproductive output (Bonduriansky 2007, Brown et al. 2017). Secondly, we predicted that early

life conditions would interact with annual environmental conditions later in life to influence responses to food deprivation. Specifically, we predict that growth will be enhanced when prey availability coincides with nutritionally primed cohorts. This may induce a ‘silver spoon’ effect, where individuals experience lifelong benefits as a result of optimal early-life environments (Grafen 1988, Madsen and Shine 2000a).

METHODS

Study Area and Data Collection

We studied five replicate populations of the western terrestrial garter snake at and around Eagle Lake, CA. These populations occur disparately in two primary habitat types that are strongly correlated with environmental conditions and observed life-history of snakes: montane meadow habitats or rocky lakeshore habitats (Bronikowski 2000). Meadow sites occur at higher elevations than lakeshore sites and are characterized by lower temperatures and greater annual fluctuations in prey availability, resulting from greater annual variation in hydrology. Lower elevation lakeshore sites display higher mean temperatures and relatively stable water during the years we study here, which affords continuous prey in the form of minnows (Arnold 1977). Diet, behavior, morphology, genetic connectivity, and thermal and physiological ecology have been well described (Kephart and Arnold 1982, Peterson and Arnold 1989, Huey 1991, Bronikowski and Arnold 1999, Manier and Arnold 2005, Sparkman and Palacios 2009, Palacios et al. 2012, Gangloff et al. 2017). Snakes emerge after spring thaw in approximately mid-April, where aggregations mate near the hibernation site before dispersing to forage until the end of September, at which point, snakes return to hibernacula to hibernate from October to March. Offspring are born between August and September (Bronikowski and Arnold 1999).

Monitoring of *T. elegans* populations was conducted during most summers from 1978-1996 through systematic visual searches from June to August, and in some years, additional surveys were conducted in May and October (Table 1.1). We used data from two lakeshore sites (PIK, GAL) and three meadow sites (PAP, MAH, NAM). Combined analysis included 1831 individual lakeshore and 2563 individual meadow snakes, with 609 and 1080 recaptures, respectively. Most individuals are only observed once, but single snakes were captured as many as 9 times. Free-ranging snakes were hand captured, measured for SVL (mm), weighed (g), sex was determined based on morphological characteristics and gravid females were palpated to determine the number of embryos (litter size). Individuals were marked with a unique identifying clip on the ventral scales or using a passive integrated transponder (PIT) tag.

For cohort analyses, we limited our data to known-age individuals based on age/size relationships, omitting individuals caught at larger sizes and therefore of unknown age. For lakeshore snakes, individuals were considered young of the year when caught at SVL's less than 275 mm, while for meadow snakes, young of the year were those less than 260 mm. First-year lakeshore snakes were those between 275 and 325 mm, and 260 and 290 for meadow snakes.

Individuals between 325 and 375 mm for lakeshore and 290 and 330 mm for meadow populations were included as second-year snakes only where there was no uncertainty about early-life cohort conditions (i.e. at least two consecutive years of either wet years with high prey or dry years when prey is less abundant).

We characterized temporal variation in resource availability using annual variation in water availability. We followed criteria developed by Miller et al. (2011), defining years to be wet, and therefore ‘high prey’ or dry with ‘low prey’ based on field notes from each year, data on snake food items, and records of annual precipitation (i.e. less than or greater than 500 mm precipitation). The abundance of breeding anurans was closely associated with precipitation levels within the Eagle Lake basin. Previous studies show that anuran tadpoles and metamorphs provide a vital but variable portion of meadow snake diets, with annual variation occurring in response to water availability. Lakeshore ecotypes rely on minnows (*Rhinichthys osculus*, *Richardsonius egregius*, *Gila bicolor*, and *Catostomus tahoensis*), which live within the lake and are more consistently available than the tadpoles at meadow sites (Kephart and Arnold 1982). Using the same classification for the same set of years, previous studies have demonstrated that wet versus dry years predicts annual differences in garter snake survival, litter size, and probability adult females are gravid (Robert and Bronikowski 2010, Miller et al. 2011, 2014). Thus, we feel confident that the classification accurately reflects conditions as they relate to food availability experienced by snakes during our study period.

Statistical Analysis

We estimated how three primary predictor variables (ecotype, sex and wet versus dry year and the interactions between these variables), were related to two measures of growth: 1) the rate of growth in overall structural size of an individual as measured by snout-to-vent length and 2) the acquisition of nutrient reserves as measured by a condition index that measures residual variation in mass corrected for body size. For each of the two measures of growth, we conducted two analyses. The first analysis used all data and only examined how variation in environmental conditions in the current year affected growth. The second only used individuals for which cohort could be determined (a smaller subset of the complete data set) to examine how the interaction between early-life conditions (i.e. was it a wet-high prey year or dry-low prey year during gestation or during the first year of life) and annual variation in conditions in later years (i.e. was the current year high prey or low prey) affected growth. The statistical models are described in detail in the following.

To estimate structural growth, we used a mark-recapture version of a von Bertalanffy growth model, modified to allow annual variability in growth. Estimated growth from mark-recapture data requires accounting for uncertainty related to age of individual, measurement error, and missing observations for individuals not recaptured in a given year. As a starting point, we used the estimator developed by Schofield et al. (2013). The length of individual i at time t where:

(1)

$$L_{it} = LFC_i + (L_{\infty} - LFC_i)(1 - K_i)^{\Delta t_i}$$

Equation (1) follows Fabens (1965), James (1991), and Wang (2004) parameterizing, where the mean response is conditioned on the observed length at first capture (LFC) for individual i . Two biologically relevant parameters are modeled by the VB function: the asymptotic length (L_{∞}) an individual approaches as they age, and the growth coefficient (K), which defines how quickly asymptotic size is reached. $1-K$ is the proportion of remaining growth (asymptotic size minus current size) that is achieved in a one-year period. The time intervals (Δt) were calculated as the number of years since an animal was first captured. We treat L_{it} as an unknown random variable, allowing us to estimate measurement error, characterized as the difference between observed length in the dataset and the true length as measure by L_{it} .

We included a random effect for individual on L_{∞} to account for differences among individuals in their asymptotic size. Repeated observations were insufficient to estimate individual variation in the growth parameter K , and we instead focus on fixed variation in this parameter. The hierarchical specification for estimating L_{∞} , allows us to draw independent posterior distributions for the mean L_{∞} for males and females, where:

$$L_{\infty i} \sim N(\mu L_{\infty}(\text{sex}_i), \sigma^2) \quad (2)$$

We assumed the variance of the variance was equal for males and females. To aid in fitting the model, we truncated the distribution to have a lower limit of 300, which is well below the expected asymptotic size for any individuals in the population. We first ran a general model to estimate average growth rates and asymptotic size for each population and for each ecotype as a function of sex. Growth models were run individually for all populations and on combined lakeshore (PIK and GAL) and meadow (PAP, MAH, and NAM) populations, respectively. The growth rate parameter, K , as a function of sex where $\text{logit}(K_{it}) \sim f(\text{sex}_i)$.

We next ran a full model to examine the influence of wet versus dry years on growth and how that varied between males and females, resulting in four values for mean growth coefficient (K). Finally, we fit the LFC parameterization of the VB growth model to examine the interaction of early-life cohort and annual prey conditions. We could not examine sex-related differences in the cohort model due to the lack of statistical power and lower certainty in differentiating males and females in young snakes (<2 years old). For our cohort models, we determined whether the birth year of an individual occurred during a wet, and therefor high prey abundance year or dry year, when nutritional resources would be scarce. To evaluate the effect of maternal environment, we similarly determined whether the year prior to parturition (i.e. year before birth) occurred during high prey (i.e. high nutrition) or low prey (i.e. low nutrition) environmental conditions. We fit the same model as in the general analysis, except now growth rate was a function of cohort type (high nutrition versus low nutrition), current year (wet-high prey versus dry-low prey) and their interaction, where $\text{logit}(K_{it}) \sim f(\text{cohort}_i, \text{year}_i)$.

We fit von Bertalanffy growth models in a Bayesian framework with JAGS v4.2 (Plummer 2003), accessed via the jagsUI (Kellner 2016) package in R (version 3.4.4; R Core Team 2014). We used weakly informative priors for model parameters. Using Markov chain Monte Carlo (MCMC), we ran models for 140,000 iterations, discarding 125,000 interactions as burn-in of the initial transient phase, adapted for 15,000 iterations, yielding a total of 45,000 samples from the stationary joint posterior distribution. In order to assure appropriate mixing of chains and model convergence we evaluated trace plots and potential scale reduction factor \hat{R} for all models using the Gelman-Rubin convergence diagnostic (Brooks and Gelman 1996).

To assess changes in nutrient reserves, we focused on a condition index, which measured the relative mass of individuals corrected for their overall structural size as measure by SVL. Most assumptions of the regression-based body condition indices are met by using the residuals from the ordinary least squares regression of the natural log of mass and the natural log of length. Previous studies have shown the index to adequately control for variation across different body sizes, and the method is desirable for capture-mark-recapture field studies, as it is least intrusive and does not require the sacrifice of animals (Jakob et al. 1996, Falk et al. 2017). We quantified changes in condition using a mixed model analysis that included fixed effects of annual prey abundance, ecotype, sex and cohort, and all possible two and three-way interactions between these predictors, as well as a random effect for individual to best predict body condition. Condition indices were calculated using external body measure of size: mass (g) and SVL (mm). Condition was estimated as the residuals from regressions of log mass on log length using the lme4 package in R (Bates et al. 2015). As with the analysis for structural size, we fit three models to the data all of which included the random effect for individual. We first used a general model to estimate average condition based on sex and reproductive status (male, non-gravid female, gravid female) and ecotype differences (lakeshore versus meadow snakes) following the linear model:

$$Y = \mu + ecotype \times sex + SVL + \varepsilon$$

The linear model included the interaction between the two categorical variables. Next we fit models which included annual variation in environmental conditions (i.e. wet-high prey versus dry-low prey year) to the complete data set. We considered all model combinations with the three main effects (sex/reproductive status, ecotype, and wet versus dry year) and all two-way interactions. We selected among models using Akaike information criterion (AIC) estimator (Akaike 1974) and fit models using the maximum likelihood methods rather than the REML to get accurate estimates of the likelihood for model selection. For animals where cohort could be determined with confidence, we also fit a set of models to examine the interaction between early-life conditions and later sensitivity to annual conditions. Based on the first two analyses and having less data available to fit the cohort-level model, we made the sex/reproductive status effect binary by dividing individuals into two groups: gravid females and males/non-gravid females. The final models presented were those best supported by the AIC model selection.

RESULTS

Growth measurements were obtained for 4362 individual *T. elegans* captured between 1978 and 1996 with 1689 recaptures for a total of 5919 observations. The largest samples for lakeshore and meadow populations were obtained from PIK (n=994) and PAP (n=1428), respectively (see Table 1.1 for sample sizes in all populations in each of the two ecotypes). Year-to-year rates of capture varied with annual rates of precipitation, as snake availability for capture corresponded to availability of prey. For example, 615 snakes were captured in PAP meadow during sampling in 1987, following a succession of four wet years, while from the same population in 1980, a dry year, just 41 snakes were obtained.

Consistent with the findings of Bronikowski and Arnold (1999), we found a significant difference in growth between the lakeshore and meadow ecotypes. Lakeshore snakes grew significantly faster (i.e. had lower values of K , which is the proportion of remaining growth not completed in a given year), than did the meadow ecotype. The mean estimated growth coefficient for male lakeshore snakes was 0.683 ± 0.077 (95% CI = 0.650 to 0.716) and 0.706 ± 0.069 (CI = 0.676 to 0.732) for female lakeshore snakes. Growth coefficients for meadow males and females were estimated at 0.767 ± 0.057 (CI = 0.746 to 0.786) and 0.767 ± 0.043 (CI = 0.746 to 0.786), respectively (Table 2).

Female *T. elegans* grew to significantly larger asymptotic sizes than males in both ecotypes, with lakeshore snakes achieving larger overall size than meadow snakes (Figures 1.1 and 1.2). Female snakes from the lakeshore ecotype were, on average, 19.1 % larger than males. The estimate for average maximum SVL (L_{∞}) was 677.232 ± 12.438 mm for lakeshore females (CI = 654.558 to 702.381) and 568.667 ± 10.551 mm for lakeshore males (CI = 549.756 to 590.666). Females from meadow populations grew to average asymptotic sizes 8.7 % larger than meadow males, with estimates of 536.095 ± 2.401 mm (CI = 531.467 to 540.960), while the average L_{∞} for meadow males was 493.306 ± 2.198 mm (CI = 489.042 to 497.606). Overall, sexual size dimorphism was greater in lakeshore snakes than meadow snakes, with males reaching asymptotic sizes 15% longer than meadow males, and lakeshore females growing 25% longer on average than their meadow analogues. Variation in asymptotic size was greater in the lakeshore ecotype than meadow populations.

We next examined how structural growth rate, K , differed between wet-high prey and dry-low prey years for both ecotype and sex for all snakes regardless of earlier life nutritional environment (Figure 1.3). In general, annual variation in environmental conditions had minimal effects when early life conditions were not accounted for (Table 1.3). Estimates for ecotype-level analysis yielded non-significant differences in growth from wet to dry years in meadow populations. Meadow females grew at similar rate, 0.764 ± 0.047 (CI = 0.747 to 0.780), when compared to males, 0.773 ± 0.065 (CI = 0.750 to 0.795) in high-prey years as well as low prey years (see table 3 for average growth relative to the maximum for both ecotypes). Lakeshore males and females grew at similar rates in wet years, and males grew significantly faster, $0.666 \pm$

0.100 (CI = 0.621 to 0.708), than females, 0.722 ± 0.083 (CI = 0.689 to 0.754), in low-prey years (Figure 1.4).

Finally, for our structural growth models, we evaluated the interaction between early life nutritional environment and ambient prey conditions, as determined by precipitation. We found no effect of gestational cohort (i.e., whether conditions in the year a snake was gestated were consistent with high nutrition or low nutrition) on growth rate, K , for the lakeshore ecotype. Lakeshore snakes grew at similar rates regardless of nutritional cohort or prey-year (Table 1.5). In contrast, we found a significant effect of nutritional cohort on growth for both wet years and dry years. Low nutrition cohorts grew faster in both wet and dry years, but this difference was most pronounced during wet years associated with greater prey availability (Figure 1.5). Similarly, when nutritional cohorts were grouped by the environment encountered during their first year of life, we found no difference in growth within the lakeshore ecotype, which grew similarly across nutritional cohort and prey years (Table 1.6). Conversely, low nutrition cohorts of meadow snakes grew faster than high nutrition cohorts in both high prey and low prey years (Figure 1.6). Additionally, low nutrition cohorts of meadow snakes grew significantly faster in high prey years than in low prey years.

Overall, gravid females are in the highest body condition, followed by non-gravid females and lastly males (Figure 1.7). Meadow snakes exhibit similar body condition index values to lakeshore snakes when gravid, but higher body condition than lakeshore snakes for both non-gravid females and males. When evaluating changes in body condition in response to prey availability across years, we find condition to be best explained by the interaction between prey year, ecotype and sex/reproductive status (gravid females and non-gravid females/males). Gravid females display higher body condition across ecotype and year (Figure 1.8). Lakeshore gravid females are in poorer condition during dry-low prey years, while meadow gravid females maintain condition but show greater variability during dry-low prey years. Meadow males and non-gravid females display higher body condition in wet-high prey years than in corresponding dry-low prey years.

Lastly, we evaluated body condition for those individuals where first-year nutritional cohort could be determined. Body condition among nutritional cohorts was best explained by an additive model with two-way interactions between nutritional cohort and prey year and nutritional cohort and reproductive status (i.e. gravid females vs. non-gravid females and males) plus an effect for ecotype. Meadow snakes were in better condition across both prey year, reproductive status and nutritional cohort groups (Figure 1.9). Gravid meadow snakes from low nutrition cohorts exhibit higher body condition than gravid females from low nutrition cohorts. However, this difference was only significant in low prey years. Non-gravid meadow snakes from low nutrition cohorts were in better condition in low prey years than high nutrition cohorts from meadow populations.

DISCUSSION

Variation in growth rates provides a mechanism for individuals to maximize fitness by balancing allocation to current and future reproductive output by modulating growth in response to environmental conditions. Our results suggest that the interaction between early and later-life environments is crucial to understanding how food availability influence the growth for the western terrestrial garter snake, *T. elegans*. This pattern was most pronounced in interactions between the nutritional environment experienced in the first year of life, and those later in life, although a similar pattern arises from the interaction between maternal environment and contemporary nutritional environment. Individuals from cohorts which experienced nutrient-poor years during gestation or their first year accelerated growth in later years, especially when resources were more abundant.

Growth rate plasticity is a nearly universal element of life-histories (Abrams and Rowe 1996). The availability and subsequent allocation of resources to growth determines the outcome of trade-offs between current and future reproduction and survival. When evaluating the influence of prey abundance on growth, we found no significant overall differences in growth during years of high prey abundance versus low prey abundance. Following the *optimization* hypothesis, growth would be expected to vary in response to fluctuating resources as a result of trade-offs between coupled fitness traits (Ricklefs 1984). In this scenario, accelerated growth would be costly (e.g. reduced survival). Conversely, where the environment is the limiting factor for fitness traits including growth, we expect that growth will always be maximized under unconstrained nutritional environments. Our results support the optimization of growth with respect to a complex of life-history trade-offs. Individuals tailor growth to maximize fitness based on the prediction that developmental environmental conditions are reflective of the environment which will be encountered as adults. A ‘silver spoon’ effect, wherein individuals born into favorable environmental conditions (high prey abundance) benefit through ontogenetic consistency in accelerated growth throughout life, has been shown in other taxa including fish, birds, snakes and humans (Grafen 1988, Madsen and Shine 2000a, Hayward et al. 2013). However, our results do not align with a silver spoon effect, but rather, individuals exposed to poor nutrition environments accelerated growth in mismatched (i.e. high prey) environments later in life.

Our results reinforce the conclusions from an earlier study which found significant divergence in the rate of growth and asymptotic body size between the lakeshore and meadow ecotypes of *T. elegans*, which has putatively driven the ecotypic differentiation observed in these populations (Bronikowski and Arnold 1999). While both ecotypes display SSD, female lakeshore snakes grow substantially larger than their male counterparts. The ‘decision’ by individuals on how to allocate finite resources is heavily conditional on reproductive status, sex and environmental conditions. Thus, it may be less beneficial for male snakes to grow beyond a threshold for mating success, as larger body size carries a metabolic cost and may increase visibility to predators. Conversely, female snakes may differentially use resources to maximize structural growth, thereby increasing size at future reproduction, enhancing reproductive output (Brown et al.

2017). The heterogeneity among-individuals in traits related to growth (e.g. maximum size and rate of growth) was greatest in the lakeshore ecotype, suggesting trade-offs between traits tied to fitness, which are maximized only when conditions are favorable (Roff 2002, Bonduriansky 2007). Anderson et al. (2008) found a strong link between faster growth and higher heterogeneity within cohorts of yellow perch and chinook salmon. Although the proximate mechanism is unclear, time to starvation was significantly shorter for fast growing individuals, while sub-optimal growth or gains in mass prior to starvation challenge increased time to starvation (Anderson et al. 2008). For fast-growing lakeshore snakes, greater variability in asymptotic body size and rate of growth relative to the maximum may reflect innate heterogeneity in growth efficiency, whereby more efficient individuals can persist in low-energy environments and greater heterogeneity of habitat use (Morinville and Rasmussen 2006, Rosenfeld et al. 2015). Populations may persist during years of reduced prey abundance or increased foraging effort and predation due to low lake levels.

Most organisms have evolved mechanisms for energy storage in order to survive periods of low food availability, and would be expected to increase the allocation to storage in response to diminishing resources (Pond 1981, Forsman and Lindell 1991). In general, we found meadow snakes to have higher body condition index values than their lakeshore counterparts. A previous study on Eagle Lake *T. elegans* by Palacios et. al (2011) found higher base levels of the insulin-like growth factor 1 (IGF-1), an important hormone in the regulation of metabolic processes including energy acquisition, storage and utilization, within the meadow ecotype as compared to lakeshore populations (Landys et al. 2006). Slow-living meadow snakes are subject to both higher overall baseline as well as stress-induced circulating glucocorticoids, which favor self-maintenance and current survival, important components to a slow pace-of-life strategy. Higher levels of IGF-1 have been associated with reduced weight loss during starvation in mammals (O'Sullivan et al. 1989). This physiological mechanism helps explain the overall higher body condition of meadow snakes, as well as the higher body condition in cohorts of individuals experiencing dietary restriction early in life. Individuals from nutrient deprived cohorts are primed to endure similar poor nutrition environments later in life, while their high nutrition counterparts are ill equipped to cope with starvation.

Our study contributes to our understanding of how phenotypic plasticity in traits like growth allow organisms to maximize fitness under a given set of environmental conditions. We show resource availability influences the allocation of energy to structural growth and nutrient reserves, resulting from complex interactions between current and past environments, highlighting the importance of long-term field studies. Early-life nutrition influences an array of life history traits including reproduction, survival and growth, and the magnitude of these effects may vary between the sexes and over time (Dmitriew and Rowe 2011, Miller et al. 2014). The response of species to changes in climate are governed by evolutionary and ecological processes and for populations to persist, evolution must keep pace with rapidly changing environments (Huey et al. 2012, Carroll et al. 2014). Climate change is expected to result in biotic shifts in

individual life-histories and populations dynamics, making many populations more vulnerable to extinction (Lande and Shannon 1996, Karl and Trenberth 2003, Melbourne and Hastings 2008). Organismal responses to these sweeping changes to environmental landscapes are limited, and forecasting ecological shifts necessitates accurate estimates of key population vital rates including survival, abundance and somatic growth (Coulson et al. 2011a). Studies within a laboratory setting may not accurately represent vital rates observed in the wild (Bonneaud et al. 2016). Furthermore, demographic dynamics in reptiles have been less well-studied than either birds or mammals, leaving major gaps in our understanding of the life-history evolution of this taxa (Andrews 1991). The spatial and temporal variation in growth within and among individuals reflect integrated responses either through genetic changes via changing selective pressures or as a plastic response to environmental change (Via et al. 1995, Bradshaw and Holzapfel 2006). Understanding how fluctuating prey abundance influences growth generating within population variability and divergence of traits between populations provide critical insights into how reptile populations will adaptively respond to future environmental conditions.

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Chapter 2: The effects of environmental variability on demography for populations of the common garter snake—*Thamnophis sirtalis*

Abstract

Sweeping anthropogenic changes pose an urgent challenge to natural ecosystems and the organisms which evolved there. For species with limited dispersal ability, fluctuating environmental conditions must be endured *in situ*, relying on adaptive capacity or phenotypic plasticity to persist (Lande and Shannon 1996, Davidson et al. 2009, Huey et al. 2012). The ability to persist is ultimately driven by vital rates like survival, somatic growth and fecundity, so it's important to understand how vital rates respond to changes in the environment. Fluctuations in environmental conditions have been shown to influence demographic traits in many species. Long-lived organisms may experience fluxes in the prevailing environment throughout life, necessitating differential allocation of resources across life-history traits. Demographic parameters such as somatic growth, survivorship, fecundity and body condition are essential traits which drive the fitness of an organism. Quantifying variation in these key traits improves our understanding of the influence of environment on demography as well as advancing our ability to predict the demographic impacts of a changing climate. For most reptiles, little is known about actual demographic rates and life-history variation. We investigate the relationship between demographic parameters and the environment for our montane populations of the common garter snake (*Thamnophis sirtalis*) using a 16-year mark-recapture data set. We quantified patterns in survival, reproduction and growth and how they varied between sexes, among populations, and in response to annual variability in weather patterns. As expected, we found that reproductive output increased in years with higher rainfall where prey availability was greater. In contrast, apparent survival varied by population and between males and females but not with respect to annual differences in environmental conditions. We found an interaction between early-life conditions and sensitivity to environments in later life, where growth was accelerated in years of higher prey availability for individuals that experienced poor conditions in their first year of life. Overall, our findings reveal spatio-temporal differences in patterns of growth and reproduction which are consistent with fluctuations in local resources. Our results provide important insights regarding demography of snakes and help elucidate the influence of annual variation in prey abundance on growth, survival and reproduction and the effect of early-life conditions. Snakes are particularly able to modulate growth throughout their lives, and the ability to modulate reproductive effort in poor-resource years may buffer adult survival from annual variation in environmental conditions. Importantly, these results reflect that our ability to predict the response of populations to fluctuating environments should incorporate multiple populations as well as early-life environment to account for context-dependent variation in demographic processes.

Keywords: *Thamnophis sirtalis*, survival, reproduction, growth, garter snake, climate change, environmental variation

The global climate is changing and the degree of climatic variation has changed over recent decades, leading to greater and lesser contrasts between precipitation and temperature fluxes (Alexander et al. 2006, Coumou and Rahmstorf 2012). Interannual variation in weather (e.g., precipitation and temperature) can result in an increase in interannual variation in demographic parameters, leading to changes in population structure, size and potentially to declines or even extinction for some species (Lawson et al. 2015, Selwood et al. 2015, van de Pol et al. 2016). Quantifying population-level processes and identifying drivers of variation in vital rates is critical for predicting changes in demography (Lynch and Lande 1993, Krebs 1996, Coulson et al. 2011b). Quantifying vital rates is also an important step in parameterizing models that predict population outcomes under future environmental conditions (Urban et al. 2016) and identifying life-history strategies that are susceptible to extinction (Mckinney 1997).

Annual variation in weather condition can profoundly influence growth, survival and reproduction, and thereby the demography and dynamics of wild populations (Krebs 1996, Gould and Nichols 1998, Hanski 1999, Baron et al. 2010, Ujvari et al. 2010). For many organisms, body size is positively linked with increased survival and reproductive output, (Sogard 1997, Brown and Weatherhead 1999a, Hall et al. 2018a), making growth a crucial component of individual life-history trajectories. Growth is determined by the rate of energy acquisition, assimilation and allocation, and because of their high phenotypic flexibility, snakes are particularly well-suited for altering growth rates (e.g. Bayne 2004). In environments where the ability to forage and prey abundance and availability is limited by annual weather conditions, organisms may often face unpredictable or inadequate food resources. Food availability and abundance is a critical environmental factor shaping trade-offs between growth, survival and reproductive output. In scarcity, animals may accelerate growth and reproduce younger or at smaller size, often because it is uncertain they will survive (Stearns 1992, Hutchings 1993).

Investment in growth is further complicated because energy allocation for growth may be divided into nutrient storage (e.g. increasing mass) or structural growth (e.g. increasing length). This illustrates differential investments in either current reproduction and survival or future reproductive output and longevity conferred by larger body size. Organisms can cope with unfavorable conditions by reducing the energy allocated for growth and reproduction and increasing stored energy to forestall starvation, should conditions worsen, thereby bolstering survival probabilities. Individuals of higher body condition—the ratio to mass to length—should have higher survival probability. Similarly, individuals of higher condition should increase future litter size, offspring size and reproductive frequency (Grindstaff et al. 2005, Lee et al. 2012, Hall et al. 2018b). Or, individuals may cope with energy constraints by either forgoing reproduction, producing litters of reduced quality (e.g. reduced litter or offspring size) or maintain reproductive output at the cost of reduced body condition, structural growth or survival (Ballinger 1977, Naulleau and Bonnet 1996, Rode et al. 2010). Individual decisions in energy trade-offs determining individual fitness are critical drivers of life history evolution in natural populations (Lack 1954, Stearns 1992, Carlson et al. 2004).

Vital rates and life-history strategies may also covary among geographically proximate populations, as a result of broad-scale exogenous (i.e. outside of intrinsic constraints of the organism) effects (Gurevitch et al. 2016). Body size influences many aspects related to fitness, thereby affecting population size, structure and density (Peters 1983, Jenkins et al. 1999, Vøllestad et al. 2002). Processes influencing survival and reproduction can also play a central role in population-level growth (Shine and Charnov 1992, Sorci et al. 1996, Ujvari et al. 2010). For example, key trade-offs such as decreasing reproductive output in order to buffer survival during unfavorable conditions, however, this would lead to decreased recruitment following poor years, and reduce overall population growth. Conversely, variation within populations and across environments may give rise to substantial heterogeneity among populations. The persistence of individual and population level variation yields diversity in the response of populations to environmental stress, thereby leading to greater stability within a species (Hanski 1998, Jorgensen et al. 2016).

The influence of environmental conditions may differ in strength and direction over ontogeny, and the consequences may manifest as carry-over effects which appear later in life or even transgenerationally (Rotem et al. 2003, Grindstaff et al. 2005, Warner et al. 2007). Within populations, early-life conditions can be shared by cohorts of individuals born within the same year, and shape how they respond to environmental variability later in life. For example, individuals experiencing a rich nutritional environment early in life may grow faster throughout life, a phenomenon known as the ‘silver spoon’ effect (Grafen 1988, Madsen and Shine 2000b). Alternately, cohorts exposed to poor nutrition during development or early life may compensate for their poor start by more efficiently exploiting resources when they become abundant and accelerating growth later in life (Wilson and Osbourn 1960, Metcalfe and Monaghan 2001, Hirose et al. 2012). This interaction between conditions experience in early-life with prevailing ecological conditions later in life influences individual fitness, shaping life-history evolution and population dynamics (Krebs 1996, Metcalf and Pavard 2007, Bonner et al. 2010). In seasonal environments, resource availability in early-life is an integral determinant of life-history traits and the effects of early-life nutrition may be direct or delayed, and may vary between the sexes (van Noordwijk and de Jong 1986, Metcalfe and Monaghan 2001).

The ability to generate reliable longitudinal data needed to estimate demographic parameters is challenging for many reptiles. Thus, reliable demographic estimates are lacking for many taxa, including squamate reptiles, which serve as important indicators for community and ecosystem monitoring (Andrews 1991). The low densities and cryptic nature of many snake species often results in low recapture rates of individuals in field studies, and longitudinal studies are logistically constrained (Parker and Plummer 1987). Long-term studies are critical for obtaining accurate estimates of growth, survival, and reproductive frequency, particularly in highly seasonal or climatically variable regions, which are essential for understanding life history evolution (Dodd Jr. 1987, 1993). The physiological processes and behavioral strategies of

reptiles are highly sensitive to environmental temperature and water availability, allowing populations to persist when resources are scarce (Pough 1980, Bradshaw 1991).

The rapid response of reptiles to shifts in environmental conditions also make them excellent study systems for understanding how climate conditions affect populations. We studied the widely distributed and locally abundant common garter snake (*Thamnophis sirtalis*)—traits that make this species well-suited for understanding snake ecology (Rossman et al. 1996).

Populations of *T. sirtalis* occur in spatially discrete montane meadows within the Eagle Lake basin in CA, USA. Annual stochastic variation in the amount of precipitation within the basin results in a resource-pulse system (Ostfeld and Keesing 2000). Wet years result in ephemeral ponds which provide ideal breeding opportunities for amphibian populations, and thereby ample prey for snake populations (Kephart and Arnold 1982, Miller, David A., Clark, W. R., Arnold, S. J. 2011, Miller et al. 2014). Our aim was to quantify key life-history traits including growth, survival, reproduction and body condition within a theoretical framework of annually shifting prey conditions, wherein years can be either high prey or low prey (Figure 2.1).

In this study, we evaluated the effects of environmental conditions on growth, survival, reproduction and body condition on 16 years of mark-recapture data of free-ranging *T. sirtalis* populations. We focused on two objectives: 1) to quantify snake vital rates and the impact of environmental conditions and 2) to evaluate which theories are supported as evident of life-history trade-offs. Increases in prey abundance are correlated with increased energy intake, and thereby reduce the need for costly trade-offs and allow organisms to maximize fitness (Roff 1992). Conversely, environments with reduced prey availability necessitate internal energy stores and adjustments in allocation to metabolism, growth and reproduction. We assessed the effect of annual variation in prey availability on key life-history parameters. First, we evaluated the annual influence of variation in prey (Figure 2.1). We predicted that high prey years would allow for increased growth, survival, reproduction and body condition, while years of reduced prey would lead to diminished fitness. In addition, we predicted growth, survival and body condition would vary between males and females as a result of differential resource allocation to maintenance and reproduction. Second, because climate conditions affect all individuals across a population on a similar temporal scale, we evaluated the influence of early-life conditions on structural body growth (e.g. increasing length) and body condition (e.g. increasing nutrient stores). To test these predictions, we used a modification of the von Bertalanffy growth model to estimate asymptotic size and growth relative to the maximum. We tested for the effects of sex, population and annual resource abundance on apparent survival using Cormack-Jolly-Seber survival models. We examined the effect of prey abundance on reproductive output using linear models to predict litter size across populations and years. Finally, we used body conditions indices to evaluate how prey abundance, sex and population influence allocation of energy to storage.

METHODS

Study populations and data collection

Free-ranging common garter snakes (*Thamnophis sirtalis*) are found in relatively high abundance in spatially discrete populations in the vicinity of Eagle Lake in Lassen County, California, USA. Snakes were hand-captured, weighted (g), measured to obtain snout-vent length (SVL [mm]), sexed, and uniquely marked by clipping ventral scales (Brown and Parker 1976). Gravid females were palpated to determine the number of embryos (litter size) before release. While capture effort varied across populations and years, sampling occurred from 1978-1996 (see Table 1) through systematic visual searches from June to August, with the greatest effort occurring across all populations in 1980, 1984 and 1985. We used data from four populations, Mahogany (MAH), Nameless (NAM), Roney Corral (RON) and McCoy North (MCN), for which there was sufficient captures and recaptures to allow us to estimate demographic parameters. A total of 1443 captures of 1056 individuals were obtained over the study period with 387 recaptures.

Environmental Data

Previous studies identified strong links between precipitation and prey availability within the Eagle Lake basin (Kephart and Arnold 1982, Bronikowski and Arnold 1999, Miller, David A., Clark, W. R., Arnold, S. J. 2011, Miller et al. 2014). Annual variation in water availability largely determines breeding conditions for local anuran populations (Western toads [*Bufo boreas*] and Pacific tree frogs [*Hyla regilla*]), and therefore, prey abundance for garter snake populations. Following criteria developed by Miller et al. (2011), we classified years as either wet, and thereby high-prey, or a dry year with low-prey using detailed field notes of the presence of breeding anurans and the stomach contents of captured snakes. High prey or low prey categorizations were used as annual predictors of vital rates. Previous work in the same study area on *Thamnophis elegans*, shows that this classification is a strong predictor of demographic variability in demographic rates in this closely related species.

Age and Early Life Classifications

To test for interactions between early-life environment and ambient environment, we identified a subset of individuals for which we were able to determine age, allowing us to place them into cohorts. Age of individuals was determined based on estimated size-age relationships using information from known young-of-the-year snakes and subsequent captures of these snakes. We classified all individuals below 275 mm as young-of-the-year, and those between 350 mm and 395 as one-year-olds. Individuals captured at larger sizes were considered of unknown age. Those between 275 mm and 350 mm, we used only individuals with two consecutive years of either wet or dry conditions for cohort year. Thus, we could evaluate both the effect of early-life cohort conditions, as well as the interaction between conditions experienced in the past and ambient environmental conditions. In order to evaluate the influence of prey availability in early life, we classified individuals experiencing dry, low-prey years during development or the first

foraging year as coming from ‘low nutrition’ cohorts and those from wet, high-prey years as ‘high nutrition’ cohorts.

Statistical analysis

To assess variation in vital rates among years, we estimated the relationship of each of our demographic variables to a categorical predictor variable that accounted for expected prey availability. Estimates were generated using a combination of standard mark-recapture estimators and generalized linear models that account for the uncertainty in detection and measurement error common in the monitoring of wild populations (Lebreton et al. 1992). We first focused on two measures of growth: 1) overall structural size as measured by snout-vent length (structural growth) and 2) nutrient reserves measured as the size-dependent mass (body condition) and how each was influenced by both annual prey condition and the combination of sex and reproductive status. For both structural body growth and body condition we evaluated both how variation in environmental conditions in the current year influence growth, as well as how early-life condition affects growth in ambient conditions (i.e., cohort effects). We next estimated sex-specific apparent survival (ϕ) and detection probability (p) and determined if survival was related to population and prey abundance. Finally, we evaluated the influence of prey availability on litter size of gravid females using linear mixed-effects models which included a random effect to account for recaptured individuals. A detailed description of the methods used for each is as follows:

Growth—To estimate structural growth, we used a von Bertalanffy growth function to estimate change in body size and maximum body size. We used a modified version adapted from Schofield et al. (2013; Chapter 1) as our starting model, where the length of individual i at time t is

$$L_{it} = LFC_i + (L_{\infty} - LFC_i)(1 - K)^{\Delta t}$$

where $L_{\infty i}$ is the asymptotic (i.e. maximum) length for individual i , and K is the growth rate at which the asymptotic size is approached. $1-K$ is the proportion of remaining growth (i.e., asymptotic size minus current size) achieved in a one-year interval. Time intervals (Δt_i) are years between captures. The response is conditioned on the observed length at first capture (LFC) for individual i . The rate of growth relative to the asymptotic size varied by individual. We assumed that K and L_{∞} differed by sex and included random effects to account for individual variation in asymptotic size, initial size at first capture, and sampling error in the length measurement (i.e. the difference between L_{it} and the observed length from our field measurements).

To test our hypotheses, we estimated the relationship between annual weather conditions (i.e., wet versus dry year) and sex to the individual growth rate, K . To evaluate variation among populations, models were run individually for all populations and then on all populations combined.

Next, to investigate the influence of early-life environment on growth, we extended the general model to allow growth rate to be a function of cohort type ('high nutrition' or low nutrition'), wet versus dry in the current year ('high prey' or 'low prey') and their interaction, where: $\text{logit}(K) \sim f(\text{cohort}_i * \text{year}_i)$. This allowed us to estimate whether early-life conditions were predictive of growth in later life and how early life conditions influenced sensitivity to annual variation in environmental conditions. To evaluate which period of early development was most sensitive to environmental conditions, we parameterized cohort models for both gestation year, when poor food availability could affect provisioning by mothers, and first-year growth, when poor conditions could directly affect juvenile snakes that are foraging on their own.

We fit all structural growth models within a Bayesian framework using the program JAGS v4.2 (Plummer 2003), accessed through package "jagsUI" (Kellner 2016) in R version 3.4.4 (R Core Team 2014). We ran models on three independent chains for 140,000 iterations each, discarding 125,000 iterations as burn-in. We used uninformative or weakly informative priors for biologically relevant parameters (asymptotic size and growth rate). Convergence was evaluated using the Gelman-Rubin convergence diagnostic, \hat{R} (Brooks and Gelman 1996) and by visually inspecting trace-plots. Model code can be found in the appendix.

Survival—Following Lebreton et al. (1992), we fit survival models that allowed for variation between males and females and across the four different populations. Apparent survival (ϕ) and detection probability (p) parameters were estimated in the program MARK 3.1 (White and Burnham 1999). We modeled data from recaptures of individuals using the default link function and variance estimation to apply the Cormack-Jolly-Seber (CJS) survival model, which allows for unequal time intervals between capture occasions (Cormack 1964, Jolly 1965, Seber 1965). Population, sex and prey year were used as categorical predictors for the global model. Simpler models were explored, and model selection was conducted in an information-theoretical framework based on Akaike's information criterion (AIC) corrected for small sample size (AIC_C) (Akaike 1974) (see Table 3 for summary of AIC_C). We limited our analysis to adults, as there were not enough recaptures of young snakes to accurately estimate survival separately and survival rates between juveniles and adults were unlikely to be the same (Bronikowski and Arnold 1999).

Reproduction—We assessed the effect of environmental conditions on reproduction using linear mixed-effects models using the package 'lme4' (Bates et al. 2015) in R version 3.4.4 (R Core Team 2014). Our response variable was litter size. Litter size was evaluated including a random-effect for individual to account for cases where multiple samples in different years came from the same individual and included SVL as a predictor to control for size, which is a strong predictor of litter size independent of annual variation in environmental conditions. To test our hypotheses, we included population and prey year as fixed effects. We explored all possible models including two- and three-way interactions among population, year, and SVL and performed model selection using AIC (Figure 2.6).

Body condition—We estimated a body condition index, which measure the relative mass of individuals corrected for their overall structural size. Body condition was calculated using external measures of body size: mass (g) and SVL (mm). Condition indices were estimated as the residuals from the ordinary least squares regression of the natural log of mass and the natural log of length, which removes heterogeneity of variance between SVL and mass. Residuals were estimated by fitting the regression using the “lme4” package in R studio. Next, we fit a linear mixed-effect model, which included a random effect for individual, to estimate average condition based on sex and reproductive status (male, non-gravid female, gravid female), population and prey-year, following the general model, $Y = \mu + population + prey-year + sex + error$, where SVL is included to account for the relationship between body size and reproductive output (Figure).

To evaluate the interaction between early-life environmental conditions and ambient resource availability, we used the reduced data set containing only individuals of known cohort that was used for the structural growth analysis. We evaluated the interaction between cohort and prey-year effects on body condition, using the same methodology as described above, reducing our sex-specific evaluation to a categorical predictor with two groups, either gravid females, or non-gravid females and males.

RESULTS

Growth—Male *T. sirtalis* grow to significantly smaller asymptotic sizes than females (Figure 2.2). The estimated mean asymptotic SVL’s was 645 mm for females (95 % CI = 629 to 662 mm), while for males, the mean asymptotic size was 526 mm (CI = 515 to 538). Female *T. sirtalis* exhibited greater variability in asymptotic sizes (standard deviation = 8.36 mm) compared to males (SD = 5.73 mm). Females reached asymptotic sizes at a slightly faster rate ($K = 0.74$, CI = 0.70 to 0.77) than males ($K = 0.75$, 0.71 to 0.79) (Table 2.2). The growth rate did not differ significantly between males and females or across high prey and low prey years.

We did find substantial variation in growth rates when we examined variation within and among populations. Male and female *T. sirtalis* from MAH grew at significantly different rates in both high prey and low prey years (Figure 2.3). Males grew faster ($K = 0.87$, CI = 0.80 to 0.92) than females ($K = 0.47$, CI = 0.39 to 0.55) in high prey years, while females grow faster ($K = 0.82$, CI = 0.77 to 0.86) than males ($K = 0.51$, CI = 0.30 to 0.65) in low prey years. Male and female *T. sirtalis* from RON grew at similar rates within years, but grew significantly faster in high prey years ($K_{male} = 0.19$, CI = 0.03 to 0.45; $K_{female} = 0.45$, CI = 0.27 to 0.63) than low prey years ($K_{male} = 0.93$, CI = 0.83 to 0.99; $K_{female} = 0.92$, CI = 0.84 to 0.98). Individuals from McCoy North (MCN) grew to the largest asymptotic sizes for both males and females, respectively ($L_{\infty} = 564$, CI = 528 to 611; $L_{\infty} = 757$, CI = 703 to 797), while male and female snakes from Mahogany (MAH) grew to the smallest asymptotic SVL’s ($L_{\infty} = 507$, CI = 493 to 523; $L_{\infty} = 603$, CI = 584 to 624).

Cohort Growth—Snakes from low nutrition first-year cohorts grew significantly faster ($K = 0.14$, $CI = 0.05$ to 0.25) in high prey years than high nutrition cohorts ($K = 0.73$, $CI = 0.59$ to 0.82) (Table 2.4). In low prey years, growth varied substantially, particularly for individuals from high nutrition cohorts (Figure 2.4).

Survival—The most parsimonious model for mark-recapture estimates of survival indicated apparent survival by sex and population and capture probability by years (Table 2.6). There was variation among populations and between males and females. However, sex dependent differences were inconsistent (males were in high condition or lower condition across populations) and CI's overlapped in all cases. In general, survival for both sexes was lowest within MCN and highest in NAM (Figure 2.6). Female survival was significantly lower (0.33 , $CI=0.17$ to 0.54) from MCN than both MAH (0.75 , $CI=0.65$ to 0.82) and NAM (0.70 , $CI=0.56$ to 0.81).

Reproduction— Litter size varied by prey year, population, and snout-vent length, as predicted by the top model (Table 2.7.). Mahogany (MAH) females produced the largest litters (effects size = 2.09 ± 0.76), while Nameless (NAM) females produced the smallest litters (effects size = -0.12 ± 0.06) (Figure 2.7.). High prey years increased litter size substantially (effects size = 0.27 ± 0.08). Similarly, SVL had a positive effect on litter size (effects size = 0.26 ± 0.02) (Table 2.8.).

Body Condition—The best model as predicted by AIC included an interaction between early-life nutritional cohort and ambient prey-year conditions with additive effects for population and sex/reproductive status (gravid females or non-gravid females and males) (Table 2.9). Overall, snakes from MCN were in the highest body condition, while those from MAH were in the poorest body condition (Figure 2.8.). Gravid females exhibited higher body condition indices across both high prey and low prey years for all populations (Table 2.10). Non-gravid females nearly always had higher body condition scores than males, with the exception of NAM in low prey years. For most populations, body condition was lowest in low prey years, apart from gravid females from MCN and NAM and males from MCN and RON.

Cohort Body Condition—When cohort was considered, body condition was best predicted by an interaction between cohort and ambient prey year with an additive effect for population and a categorical predictor for sex (gravid females or non-gravid females and males) (Table 2.12.). Populations differed in body condition, with NAM snakes in the lowest body condition and MCN in the highest (Figure 2.9.). Overall, individuals again had higher body condition in high prey years, and individuals that experienced low nutrition early in life were had lower body condition indices than those from high nutrition cohorts. Again, gravid females had higher body condition indices than males and non-gravid females with an effects size of 0.32 ± 0.015 (Table 2.11).

DISCUSSION

We show that variation in demographic parameters among and within populations is predicted by environmental variability for the common garter snake. How these relationships differ across the range of demographic parameters we measured, among different populations, and between males and female illustrate the complex interplay of life-history traits and environment. By quantifying population vital rates and how they respond to changes in environmental conditions, we are able to make important insights into the current status of these populations, and how they are likely to respond to future changes in environmental conditions. Population persistence within heterogenous environments is driven by the interaction between variability in demographic processes with changes in the environment over space and time (Fox and Kendall 2002). Comparisons between our four study populations revealed strong differences in trait means, the magnitude of variability of estimated vital rates, and their interaction with shared environments. We demonstrate that environmental variability and prey availability has the greatest impact on growth, reproduction, and body condition rather than adult survival suggesting low resource availability primarily works by affecting trade-offs between structural growth versus investment in reproduction and nutrient storage. In addition, we demonstrate that early life conditions interact with later life variability to affect rates of structural growth and changes in body condition. Our results demonstrate the substantial year-to-year variation in vital rates common in wild populations. The amount of variation in demographic parameters is governed by fluctuations in the environment, particularly, in hydrologic conditions, which determine prey availability and abundance.

Growth varied between males and females, and among sites and prey-year conditions. Snakes grew fastest *and* slowest in RON—slowest (slower growth compared to other study sites) during low-prey years and fastest during high-prey years. Our results show that the influence of food availability during development and early life as a critical determinant of the evolution of life-history traits in wild populations. Previous studies have shown that an individual's metabolism may be able to utilize energy more efficiently when developmental or early-life environments were nutrient-poor (Prentice et al. 2005). We found a strong influence of past nutritional environments on current rates of growth. Our results show that common garter snakes exposed to nutritionally poor developmental or early-life environments grew at faster rates than their well-provisioned cohort counterparts. Similar work with larval damselflies showed that those exposed to starvation achieved full compensation in body mass compared to individuals in the control group (Block et al. 2008). Growth compensation is a common phenomenon arising when individuals have been subjected to resource scarcity with subsequent accelerated growth once conditions have improved (Metcalf and Monaghan 2001, Stoks et al. 2006, Rotkopf et al. 2013). This result does not support environment-matching, where developmental or early-life conditions prime offspring phenotypes to match the environment predicted by early-life (Monaghan 2008). Rather, we found that low nutrition cohorts were better able to exploit resources when they become abundant, thereby maximizing growth and compensating for dampened growth during earlier resource paucity.

Our results suggest that sexual dimorphism in the populations we studied is primarily related to differences in asymptotic size rather than the speed at which asymptotic sizes are reached. While growth between males and females differed significantly in just one population—NAM, we observed variation in asymptotic size between males and females across all four study populations. Variation in food availability may produce variation in the degree of sexual size dimorphism (SSD), as high-prey environments elicit increased growth rate in whichever sex most benefits from increased body size (Andrews and Stamps 1994, Shine and Madsen 1997, Brown and Weatherhead 1999b). Like many snake species, where larger females exhibit higher reproductive output, female *T. sirtalis* were significantly larger than their male counterparts in all populations. Across populations, the degree of SSD varied, where the largest divergence in size was observed in MCN, which had the largest estimates of mean asymptotic size. Where food is abundant, we might expect females to maximize growth, thereby augmenting future reproductive output, while males may not gain reproductive advantage by increasing structural size.

Fitness advantages resulting from increased body size are unquestionably coupled with related fitness costs (Stearns 1989). For example, starved damselflies were able to compensate for poor early nutrition in body mass, but were less able to invest in immune response and energy storage (Block et al. 2008). We found that the population with the largest snakes, MCN, had the lowest estimate for apparent survival of the four study populations. This may suggest a trade-off between increased growth and survivorship. This relationship which is reflected in the co-occurring western terrestrial garter snake, which have diverged into two disparate ecotypes: a larger, fast-living (e.g. rapid growth, early reproduction, high reproductive output) ecotype with lower survivorship and smaller, slow-living (slower growing, later maturing, lower reproductive output) ecotypes with higher annual survivorship, supporting a trade-off between growth and survival (Bronikowski and Arnold 1999, Miller et al. 2011, Chapter 1). Trade-offs have been shown between food availability and starvation endurance such that individuals developing in environments with stable levels of prey availability are ill-equipped tolerate periods of starvation (Scharf et al. 2009). Gliwicz and Guisande (1992) found that genetically identical *Daphnia* mothers from two separate species under high and low food conditions produced offspring which varied in survivorship during subsequent periods of starvation. Mothers raised under nutritionally restrictive conditions produced offspring capable of surviving long periods of starvation, while mothers exposed to high food levels generated litters which were unable to survive for long under starvation conditions (Gliwicz et al. 1992). Conversely, Warner et. al (2015) found that growth in brown anole lizards (*Anolis sagrei*) was reduce in low prey conditions regardless of prey-conditions during gestation.

A strong positive relationship exists between female snout-vent length and litter size (Figure 2.10.). The slope of the relationship between body size and litter size was similar among populations. Consistent with this relationship, populations exhibiting larger mean female body size produced larger litters (Figure 2.7.). For females, maximizing structural growth increases future reproductive potential, and thereby lifetime fitness. Our data was insufficient to include a

sex effect in our cohort models in order to investigate the interaction between early-life environment, ambient environment and sex, yet the larger sex in sexually dimorphic species benefits most by increasing size, particularly in viviparous species (Shine 1994, Brown and Weatherhead 1999b). In general, males grow faster than females (Table 2.2), with the exception of females in MAH during high-prey conditions (Figure 2.3.). These results reflect context dependent trade-offs between growth and reproduction. In addition, resource availability has been shown to influence reproductive output across multiple taxa including mammals (Tannerfeldt and Angerbjorn 1998), birds (Meyrier et al. 2017), fish (Hutchings 1991), reptiles (Hall et al. 2018b). We found that high-prey years resulted in litters which were ~25% larger, suggesting that these populations rely on prevailing energy acquisition for reproduction.

The ability to efficiently assimilate energy and store body reserves influences survival and reproduction (Naulleau and Bonnet 1996, Benson and Bednarz 2010). Snakes in the highest overall body condition (weighed more than predicted) were in MCN and RON populations, which also had the highest estimates for litter size (Figure 2.8 and Figure 2.7.). Gravid females were in higher body condition across all populations, indicating a link between nutrient reserves and reproduction. The variability in the effect of prey abundance on growth and body condition likely indicates complex trade-offs in the investment of energy, which differ across populations and between males and females. At the population level, growth and body condition varied, suggesting local adaptation to small-scale differences in environments encountered by discrete populations. Snakes from MAH grew to smaller asymptotic sizes and exhibited lower than average body condition when compared to the other three study populations. Likewise, MCN snakes were in the highest body condition, overall, and grew to larger asymptotic sizes than snakes from the other populations yet had the lowest estimated apparent survival. Males were, in general, in lower body condition than females (gravid or non-gravid).

Early-life environment was a critical component of body condition later in life for populations of the common garter snake in our study system. High nutrition cohorts were in better body condition across all populations and prey-year interactions, suggesting an ontogenetic benefit to resource rich early-life environments. Similarly, body condition of both high and low nutrition cohorts was positively related to prevailing high-prey environments. Non-gravid females and males were in lower condition than gravid females in across all populations. The rate of acquisition of energy reserves and the trade-off between storage of body reserves and growth should determine reproductive frequency in capital breeders (Sibly and Calow 1986). There may be combined thresholds of structural size and body condition for reproduction, which could vary among populations.

Our results suggest a strong influence of prey availability on growth, body condition and litter size, but little to no effect on survival. While positive correlations in fitness traits and prey abundance are common (Weatherley and Gill 1981, Brown et al. 2017, Carvell et al. 2017), underlying mechanisms of environment and phenotype matching may cause populations to exhibit positive correlations in fitness traits, where a negative relationship is expected. The

positive influence of poor nutrition on later growth suggests a priming effect for individuals exposed to nutritionally stressful early-life environments. Although energy input is the ultimate driver of life-history evolution (Lack 1954, Stearns 1992), interactions between early and late-life environment results in direct and indirect trade-offs. Growth is frequently related to other vital rates including survival, reproductive success and maturity, and variation in these traits has implications for individual fitness as well as population dynamics (Fox and Kendall 2002). Variation in vital rates signals underlying mechanisms which link ecology and evolution of animal populations and ultimately determine population viability (McGraw and Caswell 1996, Metcalf and Pavard 2007). Studies like this one can bridge the gap between conservation management and population level vital rates which drive the evolution of life-history strategies. The information obtained from studies such as this are fundamental to determining which parameters are most strongly influenced by environmental fluctuations. These results highlight the importance of quantifying the specific responses of populations and the divers of change within an environment through comparative studies of multiple populations over time. Estimates of temporal variability in vital rates including growth, survival, and reproduction are essential to inform conservation and management strategies determine the viability of populations in the long term, particularly in the face of predicted environmental fluctuations in a rapidly changing global climate. (Karl et al. 1995, Easterling et al. 2000, Anderson et al. 2008, Buckley 2008).

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Appendix A: Chapter 1 Tables

Table 1.1. Summary of study sites. Sample sizes by populations and ecotype, years studied, and total observations and recaptures, including totals summed from all populations within each ecotype.

Study Sites	Site Code	Years Studied	Observations	Recaptures
Lakeshore			2634	649
Totals				
Pikes	PIK	1978-1988; 1994-1995	1353	408
Gallatin	GAL	1980-1986; 1988; 1994-1995	1027	201
Meadow Totals			3841	1220
Papoose	PAP	1979-1989; 1992; 1994-1996	2040	713
Mahogany	MAH	1978-1980; 1982-1989; 1994-1996	896	275
Nameless	NAM	1980; 1982-1988	603	92

Table 1.2. Estimates of von Bertalanffy growth model for male and female *T. elegans*. Results for average growth coefficient (μK) and asymptotic size (L_∞) from sex-specific VB growth model with mean estimates and 95% confidence intervals.

μK Estimate	Confidence Interval		L_∞ Estimate	Confidence Interval		Sex	Ecotype
	2.5	97.5		2.5	97.5		
0.683305	0.650446	0.715653	568.667	549.756	590.666	Male	Lakeshore
0.705577	0.676121	0.731648	677.232	654.558	702.381	Female	Lakeshore
0.7665622	0.7455466	0.7856666	493.306	489.042	497.606	Male	Meadow
0.7665622	0.7455466	0.7856666	536.095	531.467	540.96	Female	Meadow

Table 1.3. Summary of sex-specific results for growth rate during high prey and low prey years. Estimates of the mean growth coefficient (μK) for lakeshore and meadow ecotypes of *T. elegans*, including mean values and 95% confidence intervals across high and low prey conditions.

<u>Lakeshore Ecotype</u>				
High Prey Years	Mean Estimate (μk)	95% Confidence Interval		
		2.5	97.5	
Males	0.6961434	0.657461	0.7330201	
Females	0.6980438	0.6650765	0.7280992	
Low Prey Years				
Males	0.6661893	0.6212836	0.708064	
Females	0.7215172	0.6891182	0.7538032	
<u>Meadow Ecotype</u>				
High Prey Years	Mean Estimate (μk)	95% Confidence Interval		
		2.5	97.5	
Males	0.7725911	0.7498852	0.7946197	
Females	0.7642278	0.7470613	0.7798856	
Low Prey Years				
Males	0.745167	0.6980438	0.7856666	
Females	0.7277031	0.6833045	0.7663832	

Table 1.4. Estimated growth coefficients for gestational cohorts of *T. elegans*. Summary of average growth coefficients from fast-living Lakeshore and slow-living meadow ecotypes of *T. elegans* from either high or low maternal nutrition cohorts across high and low prey years.

Lakeshore Ecotype				
	High Prey Years		Low Prey Years	
	μK	95% Confidence Interval	μK	95% Confidence Interval
High Nutrition	0.7039	(0.6383, 0.7575)	0.7074	(0.6288, 0.7676)
Low Nutrition	0.7377	(0.6959, 0.7733)	0.7358	(0.6957, 0.7714)
Meadow Ecotype				
	High Prey Years		Low Prey Years	
	μK	95% Confidence Interval	μK	95% Confidence Interval
High Nutrition	0.7612	(0.7191, 0.8004)	0.7789	(0.6651, 0.8542)
Low Nutrition	0.6595	(0.5681, 0.7371)	0.6243	(0.5237, 0.7043)

Table 1.5. Estimated growth coefficients for first-year cohorts of *T. elegans*. Results for average growth coefficient (μK) for high nutrition and low nutrition first-year cohorts during high prey years and low prey years from the VB growth model with mean estimates and 95% confidence intervals.

Lakeshore Ecotype						
	High Nutrition Cohorts			Low Nutrition Cohorts		
	μK	95% Confidence Interval		μK	95% Confidence Interval	
		2.5	97.5		2.5	97.5
High Prey Years	0.7247207	0.6787428	0.7654868	0.7480049	0.7043294	0.7873458
Low Prey Years	0.7711824	0.686111	0.827641	0.7275049	0.6846015	0.7674557
Meadow Ecotype						
	High Nutrition Cohorts			Low Nutrition Cohorts		
	μK	95% Confidence Interval		μK	95% Confidence Interval	
		2.5	97.5		2.5	97.5
High Prey Years	0.7277031	0.6904021	0.7636869	0.4434924	0.298385	0.5719961
Low Prey Years	0.7576796	0.5555201	0.8259225	0.6389939	0.541405	0.7164663

Table 1.6. AIC table for cohort body condition for populations of *T. elegans*. Linear mixed-effects models for body condition of the common garter snake in northeastern California. All models include a random effect for individual to control for non-independence of repeat measures. Predictor variables are categorical: Cohort (High Nutrition or Low Nutrition), Prey-Year (High Prey or Low Prey), Ecotype (Lakeshore or Meadow), Sex Effect (Gravid or Non-gravid/males).

Model	AIC	ΔAIC	No. Fixed Parameters
Cohort x Prey-Year + Ecotype + Cohort x Sex Effect	-3045.474	0	7
Cohort x Prey-Year + Ecotype + Sex Effect	-3044.478	0.996	6
Cohort x Prey-Year + Cohort x Ecotype + Cohort x Sex Effect	-3043.775	1.699	8
Cohort x Prey-Year + Cohort x Ecotype + Sex Effect	-3042.834	2.64	7
Prey-Year + Ecotype + Cohort + Sex Effect	-3007.662	37.812	5
Prey-Year + Cohort x Ecotype + Sex Effect	-3006.249	39.225	6
Prey-Year + Ecotype + Cohort x Sex Effect	-3006.130	39.344	6
Prey-Year + Cohort x Ecotype + Cohort x Sex	-3004.694	40.78	7
Null (Intercept only)	-2583.658	461.816	1

Appendix B: Chapter 2 Tables

Table 2.1. Summary table of study sites for *T. sirtalis* populations. Summary of study populations, number of observations, recaptures and years studied.

Study Site	Site Code	Total Captures	Recaptures	Years Studied
Mahogany	MAH	597	139	1978-1989; 1993-1994
Roney Corral	RON	411	101	1979-1981; 1984-1986
Nameless	NAM	248	73	1980; 1982; 1984-1988; 1994
McCoy North	MCN	187	74	1979-1981; 1983-1985; 1987-1988

Table 2.2. VB growth estimates for male and females. Estimates of mean growth rate relative to the maximum (K) and asymptotic length (L_{∞}) for each population and combined analysis. Larger values of K represent slower overall growth rate per year. Estimates represent means with 95% confidence intervals.

Population	Sex	K	L_{∞}
MAH	Male	0.668 (0.556, 0.750)	506.954 (492.546, 522.862)
	Female	0.644 (0.566, 0.706)	602.512 (584.167, 623.982)
RON	Male	0.748 (0.682, 0.800)	520.53 (503.07, 540.007)
	Female	0.797 (0.740, 0.843)	671.135 (635.241, 726.906)
NAM	Male	0.565 (0.231, 0.729)	552.125 (528.813, 581.562)
	Female	0.818 (0.749, 0.865)	673.458 (638.166, 715.883)
MCN	Male	0.644 (0.343, 0.806)	563.508 (527.967, 610.72)
	Female	0.694 (0.433, 0.808)	757.417 (703.237, 797.305)
COMBINED	Male	0.750 (0.706, 0.787)	526.755 (516.161, 538.345)
	Female	0.738 (0.699, 0.771)	645.882 (630.411, 663.007)

Table 2.3. Estimates of asymptotic size (L_{∞}) for *T. sirtalis*. Estimates of asymptotic snout-to-vent length generated from the von Bertalanffy growth model for male and female common garter snakes. Mean estimates with corresponding 95% credible intervals are shown for model estimates. Using the slope of the log transformed linear relationship between mass and length, we calculated the % difference between mean estimates for L_{∞} between males and females from each of the four study populations.

Population	Asymptotic Length (L_{∞})		% Diff in SVL	% Diff in Body Vol.
	Males	Females		
MAH	509.737 (494.691, 525.991)	597.511 (581.605, 614.594)	17.2195	62.5109
RON	518.305 (502.935, 534.524)	660.778 (633.454, 697.254)	27.4883	107.21
NAM	552.215 (528.845, 581.408)	668.482 (632.937, 713.519)	21.0547	77.3963
MCN	562.596 (526.92, 609.893)	758.081 (702.276, 797.641)	34.7469	144.657

Table 2.4. Estimated growth coefficients for first-year cohorts of *T. sirtalis*. Results for average growth coefficient (K) for high nutrition and low nutrition first-year cohorts during high prey years and low prey years from the VB growth model with mean estimates and 95% confidence intervals.

	Lakeshore Ecotype					
	High Nutrition Cohorts			Low Nutrition Cohorts		
	K	95% Confidence Interval		K	95% Confidence Interval	
		2.5	97.5		2.5	97.5
High Prey Years	0.7283	0.5927	0.8164	0.1431	0.0511	0.2469
Low Prey Years	0.7060	0.6219	0.8235	0.7673	0.7077	0.8153

Table 2.5. AIC table for Cormack-Jolly-Seber survival models. Estimates obtained from program MARK, for annual apparent survival of the common garter snake in northeastern California. Groups represent males and females from each of the four populations.

Model	ΔAIC_c	AIC _c Weight	Model Likelihood	No. Params	Deviance
ϕ (Group) p (Population x Year)	0	0.987	1.000	41	218.895
ϕ (Group) p (Group x Year)	10.267	0.006	0.006	73	159.481
ϕ (Sex) p (Group x Year)	10.679	0.005	0.005	67	173.216
ϕ (Group x Year) p (Group)	11.832	0.003	0.003	69	169.942
ϕ (Population) p (Group x Year)	263.156	0.0000	0.0000	194	114.984
ϕ (Group x Year) p (Group + Year)	11261.973	0.0000	0.0000	75	11406.719

Table 2.6. Apparent survival by population and sex. Estimate of apparent survival (ϕ) by population and sex of *T. sirtalis* generated using the CJS model in the program MARK.

Estimate of ϕ	95% Confidence Intervals		SE	Population	Sex
	Lower	Upper			
0.676	0.494	0.817	0.085	RON	Females
0.751	0.567	0.874	0.080	RON	Males
0.690	0.579	0.783	0.053	MAH	Females
0.515	0.381	0.646	0.069	MAH	Males
0.698	0.515	0.834	0.084	NAM	Females
0.650	0.391	0.843	0.123	NAM	Males
0.301	0.161	0.492	0.087	MCN	Females
0.496	0.364	0.629	0.069	MCN	Males

Table 2.7. AIC table for litter size models predicted for populations of *T. sirtalis*. Summary of AIC model ranking for linear models predicting litter size. All models included an effect for snout-vent length (SVL) to control for known body size.

Model	AIC	ΔAIC	No. Fixed Parameters
Prey Year + Population + SVL	983.410	0	6
Population x SVL + Prey Year	988.057	4.647	9
Population x Year	988.540	5.129	9
Population + SVL	993.583	10.173	5
Population x Prey Year x SVL	994.457	11.046	15
Year + SVL	996.519	13.109	3
Population x SVL	997.481	14.071	8
Null Model	1004.475	21.065	2

Table 2.8. Fixed effects for relative litter size for populations of *T. sirtalis*. from linear mixed effects model. Response variable, litter size, is best predicted using an additive model with predictor variables of population, prey year (dry-low prey or wet-high prey) and snout-to-vent length (SVL).

Fixed Effects	Estimate	SE
MAH (Intercept)	2.089	0.076
Wet Year	0.266	0.078
MCN	0.182	0.083
NAM	-0.124	0.064
RON	0.112	0.051
SVL	0.259	0.022

Table 2.9. AIC table for relative body condition models for *T. sirtalis* populations. Linear mixed effects models for body condition of the common garter snake in northeastern California. All models include a random effect for individual to control for non-independence of repeat measures.

Model	AIC	Δ AIC	No. Fixed Parameters
Year x Sex + Sex x Population + Population x Year	-733.050	0	18
Year x Sex + Population	-668.463	64.587	9
Sex x Population + Year	-667.717	65.333	13
Year + Sex + Population	-663.670	69.381	7
Year x Sex x Population	-618.977	114.073	24
Sex x Population	-606.782	126.269	12
Population x Year + Sex	-493.521	239.529	9
Sex x Year	-364.607	368.443	6
Population x Year	-345.215	387.835	8

Table 2.10. Fixed effects for body condition model. Summary of fixed effects results from linear model using body condition as a response variable predicted by three two-way interactions: population (MAH, MCN, NAM and RON) x sex/reproductive status (male, non-gravid female, or gravid female) + prey year (high prey or low prey) x sex/reproductive status + population x prey year

Fixed effects	Estimate	SE
Non-gravid Female (Intercept)	-0.175	0.014
Gravid Female	0.224	0.036
Male	-0.055	0.019
High Prey Year	0.176	0.024
MCN	0.326	0.036
NAM	-0.049	0.029
RON	0.289	0.021
Gravid Female x High Prey Year	0.036	0.041
Male x High Prey Year	-0.064	0.027
Gravid Female x MCN	-0.019	0.056
Male x MCN	-0.038	0.043
Gravid Female x NAM	-0.076	0.045
Male x NAM	0.060	0.036
Gravid Female x RON	0.032	0.041
Male x RON	-0.026	0.029
MCN x High Prey Year	-0.165	0.038
NAM x High Prey Year	0.084	0.035
RON x High Prey Year	-0.169	0.031

Table 2.11. AIC table for cohort body condition for populations of *T. sirtalis*. Linear mixed-effects models for body condition of the common garter snake in northeastern California. All models include a random effect for individual to control for non-independence of repeat measures. Predictor variables are categorical: Cohort (High Nutrition or Low Nutrition), Prey-Year (High Prey or Low Prey), Population (MAH, RON, NAM, MCN), Sex Effect (Gravid or Non-gravid/males).

Model	AIC	ΔAIC	No. Fixed Parameters
Cohort x Prey-Year + Population + Sex Effect	-728.1511	0	8
Cohort x Prey-Year + Population + Cohort x Sex Effect	-726.3608	1.7903	9
Cohort x Prey-Year + Cohort x Population + Sex Effect	-723.3452	4.8059	11
Prey-Year + Population + Cohort + Sex Effect	-722.8139	5.3372	7
Cohort x Prey-Year + Cohort x Population + Cohort x Sex Effect	-721.4941	6.657	12
Prey-Year + Cohort x Population + Sex Effect	-720.9778	7.1733	10
Prey-Year + Population + Cohort x Sex Effect	-720.8147	7.3364	8
Prey-Year + Cohort x Population + Cohort x Sex Effect	-718.9778	9.1733	11
Cohort x Prey-Year x Population	-371.637	356.5141	16
Cohort x Population	-57.47549	670.67561	8

Table 2.12. Fixed effects for cohort body condition model. Summary results from linear mixed effects model. Response variable, body condition, is best predicted with a two-way interaction between early-life nutritional cohort (high nutrition or low nutrition) and ambient prey year (high prey or low prey) with additive effects for predictor variables of population and a sex effect (gravid females or non-gravid females and males).

Fixed Effects	Estimate	SE
MAH (Intercept)	-0.316	0.017
High Nutrition Cohort	0.071	0.010
High Prey Year	0.176	0.024
MCN	0.184	0.021
NAM	0.073	0.016
RON	0.242	0.013
Gravid Female	0.322	0.015
High Nutrition Cohort x High Prey Year	-0.041	0.015

Appendix C: Chapter 1 Figures

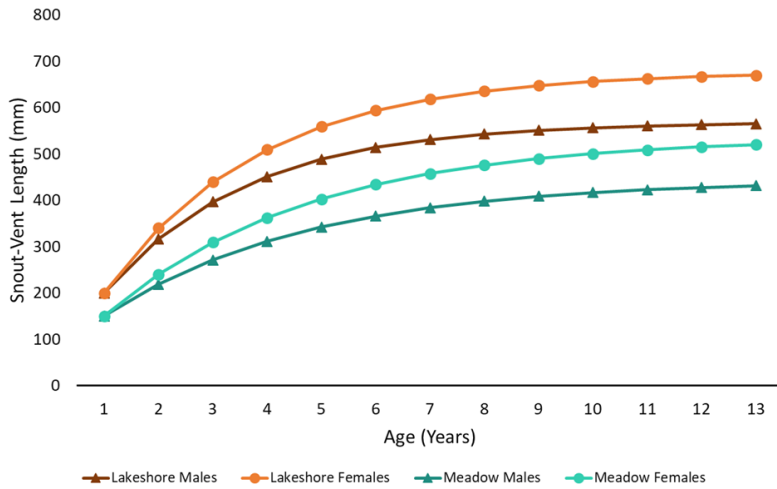


Figure 1.1. Growth curves for lakeshore and meadow ecotypes of the western terrestrial garter snake. von Bertalanffy growth curves for male and female western terrestrial garter snakes from northern California populations consisting of divergent ecotypes. Curves depict the approach to asymptotic size as individuals age. Lakeshore ecotypes grow to larger asymptotic size more rapidly than the slower-growing meadow ecotype.

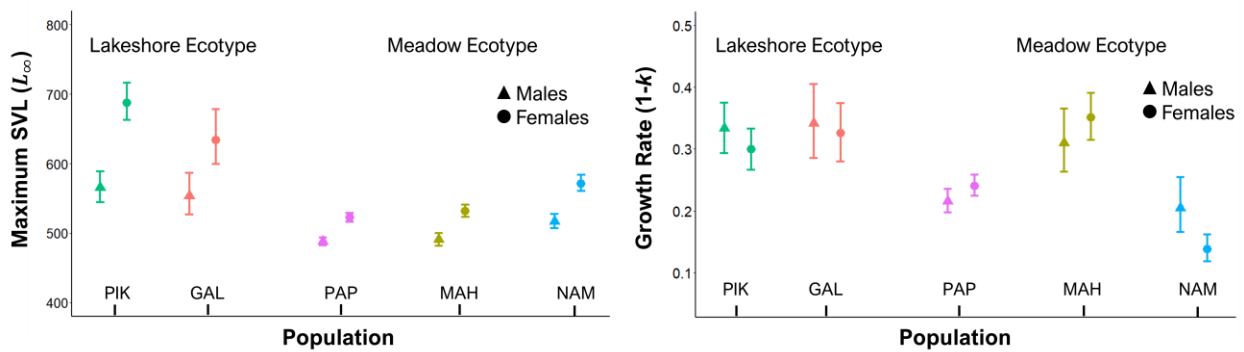


Figure 1.2. Mean growth parameters estimated from the VB growth model. (A) Average maximum snout-to-vent length (L_{∞}) and (B) average growth rate (K) by population for both Lakeshore and Meadow ecotypes. Growth rate is reported as the inverse such that higher values depict faster growth. Bars indicated 95% confidence intervals.

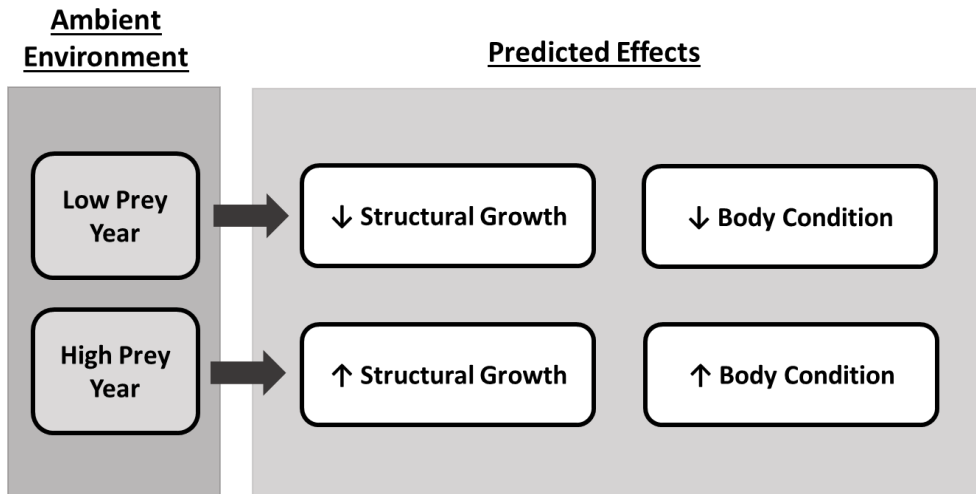


Figure 1.3. Theoretical schematic of predicted effects of prey conditions on structural growth and body condition. Annual fluctuations in prey are classified as either low or high.

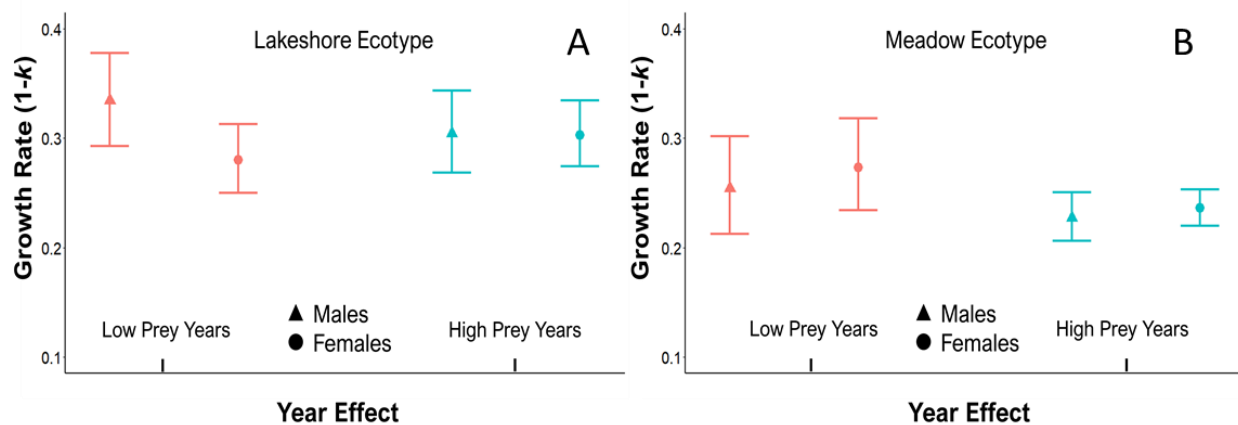


Figure 1.4. Low and high prey year growth for male and female *T. elegans*. Average growth rate for males and females by population for both Lakeshore (A) and Meadow (B) ecotypes during either low prey or high prey years. Bars indicated 95% confidence intervals.

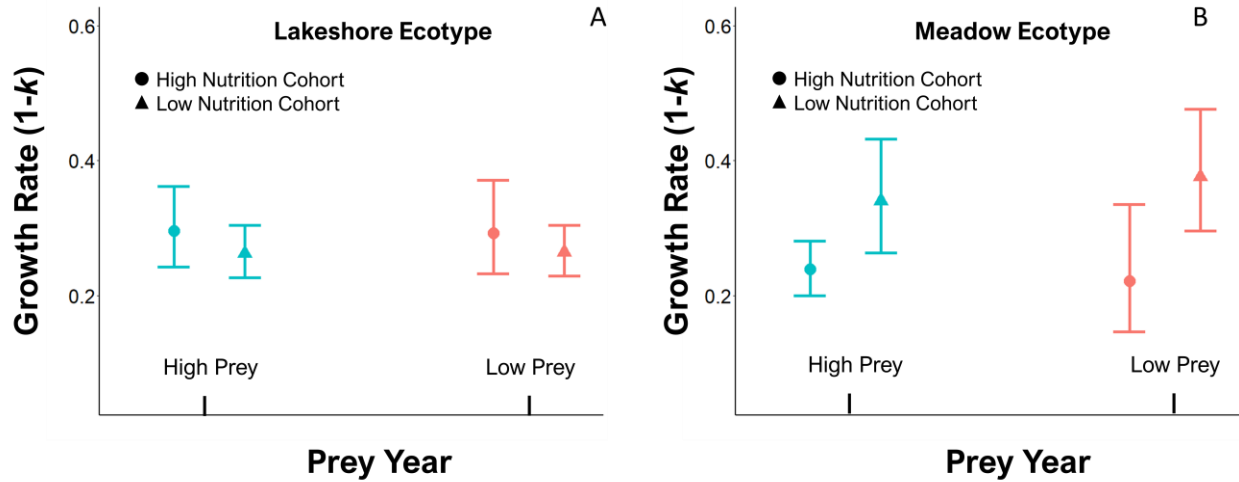


Figure 1.5. Gestational cohort mean growth for high and low prey years. Average growth rate for gestational cohorts from either low nutrition and high nutrition years during gestation by population for both Lakeshore and Meadow ecotypes during either low prey or high prey years. Bars indicated 95% confidence intervals.

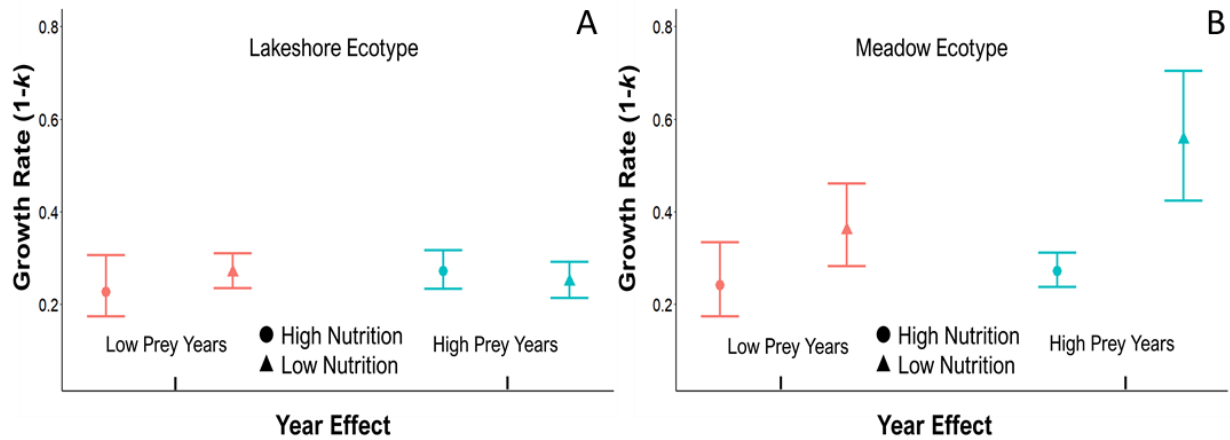


Figure 1.6. First foraging year cohort mean growth for high and low prey years. Average growth rate for cohorts grouped by nutritional environment (high nutrition or low nutrition) during the first year of life for both Lakeshore and Meadow ecotypes during either low prey or high prey years.

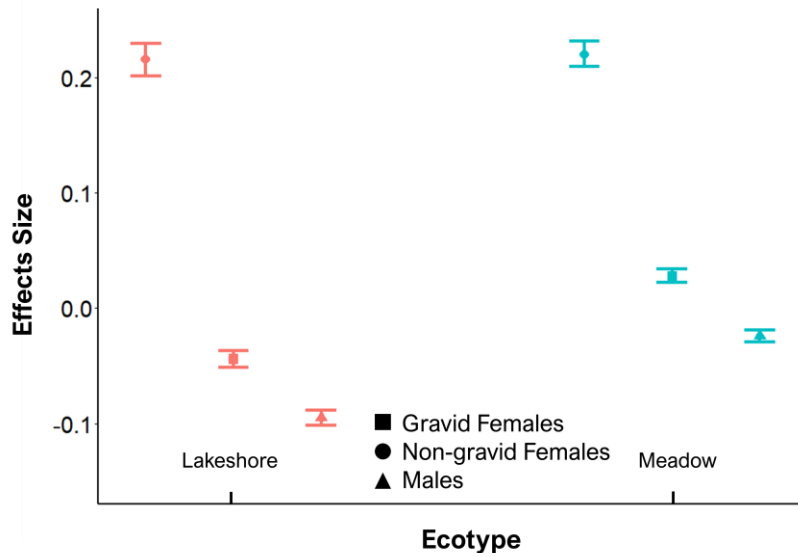


Figure 1.7. Relative body condition across two ecotypes of *T. elegans*. Average body condition of lakeshore and meadow snakes by sex and reproductive status, ignoring the effect of prey-year. Gravid females from both ecotypes exhibit similar body condition, while non-gravid females and males from meadow populations are in better condition than lakeshore non-gravid females and males. Bars indicated 95% confidence intervals.

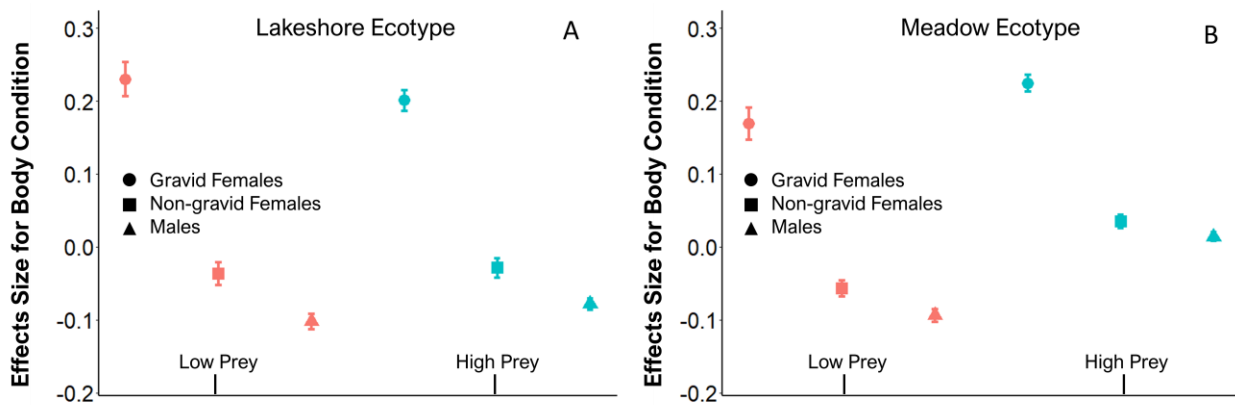


Figure 1.8. Relative body condition across two ecotypes of *T. elegans* in low prey and high prey environments. Effects size for body condition predicted by most parsimonious linear model with the form Body Condition \sim Year*Sex + Ecotype*Sex + Ecotype*Year. Fast-living lakeshore snakes (A) and slow-living meadow snake (B) vary by sex and reproductive status across prey years.

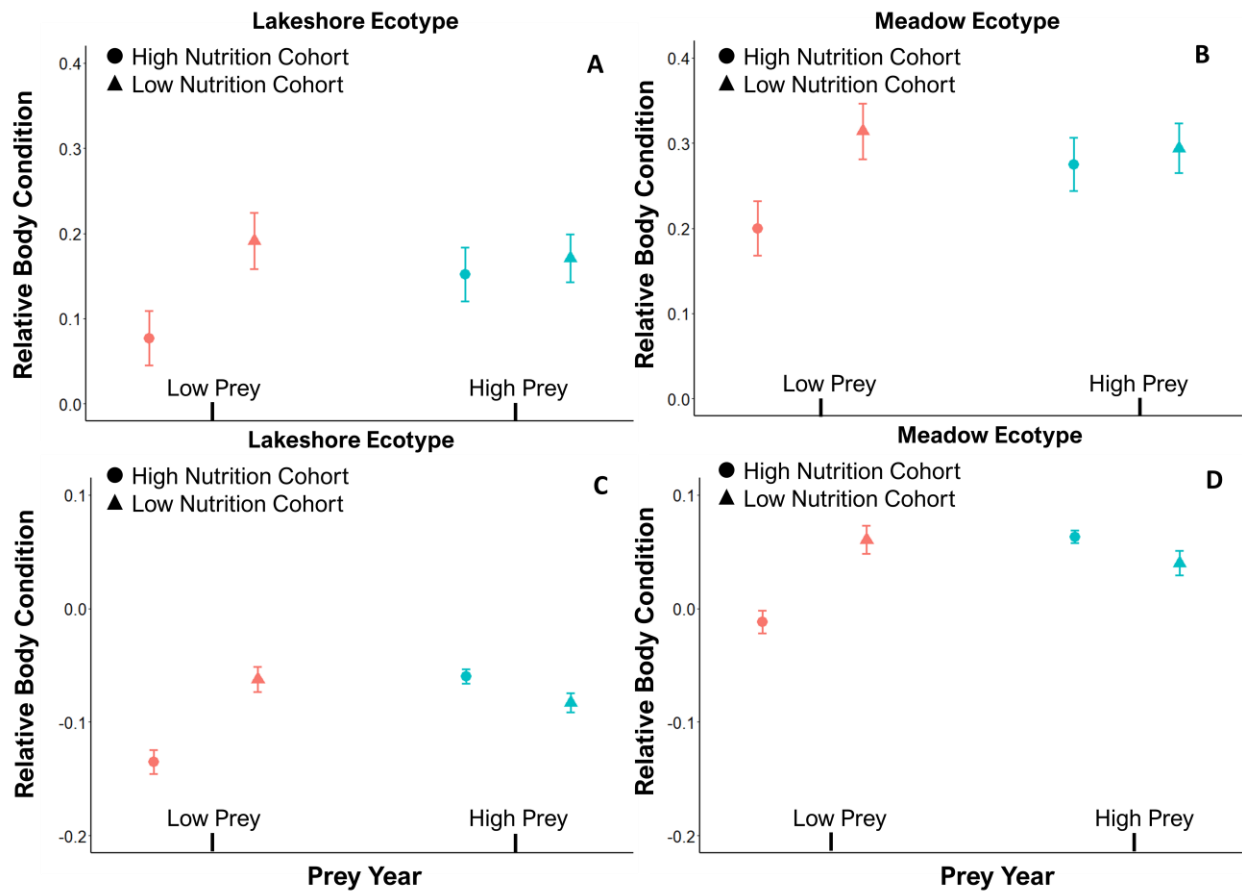


Figure 1.9. Relative condition predicted by early-life cohort and ambient prey environment. Body condition was best predicted by an interaction between early-life cohort and prey-year environment, an interaction between cohort and sex effect (gravid or non-gravid females/males) with an additive effect for ecotype (lakeshore or meadow). Panel A) shows the relative body condition of gravid lakeshore snakes in high and low prey conditions, B) shows gravid meadow snakes, C) show non-gravid lakeshore snakes, and D) depicts non-gravid meadow snakes.

Appendix D: Chapter 2 Figures

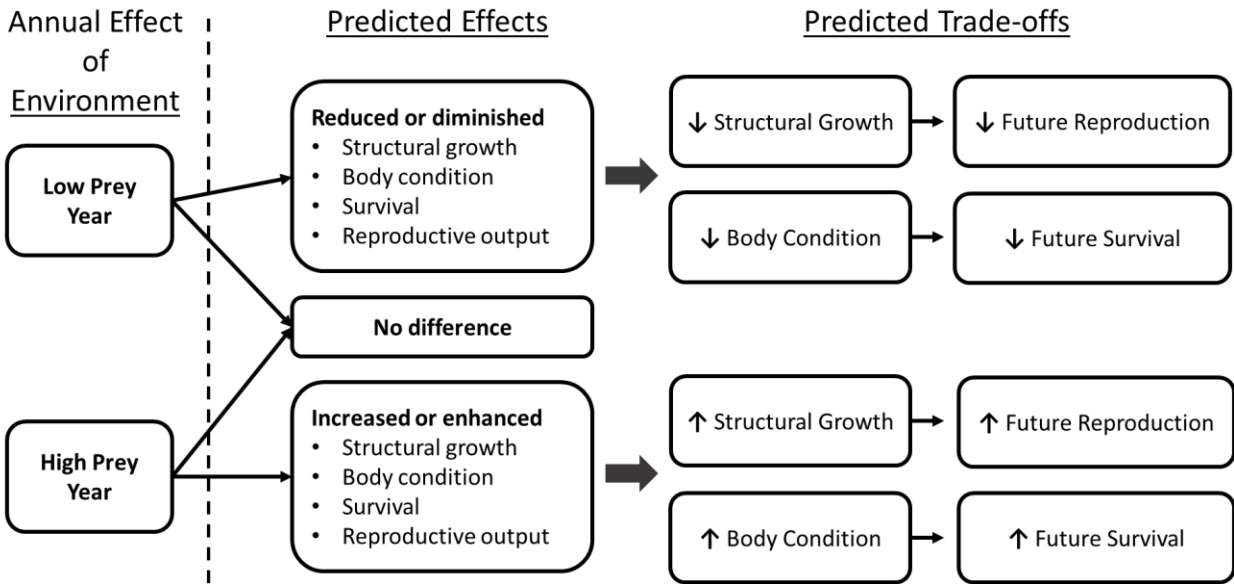


Figure 2.1. Theoretical schematic of predicted effects of environmental variation on life-history-traits in free-living populations of the common garter snake (*Thamnophis sirtalis*). Variation in environmental conditions (e.g. prey abundance) affect population vital rates including growth, body condition, survival and reproduction.

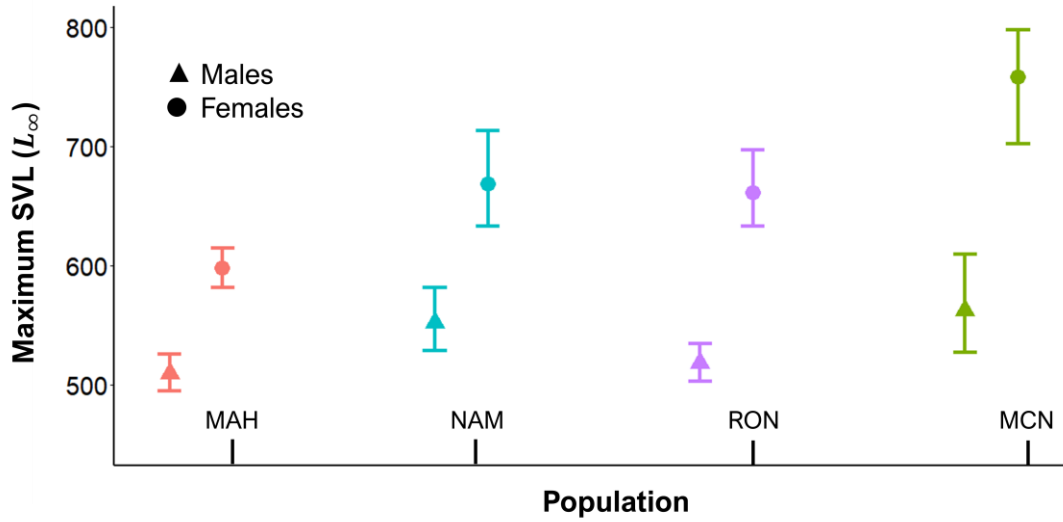


Figure 2.2. Estimates of asymptotic size (L_{∞}) for populations of *T. sirtalis*. Estimates from the von Bertalanffy growth model for maximum snout-to-vent (L_{∞}) across the four study populations, Mahogany (MAH), Nameless (NAM), Roney Corral (RON) and McCoy North (MCN). Points represent mean estimates and error bars depict the 95% credible intervals. Populations are grouped by males (triangles) and females (circles).

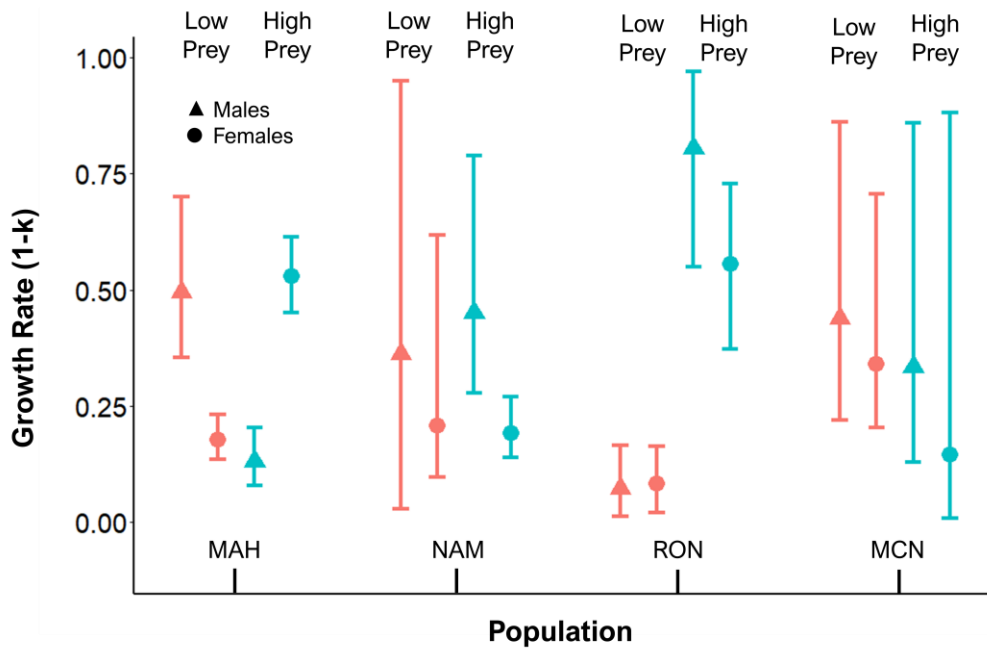


Figure 2.3. Population and sex-specific growth rates for *T. sirtalis* in low prey and high prey environments. The inverse of the von Bertalanffy growth coefficient (higher values indicate faster growth) between males (triangles) and females (circles) across four study populations in either low prey or high prey environments. Mean estimates are indicated by points, while error bars indicate the 95% confidence intervals.

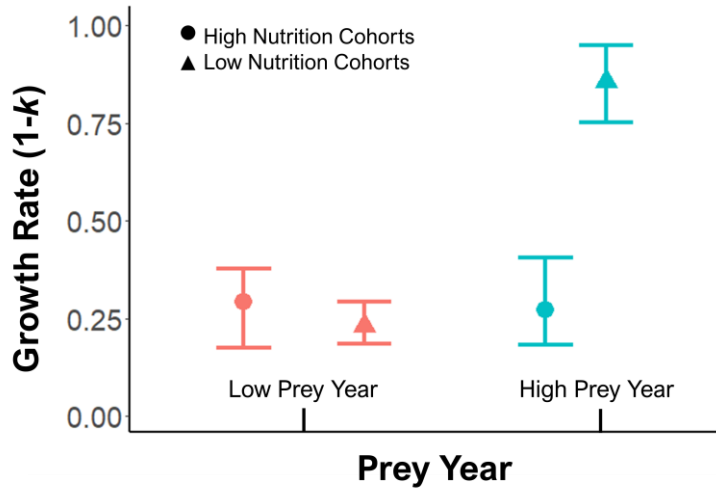


Figure 2.4. First-year cohort growth rate in low and high prey environments. The inverse of the von Bertalanffy growth coefficient (K), points represent the posterior mean estimate of K for first-year cohorts in low prey (red) and high prey years (blue). Error bars show 95% confidence intervals. Circles represent individuals from high nutrition cohorts and triangles depict those from low nutrition cohorts.

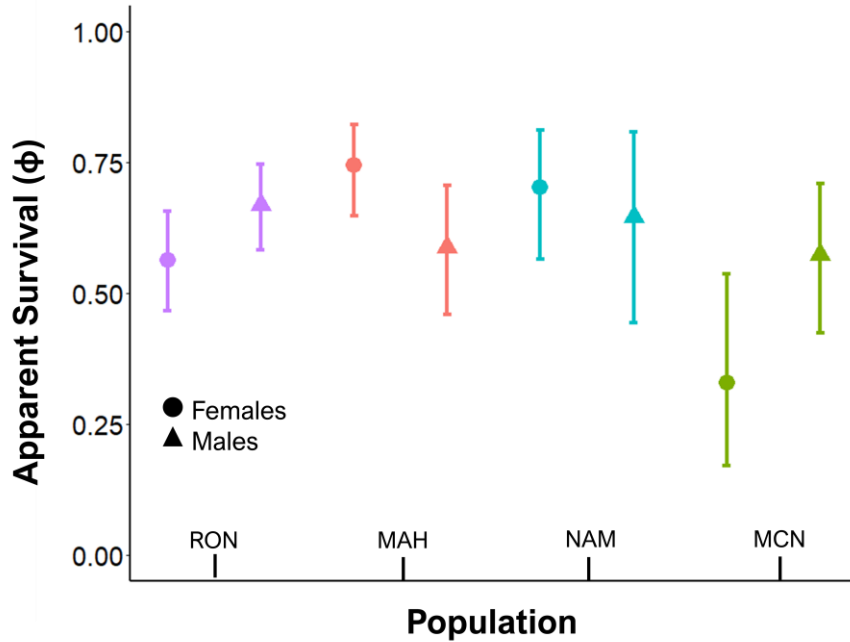


Figure 2.5. Estimates of sex-specific apparent survival by population from CJS survival models generated in the program MARK. Points indicate mean survivorship and error bars depict the 95% confidence interval. Estimates are shown for males (triangles) and females (circles) from each of the four study populations.

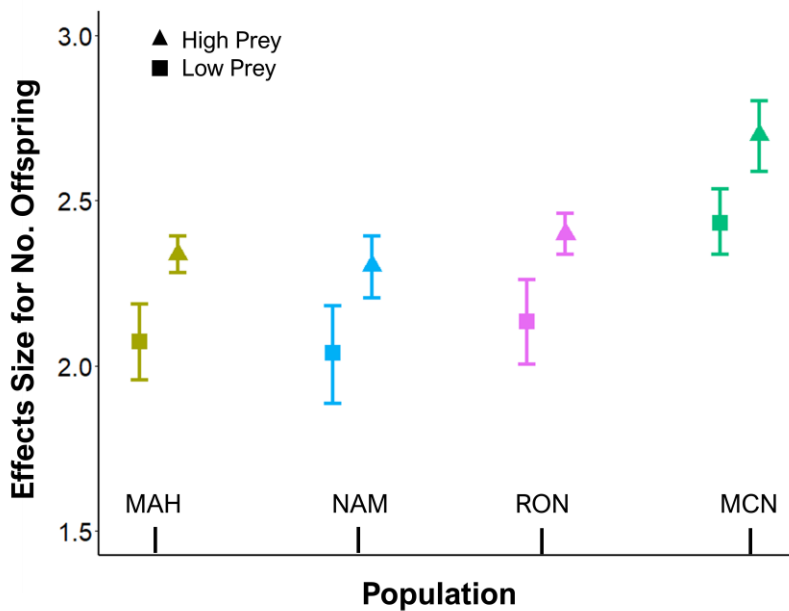


Figure 2.6. Effect of population and prey-year conditions on litter size. Mean effects size by population for predicted litter size given year effect (high-prey or low-prey). Points depict mean estimates and error bars indicate 95% confidence intervals. The general model is $Litter\ size \sim Prey-Year + Population + SVL$

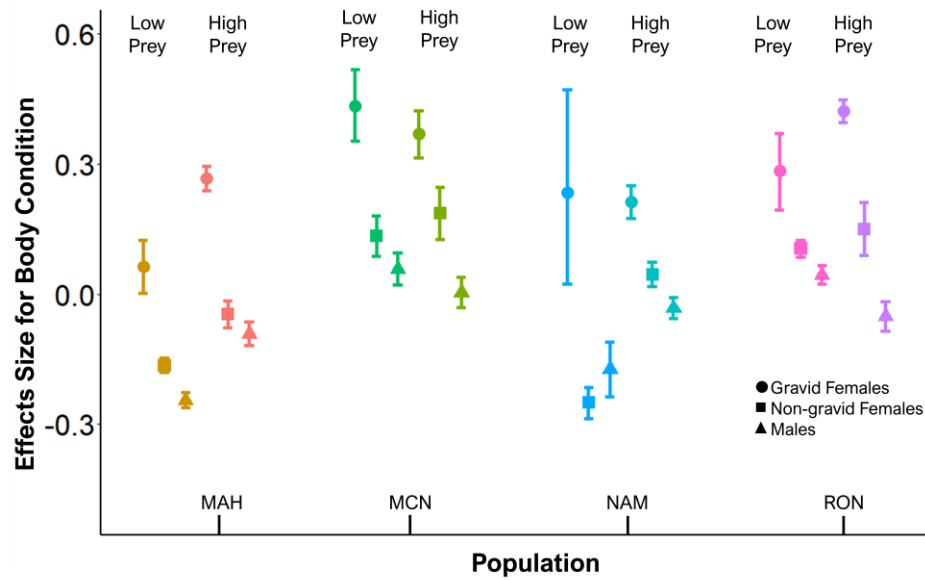


Figure 2.7. Effect of population, sex/reproductive status and prey-year conditions on body condition. Variation in body condition of the common garter snake, as measured by residuals from the linear regression of ln-transformed body mass versus ln-transformed snout-vent length across high prey and low prey years within populations. Snakes are grouped by sex/reproductive status into three groups: gravid females, non-gravid females and males. Points represent mean effects size, and error bars depict the 95% confidence interval.

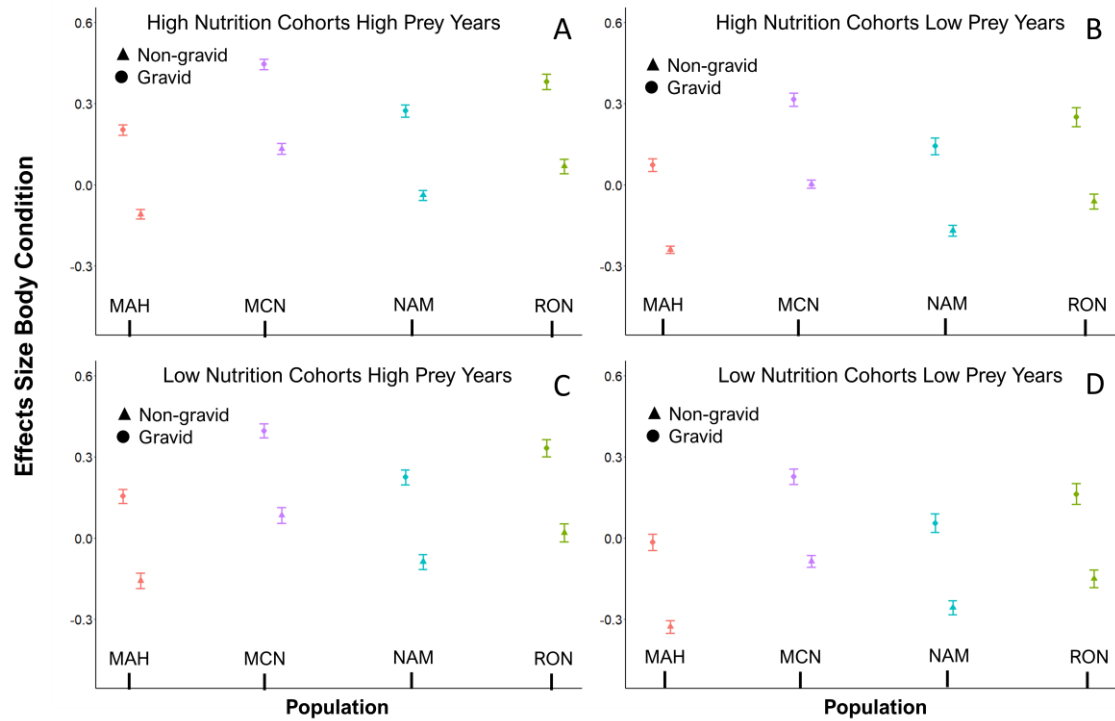


Figure 2.8. Effect of early-life cohort, population, sex/reproductive status and prey-year conditions on body condition Mean effect size of body condition predicted by the interaction between early-life nutritional cohort and prey-year with an additive effect for population and sex effect (gravid or non-gravid) for each of four study populations of *T. sirtalis*. Panel A) depicts high nutrition cohorts in high prey years, while B) shows high nutrition cohorts in low prey years. Similarly, panels C) and D) show low nutrition cohorts across high and low prey years.

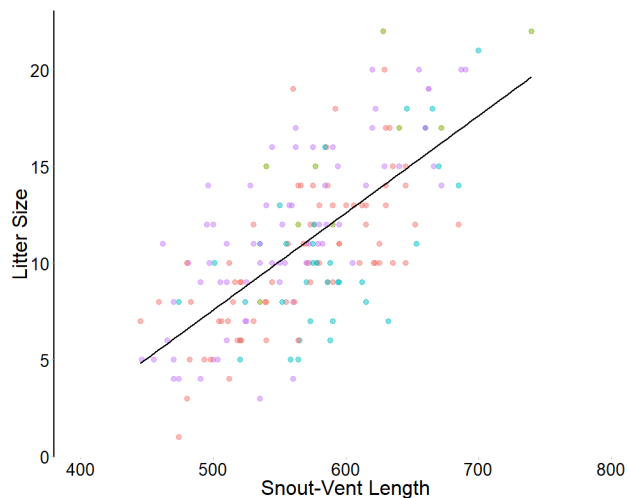


Figure 2.9. Relationship between snout-vent length and litter size in populations of *T. sirtalis*. Litter size (number of embryos) plotted against snout-vent length for the common garter snake. Trend line shows the average relationship for all four study populations.