

# An empirical test of evolutionary theories for reproductive senescence and reproductive effort in the garter snake *Thamnophis elegans*

Amanda M. Sparkman<sup>1</sup>, Stevan J. Arnold<sup>2</sup> and Anne M. Bronikowski<sup>1,\*</sup>

<sup>1</sup>Department of Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA 50011, USA

<sup>2</sup>Department of Zoology, Oregon State University, Corvallis, OR 97331, USA

Evolutionary theory predicts that differential reproductive effort and rate of reproductive senescence will evolve under different rates of external mortality. We examine the evolutionary divergence of age-specific reproduction in two life-history ecotypes of the western terrestrial garter snake, *Thamnophis elegans*. We test for the signature of reproductive senescence (decreasing fecundity with age) and increasing reproductive effort with age (increasing reproductive productivity per gram female) in replicate populations of two life-history ecotypes: snakes that grow fast, mature young and have shorter lifespans, and snakes that grow slow, mature late and have long lives. The difference between life-history ecotypes is due to genetic divergence in growth rate. We find (i) reproductive success (live litter mass) increases with age in both ecotypes, but does so more rapidly in the fast-growth ecotype, (ii) reproductive failure increases with age in both ecotypes, but the proportion of reproductive failure to total reproductive output remains invariant, and (iii) reproductive effort remains constant in fast-growth individuals with age, but declines in slow-growth individuals. This illustration of increasing fecundity with age, even at the latest ages, deviates from standard expectations for reproductive senescence, as does the lack of increases in reproductive effort. We discuss our findings in light of recent theories regarding the phenomenon of increased reproduction throughout life in organisms with indeterminate growth and its potential to offset theoretical expectations for the ubiquity of senescence.

**Keywords:** reproductive effort; garter snake; life history; senescence

## 1. INTRODUCTION

Classical evolutionary theories of senescence predict that physiological deterioration with age results from the declining power of natural selection at late ages (Medawar 1952; Williams 1957). The age-specific trajectory of mutation/selection balance for any given group depends on the relative proportions of old and young adults and on the pattern of reproduction (Hamilton 1966). Thus, changes in extrinsic forces of mortality that selectively increase the value of older individuals should select for delayed senescence. However, more recent theoretical investigations have suggested that the case of a near absence of senescence, or negligible senescence, can result if older individuals have high reproduction and a high probability of survival that completely offsets their declining numbers (Finch 1998; Gasser *et al.* 2000; Vaupel *et al.* 2004; reviewed in Williams *et al.* 2006).

Although many studies have documented actuarial senescence in wild populations (e.g. McDonald *et al.* 1996; Bonduriansky & Brassil 2002; Bronikowski *et al.* 2002), tests for the persistence and evolution of reproductive senescence in nature are relatively rare (but see Packer *et al.* 1998; Bérubé *et al.* 1999; Holmes *et al.* 2003). Such studies in mammals and birds have revealed convincing evidence for declining reproduction at late ages and, in some cases, a substantive post-reproductive lifespan. In contrast, ectotherms, and reptiles in

particular, remain enigmatic with regard to evolutionary theories of senescence. Specifically, several studies suggest that some ectotherms may not show any signs of reproductive decline, and even where senescence is evident, it may not exhibit the predicted response to extrinsic mortality (e.g. Congdon *et al.* 2001, 2003; Miller 2001; Reznick *et al.* 2002, 2004). Senescence has, however, been documented in some fish, and the lack of clear illustrations of senescence in reptiles may be due in part to the difficulties of studying secretive species, such as snakes, and obtaining long-term data on long-lived organisms. Alternatively, it has been suggested that the apparent absence of a decline in reproduction with age may be a consequence of the indeterminate growth exhibited by many of these species, a trait that may delay (or prevent) the onset of reproductive senescence and even facilitate an increase in fecundity throughout life (Finch 1998; Reznick *et al.* 2002; Vaupel *et al.* 2004).

Here, we present intraspecific data on age-specific reproduction for five populations of the garter snake *Thamnophis elegans* that reside in close geographical proximity. These populations are derived from the same ancestral source population, but have been differentiated into two distinct, genetically diverged ecotypes that differ in scalation, coloration and life history (Bronikowski & Arnold 1999; Bronikowski 2000; Manier & Arnold 2005). These two ecotypes provide an ideal model for the microevolution of life history. One ecotype, which occupies lakeshore habitats, exhibits fast growth, early

\* Author for correspondence (abroniko@iastate.edu).

maturation, large adult body size, high annual reproduction and low annual survival. In contrast, the second ecotype, which occupies mountain meadow habitats, exhibits slow growth, late maturation, small adult body size, low annual reproduction and high annual survival (Bronikowski & Arnold 1999). A common garden experiment has shown that the ecotypic difference in growth has a genetic basis (Bronikowski 2000). Furthermore, the respective lifespans of the two ecotypes reflect these fast/slow life-history strategies, with the fast-growth lakeshore snakes maintaining a shorter median lifespan than the slow-growth meadow snakes, both in the field (2 and 5 years, respectively) and in the laboratory (4 and 8 years, respectively; A. M. Bronikowski & S. J. Arnold, 1999 unpublished data). This article provides a detailed ecotypic comparison of how reproductive traits covary with age. We explore this comparison using theory for the evolution of life history and senescence.

Classical theory (e.g. Williams 1957) predicts that individuals of the long-lived, slow-growth (meadow) genotype should exhibit concomitantly slow reproductive decline, while short-lived, fast-growth (lakeshore) individuals should exhibit a more rapid decline in reproductive function. We test whether differences in age-specific reproductive trajectories conform to these theoretical expectations using approximately 250 reproductive *T. elegans* individual females collected between the years of 1975 and 1994. We anticipate that lakeshore populations will exhibit an increase in reproduction at early ages at a faster rate than meadow populations, in association with faster growth rates. For the dynamics of age-specific reproduction at later ages, we propose two alternate hypotheses to a null model of no senescence: (H1) Reproductive success will decline in populations of both ecotypes at later ages, but will decline more rapidly in lakeshore snakes, indicative of a faster rate of ageing. (H2) Reproductive success will not decline in lakeshore snakes, due to a truncated lifespan, but decline will be evident in meadow snakes, which may live long enough to exhibit senescence. Finally, because reproductive effort includes both live and non-live births, we examine the incidence of reproductive failure, characterized by delivery of yolks and/or stillborns, in addition to testing for declines in reproductive success, because increasing dead litter mass with age could also be indicative of reproductive senescence.

## 2. MATERIAL AND METHODS

### (a) Study organisms and data collection

Our study populations of *T. elegans* reside in the vicinity of Eagle Lake in Lassen County, CA, at the northern end of the Sierra Nevada range. We collected snakes from two lakeshore habitats, which are characterized by continuous prey availability and warm temperatures, and three mountain meadow habitats, which exhibit highly variable prey availability and cooler temperatures (Kephart 1982; Kephart & Arnold 1982; Bronikowski & Arnold 1999). Approximately, 250 pregnant female snakes were collected from 1975 to 1994 as part of a large mark/recapture study. Within this larger study, all animals were collected by active searching (i.e. not only catching animals out foraging or basking, but also beneath retreat rocks, hidden at the base of vegetation, etc.). Each female contributed a single litter to this study; we

excluded repeated measures within females. Thus, this is a cross-sectional study of age-specific reproductive parameters. Pregnant females were maintained in captivity for the duration of pregnancy on thermal gradients that permitted thermoregulation (Arnold 1988). All neonates, stillborns and yolks (undeveloped embryos) were counted, weighed and measured upon parturition. Total, live and dead litter mass (defined as the combined weight of stillborns and undeveloped yolks) were calculated for each female along with average individual live offspring mass. Female snout-vent length (SVL) and mass were measured postpartum. In addition to these pregnant females, we sampled 20 non-pregnant females (randomly with respect to size/age) from each population to determine ages of non-reproducing female to compare with the age-distributions of pregnant females.

### (b) Age determination

Many dams were marked as neonates; these animals provided data on exact age. When exact age was unknown we used one of the two methods to estimate age. Since the snakes in this region hibernate from October to April, we were able to determine age histologically using the technique of skeletochronology by counting annual growth rings (annuli) in a single vertebra from each animal (Waye & Gregory 1998). In cases where the annuli were indistinguishable (e.g. in animals that had been preserved many years ago), we used the close relationship between age and size within each ecotype to estimate age (Pearson's correlation: Lakeshore:  $r=0.8482$ ,  $p<0.0001$ ,  $n=19$ ; Meadow:  $r=0.9272$ ,  $p=0.0009$ ,  $n=8$ ). Von Bertalanffy growth equations were used to estimate age for these latter dams (eqns described in Bronikowski & Arnold 1999). In cases in which age was known to be at least 15 years, dams were designated as 15+ years to increase sample sizes in this final age class.

### (c) Statistical analyses

#### (i) Age distributions

Female age within the two ecotypes exhibited non-normal distributions, so we  $\log_e$  transformed and tested for differences between the lakeshore and the meadow ecotypes and between the gravid and the non-gravid females with analysis of variance.

#### (ii) Reproductive success

The dependent variables were single observations per female pooled across the 20 years of observation. Live litter mass was analysed with analysis of covariance (ANCOVA) with the following linear model

$$Y = \mu + \text{age} + \text{ecotype} + \text{population}(\text{ecotype}) + \text{age} \\ \times \text{ecotype} + \text{age} \times \text{population}(\text{ecotype}) + \epsilon,$$

where  $\mu$  is the population mean; age is a covariate; ecotype is the fixed effect of meadow versus lakeshore habitat; population nested within ecotype represents the effect of two lakeshore (L1 and L2) and three meadow (M1, M2 and M3) populations; and  $\epsilon$  is an error term (Proc GLM in SAS v. 9.1). Population nested within ecotype was treated as a fixed, rather than a random, effect to reflect complex microhabitat variation among populations. The interaction between maternal age and population nested within ecotype did not exhibit any significant effects and was therefore removed from the model. (However, note that the statistical power of the interaction of age with population was  $\beta<0.80$ .) Since the

results for total and live litter were in agreement, we discuss live litter mass hereafter. In addition to live litter mass, live litter size, average size of live offspring and relative clutch mass (RCM, defined as the residuals of the regression of total litter mass on post-parturient maternal mass) were also analysed using the same model. Parallel analyses were performed with SVL rather than age as the covariate to provide a comparison to other studies, but since the outcomes of both ANCOVAs supported the same conclusions, results are discussed primarily in terms of age (with the exception of RCM, for which both age and SVL are discussed).

### (iii) Reproductive failure

Analyses of total dead litter mass and the number of stillborns were first performed using the model detailed above. Dead litter mass and number of stillborns yielded a significant relationship to maternal age, so in order to determine the relationship between these variables and changes in litter mass/size with age, we expressed these parameters as a proportion of total litter mass/size for each individual. After arcsine transformation of this ratio, the data were analysed using ANCOVA. Finally, the presence or absence of dead litter components (i.e. yolks and/or stillborns) was analysed using logistic analysis.

Since the lakeshore sites had few old females, we ran all analyses (i.e. for both reproductive success and failure) with and without the six lakeshore females that were more than 10 years of age. The exclusion of these females did not significantly alter the results or our conclusions regarding age-specific reproduction.

## 3. RESULTS

### (a) Age distributions

Ages of reproductive females ranged from 2 to 15 years within lakeshore populations (characterized by fast-growth individuals); non-gravid females ranged from 2 to 9 years of age. In meadow (slow-growth) populations, the age of reproductive females ranged from 3 to 15 years of age; non-gravid females ranged in age from 4 to 13 years. Within ecotype, the mean age of gravid and non-gravid females was indistinguishable in lakeshore habitat (gravid: 3.9 years; non-gravid: 4.2 years,  $p=0.5229$ ). In meadows, the mean age of non-gravid females was less than that of gravid females (gravid: 7.6 years; non-gravid: 6.1 years,  $p=0.0004$ ). Thus, for any given population, the pool of non-gravid females in any given year is on average the same ages or younger than the reproducing females, i.e. the non-gravid group of females is not composed of post-reproductive or otherwise reproductively senescent females.

Between ecotypes, the ages for both categories of females (gravid and non-gravid) differed significantly. Reproductive females averaged 3.9 years in lakeshore (fast-growth) sites and 7.6 years in meadow (slow-growth) sites ( $p<0.0001$ ; figure 1). Most reproductive lakeshore snakes fell in the range 2–6 years, with a few individuals from one lakeshore population (L2) reaching the age of 15+ years. The age distribution of reproductive meadow females was significantly shifted towards older ages, with broad representation in the range 4–15+ years (Kolmogorov-Smirnov  $D=0.667$ ,  $p<0.0001$ ,  $n=249$ ), with the maximum difference ( $D$ ) occurring at age 4 years (figure 1).

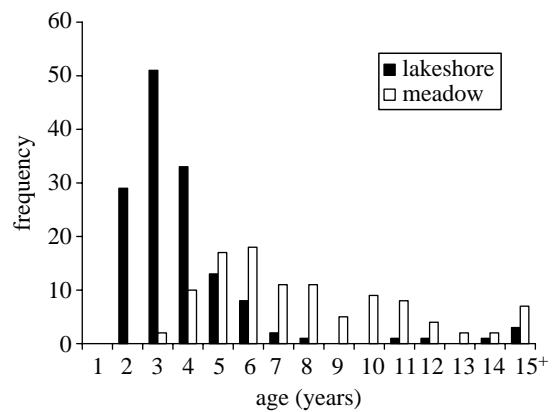


Figure 1. Histogram of maternal ages. The distributions of pregnant females differed between the two ecotypes (see §3 for details).

### (b) Reproductive success

Age and source population significantly affected live litter mass and live litter size (number of live offspring; table 1). Live litter mass increased significantly with dam age in both ecotypes with those few fast-growth individuals in the 15+ category having the highest litter masses overall (figure 2). L1 had significantly greater live litter mass than L2; both lakeshore sites had significantly greater live litter mass than the meadow sites, which were equivalent (ranking of live litter mass: L1 > L2 > M1 = M2 = M3). The significant interaction between age and ecotype (table 1) reflects that populations of fast-growth individuals exhibited a much faster increase in reproductive success with age than populations of slow-growth individuals, in which only a slight increase is evident with age (fast: slope = 3.2 g offspring per year,  $p<0.0001$ ; slow: slope = 0.42 g offspring per year,  $p=0.0137$ ; figure 2). Like live litter mass, the dam age by ecotype interaction significantly affected litter size; litter size increased with age in fast-growth snakes but remained constant in slow-growth snakes (L: slope = 0.89 offspring per year,  $p<0.0001$ ; M: slope = 0.02 offspring per year,  $p=0.8125$ ).

Average offspring mass varied with age; older dams gave birth to larger offspring (table 1, figure 3). There was no interaction between age and ecotype, which indicates that average offspring mass increases in a similar fashion in fast- and slow-growth snakes (L: slope = 0.05 g per year,  $p=0.047$ ; M: slope = 0.07 g per year,  $p<0.001$ ) (figure 3).

RCM (gram offspring per gram dam) was significantly affected by the interaction between age and ecotype (table 1). RCM remained constant with age (slope = 0.37 g/g per year,  $p=0.1465$ ,  $n=141$ ) in lakeshore females, but increased slightly with SVL (slope = 0.03 g/g per mm,  $p=0.0267$ ,  $n=141$ ). In contrast, RCM showed a strong decrease with both age and SVL in meadow females (age: slope = -0.67 g/g per year,  $p=0.0011$ ,  $n=89$ ; SVL: slope = -0.05 g/g per mm,  $p<0.0004$ ,  $n=89$ ; figure 4).

### (c) Reproductive failure

Maternal age significantly affected the dead litter mass and the number of stillborns (table 2). However, when these dependent variables were expressed as arcsine-transformed proportions of total reproductive output (total litter mass and total litter size, respectively), no effects were found to be significant (table 2). Thus, although

Table 1. Analysis of covariance of parameters of reproductive success. (\*, denote significant effects.)

	source of variation	d.f.	type III MS	<i>F</i>	<i>p</i>
litter mass	age	1	5576	79.8	<0.0001*
	ecotype	1	4	0.1	0.8200
	population(ecotype)	3	416	6.0	<0.0001*
	age × ecotype	1	3224	46.1	<0.0001*
	error	239			
litter size	age	1	385	55.7	<0.0001*
	ecotype	1	1.00	0.1	0.7043
	population(ecotype)	3	129.3	6.2	0.0004*
	age × ecotype	1	280.31	40.4	<0.0001*
	error	238			
average individual offspring mass	age	1	3.43	13.1	<0.0001*
	ecotype	3	0.332	1.3	0.2618
	population(ecotype)	1	2.39	9.1	<0.0001*
	age × ecotype	1	0.08	0.3	0.5799
	error	232			
relative clutch mass (RCM)	age	1	6.68	0.1	0.7400
	ecotype	1	57.68	1.0	0.3302
	population(ecotype)	3	800	4.4	0.0050*
	age × ecotype	1	417.97	6.9	0.0092*
	error	223			

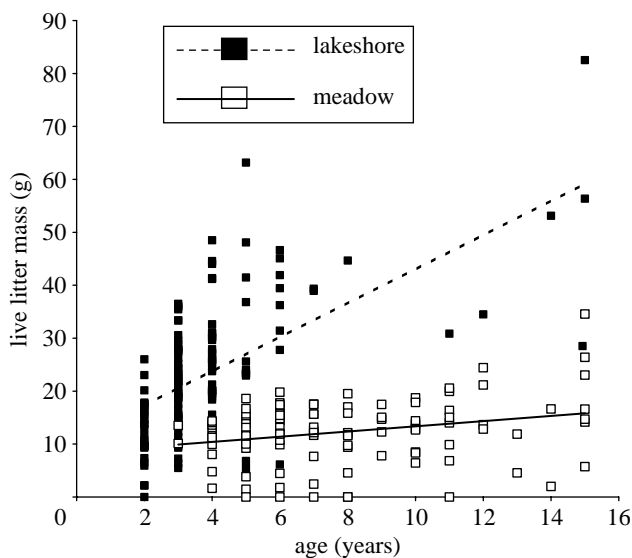


Figure 2. Total live litter mass as a function of maternal age. Total litter mass increased with age in both ecotypes but at a faster rate in lakeshore populations.

dead litter mass and number of stillborns increased with age for both ecotypes (figure 5a), they remained as constant proportions of total litter mass per litter size (figure 5b). Similarly, there was no significant increase in the incidence of litters containing yolks or stillborns with age ( $p > 0.20$ ).

#### 4. DISCUSSION

In many organisms, reproductive success increases with age early in adulthood (Clutton-Brock 1984; Cameron *et al.* 2000 and references therein). This increase can be attributed both to morphological development and learning, which results in improvements in such skills as resource and mate acquisition, and parental care. Increasing body size throughout life in organisms with indeterminate growth has been shown to be a particularly important factor in increasing reproductive success, and

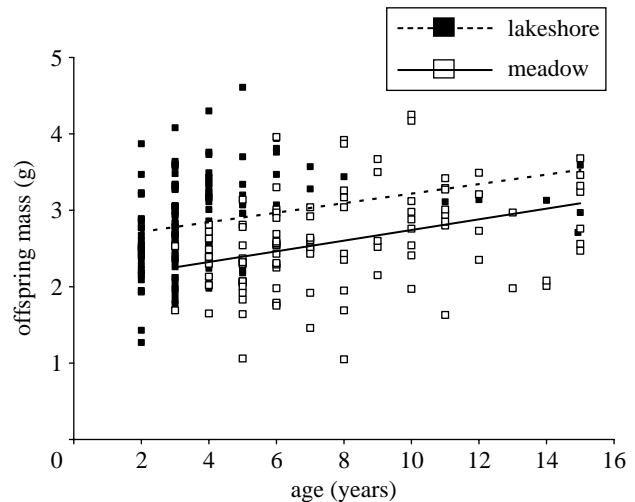


Figure 3. Average live offspring mass as a function of maternal age. Offspring size increased with age at a similar rate in both lakeshore and meadow snakes.

may be attributed to an increase in internal space for offspring development, as well as general improvement in body condition (reviewed in Roff 1992). In general, most studies to date have examined female reproductive success in squamates primarily as a function of body size. Only recently has reproductive success been examined in individuals of known age in wild populations. In these studies, up to 8 years of data on natural snake and lizard populations have been analysed (e.g. Madsen & Shine 1992; Olsson & Shine 1996; Diller & Wallace 2002; Stanford & King 2004). However, owing to lack of data on older animals, senescence has rarely been examined in squamates. Here, with 20 years of age-specific data, we test evolutionary hypotheses of reproductive senescence and reproductive effort.

Age-specific trends in fecundity and offspring size showed no evidence of senescence. We found that the lakeshore (fast-growth) snakes began reproducing at earlier ages and exhibited a greater increase in

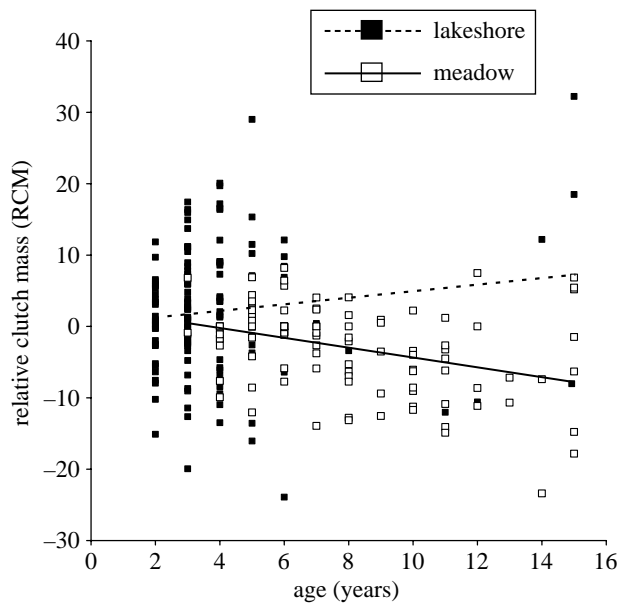


Figure 4. Relative clutch mass (RCM) as a function of maternal age. RCM remained constant with age for lakeshore snakes but declined in meadow snakes.

reproduction with age than the meadow snakes. This lakeshore trajectory of increasing reproduction with advancing age neither plateaued nor decreased in late age. In slow-growth meadow snakes, the rate-of-change in reproduction differed from that of the lakeshore females, but again did not decrease within the longest-lived age-classes. Furthermore, it is evident that older dams in both ecotypes produced larger offspring than their younger counterparts, while older lakeshore females also produced increasingly large litters. It is likely that these age-specific trends continue throughout the lifespan of these female snakes, as the oldest individuals are close to the maximum lifespan that we have observed in the field (18 years of age in both ecotypes).

Although dead litter mass and number of stillborns increased with age, they did not change in proportion to total litter mass/size. This result begs the as yet unanswerable question: why not invest more energy into converting this fixed proportion of reproductive effort from failure to success, rather than into producing more total eggs, which means more reproductive dead ends (yolks and stillborns). Nevertheless, our findings are consistent with the previous reports in snakes and turtles (e.g. Luiselli *et al.* 1996; Congdon *et al.* 2003). Although an interesting phenomenon, these results provide no evidence for reproductive senescence via a disproportionate increase in reproductive failure with age. Thus, for these ectothermic vertebrates, we have found that at least one endothermic hallmark of ageing, declining age-specific reproduction, is not only absent, but is also opposite in predicted sign. We focus below on theories for the evolution of reproductive effort and senescence both with respect to local habitat differences and the larger question of the effects of indeterminate growth.

Life-history models predict that reproductive effort will increase with age as a function of expected remaining lifespan (reviewed in Roff 1992; Charlesworth 1994). One measure of reproductive effort, RCM, did not change with age in fast-growth snakes, although it did exhibit slight increases with body size. This is contrary to what has

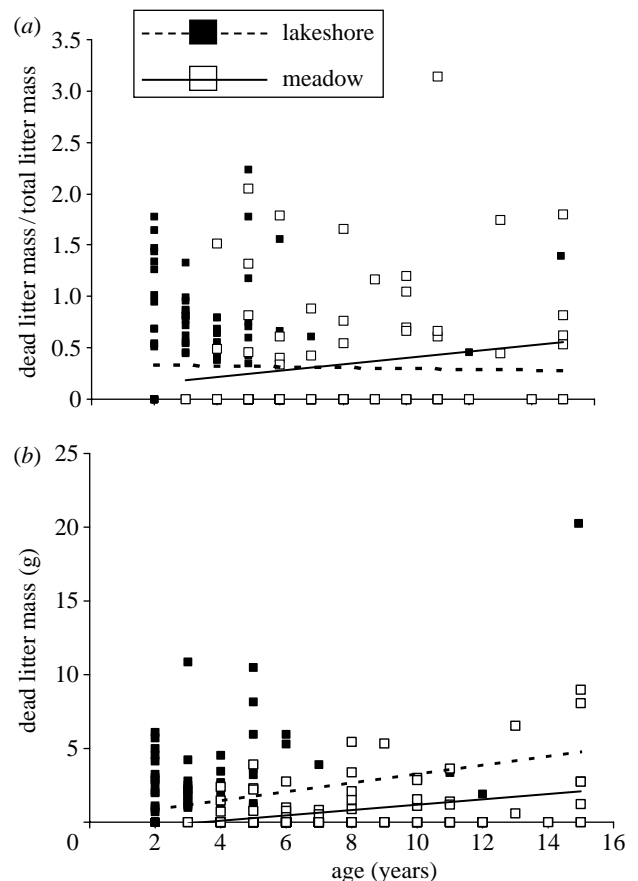


Figure 5. Dead litter mass as a function of maternal age. Dead litter mass increased with age in both ecotypes (a), but remained constant when expressed as an arcsine-transformed proportion of total litter mass (b).

been reported for a wide variety of other snakes. Intraspecific RCM tends not to increase with size in snakes (e.g. Pianka & Parker 1975; Seigel *et al.* 1986; Madsen & Shine 1992) and is thought to be limited largely by abdominal volume (e.g. Vitt & Congdon 1978). In some cases, however, size-dependent increases in RCM have been reported, and in the viviparous smooth snake *Coronella austriaca* the slope is steeper than in the lakeshore *T. elegans* (Luiselli *et al.* 1996). Since larger RCMs are thought to be associated with a variety of costly factors (e.g. decreased mobility, increased basking and high energetic costs) that may increase vulnerability to predators and other hazards, Luiselli *et al.* (1996) speculate that larger *C. austriaca* females may be able to afford larger RCMs because (i) they may be large enough to deter predators by size alone or (ii) they may have undergone an ontogenetic switch to larger prey and so may experience an enhanced energy intake. The first possibility may apply to our lakeshore populations. In these populations, American Robins (*Turdus migratorius*) and Brewer's blackbirds (*Euphagus cyanocephalus*) attack small snakes but cannot prey on adult *T. elegans*.

Interestingly, RCM in meadow snakes showed a strong trend in the opposite direction: they exhibited a marked decrease in RCM with age (and body size). In other words, older and larger snakes invested less in reproduction per gram body mass than younger, smaller snakes. Meadow habitats are characterized by larger avian predators such as sandhill cranes (*Grus canadensis*), red-tailed hawks (*Buteo jamaicensis*) and golden eagles (*Aquila chrysaetos*) on the

Table 2. Analysis of covariance of two parameters of reproductive failure, dead litter mass and number of stillborns. (And analysis of the same expressed as arcsine-transformed proportion of total litter mass and proportion of total litter size, respectively. \*,  $p < 0.05$ .)

source of variation		untransformed				arcsine transformed			
		d.f.	type III MS	<i>F</i>	<i>p</i>	d.f.	type III MS	<i>F</i>	<i>p</i>
dead litter mass	age	1	121.2	15.0	<0.0001*	1	0.359	0.96	0.3288
	ecotype	1	10.77	1.4	0.2494	1	0.494	1.32	0.2542
	population(ecotype)	3	18.61	2.3	0.0778	3	0.199	0.53	0.6613
	age × ecotype	1	0.8	0.1	0.7528	1	0.692	1.85	0.1756
	error	229				241			
stillborn number	age	1	9.12	6.0	0.0147*	1	0.3012	0.89	0.3461
	ecotype	1	0.62	0.4	0.5219	1	0.1975	0.58	0.4453
	population(ecotype)	3	1.4	0.9	0.4286	3	0.3822	1.13	0.3372
	age × ecotype	1	0.48	0.3	0.5704	1	0.3013	0.89	0.3460
	error	238				238			

one hand, and a lack of retreat rocks on the other. Thus, large gravid females may be at a greater risk than smaller females, which may be less conspicuous and more mobile. We are currently testing the hypothesis that predator suites have been a major evolutionary pressure for slow growth and small adult body size in meadow populations (as well as fast growth and large body size in lakeshore populations). In meadows, slower age-specific growth rates may represent a compromise between escape from predation (where small body size is beneficial) and increased reproduction (where large body size is beneficial).

Remarkably, lakeshore females increased reproductive success even at the latest ages. This suggests that the paucity of older reproductive females captured in lakeshore sites may be a direct consequence of higher levels of extrinsic mortality rather than faster senescence, the latter being a predicted cost of fast growth and high reproduction. From the mark/recapture data, we have reported elsewhere that mortality for lakeshore juveniles and adults is twice that of the meadow animals (Bronikowski & Arnold 1999 and unpublished data). That fast growth and greater reproductive success in lakeshore snakes relative to meadow snakes does not result in either shortened maximum lifespan (although median lifespan is smaller) or decreased late-age reproduction appears to contradict classical theory (e.g. disposable soma theory: Kirkwood 1977; antagonistic pleiotropy theory: Williams 1957). This is particularly striking because there is a genetic component to the ecotypic difference in growth (Bronikowski 2000).

The apparent contradiction may be a consequence of indeterminate growth. Reznick *et al.* (2002) suggest that many fish are long-lived because their capacity for indeterminate growth has allowed them to increase fecundity with age, long past maturity. This continuing rise in fecundity may result in increased selection against deleterious alleles that are expressed at older ages, resulting in the evolution of delayed, or negligible senescence (see Finch 1998). Theoretically, increasing age-specific fecundity could completely offset the decline in the strength of selection that naturally occurs because there are fewer older than younger individuals (Vaupel *et al.* 2004). Thus, lakeshore snakes may be an example of what might be termed 'perfect indeterminate fecundity', which completely offsets the trend for strength of selection

to decrease with age. However, other trends indicate that the question may not be so easily resolved. Growth in meadow snakes after maturity slows at a more rapid rate than in lakeshore snakes (Bronikowski & Arnold 1999). Nevertheless, meadow snakes show no indications of reproductive senescence. Likewise, Congdon *et al.* (2003) have suggested that indeterminate growth cannot be the only factor involved in delaying senescence in turtles. They examined ageing in painted turtles (*Chrysemys picta*), which exhibit indeterminate growth, and Blanding's turtles (*Emydoidea blandingii*), which do not, and found no decline in reproductive success or survivorship with age in either species.

Evolutionary theories of senescence are based on the assumption that in a situation in which there are fewer old than young individuals, the conditions for the evolution of senescence are created. These theories are increasingly being challenged and refined. Ongoing generalizations of the theory include factors as diverse as inclusive fitness, immune function and interactions between sources of mortality (Lee 2003; Williams & Day 2003; Bronikowski & Promislow 2005) as well as alternative theoretical perspectives on the effects of age-specific mutations (see Baudisch 2005). Despite the apparent absence of a trade-off between fast growth and age-specific reproductive success in our system, there may be costs associated with other components of fitness. For instance, laboratory guppies (*Poecilia reticulata*) derived from sites with high extrinsic mortality show earlier maturation and higher reproductive investment than their low extrinsic mortality counterparts. Nevertheless, strains from high mortality environments do not suffer the double cost of reduced survival and increased reproductive senescence. However, they do exhibit a more substantial decline in swimming performance than strains from low-mortality environments (Reznick *et al.* 2004). With regard to our system, it is possible that *T. elegans* in lakeshore environments incur a cost that we have not assessed. For example, we have not determined whether there is an ecotypic difference in investment in somatic maintenance. We are currently assessing oxidative damage and repair mechanisms in the two ecotypes. However, even if there were no differences in cellular damage and repair, ecological trade-offs might make the fast-growth life-history strategy suboptimal in other settings. Thus, in

meadow environments a slow-growth life history may be a bet-hedging response to factors such as unpredictable food resources (Bronikowski & Arnold 1999). Whatever the case, it is clear that there is still much to be learned regarding the relationship between age and reproduction in organisms exhibiting diverse patterns of growth.

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