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**Costs of Reproduction in a Temperate-zone Lizard, *Elgaria coerulea***

by

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B.Sc., University of Toronto, 1991  
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in  
the Department of Biology

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### ABSTRACT

Understanding why organisms possess certain combinations of life-history traits is important to our understanding of how natural selection operates. Combinations of life-history traits evolve in response to the costs of current reproduction to both survival and future reproduction. Reproductive costs have been broadly categorised into two types: 1) survival costs, and 2) potential fecundity costs. As a means of predicting and explaining variation in reproductive investment in lizards and snakes, Shine and Schwarzkopf (1992) attempted to determine the relative importance of the two kinds of costs to individual lifetime fitness (the SS model). They concluded that most lizard species are unlikely to make trade-offs between current and future reproduction (fecundity costs). In this study of a temperate-zone lizard, *Elgaria coerulea*, I have three main objectives: 1) to provide the first natural history data for a Canadian population of this species, 2) to describe life-history traits for this population, and 3) to formally test the predictions of the SS model and discuss its potential predictive power.

Individual *Elgaria coerulea* occupy relatively small areas, thus minimising costs associated with a long-distance migration. In addition to having limited movement, *Elgaria coerulea* rely on hiding as one of their main anti-predator strategies, although there is sex-dependent variation in their retreat-site selection. Emergence patterns of male *Elgaria coerulea* did not change over their reproductive cycle. In contrast, the probability of capturing an adult female in the open steadily increased over the summer. These results suggest that the benefits of emerging from cover outweigh the costs in females, but not males.

Annual survival rate of adult females was 44% and juvenile survival rate was 22%. The survival rate of adult males likely fell in between these values, but I was not able to estimate it directly because of small sample sizes. I infer from the female's relatively high survival rate that the necessity for gravid females to spend more time in the open during

gestation does not translate simply to increased mortality.

Gravid females have reduced sprint speed and sprint speed was inversely related to the burden of the clutch. Therefore, gravid females presumably could reduce their predation risk by remaining closer to cover than males or juveniles. However, this is not the case; all northern alligator lizards remained close to cover. Thus, the lack of shift in anti-predator behaviour of gravid females may be a result of all *Elgaria coerulea* relying on crypsis rather than sprinting as an anti-predator defence. I did detect a difference in body coloration. Gravid females had more black pigmentation than males or juveniles. The black pigmentation may help females blend in with their background better than males, thereby reducing predation risk, or help increase their body temperature at a quicker rate.

Another important anti-predator strategy in *Elgaria coerulea* is tail autotomy, and once again I measured variation in this trait between males and females. Gravid females never lose small parts of their tails, perhaps giving them extra time to escape from a predator. Furthermore, recent tail loss was not seen in gravid females during late gestation. By contrast, males were equally likely to autotomise at any time of the year. Females may be less likely than males to lose their tails because of the potential reproductive gain by females with intact tails. Females with intact tails had a higher probability of being reproductive and females with longer tails had larger newborn.

Finally, I show that some *Elgaria coerulea* trade current reproduction for growth. Examination of reproductive costs in *Elgaria coerulea* revealed problems with incorporating cold-climate reptile species into the SS model. Because cold-climate species spend significant time in hibernation each year they have relatively short interclutch intervals. For these species the SS model predicts that trade-offs between current and future reproduction are more likely. The likelihood of fecundity costs also increases, given that concurrent growth and reproduction may be more prevalent than previously believed, as is evident in *Elgaria coerulea*. Both of these factors need to be incorporated into the SS model to increase our ability to make predictions about the evolution of reproductive effort in cold-climate species.

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## Chapter 1

### General Introduction

Life-history traits (e.g. size at birth, age at first reproduction, survival rate) and the trade-offs between them, over the reproductive lifespan of the individual, directly and indirectly influence individual's lifetime fitness. Thus, understanding why organisms possess certain combinations of life-history traits is important to our understanding of how natural selection operates. In general, the study of life-history traits has proceeded in two directions: description of these traits through field documentation and experimental research, and development of life-history theory (Stearns, 1976). These lines of research are inter-connected, each constantly providing information for the advancement of the other. Description of life-history traits of many organisms has revealed a wide range of trait combinations. Examination of this variation provides a basis for the development of life-history theory, which is a body of related hypotheses used to explain extant life-history combinations, and predict the combinations of traits that will evolve in organisms in specific situations (Stearns, 1976). Hypotheses can be tested directly with life-history data from appropriately studied species. This process helps clarify our thinking about the evolution of life-histories and allows the development of better predictive models.

The focused investigation of variation in life-history traits began with Fisher (1930). He noted that energy budgets of organisms are partitioned among reproduction, growth and maintenance. This led him to ask what physiological mechanism controls resource allocation and under what circumstances it is profitable to divert a greater or lesser share of available resources towards reproduction. Williams (1966) refined these ideas by dis-

tinguishing between resources invested in current reproduction (reproductive effort) and resources saved for the future (residual reproductive effort). Because energy allocated to one cannot be allocated to the other, there will be a trade-off between reproductive effort and residual reproductive effort resulting in an energetic cost associated with current reproduction. Williams (1966) theorised that combinations of life-history traits evolved in response to the costs of current reproduction to both survival and future reproduction.

Costs of reproduction have been broadly categorised into two types: 1) survival costs, and 2) potential fecundity costs (Bell, 1980). Survival costs and fecundity costs may function separately or they may be linked, but they are rarely simple. To date, most field studies of variation in reproductive effort have been on birds and this limits the kinds of questions that can be asked. All birds are oviparous, most have some form of parental care, and most grow little after maturity. However, lizards provide an excellent opportunity to study adaptive life-history responses to the costs of reproduction because they have a wider range of reproductive strategies (Shine, 1980, 1988b). Variation in parental investment, both between and within species provides an opportunity to study trade-offs between current reproduction and survival. In addition, many reptiles grow significantly after maturity, so there is potential for reducing current reproduction for enhanced future reproduction (Schwarzkopf, 1994), given that clutch size usually increases with body size in reptiles.

As a means of predicting and explaining variation in reproductive investment in lizards and snakes, Shine and Schwarzkopf (1992) attempted to determine the relative importance of costs associated with reproduction to individual lifetime fitness. They considered two life-history characteristics (relative clutch mass, and survival rate) to create a simple simulation model (SS model) that predicted the level above which individuals should

trade-off between current and future reproduction. They concluded that many lizard species fall below the predicted trade-off curve (Shine and Schwarzkopf, 1992), and suggested that the low relative clutch mass and/or low adult survival rate of most lizard species makes them unlikely to make trade-offs between current and future reproduction.

There has been much discourse since the SS model was originally proposed (Niewiarowski and Dunham, 1994, 1998; Shine et al., 1996), but there has been no formal test of its predictions. This is important because Shine and Schwarzkopf (1992) use their model predictions to encourage researchers to focus only on collecting data on survivorship and its relationship with reproductive patterns. They opined that research on fecundity costs should be abandoned, because they inferred that fecundity costs are unimportant in determining life-history evolution in lizards. In this study of a temperate-zone lizard, *Elgaria coerulea*, I have three main objectives: 1) to provide the first natural history data for a population of this species at its northern geographic limits, 2) to describe life-history traits for this population, and 3) to formally test the predictions of the SS model (Shine and Schwarzkopf, 1992) and discuss its potential predictive power. The specific objectives of each chapter are presented below.

## Objectives

In Chapter 2 I describe and compare habitat use and movement patterns of *Elgaria coerulea*, a viviparous lizard, and of a syntopic lizard, *Eumeces skiltonianus* which is oviparous. I address the following objectives: 1) to determine the characteristics of hibernation and summer sites for each species, 2) to determine the extent of movement in both species, particularly whether migration occurs between summer and winter habitats, and



3) to discuss the extent to which both species co-occur in habitat patches at the study site.

In Chapter 3 I delineate patterns of retreat-site selection and emergence in *Elgaria coerulea*. In particular, I address age- and sex-related variation in these traits and how these traits vary over the course of the activity season. In this chapter I have the following objectives: 1) to determine seasonal and daily variation in retreat-site selection, emergence patterns, and proximity to cover, 2) to test for age- and sex-related differences in capture-site temperature, retreat-site selection, emergence patterns, proximity to cover, and sprint speed, and 3) to speculate about the circumstances under which it is more favourable for an ectotherm to be in the open rather than hidden.

In Chapter 4 I present a variety of life-history traits of *Elgaria coerulea*, focusing on the differences between adult males and females. I measure survival rates using mark-recapture data, taking into account recapture rates of lizards. Furthermore, I test for sexual dimorphism in survival rates, head width, body size, tail autotomy, and colour pattern.

In the final chapter of the thesis I test for the presence of trade-offs among current reproduction, future reproduction, and survival. I accomplish this test using reproductive data presented in this chapter and additional life-history data from preceding chapters. I discuss the results in light of the predictions the SS model and the ensuing debate in the literature (Niewiarowski and Dunham, 1994, 1998; Shine et al., 1996).

## Chapter 2

# Habitat Use and Movement Patterns

### Introduction

Animals often have different habitat requirements for different activities or functions. These habitats may be spatially separated, necessitating movement between them. This issue is significant on two fronts: 1) availability of suitable habitat in a favourable spatial configuration may be a key factor limiting the distribution and abundance of species; and 2) manipulation of habitat is a potentially important technique in conservation and management. Furthermore, the need for a diversity of accessible habitats by species means that habitat fragmentation, as a result of human activities is a serious issue in wildlife conservation. In reptiles, particularly at higher latitudes, two major habitat requirements are hibernation sites and incubation/gestation sites (Etheridge et al., 1983; Gregory, 1984; Burger and Zappalorti, 1986; Burger et al., 1988; Brown and Brooks, 1994; Prior and Weatherhead, 1996; Litzgus et al., 1999). In some northern populations of reptiles, suitable summer and winter sites are so far apart that long-distance migration is a regular feature of their annual cycle (Weintraub, 1966; Gregory and Stewart, 1975; Brown and Parker, 1976; Brown and Brooks, 1994).

The requirements of squamates for hibernation and incubation/gestation are quite different. Hibernation sites must be structurally stable, below the frost-line, and sufficiently humid to prevent over-winter dehydration. Incubation/gestation, by contrast, requires nest sites that provide high temperatures and sufficient moisture content for developing embryos, and must also be a refuge from predators. Nest sites that fit these criteria may be limiting

(Cooper et al., 1983; Hecnar, 1994), particularly for reptiles living in cooler climates. Choice of basking sites is important for gravid viviparous females because basking by gravid females may increase the risk of predation (Huey and Slatkin, 1976; Shine, 1980; Madsen, 1987) due to their reduced mobility (Vitt and Congdon, 1978; Bauwens and Thoen, 1981; Seigel et al., 1987; Sinervo et al., 1991).

Most studies of movements between habitats by squamates have been done on snakes (reviewed in Gregory et al., 1987), which are often amenable to radiotelemetry (reviewed in Fitch, 1987). However, we have little understanding of seasonal habitat use and movement patterns of small lizards. The consequences of different movement patterns have important implications, both in theory and applied management. For example, extensive movement may foster higher levels of gene flow, compared to the more isolated populations of less mobile species. Extensive movements may carry greater risks of exposure to agents of mortality such as predators. In human-influenced areas, roads may cause extensive mortality to mobile species, although roads may also act as barriers that isolate and deter movements (Trombulak and Frissell, 2000). In snakes, roads may also be attractive as temporary basking sites, further increasing the risk of mortality (Bernardino and Dalrymple, 1992; Ashley and Robinson, 1996). If lizards have similar seasonal movement patterns to snakes, they likely face the same risks and barriers.

My first objective was to determine the characteristics of sites used for hibernation and the activity season for two lizard species near the northern limits of their geographic range, *Elgaria coerulea* and *Eumeces skiltonianus*. My second objective was to determine the extent of movement in both species, particularly whether migration occurs between summer and winter habitats. I also discuss the extent to which both species co-occur in

southeastern British Columbia and to what extent habitat choice is influenced by that co-occurrence. I used mark-recapture (PIT-tags and toe-clips) to do this. In addition to addressing fundamental questions about the biology of these animals, my results also have important implications for their management.

## Materials and Methods

### *Study Species and Study Site*

The two study species are found in the western United States and reach the northern limits of their distribution in southern British Columbia (Stebbins, 1966). Although they are both diurnal and sometimes found in the same habitat *Elgaria coerulea* is viviparous and *Eumeces skiltonianus* is oviparous. All protocols were done with the approval of the University of Victoria Animal Care Committee and all necessary permits for field study were obtained.

I conducted this study during the summers of 1996-1998 from mid-April to mid-September on the west side of the Creston Valley, 10 km west of Creston, British Columbia, Canada (49°6' N, 116°31' W; elevation 597 m; Fig. 2.1). Mean daily maximum air temperatures from April - September 1996 ranged from 6.5°C to 35.0°C. Mean daily minimum air temperatures in the same period ranged from -0.6°C to 18.3°C (Environment Canada, 1996).

For mark-recapture, I used four primary study sites (hand capture and trapping; Pat's Hill, Hydro, East Clearing, and Lone Pine Hill) and six secondary sites (hand capture only; Dewdney, Office, Sign Slope, Trail, Junction, and West Creston). In 1998, Pat's Hill was used to track animals with PIT-tag implants. All sites were separated from each other

by distances of 500 m or greater.

### *Mark-recapture*

On average, the primary sites were visited four times a year and the secondary sites were visited two times per year over three years (1996-1998). Upon capture I recorded the following data: ground temperature in the open, temperature at the capture site, lizard's capture position (open or under cover), distance to nearest rock > 10 cm in length, distance to nearest shrub > 1 m in base diameter, distance to forest edge (to the nearest 5 m), rock area, and mean rock thickness (cm). Temperatures were measured using a Smart2 precision indoor - outdoor thermometer to the nearest 0.1°C. Ground temperature is the temperature in the open, at ground level, of the nearest site to the captured lizard that was exposed to sun. I gave each rock a unique number to determine if it was used by more than one lizard over time and to determine if lizards show site fidelity.

At each primary site I set up an array of portable traps. All trap numbers, sessions and duration are averages. In 1997, twelve traps were set for three sessions of three days each. In 1998, thirty traps were set for four sessions of five days each. In both years, traps were checked from one to three times a day depending on the weather.

The traps were made of 0.5 cm wire-mesh. They were tube-shaped, and 34 cm in length and 10.5 cm in diameter. A wire-mesh funnel was sewn into one end using 30 lb braided fishing line. A removable sponge was inserted into the other end. Lizards entered a trap through a 3.5 cm opening in the funnel and were unable to escape. Traps were covered with a cloth in the spring and fall, and a piece of wood in the summer, to provide shade.

### *PIT-tags and Mapping*

In 1998, I implanted AVID PIT (passive integrated transponder) tags in thirteen *Elgaria coerulea* (three adult males, five adult females, four juvenile males, one juvenile female) and six *Eumeces skiltonianus* (five adult males and one adult female) from Pat's Hill. These tags do not appear to affect growth rates or locomotor performance of neonatal snakes (Keck, 1994; Jemison et al., 1995). Roark and Dorcas (2000) urged caution in use of PIT tags because of their potential to move through the body and be expelled via the gut. In my study, none of the recaptured PIT-tagged lizards had lost their tags.

The PIT-tags were 14 mm x 2.1 mm and weighed 0.08 g. They were implanted by making a small incision (two millimetres) in the side of a lizard and injecting the tag under the skin, using a specially designed needle and syringe. Animals were left to recover for one day in the laboratory before release. All animals fully recovered and later recaptures in the field indicated complete healing of the small incision. The tags were read by passing a reader within eighteen centimetres of the animal. Measurements of rock thickness in 1996-97 indicated that, on average, lizards were under rocks less than eighteen centimetres. Therefore, I expected to be able to scan cover objects and identify animals sitting under them without disturbing the animals.

I implanted PIT-tags from May 4-7 and June 14-17. In May I scanned for 480 minutes over three days, but only one (of seven) *Elgaria coerulea* were detected and two (of five) *Eumeces skiltonianus* were detected. Therefore, scanning during the remaining three visits to the site was done opportunistically, rather than on a formal schedule.

I used a tape measure and compass to construct detailed fine-scale maps of the rock locations at each site.

I used R (Thaka and Gentleman, 1996) for all statistical analyses.

## Results

### *Species Co-occurrence*

*Elgaria coerulea* and *Eumeces skiltonianus* co-occurred at seven of the ten sites (Table 2.1). *Elgaria coerulea* was the only species that occurred at the other three sites. At four sites where the species co-occurred, *Elgaria coerulea* was predominant. The two species co-occurred in approximately equal numbers at two sites and *Eumeces skiltonianus* predominated at only one site.

At the seven sites where the two species co-occurred there was no difference in location and they were frequently found using the same rocks, although at different times. In fact, for either species, I found only copulating lizards or newborn (presumed to be from the same litter) together under a single rock at the same time.

### *Hibernation and Summer Sites*

I categorised all capture sites of lizards made before April 30 and after September 1 as hibernation sites. I was present at the study site before lizards emerged from hibernation in the spring. Weather was typically cool, and some snow cover was common until the end of April. Temperatures began to decline in early September, although snow was not present at this time. *Elgaria coerulea* captured at hibernation sites were near captures made during the summer at the four primary study sites (Fig. 2.2). A similar pattern existed in *Eumeces skiltonianus* at the only primary study site (Pat's Hill) where they were abundant.

Given that both species were found in the same location throughout the year I pooled all data from hibernation site and summer site captures to look for differences in habitat use

between the two lizard species. Most lizards of both species were found under rocks (Table 2.2). Using ANOVA I compared proximity to cover and cover object size among three categories of lizards: 1) *Elgaria coerulea* when they were the only lizard present at a site, 2) *Elgaria coerulea* when they were syntopic with *Eumeces skiltonianus*, and 3) *Eumeces skiltonianus* when they were syntopic with *Elgaria coerulea*. Note that there were no sites that contained only *Eumeces skiltonianus*. Rock area ( $F = 3.92$ ,  $df = 2, 335$ ,  $P = 0.02$ ), rock thickness ( $F = 7.28$ ,  $df = 2, 336$ ,  $P < 0.001$ ) and distance to the nearest forest edge ( $F = 6.99$ ,  $df = 2, 488$ ,  $P = 0.001$ ) all differed among the three categories of lizards (Fig. 2.3). The distance to the nearest rock ( $F = 2.72$ ,  $df = 2, 491$ ,  $P = 0.18$ ) and the distance to the nearest shrub ( $F = 2.72$ ,  $df = 2, 489$ ,  $P = 0.07$ ) did not differ among the three categories ( $F = 1.70$ ,  $df = 2, 491$ ,  $P = 0.18$ ) (Fig. 2.3). Pair-wise t-tests revealed that *Elgaria coerulea* were under larger, thicker rocks than *Eumeces skiltonianus* at sites where they were syntopic with *Eumeces skiltonianus*. Both lizard species were found at similar distances from rocks, shrubs or forest edges. *Elgaria coerulea* were under larger, thicker rocks, and farther from shrubs and forest edges (but not rocks) when they were syntopic with *Eumeces skiltonianus*, than when they were allotopic.

I compared the species of shrub that was nearest to the lizard when it was found, between the two lizard species at the two sites where they were abundant (Pat's Hill and Dewdney). The five most common shrub species were compared at Pat's Hill and the top three at Dewdney using Chi-square analysis. Both lizard species were associated with similar shrub species (Pat's Hill:  $\chi^2 = 2.75$ ,  $df = 4$ ,  $P = 0.60$ ; Dewdney:  $\chi^2 = 1.40$ ,  $df = 2$ ,  $P = 0.50$ ). Most lizards were found near Mallow Nine Bark (*Physocarpus malvaceus*), Ocean Spray (*Holodiscus discolor*), Mock Orange (*Philadelphus lewisii*), and Snowberry



(*Symphorocarpus albus*).

Similarly, I compared the associations with the immediately surrounding substrate (e.g. soil, grass, moss, leaf litter, etc.) of the two species at Pat's Hill. Both lizard species were associated with similar surrounding substrate ( $\chi^2 = 3.55$ ,  $df = 2$ ,  $P = 0.17$ ); most lizards associated with grass and moss.

All sites were located on forest edges, but the most common tree species in the nearest forest edge differed between sites. At Pat's Hill, where *Elgaria coerulea* and *Eumeces skiltonianus* were equally abundant, there was no difference between the two lizard species in their occurrences near either tree species ( $\chi^2 = 0.18$ ,  $df = 1$ ,  $P = 0.67$ ). The two most common tree species (that individual lizards were captured nearest) were Ponderosa Pine *Pinus ponderosa* (*Elgaria coerulea*: 63% of captures; *Eumeces skiltonianus*: 57% of captures) and Douglas-fir *Pseudotsuga menziesii* (*Elgaria coerulea*: 37% of captures; *Eumeces skiltonianus*: 42% of captures). I was not able to test the differences between the lizard species at the other site where both lizard species were commonly found (Dewdney) but a similar pattern existed. The most common tree species was Douglas-fir *Pseudotsuga menziesii* (*Elgaria coerulea*: 91% of captures; *Eumeces skiltonianus*: 100% of captures), which also dominated at the four sites where *Elgaria coerulea* were most abundant (Hydro: 100% of captures; Office: 100% of captures; East Clearing: 100% of captures and Lone Pine Hill: 99% of captures). The most common tree species at the one site where *Eumeces skiltonianus* were most abundant was Trembling Aspen *Populus tremuloides* (*Elgaria coerulea*: 71% of captures; *Eumeces skiltonianus*: 96% of captures).

Neither lizard species was commonly found on roads, even though six of the ten sites were bordered on one side by a road.

### *Distances between Capture Locations*

Minimum distances moved were not corrected for the time between captures as there was no relationship between distance moved and days between captures (Fig. 2.4). In addition, the habitat was level and there were no barriers between capture sites at a study site. Therefore, raw straight-line distance was used as the measure of the distance between capture sites.

Twenty-seven percent (90 of 334) of all marked *Elgaria coerulea* were recaptured over the three years and twenty-five percent (25 of 101) of all *Eumeces skiltonianus* were recaptured. Of these recaptures, neither *Elgaria coerulea* nor *Eumeces skiltonianus* were caught very far from a previous capture location (*Elgaria coerulea*: mean = 16.1 m, SE = 5.56, N = 90; *Eumeces skiltonianus*: mean = 8.0 m, SE = 2.67, N = 25). Over the three-year study, only one *Elgaria coerulea* moved from one study site to another, a distance of approximately 750 meters. No individual *Eumeces skiltonianus* was detected at a second site, although neither of the two main *Eumeces skiltonianus* sites were within one kilometre.

I compared distances between capture locations within the same year (1996, 1997, or 1998) to those between capture years (1996 to 1997, 1997 to 1998, and 1996 to 1998) using ANOVA. There was no significant difference in the distances regardless of how far apart in time *Elgaria coerulea* ( $F_{5,84} = 0.62$ ,  $P = 0.68$ ) or *Eumeces skiltonianus* ( $F_{5,19} = 0.54$ ,  $P = 0.74$ ) were captured.

*Elgaria coerulea* were equally likely to make both short and long distance moves within or between seasons (Fig. 2.5a). This is particularly evident for the 1998 data, as the movement study was more intensive that year. A similar plot of only the within-season data shows that lizards did not make long-distance moves from hibernation sites to summer

sites (Fig. 2.5b). *Eumeces skiltonianus* showed similar movement patterns, both within and between seasons.

There was no significant difference in the mean distance between captures of adult male *Elgaria coerulea* and that of newborns, juveniles or adult females ( $F_{3,84} = 0.68$ ,  $P = 0.57$ ). This was also true for male *Eumeces skiltonianus* compared to female *Eumeces skiltonianus* ( $t = 0.68$ ,  $df = 22$ ,  $P = 0.51$ ). Although the mean distances did not differ, males of both species moved the largest individual distances between capture locations.

### *Site Fidelity*

Some captures were made at sites where lizards had been previously caught (*Elgaria coerulea*: 9% of 282 captures; *Eumeces skiltonianus*: 10% of 92 captures). Some of these repeat captures were of the same animal recaptured at the same location (*Elgaria coerulea*: seven of twenty-six (26.9%) repeat captures; *Eumeces skiltonianus*: four of nine (44.4%) repeat captures). In all other instances different lizards were captured at different times at the same location.

There was no difference in the surface area or thickness of rocks recorded once or more than once for either *Elgaria coerulea* (rock area:  $t = 0.62$ ,  $df = 31.8$ ,  $P = 0.55$ ; rock thickness:  $t = 0.67$ ,  $df = 27.3$ ,  $P = 0.51$ ) or *Eumeces skiltonianus* (rock area:  $t = 1.25$ ,  $df = 8.8$ ,  $P = 0.24$ ; rock thickness:  $t = 1.01$ ,  $df = 9.2$ ,  $P = 0.34$ ). Similarly, distance to the next nearest rock for both *Elgaria coerulea* ( $t = 0.87$ ,  $df = 36.3$ ,  $P = 0.39$ ) and *Eumeces skiltonianus* ( $t = 0.15$ ,  $df = 10.9$ ,  $P = 0.88$ ) did not differ between single-use or multiple-use rocks. Distance to the nearest shrub did not differ between single-use or multiple-use rocks for both *Elgaria coerulea* ( $t = 0.29$ ,  $df = 26$ ,  $P = 0.77$ ) and *Eumeces skiltonianus* ( $t = 1.29$ ,  $df = 27.6$ ,  $P = 0.21$ ), nor did distance to the nearest forest edge vary between single-use or

multiple-use rocks for both *Elgaria coerulea* ( $t = 0.84$ ,  $df = 32.5$ ,  $P = 0.41$ ) and *Eumeces skiltonianus* ( $t = 0.74$ ,  $df = 11.3$ ,  $P = 0.48$ ).

### *Response to Disturbance*

*Eumeces skiltonianus* were more secretive than *Elgaria coerulea*. A Chi-square test of the capture location frequencies indicated that fewer *Eumeces skiltonianus* were seen in the open, either in vegetation or on a hard substrate ( $\chi^2 = 43.31$ ,  $df = 5$ ,  $P < 0.001$ ). Although *Eumeces skiltonianus* were rarely captured or sighted in vegetation unlike *Elgaria coerulea*, when disturbed *Eumeces skiltonianus* typically ran towards a shrub for cover. In contrast, *Elgaria coerulea* typically ran to a nearby rock for cover. Only copulating *Elgaria coerulea* were unresponsive to human presence, even tolerating being picked up while they remained together.

### **Discussion**

*Elgaria coerulea* and *Eumeces skiltonianus* are frequently found at the same sites in the Creston valley. This pattern of overlap was also reported between *Eumeces skiltonianus* and *Elgaria multicarinatus* in California (Block and Morrison, 1998). Nonetheless, some sites are dominated by one species. Why this should be is not clear. The proximity to cover and cover object size differs for *Elgaria coerulea* when they are allotopic in contrast to when they are syntopic with *Eumeces skiltonianus*. This may indicate competitive interactions between the two species, but that hypothesis would need to be tested experimentally. Throughout this study, I did not witness direct interactions between the two species, although I did not perform experiments to test for the presence and effects of competition. It is possible that the differences in habitat use of *Elgaria coerulea* (syntopic versus allotopic)

simply reflect site differences in habitat structure (i.e. rock sizes, shrub density). If there is no competition between the two species then perhaps the pattern of site occupation is due simply to historical reasons.

For both *Elgaria coerulea* and *Eumeces skiltonianus* captures at hibernation sites were near captures made during the summer. This suggests that hibernation and reproduction sites are in the same general area. In addition, individuals of both species were recaptured within ten meters (on average) of a previous capture. Both these factors indicate that a population requires a relatively small area. Stewart (1985) also found that most recaptures of individual *Elgaria coerulea* were within a ten metre radius of the original capture point. This is in contrast to a previous study (Vitt, 1973), in which *Elgaria coerulea* were gregarious around localised dens in early April and then from late April through August they were dispersed away from the den sites. Thus, the degree to which I can extrapolate from one population to another is questionable. Presumably, different movement patterns result from the different spatial arrangement of essential resources. I did not measure conditions required for hibernation and other activities, or their availability, but comparisons of such parameters between different habitats might explain different patterns of habitat use.

Because *Elgaria coerulea* and *Eumeces skiltonianus* have high site-fidelity and do not make large movements between hibernation or reproduction sites, they rarely need to cross roads. In addition, they are apparently not attracted to roads as basking locations. Roads may be barriers between populations, limiting gene flow and eliminating colonisation of new areas. Although not shown in lizards, this phenomenon has been observed in populations of mammals and carabid beetles (Oxley et al., 1974; Mader, 1984). The impact of habitat

fragmentation on these lizards, including the effects of roads, awaits more detailed knowledge of dispersal patterns, especially of young animals.

Both lizard species were rarely found in the open and were more often under rocks than in vegetation or under logs. They rarely strayed far from available cover, remaining closest to rocks but typically within two meters of a shrub. For reptiles, retreat sites can serve as protection from lethal ground temperatures and predators (Huey et al., 1989; Downes and Shine, 1998). In the summer, maximum air temperatures in Creston can reach 35°C with ground temperatures exceeding 40°C, lethal for a reptile in the open in midafternoon (Huey et al., 1989). I know little about their thermal biology, but there are seasonal patterns of retreat-site selection (Chapter 3). Retreat sites also would provide refuge from predators. The main predators of either lizard species are unknown but *Elgaria coerulea* carcasses have been seen on nearby nest boxes, presumably left by avian predators.

It appears that some retreat sites are more important than others. Although I found no physical differences between these 'preferred' locations and 'single-use' locations, it is possible that these 'preferred' locations had better thermoregulatory properties in addition to their proximity to available cover. Further study would reveal if lizards are selecting rocks non-randomly within the habitat by comparing rocks that lizards used to rocks that were not used.

Distances between capture locations indicated site fidelity for both species, although some adult males moved greater distances. Higher activity and longer movements in males have been shown in other lizard species (Marler and Moore, 1988; Parker, 1994) and may be due to mate-seeking behaviour. The lesser distances between capture locations of females may be due to the fact that nesting *Eumeces skiltonianus* females guard their eggs (Shine,

1988b) and gravid *Elgaria coerulea* females have reduced mobility (Chapter 5).

*If* lizards are dependent on specific retreat sites it may have broad effects on the population biology of these animals. In areas where other factors are not limiting, the availability of retreat sites may determine the upper limit for species abundance on a local scale (Bustard, 1969, 1970). For retreat-site availability to be limiting, retreat sites must be vital to the biology of the animal and there must be a limit on the number of individual lizards able to use each site simultaneously. Use of a rock by more than one *Elgaria coerulea* or *Eumeces skiltonianus* was rare in this study, regardless of the size of the rock.

Their necessity for cover means that any disturbance or removal of rocks in the area would be detrimental to both species. Rock collecting is thought to be detrimental to Velvet Geckos (*Oedura lesueurii*) (Schlesinger and Shine, 1994) and Broad-headed Snakes (Shine et al., 1998b) in southern Australia. *Elgaria coerulea* and *Eumeces skiltonianus* are similar to these reptiles in that they rely heavily on retreat sites and show some site fidelity. Both of these features make them susceptible to retreat-site disturbance.

Although both lizards were most commonly captured under rocks they also remained quite close to shrubs. In addition, disturbed *Eumeces skiltonianus* preferentially ran towards shrubs for cover. *Elgaria coerulea* and *Eumeces skiltonianus* were most frequently found nearest four shrub species. Proximity to these shrub species might merely reflect their availability at the site. All four of these shrubs are dense and provide cover close to the ground, allowing the lizards to disappear easily into the vegetation. Both lizard species are insectivores (Gregory and Campbell, 1984) and may use shrubs for foraging.

The association of *Elgaria coerulea* and *Eumeces skiltonianus* with forests is unclear. All sites were in forest clearings but the lizards may not have been utilising the forests

themselves. *Elgaria coerulea* sometimes are captured within forests (Gregory and Campbell, 1984), but they are most commonly seen in clearings. This may in part be due to the difficulty of seeing and capturing a lizard in the forest compared to in an open clearing. However, the consistent capture and recapture of both species in the clearings suggests that even if they were venturing into the forests they still returned to the clearing. An intensive movement study would need to be conducted to properly determine their association with forests.



Table 2.1: Sizes of the ten study sites and total number of individuals of *Elgaria coerulea* and *Eumeces skiltonianus*.

| Site             | Size (m <sup>2</sup> ) | <i>E. coerulea</i> |            | <i>E. skiltonianus</i> |            | TOTAL      |
|------------------|------------------------|--------------------|------------|------------------------|------------|------------|
|                  |                        | (N)                | (%)        | (N)                    | (%)        |            |
| <b>Primary</b>   |                        |                    |            |                        |            |            |
| Pat's Hill       | 22 500                 | 61                 | 61         | 39                     | 39         | 100        |
| Hydro            | 60 000                 | 51                 | 93         | 4                      | 7          | 55         |
| East Clearing    | 30 000                 | 50                 | 100        | 0                      | 0          | 50         |
| Lone Pine Hill   | 52 500                 | 65                 | 100        | 0                      | 0          | 65         |
| <b>Secondary</b> |                        |                    |            |                        |            |            |
| Dewdney          | 70 000                 | 36                 | 59         | 25                     | 41         | 61         |
| Office           | 90 000                 | 47                 | 94         | 3                      | 6          | 50         |
| Sign Slope       | 10 000                 | 3                  | 75         | 1                      | 25         | 4          |
| Trail            | 2 500                  | 6                  | 100        | 0                      | 0          | 6          |
| Junction         | 1 250                  | 4                  | 67         | 2                      | 33         | 6          |
| West Creston     | 22 500                 | 7                  | 21         | 27                     | 79         | 34         |
| <b>Total</b>     |                        | <b>334</b>         | <b>100</b> | <b>100</b>             | <b>100</b> | <b>435</b> |

**Table 2.2: Locations of all captured (including recaptures) and sighted (not captured) lizards. Data include both hibernation site and summer site captures.**

**A. *Elgaria coerulea***

| Location      | Captured   |            | Sighted    |            | Total      |            |
|---------------|------------|------------|------------|------------|------------|------------|
|               | (N)        | (%)        | (N)        | (%)        | (N)        | (%)        |
| Under rock    | 271        | 61         | 47         | 34         | 318        | 55         |
| In vegetation | 59         | 13         | 21         | 15         | 80         | 14         |
| On dirt/rock  | 27         | 6          | 24         | 18         | 51         | 9          |
| Under log     | 4          | 1          | 1          | 1          | 5          | 1          |
| On road       | 2          | 0.5        | 0          | 0          | 2          | 0.3        |
| Unknown       | 79         | 18         | 42         | 31         | 121        | 21         |
| <b>Total</b>  | <b>442</b> | <b>100</b> | <b>137</b> | <b>100</b> | <b>579</b> | <b>100</b> |

**B. *Eumeces skiltonianus***

| Location      | Captured   |            | Sighted   |            | Total      |            |
|---------------|------------|------------|-----------|------------|------------|------------|
|               | (N)        | (%)        | (N)       | (%)        | (N)        | (%)        |
| Under rock    | 112        | 83         | 55        | 60         | 167        | 74         |
| In vegetation | 2          | 1          | 5         | 5          | 7          | 3          |
| On dirt/rock  | 1          | 1          | 2         | 1          | 3          | 1          |
| Unknown       | 19         | 14         | 29        | 32         | 48         | 21         |
| <b>Total</b>  | <b>135</b> | <b>100</b> | <b>91</b> | <b>100</b> | <b>226</b> | <b>100</b> |

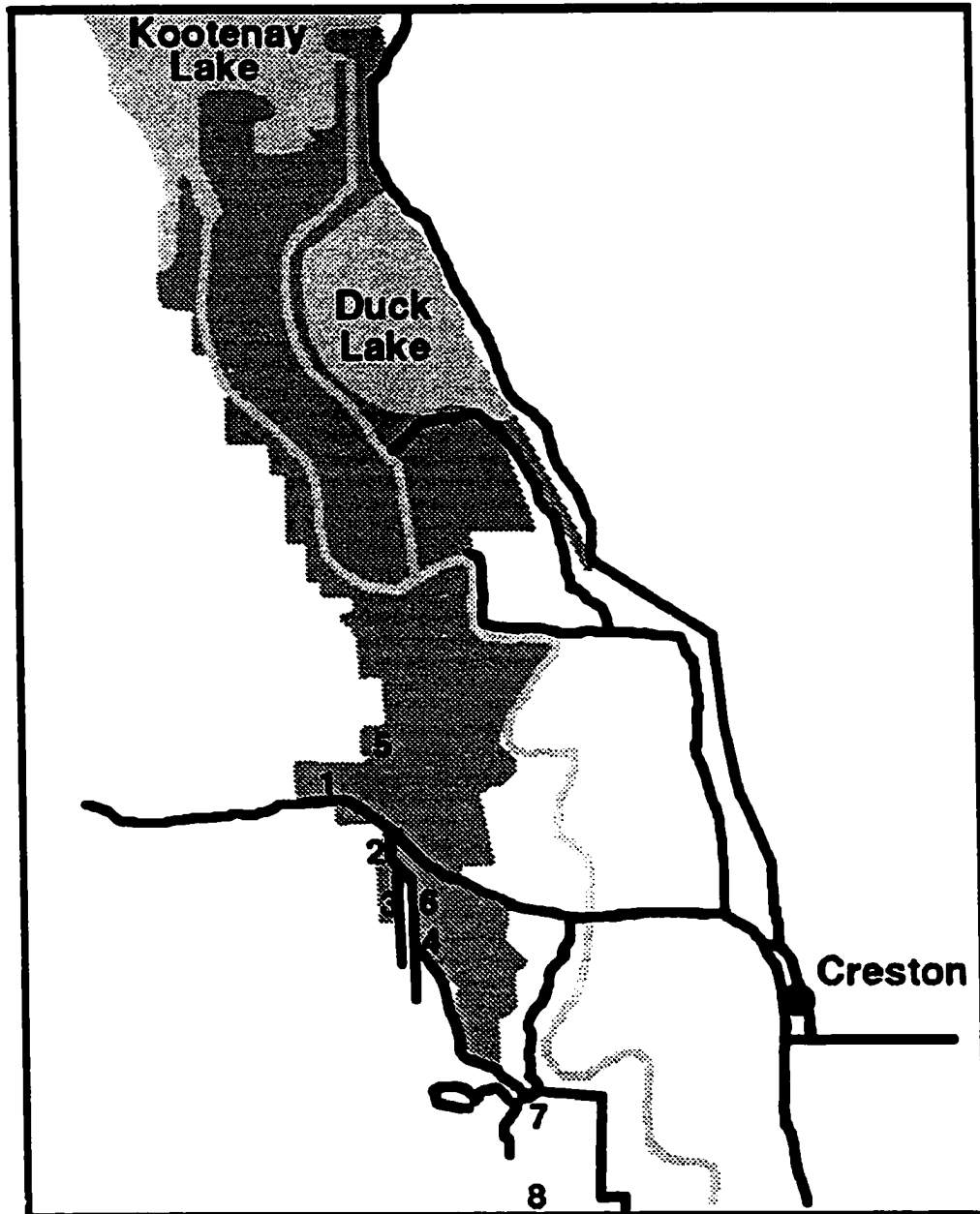


Figure 2.1: Map of the primary (1 = Pat's Hill, 2 = Hydro, 3 = East Clearing, and 4 = Lone Pine Hill) and secondary sites (5 = Dewdney, 6 = three sites: Office, Sign Slope, and Trail, 7 = Junction, and 8 = West Creston) located on and nearby the Creston Valley Wildlife Management Area, ten kilometres west of the Creston, British Columbia.

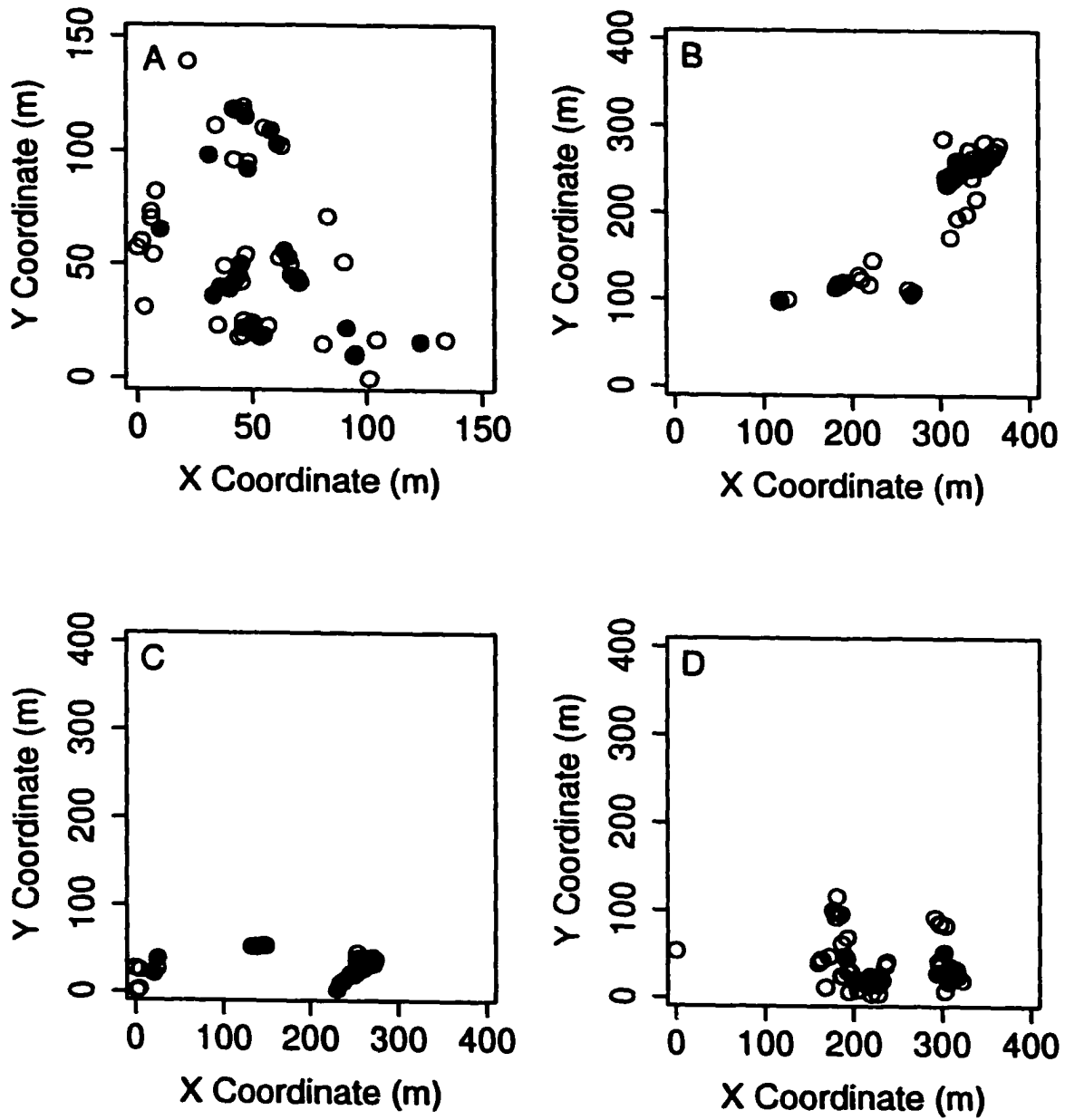


Figure 2.2: Hibernation (closed circle) and summer sites (open circle) for *Elgaria coerulea* at four primary sites: (A) Pat's Hill, (B) Balance Rock (Hydro), (C) Balance Rock (East Clearing), and (D) Lone Pine Hill.

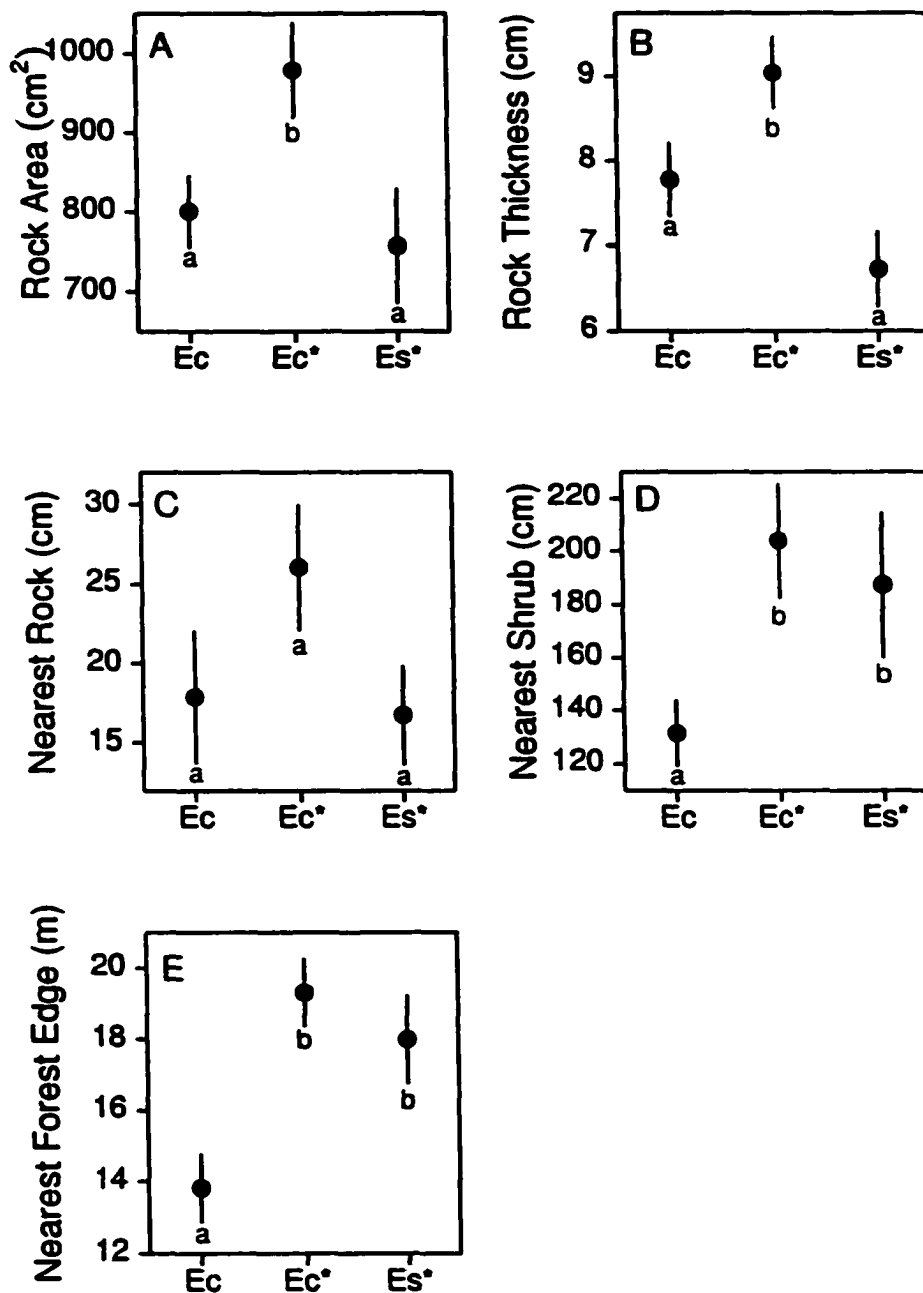


Figure 2.3: Comparisons of proximity to cover and cover object size for three categories of lizards: (1) *Elgaria coerulea* when they were the only lizard present at a site (Ec), (2) *Elgaria coerulea* when they were syntopic with *Eumeces skiltonianus* (Ec\*), and (3) *Eumeces skiltonianus* when they were syntopic with *Elgaria coerulea* (Es\*). Categories that do not differ at P less than or equal to 0.05 are shown with the same letter.

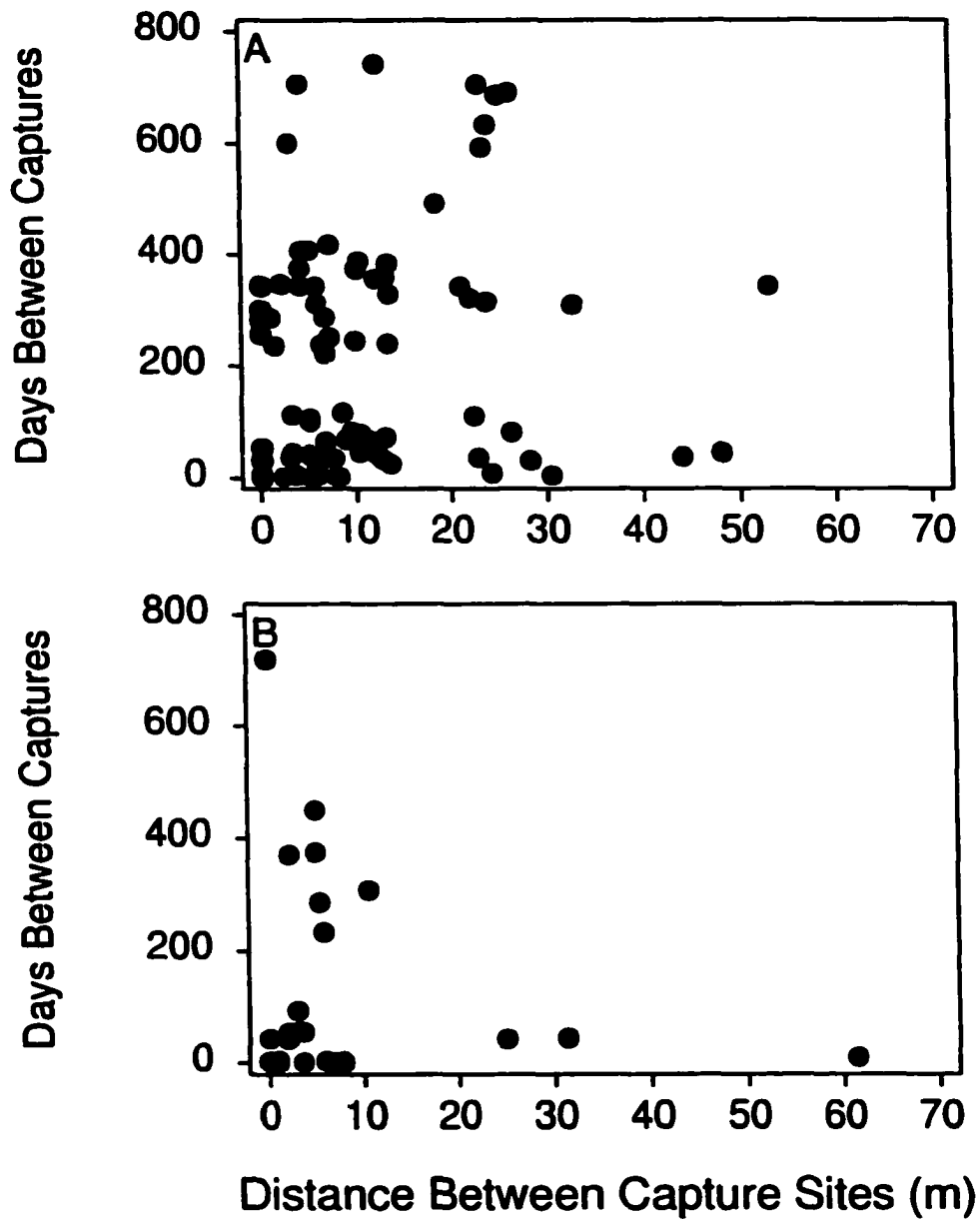


Figure 2.4: Days between capture sites and distance travelled (m) by (A) *Elgaria coerulea* and (B) *Eumeces skiltonianus* from CVWMA, Creston, British Columbia collected in 1996-1998. One outlier, an adult male *Elgaria coerulea* that was recaptured more than 500 m from his original capture after 330 days, was omitted from the plot.

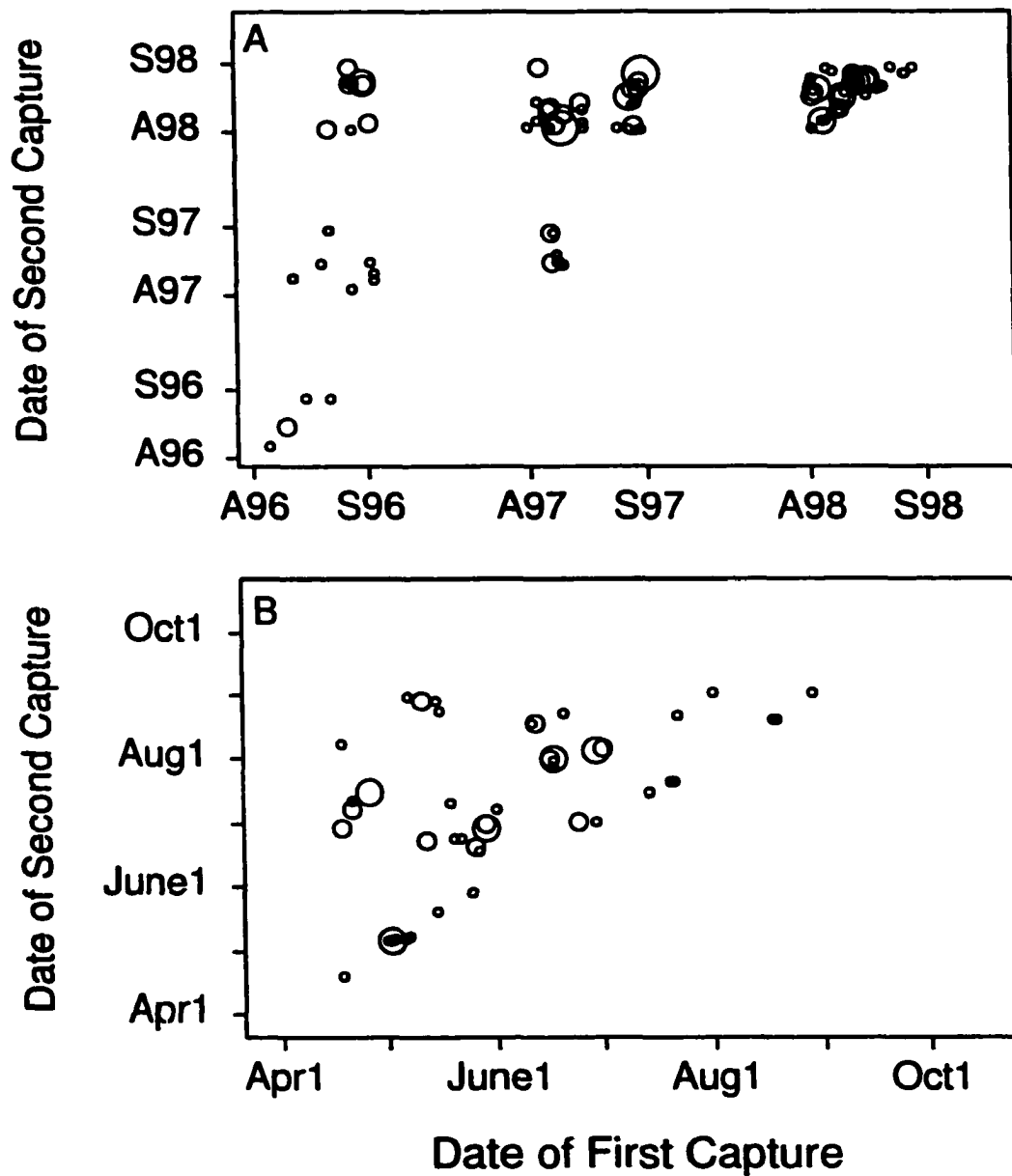


Figure 2.5: Distance between locations of first and second captures for (A) 1996-1998 and (B) within 1998 for *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. Distances travelled between capture locations are in four categories that correspond to dot size: < 10 m, 10-25 m, 25-50 m and > 50 m (A = April S = September).

## Chapter 3

# Retreat-site Selection and Emergence Patterns

## Introduction

Reproductive activities frequently make animals more susceptible to predation risk (see Magnhagen, 1991). Therefore, the challenge is for animals to minimise predation risk while successfully undertaking reproduction. To do this, animals utilise a large variety of anti-predator strategies, ranging from swift escape to hiding. For animals that rely on hiding it is important to find suitable habitat to provide cover from predators. Such habitat may take the form of vegetation that allows individuals to use crypsis. Other animals use retreat sites, hiding under rocks or logs. Selection of a suitable retreat site is typically nonrandom and is influenced by factors such as humidity (Shoemaker et al., 1992) and temperature (Huey et al., 1989; Wehner et al., 1992).

Retreat-site selection has been shown in several species of ectotherms. Animals avoid lethal high and low temperatures by selecting different retreat sites throughout the season or throughout the day (Bustard, 1967; Ruben, 1976; Huey et al., 1989; López et al., 1998; Webb and Shine, 1998). Individuals also trade off the costs and benefits of remaining under cover. The decision to emerge from a retreat site and risk predation is determined by the need to satisfy requirements (e.g. temperature regulation, foraging, mating, gestation) and by perceived threat (Avery, 1982; Huey, 1982; Cooper, 1998; Martín and López, 1999, 2001).

As the thermal environment changes throughout the season, emergence patterns also vary. In the spring and fall many ectotherms have a unimodal basking pattern, emerging



only in midday, while switching to a bimodal pattern during the warmer months (Porter et al., 1973; Huey et al., 1977; Bauwens et al., 1996). There is also variation in the time of the day individuals emerge from a retreat site. Some emerge to bask in early morning (Stebbins and Barwick, 1968; Díaz, 1991; Bauwens et al., 1996). Others warm themselves under cover before emerging, possibly to avoid exposure to predators while basking (Bustard, 1967; Schlesinger and Shine, 1994; Bauwens et al., 1999).

Response to the thermal environment through retreat-site selection and emergence patterns is not uniform and has been shown to depend on the size and sex of the animal and its behavioural requirements. Larger animals need more time to alter their body temperature than smaller animals because of differences in surface-volume ratios (Porter et al., 1973). This may explain the difference in basking patterns for juveniles and adults of the same species (Simon and Middendorf, 1976; Middendorf and Simon, 1988). During breeding, male lizards emerge earlier in the morning from retreat sites and bask more frequently than adult females or sub-adults (Damme et al., 1987; Bauwens et al., 1990). This is likely the result of their need to defend territories, seek mates, and undergo sperm production, all of which require surface activity (Licht, 1971; Vitt, 1973; Stamps, 1977).

Female reptiles also modify their emergence patterns during reproduction as reproductive females bask more frequently, for longer periods and in more open positions than males and non-reproductive females (Luiselli et al., 1996; Krawchuk and Brooks, 1998). Retreat-site selection and alteration of emergence patterns may be most important in viviparous reptiles in which basking duration and frequency may affect gestation length and offspring quality (Beuchat, 1988; Shine and Harlow, 1993). In addition, the ability to flatten the body is impaired during pregnancy in viviparous lizards. This reduces heating

rates and may increase the time they need to spend basking (Tosini and Avery, 1996).

The increased basking of reproductive males and females, however, is not cost-free. Gravid females and breeding males may be more vulnerable to predation because of increased basking. In particular, gravid females of viviparous species have reduced locomotor abilities (see Schwarzkopf and Shine, 1992). In both lizards and snakes, reproducing females have been shown to compensate by shifting their anti-predator strategy towards a more sedentary cryptic strategy (Brodie, 1989; Cooper et al., 1990; Schwarzkopf and Shine, 1992) and utilising habitat with more rock cover than non-gravid females (Charland and Gregory, 1995).

Much of the previous research on retreat-site selection and emergence patterns has focused on open, active ectotherms, particularly species where males defend mates and territories. There has been less emphasis on sedentary species that use cryptic strategies of anti-predator defence. *Elgaria coerulea* (Baird and Girard) are very secretive and are believed to frequently abandon thermoregulatory efforts in favour of staying hidden (Vitt, 1973).

I am interested in whether this secretive species exhibits age- and/or sex-related differences in retreat-site selection, emergence patterns and anti-predator behaviour. In this chapter I address the following objectives: 1) determine seasonal and daily variation in retreat-site selection, emergence patterns, and proximity to cover, 2) test for age- and/or sex-related differences in capture-site temperature, retreat-site selection, emergence patterns, proximity to cover, and sprint speed, and 3) speculate about the circumstances under which it is more favourable for an ectotherm to be in the open rather than hidden.

## Materials and Methods

### *Study Species and Study Site*

*Elgaria coerulea* are found in western United States and reach the northern limits of their distribution in southern British Columbia (Stebbins, 1966). They are viviparous.

I conducted this study during the summers of 1996-1998 from mid-April to mid-September on the west side of the Creston Valley, 10 km west of Creston, British Columbia, Canada (49°6' N, 116°31' W; elevation 597 m; Fig. 2.1). Mean daily maximum air temperatures from April - September 1996 ranged from 6.5°C to 35.0°C. Mean daily minimum air temperatures in the same period ranged from -0.6°C to 18.3°C (Environment Canada, 1996).

For mark-recapture studies, I used four primary study sites (hand capture and trapping: Pat's Hill, Hydro, East Clearing, and Lone Pine Hill) and six secondary sites (hand capture only: Dewdney, Office, Sign Slope, Trail, Junction, and West Creston). All sites were separated from each other by distances of 500 m or greater.

### *Mark-recapture*

On average, I visited the primary sites four times a year and the secondary sites two times per year over three years (1996-1998). All visits were made during the daytime. I marked all lizards with a unique toe-clip (Swingland, 1978) and kept the clipped toes in 10% formalin for skeletochronological determination of age. No more than two toes per foot were clipped from any animal.

I recorded the following data upon capture: ground temperature in the open, temperature at the capture site, lizard's capture position (open or under cover), distance to the

nearest rock >10 cm in length and that they are not currently using a cover object, distance to the nearest shrub >1 m in diameter of the entire shrub, distance to the forest edge to the nearest 5 m, rock area, and mean rock thickness (cm). Temperatures were measured using a Smart2 precision indoor-outdoor thermometer to the nearest 0.1°C. Ground temperature is the temperature in the open, at ground level, of the nearest site to the captured lizard that was exposed to sun. I recorded distance to the nearest rock for all lizards and set it equal to 0.1 (to allow a log transformation) for lizards captured under a rock. I gave each rock a unique number to determine if it was used by more than one lizard over time and to determine if lizards showed site fidelity. I categorised time of day into four arbitrary categories: 6 to 10am, 10am to 1pm, 1 to 4pm, or 4 to 8pm.

Upon capture I measured head width, snout-vent length (SVL), tail length, and mass of all lizards. Snout-vent length and tail length were measured by pressing the lizard against a plastic surface using foam. The distance along the centre of the lizard was traced onto the plastic, transferred onto paper and measured. I recorded tail loss state (yes or no) based on the presence of a previous tail break. In lizards that had lost their tails I measured the distance from the vent to the tail break (middle length) and the distance from the break to the tail tip (regenerated length). I determined sex in adults only. Individuals greater than 71 mm SVL were classed as adults as this is the minimum breeding size for females (Chapter 5).

### *Sprint Speed*

I raced all lizards within two days of capture. They were held in the laboratory in ventilated plastic containers and provided with water *ad libitum*. A trial commenced by placing lizards in separate, ventilated plastic containers within a styrofoam thermal

chamber. I kept them in this chamber until the temperature inside the plastic chambers was close to 32°C (mean = 33.2°C, range = 25.2 - 40.8°C, n = 84, SE = 0.23). I held them at this temperature for an hour and then raced each lizard three times with 45 minute rests in between. I chased each lizard down a 1.5 m rubber-floored track towards a pillow case, which provided cover. The trial in which a lizard ran the fastest was recorded as its maximal sprint speed.

After all three races were completed I measured snout-vent length (SVL), tail length, back leg length and mass of all lizards. I calculated relative tail length by first calculating the relationship between snout-vent length and tail length for all lizards that had never lost their tails. The relative tail length is the difference between the actual tail length and the predicted tail length. This regression was done separately for males and females because males grow relatively longer tails than females (Chapter 4). I calculated relative back leg length by first calculating the quadratic relationship between snout-vent length and back leg length for all lizards. Relative leg length is the difference between the actual leg length and the predicted leg length. I determined sex in adults only. I raced 84 lizards over two years (1997-98): 13 juveniles, 35 adult males, 20 adult non-gravid females, and 16 adult gravid females.

### *Statistical Analyses*

The mark-recapture dataset included some repeat observations from individuals (15% of the 227 observations). These were not considered a problem because more than half of these repeat observations (53%) were in different years and therefore individuals had grown and in some cases (19%) changed from juveniles to adults. In addition, most individuals (75%) with repeat observations were only represented twice, with the remainder

represented three times. I feel that their inclusion does not bias the results towards the behaviour of any one individual, while providing the necessary sample size to draw conclusions from the data.

Stepwise regression was used to select the best models for both logistic and linear regression models. For logistic regression models, the minimal adequate model was chosen on the basis of minimising Akaike's information criterion (AIC). The criterion often performs better than decisions based on statistical significance alone (Burnham et al., 1995). For linear regression models, the minimal adequate model was chosen on the basis of minimising Mallows's  $C_p$  (Mallows, 1973). Mallows's  $C_p$  is considered an approximation to AIC (Venables and Ripley, 1999) and is closely related to the adjusted  $R^2$  (Draper and Smith, 1981). I used R (Ihaka and Gentleman, 1996) for all statistical analyses.

## Results

### *Capture Site Temperature*

*Elgaria coerulea* were found at a wide range of capture-site temperatures (range = 9.5 - 35.9), although 80% were found between 18 and 29.9°C and 50% between 20.4 and 26.9°C (mean = 23.7, median = 23.6). There was no difference in the average capture-site temperature of newborns, juveniles, adult males or females ( $F_{3,236} = 0.81$ ,  $P = 0.49$ ).

Capture-site temperature increased with open ground temperature ( $F_{1,232} = 188.75$ ,  $P < 0.001$ ; Model 1 in Table 3.1; Fig. 3.1). The interaction term ground temperature by open/cover was retained in the second best model which differed slightly from the best model. Therefore, the relationship between ground temperature and capture-site temperature tended to differ for lizards captured in the open compared to those under cover, albeit

not significantly ( $F_{1,232} = 1.86$ ,  $P = 0.17$ ; Fig. 3.1). This interaction suggested that there was little difference in the capture-site temperature of lizards in the open or under cover at low ground temperatures but lizards in the open at high temperatures were at higher capture-site temperatures than those under cover. Nonetheless, their capture-site temperatures were still not as high as ground temperature. This is likely due to the fact that lizards in the open were often in a crevice or vegetation, thereby obtaining some shade from the direct sunlight. Capture-site temperature did not differ among juveniles, adult males, or adult females.

#### *Retreat-site Selection*

Almost all *Elgaria coerulea* used rocks as retreat sites (only 2% were captured under logs). Although rock thickness and rock area are related ( $R = 0.37$ ,  $N = 173$ ,  $P < 0.001$ ), I tested them in separate models to determine if they were influenced by different factors. Both rock thickness ( $F_{1,171} = 5.35$ ,  $P = 0.02$ ; Fig. 3.2a) and rock area ( $F_{1,171} = 12.05$ ,  $P = 0.001$ ; Fig. 3.2b) increased with julian date (Models 2a and 2b in Table 3.1). Adult females and males selected rocks of similar thickness ( $t = 0.68$ ,  $df = 173$ ,  $P = 0.50$ ) and juveniles selected the thinnest rocks ( $t = 2.46$ ,  $df = 173$ ,  $P = 0.02$ ; Fig. 3.2a). Adult males used the largest rocks, followed by adult females and juveniles ( $F_{1,171} = 2.58$ ,  $P = 0.08$ ). Rock thickness also decreased the capture-site temperature of lizards under rocks relative to ground temperature ( $F_{1,172} = 2.81$ ,  $P = 0.10$ ; Model 3 in Table 3.1). Rock area did not affect capture-site temperature.

### *Emergence from Retreat Sites*

There were more adult female lizards in the open than males or juveniles (Fig. 3.3a; Model 4 in Table 3.1), but the percentage in the open varied with julian date ( $\chi^2 = 7.26$ ,  $df = 2$ ,  $P = 0.03$ ). Julian date was a better predictor than ground temperature. Adult males were in the open equally often in the spring (April-May) compared to the summer (June-Sept.). In contrast, juveniles and adult females were more often in the open in summer than in spring.

A larger model including the interaction term time of day by julian date and the main effect of time of day was marginally worse (AIC = 214.89) suggesting that these terms may influence the probability of emergence. I interpret the interaction term between time of day category and julian date with caution ( $\chi^2 = 8.08$ ,  $df = 3$ ,  $P = 0.04$ ). In the spring, there were more animals in the open in late morning (10am to 1pm) and early afternoon (1 to 4pm; Fig. 3.3b). In the summer the probability of a lizard emerging from a retreat site increased in all four time categories, but the largest change was seen in the late afternoon category (4 to 8pm). By late July, the likelihood of a lizard being in the open was higher in late afternoon (4 to 8pm) than at any other time of day.

### *Proximity to Cover*

Distance to the nearest rock differed for the times of day categories for each of the sex/age categories ( $F_{6,215} = 2.93$ ,  $P = 0.01$ ; Model 5 in Table 3.1; Fig.3.4). Juveniles were farthest from rocks in late morning (10am to 1pm) and closest to rocks in early morning (6 to 10am). Adult males were farthest from rocks in late afternoon (4 to 8pm) and closest to rocks in late morning (10am to 1pm). Adult females were farthest from rocks in early morning (6 to 10am) and closest to rocks in early afternoon (1 to 4pm).



### *Sprint Speed*

The mean sprint speed was 1.13 m/s (SE = 0.03, n = 84). Sprint speed increased with relative tail length ( $F_{1,79} = 8.54$ ,  $P = 0.01$ ; Model 6 in Table 3.1; Fig. 3.5). Juveniles were not significantly faster than adult gravid females ( $t = 0.59$ ,  $P = 0.56$ ; Fig. 3.5), but both adult males and adult non-gravid females were significantly faster than adult gravid females ( $t = 3.65$ ,  $P = 0.001$ ;  $t = 3.32$ ,  $P < 0.001$ ; Fig. 3.5).

### **Discussion**

This study showed that although remaining hidden is believed to be of primary importance for predator avoidance by *Elgaria coerulea*, their cover-use behaviour is influenced by time of year, time of day, age and sex. In this study, the thickness and size of rocks used as retreat sites increased from April to September. A similar pattern was shown in broad-headed snakes, which, in the spring, actively selected thin (<15 cm), unshaded rocks, used cliff-top crevices exposed to the afternoon sun and avoided cooler crevices (Webb and Shine, 1998). During the summer they avoided thin, exposed rocks, which became too hot (>40°C). Some snakes used thicker, more shaded rocks and others abandoned the rock outcrop and moved to the woodland. A similar pattern may be the case in male *Elgaria coerulea* as fewer were captured in the summer months.

These seasonal shifts in retreat-site use presumably are due to avoidance of lethal temperatures. Analyses of temperatures under rocks of various sizes and shapes in the summer indicated that garter snakes *Thamnophis elegans* selecting thin rocks (<20 cm) would die of heat stress in midafternoon and would have strongly impaired physiological capacity from cold at night (Huey et al., 1989). Snakes selecting thick rocks (>40 cm) would

not experience such extreme temperatures but neither would they warm to their preferred  $T_b$ . Snakes selecting rocks of intermediate size would never overheat and would achieve preferred  $T_b$  for long periods.

There is also seasonal and daily variation in emergence patterns in *Elgaria coerulea*. In the spring, the probability of being captured in the open was highest in late morning (10am to 1pm) and early afternoon (1 to 4pm), although there was less than a 25% chance of finding an individual in the open even at these times. This pattern of finding the highest number of animals in the open in the middle of the day (unimodal pattern) is commonly seen in the spring and fall in reptiles. In the warmer months many reptiles switch to a bimodal pattern, emerging in the morning and evening, but remaining under cover in the heat of the day (Mayhew, 1968; Pianka, 1971; Porter et al., 1973; Avery, 1976; Huey and Slatkin, 1976; Huey et al., 1977; Damme et al., 1987; King, 1980; Braña, 1991; Díaz, 1994; Bauwens et al., 1996). This shift to a bimodal pattern is evident in *Elgaria coerulea*. From July through September the highest probability of capturing a lizard in the open occurred from 4 to 8pm with the next highest time period being 10am to 1pm.

The low percentages of lizards found in the open in the spring and the highest percentages in the open in late afternoon in the summer suggests that *Elgaria coerulea* do not warm up by basking in the open. They likely warm themselves by adopting the temperature of their retreat sites and initiate surface activity when their body temperature exceeds some threshold. This behaviour has been recorded in many other reptiles (Licht et al., 1966; Bustard, 1967, 1968; Werner and Whitaker, 1978; Schlesinger and Shine, 1994; Bauwens et al., 1999). Late-afternoon activity also might be a response to lower predation pressure at this time of day. *Elgaria coerulea* carcasses have been found on nearby nest-

boxes (Gary Burness, personal communication), presumably left by foraging raptors. As most raptors are diurnal hunters (Ehrlich et al., 1988), emergence in the late afternoon by *Elgaria coerulea* might help them avoid predation by raptors.

There is also daily variation in the proximity of lizards to cover but this differs for the different sex-age classes. Individuals were close to cover from 1 to 4pm. Similar to their use of thicker rocks in the summer, this may reflect the need to avoid lethal high temperatures. Females and juveniles were farthest from cover in the morning (6 to 10am and 10am to 1pm), whereas males were farthest from cover in the afternoon (4 to 8pm). This variation might be a reflection of different foraging tactics, but data on foraging are lacking.

Age- and sex-related differences were not found in capture-site temperatures, although female *Elgaria coerulea* have been shown to have higher body temperatures and lower variance in body temperatures than males (Stewart, 1984). My inability to detect a difference may be a reflection of measuring capture-site temperatures rather than cloacal temperatures as used by Stewart (1984). Nonetheless, I did find wide variation in capture-site temperatures, which is consistent with the wide variation in body temperatures found in Washington and California populations of *Elgaria coerulea* (Vitt, 1973; Stewart, 1984) and Southern Alligator Lizards *Elgaria multicarinata* (Kingsbury, 1994). This wide range may be indicative of no or limited thermoregulation, as in the lizard *Podarcis hispanica*, whose use of micro-sites was more similar to the predictions of the 'no thermoregulation' hypothesis than those of the 'only thermoregulation' hypothesis (Bauwens et al., 1996). The wide range (particularly the low body temperatures) also could be indicative of a species that continues to be active when thermoregulation is more difficult (Kingsbury,

1994). Kingsbury (1994) believes this to be the case for the Southern Alligator Lizards and it is a likely explanation for its close relative, *Elgaria coerulea*. This suggests facultative thermoregulation rather than obligate thermoregulation.

The wide range of body temperatures of alligator lizards is also an indication of their priorities. Both *Elgaria coerulea* and *E. multicaudatus* prefer to stay hidden, but *E. multicaudatus* will select warm shelter when available (Kingsbury, 1993). In both species, their reliance on hiding forces them to live in thermally marginal habitats, such as dense brush or forests. They are able to utilise this habitat by being facultative thermoregulators and operating at low body temperatures in some circumstances. Although low body temperatures do have a cost, impairing burst speed and endurance (Bennett, 1980), these costs are less important in either *Elgaria coerulea* or *E. multicaudatus*, which do not rely on speed to capture prey as they largely eat slowly moving prey that move within striking distance of the lizard (Cunningham, 1956). Anti-predator behaviour in *Elgaria coerulea* is also less reliant on sprint speed as *Elgaria coerulea* initially use crypsis to avoid predators and rely on biting, defecation and tail autotomy if captured (Rutherford, personal observation).

I did detect age-variation in retreat-site selection. Adult males and females selected thicker rocks than juveniles, with no difference between the former two groups. Adult males also used the largest rocks, followed by adult females and juveniles. It is unclear why males would select larger, thicker rocks than females and juveniles. It may be a function of the areas where males are located, making larger, thicker rocks more available to them than to females or juveniles. Larger, thicker rocks may offer a more stable thermal environment (Huey et al., 1989), although it is unclear why this would be more important to males than females or juveniles.

There was also age- and sex-related variation in emergence patterns. For males, the probability of being found in the open did not change from April to September. Changes in emergence patterns based on reproductive cycles have been shown for male lizards (Damme et al., 1987; Bauwens et al., 1990; Firth and Belan, 1998). Lack of evidence for it in *Elgaria coerulea* may reflect differences between facultative and obligate thermoregulation. Although spermatogenesis is known to occur in this species in late fall and early spring (Vitt, 1973), individuals may be able to accomplish spermatogenesis without significantly modifying their emergence patterns and exposing themselves to increased predation pressure.

In contrast, accomplishing gestation without modifying emergence patterns may not be possible. I found that the probability of capturing an adult female in the open steadily increased over the summer. This pattern has been shown in other reptiles (Damme et al., 1987; Luiselli et al., 1996; Krawchuk and Brooks, 1998). Spending more time in the open makes gravid females more vulnerable to predation and reduced sprint speeds make them less likely to escape a predator if pursued. Given these factors, females should remain closer to cover. However, females did not consistently remain closest to cover and for all three sex-age classes (juveniles, adult males, and adult females) proximity to cover varied with time of day. Regardless of this variation, all individuals consistently remained close to cover (Chapter 2), demonstrating their reliance on crypsis rather than sprinting as an anti-predator defence. Given this strategy, I would not expect to see a shift in anti-predator behaviour by gravid females, regardless of a reduction in sprint speed.

Juveniles also demonstrated a shift in emergence patterns with a marked increase in the probability of being captured in the open in August and September. This pattern

may be the result of an influx of juveniles into the population as parturition occurs at this time of year. It is possible that this increase in the probability of being captured in the open also reflects an increase in foraging as juveniles prepare for hibernation.

Emergence patterns of male *Elgaria coerulea* do not change in response to their reproductive cycle, although gestation does significantly alter emergence patterns of females. These results suggest that the benefits of emerging from cover outweigh the costs only in female, and not male, *Elgaria coerulea*. However, this study is only a first step in evaluating the factors that influence a lizard's cover-use behaviour. A description of mate-searching behaviour in male *Elgaria coerulea* may reveal why males do not spend more time in the open in the spring, compared to the summer and fall. In addition, further work on anti-predator behaviour and predation rates in *Elgaria coerulea*, particularly gravid females, will determine if gravid females incur costs as a result of their change in cover-use behaviour during gestation.

Table 3.1: A series of models testing the effects of age and sex on retreat-site selection, emergence patterns and sprint speed in *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. Tested models with the terms retained in the best model are shown in italics. For models 1 and 4, additional terms retained in the next best model are shown in brackets. Ground temperature and distance to the nearest rock were log transformed to correct non-normal distributions. Julian date and ground temperature were tested in separate models because they were highly correlated ( $R = 0.438$ ).

| No. | Dependent Variable | Terms  | F/AIC  | df     | P       | Adj. R <sup>2</sup> |
|-----|--------------------|--|--------|--------|---------|---------------------|
| 1   | capture-site temp. | <i>ground temp., open/cover, (gr. temp. by open/cover), sex/age, ground temp. by sex/age, sex/age by open/cover</i>  | 64.31  | 3,232  | < 0.001 | 0.447               |
| 2a  | rock thickness     | <i>date, sex/age, date by sex/age</i>  | 3.90   | 3,171  | 0.01    | 0.048               |
| 2b  | rock area          | <i>date, sex/age, date by sex/age</i>  | 5.74   | 3,171  | 0.001   | 0.076               |
| 3   | capture-site temp. | <i>ground temp., rock thickness or area, sex/age, ground temp. by sex/age, rock thick. or area by sex/age</i>  | 54.15  | 2,172  | < 0.001 | 0.379               |
| 4   | prob.(emergence)   | <i>date, sex/age, date by sex/age, (time, date by time), tail loss state, time by sex/age, tail loss by sex/age</i>  | 211.35 | 211    |         |                     |
| 5   | distance from rock | <i>time, sex/age, time by sex/age, date, tail loss state, date by time, date by sex/age, tail loss state by sex/age</i>  | 2.24   | 11,215 | 0.013   | 0.057               |
| 6   | sprint speed       | <i>age/repro., rel. tail, site, chamber temp., rel. SVL, rel. back leg, age/repro. by chamber temp., age/repro. by rel. SVL, age/repro. by rel. tail, age/repro. by rel. leg</i> | 8.13   | 4,79   | <0.001  | 0.256               |

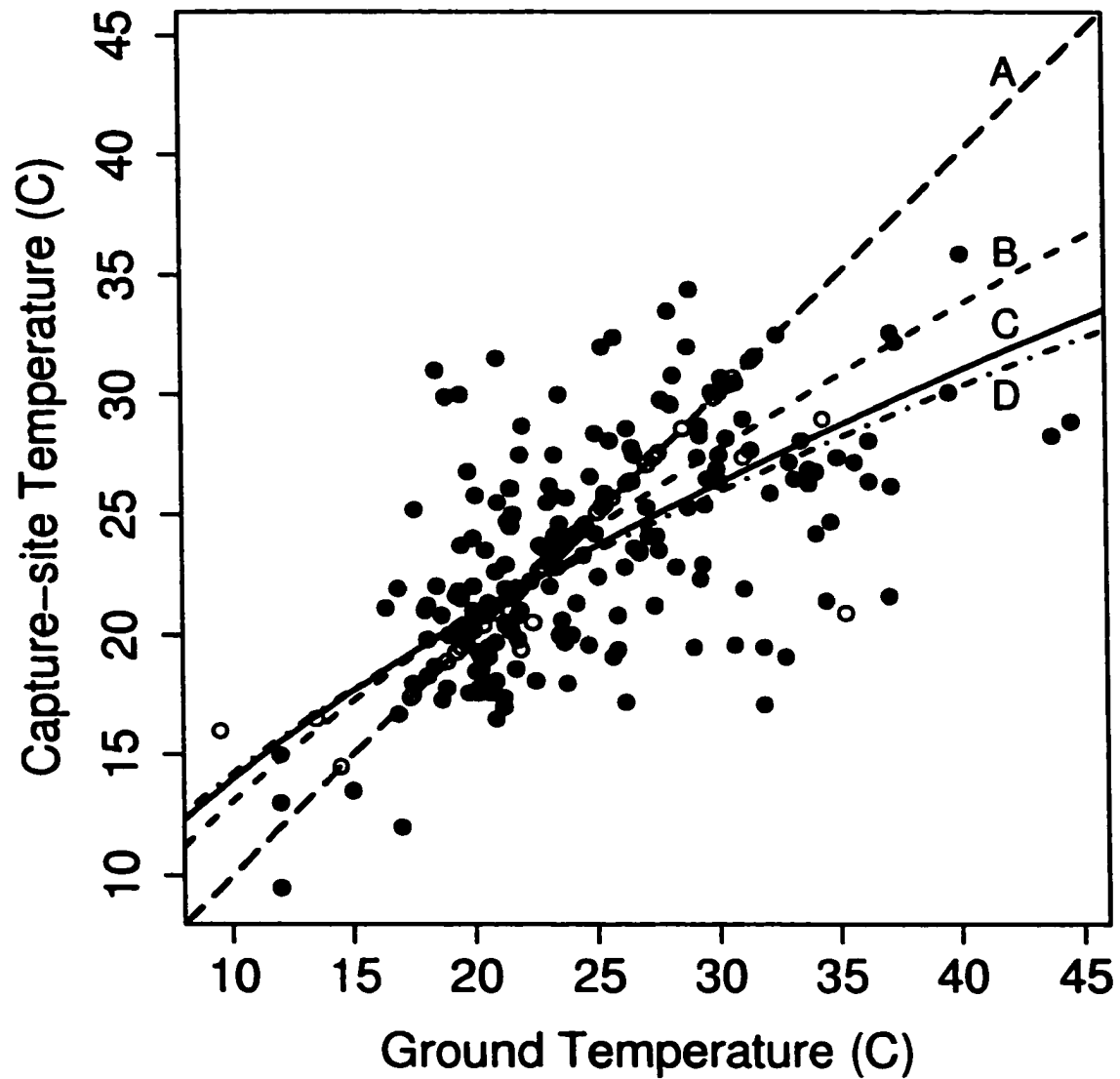


Figure 3.1: Open ground temperature (C) vs capture-site temperature (C) for *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. Regression lines are shown for the (A) ground temperature equal to capture-site temperature, (B) lizards captured in the open (open circles), (C) total data set, and (D) lizards captured under cover (closed circles). Lines (B)-(D) are curved because the tested relationships were between log-transformed variables.



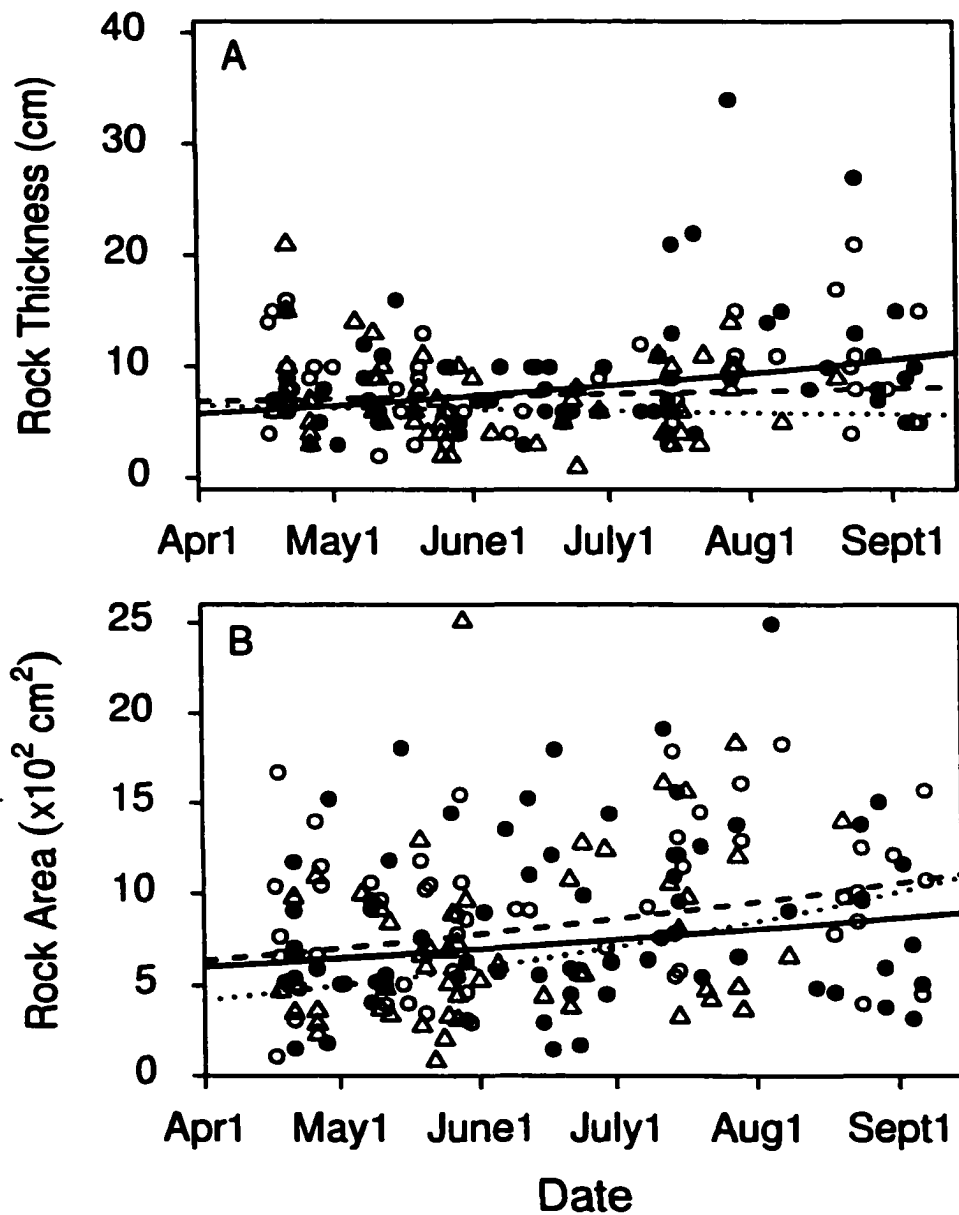


Figure 3.2: Julian date vs (A) rock thickness and (B) rock area. Regression lines are shown for juveniles (triangle, short-dashed line), adult males (open circle, long-dashed line), and adult females (closed circle, solid line) *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998.

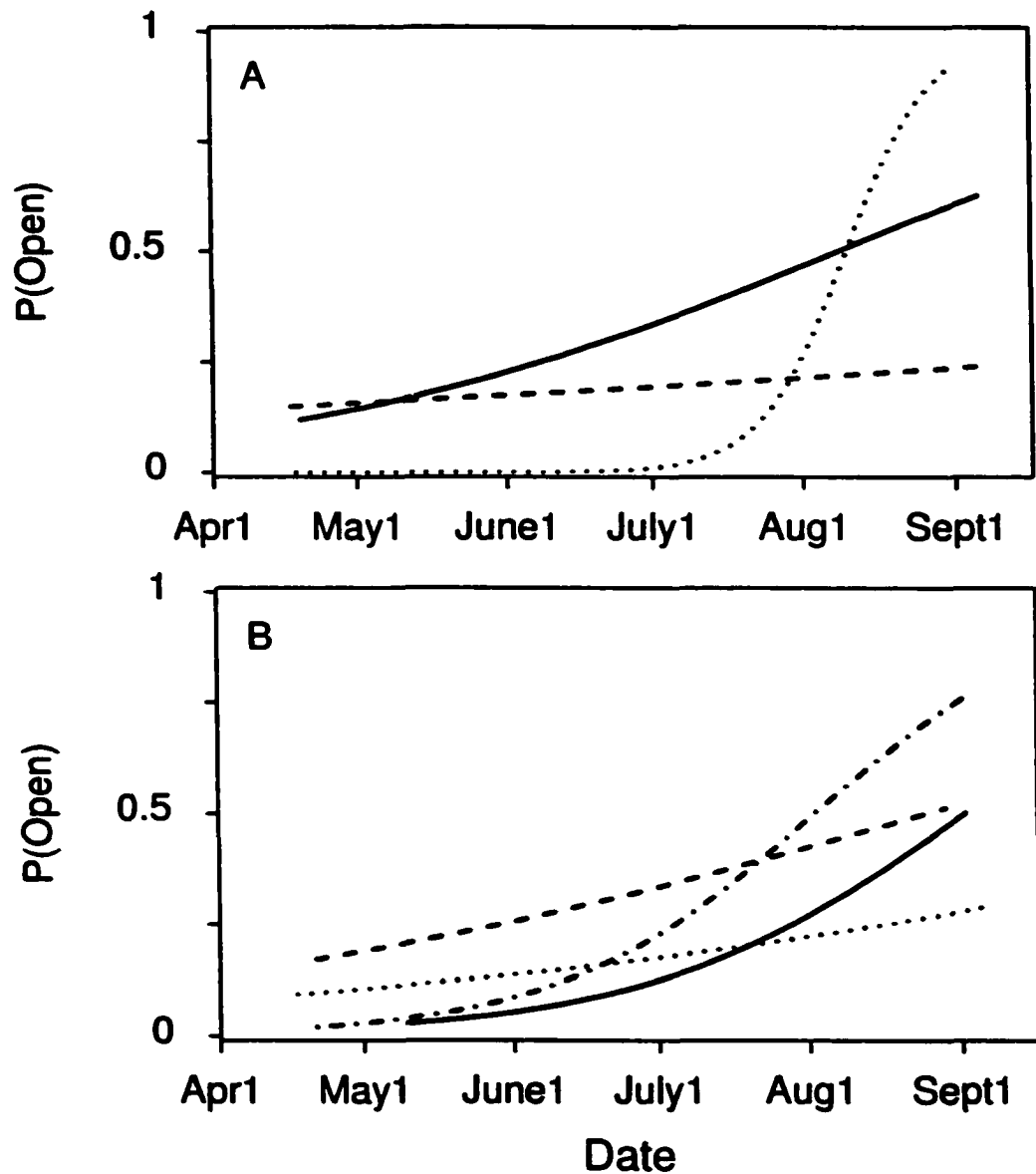


Figure 3.3: Julian date vs probability of being in the open for (A) sex/age categories and (B) time of day categories. In (A) probability curves are shown for juveniles (short-dashed line), adult males (long-dashed line), and adult females (solid line) *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. In (B) probability curves are shown for 6 to 10am (solid line), 10am to 1pm (long-dashed line), 1 to 4pm (short-dashed line), and 4 to 8pm (short- and long-dashed line).

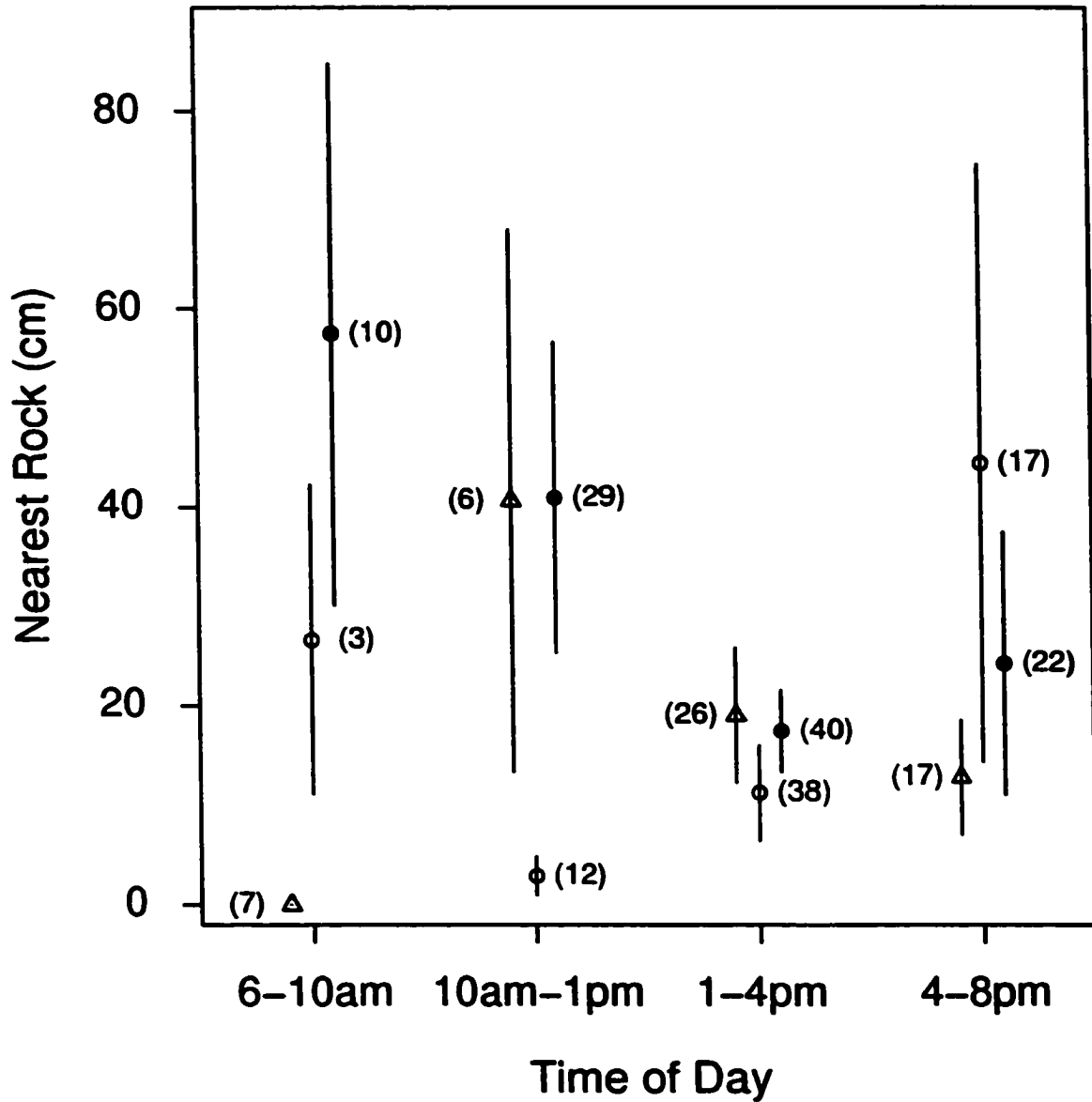


Figure 3.4: Mean distance to the nearest rock (cm)  $\pm$  SE for four time of day categories. Plotted are juvenile (triangle), adult male (open circle), and adult female (closed circle) *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. Sample sizes are shown in parentheses.

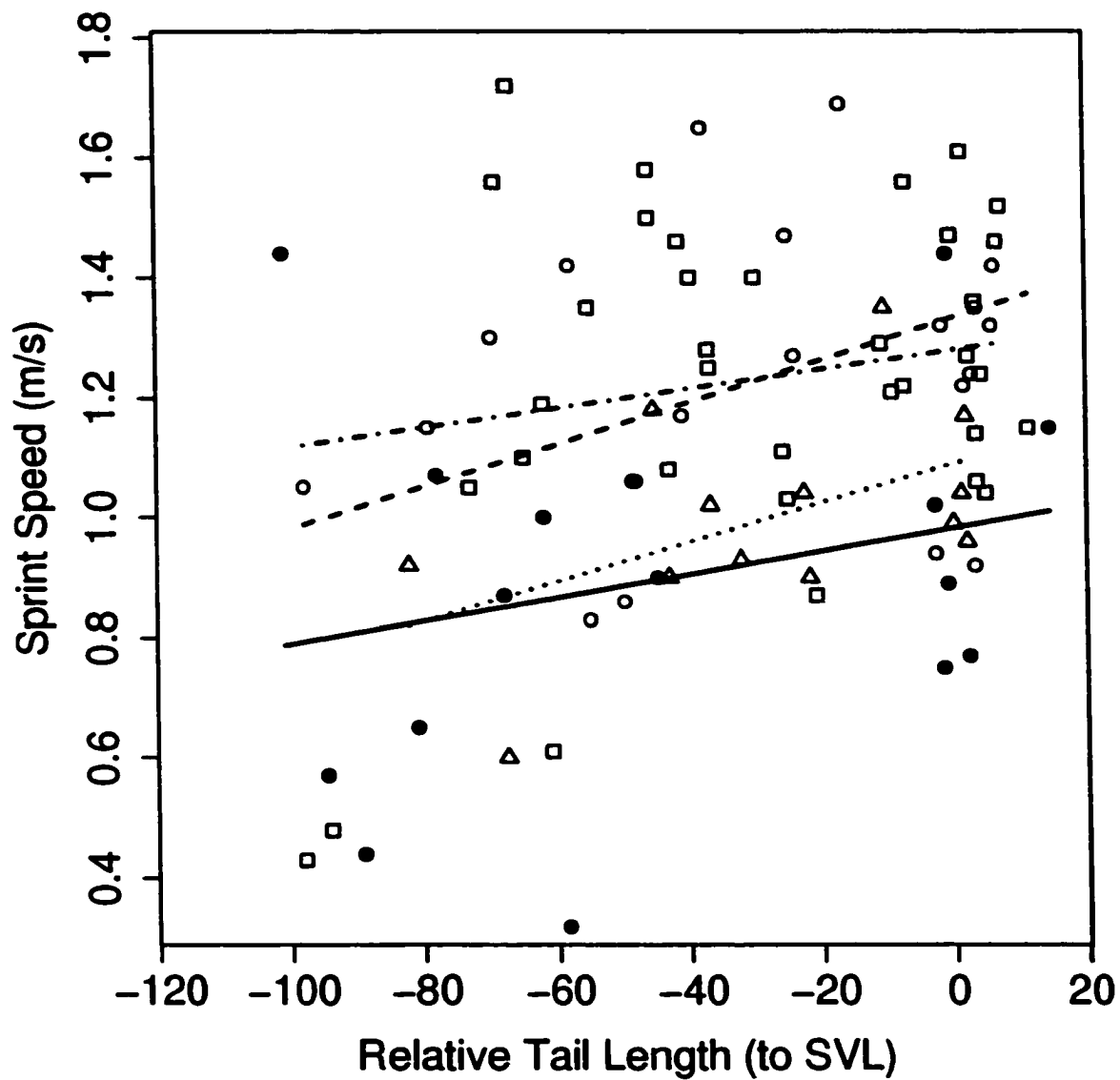


Figure 3.5: Sprint speed (m/s) vs relative tail length (to SVL) for *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1997-1998. Four age/reproductive categories are shown: juveniles (triangle; short dashes), adult males (square; long dashes), adult non-gravid females (open circle; short-long dashes) and adult gravid females (closed circle; solid line).

## Chapter 4

# Sexual Dimorphism in Survival Rates and Morphometry

### Introduction

Sexual size dimorphism, wherein one sex is larger than the other in some body measurement, is a characteristic of many animal species (Selander, 1972; Crook, 1972; Woolbright, 1983) and widespread in reptiles (Schoener, 1977; Fitch, 1981; Stamps, 1983). The factors determining these sexually dimorphic traits are complex and could involve both natural and sexual selection (Slatkin, 1984; Koenig and Albano, 1986; Shine, 1989; Smith, 1991).

The idea that sexual selection causes sexual size dimorphism was first suggested by Darwin (1871). Through intraspecific aggression, courtship, and mating there is selection pressure for large combat structures, such as increased body size and head size. In lizards, several studies have demonstrated that sexual dimorphism of head and body size is due to sexual selection (Schoener, 1975; Trivers, 1976; Carothers, 1984; Vitt and Cooper, 1985; Anderson and Vitt, 1990; Bull and Pamula, 1996). Larger bodies are advantageous in securing and retaining mates, while wider heads are beneficial as males hold females in their jaws during copulation. Alternatively, dimorphism in head size is also the result of resource partitioning, whereby males eat larger prey than female conspecifics (Schoener, 1967; Powell and Russell, 1984; Best and Pfaffenberger, 1987; Preest, 1994).

An additional mechanism proposed to account for sexual size dimorphism in body size is differential mortality between the sexes (Dunham, 1981; Stamps, 1983; Stewart, 1984, 1985). This may cause an apparent size dimorphism due to unequal ages of the sexes. Few

studies have looked for this effect in lizards and the results are equivocal. Tinkle (1972) and Parker (1994) reported that adult male lizards tended to have lower survival rates than adult female lizards, but Smith (1996a) found the opposite trend.

Differential survival may be the result of variation in anti-predator strategies between adult males and females. A common anti-predator strategy in lizards, some salamanders, and a few rodents is tail autotomy (Robinson et al., 1970; Morton, 1973; Edmunds, 1974; Maiorana, 1977; Arnold, 1988). In lizards, several studies have demonstrated sexual dimorphism in tail length (Barbadillo and Bauwens, 1997), tail break points (Barbadillo et al., 1995), tail break frequency (e.g. Tinkle and Ballinger, 1972; Vinegar, 1975; Brown and Ruby, 1977; Parker, 1994; Smith, 1996b; Wilson and Booth, 1998), ease of tail autotomy (Fox et al., 1998), percent lipid content (Vitt and Cooper, 1986), and regeneration rates (Congdon et al., 1974; Vitt, 1981). These differences are believed to be due to the differences between males and females in the costs of tail autotomy and tail regeneration. A handful of studies have compared field survival rates of tailed and tailless lizards. In some cases, lizards with incomplete tails had lower survival rates during hibernation (Bauwens, 1981), or the active season (Wilson, 1992; Fox and McCoy, 2000), whereas other studies found no difference between survival rates of lizards with or without tails (Althoff and Thompson, 1994; Smith, 1996b; Niewiarowski et al., 1997).

Differential survival between males and females also may be the result of colour pattern variation. In one of the few studies to compare survival rates of different colour patterns in males and females, Forsman and Shine (1995) found that the relationship between colour pattern and survival differed for the two sexes in a scincid lizard. Striped gravid females survived better than non-striped females, but striped males had lower survival than

control males. In reptiles, an individual's colour pattern can influence its anti-predator strategy (Andrén and Nilson, 1981) and its thermoregulatory abilities (Gibson and Falls, 1979). The pattern detected by Forsman and Shine (1995) may be the result of variation in the anti-predator strategies and thermoregulatory abilities of the male and female scincid lizards.

Comparison of survival rates of male and female lizards under natural conditions has been limited by the fact there are few dependable data on lizard age and survival due to low recapture rates (see Shine and Charnov, 1992). Few previous studies calculated survival rates using separately estimated recapture probabilities, making their estimates potentially less reliable. Recently developed methods of analysis of mark-recapture data allow separate estimation of survival and capture probabilities (Lebreton et al., 1992), producing dependable survival estimates.

In this study I measured survival rates of *Elgaria coerulea* (Family: Anguidae), taking into account their recapture rates. I then tested for sexual dimorphism in survival rates, head width, body size, tail autotomy, and colour pattern. In the family Anguidae, sexual dimorphism in body size, head size and colour pattern is rare (Fitch, 1938; Tihen, 1949; Taylor, 1956; Fitch, 1981; Vitt, 1985; Kargas and Wright, 1987; Knight and Duerre, 1987; Vial and Stewart, 1989). Demonstration of the presence of sexual dimorphism suggests that these traits are under selection and comparison with other lizard species may shed light on possible causes.

## **Materials and Methods**

### ***Study Site***

I conducted this study during the summers of 1996-1998 from mid-April to mid-September on the west side of the Creston Valley, 10 km west of Creston, British Columbia, Canada (49°6' N, 116°31' W; elevation 597 m; Fig. 2.1). Mean daily maximum air temperatures from April - September 1996 ranged from 6.5°C to 35.0°C. Mean daily minimum air temperatures in the same period ranged from -0.6°C to 18.3°C (Environment Canada, 1996).

For mark-recapture studies, I used four primary study sites (hand capture and trapping: Pat's Hill, Hydro, East Clearing, and Lone Pine Hill) and six secondary sites (hand capture only: Dewdney, Office, Sign Slope, Trail, Junction, and West Creston). All sites were separated from each other by distances of 500 m or greater.

### ***Mark-recapture***

On average, I visited the primary sites four times a year and the secondary sites two times per year over three years (1996-1998). I marked all lizards with a unique toe-clip (Swingland, 1978) and kept the clipped toes in 10% formalin for skeletochronological determination of age. I clipped no more than two toes per foot.

Upon capture I measured head width, snout-vent length (SVL), tail length, and mass of all lizards. Snout-vent length and tail length were measured by pressing the lizard against a plastic surface using foam. The distance along the centre of the lizard was traced onto the plastic, transferred onto paper and measured. I recorded tail loss state (yes or no) based on the presence or absence of a previous tail break. In lizards that had lost



their tails I measured the distance from the vent to the tail break (middle length) and the distance from the break to the tail tip (regenerated length). I determined sex in adults only. Individuals greater than 71 mm SVL were classed as adults as this was the minimum breeding size for females (Chapter 5).

#### *Skeletochronological Determination of Age*

I prepared the toe-clip samples using standard paraffin histology techniques, until they were embedded in paraffin in separate blocks. I counted growth layers using the same technique as Waye and Gregory (1998). The number of rings was determined by a single reader, but ring counts were verified by known-aged animals when possible.

#### *Colour and Mottling Scoring*

I scored colours by comparison to Munsell Soil Color charts, which give values for colour (hue), saturation (value) and chroma. These standards have been previously used to measure colours from other lizard species (see Molina-Borja et al., 1997). I did colour estimation in a consistent environment in the laboratory within a white box under a 60w light bulb. All colour scoring was done by me to avoid intra-individual colour perception variation. I then reduced the resulting seventeen different colour scores to five ranked colour scores (darkest to lightest): dark brown (5), grey brown (4), medium brown (3), light brown (2), and yellow brown (1) by grouping all colour scores that were not distinguishably different to my eye. I did the grouping on two separate occasions and the same grouping pattern resulted each time. I determined mottling by scoring the percent black on lizard's backs (0, 1, 5, 10 or 20%), using the Munsell chart for estimating proportions of mottles and coarse fragments. Percent black was converted to ranks one through five, with one

being the lowest.

The relationship between air temperature and colour was determined by recording lizard colour at a high temperature (mean = 32.1, range = 27.6 - 34.0). I then placed each lizard in the refrigerator for 5 minutes. A low temperature (mean = 5.13, range = 1.5 - 8.8) colour was recorded immediately upon removal of the lizard from the refrigerator. Colour did not change with temperature (paired t-test  $P = 0.46$ ,  $df = 43$ ).

### *Statistical Analyses*

I used stepwise regression (Ihaka and Gentleman, 1996) to select the best models for both logistic and linear regression analyses. For logistic regression models, the minimal adequate model was chosen on the basis of minimising Akaike's information criterion (AIC). This criterion often performs better than decisions based on statistical significance alone (Burnham et al., 1995). For linear regression models, the minimal adequate model was chosen on the basis of minimising Mallows's  $C_p$  (Mallows, 1973). Mallows  $C_p$  is considered an approximation to AIC (Venables and Ripley, 1999) and is closely related to the adjusted  $R^2$  (Draper and Smith, 1981).

I determined survival rates using MARK analysis of deviance of mark-recapture data (White and Burnham, 1999). This determines maximum likelihood estimates of the deviance of models incorporating parameters for survival ( $\phi$ ) and recapture probabilities ( $P$ ) as a function of group (juvenile, adult male or adult female;  $g$ ), over-winter vs within year ( $ow$ ), and spring vs summer ( $spr$ ). I divided each year into three time periods (Spring: April and May, Summer: June and July, and Fall: August and September). Time intervals of two months between visits within a year and seven months between fall and spring were included in the analysis allowing estimates of survival rates per month. Data from three

sites (Lone Pine Hill, Hydro and Pat's Hill) were included in the analysis, although site differences were not examined due to limited data.

I used the model with the most parameters [ $\phi$ (group by over-winter)  $P$ (group by spring); deviance = 145.74; deviance df = 22] to determine the fit of the model (Cooch and White, 1998). A bootstrap Goodness of Fit test with 100 iterations determined that the observed deviance was 'quite likely' because 96 of the 100 simulated values exceeded the observed value. An additional means of evaluating the fit of the model is to calculate  $\hat{c}$  which can be done in two ways: 1) observed deviance / mean of simulated deviances =  $145.74 / 180.67 = 0.807$ , or 2) observed  $\hat{c}$  / mean of simulated  $\hat{c}$ 's =  $6.625 / 4.74 = 1.398$ . If the model fits the data perfectly then we expect a  $\hat{c}$  of 1.0. The highest adjusted  $\hat{c}$  of 1.398 was used to calculate quasi-likelihood adjusted AIC (QAIC).

The minimal adequate model was selected as the one with the lowest QAIC, and the highest QAIC weight (Cooch and White, 1998). Terms retained in this model indicated significant differences in the survival or recapture estimates for different groups (adult females, adult males, or juveniles), or different times of the year (over-winter vs within season survivorship rates and spring vs summer recapture rates). Effects were also tested using likelihood ratio tests (LRT), in which the general model containing the term was compared to a nested model without the term. The difference in deviance was  $\chi^2$  distributed with degrees of freedom equal to the difference in the number of parameters of the two models.

## Results

### *Survival*

Age distributions show patterns of survival if the population is stable in size with a stationary age distribution (Caughley, 1977). I assumed this was true for these populations of *Elgaria coerulea*. Age distributions of captured lizards reveal patterns of age- and sex-specific survival rates and longevity (Fig. 4.1). There were few one-year-olds captured compared to the number of newborn, but the differences in the numbers of individuals captured in other age classes was minimal. The oldest individual captured was an eight year old male. Sex ratios were equal in the three- to eight-year-old age categories of the pooled data (site and year;  $\chi^2 = 6.99$ ,  $df = 5$ ,  $P = 0.22$ ; Fig. 4.1). Sex ratios varied from year to year at the sites, and recruitment was lower in 1996 and varied from year to year; these effects are likely a consequence of small sample sizes.

A test of the factors influencing survival and recapture rates results in a minimal adequate model (Model 3 in Table 4.1a) that suggests that juveniles, adult females and adult males had different survival rates although group differences were only marginally significant in a likelihood ratio test (Table 4.1b). Annual female survival (0.435) was higher than annual juvenile survival (0.216) although male survival could not be estimated in the minimal adequate model due to small sample sizes (Fig. 4.2). The best model that allowed estimation of male survival was model 16 in Table 4.1a. This model estimated that male survival rates were between female and juvenile survival rates (Fig. 4.2). Unfortunately, this does not provide strong evidence that male and female survival rates were significantly different because of the low weight for this model. To determine the relationship between juvenile, adult female and adult male survival rates I examined an additional model, in

which I estimated adult survival by grouping adult males and females and compared this to juvenile survival (Model 4 in Table 4.1a). This model had a higher QAIC than either models 3 or 5 (Table 4.1a), providing indirect evidence that juvenile, adult female and adult male survival rates were significantly different from one another.

Survival rates did not differ between over-winter periods and within seasons, as indicated by the lack of inclusion of this term in the minimal adequate model (Table 4.1a) and the likelihood ratio test (Table 4.1b).

Recapture rates differed among the three groups (juveniles, adult females, adult males) and the two times of year (spring, summer) as evidenced by the retention of the interaction term in the minimal adequate model (Table 4.1a) and the likelihood ratio test (Table 4.1b). Recapture rates were higher in the summer than the spring for females and juveniles while the opposite was true for males (Fig. 4.2).

#### *Morphometry and Colour*

Head width of adult males increased with snout-vent length faster than did head width of adult females ( $F_{1,191} = 12.22$ ,  $P < 0.001$ ; Model 1 in Table 4.2; Fig. 4.3a). Tail length of adult males increased faster with body size (SVL) than did tail length of adult females ( $F_{1,56} = 2.72$ ,  $P = 0.10$ ; Model 2 in Table 4.2; Fig. 4.3b).

Of the 330 lizards captured, 183 (55.5%) had previously lost their tails. A small number ( $N = 3$ ; 0.9%) were initially captured with intact tails but in subsequent captures had lost their tails. The probability of tail loss differed between sites in a logistic regression (deviance = 18.27, deviance df = 5,  $P = 0.003$ ; Model 3 in Table 4.2). This was largely due to a lower tail loss percentage at East Clearing (34.2% compared to 51.7% or greater at all other sites;  $z = -2.72$ ,  $P = 0.006$ ). The significance of the sex/age category is not surprising

since the likelihood of a lizard having lost its tail increases as it grows. This is due to the fact that once a lizard has lost its tail it is forever classed as a tail loss. Juveniles had significantly lower tail loss percentages than adult females (40.7%;  $z = -2.84$ ,  $P = 0.004$ ) but there was no significant difference between adult males and adult females (67%;  $z = 0.54$ ,  $P = 0.59$ ).

I captured only twenty-two animals that had recently lost their tails. A recent tail loss was defined as any animal with a regenerated portion less than 5 mm in length. Tail loss occurs throughout the season for juveniles and adult males although most juveniles with recent tail loss were captured in August. Adult females with recent tail loss were captured only in June and July (Fig. 4.4).

Lizards can autotomise varying portions of their tails. I compared the amount of tail lost in adult males and females by subtracting the amount of original tail remaining (middle length) from the predicted tail length. Predicted tail length was determined by separately regressing (males and females) SVL vs tail length in lizards with intact tails. Predicted tail length was included in the model (Model 4 in Table 4.2) to control for the fact that lizards with longer tails have the potential to lose more of their tails than lizards with shorter tails. As expected, the amount of tail loss increased with predicted tail length (Model 4 in Table 4.2). The model including all terms had a Cp only marginally higher (Cp = 3.7, np = 3 compared to Cp = 3.4, np = 2). Therefore, there is a tendency for the relationship between predicted tail length and amount of tail loss to differ for males and females (Fig. 4.5). In lizards with short tails males lose more of their tails, whereas in lizards with long tails females lose more of their tails (Fig. 4.5). Females also never lost just tail tips. The range of the amount of tail lost was 46.6 - 133.8 mm for females compared to

### 3.3 - 132.2 mm for males.

I calculated tail regrowth rates by dividing the regenerated length by the number of days between measures and multiplying by 30 to get a monthly rate. Tail regrowth rates were variable (mean = 2.7, SD = 3.39, range = -1.4 to 16.8 mm/month; Fig. 4.6). There was no difference in regrowth rates of males and females. Regrowth rates decreased with age (Model 5 in Table 4.2). Two older females showed very high tail regrowth rates and were obvious outliers. It is unclear why they exhibited higher growth rates than similar-aged animals. When the two outlying females were removed from the data set the effect of age on tail regrowth rates became very significant ( $F_{1,37} = 23.24$ ,  $P < 0.001$ , Adjusted  $R^2 = 0.382$ ; Fig 4.7).

Plots of recaptured individuals showed that rapid body growth (SVL) occurred in both males and females until approximately four years of age. At this time males slowed body growth substantially while females continued to grow, although at a slower rate (Fig. 4.8a). An examination of all captured individuals showed that adult females had longer bodies than adult males of the same age ( $F_{1,138} = 40.35$ ,  $P < 0.001$ ; Model 6 in Table 4.2; Fig. 4.8b).

Colour rank differed among the sex/age categories (newborn, juvenile, adult male and adult female) at the three sites (Hydro, Lone Pine Hill and Pat's Hill;  $\chi^2 = 23.02$ ,  $df = 12$ ,  $P = 0.03$ ; Model 7 in Table 4.2; Fig. 4.9). At Hydro and Pat's Hill newborn lizards were lighter but juveniles, adult males and adult females did not differ. At Lone Pine Hill there was no difference among the sex/age categories. Percent black rank differed among the sex/age categories ( $\chi^2 = 188.35$ ,  $df = 3$ ,  $P < 0.001$ ; Model 8 in Table 4.2; Fig. 4.9) and sites ( $\chi^2 = 11.41$ ,  $df = 2$ ,  $P < 0.001$ ). Newborn and juvenile lizards did not differ but they

were less black than adult males, which had less black than adult females. Percent black overall was highest at Pat's Hill and lowest at Hydro.

## Discussion

This study showed clear evidence of sexual dimorphism in morphometric traits of an Anguid lizard, *Elgaria coerulea*. Adult females were larger, had narrower heads and shorter tails, and more black mottling on their backs than adult males. I provide also one of very few reliable estimates of juvenile and adult lizard survival rates under natural conditions and indirect evidence that adult females had higher survival rates than males.

Annual survival rate of adult females was 44% and juvenile survival rate was 22%. The survival rate of adult males likely falls in between, although I was not able to estimate their survival rate due to small sample sizes. These estimates are substantially lower than those of Stewart (1985), who estimated annual adult survival to be 73% and annual juvenile survival to be 54% in a California population of *Elgaria coerulea*. The estimates of Stewart (1985) did not incorporate recapture rates, although this alone does not explain why they were higher than the estimates from this study, as incorporation of recapture rates should produce higher survival estimates. It is more likely that the differences are due to variation in age at maturity, longevity, climate or predation pressure between the two locations.

Published data on survival rates in other lizard species reveal that rates are highly variable among species (8 to 90%) and are positively correlated with age at maturity (Shine and Charnov, 1992). The age and size at maturity of *Elgaria coerulea* in this study was consistent with estimates from the California population of *Elgaria coerulea* (Stewart, 1985); therefore the lower survival rates are not due to differences in age at maturity between the



two populations. The age range of the lizards from this study was also consistent with those in the California population (Stewart, 1985), which contradicts the differences seen in the survival rates of the two populations. Few old individuals were captured in the California population, which is also similar to this study.

The colder climate of the population of *Elgaria coerulea* in this study may be the reason survival rates are lower than in the California population of this species. Given that I did not detect a difference between over-winter and within season survival rates I suggest that the reduced survival of these lizards is not solely due to hibernation mortality during the colder winters. In addition, variation in survival rates has been linked to variation in predation pressure among populations of *Sceloporus undulatus* (Tinkle and Ballinger, 1972). It is possible that higher predation pressure on lizards in this study resulted in their lower survival rates. Tail break frequencies have been positively correlated with heavier predation (Schoener, 1979; Fox et al., 1994; Pérez-Mellado et al., 1997). In this study, frequencies were generally greater than 50%, suggesting that predation pressure is high. In addition, individuals with broken tails have been shown to have reduced survival (Wilson, 1992; Fox and McCoy, 2000). More than half of the individuals, in this study, had lost their tail at some point; this also may have contributed to the lower survival rates I observed.

Although I was not able to estimate male survival, limited indirect evidence suggests that it is lower than female survival. Stewart (1985) also found that survival rates of adult females were higher than those of adult males in this species. This sexually dimorphic pattern has been demonstrated in another lizard species, *Sceloporus undulatus* (Tinkle, 1972; Parker, 1994). Lower survival rates of males have been suggested to be the result of their higher activity and movements (Marler and Moore, 1988; Parker, 1994). Limited data

on their movements suggests that male *Elgaria coerulea* are more active and mobile than females (Chapter 2).

Why did the two sexes differ in recapture rates? Males had higher recapture rates in the spring than the summer, whereas females showed the opposite pattern. These differences likely reflect behaviour patterns of the two sexes. In the spring, males actively seek females and were more obvious and accessible on the study site, but they virtually disappeared during the summer. Without having tracked these animals I cannot say whether they left the study site or if they spent less time foraging and basking, making themselves more difficult to capture. In contrast, during the summer months, most adult females are gestating and therefore foraging and basking, making themselves easier targets for capture. They also had slower sprint speeds (Chapter 3), making them easier to capture by hand.

Sexual dimorphism in body size of lizards often has been attributed to sexual dimorphism in survival rates (Dunham, 1981; Stamps, 1983; Stewart, 1984, 1985). However, my data clearly show that sexual dimorphism in size of *Elgaria coerulea* is not attributable solely to differential mortality. So why are females larger? Perhaps larger females have higher fecundity, a mechanism proposed in a variety of taxa (Selander, 1972; Ralls, 1976; Shine, 1989; Karlsson and Wickman, 1990; Madsen and Shine, 1994; Braña, 1996). In my study population, female body size is positively correlated with clutch size (Chapter 5). This suggests that larger body size is due to selection for increased fecundity, although I did not test this (see Shine, 1988a; Madsen and Shine, 1994).

In addition to being larger, females had more black mottling on their backs than adult males. Melanistic snakes warm faster (Gibson and Falls, 1979; Forsman, 1995), but are subject to heavier predation (although there are sex differences) (Andrén and Nilson,

1981; Forsman, 1995). *Elgaria coerulea* have a limited reproductive season so the dark pigmentation may confer a reproductive advantage on females. Darker females will warm faster than lighter females, thereby keeping developing embryos at optimal developmental temperatures for longer periods and shortening the gestation period. Males will not benefit from this advantage; there might even be selection for reduced black mottling if it reduces their risk of predation.

Adult *Elgaria coerulea* also differ in head width; males have wider heads than females. Larger male head width is common in lizards and may be a result of the importance of head width in both intrasexual or intersexual interactions, or may reflect resource partitioning of the two sexes (see Herrel et al., 1999). During copulation, male *Elgaria coerulea* hold female heads in their jaws with such force as to often leave scars on female heads (Rutherford, personal observation). In addition, copulations are lengthy (up to twelve hours). This suggests an advantage for larger heads during intersexual interactions, although I have no evidence that males with larger heads have higher reproductive success. I witnessed no male-male interactions during this study, although male-male aggression has been documented in this genus (Bowker, 1988). Therefore, wider heads may also be advantageous during agonistic interactions. To date, diet of *Elgaria coerulea* is unknown so it is also possible that larger head width in males is due to resource partitioning.

Female *Elgaria coerulea* have shorter tails than males, never lose small amounts of their tails, appear to suffer higher tail loss in June and July, and are capable of quick tail growth. Tail length is known to increase survival (Bauwens, 1981; Wilson, 1992; Fox and McCoy, 2000). If males suffer higher predation than females due to their increased movement (Marler and Moore, 1988; Parker, 1994), selection will favour increased tail length

in males as long as the benefits of investing in tail growth outweigh the cost of not being able to invest this energy elsewhere (e.g. body growth, maintenance, reproduction), or the potential cost of having a longer tail. The ratio of costs to benefits likely differs for males and females given their differences in reproductive investment. This may explain why selection might result in longer tails in males than females. An alternative explanation for the longer tails of males is the need to accommodate intromittent organs while still maintaining the equivalent number of autotomous vertebrae as females (Barbadillo et al., 1995). I have no data on this point.

Variation is also evident in tail autotomy patterns of males versus females. Both the 'decision' to autotomise a tail and the amount of tail autotomised are variable (Arnold, 1984), likely related to the costs and benefits of losing a tail. Although males and females do not differ in tail loss rates, there appear to be differences in the likelihood of autotomy. Recent tail loss was not seen in females during late gestation (August) and hand-capture of females suggests they are less likely to autotomise at this time (Rutherford, personal observation). In contrast, males seemed equally likely to autotomise at any time of the year. In addition, females never shed less than 46 mm of a tail. A comparison among geckos suggests that slower species are more likely to autotomise larger portions of their tails (Arnold, 1984). The autotomised part of the tail remains active for several minutes after autotomy. Therefore, loss of a larger part of the tail may increase handling time by the predator, of the autotomised part, which can increase escape time for the lizard (Dial and Fitzpatrick, 1983). Longer escape times may be necessary as gravid female *Elgaria coerulea* sprint speeds are approximately 0.4 m/s slower than males (Chapter 3). It would take a gravid female an additional second to travel a distance of two metres. Tail regrowth rates

of *Elgaria coerulea* are highly variable, but generally low compared to other species and inconsistent with the hypothesis that loss rates are positively correlated with regeneration rates (Vitt et al., 1977). Nonetheless, some females had higher tail regeneration rates, which was likely influenced by the immediate benefits of a longer tail. This tail growth may provide a reproductive payoff as females with longer tails have larger litters (Chapter 5).

Lizards are often seen as ‘model organisms’ for the study of life histories. However, most studies have focused on reproductive traits and very few have provided reliable, mark-recapture estimates of survival rates, as I have attempted here. Determination of survival rates is central to explaining lifetime patterns of reproductive output. In this study, I also argue that sexual size dimorphism is a potentially important link between reproductive and survival traits. The next step is to test specific hypotheses that explain this morphometric dimorphism.

Table 4.1: MARK analysis of deviance of mark-recapture data from CVWMA, Creston, British Columbia collected in 1996-1998. A) Maximum likelihood estimates of the deviance of models incorporating parameters for survival ( $\phi$ ) and recapture probabilities ( $P$ ) as a function of group (juvenile, adult male or adult female;  $g$ ), over-winter vs within year ( $ow$ ), and spring vs summer ( $spr$ ). The minimal model is shown in bold. B) Likelihood ratio tests of the effect of group ( $g$ ) and over-winter vs within-year ( $ow$ ) on survival and recapture probabilities.

| A        |                             |                               |          |               |              |
|----------|-----------------------------|-------------------------------|----------|---------------|--------------|
| Model    | Survival                    | Recapture                     | np       | QAIC          | Weight       |
| 1        | $\phi(g^*ow)$               | $P(g^*spr)$                   | 12       | 328.64        | 0.015        |
| 2        | $\phi(ow)$                  | $P(g^*spr)$                   | 8        | 324.86        | 0.101        |
| <b>3</b> | <b><math>\phi(g)</math></b> | <b><math>P(g^*spr)</math></b> | <b>9</b> | <b>322.27</b> | <b>0.368</b> |
| 4        | $\phi(ad. vs juv.)$         | $P(g^*spr)$                   | 8        | 323.66        | 0.183        |
| 5        | $\phi()$                    | $P(g^*spr)$                   | 7        | 322.78        | 0.283        |
| 6        | $\phi(g^*ow)$               | $P(spr)$                      | 8        | 346.57        | 0.000        |
| 7        | $\phi(g^*ow)$               | $P(g)$                        | 9        | 331.59        | 0.003        |
| 8        | $\phi(g^*ow)$               | $P()$                         | 7        | 345.42        | 0.000        |
| 9        | $\phi(g)$                   | $P(g)$                        | 6        | 327.50        | 0.027        |
| 10       | $\phi(ow)$                  | $P(g)$                        | 5        | 330.72        | 0.005        |
| 11       | $\phi(g)$                   | $P(spr)$                      | 5        | 353.89        | 0.000        |
| 12       | $\phi(ow)$                  | $P(spr)$                      | 4        | 374.44        | 0.000        |
| 13       | $\phi()$                    | $P(g)$                        | 4        | 328.80        | 0.000        |
| 14       | $\phi()$                    | $P(spr)$                      | 3        | 373.12        | 0.000        |
| 15       | $\phi()$                    | $P()$                         | 2        | 372.41        | 0.000        |
| 16       | $\phi(g)$                   | $P()$                         | 4        | 352.48        | 0.000        |
| 17       | $\phi(ow)$                  | $P()$                         | 3        | 372.51        | 0.000        |

| B        |            |    |          |         |
|----------|------------|----|----------|---------|
| Effect   | Comparison | df | $\chi^2$ | $P$     |
| $g$      | 3 vs 5     | 2  | 4.76     | 0.09    |
| $ow$     | 1 vs 3     | 3  | 0.09     | 0.99    |
| $g^*spr$ | 3 vs 16    | 5  | 40.70    | < 0.001 |

**Table 4.2: A series of models of morphometric comparisons of male and female *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. Tested models with the terms retained in the best model are shown in italics and additional terms retained in the next best model if there was little difference between models are shown in brackets. The dependent variable in model 3 (tail loss) is categorical; all other dependent variables are continuous. Predicted tail length was included in model 4 to control for the fact that lizards with longer tails have the potential to lose more of their tails than lizards with shorter tails. For colour rank and percent black rank (models 7 and 8) I used the Scheirer-Ray-Hare extension of the Kruskal-Wallis test to do a two-way anova on ranked data (Sokal and Rohlf, 1995, p.446).**

| No. | Dependent Variable        | Terms   | F/AIC  | df     | P       | Adj. R <sup>2</sup> |
|-----|---------------------------|---|--------|--------|---------|---------------------|
| 1   | head width                | <i>SVL, sex, SVL by sex</i>                                       | 104.7  | 3,191  | < 0.001 | 0.616               |
| 2   | tail length (intact only) | <i>SVL, sex, SVL by sex</i>                                       | 46.17  | 3,57   | < 0.001 | 0.693               |
| 3   | tail loss                 | <i>site, sex/age, site by sex/age</i>                             | 345.23 | 258    |         |                     |
| 4   | tail length lost          | <i>predicted tail length, (sex, sex by predicted tail length)</i> | 47.22  | 1,164  | < 0.001 | 0.219               |
| 5   | tail regrowth rate        | <i>starting age, sex, starting age by sex</i>                     | 2.60   | 1,37   | 0.115   | 0.04                |
| 6   | SVL                       | <i>age, sex, age by sex</i>                                       | 87.03  | 2,138  | < 0.001 | 0.551               |
| 7   | colour rank               | <i>sex/age, site, sex/age by site</i>                             | 11.14  | 19,405 | < 0.001 | 0.312               |
| 8   | percent black rank        | <i>sex/age, site, sex/age by site</i>                             | 83.72  | 5,373  | < 0.001 | 0.523               |

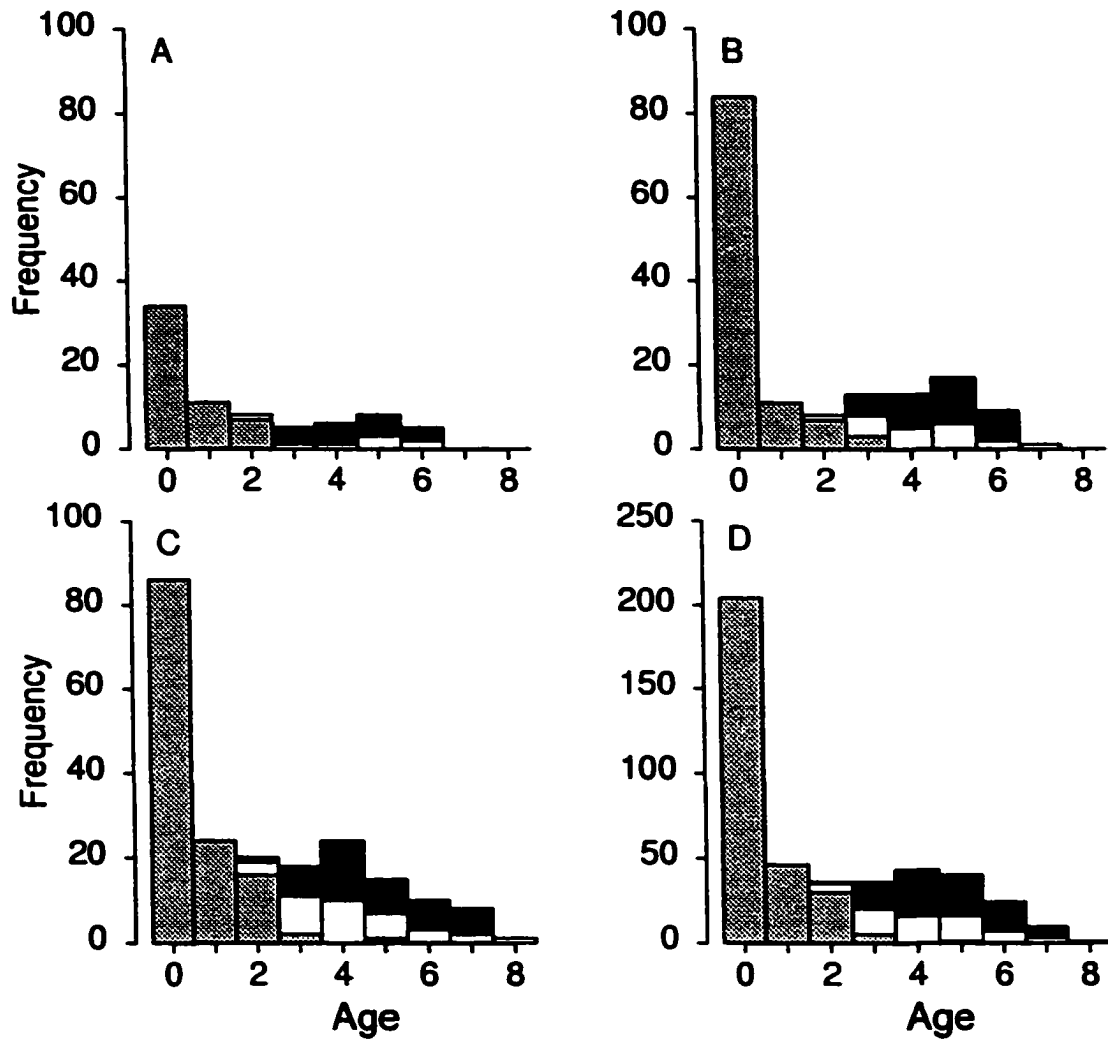


Figure 4.1: Age distributions for juvenile (grey), adult male (white), and adult female (black) *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. Plotted for (A) 1996, (B) 1997, (C) 1998, and (D) all years combined.



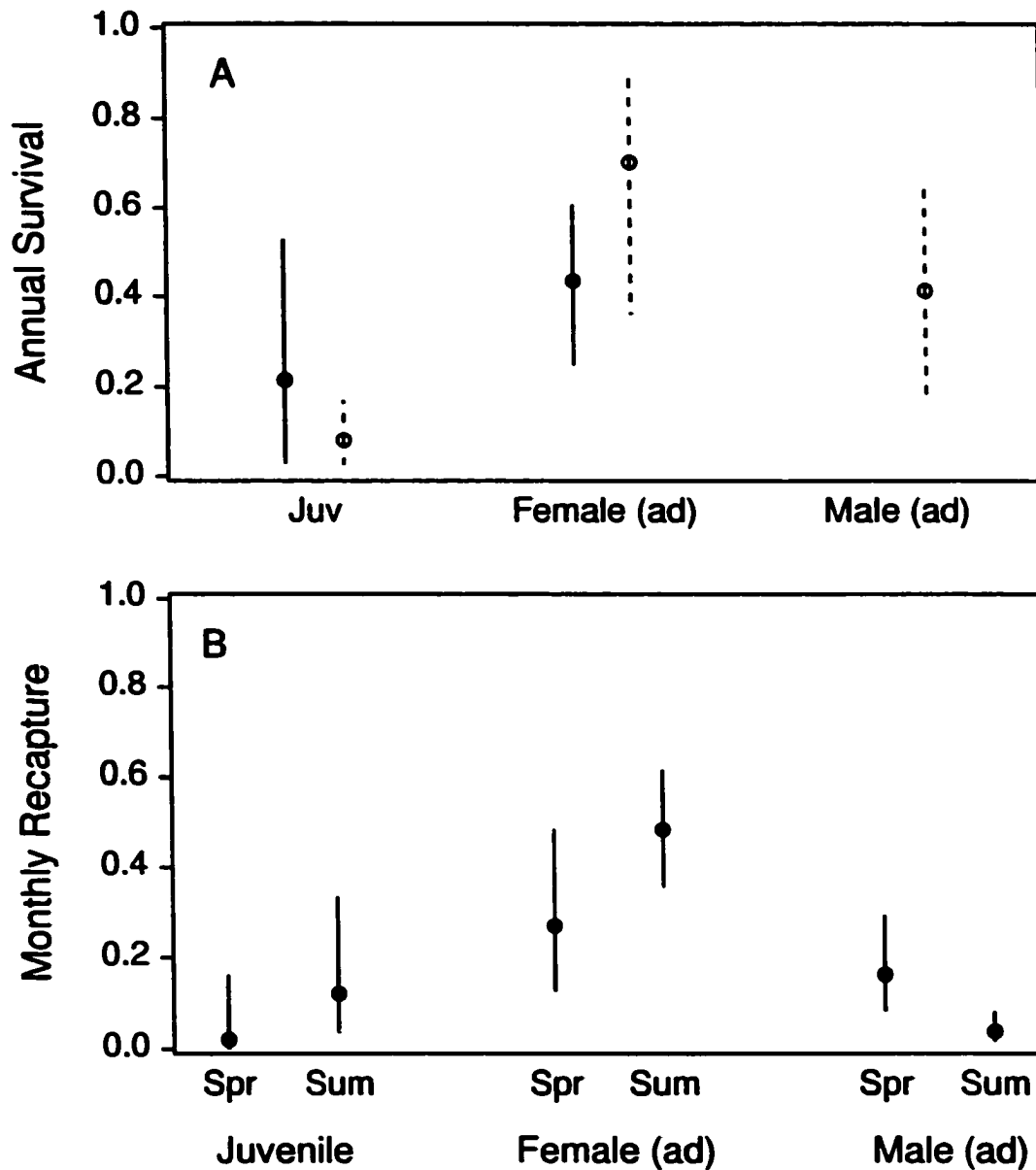


Figure 4.2: Maximum likelihood estimates and 95% confidence limits from the minimal adequate model of (A) annual survival rates for juvenile, adult female and adult male, and (B) monthly recapture rates for juvenile, adult female and adult male *Elgaria coerulea* from CVWMA, Creston, British Columbia captured in the spring and summer capture periods of 1996-1998. Open circle survival rates shown in (A) are estimates from model 16 ( $\phi(g)P()$ ) because this was the best model in which male survival could be estimated. The recapture rate in this model was 0.222 (0.033, 0.294).

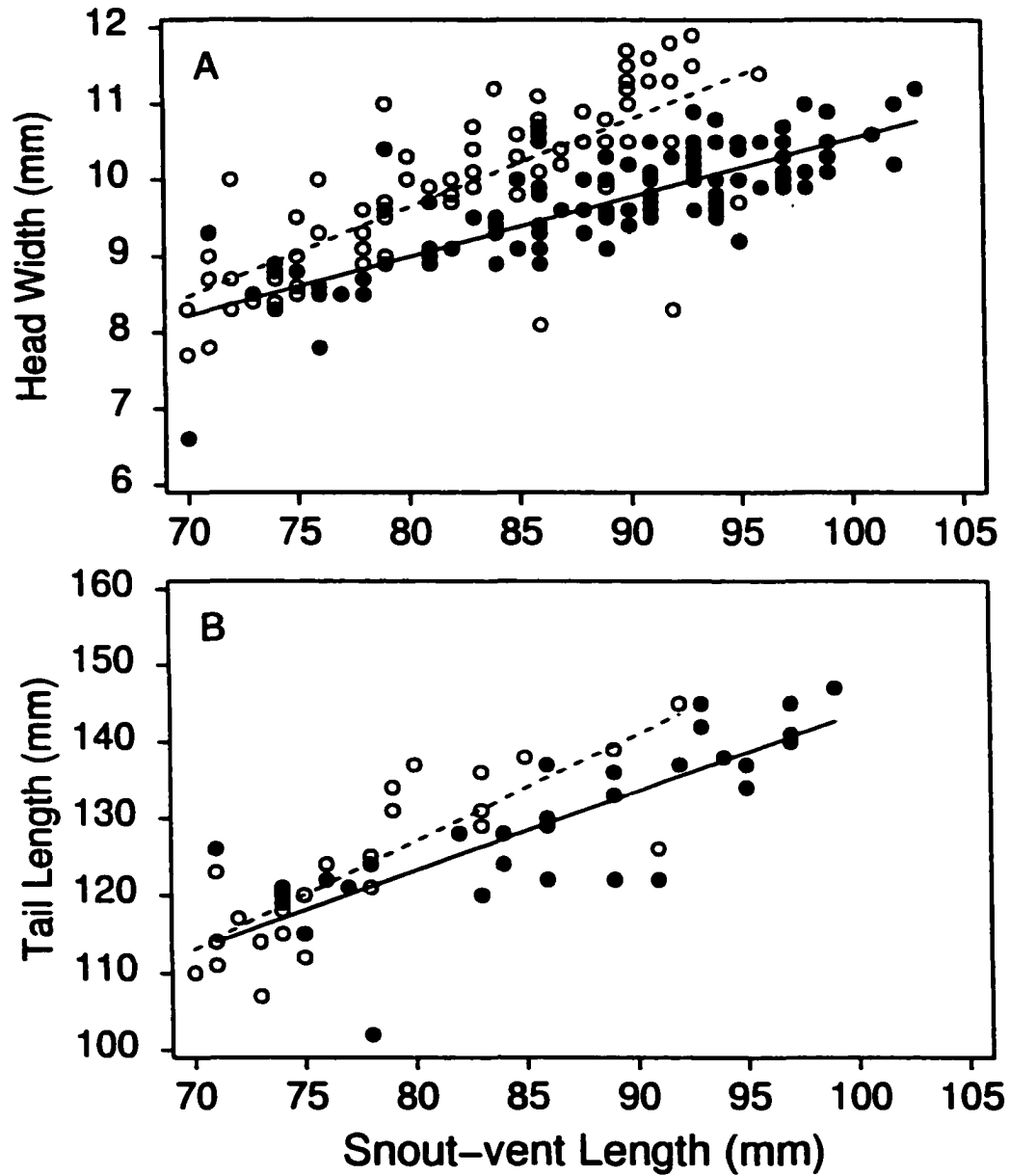


Figure 4.3: Snout-vent length (mm) vs (A) head width (mm) and (B) tail length (mm) (based only on lizards that had never lost their tails) for adult *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. Regression lines are shown for males (open circle, dashed line) and females (closed circle, solid line).

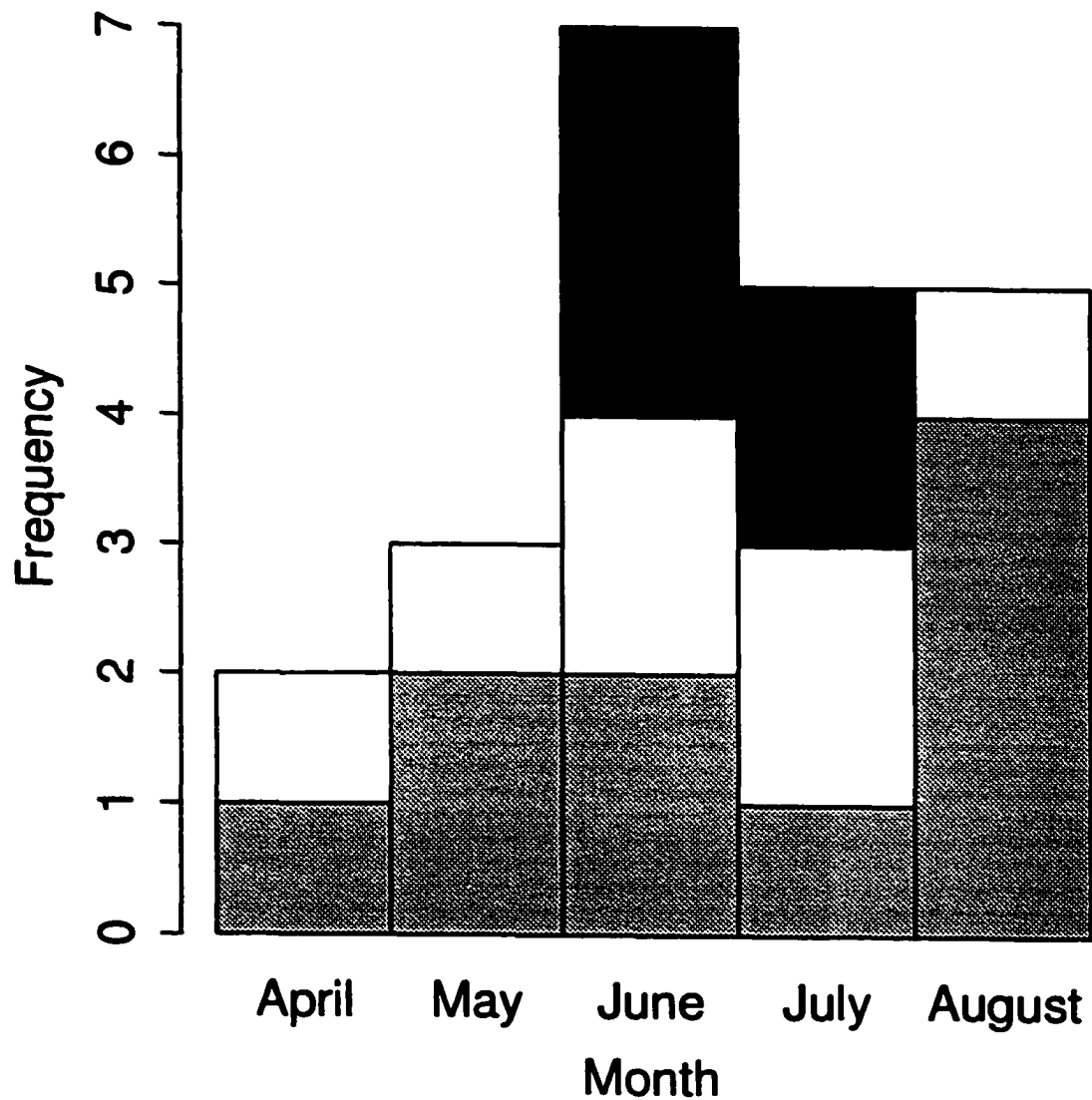


Figure 4.4: Distribution of captures of *Elgaria coerulea* that had recently lost their tails from CVWMA, Creston, British Columbia collected in 1996-1998. Juveniles are in gray, adult males in white and adult females in black.

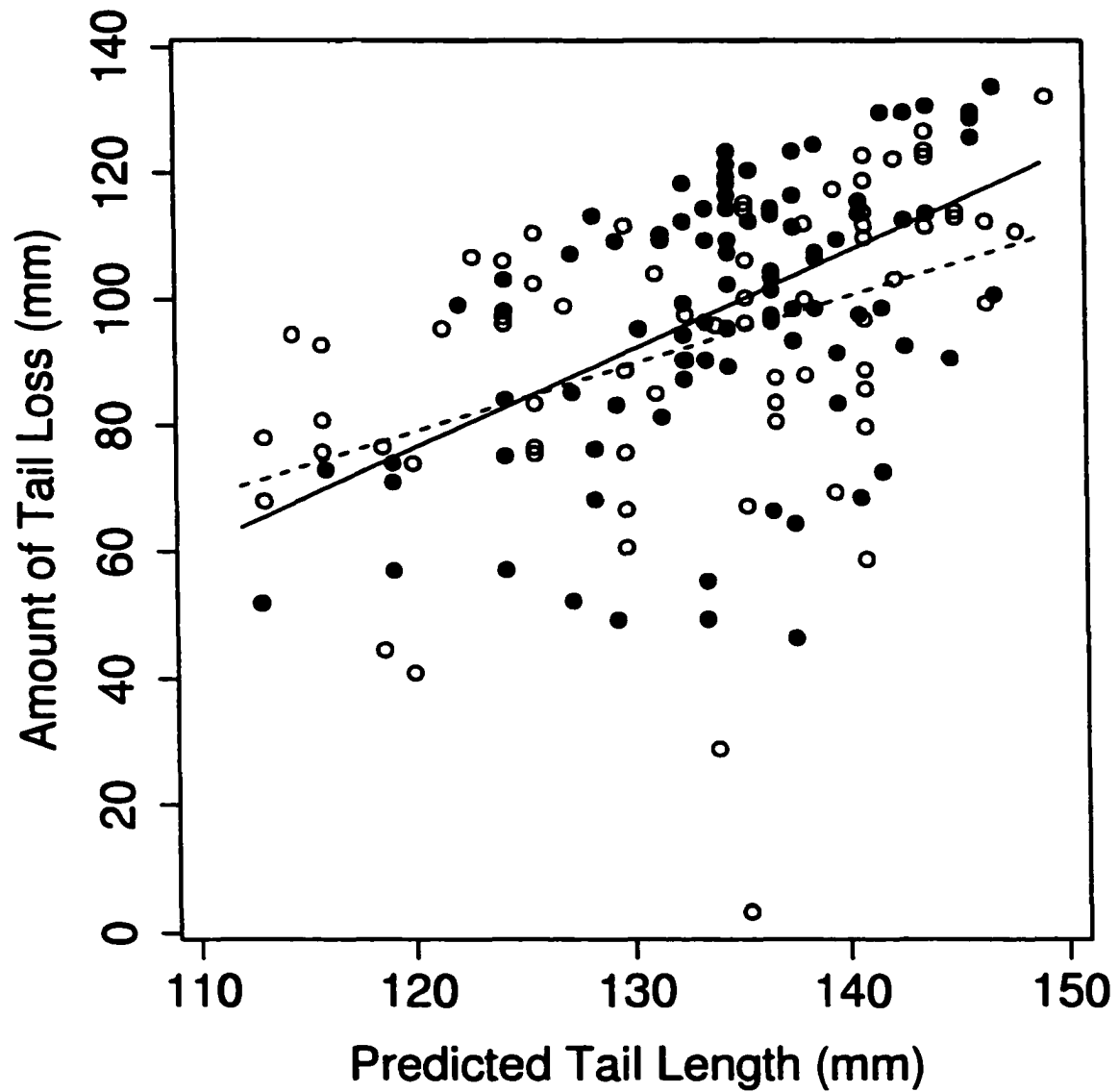


Figure 4.5: Predicted tail length (mm) vs amount of tail loss (mm) for *Elgaria coerulea* that have lost their tails from CVWMA, Creston, British Columbia collected in 1996-1998. Regression lines are shown for males (open circle, dashed line) and females (closed circle, solid line).

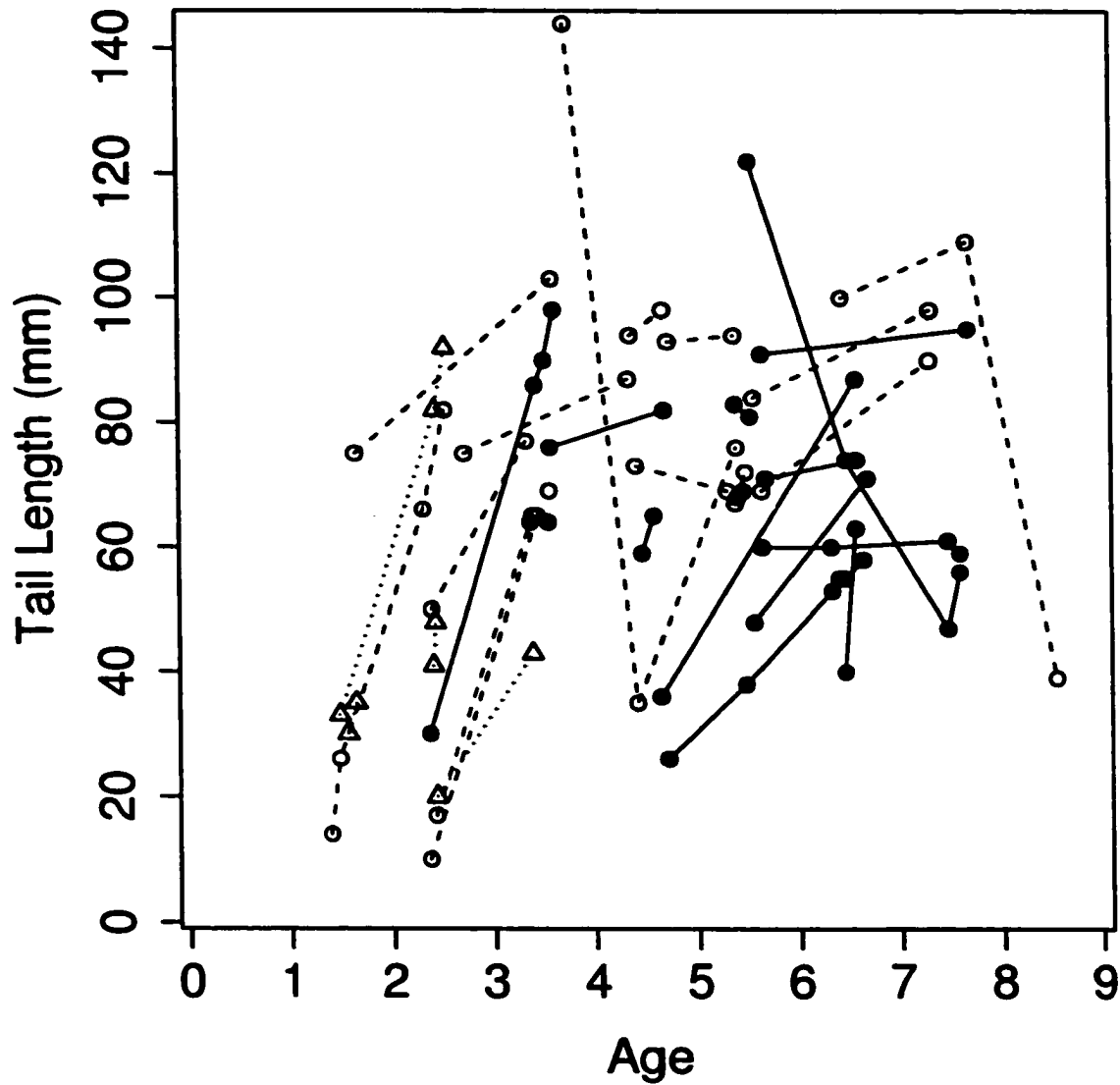


Figure 4.6: Age vs tail length (mm) for recaptured *Elgaria coerulea* that had lost their tails from CVWMA, Creston, British Columbia collected in 1996-1998. Line segments are plotted for individuals that are categorised according to sex/age category: juveniles (triangle, short-dashed line), males (open circle, long-dashed line) and females (closed circle, solid line). The decreases in tail length indicate tail loss between recaptures.

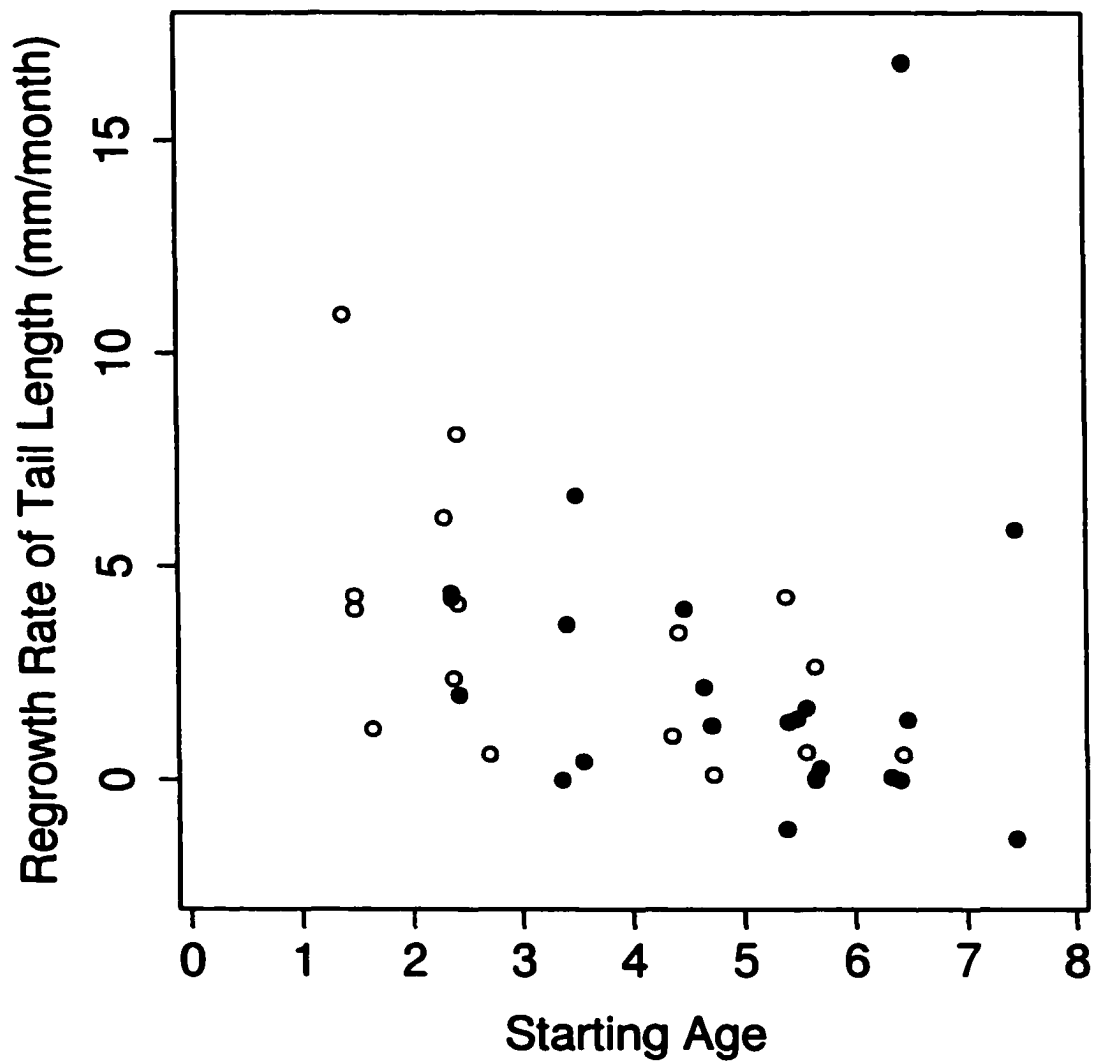


Figure 4.7: Starting age vs tail regrowth rate (mm/month) for adult *Elgaria coerulea* that have lost their tails from CVWMA, Creston, British Columbia collected in 1996-1998. Males are open circles and females are closed circles.

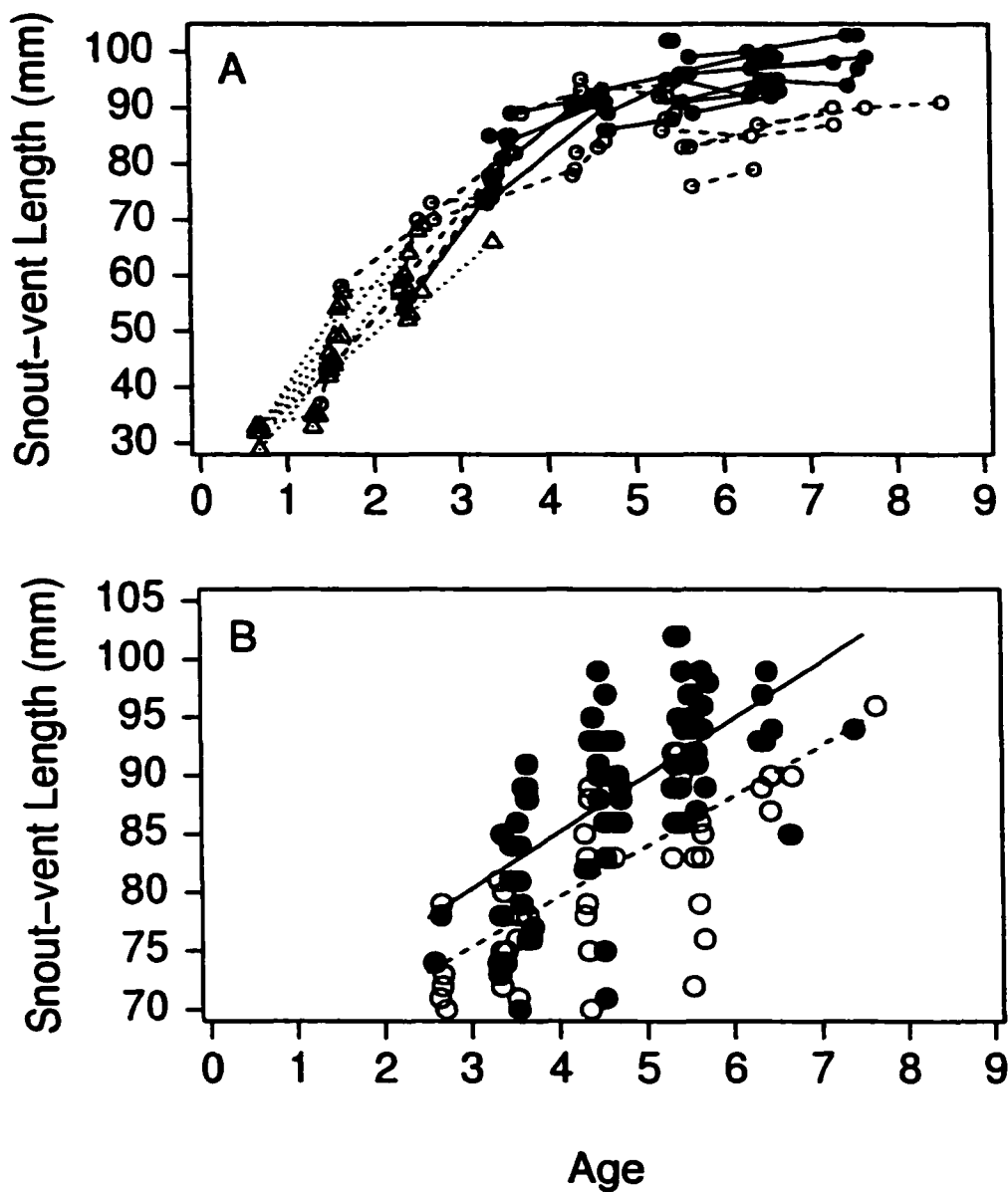


Figure 4.8: Age vs snout-vent length (mm) for (A) recaptured, and (B) adult *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. In (A) line segments are plotted for individuals that were recaptured throughout the study. Lizards are categorised according to sex/age category: juveniles (triangle, short-dashed line), males (open circle, long-dashed line) and females (closed circle, solid line). In (B) all captures of adult lizards are plotted (including recaptured animals). Regression lines are shown for males (open circle, dashed line) and females (closed circle, solid line).

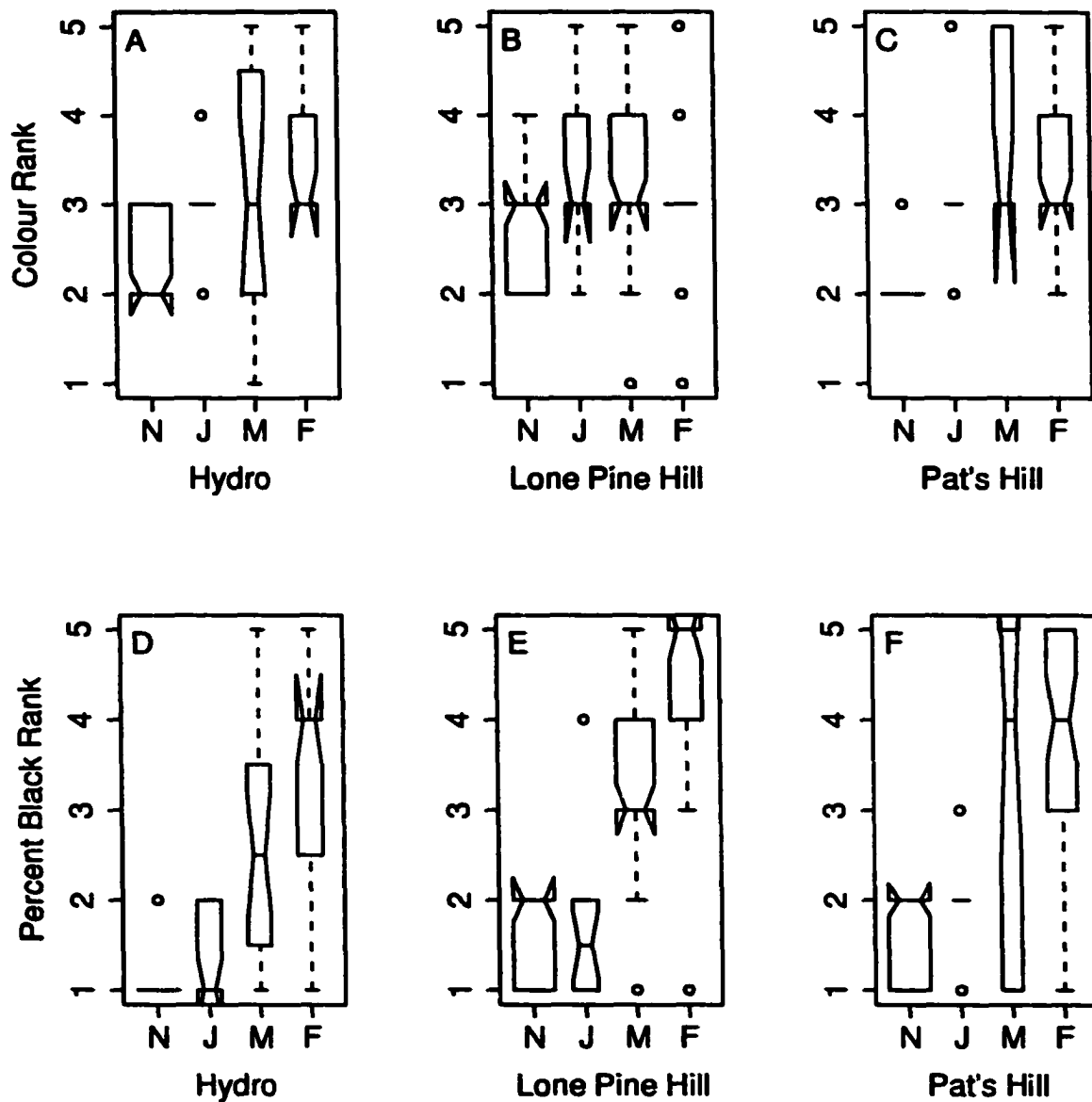


Figure 4.9: Box plots of colour rank (A) to (C) and percent black rank (D) to (F) for newborn (N), juvenile (J), adult male (M), and adult female (F) *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. Plotted for three sites: Hydro, Lone Pine Hill and Pat's Hill. Overlapping notches in the boxplots indicate medians that are not significantly different at the 5 percent level. The width of the box is the square root of the sample size.



## Chapter 5

# Testing the Shine and Schwarzkopf Model

### Introduction

Costs of reproduction have had central importance in theories of life-history evolution since first formalised by Williams (1966). Since that time empiricists have attempted to characterise these costs (reviewed by Reznick et al., 2000), broadly categorising them into two types: 1) survival costs, and 2) potential fecundity costs (Bell, 1980). Shine (1980) reviewed available data on reproductive costs in squamate reptiles and evaluated them in the context of these two categories. Survival costs arise because reproducing females are more vulnerable to predation than non-reproducing females, for two reasons: 1) the physical burden of the clutch makes them less able to escape from predators, and 2) they are more exposed to predators due to increased basking (see Shine, 1980). Potential fecundity costs arise when a female devotes energy to current reproduction instead of growth. In many reptile species clutch mass and fecundity increase with body size. Hence, energy devoted to reproduction instead of growth may reduce a female's future reproductive output (Shine, 1980).

The two kinds of reproductive costs (survival and potential fecundity) operate in different ways and each may be more or less important in a particular population (Shine and Schwarzkopf, 1992). Shine and Schwarzkopf (1992) proposed a model (SS model) to explain the relative importance of the two kinds of costs in various squamate reptiles. The SS model considered two life-history characteristics (relative clutch mass and survival rate) and predicted the levels of relative clutch mass (RCM) and survival rate above which individuals

should trade off current for future reproduction (see Figure 1, Shine and Schwarzkopf, 1992). They then summarised data on five families of lizards (Agamidae, Iguanidae, Teiidae, Lacertidae, Xantusiidae) and showed that many lizard species (83%) fall below the predicted trade-off curve (Shine and Schwarzkopf, 1992). This suggested that the low relative clutch mass and/or low adult survival rate of most lizard species make them unlikely to make trade-offs between current and future reproduction.

Niewiarowski and Dunham (1994, 1998) criticised the prediction that fecundity costs are not important in squamate reptiles and proposed an alternative model (ND model). This model suggested that the potential fecundity trade-off may be more common than the SS model predicted, particularly in species with short interclutch intervals (see Figure 2, Niewiarowski and Dunham, 1994). The main difference between the two models is that the ND model (Niewiarowski and Dunham, 1994) calculated growth increments on a daily basis as opposed to the annual basis used in the SS model (Shine and Schwarzkopf, 1992). Modelling growth as daily, instead of annual, implies that females are capable of simultaneous growth and reproduction. Shine et al. (1996) doubted that simultaneous growth and reproduction is biologically realistic, because it is unlikely that energy 'saved' by a reproducing female (due to a decrement in RCM) will cause an immediate increase in her body size. Yet, growth during gestation has been shown in a few limited studies (Vitt, 1982; Colli, 1991; Niewiarowski and Dunham, 1998). Nonetheless, there are few field data available, making it difficult to identify general patterns (Niewiarowski and Dunham, 1998). Both Shine et al. (1996) and Niewiarowski and Dunham (1998) agree that additional empirical data are needed to investigate the possibility of simultaneous growth and reproduction in species with brief interclutch intervals.

This adjustment to the SS model had little effect for longer interclutch intervals, such that the two models generated identical results for one or fewer clutches per year. However, this assumes that all non-reproductive time is available for growth, which is not always the case. Many cold-climate reptiles reproduce only once per year, but effectively have a short interclutch interval because they spend a long period each year in hibernation. The short annual period of activity constrains them to one reproductive attempt per year, especially if they are viviparous. To date, there are very few data available on growth patterns of reproductive females in cold-climate reptiles (but see Luiselli et al., 1996).

In this study, I test for the presence of trade-offs among current reproduction, future reproduction, and survival in a cold-climate lizard, the alligator lizard, *Elgaria coerulea*. I test whether or not female lizards make trade-offs throughout their lifetime under natural conditions. Also, I provide evidence of concurrent growth and reproduction in this species. This indicates that the ND model may be biologically realistic, and that potential fecundity trade-offs may be more common than initially proposed. In light of these results I discuss how cold-climate reptile species fit into these models and make predictions about fecundity trade-offs for such species.

## Materials and Methods

### *Study Species and Study Site*

*Elgaria coerulea* is a viviparous lizard found in the western United States and reaches the northern limits of its distribution in southern British Columbia (Stebbins, 1966). I conducted this study during the summers of 1996-1998 from mid-April to mid-September on the west side of the Creston Valley, 10 km west of Creston, British Columbia, Canada (49°6'

N, 116°31' W; elevation 597 m; Fig. 2.1). Mean daily maximum air temperatures from April - September 1996 ranged from 6.5°C to 35.0°C. Mean daily minimum air temperatures in the same period ranged from -0.6°C to 18.3°C (Environment Canada, 1996).

For mark-recapture studies, I used four primary study sites (hand capture and trapping: Pat's Hill, Hydro, East Clearing, and Lone Pine Hill) and six secondary sites (hand capture only: Dewdney, Office, Sign Slope, Trail, Junction, and West Creston). All sites were separated from each other by distances of 500 m or greater.

### *Mark-recapture*

On average, the primary sites were visited four times a year and the secondary sites were visited two times per year over three years (1996-1998). I marked all lizards with a unique toe-clip (Swingland, 1978) and kept the clipped toes in 10% formalin for skeletochronological determination of age. I clipped no more than two toes per foot. Upon capture I measured head width, snout-vent length (SVL), tail length, and mass of all lizards. Snout-vent length and tail length were measured by pressing the lizard against a plastic surface using foam. The distance along the centre of the lizard was traced onto the plastic, transferred onto paper and measured. I recorded tail loss state (yes or no) based on the presence or absence of a previous tail break. In lizards that had lost their tails I measured the distance from the vent to the tail break (middle length) and the distance from the break to the tail tip (regenerated length).

### *Skeletochronological Determination of Age*

I prepared the toe-clip samples using standard histological techniques, until they were embedded in paraffin in separate blocks. I counted growth layers using the same

technique as Waye and Gregory (1998). The number of rings was determined by a single reader, and ring counts were verified by known-age animals when possible.

### *Reproductive Output*

I brought all gravid females to the laboratory to complete gestation. On average, females were in the laboratory for 38 days ( $N = 59$ ,  $SD = 21.4$ , range = 1 to 89). I fed the lizards crickets and provided water ad libitum. In 1996 I housed the females in tupperware containers with a cloth for cover and a heating pad at one end for heat. In 1997 and 1998 they were housed in wood enclosures with a soil substrate and rock cover. I provided an overhead light bulb for a heat source. I measured females upon capture, throughout their pregnancy and postpartum; neonates were measured within 24 hours of birth. I marked and measured all newborn lizards and returned both mother and offspring to the mother's capture site within 72 hours of parturition. Clutch size and clutch mass included both live and dead young. Dead young, although obviously not demographically important, still represent an energetic investment by the female.

### *Sprint Speed*

I raced all lizards within two days of capture. They were held in the laboratory in ventilated plastic containers and provided with water ad libitum. A trial commenced by placing lizards in separate, ventilated plastic containers within a styrofoam thermal chamber. I kept them in this chamber until the temperature inside the plastic chambers was close to  $32^{\circ}\text{C}$  (mean =  $33.2^{\circ}\text{C}$ , range =  $25.2 - 40.8^{\circ}\text{C}$ ,  $n = 84$ ,  $SE = 0.23$ ). I held them at this temperature for an hour and then raced each lizard three times with 45 minute rests in between. I chased each lizard down a 1.5 m rubber-floored track towards a pillow

case, which provided cover. The trial in which a lizard ran the fastest was recorded as its maximal sprint speed. After all three races were completed I measured snout-vent length (SVL), tail length, and mass of all lizards. I raced sixteen gravid females over two years (1997-98).

### *Statistical Analyses*

I calculated relative tail length by first calculating the relationship between snout-vent length and tail length for all lizards that had never lost their tails. The relative tail length is the difference between the actual tail length and the predicted tail length. This regression was done separately for males and females because males grow relatively longer tails than females (Chapter 4).

I calculated body condition using a regression of mass against snout-vent length and tail length for all adult lizards (male and female) captured during the study (1996-1998). To compare body conditions, I classified lizards into two time periods: spring and fall. Spring was the period up to May 31 as this was the last date breeding pairs were seen in the field. Fall was defined as the period after August 18 as this was the first date females gave birth. I calculated two body condition estimates for the trade-off analysis: early and late body condition. These measures were similar to spring and fall body condition, but because I had limited data I extended each time period to incorporate as many animals as possible. Early body condition was calculated for lizards captured prior to June 30. Although this date is later than the date used for spring condition (May 31), it is still a good estimate of condition at the start of pregnancy because plots of weight gain of gravid females show that weight gain due to the pregnancy does not commence until after June 30. For late condition estimates, I used lizards captured after August 1 (males and non-gravid females),

or in the case of gravid females I used their post-partum mass and body measurements.

To determine which factors determined whether a newborn was dead or alive I used a logistic regression with newborn lizards categorised as alive or dead (Model 1 in Table 5.1). I then tested for the effects of maternal characteristics (SVL, relative tail length, and year) on clutch size, mean newborn body condition, and mean newborn snout-vent length using ANCOVA (Models 2-4 in Table 5.1). To determine the factors predicting whether a female was reproductive or not I used a logistic regression (reproductive or not), including only known gravid and non-gravid females (Model 5 in Table 5.1).

I tested for fecundity costs by regressing residual clutch mass against year, early body condition, growth rate of snout-vent length, growth rate of tail length, and late body condition. A negative relationship between growth rates of either snout-vent length or tail length, and residual clutch mass indicates a trade-off between current reproduction and growth. To calculate residual clutch mass, I used the positive relationship between clutch mass and snout-vent length ( $F_{1,57} = 3.74$ ,  $P = 0.06$ ) and subtracted the predicted clutch mass from the measured clutch mass. I used residual clutch mass rather than relative clutch mass (RCM) because RCM is a ratio variable and introduced spurious correlations in my analyses, as follows. In my regression, I used growth rates of snout-vent length and tail length as independent variables. Thus, lizards that grow will also increase post-partum mass (the denominator of the standard RCM measure), which will automatically reduce the RCM of those females, regardless of whether a trade-off between reproduction and growth really exists.

The regression to test for fecundity costs was done for two groups of lizards: 1) only gravid females (Model 6 in Table 5.1), and 2) gravid females plus two non-gravid adult

females and three adult males (Model 7 in Table 5.1). I included males in the analysis because I had only two non-gravid females. Although males may invest energy differently than females, they are similar to non-gravid females in that they are not currently investing in reproductive output. Males and non-gravid females were given a clutch mass of zero and residual clutch mass was calculated using the same equation as for gravid females. Year was not included in the second analysis because all males and non-gravid females were collected in 1998, and year was not significant in the first analysis (only gravid females).

I considered two ways in which reproduction might compromise survival: 1) reduction in post-partum condition, which may reduce over-winter survival, and 2) reduced sprint speed due to the burden of the clutch. There is evidence of survival costs if there is a negative relationship between residual clutch mass and late body condition in the above analysis with only gravid females (Model 6 in Table 5.1). A negative relationship between clutch burden and sprint speed also may indicate survival costs. I tested the effect of body size, relative tail length, and clutch burden on sprint speed (Model 8 in Table 5.1). The clutch burden of a gravid female was the difference between the mass of a gravid female and the predicted mass of a non-gravid lizard. The predicted mass was determined by regressing mass against snout-vent length and tail length for all non-gravid adults (males and females).

Stepwise methods were used to select the best models for both logistic and linear regressions. For logistic regression models, the minimal adequate model was chosen on the basis of minimising Akaike's information criterion (AIC). The criterion often performs better than decisions based on statistical significance alone (Burnham et al., 1995). For linear regression models, the minimal adequate model was chosen on the basis of minimising



Mallow's  $C_p$  (Mallows, 1973). Mallow's  $C_p$  is considered an approximation to AIC (Venables and Ripley, 1999) and is closely related to the adjusted  $R^2$  (Draper and Smith, 1981). All statistical analyses were performed using R (Ihaka and Gentleman, 1996).

## Results

### *Breeding Size and Age*

Reproductive females ranged in snout-vent length (SVL) from 71 to 103 mm, tail length from 22 to 145 mm, and age from 3 to 7 (see Table 5.2). Males and females were classed as adults at 71 mm SVL based on minimum female breeding size. Most individuals reach breeding size by three years of age, although six adults (five males and one female) were two years of age (see Figure 4.1 in Chapter 4). There were no differences in snout-vent length ( $F_{2,56} = 0.73$ ,  $P = 0.49$ ), tail length ( $F_{2,56} = 0.10$ ,  $P = 0.90$ ) or age ( $F_{2,56} = 1.41$ ,  $P = 0.25$ ) of gravid females among years (Table 5.2).

### *Variation in Reproductive Output*

Coefficients of variation within litters were low for head width (range = 0 to 5.0), snout-vent length (range = 0 to 6.9), tail length (range = 0 to 7.1 with an outlier at 30.8 mm due to an individual with a very short tail in that litter) and mass (0 to 15.8 with an outlier at 69 g due to an individual with low mass in that litter).

Coefficients of variation also were low between litters born in the same year for head width, snout-vent length, and tail length, but they were higher for mass (Table 5.2). I used a nested ANOVA (litters within years) to test for significant variation between litters nested within years, and among years. All morphological measurements (head width, snout-vent length, tail length, mass, and condition) varied significantly between litters nested within

years (head width:  $F_{55,207} = 3.14$ ,  $P < 0.001$ ; snout-vent length:  $F_{55,207} = 2.99$ ,  $P < 0.001$ ; tail length:  $F_{55,207} = 2.13$ ,  $P < 0.001$ ; mass:  $F_{55,207} = 4.25$ ,  $P < 0.001$ ; condition:  $F_{55,207} = 2.19$ ,  $P < 0.001$ ). Only head width, mass and condition varied among years (head width:  $F_{2,207} = 28.93$ ,  $P < 0.001$ , mass:  $F_{2,207} = 12.98$ ,  $P < 0.001$ , and condition:  $F_{2,207} = 18.17$ ,  $P < 0.001$ ; Table 5.2).

#### *Dead Newborn and Deformities*

In total there were 25 dead newborn among the 59 litters (9.4%). Most litters consisted of more than 80% live offspring (Table 5.2). Within a clutch, dead offspring were smaller in all measures except body condition, which did not differ between live and dead offspring (head width:  $F_{8,214} = 2.68$ ,  $P = 0.01$ ; snout-vent length:  $F_{11,220} = 14.89$ ,  $P < 0.001$ , tail length:  $F_{11,220} = 8.86$ ,  $P < 0.001$ ; and mass:  $F_{11,220} = 12.34$ ,  $P < 0.001$ ). Deformities in living newborn were rare (1.1%), but all deformed living newborn were found in 1998 (2.8% of those born alive in 1998).

The probability of a newborn being alive varied among years (Model 1 in Table 5.1;  $\chi^2 = 14.23$ ,  $df = 2$ ,  $P = 0.001$ ); it was lowest in 1996 and highest in 1997 (Table 5.2). This might be attributed to a change in the housing and birthing conditions in 1997 and 1998. Newborn condition and snout-vent length increased the probability of being alive ( $\chi^2 = 4.50$ ,  $df = 1$ ,  $P = 0.03$ ;  $\chi^2 = 14.39$ ,  $df = 1$ ,  $P < 0.001$ ; Fig. 5.1). Neither newborn relative tail length nor clutch size had an effect on whether a newborn was alive or dead at birth ( $\chi^2 = 0.74$ ,  $df = 1$ ,  $P = 0.39$ ;  $\chi^2 = 0.21$ ,  $df = 1$ ,  $P = 0.65$ ).

### *Factors Affecting Reproductive Output*

Clutch size increased with maternal snout-vent length (Model 2 in Table 5.1; Fig. 5.2a). There was no effect of mean newborn mass on clutch size, indicating that there was no detectable trade-off between size and number of offspring. Similar analyses were done against mean newborn condition and mean snout-vent length per litter of live and dead young (Models 3 and 4 in Table 5.1). I wanted to determine which maternal characteristics were important predictors of condition and snout-vent length in newborn, because both measures were significant predictors of the probability of a newborn being alive, and might also have influenced future survival. No maternal traits affected mean newborn condition, but condition did vary from year to year (Model 3 in Table 5.1) and was highest in 1996 (Fig. 5.2b). Mean newborn snout-vent length increased with maternal relative tail length (Model 4 in Table 5.1; Fig. 5.2c). In both Models 3 and 4 (Table 5.1) there was no significant effect of clutch size, indicating that there was no detectable trade-off between size (or quality) and number of offspring.

### *Reproductive Frequency*

Of the 75 adult females captured after July 1st 50 were gravid and 25 were not gravid. I separated the 25 non-gravid females into those caught before August 18 (known non-gravid) and those after August 18 (possibly postpartum). August 18 is the earliest date that lizards were born in any year. The majority of adult females captured in the summer were gravid (range = 65 to 71% from 1996-98). Only a fraction of adult females were definitely known not to have reproduced in any given year (range = 0 to 18% from 1996-98) because they were not gravid when all other reproductive females were gravid. If the females with unknown reproductive state were reproductive, then the proportion of

reproductive females could be as high as 82 - 100%

Estimates of breeding frequency based on the percentage of captured females that are reproductive may over-estimate breeding frequency because reproductive animals are easier to catch (Bonnet and Naulleau, 1996). Temporal patterns of individual females can reveal much lower estimates. I assumed that all captured females for which reproductive status was uncertain (either spring or late fall captures) were in fact reproductive, because reproductive animals are easier to catch (Bonnet and Naulleau, 1996). Even with this assumption, most females exhibited triennial breeding patterns, with very few females (10%) reproducing in consecutive years (Table 5.3).

Larger females were more likely to be pregnant (Model 5 in Table 5.1;  $\chi^2 = 16.31$ ,  $df = 1$ ,  $P < 0.001$ ) and females with intact tails were more likely to be pregnant than those that had lost their tails ( $\chi^2 = 2.78$ ,  $df = 1$ ,  $P = 0.10$ ; Model 1 in Table 5.1; Fig. 5.3).

I compared the post-partum body condition of females that reproduced in the following year to females that did not reproduce in the following year. I used a t-test using separate estimates for variance with the Welch modification to the degrees of freedom (Ihaka and Gentleman, 1996). As above, I assumed that all captured females for which reproductive status was uncertain (spring or late fall captures) were in fact reproductive. There was no difference between post-partum body condition of females that skipped reproduction and females that reproduced in consecutive years ( $t = 0.39$ ,  $df = 3.41$ ,  $P = 0.72$ ).

#### *Growth During Gestation*

Substantial body growth (15 mm) occurred during gestation in two gravid females less than 80 mm snout-vent length. Their growth rates were 3.9 and 2.5 mm per week. I had growth rate data on seven other individuals (six adult males and one adult non-gravid

female) that were similar in size (70 to 80 mm), and were recaptured within the same season and spent their growth time in the field. They had growth rates ranging from 0 to 0.91 mm per week, which is lower than the growth rates of the gravid females that grew.

Tail growth greater than 5 mm occurred in ten gravid females, all of which had tail lengths less than 70 mm. Gravid females with tail lengths less than 70 mm had growth rates ranging from 0.0 to 6.4 mm per week (mean = 1.3, sd = 1.56, N = 21). I compared the ten gravid females that grew tails to the forty-nine gravid females without substantial tail growth, using a t-test, with Welch's approximation to the degrees of freedom for unequal variance (Ihaka and Gentleman, 1996). The ten gravid females whose tails grew were not smaller ( $t = 0.45$ ,  $df = 23.4$ ,  $P = 0.66$ ) or younger ( $t = 0.28$ ,  $df = 13.7$ ,  $P = 0.79$ ), but they did have significantly shorter tails (mean = 43.9 vs 93.9;  $t = 7.55$ ,  $df = 28.7$ ,  $P < 0.001$ ) than those gravid females with tail growth less than 5 mm.

### *Body Condition*

I compared the relationship between snout-vent length and tail length, and mass of five groups (spring males, spring females, fall males, fall females of unknown reproductive state, and known post-partum females; Model 6 in Table 5.1).

The slope of the line relating snout-vent length to mass was significantly greater for fall males as compared to fall females ( $t = 3.04$ ,  $df = 1$ ,  $P = 0.003$ ) and almost significantly greater for spring females compared to fall females ( $t = 1.81$ ,  $df = 1$ ,  $P = 0.07$ ; Model 6 in Table 5.1; Fig. 5.4). The relationship between tail length and mass did not differ among the five groups (Model 6 in Table 5.1).

### *Costs of Reproduction*

Tests for trade-offs between reproduction and growth revealed an inverse relationship between growth rate of snout-vent length and residual clutch mass ( $F_{1,18} = 9.45$ ,  $P = 0.007$ ; Fig. 5.5a), but only when gravid and non-gravid lizards (non-gravid females and males) were both included in the analysis (Model 8 in Table 5.1). Among only gravid females there was no significant relationship between growth rate of snout-vent length and residual clutch mass (Model 7 in Table 5.1; Fig. 5.5a). Residual clutch mass increased with early body condition in both cases: 1) only gravid females (see Model 7 in Table 5.1 for F statistic), and 2) both gravid and non-gravid lizards ( $F_{1,18} = 19.51$ ,  $P < 0.001$ ; Model 8 in Table 5.1; Fig. 5.5b).

The analyses for survival costs of reproduction showed that post-partum body condition was not related to residual clutch mass (Model 7 in Table 5.1). Few females (2 of 54; 4%) died during parturition. One female that died was in very poor condition (the lowest of all post-partum females). Although condition could not be measured in the other female, she was six years of age and near the end of her apparent lifespan. Sprint speed of gravid females decreased with clutch burden (Model 9 in Table 5.1;  $F_{1,13} = 4.61$ ,  $P = 0.05$ ; Fig. 5.6a) and with snout-vent length ( $F_{1,13} = 3.88$ ,  $P = 0.07$ ; Fig. 5.6b).

### *Projected Lifetime Offspring Production*

Is it advantageous for female *Elgaria coerulea* to trade-off between growth and reproduction? I examined this question by classifying females according to whether they invested in body growth or not, and comparing their potential lifetime offspring production. If a growth strategy produces higher lifetime offspring production than a no-growth strategy, then the growth strategy should be favoured by natural selection. I used my mea-

sured values of clutch mass, survival rates (see Chapter 4), probability of reproduction, and growth rates of female *Elgaria coerulea* to compare lifetime offspring production under two strategies. In the first strategy (growth) females invest in body growth and reduce current reproduction, but increase future reproduction. In the second strategy (no growth), females do not invest in body growth, thereby not reducing current reproduction, and continue to reproduce at the current rate.

I calculated projected lifetime offspring production using Equation A.1 (see Appendix A), a variant of Equation 2 from Shine and Schwarzkopf (1992). The equation is a summation of  $R_0$  (net reproductive rate) for each year of life up to the known lifespan of the population (seven years of age in this case). I calculated lifetime offspring production under both strategies for sixteen of the eighteen females considered in the trade-off analysis. Two females were omitted because they were seven years of age, thus theoretically in their final year of life (according to my data). The group was divided in two: 1) growers (included five gravid and two non-gravid females), and 2) non-growers (nine gravid females).

I compared the two strategies (growth and no growth) for the two groups of females (growers and non-growers), using one-tailed pairwise t-tests. See Appendix A for details of how I calculated lifetime offspring production for the two strategies in growers and non-growers. For the growers, there was no difference between lifetime offspring production under the growth strategy compared to the no-growth strategy ( $t = 0.03$ ,  $df = 6$ ,  $P = 0.51$ ). Two young female growers had higher lifetime offspring production under the growth strategy as compared to the no-growth strategy, although the differences were not significant ( $t = 1.40$ ,  $df = 1$ ,  $P = 0.20$ ). This was not the case in non-growers; the growth strategy resulted in significantly lower lifetime offspring production than the no-growth strategy ( $t$

= 12.92,  $df = 8$ ,  $P < 0.001$ ).

## Discussion

### *Costs of Reproduction*

This study shows that some female *Elgaria coerulea* trade body growth for reproductive output in a natural population. My projected calculations of lifetime offspring production suggest that young females can increase their lifetime offspring production by growing. The other females that grew saw no increase, but also no decrease, in lifetime offspring production. Females that did not grow would have seen a decline in lifetime offspring production had they invested in body growth.

Investment in body growth reduces current reproduction. So which individuals make the trade-off between growth and reproduction and why? If females are in good condition and it is a 'better' reproductive year, then they should invest in body growth. Only young females increase their lifetime offspring production by investing in growth at the expense of reproduction. This could be considered a fecundity trade-off because they realise a reproductive benefit from investment in body growth. Other females invested in snout-vent length growth, but this investment did not increase or decrease lifetime offspring production. They grew enough to balance the loss in current reproduction by an increase in future reproduction. Given that they realised no reproductive benefit, it seems unlikely that the reason for growing was related to reproduction. It is possible that there is a survival benefit. If survival probability increases with body size then these females might have been making a survival trade-off. They reduced their current reproduction because they invested in body growth, which may have increased their survival rate. However, they decreased



current reproduction only by an amount that did not reduce lifetime offspring production.

I was able to detect the trade-off between growth and reproduction because I measured female condition in the spring. In previous studies, the ability to detect a trade-off has been weakened by lack of knowledge about a female's stored energy or her ability to acquire resources (van Noordwijk and de Jong, 1986; de Jong and van Noordwijk, 1992). Few field studies on squamate reptiles have been able to do this because of low recapture rates within a season (but see Sinervo and DeNardo, 1996; Doughty and Shine, 1997). In this study, I measured energy reserves before and after reproduction. My ability to control for variation in spring condition provided the power necessary to detect the trade-off between growth and reproduction. In addition, the strong relationship between spring condition and clutch mass (corrected for body size) showed that there was considerable variation in female body condition and that reproductive output was strongly influenced by body condition.

Although spring condition strongly influenced clutch mass (corrected for body size), there was no relationship between clutch mass and post-partum condition. Some previous studies have found a negative relationship (Madsen and Shine, 1993), but other studies have not (Doughty and Shine, 1997). Only four percent of female *Elgaria coerulea* died during parturition, fewer than in a temperate-zone snake species (20%; (Madsen and Shine, 1993)). The differences may lie in the female's eating habits during gestation. Some viviparous snake species are known to eat very little during gestation (Gregory et al., 1999; Farr, 1988), and energy allocated to reproduction is at a cost to post-partum condition (Gregory and Skebo, 1998). Female *Elgaria coerulea* feed during pregnancy (Rutherford, personal observation), perhaps at the same rate as non-gravid lizards. This may make gravid females better able to allocate resources towards both reproduction and condition.

The lack of relationship between clutch mass (corrected for body size) and postpartum condition suggests that female *Elgaria coerulea* do not trade-off between reproduction and over-winter survival. Although I could not compare survival rates of reproductive and non-reproductive females, there is no difference between over-winter survival and summer survival rates (Chapter 4). Therefore, while females were in significantly poorer condition in the fall compared to the spring, this does not necessarily translate to higher mortality during hibernation.

Clutch burden (an estimate of relative clutch mass) did reduce sprint speed, but this may not indicate a trade-off between reproduction and survival for several reasons. First, *Elgaria coerulea* spend little time basking in the open, and when they are exposed they stay very close to available rock cover (Chapter 2). In addition, gravid females do not stay closer to cover than males or juveniles (Chapter 3), indicating that there is no shift in behaviour to compensate for the reduced sprint speed of gravid females as has been shown in other vertebrates (Brodie, 1989; Braña, 1993; Rodewald and Foster, 1998). This suggests that *Elgaria coerulea* does not rely on sprinting as an anti-predator tactic. Therefore, the negative relationship between sprint speed and clutch burden may be inconsequential and not represent a survival cost of reproduction.

It is more likely that *Elgaria coerulea* rely on crypsis and tail autotomy as anti-predator strategies. These lizards are mottled brown in colour and their initial reaction to a human predator is to remain stationary (Rutherford, personal observation). Adult females have more black mottling on their backs than males or juveniles (Chapter 4), although this is fixed and does not vary with reproductive state. This may make them more conspicuous to predators than are males, but there would be no difference between gravid and non-gravid

females in visibility. Therefore, if there is a survival cost associated with the black mottling the cost could not be reduced by not reproducing.

Tail autotomy is common in *Elgaria coerulea* (56%) and tail loss is known to reduce survival in some lizard species (Wilson, 1992; Fox and McCoy, 2000). In *Elgaria coerulea* there was no difference between adult males and females in rates of tail loss (Chapter 4), suggesting that gravid females do not suffer a higher survival cost because of tail autotomy than adult males. Tail loss in female *Elgaria coerulea* may constitute a fecundity cost because a female with an intact tail is more likely to be reproductive than a similar-sized female that has lost her tail. Although there was no difference in tail loss rates, adult males and females did differ in the amount of tail loss; females never lost only small portions of their tails (Chapter 4). This difference will result in higher survival costs for females compared to males if the length of the tail affects their ability to survive another predation event. A fecundity cost may result because females with longer tails tended to have larger clutches.

#### *Shine and Schwarzkopf Model*

These results demonstrate fecundity costs of reproduction in a temperate-zone lizard. This result contradicts the SS model, which predicts that a species with such a low relative clutch mass (0.32) and survival rate (0.43; Figure 5.7) would be less likely to make trade-offs between current and future reproduction. So why do the predictions of the SS model not hold true?

There are two factors to consider. The first reason that predictions of the SS model may not hold true lies in consideration of reproductive frequency. Predictions about the importance of fecundity costs for cold-climate reptiles are made using the curves for re-

productive frequencies of one or one-half per year (Shine and Schwarzkopf, 1992). In the SS model these species have a long interclutch interval. I argue that this is not realistic for cold-climate species. Female *Elgaria coerulea* are at best capable of a single clutch per year due to a short activity season. The remainder of the year is spent in hibernation, during which time no growth occurs, resulting in a short interclutch interval. This suggests that the placement of cold-climate species on the RCM-survivorship trajectory needs to be reconsidered. If they are more like the hypothetical species that produces five clutches per year because they have a short interclutch interval, then their RCM-survivorship trajectory is lower. The SS model would then predict that many cold-climate reptiles might make trade-offs between current and future reproduction.

The second reason that the predictions of the SS model may not hold true is that the RCM-survivorship trajectory is influenced by the method of modelling growth. In a re-examination of the SS model Niewiarowski and Dunham (1994) discovered that the RCM-survivorship trajectory from the ND model was increasingly lower than the RCM-survivorship trajectory from the SS model as reproductive frequency increased and interclutch interval decreased. The ND model used daily growth increments instead of annual growth increments used in the SS model. The even lower RCM-trajectories of the ND model predict that species with very low RCM and very low survival rates might trade-off current for future reproduction. Whether calculating daily growth increments is reasonable depends on whether females are capable of concurrent growth and reproduction. Reproductive female *Elgaria coerulea* clearly are capable of concurrent growth and reproduction.

### ***Reproductive Frequency***

Within my trade-off analysis of gravid females there was a trend for body growth to reduce clutch mass (corrected for body size). The relationship became significant only when non-gravid lizards (male and female), which had a clutch mass of zero, were included in the analysis. Therefore, the trade-off between growth and reproduction was evident only when non-reproductive lizards were considered.

Females of many cold-climate reptiles, mainly snakes, are known to reproduce less often than annually (Fitch, 1970; Bull and Shine, 1979), and *Elgaria coerulea* appear to fit this pattern. Reproduction can involve significant 'costs' that are independent of litter size (Bull and Shine, 1979). Under such circumstances natural selection should favour females that delay reproduction until they can produce a larger litter (e.g. Naulleau and Bonnet, 1996; Shine and Madsen, 1997; Shine et al., 1998a). In *Elgaria coerulea* clutch mass increases with body condition and snout-vent length. Reproduction did not significantly reduce body condition, a pattern also shown in *Eulamprus tympanum* (Schwarzkopf, 1993). In water skinks (Schwarzkopf, 1993) and alligator lizards from this study it may be that energy limitation is not an important cause of missed reproduction. Some female *Elgaria coerulea* are capable of annual reproduction, and some are capable of both growth and reproduction; but perhaps not all females are capable of these reproductive strategies. Perhaps less than annual reproduction in this species is a result of females trading off growth for reproduction, rather than a consequence of their inability to gather enough resources for reproduction. If this is the case, then examination of the causes of missed reproduction in species with biennial or triennial reproductive frequencies may reveal patterns of life-history trade-offs.

### *Conclusions*

This study is important because it showed evidence of a trade-off between current reproduction and growth in a natural population of a temperate-zone lizard, *Elgaria coerulea*. Projected calculations of lifetime offspring production under two different scenarios (growth and no growth) suggested that trading growth for reproduction will not always increase lifetime production of offspring, even though it will always increase future reproductive output. This increase may not be enough to compensate for the reduced reproductive output due to their investment in body growth, resulting in lower lifetime production of offspring overall. Thus, in some circumstances body growth may increase lifetime offspring production, but in other cases it may increase survival. Therefore, in this species there appears to be both a trade-off between current and future reproduction, and a trade-off between current reproduction and survival. Cold-climate species have annual (or biennial and triennial) reproductive frequencies, but due to hibernation they have relatively short interclutch intervals. If I consider these species to be more similar to species with short interclutch intervals, then the SS model predicts that trade-offs between current and future reproduction are more likely. In addition, I showed that concurrent growth and reproduction does occur. This means that the ND model may be reasonable, because it predicts that species with very low relative clutch mass and survival rates may benefit from trading off current for future reproduction.

Although there are many questions left unanswered, this study provides one of the first tests of a model that predicts reproductive effort in reptiles. Whether the model passes or fails tells us little about the evolution of reproductive effort. Instead, we benefit from evaluating why the model is weak, and discussion about its short-comings. This process

**helps us clarify our thinking about the evolution of costs of reproduction and further develop predictive models.**

Table 5.1: Tested models (with the terms retained in the best model are shown in italics) and test statistics for *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. In model 5, age was tested separately from SVL and relative tail length was tested separately from tail loss state due to the correlation between age and SVL ( $t = 6.76$ ,  $df = 44$ ,  $P < 0.001$ ), and relative tail length and tail loss state ( $t = 10.2$ ,  $df = 57$ ,  $P < 0.001$ ). Model 7 includes only gravid females, while Model 8 additionally includes two non-gravid adult females and three adult males. Condition estimates were the residuals of a regression of snout-vent length and tail length on mass. Relative tail length was the residual of the regression of tail length versus snout-vent length.

| No. | Dependent Variable     | Terms  | F/AIC  | df     | P       | Adj. R <sup>2</sup> |
|-----|------------------------|--|--------|--------|---------|---------------------|
| 1   | Probability(alive)     | <i>year, SVL, condition, clutch size, relative tail length</i>                                     | 150.27 | 289    |         |                     |
| 2   | clutch size            | <i>SVL, relative tail length, year, mean newborn mass</i>  | 2.79   | 1,57   | 0.10    | 0.03                |
| 3   | mean newborn condition | <i>year, SVL, relative tail length, clutch size</i>  | 7.85   | 2,56   | < 0.001 | 0.19                |
| 4   | mean newborn SVL       | <i>relative tail length, year, clutch size, SVL</i>  | 3.30   | 1,57   | 0.07    | 0.04                |
| 5   | Probability(pregnant)  | <i>SVL, tail loss state, year, SVL by tail loss state, age*, relative tail length*</i>             | 37.31  | 56     |         |                     |
| 6   | mass                   | <i>SVL, tail length, condition category, SVL by condition category, tail by condition category</i> | 48.4   | 10,175 | < 0.001 | 0.72                |
| 7   | residual clutch mass   | <i>early condition, growth rate of SVL, year, growth rate of tail length, late condition</i>       | 7.03   | 1,14   | 0.02    | 0.29                |
| 8   | residual clutch mass   | <i>early condition, growth rate of SVL, growth rate of tail length, late condition</i>             | 14.48  | 2,18   | < 0.001 | 0.57                |
| 9   | speed                  | <i>SVL, clutch burden, relative tail length</i>  | 4.25   | 2,13   | 0.04    | 0.30                |



**Table 5.2: Yearly means and coefficients of variation (CV) for size and age of reproductive females, litter size and newborn size of *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. Samples size are indicated in brackets for each year. \* indicates significant differences from year to year at  $\alpha < 0.05$ . Condition estimates were the residuals of a regression of snout-vent length and tail length on mass. Clutch size and clutch mass included both live and dead young.**

| Variable                 | 1996 (12) |      | 1997 (23) |      | 1998 (24) |      |
|--------------------------|-----------|------|-----------|------|-----------|------|
|                          | Mean      | CV   | Mean      | CV   | Mean      | CV   |
| Female SVL (mm)          | 91.9      | 6.1  | 93.5      | 4.7  | 91.5      | 7.9  |
| Female tail length (mm)  | 87.9      | 44.8 | 84.2      | 39.9 | 88.8      | 40.6 |
| Female age (yrs.)        | 4.7       | 20.0 | 5.1       | 18.8 | 5.4       | 22.0 |
| Post-partum condition*   | 0.32      |      | -1.16     |      | -0.98     |      |
| Clutch mass (g)          | 3.43      | 29.5 | 3.62      | 24.1 | 3.41      | 34.4 |
| Clutch size              | 4.6       | 28.6 | 5.1       | 24.4 | 4.9       | 31.0 |
| Number of live young*    | 3.6       | 42.0 | 5.0       | 30.7 | 4.5       | 41.4 |
| Percent live*            | 77.1      |      | 96.5      |      | 92.6      |      |
| Newborn head width (mm)* | 4.6       | 1.9  | 4.4       | 2.0  | 4.5       | 1.9  |
| Newborn SVL (mm)         | 32.5      | 2.2  | 32.6      | 2.2  | 32.3      | 3.1  |
| Newborn tail length (mm) | 38.1      | 2.9  | 38.4      | 3.5  | 37.8      | 4.5  |
| Newborn mass (g)*        | 0.76      | 7.6  | 0.71      | 8.6  | 0.71      | 8.1  |
| Newborn condition*       | 0.04      |      | -0.02     |      | 0.00      |      |

**Table 5.3: Sets of capture-recapture data providing estimates of breeding frequencies of female *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. Females are classed as reproductive (R) or non-reproductive (NR) in each year.**

| <b>1996</b> | <b>1997</b> | <b>1998</b> | <b>N</b> | <b>%</b> | <b>Type</b> |
|-------------|-------------|-------------|----------|----------|-------------|
| R           | NR          | NR          | 6        | 11       | Triennial?  |
| NR          | NR          | R           | 20       | 38       | Triennial?  |
| NR          | R           | NR          | 20       | 38       | Biennial?   |
| R           | NR          | R           | 2        | 4        | Biennial    |
| R           | R           | NR          | 1        | 2        | Annual?     |
| NR          | R           | R           | 1        | 2        | Annual?     |
| R           | R           | R           | 3        | 6        | Annual      |

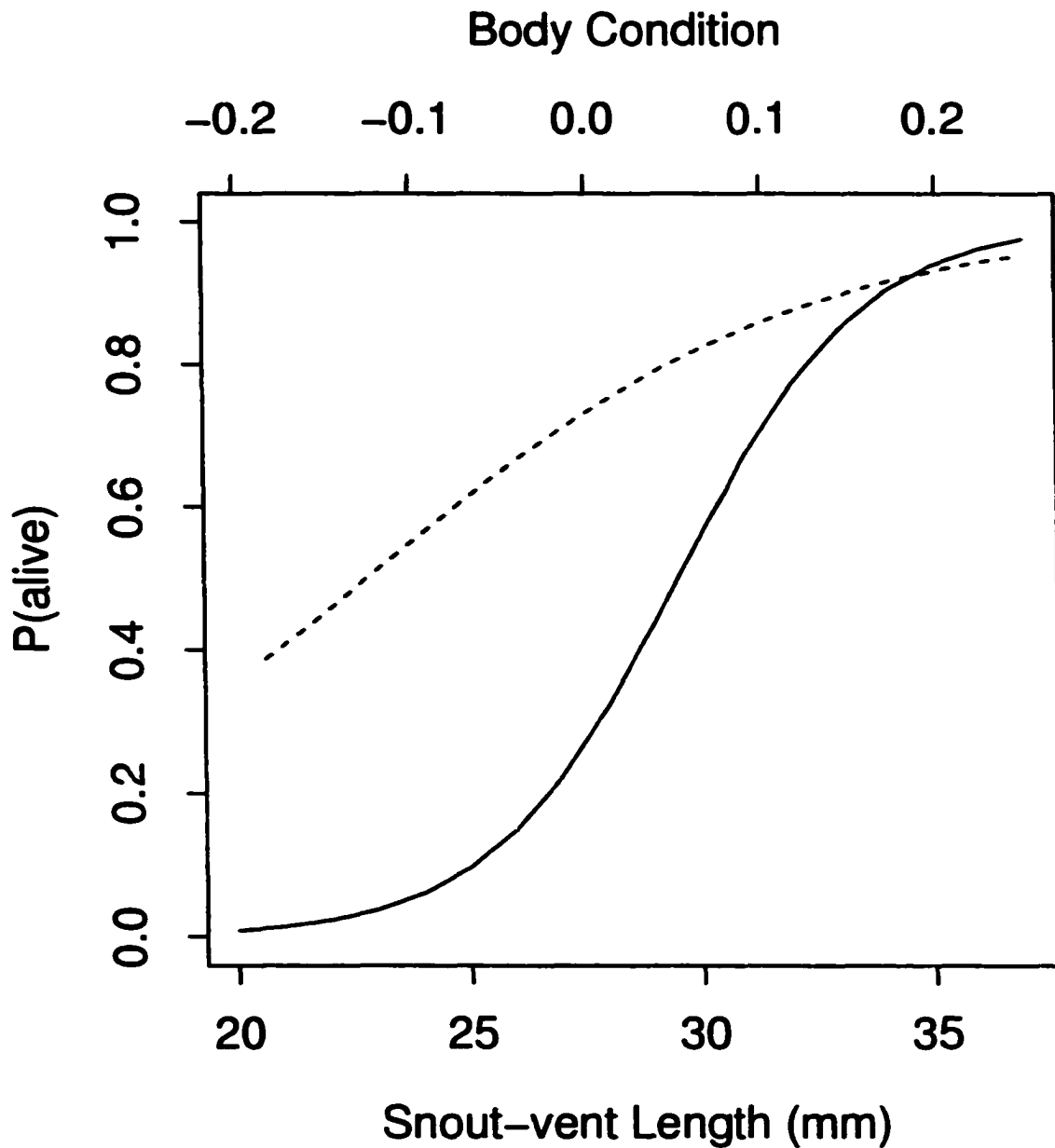
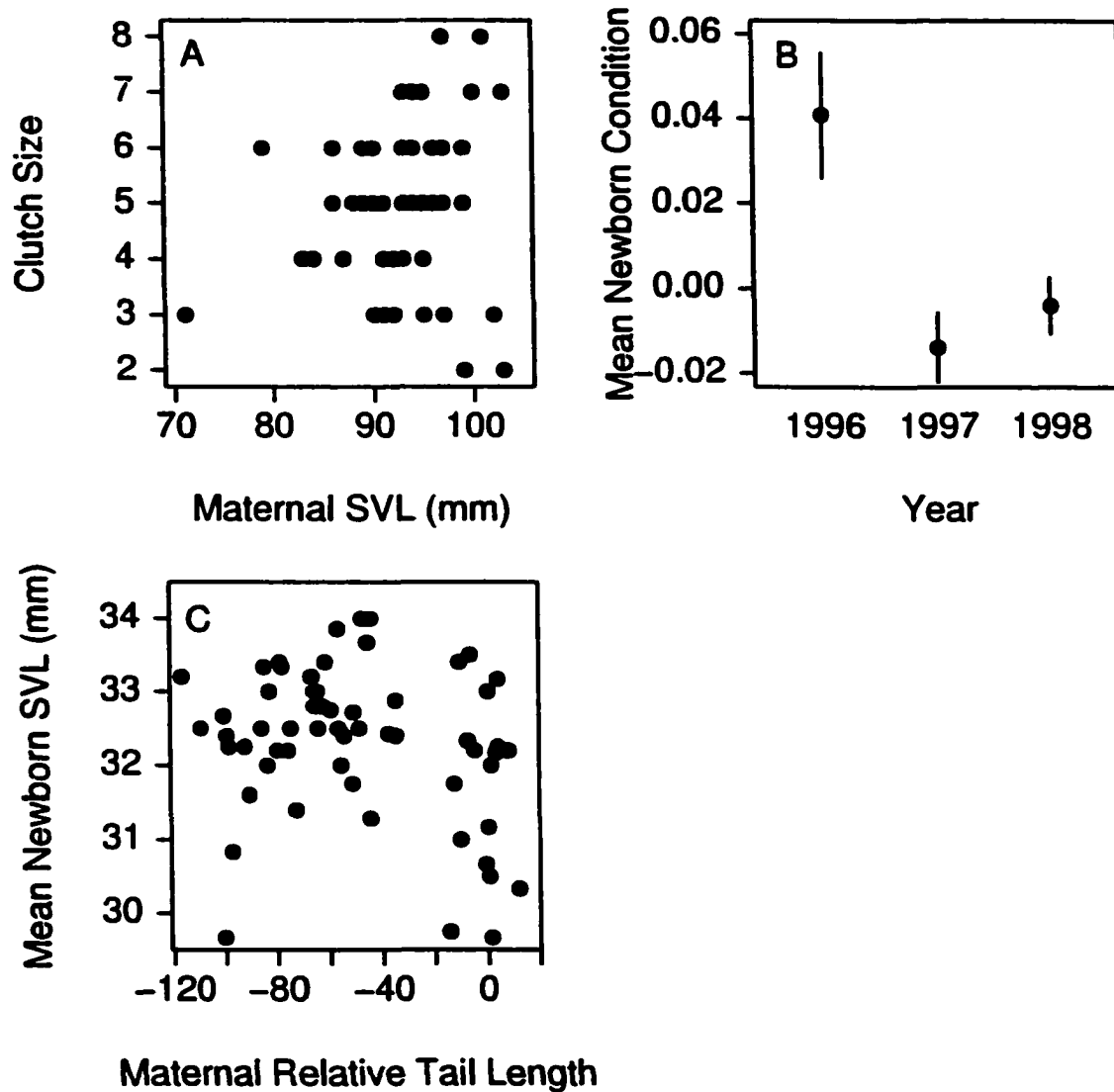


Figure 5.1: Newborn snout-vent length (solid line) and body condition (dashed line) versus the probability of being alive for newborn *Elgaria coerulea* from CVWMA, Creston, British Columbia born in 1996-1998.



**Figure 5.2:** Plots of significant factors affecting three reproductive traits: (A) clutch size, (B) mean newborn condition ( $\pm$  SE), and (C) mean newborn snout-vent length. Condition estimates were the residuals of a regression of snout-vent length and tail length on mass. Relative tail length was the residual of the regression of tail length versus snout-vent length.

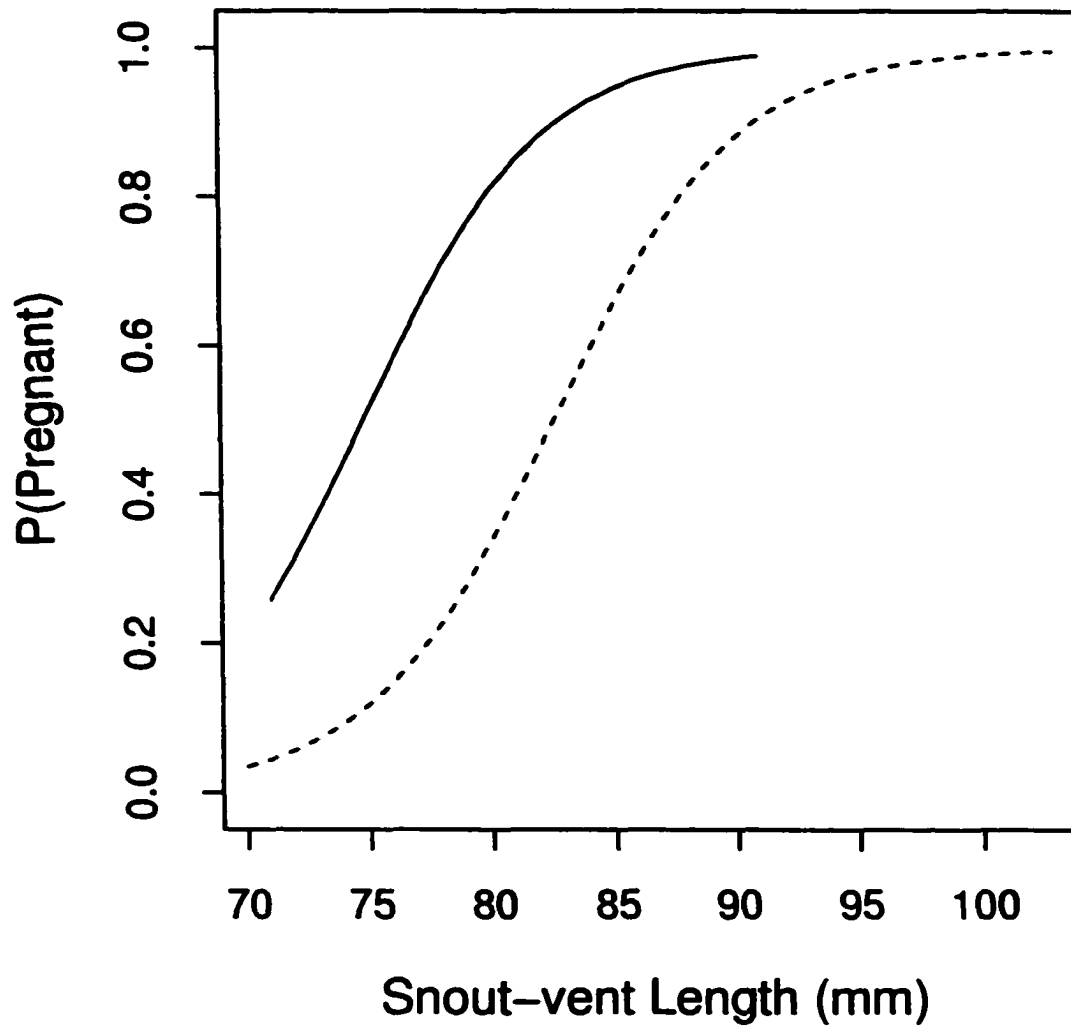


Figure 5.3: Snout-vent length versus the probability of being pregnant plotted for female *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998 with intact tails (solid line) and lost tails (dashed line). Plotted are the predicted probabilities from a logistic regression of snout-vent length versus reproductive state (gravid or not) for two groups of lizards (lost and intact tails).

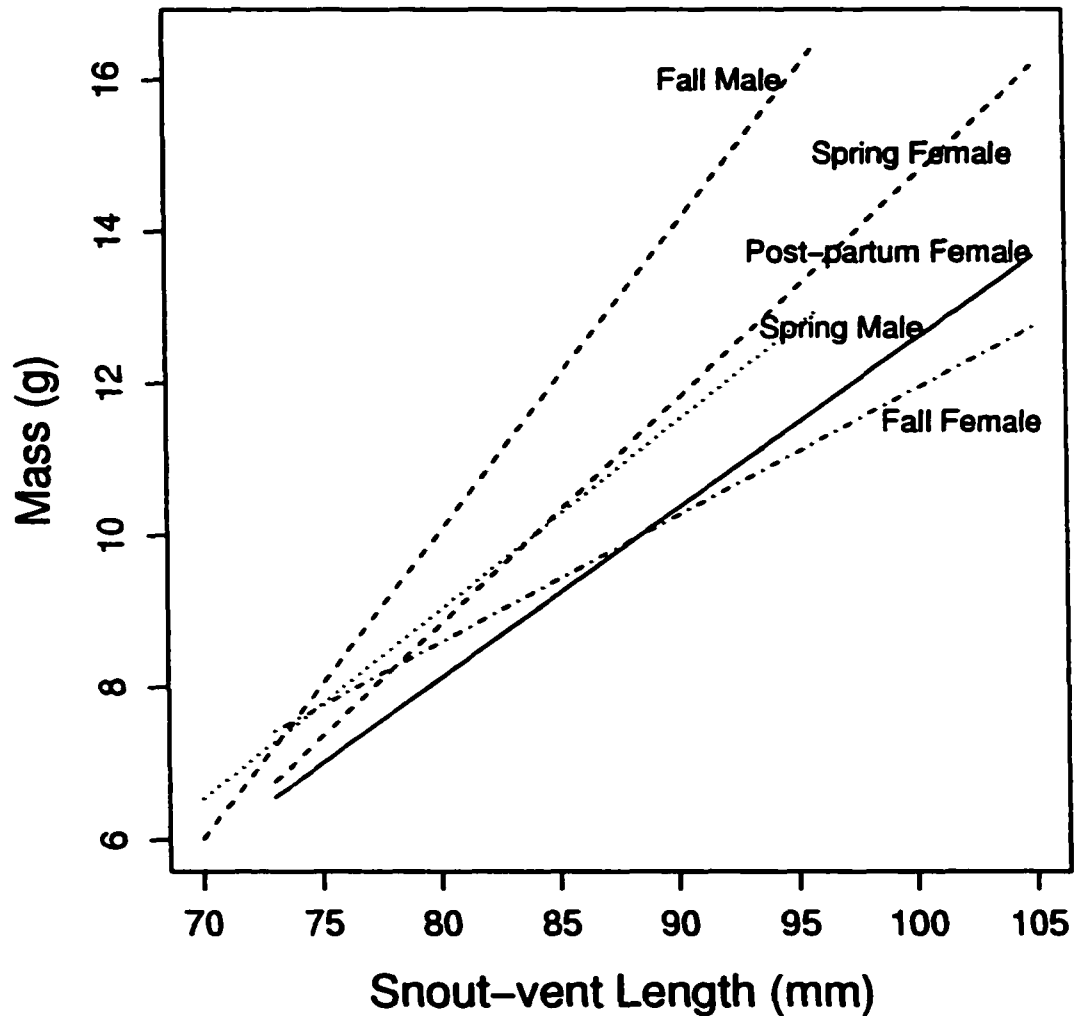


Figure 5.4: Snout-vent length (mm) versus mass (g) for spring male (short-dashed line), fall male (long-dashed line), spring female (mid-dashed line), fall female of unknown reproductive state (long and short-dashed line), and known post-partum female (solid line) adult *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998.

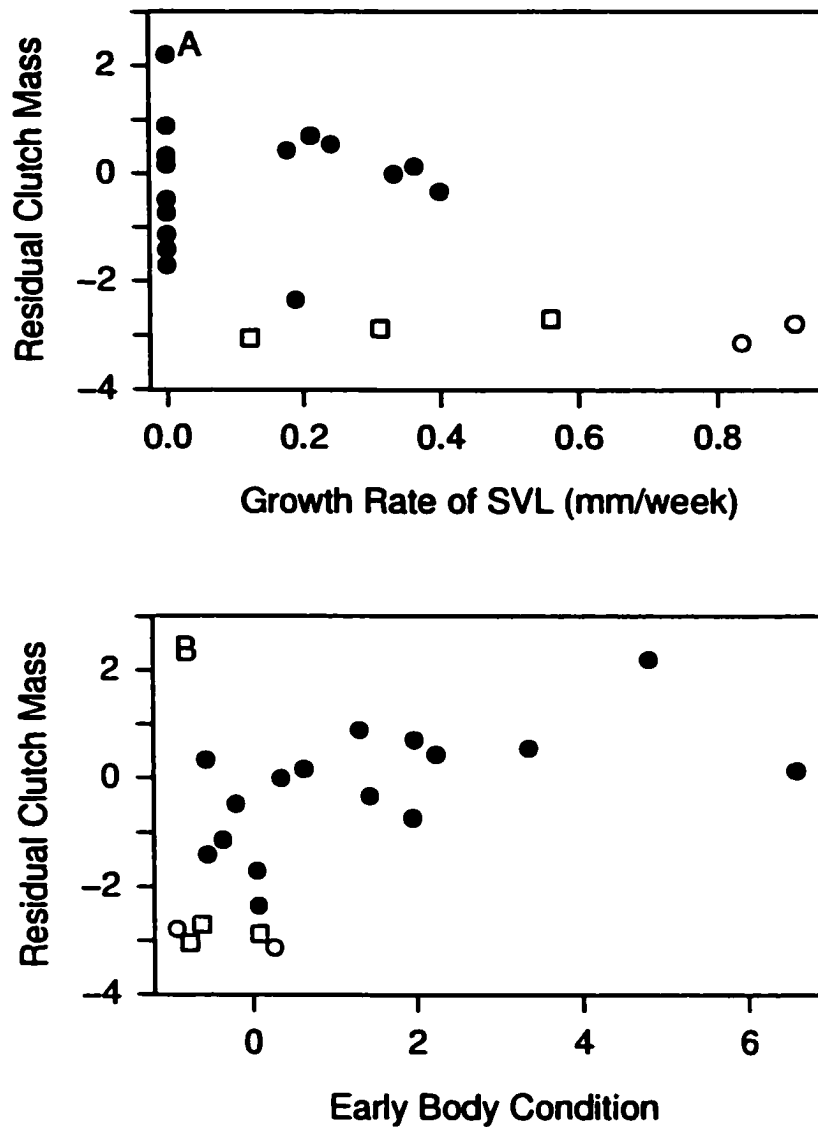


Figure 5.5: (A) Growth rate of snout-vent length (mm/week), and (B) early body condition versus residual clutch mass for adult *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. Gravid females are shown with filled circles, non-gravid females with open circles, and males with open squares. Non-gravid females and males were given a clutch mass of zero. For all lizards, residual clutch mass was calculated from a regression of snout-vent length versus clutch mass. I calculated early body condition for lizards captured prior to June 31, from the residuals of a regression of snout-vent length and tail length against mass for all adult lizards.

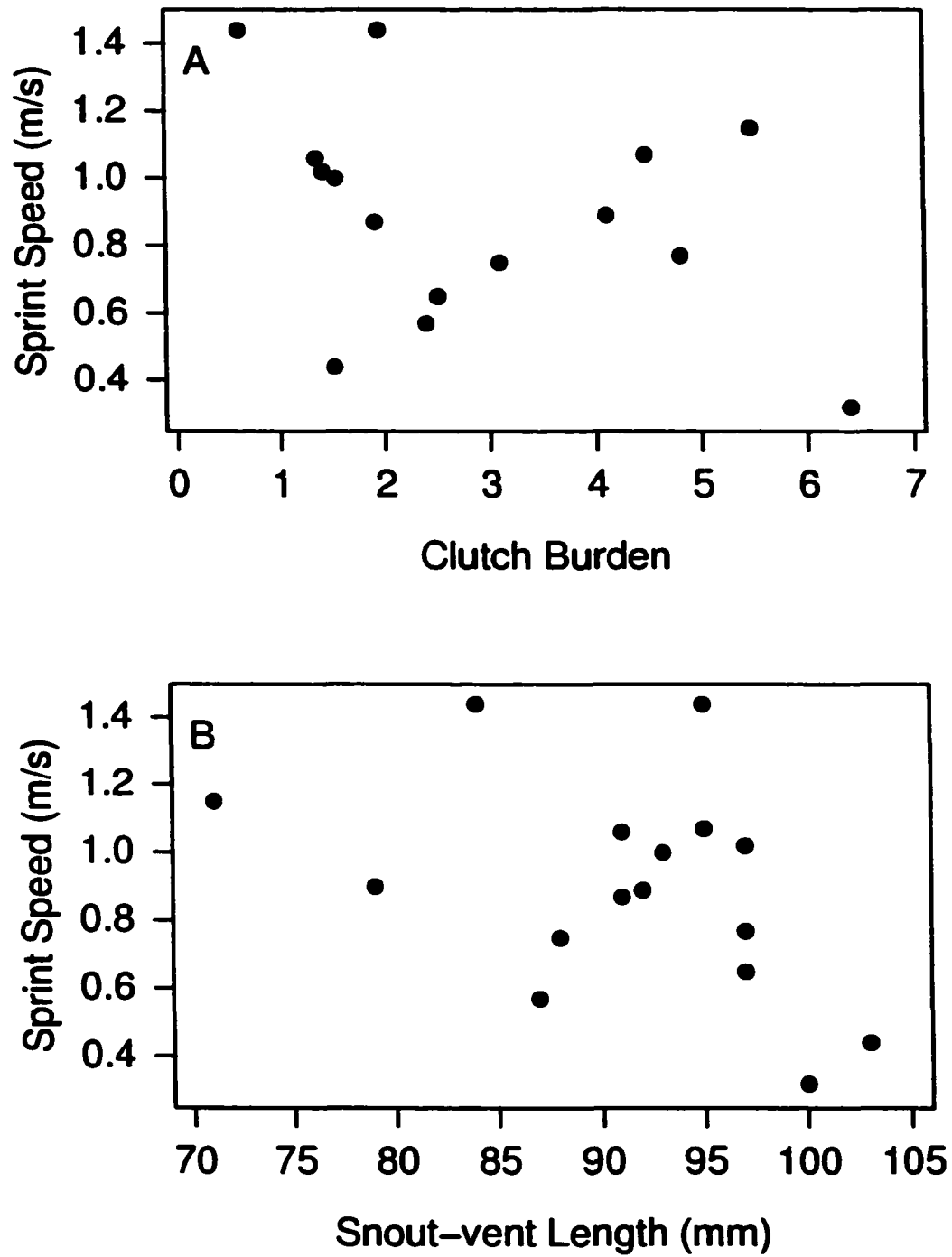


Figure 5.6: (A) Estimated clutch burden, and (B) snout-vent length (mm) versus sprint speed (m/s) for gravid female *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998.



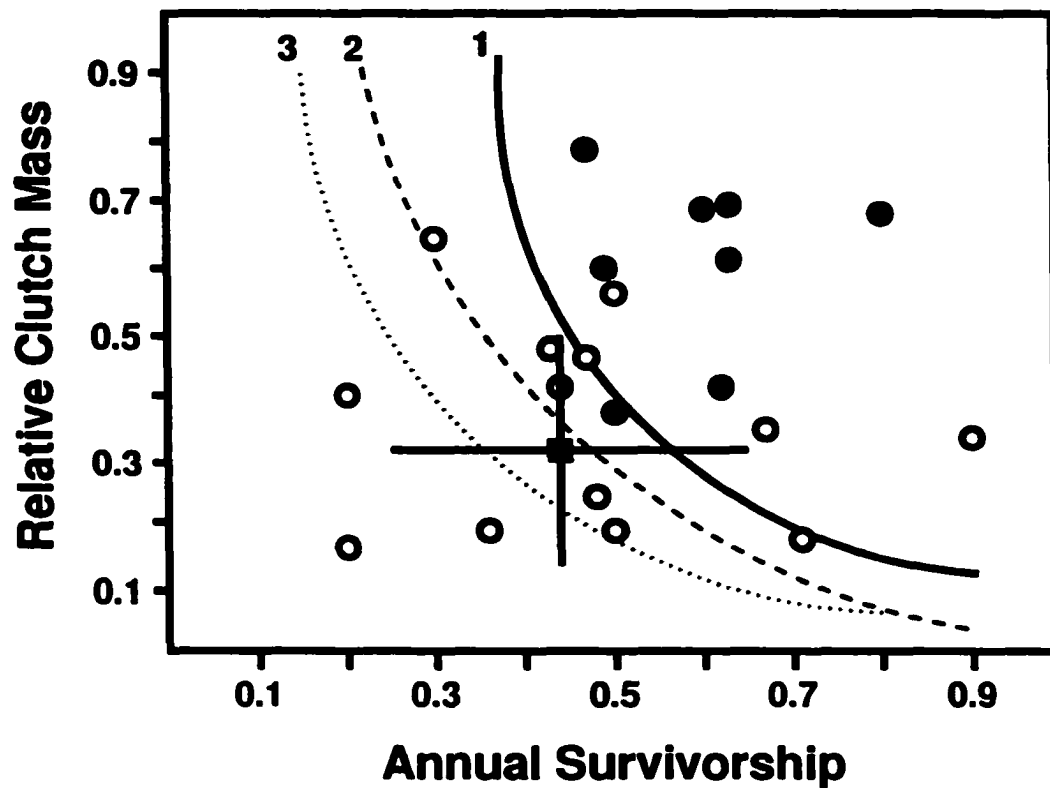


Figure 5.7: Calculated trade-off lines relating annual survivorship and relative clutch mass (reproduced from Shine and Schwarzkopf (1992)). Lines are shown for number of clutches equal to 1, 2, and 3. Published data for lizards (open circles) and snakes (closed circles) are superimposed on the trade-off lines. Means and 95% confidence limits for survival rate and relative clutch mass of *Elgaria coerulea* from this study are shown (open square).

## Chapter 6

### General Conclusions

1. Hibernation in *Elgaria coerulea* occurred in the same habitat where lizards were active during the summer. They were syntopic with another lizard species, *Eumeces skiltonianus*, at many of the study sites, although some sites had only one of the species. Individuals of either species were recaptured on average within ten metres of a previous capture. Both species were rarely found in the open and more often under rocks than in vegetation or under logs; they also remained close to shrubs and forest edges. Therefore, *Elgaria coerulea* are secretive, and do not incur the energetic cost, or increased predation risk associated with a long-distance migration.
2. *Elgaria coerulea* had seasonal variation in both retreat-site selection and emergence patterns. Lizards selected thicker rocks and fewer emerged at midday during the summer compared to spring, perhaps to avoid lethal, high temperatures. Adult males used larger, thicker rocks than adult females and juveniles. Emergence patterns also differed between the sexes. The probability of capturing an adult female in the open steadily increased over the summer, while there was no change in male emergence patterns over the season. Thus, while remaining under cover is important in *Elgaria coerulea*, specific circumstances (lethal temperatures and gestation) will modify their cover-use.
3. There was sexual dimorphism in morphometric traits in *Elgaria coerulea*. Adult females were larger, had narrower heads and shorter tails, and more black mottling on their backs than adult males. Annual survival rate of adult females was 44% and

juvenile survival rate was 22%. The survival rate of adult males likely fell in between, although I was not able to estimate their survival rate due to small sample sizes. The patterns of sexual size dimorphism seen in *Elgaria coerulea* may be a potentially important link between reproductive and survival traits.

4. *Elgaria coerulea* trade-off current reproduction for growth in a natural population. My projected calculations of lifetime offspring production suggest that young females can increase their lifetime offspring production by growing. The other females that grew saw no increase, but also no decrease, in lifetime offspring production. Females that did not grow would have seen a decline in lifetime offspring production had they invested in body growth. Thus, in some circumstances body growth may increase lifetime offspring production, but in other cases it may increase survival. Although spring condition strongly influenced clutch mass, there was no relationship between clutch mass and post-partum condition suggesting that female lizards do not trade-off between reproduction and over-winter survival. Clutch burden reduced sprint speed, but this may not indicate a trade-off between reproduction and survival if *Elgaria coerulea* do not rely on sprinting as an anti-predator tactic.
5. The predictions of the SS model may not hold true because of problems with incorporating cold-climate reptile species into the model, and because concurrent growth and reproduction may be more prevalent than previously believed. Thus, the ND model may be reasonable, because it predicts that species with very low relative clutch mass and survival rates may benefit from trading off current for future reproduction.

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## Appendix A

### Projected Lifetime Offspring Production

I calculated projected lifetime offspring production using Equation A.1, a variant of Equation 2 from Shine and Schwarzkopf (1992).

$$R_0 = \sum_{i=i+1}^n (S)^i (\text{Prob. of Reproduction})(\text{Predicted Clutch Mass}) \quad (\text{A.1})$$

Annual survival ( $S$ )<sup>*i*</sup> was estimated from mark-recapture data (Chapter 4) and calculated as a constant survival probability raised to the power of year. This value started at one for the female's current year and increased by one until the female reached seven years of age, the maximum age recorded in this population. For example, a five-year-old female would have had three possible reproductive attempts ( $n = 3$ ).

Probability of reproduction was considered because there is a strong relationship between snout-vent length and probability of reproduction (Fig. 5.3). This was done separately for females that had lost their tails (Equation A.2) and for those with intact tails (Equation A.3).

$$\text{Prob. of Reproduction} = \frac{\exp(-21.9316 + 0.2657 * SVL)}{1 + \exp(-21.9316 + 0.2657 * SVL)} \quad (\text{A.2})$$

$$\text{Prob. of Reproduction} = \frac{\exp(-20.8512 + 0.2788 * SVL)}{1 + \exp(-20.8512 + 0.2788 * SVL)} \quad (\text{A.3})$$

$$\text{Predicted Clutch Mass} = -0.47127 + 0.04296 * SVL \quad (\text{A.4})$$

I calculated predicted clutch mass from the regression between clutch mass and

snout-vent length. I then added a clutch mass adjustment to this predicted clutch mass. The clutch mass adjustment considered year of reproduction, capture condition, and growth rate in snout-vent length, all factors known to influence clutch mass. The coefficients were taken from the regression analysis of these factors on residual clutch mass. The adjustments for 1997 and 1998 were calculated using Equations A.5 and A.6 respectively.

$$\text{Adjustment} = 0.5946 * \text{Condition} - 1.6726 * \text{Growth Rate} \quad (\text{A.5})$$

$$\text{Adjustment} = -0.7939 + 0.5946 * \text{Condition} - 1.6726 * \text{Growth Rate} \quad (\text{A.6})$$

For growers, I calculated their predicted clutch mass under strategy 1 (growth) using their actual growth rate in snout-vent length. I calculated their predicted clutch mass under strategy 2 (no growth) using a growth rate of zero. For non-growers, I calculated their predicted clutch mass under strategy 1 (growth) using an average growth rate of similar-aged reproductive females. I calculated their predicted clutch mass under strategy 2 (no growth) using their actual growth rate of zero change in snout-vent length.

Predicted clutch mass in subsequent years was calculated using Equation A.4, substituting in their final snout-vent length after growth for strategy 1 (growth) and using their initial snout-vent length for strategy 2 (no growth). I did not adjust their predicted clutch mass in subsequent years using year or condition effects because this would be purely hypothetical.