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How age, sex, and reproductive condition affect retreat-site selection and emergence patterns in a temperate-zone lizard, *Elgaria coerulea*¹

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Abstract: Minimising predation risk is critical to fitness in all animals. For animals that utilise retreat sites as an anti-predator strategy, there are many factors that influence retreat site selection and determine when to emerge from a hiding place. In this paper we test for seasonal and daily variation in cover use in a temperate-zone lizard (*Elgaria coerulea*). We also test for age- and sex-related differences in capture-site temperature, cover use, and sprint speed. We conducted a mark-recapture study on *Elgaria coerulea* in south-eastern British Columbia, Canada. We recorded temperature, precipitation, lizard's position, proximity to cover, and rock size. The results showed seasonal variation in both retreat-site selection and emergence patterns. Lizards selected thicker rocks 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 male emergence declined over the season. The tendency to be in the open also increased with the amount of rain that fell the previous day. This study shows that while remaining under cover is important in *Elgaria coerulea*, specific circumstances (lethal temperatures, reproduction, precipitation) will modify their cover use.

Keywords: lizards, temperature selection, retreat sites, cost of reproduction.

Résumé : Pour tous les animaux, minimiser les risques de prédation influence grandement le succès reproducteur. Chez les animaux qui utilisent les caches comme stratégie anti-prédateur, il existe plusieurs facteurs qui influencent le choix des caches et qui déterminent quand l'animal peut sortir de sa cachette. Dans cet article, nous vérifions les variations saisonnières et journalières de l'utilisation d'un couvert par un lézard des régions tempérées, *Elgaria coerulea*. Nous tentons également de connaître les différences d'âge et de sexe en ce qui concerne la température des lieux de capture, l'utilisation du couvert et la vitesse de course des lézards. Nous avons mené une étude de marquage-recapture d'*Elgaria coerulea* dans le sud-est de la Colombie britannique, au Canada. Nous avons mesuré la température, les précipitations, la position des lézards, la proximité du couvert et la taille des rochers servant de couvert. Il existe une variation saisonnière dans le choix des caches et dans les patrons de sortie des caches. Les lézards se réfugient sous de plus gros rochers en été qu'au cours du printemps, peut-être pour se protéger de températures trop élevées pouvant être mortelles. Les mâles adultes utilisent des rochers de plus grandes dimensions que les femelles et les jeunes. Les patrons de sortie du couvert sont également différents entre les sexes. En effet, la probabilité de capturer une femelle adulte en milieu ouvert s'accroît pendant l'été, alors que les mâles s'exposent de moins en moins au cours de la saison. Les sorties en milieu ouvert augmentent également avec la quantité de pluie tombée le jour précédent. En conclusion, bien qu'il soit important pour *Elgaria coerulea* de rester sous couvert, des circonstances spécifiques, comme une température létale, la reproduction ou les précipitations, peuvent inciter les lézards à sortir de leurs caches.

Mots-clés : lézards, sélection de la température, caches, coût de la reproduction.

Nomenclature: Good, 1988.

Introduction

Key activities undertaken by an animal (*e.g.*, foraging, finding mates) can make it more susceptible to predation; therefore, the challenge is to minimise risk of predation while successfully completing those activities (Magnhagen, 1991). 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 non-random and is influenced

by factors such as humidity (Shoemaker *et al.*, 1992) and temperature (Huey *et al.*, 1989; Wehner, Marsh & Wehner, 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; Lopez, Salvador & Martin, 1998; Webb & Shine, 1998). Individuals also trade off the costs and benefits of remaining under cover. The decision to emerge from a retreat site and to risk predation is determined by factors such as temperature, precipitation, the need to satisfy other requirements (*e.g.*, basking, foraging, mating, gestation) and perceived threat (Avery, 1982; Huey, 1982; Jones, Waldschmidt & Potvin, 1987; Cooper, 1998; Lorenzon *et al.*, 1999; Martin & Lopez, 1999, 2001).

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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, Pianka & Hoffman, 1977; Bauwens, Hertz & Castilla, 1996). There is also variation in the time of the day that individuals emerge from a retreat site. Some emerge to bask in early morning (Stebbins & Barwick, 1968; Diaz, 1991; Bauwens, Hertz & Castilla, 1996). Others warm themselves under cover before emerging, possibly to avoid exposure to predators while basking or while still cool (Bustard, 1967; Schlesinger & Shine, 1994; Bauwens, Castilla & Mouton, 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 compared to smaller animals because of differences in surface-volume ratios (Porter *et al.*, 1973). This may explain the difference in basking patterns of juveniles and adults of the same species (Simon & Middendorf, 1976; Middendorf & Simon, 1988). In addition, breeding male lizards emerge from retreat sites earlier in the morning and bask more frequently than adult females or sub-adults (Van Damme, Bauwens & Verheyen, 1987; Bauwens *et al.*, 1990). This is likely the result of their need to defend territories, seek mates, and undergo spermatogenesis, all of which require surface activity (Licht, 1971; Vitt, 1973; Stamps, 1977).

Female reptiles also modify their emergence patterns during reproduction: reproductive females bask more frequently, for longer periods, and in more open positions than males and non-reproductive females (Luiselli, Capula & Shine, 1996; Krawchuk & 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 & 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 that pregnant females need to spend basking (Tosini & 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 (Schwarzkopf & 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 & Shine, 1992) and utilising habitat with more rock cover than non-gravid females (Charland & Gregory, 1995).

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

We are interested in whether this species exhibits age- and/or sex-related differences in retreat-site selection, emergence patterns, and anti-predator behaviour. In this paper we 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) generalize about the circumstances under which it is more favourable for an ectotherm to be in the open rather than hidden.

Methods

STUDY SPECIES AND STUDY SITE

Elgaria coerulea are viviparous lizards found in the western United States, reaching the northern limits of their distribution in southern British Columbia (Stebbins, 1966). Very little is known about their competitors and predators. At our study site, one potential competitor for food and retreat-sites is the western skink (*Eumeces skiltonianus*) (Rutherford & Gregory, in press). Other competitors may include common garter snakes (*Thamnophis sirtalis*) and long-toed salamanders (*Ambystoma macrodactylum*), which were found in early spring at some sites, although few were seen during the remainder of the summer. Potential predators include rubber boas (*Charina bottae*) and raptors such as the american kestrel (*Falco sparverius*). Rubber boas are nocturnal constrictors (Gregory & Campbell, 1984), and we did find small lizards in the stomach contents of rubber boas captured during our study. Raptors are diurnal foragers (Ehrlich, Dobkin & Wheye, 1988), hunting from poles, trees, and wires, and are commonly seen in the area. *Elgaria coerulea* carcasses have been found on nearby nest boxes (G. Burness, pers. comm.), presumably left by foraging raptors.

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

All study sites were located on the Aldridge formation, which is composed of siliciclastic and carbonate rocks of the Middle Proterozoic age (Brown, Doughty & Stinson, 1994). This formation is characterized by rusty weathering, caused by disseminated pyrite and pyrrhotite. The soil group classification is Eutric Brunisol, a coarse-textured soil with a pH generally above 6.0 (Canada Soil Survey Committee, 1978). The soil has a subhumid moisture regime, meaning that there can be varying periods of significant water deficits during the growing period, and a cold cryoboreal soil climate classification (120 to 180 growing season days over 5°C). The predominant available cover objects are rocks, which range in size from small pebbles to rocks greater than a metre across. There are few downed logs at any of the study sites. All sites have moderate slope (approximately 10%), and no major runoff occurs through any of the sites. The locations of the rocks and shrubs changed very little over the three years of the study.

The study sites are located in the Interior Douglas-fir biogeoclimatic zone. The most common shrub species are mallow nine bark (*Physocarpus malvaceus*), ocean spray (*Holodiscus discolor*), mock orange (*Philadelphus lewisii*), and snowberry (*Symphoricarpos albus*). The most common tree species are ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). Further discussion of the association between *Elgaria coerulea* and habitat structures can be found in Rutherford and Gregory (in press).

Mean daily maximum air temperatures from April to September 1996 ranged from 6.5°C to 35.0°C. Mean daily -0.6°C to 18.3°C (Environment Canada). Figure 1 provides a snapshot of available temperatures in two locations (unshaded open location and under a nearby rock) for three rock-open combinations. Rock sizes were a) thickness = 8 cm, area = 950 cm², b) thickness = 14 cm, area = 3,000 cm², and c) thickness = 18 cm, area = 1,900 cm². We took temperatures every 24 minutes from August 27 to September 5, 1996 using a Hobo temperature data logger. The voluntary maximum of 36°C for gravid *Thamnophis elegans* (Scott, Tracy & Pettus, 1982), a snake species that is syntopic with *Elgaria coerulea* at our study sites and often uses similar cover objects, was more often exceeded at the location in open than at the location under the rock.

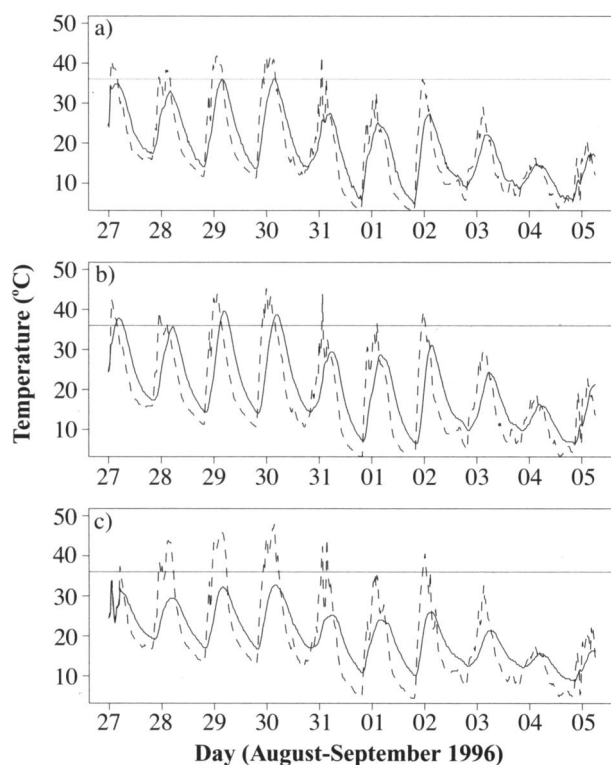


FIGURE 1. Temperatures at an open, unshaded site (dashed line) and under a nearby rock (solid line) at the Hydro study site, Creston Valley Wildlife Management Area, Creston, British Columbia for three rock-open combinations. Rock sizes were a) thickness = 8 cm, area = 950 cm², b) thickness = 14 cm, area = 3,000 cm², and c) thickness = 18 cm, area = 1,900 cm². Temperatures were taken every 24 minutes from August 27 to September 5, 1996 using a Hobo data logger. The voluntary thermal maximum (36°C) of a potentially comparable snake species, gravid *Thamnophis elegans* (Scott, Tracy & Pettus, 1982) is shown by the solid horizontal line.

MARK-RECAPTURE

On average, we visited the primary sites four times a year and the secondary sites two times a year over three years (1996-1998). Within each year, there was an average of 32 days and a minimum of 15 days between visits to the primary sites. The secondary site visits were an average of 39 days and a minimum of 14 days apart. All visits were made during the daytime. We 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.

We recorded the following data immediately upon hand capture of a lizard: 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 (other than their current cover object), distance to the nearest shrub > 1 m in base diameter, 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. We 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. We gave each rock a unique number to determine whether it was used by more than one lizard over time and to determine whether lizards showed site fidelity. We categorised time of day into four arbitrary categories: 06h00 to 10h00, 10h00 to 13h00, 13h00 to 16h00, and 16h00 to 20h00 (Mountain Standard Time).

We measured head width, snout-vent length (SVL), tail length, and mass of all lizards upon capture. We recorded tail-loss state (yes or no) based on the presence of a previous tail break. In lizards that had lost their tails we measured the distance from the vent to the tail break (middle length) and the distance from the break to the tail tip (regenerated length). We determined sex in adults only. Individuals with an SVL greater than 70 mm were classed as adults, as this is the minimum breeding size for females (Rutherford, 2002).

SPRINT SPEED

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

After all three races were completed, we measured snout-vent length (SVL), tail length, back leg length, and mass of the lizard. We calculated relative tail length by first calculating the quadratic 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 (Rutherford, 2002). We 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. We 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 dataset for Models 1, 2, 3, and 5 (Table I) included some repeat observations of 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. Their inclusion should not have biased the results unduly towards the behaviour of any one individual, and it provided the necessary sample size to draw conclusions from the data. Analyses to determine the factors predicting the probability of emergence (Model 4 in Table I) included only 1996 data. We used the precipitation (mm) that fell on the previous day as one of the independent variables.

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, White & Anderson, 1995). For linear regression models, the minimal adequate model was chosen on the basis of minimising Mallows' Cp (Mallows, 1973). Mallows' Cp is considered an approximation to AIC (Venables & Ripley, 1999) and is closely related to the adjusted R^2 (Draper & Smith, 1981). All statistical analyses were performed using *R* (Ihaka & Gentleman, 1996).

Results

CAPTURE SITE TEMPERATURE

Elgaria coerulea were found at a wide range of temperatures (range = 9.5-35.9), although 80% were found between 18°C and 29.9°C and 50% between 20.4°C 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 I; Figure 2). 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 ($F_{1,232} = 1.86$, $P = 0.17$; Figure 2). 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, which provided some shade from the direct sunlight. Capture-site temperature did not differ among juveniles, adult males, or adult females.

RETREAT-SITE SELECTION

Almost two-thirds (62%) of captured *Elgaria coerulea* were found under cover. Almost all those lizards used rocks as retreat sites (only 2% were captured under logs). Although rock thickness and rock area are related ($r = 0.37$, $N = 173$, $P < 0.001$), we tested them in separate models to determine whether they were influenced by different factors. Both rock thickness ($F_{1,171} = 5.35$, $P = 0.02$; Figure 3a) and rock area ($F_{1,171} = 12.05$, $P = 0.001$; Figure 3b) increased with date (Models 2a and 2b in Table I). Adult females and males selected rocks of similar thickness ($t = 0.68$, $df = 173$, $P = 0.50$), and juveniles selected the thinnest rocks ($t = 2.46$,

TABLE I. Tested models with terms retained in the best model are shown in italics. All terms are continuous except: open/cover (in the open or under cover), sex/age (newborn [only included in Model 1], juvenile, adult male, or adult female), time (06h00 to 10h00, 10h00 to 13h00, 13h00 to 16h00 or 16h00 to 20h00), and age/repro (juvenile, adult male, adult non-gravid female, or adult gravid female). Interactions terms are indicated with by (e.g. ground temperature by open/cover). 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. Date and ground temperature were tested in separate models because they were highly correlated ($R = 0.438$). The F or AIC column shows F values for all models except 4, where AIC is reported (F or AIC).

No.	Dependent variable	Terms	F or AIC	df	P	Adj. R^2
1	capture-site temp.	<i>ground temp.</i> , <i>open/cover</i> , (gr. temp. by open/cover), sex/age, ground temp. by sex/age, sex age by open/cover	64.31	3,232	<0.001	0.447
2a	rock thickness	<i>date</i> , <i>sex/age</i> , date by sex/age	3.90	3,171	0.01	0.048
2b	rock area	<i>date</i> , <i>sex/age</i> , date by sex/age	5.74	3,171	0.001	0.076
3	capture-site temp.	<i>ground temp.</i> , <i>rock thickness</i> or area, sex/age, ground temp. by sex/age, rock thick. or area by sex/age	54.15	2,172	<0.001	0.379
4	prob. (emergence)	<i>date</i> , <i>sex/age</i> , <i>time</i> , date by sex/age, (precipitation), tail loss state, date by time, date by precipitation, time by sex/age, tail loss by sex/age	62.4	66		
5	distance from rock	<i>time</i> , <i>sex/age</i> , time by sex/age, date, tail loss state, date by time, date date by sex/age, tail loss state, by sex/age	2.24	11,215	0.013	0.057
6	sprint speed	<i>age/repro.</i> , <i>rel. tail</i> , site, chamber temp., rel. SVL, rel. back leg, age/repro. by rel. SVL, age/repro. by rel. tail, age/repro. by rel. leg	8.13	4,79	<0.001	0.256

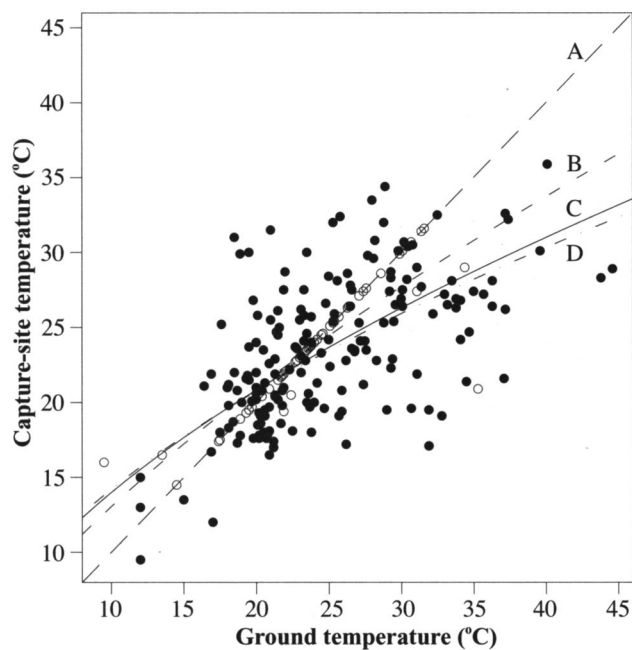


FIGURE 2. Open ground temperature ($^{\circ}\text{C}$) versus capture-site temperature ($^{\circ}\text{C}$) for *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. Regression lines are shown for the (A) ground temperature equal to capture-site temperature, (B) lizards captured in the open (open circles) ($N = 57$), (C) total data set ($N = 236$), and (D) lizards captured under cover (closed circles) ($N = 179$). Lines B-D are curved because the tested relationships were between log-transformed variables.

$df = 173$, $P = 0.02$; Figure 3a). 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 I). Rock area did not affect capture-site temperature.

EMERGENCE FROM RETREAT SITES

The percentage of lizards in the open varied with date for each of the sex/age classes ($\chi^2 = 5.91$, $df = 2$, $P = 0.05$; Figure 4a; Model 4 in Table I). Adult males were in the open more often in the spring (April-May) compared to the summer (June-September). In contrast, juveniles and adult females were more often in the open in summer than in spring.

Lizards were more likely to be in the open from 13h00 to 16h00 than any other time of day ($N = 28$, 53.6% in the open). They were equally likely to be in the open in early morning (06h00 to 10h00) and late afternoon (16h00 to 20h00; $N = 11$, 36.4% for both time periods). The fewest lizards were seen in the open in mid-morning (10h00 to 13h00; $N = 26$, 23.1%)

The probability of capturing a lizard in the open tended to increase with the amount of precipitation that fell on the previous day ($\chi^2 = 2.05$, $df = 1$, $P = 0.15$; Figure 4b; Model 4 in Table I). This term was retained in the next-best model, which was only marginally worse.

PROXIMITY TO COVER

Distance to the nearest rock differed for the time-of-day categories for each of the sex/age categories ($F_{6,215} = 2.93$, $P = 0.01$; Model 5 in Table I; Figure 5). Juveniles were farthest from rocks in late morning (10h00 to 13h00) and

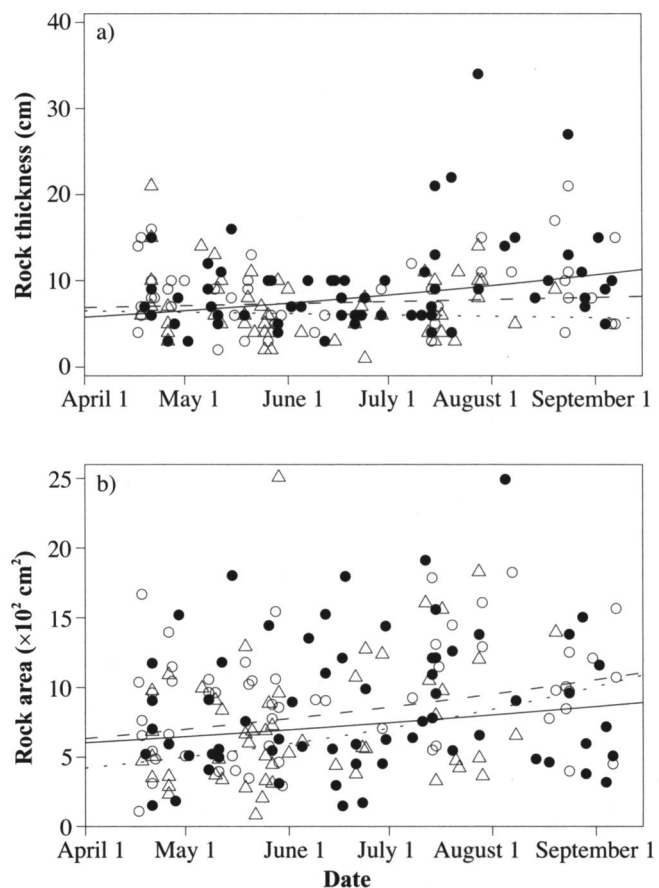


FIGURE 3. Date versus a) rock thickness and b) rock area. Regression lines are shown for juveniles (triangle, short-dashed line), adult males (open circle, long-dashed line), and adult females (closed circle, solid line) *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998.

closest to rocks in early morning (06h00 to 10h00). Adult males were farthest from rocks in late afternoon (16h00 to 20h00) and closest to rocks in late morning (10h00 to 13h00). Adult females were farthest from rocks in early morning (06h00 to 10h00) and closest to rocks in early afternoon (13h00 to 16h00).

SPRINT SPEED

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

Discussion

This study showed that although remaining hidden is believed to be of primary importance to *Elgaria coerulea*, their cover-use behaviour is influenced by time of year, time of day, precipitation, 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 ($< 15 \text{ cm}$), unshaded rocks, used cliff-top crevices

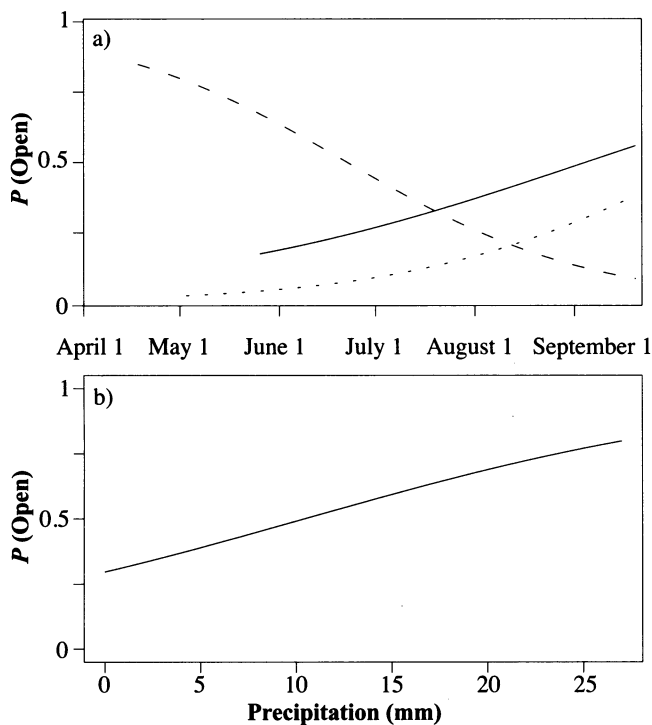


FIGURE 4. Factors affecting the probability of being in the open for *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. a) Date versus probability of being in the open for sex/age categories (juveniles [short-dashed line], adult males [long-dashed line], and adult females [solid line]). b) Precipitation (mm) from 24 hours prior to capture versus probability of being in the open.

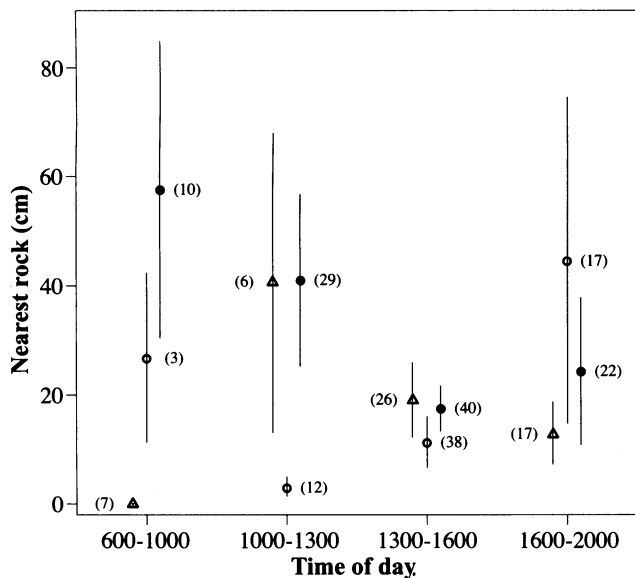


FIGURE 5. Mean distance to the nearest rock (cm) \pm SE for four time-of-day categories. Plotted are juvenile (triangle), adult male (open circle), and adult female (closed circle) *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1996-1998. Sample sizes are shown in parentheses.

exposed to the afternoon sun, and avoided cooler crevices (Webb & Shine, 1998). During the summer, they avoided thin, exposed rocks, which became too hot ($> 40^{\circ}\text{C}$). Some snakes used thicker, more shaded rocks, and others abandoned the rock outcrop and moved to the woodland. A simi-

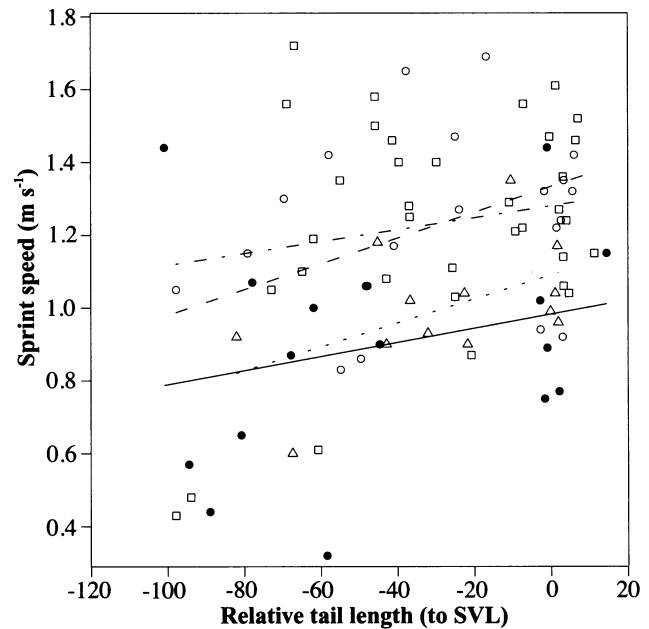


FIGURE 6. Sprint speed (m s^{-1}) versus relative tail length (to SVL) for *Elgaria coerulea* from CVWMA, Creston, British Columbia collected in 1997-1998. Four age/reproductive categories are shown: juveniles (triangle; short dashes), adult males (square; long dashes), adult non-gravid females (open circle; short-long dashes), and adult gravid females (closed circle; solid line).

lar pattern may be the case in male *Elgaria coerulea*, as fewer were captured in the summer months than in spring (Rutherford, 2002).

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 in California indicated that garter snakes (*Thamnophis elegans*) selecting thin rocks (< 20 cm) would die of heat stress in midafternoon or 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 body temperature (T_b). Snakes selecting rocks of intermediate size would never overheat and would achieve preferred T_b for long periods.

The probability of capturing a lizard in the open increased with the amount of precipitation that fell the previous day. This may indicate that, following a rainfall, lizards are more active and thus more likely to be captured in the open. Increased activity associated with wetter conditions has been reported in other lizard species (Stamps, 1976; Crowley, 1987; Jones, Waldschmidt & Potvin, 1987). There are several possible explanations: lizards may be able to move about because they are not concerned about dehydration, or they may be responding to the increase in food availability often associated with precipitation (Smith, 1996; Lorenzon *et al.*, 1999).

There is also seasonal and daily variation in emergence patterns in *Elgaria coerulea*. The probability of being captured in the open was highest in early afternoon (13h00 to 16h00), followed by early morning (06h00 to 10h00) and late afternoon (16h00 to 20h00). The fact that the highest percentages were captured in the open in the afternoon sug-

gests 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 & Whitaker, 1978; Schlesinger & Shine, 1994; Bauwens, Castilla & Mouton, 1999). Afternoon activity also might be a response to lower predation pressure by foraging raptors at this time of day. As most raptors are visual hunters (Ehrlich, Dobkin & Wheye, 1988), emergence in the late afternoon, when there is less light, might help *Elgaria coerulea* 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 remained close to cover from 13h00 to 16h00. 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 (06h00 to 10h00 and 10h00 to 13h00), whereas males were farthest from cover in the afternoon (16h00 to 20h00). This variation might be a reflection of different foraging strategies, but data on foraging are lacking.

We detected age-related variation in retreat-site selection. Adult males and females selected thicker rocks than juveniles, with no difference between the first 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. Male recapture patterns suggest that during the summer they occupy habitats different from those of females (Rutherford, 2002). If these habitats differ in their rock structure, this may explain the differences in rock thickness and area between males, females, and juveniles. An intensive movement study is necessary to address this issue.

There was also age- and sex-related variation in emergence patterns. For males, the probability of being found in the open was highest in spring and declined throughout the summer. Changes in emergence patterns based on reproductive cycles have been shown for male lizards (Van Damme, Bauwens & Verheyen, 1987; Bauwens *et al.*, 1990; Firth & Belan, 1998). Spermatogenesis is known to occur in *Elgaria coerulea* in late fall and early spring (Vitt, 1973). Individuals likely accomplish spermatogenesis and find mates by modifying their emergence patterns and exposing themselves to increased predation pressure. Once this is completed they spend less time in the open.

Accomplishing gestation without modifying emergence patterns also is not possible. We 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 (Van Damme, Bauwens & Verheyen, 1987; Luiselli, Capula & Shine, 1996; Krawchuk & 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 (23 cm on average; Rutherford &

Gregory, in press), demonstrating their reliance on crypsis rather than sprinting as an anti-predator defence. Given this strategy, we 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 an 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 since parturition occurs at this time of year. There is typically a month between parturition and hibernation, and neonates do not retain yolk at parturition (Stewart & Castillo, 1984). 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* changed in response to their reproductive cycle, just as gestation significantly altered emergence patterns of females. These results suggest that the benefits of emerging from cover outweigh the costs in female, and 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 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 whether gravid females incur costs as a result of their change in cover-use behaviour during gestation.

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