Ecology of the Introduced European Wall Lizard, *Podarcis muralis*, near Victoria, British Columbia

by

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Abstract

Determining the past, present and future effects of alien species on native biodiversity is a globally recognized problem. The Wall Lizard, *Podarcis muralis,* was introduced to Vancouver Island from Europe in 1970. To assess potential competitive interactions with the native Northern Alligator Lizard (*Elgaria coerulea*), I investigated several aspects of *P. muralis* ecology. Diffusion along manmade corridors (e.g. roads and powerlines) and human-facilitated jump dispersal are contributing to range expansion; three separate populations currently exist. Reproductive output of *P. muralis* was not affected by amount eaten while gravid, but feeding level and incubation temperature affected offspring phenotypes. In comparative tests of locomotor performance, *P. muralis* was faster than *E. coerulea,* but only at moderate temperatures. I found no effect of *P. muralis* odour on *E. coeruela* behaviour, but *E. coeruela* avoided cover objects that housed *P. muralis*. These two species use similar habitats, but were found on different substrates and mesoslopes. Based on the results of these experiments there is a potential for competition between these two lizard species.

Table of Contents

Page

Title Page i

Abstract ii

Table of Contents iii

List of Tables v

List of Figures vi

General Introduction 1

Chapter 1: *Podarcis muralis* on Vancouver Island

Introduction 6

Methods 7

Results and Discussion 8

Chapter 2: Life-History Characteristics of *Podarcis muralis* on Vancouver Island

Introduction 20

Methods 24

Results 26

Discussion 30

Chapter 3: Locomotor Performance of *Podarcis muralis* and *Elgaria coerulea*

Introduction 39

Methods 40

Results 43

Discussion 51

Chapter 4: Habitat Use of *Podarcis muralis* and *Elgaria coerulea*

Introduction 55

Methods 56

Results 57

Discussion 59

Chapter 5: Behaviour of *Elgaria coerulea* and *Podarcis muralis* in Paired Encounters

Introduction 65
Methods 67
Results 71
Discussion 77
Conclusions 82
Literature Cited 85

List of Tables

Page

Table 1.1 Collection of anecdotal sighting information produced 10 locations where *Podarcis muralis* were likely to be found and 3 where presence was unlikely. Field surveys either confirmed (Yes) or were unable to confirm (No) *Podarcis muralis* presence at these sites. Field surveys were not undertaken at five of the sites (*); hence no information is available. 11

Table 1.2 Distances between the original release site and two satellite populations calculated in kilometers by air and by the most direct road route. 13

Table 2.1 Partial correlations (controlling for SVL) between female and clutch characteristics. 29

Table 3.1 Results of repeated measures ANOVA comparing maximum velocity of *Podarcis muralis* and *Elgaria coerulea* at three temperatures (high = 33°C; room = 22°C; low = 11°C). 46

Table 3.2 Results of one-way ANOVA comparisons of maximum velocity between species at low (11°C), room (22°C) and high (33°C) temperatures and between temperatures for each species (Pm = *Podarcis muralis*, Ec = *Elgaria coerulea*). 48

Table 4.1 Mean values and standard deviations for habitat variables collected at *Podarcis muralis* (Pm), *Elgaria coerulea* (Ec) and associated random locations. Significant comparisons between Pm and Ec sites (independent samples t-test, $P < .05$; superscript circle), Pm and Pm random locations (paired t-test, $P < .05$; superscript triangle), and Ec and Ec random locations (paired t-test, $P < .05$; superscript square) are summarized. 58

List of Figures

Page

Fig. 1.1 Newspaper advertisement placed in the Saanich News July 31 and August 2, 2002. 9

Fig. 1.2 Locations of three confirmed *Podarcis muralis* populations. Location **A** is the original release site, **B** is located at Stellys Cross Road and Wallace Drive, and **C** is located at Clinton Place east of the Vancouver Island Regional Correctional Centre on Wilkinson Road. 12

Fig. 1.3 Overhead photo of *Podarcis muralis* original release site and surrounding area. The location of an apparantly isolated population of *Podarcis muralis* at Tod Inlet in Gowland-Tod Provincial Park is indicated by **A**. The location of original introduction site at the end of Rudy Road is indicated by **B**. The red line indicates where *Podarcis muralis* were found along the powerline and east ditch of Wallace Drive. **C** indicates another *Podarcis muralis* sighting, the powerline between the red line and point **C** was not searched therefore presence of lizards was not confirmed along this corridor. 14

Fig. 1.4 **A** marks the location of a veterinary clinic at the corner of Stellys Cross Road and Wallace Drive. Many *Podarcis muralis* of all size groups have been observed around the clinic's main building, outbuildings and ditches. Further searches (red line) indicate that the lizards have spread along the north ditch of Stellys Cross Road, east ditch of Tomlinson Road, both sides of Holm Road and the west ditch of Wallace Drive (north of Stellys intersection). Reliable information indicates *Podarcis muralis* are established at **B** (the Saanich Fairgrounds) and in the residential areas of Brentwood Bay (further west along Stellys Cross Road), although neither was confirmed. 15

Fig. 1.5 The blue diamond indicates a confirmed *Podarcis muralis* population on a cul de sac (Clinton Place) in a in a residential neighborhood. Individuals were first observed in 2000 and have been seen on the sides of houses, on decks and along driveways. 17

Fig. 2.1 Boxplots of female A) SVL, B) mass and C) body condition from two feeding treatments. 27

Fig. 2.2 Dates of clutch deposition for two experimental feeding treatments (squares - high feeding, circles – low feeding). Experiment took place in 2002. 28

Fig. 2.3 Effect of incubation treatment (high or low temperature) on the length of incubation period in days. 31

Fig. 2.4 Effect of incubation temperature on A. *Podarcis muralis* hatchling SVL (mm) and B. *Podarcis muralis* hatchling mass (g). 32

Fig. 2.5 Effect of maternal feeding regime on the mass of wall lizard hatchlings incubated at a relatively low temperature (26°C). 33

Fig. 3.1 Linear regression of *Podarcis muralis* snout-vent length (mm) versus maximum velocity (m/ s) with coefficients of determination (Rsq). Three temperature treatments were analyzed: low (squares; short dashes; $P = .1658$), room (asterisks; solid line; $P = .6299$) and high (triangles; long dashes; $P = .6796$). 44

Fig. 3.2 Linear regression of *Elgaria coerulea* snout-vent length (mm) versus maximum velocity (m/ s) with coefficients of determination (Rsq). Three temperature treatments were analyzed: low (squares; short dashes; *P* 45

= .4782), room (asterisks; solid line; $P = .4434$) and high (triangles; long dashes; $P = .4193$).

Fig. 3.3 Estimated marginal means velocity for each lizard species (*Podarcis muralis* - open circles; *Elgaria coerulea* - closed circles) at three temperatures (low = 11°C, room = 22°C, high = 33°C). Means labeled with the same letter are not statistically different, while those with different labels are. 47

Fig. 3.4 Maximum velocity (m/s) versus snout-vent length (mm) at room temperature (22°C) for *Podarcis muralis* male (circles; long dash) and female (squares; short dash). 49

Fig. 3.5 Maximum velocity (m/s) versus snout-vent length (mm) at room temperature (22°C) for *Elgaria coerulea* males (circles; long dashes) and females (squares; short dashes). 50

Fig. 4.1 Number of *Podarcis muralis* (Pm; black bars) and *Elgaria coerulea* (Ec; white bars) sightings at various locations (on log, on rock, on cement, on dirt, on moss, on wood, on dirt/rock, in dead vegetation, in vegetation, under rock). Chi-square tests analyzed three categories created by grouping similar substrate categories. These groupings were: 1)on log, on rock, on cement, on moss, on wood, 2) on dirt, on dirt/ rock, on dead vegetation and 3) in vegetation, under rock. 60

Fig. 4.2 Number of *Podarcis muralis* (Pm; black bars) and *Elgaria coerulea* (Ec; white bars) sightings at various mesoslope locations (crest, upper, middle, lower, toe, level). Chi-square tests analyzed three categories created by grouping similar mesoslope categories. These groupings were: 1) crest, upper, 2) middle and 3) lower, toe, level. 61

Fig. 5.1 Experiment 3 cage set up. A *Podarcis muralis* held captive in a tube, or a control tube (empty tube), was placed under one of the two cover objects. 70

Fig. 5.2 Proportion of time (total time minus time spent trying to escape) that *Elgaria coerulea* spent on areas scented with *Podarcis muralis* odour vs. unscented. Boxes represent the interquartile range, the vertical lines extend to the highest and lowest values and the horizontal black lines indicate the median (n = 9). 72

Fig. 5.3 Retreats as a proportion of total approaches for each species (Pm = *Podarcis muralis*, Ec = *Elgaria coerulea*, neither = neither species retreated). Vertical lines are approximate 95% confidence limits. 74

Fig. 5.4 Approaches by each species as a proportion of total approaches (Pm = *Podarcis muralis*, Ec = *Elgaria coerulea*). Vertical lines are approximate 95% confidence limits. 75

Fig. 5.5 Total time that each *Podarcis muralis* (Pm) and *Elgaria coerulea* (Ec) spent under cover. Boxes represent the interquartile range, the vertical lines extend to the highest and lowest values and the horizontal black lines indicate the median (n = 9). 76

Fig. 5.6 Proportion of observations of *Elgaria coerulea*, relatively close to, or far from, a *Podarcis muralis* individual held captive in a tube (white bars) or an empty tube (black bars). Observations of basking are also shown (n = 9). 78

General Introduction

Plants, animals and microbes are being transported from their native ranges and becoming established as alien or invasive species at an ever-increasing rate (Peterson and Vieglais 2001). Accidental movement and subsequent establishment of organisms commonly occurs with the transportation of commercial goods, while intentional movement of organisms occurs through activities such as agriculture and the pet trade. Consequences include negative impacts on the economy, human health and biodiversity (Davis 2003). Alien species rank second, behind habitat degradation and destruction, in the top five threats to North American biodiversity (Wilcove et al. 1998).

Alien species are those introduced into new habitats through human intervention (Sandlund et al. 1999). When alien species (also known as introduced, non-native or exogenous) become a threat to native biological diversity, these species are considered invasive or aggressive (Sandlund et al. 1999). In situations in which the direct cause of species extinction can be identified, invasive species are the number one cause (McNeely 1999). Crooks and Soulé (1999) predict that invasive species will surpass habitat loss and fragmentation as the leading cause of loss of biodiversity for two reasons: 1) the habitat available for alteration or destruction is rapidly declining; and 2) altered habitats are especially vulnerable to invasion by non-native species. Invasive species often do best in urban environments due to disturbance of habitat and the subsequent creation of niches (McNeely 1999).

Once an invasive species has become established, there may be a lag time before explosive population growth and range expansion occur. Changes in environmental factors (e.g. habitat and food resources, climate, dispersal vectors, interspecific interactions and intraspecific interactions) and genetic factors (e.g. local genetic adaptation) may cause an increase in alien species' fitness that is followed by an increase in population growth rate (Crooks and Soulé 1999). Data on the life-history characteristics of invasive species help explain such population and range expansion, and allow identification of effects on native species and development of management strategies.

Even without explosive population growth, invasive species can cause population declines, extirpations of native species, and restructuring of natural ecosystems (Williamson 1996). Invasive species can cause these effects through predation, competition, the introduction of pathogens and parasites, homogenization of native species' genetic structure, and loss of genes through interbreeding of native and introduced species (Williamson 1996, Hindar 1999). Competitive effects could be indirect, through competition for resources such as food and space, or direct, through interspecific aggression.

Globally, most invasive species are plants, but examples of invasive species from virtually every taxonomic group can be found. The subject of this thesis is the Wall Lizard, *Podarcis muralis*, a species native to Europe and introduced in North America. *Podarcis muralis* is currently found in two American states, Ohio (Vigle 1977, Hedeen 1984) and Kentucky (Draud and Ferner 1994), and at one site in Canada, southern Vancouver Island, British Columbia (Allan et al. 1993). The Kentucky populations were created when homeowners took lizards from Cincinnati, Ohio and released them in their gardens (Deichsel and Gist 2001). Italian wall lizards, *Podarcis sicula*, also are established at two sites in the USA, Long Island, New York (Gossweiler 1975) and Topeka, Kansas (Deichsel and Miller 2000). Both species of lizard appear to be restricted to urban or human-altered habitats in North America; for example, they are both commonly found on trash and wood piles, cement and brick walls, roadsides and railways.

Currently, over 6 km^2 is inhabited by wall lizards in Cincinnati (Deichsel and Gist 2001). None of the three native lizard species from this region are found in this area of Cincinnati, so that interspecific competition between *Podarcis muralis* and native lizards has not been observed (Hedeen 1984). However, on Vancouver Island, *Podarcis muralis* has been introduced into areas occupied by the native Northern Alligator Lizard (*Elgaria coerulea*), raising the possibility of competitive interactions. This possibility is reinforced by apparent similarities in habitats used by wall lizards and alligator lizards. As the range of *Podarcis muralis* expands on Vancouver Island, potential effects on *Elgaria coerulea* will increase as well.

The impact of *Podarcis muralis* on *Elgaria coerulea* might be indirect, through competition for resources such as food, or direct, through interspecific aggression. Boag (1973) studied the spatial relationships and behaviour of an Italian population of *Podarcis muralis* and found that both males and females maintained and defended territories through threatening behaviours. The population was composed of both resident individuals that maintained territories through displays of dominance, and non-resident individuals or transients that moved through the habitat and settled whenever territories became available (Boag 1973).

High levels of intraspecific aggression have been documented in both native and introduced populations of *Podarcis muralis.* Potentially these behaviours could occur on an interspecific level on Vancouver Island if introduced populations of *Podarcis muralis*, now or in the future, overlap spatially with native lizard populations. *Elgaria coerulea* have been shown to have high fidelity to retreat sites and move only short distances from these sites (Rutherford and Gregory 2003a). If aggression by *Podarcis muralis* results in a reduction in the availability of suitable retreat sites for *Elgaria coerulea*, negative effects, such as increased predation on *Elgaria coerulea*, would likely result, causing subsequent reduction in both abundance and distribution.

The ability of *Podarcis muralis* to achieve high densities and population growth rate relative to *Elgaria coerulea* could exacerbate these potential negative effects. *Podarcis muralis* have a clumped distribution, in which breeding colonies of relatively high lizard density are centred on areas of preferred habitat (Brown et al. 1995). Population densities of wall lizards have been estimated to range from 100 individuals/ hectare in Italy (Dexel 1984) to over 600 individuals/ hectare in Cincinnati (Kwiat and Gist 1987). By comparison, population densities of *Elgaria coerulea* in California have been estimated at 95-111 individuals/ hectare (Stewart 1985).

Podarics muralis and *Elgaria coerulea* differ in their reproductive modes and strategies. *Podarcis muralis* is oviparous and individual females can deposit from 1-3 clutches per active season (Kwiat and Gist 1987, Ji and Brana 2000). *Elgaria coerulea*, however, are viviparous and produce only a single litter in any year. The possibility of multiple clutches per season presumably allows *Podarics muralis* to achieve the densities mentioned above and gives them the flexibility needed to respond to variations in the availability of food resources needed for reproduction.

The broad aims of my thesis are to document the establishment and spread of *Podarcis muralis* on the Saanich Peninsula of Vancouver Island and to describe aspects of the life history and ecology of this species that are pertinent to potential interactions with *Elgaria coerulea*. In the first chapter I document the history of the introduction and identify patterns of spread and contributing factors to range expansion. Next, I test for the influence of capital versus income breeding on reproductive output of wall lizards, as well as the effect of incubation temperature on offspring phenotype. I also compare the locomotor performance and habitat use of *Podarcis muralis* and *Elgaria coerulea*. Finally in Chapter 5, I make direct tests of behavioural interactions between the two species.

Chapter 1

Podarcis muralis on Vancouver Island

Introduction

The first known introduced population of *Podarcis muralis* to become established in North America was in Cincinnati, Ohio. In September 1951 or 1952, a resident there released approximately 10 European wall lizards from northern Italy (Deichsel and Gist 2001). Since then *Podarcis muralis* has become firmly established in the Cincinnati area and population densities of 600 individuals/ hectare are estimated where preferred habitat is present (Kwiat and Gist 1987). Dispersal of this lizard has occurred primarily through diffusion (along railways) and secondarily through jump-dispersal (human capture and release, creating satellite populations; Hedeen and Hedeen 1999). Movement along railways and rights-of-way has been observed to produce higher dispersal rates compared to this lizard's spread through residential and commercial areas (Hedeen and Hedeen 1999). In Cincinnati, railways appear to provide a continuous corridor of favourable habitat that is aiding the dispersal of *Podarcis muralis* (Hedeen and Hedeen 1999). In addition, a set of satellite populations south of the Ohio River in Kentucky were created by homeowners releasing *Podarcis muralis* into their gardens (Draud and Ferner 1994, Deichsel and Gist 2001).

Comparisons of temperature and precipitation data from the source region of *Podarcis muralis* in Italy and Cincinnati reveal similar climatic regimes (Hedeen 1984). This suggests that *Podarcis muralis* was probably somewhat "pre-adapted" to the environmental conditions of Cincinnati (Hedeen 1984). Within the native range of *Podarcis muralis* in Europe, this lizard is commonly associated with anthropogenic landscapes and is believed to have spread from dry, rocky regions into its current range subsequent to human agricultural, industrial and residential developments (Hedeen 1984). Thus, Hedeen (1984) suggests that the success of *Podarcis muralis* in Cincinnati can be attributed to the fact that these lizards were already adapted to survival amongst human developments in a similar climate. Furthermore, establishment and spread of a similar species, *Podarcis sicula*, in Long Island, New York may have been facilitated by a lack of natural predators (Gossweiler 1975).

A third North American population of *Podarcis muralis* has become established on the Saanich peninsula near Victoria, British Columbia. Twelve animals were released in 1970 when a private zoo located on Rudy Road closed (Deichsel and Schweiger *in press*). I undertook an analysis of the wall lizard populations around Victoria, combining the original release site, confirmed sites and suspected sites to shed light on the range, distribution and dispersal pattern of this lizard in this area.

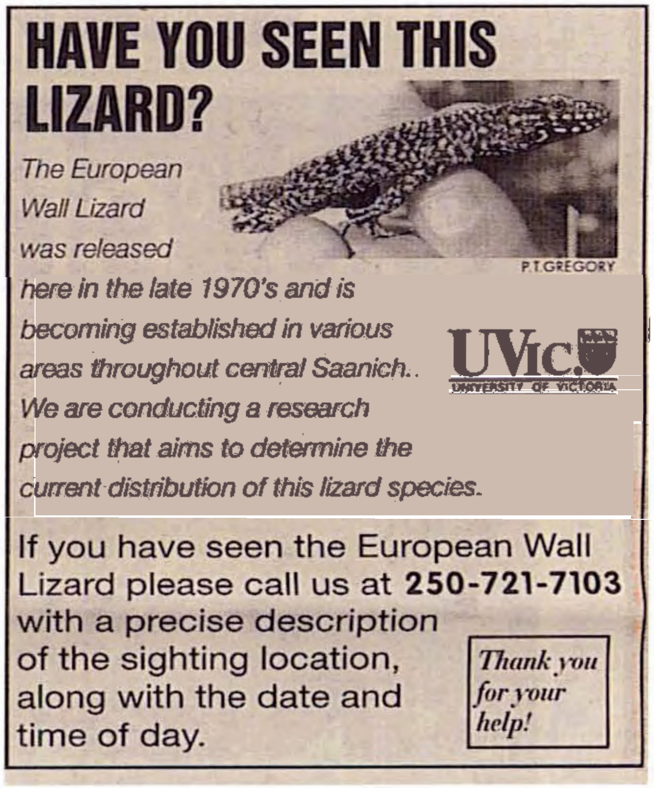
Methods

I collected anecdotal sighting information and did field searches to determine the current distribution of *Podarcis muralis* on Vancouver Island. I contacted Ministry of Water, Land and Air Protection (WLAP) staff to request sighting data and placed a newspaper advertisement to facilitate the gathering of sighting information from the public. The advertisement appeared in the Saanich News in the July 31/ 02 and August 2/ 02 issues. Potential *Podarcis muralis* locations were categorized as likely or unlikely to have populations. The criteria used (in order of importance) were location, number of sightings/ accuracy of lizard description and relative confidence of Ministry of WLAP staff. Human-altered locations versus natural or minimally disturbed locations, and sites with a greater total number of sightings/ accurate *Podarcis muralis* descriptions, were considered more likely to contain *Podarcis muralis*. A site also was considered more likely to contain *Podarcis muralis* when Ministry of WLAP staff were confident in the sighting information, usually through personal experience or a trusted source. I used the combined results from all three criteria to designate each site as likely or unlikely to be populated by *Podarcis muralis*.

I undertook field searches at several of the sites likely inhabited by *Podarcis muralis* and assigned a rating of confirmed, unable to confirm, or no information to each site. Repeated searches during optimal weather focused on habitat features apparently important to lizards, for example, sunny open areas with cover objects. When presence was confirmed, I searched the surrounding areas to determine the extent of *Podarcis muralis* expansion.

Results and Discussion

Ministry of WLAP staff, who had been compiling and investigating sightings reported to their office, provided a list of 11 sites (D. Fraser *pers. comm.*). Two additional sightings were obtained from members of the public who had an interest in the research; I was connected with them through contacts in the UVic biology department. The newspaper advertisement (Fig. 1.1) resulted in only one response; I



HAVE YOU SEEN THIS LIZARD?

P.T.GREGORY

The European Wall Lizard was released here in the late 1970's and is becoming established in various areas throughout central Saanich.. We are conducting a research project that aims to determine the current distribution of this lizard species.

UVic UNIVERSITY OF VICTORIA

If you have seen the European Wall Lizard please call us at **250-721-7103** with a precise description of the sighting location, along with the date and time of day.

Thank you for your help!

Fig. 1.1 Newspaper advertisement placed in the Saanich News July 31 and August 2, 2002.

believe this method was unsuccessful due to the advertisement's location in the paper, which was amongst business advertisements. Placement in the classified advertisements or as a separate news piece would have highlighted the information better and attracted more readers to the details of the request. An alternative would have been to place posters in neighborhoods (e.g. at mailboxes and bulletin boards) where *Podarcis muralis* were suspected to be present, thereby increasing exposure to members of the public who have a relatively high potential for contact with the lizard.

Of the 13 sites, 10 were categorized likely and 3 unlikely to have *Podarcis muralis* populations (Table 1.1). Between Apr. – Sept. 2002 and Apr. – May 2003, I searched eight sites and confirmed populations at six. The sites were grouped into three main areas: the original release site, Stellys Cross Road and Wallace Drive, and Clinton Place (Fig. 1.2). The habitats between the three sites did not contain *Podarcis muralis*; the distances between them were calculated by air and by road (Fig. 1.2, Table 1.2).

The latter two sites appeared to be satellite populations created by the collection and movement of lizards over relatively long distances (jump dispersal). Additional searches around the original release site and the Stellys-Wallace site indicated that the lizards were spreading along ditches, fence lines and power lines (Figs. 1.3 and 1.4). This diffusion has occurred over several generations and likely will continue along roads, power lines etc. until some type of barrier is reached (e.g. forest, fields).

Table 1.1 Collection of anecdotal sighting information produced 10 locations where *Podarcis muralis* were likely to be found and 3 where presence was unlikely. Field surveys either confirmed (Yes) or were unable to confirm (No) *Podarcis muralis* presence at these sites. Field surveys were not undertaken at five of the sites (*); hence no information is available.

SITE	**LIKELY**	**PRESENCE CONFIRMED**
1	end of Rudy Rd. (original introduction site)	Yes
2	Stellys Cross Rd. and Wallace Dr. (veterinarian clinic and surrounding area)	Yes
3	area around water filled quarry pit (on Wallace Dr. just south of Benvenuto Rd.)	Yes
4	rock walls in front of horse barns on Saanich Fairgrounds	*
5	powerline on Department of National Defense test grounds	Yes
6	Clinton Pl. (residential areas near Wilkinson Rd. jail)	Yes
7	residential areas of Brentwood Bay	*
8	Tod Inlet	Yes
9	Keetings Elementary School	*
10	Triangle Mountain	*
	UNLIKELY	
11	Christmas Hill	No
12	Finlayson Rd. near Quadra	*
13	north side of Bear Hill	No

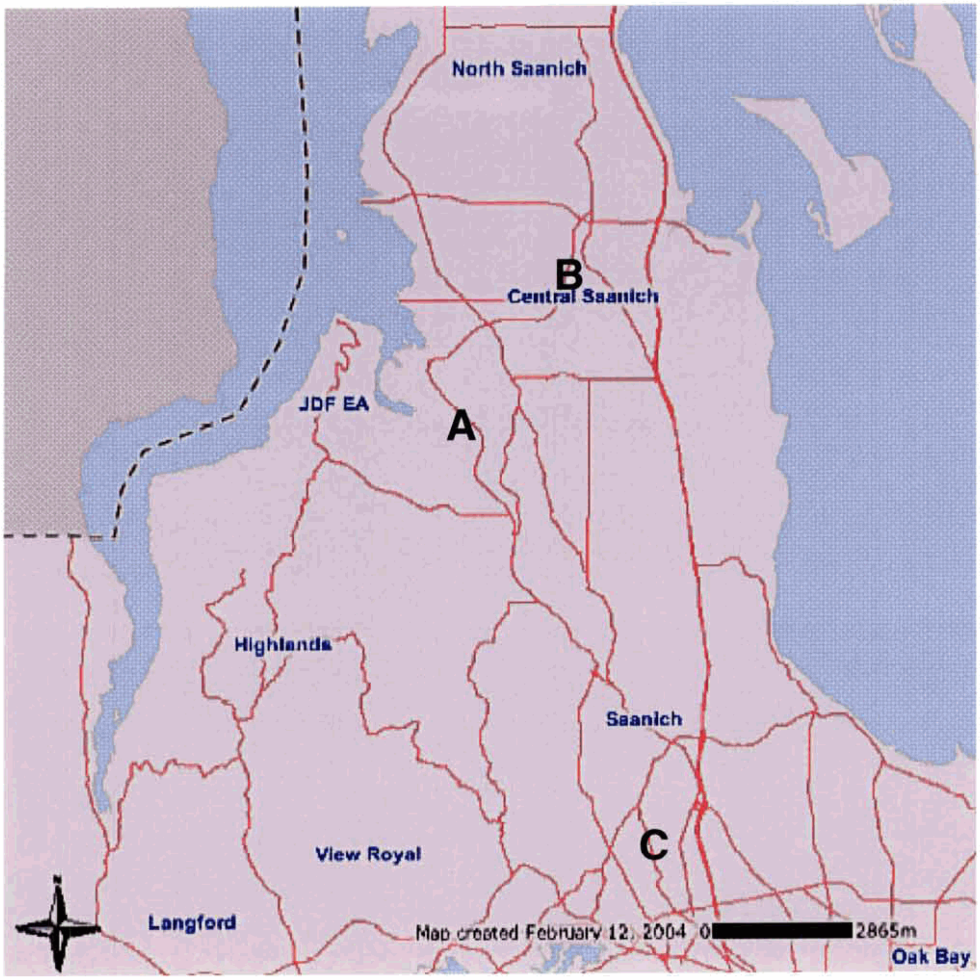


Fig. 1.2 Locations of three confirmed *Podarcis muralis* populations. Location **A** is the original release site, **B** is located at Stellys Cross Road and Wallace Drive, and **C** is located at Clinton Place east of the Vancouver Island Regional Correctional Centre on Wilkinson Road.

Table 1.2 Distances between the original release site and two satellite populations calculated in kilometers by air and by the most direct road route.

		Stellys Cross Road and Wallace Drive	Clinton Place
Original Release Site	distance by air (km)	3.7	9.5
	distance by road (km)	5.4	11.8

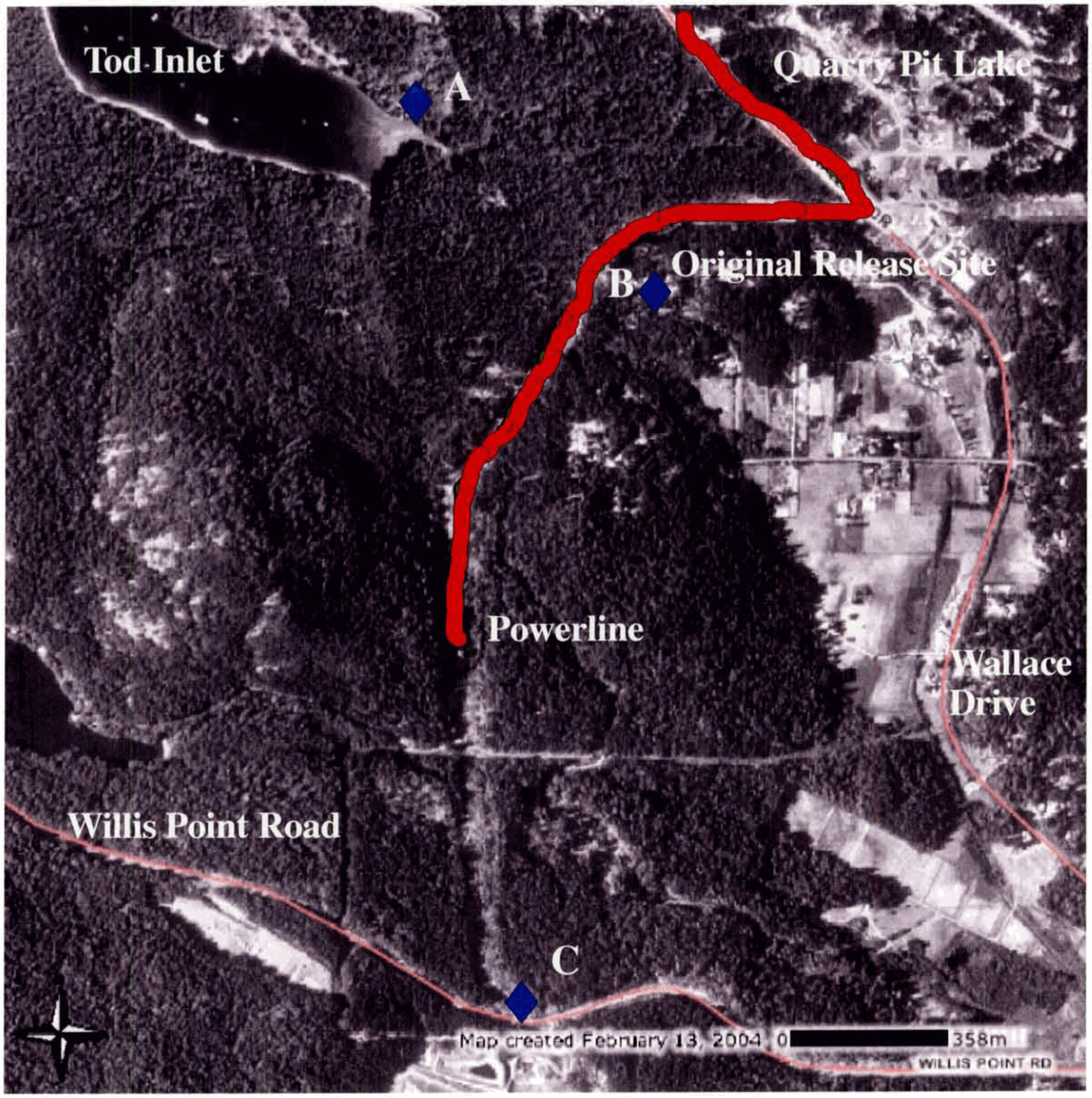


Fig. 1.3 Overhead photo of *Podarcis muralis* original release site and surrounding area. The location of an apparantly isolated population of *Podarcis muralis* at Tod Inlet in Gowland-Tod Provincial Park is indicated by **A**. The location of original introduction site at the end of Rudy Road is indicated by **B**. The red line indicates where *Podarcis muralis* were found along the powerline and east ditch of Wallace Drive. **C** indicates another *Podarcis muralis* sighting, the powerline between the red line and point **C** was not searched therefore presence of lizards was not confirmed along this corridor.

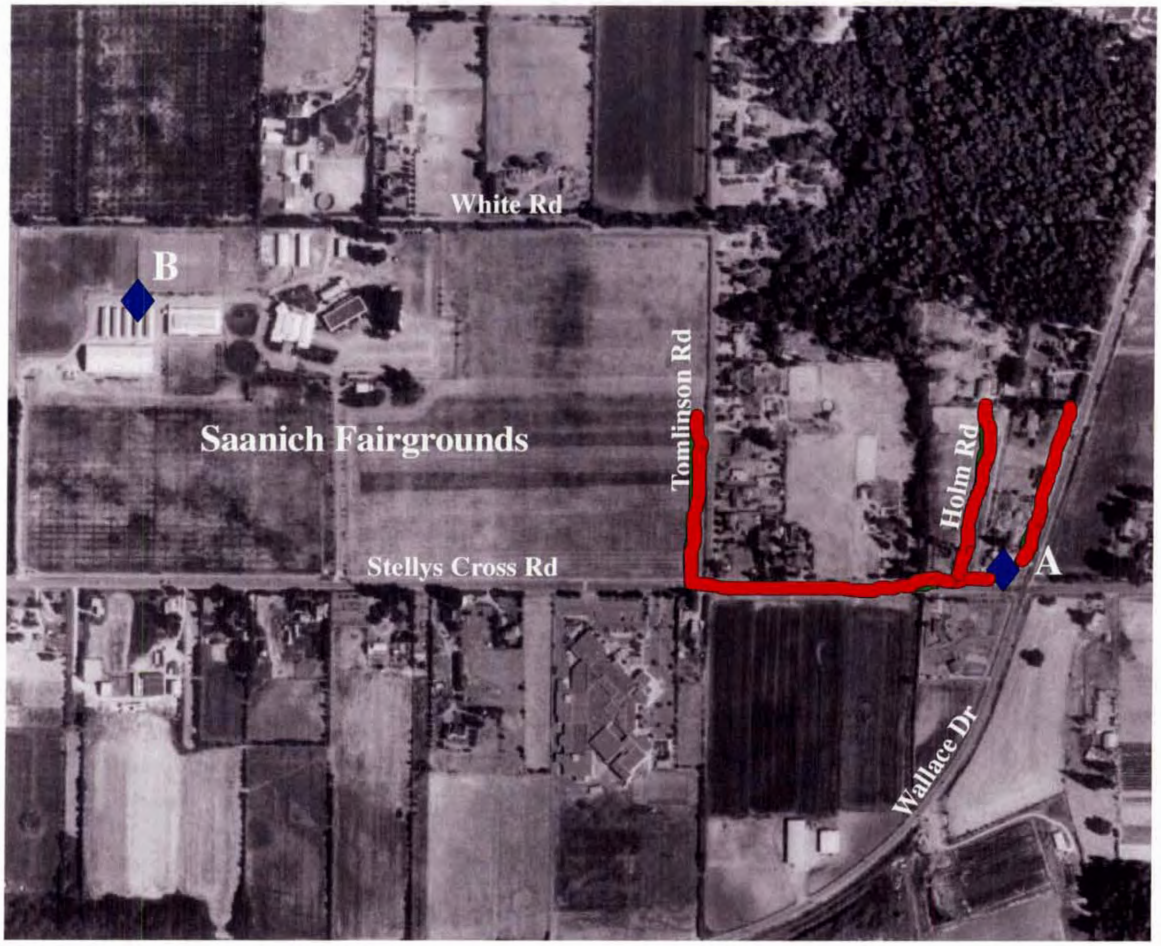


Fig. 1.4 **A** marks the location of a veterinary clinic at the corner of Stellys Cross Road and Wallace Drive. Many *Podarcis muralis* of all size groups have been observed around the clinic's main building, outbuildings and ditches. Further searches (red line) indicate that the lizards have spread along the north ditch of Stellys Cross Road, east ditch of Tomlinson Road, both sides of Holm Road and the west ditch of Wallace Drive (north of Stellys intersection). Reliable information indicates *Podarcis muralis* are established at **B** (the Saanich Fairgrounds) and in the residential areas of Brentwood Bay (further west along Stellys Cross Road), although neither was confirmed.

Confirmation of presence of *Podarcis muralis* was not difficult and required only visual sightings of individuals active in the open. Searching under cover objects was not necessary at any of the sites, providing that the search occurred during warm, dry weather. When *Podarcis muralis* were present they were easily observed moving in the habitat; they retreated to cover when frightened but almost always came back out within minutes if the searcher remained still. This behaviour suggests that areas where the presence of *Podarcis muralis* could not be confirmed have a very high probability of not having populations, relative to the possibility that lizards were present but not observed.

The original release site power line is primarily bordered by mature forest (Fig. 1.3). Searches within the forest revealed that *Podarcis muralis* were found only within a few metres of the edge. Adjacent to the ditches at Stellys-Wallace are large uniform fields of various tall grass species; *Podarcis muralis* were easily located on the roadsides and fence lines bordering the fields, but were not located in the fields themselves (Fig. 1.4). The lizards were observed on the fences and retreated to the grasses and similarly were observed on the mowed roadsides, but retreated to nearby tall grass when disturbed. *Podarcis muralis* also were observed basking on piles of cut grass in the ditches and roadsides. The third area, Clinton Place, is a residential area bordered by homes and scrubby fields (Fig. 1.5). Lizards at this site were observed on the sides of houses, in driveways and flower gardens (K. Ovaska *pers. comm.*).

Why were *Podarcis muralis* not observed in forests and fields? Presumably, forests are too cool most of the time, as are fields when the vegetation grows thick

Fig. 1.5 The blue diamond indicates a confirmed *Podarcis muralis* population on a cul de sac (Clinton Place) in a in a residential neighborhood. Individuals were first observed in 2000 and have been seen on the sides of houses, on decks and along driveways.

and tall. The latter, however, probably are unsuitable habitat even when the vegetation is short, due to a lack of cover for hiding. Conversely, residential areas do not appear to be a barrier to movement of wall lizards. Juvenile *Podarics muralis* were documented at the Clinton Place location, indicating a reproducing population. In Cincinnati, Ohio, diffusion of *Podarcis muralis* into residential and commercial areas also has occurred (Hedeen and Hedeen 1999).

The ability of *Podarcis muralis* to survive in residential areas will become important in the future as these lizards spread along roads, etc. and encounter subdivisions, rural homes and high-density housing. Increased contact with humans increases the probability of human-aided jump dispersal, which will further increase the range and distribution of this non-native lizard species. Education on the potential future effects of *Podarcis muralis* and introduced species in general is needed to enlighten and empower the public to make appropriate decisions with respect to the ecology of the places where they live.

As *Podarcis muralis* increases its range and numbers, it may begin to have more widespread effects on the ecosystems into which it has been introduced. For example, the presence of a novel organism could upset the food chain, resulting inintertrophic effects (Davis 2003). High densities of foraging *Podarcis muralis* could compete for food with any native organism that eats invertebrates, not just *Elgaria coerulea*. *Podarcis muralis* are also potential prey for other predators and thus could be exploited as a food source, perhaps supporting higher populations of predators and thereby indirectly having negative effects on other prey species (Roemer et al. 2002).

Thus, it is important to determine what factors favour the success of *Podarcis muralis* on Vancouver Island and the potential effects this species may have on native species, in order to develop appropriate mitigating strategies.

Chapter 2

Life-History Characteristics of *Podarcis muralis* on Vancouver Island

Introduction

Life-history theory attempts to explain the evolution of life cycles and the causes of differences in fitness between different life cycles (Stearns 1992). A life history is defined as “a set of coadapted traits designed, by natural selection, to solve particular ecological problems”(Stearns 1976). The principal life-history traits include: size at birth, growth pattern, age at maturity, size at maturity, number, size and sex ratio of offspring, age- and size-specific reproductive investments and mortality schedules, and length of life (Stearns 1992). Trade-offs occur when change in one trait results in a benefit, but is linked to change in another trait that results in a cost, leading to variation in fitness (Stearns 1992). Examples of trade-offs between traits include: current reproduction versus survival, current reproduction versus future reproduction, and number versus size of offspring (Stearns 1992).

A focus of much research on life histories has been the cost of reproduction. Reproductive costs can be divided into ‘survival costs’, which reduce the future survival of the reproducing organism, and ‘fecundity costs’, which may reduce the organism’s ability to reproduce in the future (Bell 1980, Shine and Schwarzkopf 1992). Fecundity costs can be broken down further: ‘direct fecundity costs’ result from usage of energy stores that could be used in future reproduction, whereas ‘indirect fecundity costs’ reduce fecundity when growth rate is reduced (Schwarzkopf 1994). The latter applies in cases in which clutch size is correlated with body size (e.g. most squamate reptiles). The concept of ‘capital’ versus ‘income’ breeders complements the idea of fecundity costs. Species that support reproductive investment through gathering resources during the reproductive period are defined as income breeders, whereas species that utilize previously gathered resources are categorized as capital breeders (Stearns 1992, Shine and Schwarzkopf 1992, Schwarzkopf 1994, Bonnet et al. 1998).

Typically, within a population, life-history traits are highly variable. Although some of this variation presumably is genetic, much of it is attributable to phenotypic plasticity (Ferguson and Talent 1993). The term phenotypic plasticity describes "all types of environmentally induced phenotypic variation" (Stearns 1989). Sources of variation in life-history traits include ecotypic adaptations and proximal environmental factors (Ballinger 1983). Environmental conditions can affect individuals physiologically to produce various life-history phenotypes (Ballinger 1983), which, when plotted against environmental conditions, result in a reaction norm (Stearns 1989). Such phenotypic variations can be nonadaptive, maladaptive or adaptive (Stearns 1989). For example, grasshoppers display an adaptive reaction norm in which mandible shape develops differently depending on the type of leaves available, resulting in increased growth rate and reproduction (Thompson 1988).

Life-history theory has obvious links to population dynamics and consequently has been linked to conservation issues (Kolar and Lodge 2001). For example, one of the most serious current threats to native faunas and floras is that of invasive species (Wilcove et al. 1998). What features make an invasive species successful are not entirely clear, but life histories that produce a high intrinsic rate of increase of a population seem to play an important role in many cases (Ludsin and

Wolfe 2001). Thus, studies that focus on the potential impacts of native species need to address this issue.

The subject of this study is an introduced population of the European wall lizard (*Podarcis muralis*) near Victoria, on Vancouver Island (refer to Chapter 1 for details of release). Wall lizards of two species (*Podarcis muralis* and *Podarcis sicula*) have become successfully established at several locations in North America (Vigle 1977, Hedeen 1984, Deichsel and Gist 2001, Draud and Ferner 1994, Gossweiler 1975, Deichsel and Miller 2000) and, because of their high densities and apparently high population growth rates (Kwiat and Gist 1987), they pose a potential threat, presumably via competition, to native species of lizards.

Such competitive interactions will be exacerbated when invasive species have life histories that favour their population growth over that of native species. For example, on Vancouver Island, the native alligator lizard (*Elgaria coerulea*) is viviparous and produces only one brood per year (Vitt 1973), whereas its potential competitor, *Podarcis muralis*, is oviparous and capable of producing multiple clutches per year (Kwiat and Gist 1987, Ji and Braña 2000).

Here, I address two aspects of wall lizard life histories on Vancouver Island. First, I ask to what extent reproduction in female wall lizards is dependent on capital versus income. Presumably, a relatively high dependence on income would allow lizards, under favourable circumstances, to respond rapidly to variations in food supply and thereby increase their numbers very quickly and with little time lag. I test this idea by dividing lizards into low- and high-feeding groups and then measuring their respective reproductive outputs. I anticipated that, if wall lizards are primarily capital breeders, then initial clutches in the two feeding groups should not differ significantly. However, if income was more critical, then lizards feeding at a higher rate should produce more and/ or bigger eggs. In either case, though, subsequent clutches should be smaller or less frequent in lizards that eat less.

Second, I test the influence of incubation temperature (crossed with feeding regime) on phenotypes (body sizes) of hatchling lizards. Developmental temperature is a well-known influence on offspring traits, including size, in *Podarcis muralis* (Braña and Ji 2000) and other squamate reptiles (Wapstra 2000, Webb et al. 2001). In introduced species such as *Podarcis muralis*, successful invasion is partly due to rapid population growth, which in turn depends on both high survivorship and reproductive rate. If early survivorship is related to body size at hatching (Wapstra 2000), then one adaptive trait of wall lizards might be a relative insensitivity of hatchling size to moderate variation in incubation temperature. I chose incubation temperatures of 26 and 31 °C because they are within the normal range of incubation temperatures experienced by typical temperate-zone lizards, yet far enough apart to influence phenotypes (Braña and Ji 2000, Ji et al. 2002).

Because lizards have emerged, in recent years, as an important taxon for the study of life-history evolution (e.g. Ferguson and Talent 1993, Angilletta and Sears 2000, Seigel and Ford 2001, Haenel and John Alder 2002), a wealth of published data exists for comparative interpretation of my data.

Methods

From 18 April – 10 May 2002, I captured large adult male and female *Podarcis muralis*, using a dental-floss noose, from a powerline adjacent to the original release site of *Podarcis muralis* on Vancouver Island (see Chapter 1, Fig. 1.3). I then recorded mass (g), snout-vent length (SVL, mm), tail length (mm) and sex for each captive individual. I regressed mass versus SVL for all females and used the residuals from that regression as indices of body condition. Pairs of males and females were placed in separate 45 X 25 X 30 cm plastic cages with mesh lids. Each cage included substrate (sterilized soil and pebbles, approximately 5 cm deep), a water dish, 1-2 pieces of bark and an egg-laying chamber. The egg-laying chamber was a 10 cm diameter plastic pot with an entrance hole cut in it and filled with 5 cm of moistened perlite. I placed heat lamps set on a 12-hour light/dark cycle above each cage at one end only. A total of 34 male-female pairs of lizards were divided into two feeding groups (17 pairs each) and were fed approximately every second day (3-4 days per week). Each 'high feeding' pair received ~3 grams of crickets per week while the 'low feeding' pairs received ~1 gram per week. The aim of this part of the experiment was to test the influence of varying levels of 'income' on reproductive output.

Following oviposition by females, I counted the eggs, removed them from the parental cages, and placed them in incubators. Each egg's mass (g), length (mm) and width (mm) were determined using a digital scale and calipers. Eggs that were stuck together or had substrate stuck to them were not separated or cleaned, so I could not obtain all measurements from them. I divided each clutch into two groups; half were placed in a 26°C incubator (low-temperature treatment) and the other half in a 31°C incubator (high-temperature treatment). Thus I could test the effects of incubator temperature on phenotype of offspring, without confounding them with feeding or family effects. Eggs were placed in the incubator in the exact position in which I found them (i.e. same side up and same orientation). Eggs from each clutch were placed in a 50 ml glass beaker two thirds full of moist perlite (equal parts perlite and water by weight); to prevent evaporation and drying of the perlite, I placed clear plastic wrap over the beaker and secured it with an elastic band.

After the first hatchling emerged, I checked the incubators at least twice (morning and afternoon) per day. Hatchlings were removed from the incubator and mass (g), SVL (mm), and tail length (mm) were measured promptly. Next, I placed the hatchlings in a cage containing the same components as the parental cages, and fed them fruit flies and small meal worms (~1 mm diameter) ad lib.)

All analyses were performed using SPSS 11.0 with a rejection level of *P* = .05. For the capital – income breeding experiment, I analyzed differences in morphology (SVL, mass, body condition) and clutch size using t-tests. Date of clutch deposition was analyzed using the Mann-Whitney U test. Differences in egg characteristics between feeding treatments were determined using nested ANOVA (clutches nested in treatments). Phenotypic plasticity was analyzed using Chi-square tests to compare hatching success, and t-tests to compare incubation period, between treatments. I used nested ANOVA to compare hatchling characteristics between incubation temperatures and between maternal feeding regimes (low temperature incubation treatment only).

Results

Capital – Income Breeding

Females from the two feeding groups did not differ significantly in initial SVL ($t = -1.26$, $P = .277$), mass ($t = -1.97$, $P = .067$) or body condition ($t = -1.68$, $P = .113$; Fig. 2.1). Females from the low feeding group (8 clutches, 44 eggs) deposited their clutches earlier than those from the high feeding group (10 clutches, 44 eggs; $Z = 2.711$, $P = .007$; Fig 2.2). There was no significant difference in clutch size ($t = 11.537$, $P = .144$), egg width ($F_{1,38} = 3.55$, $P = .078$), egg length ($F_{1,39} = .001$, $P = .973$) or egg mass ($F_{1,41} = .000$, $P = .985$) between high and low feeding treatments. I tested correlations among morphological measurements of females (e.g. mass, body condition) and clutch characteristics (e.g. number of eggs in clutch; average weight, length and width of eggs), controlling for SVL via partial correlation, for all females combined, and then separately for each group. Although females from both feeding groups deposited eggs, none did so more than once. Strength and directions of correlations between female and clutch characteristics were inconsistent between treatments and the overall sample (Table 2.1). Although lack of significance in some cases was due to small sample sizes, there were some clear differences between the feeding treatments (e.g. number of eggs vs. postpartum mass, number of eggs vs. mean egg length) that demand explanation.

Phenotypic Plasticity

In total, 44 eggs per treatment were incubated, but hatching success was low. A lower proportion of eggs hatched in the high incubation temperature treatment (7

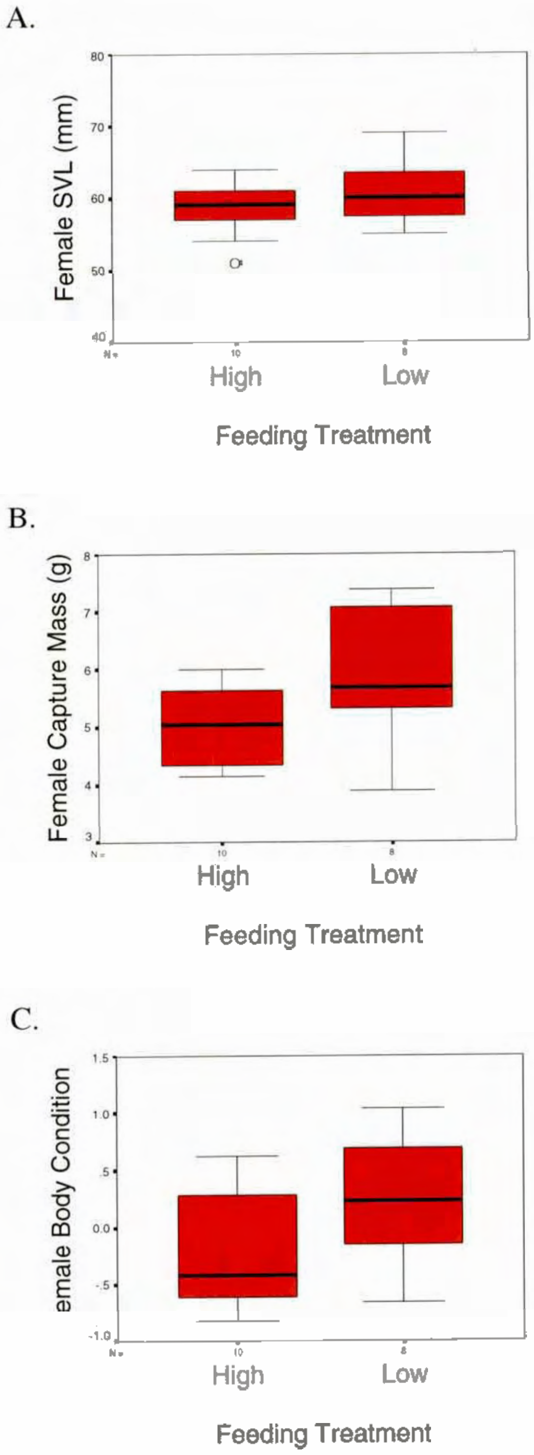


Fig. 2.1 Boxplots of female A) SVL, B) mass and C) body condition from two feeding treatments.

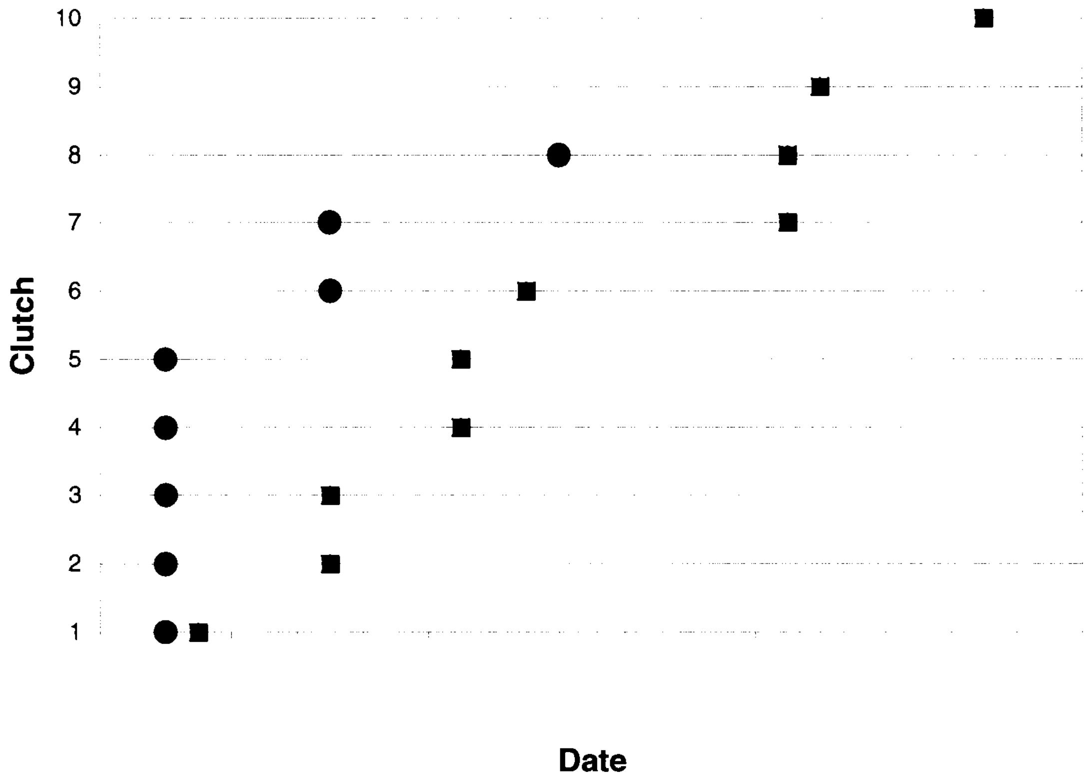


Fig. 2.2 Dates of clutch deposition for two experimental feeding treatments (squares - high feeding, circles – low feeding). Experiment took place in 2002.

Table 2.1 Partial correlations (controlling for SVL) between female and clutch characteristics.

	CORRELATION COEFICIENT		
		Feeding Treatment	
Characteristics	All Clutches n = 18	High n = 10	Low n = 8
# Eggs in Clutch – Postpartum Mass	-.0345	.7997*	-.2485
# Eggs in Clutch – Body Condition	.5708*	.4997	.6078
# Eggs in Clutch – Mean Egg Length	-.7715*	-.8517*	.6537
Postpartum Mass – Body Condition	.2411	.8384*	.4613
Mean Egg Mass – Mean Egg Width	.8942*	.8994*	.8214

*correlation is significant at $P = .05$

hatchlings, 16% success) than in the low (16 hatchlings, 36% success; $\chi^2 = 4.768$, df = 1, $P = .029$). Incubation period was significantly longer for the low temperature treatment ($t = -11.72$, $P = .000$; Fig. 2.3). Nested ANOVAs of hatchling characteristics indicated that hatchling SVL ($F_{1,7} = 12.10$, $P = .002$), tail length ($F_{1,7} = 6.08$, $P = .022$) and mass ($F_{1,7} = 12.90$, $P = .002$) were statistically different between high and low temperature incubation treatments (Fig. 2.4); lower incubation temperatures resulted in higher hatchling SVL, tail length and mass.

The very small number of hatchlings I obtained at the higher incubation temperature prevented complete factorial analysis of the effects of feeding regime and incubation temperature on hatchling characteristics. I thus tested the effect of maternal feeding regime only at low temperature incubation. Nested ANOVA (clutches nested within treatments) indicated that hatchling mass was significantly higher for the high versus low maternal feeding regime ($F_{1,6} = 7.95$, $P = .014$; Fig. 2.5).

Discussion

This experiment was marred by two unexpected problems: failure of many females to lay any eggs (and of any females to produce more than one clutch); and poor incubation success. I suspect that females that deposited a clutch likely were already gravid when collected and that none became gravid in captivity. I did not expect that all females would deposit multiple clutches since the probability of depositing a second or third clutch in a season depends on body size (Ji and Braña 2000). However, Ji and Braña (2000) found that females from 56.1 – 65.0 mm SVL

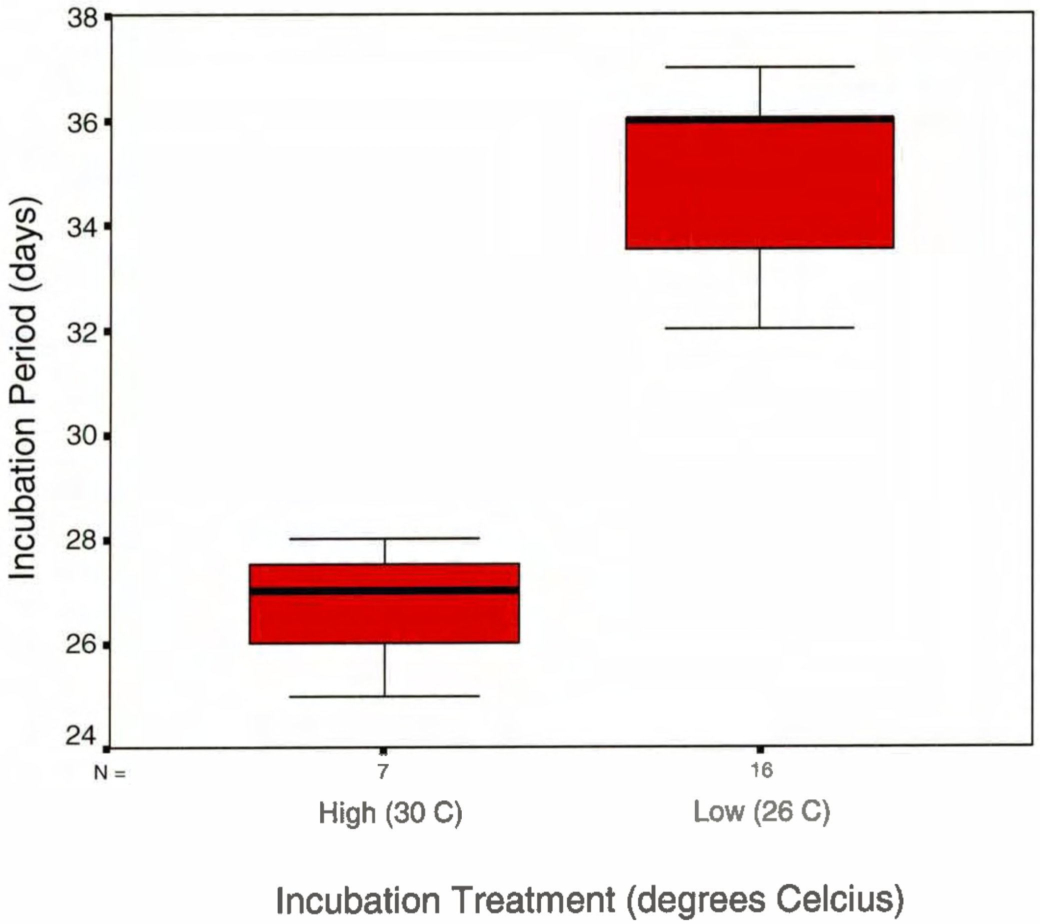


Fig. 2.3 Effect of incubation treatment (high or low temperature) on the length of incubation period in days.

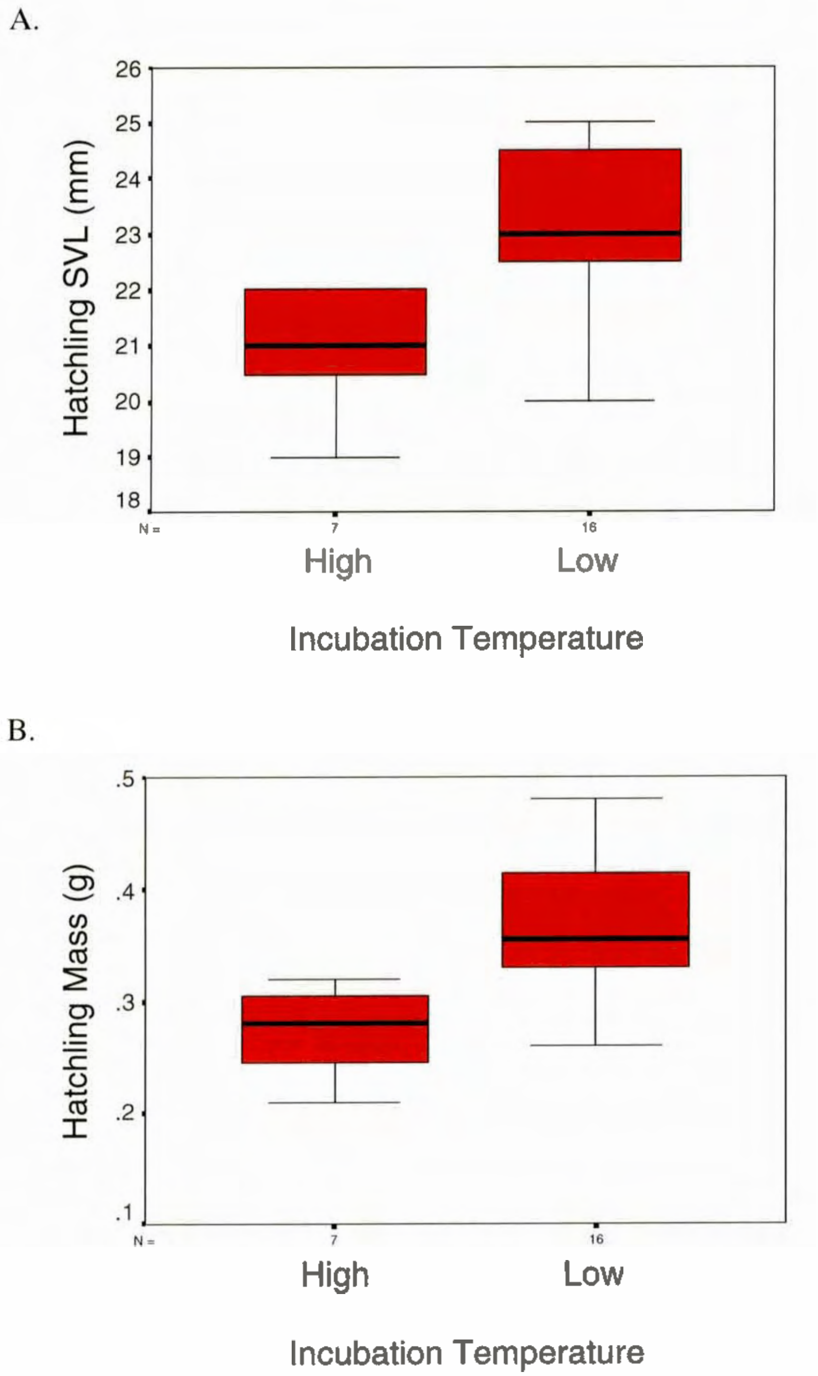


Fig. 2.4 Effect of incubation temperature on A. *Podarcis muralis* hatchling SVL (mm) and B. *Podarcis muralis* hatchling mass (g).

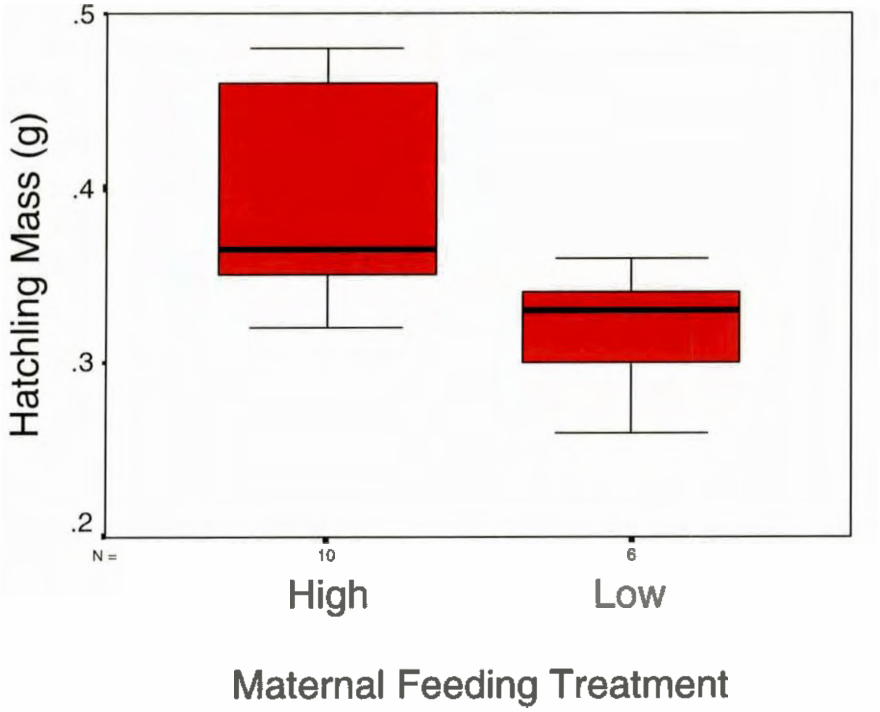


Fig. 2.5 Effect of maternal feeding regime on the mass of wall lizard hatchlings incubated at a relatively low temperature (26°C).

deposited three clutches in one season. Because seventy-five percent of the females in my experiment fit into this range, I therefore expected multiple clutches from at least some of the females. A likely problem was the captive environment. Although I attempted to provide conditions that were as natural as possible (e.g. substrate and cover objects), lighting was artificial. I also provided no opportunity for mate choice. However, in retrospect, the most serious deficiency in this experiment was an insufficiently high feeding regime.

Other experiments have used larger enclosures in greenhouse conditions where numbers of male and female *Podarcis muralis* were placed together in a single captive environment (Ji and Braña 2000). This allows for natural light cues and better enables individuals to interact as they would in their natural habitat. Due to the introduced status of *Podarcis muralis* in Victoria and concerns over escapement and further establishment of satellite populations, outdoor enclosures pose risks not encountered by researchers working in this lizard's native range. Although increased expense would be incurred, this approach is highly recommended if an experiment of this type is repeated. For example, two much larger semi-natural enclosures located in full natural light, one exposed to a high feeding regime and the other to a low feeding regime, could be employed. As females became gravid they could be removed and placed in individual cages until clutch deposition occurred, following which they would be returned to the appropriate large enclosure until gravid again.

Despite these difficulties, my data nonetheless suggest that *Podarcis muralis* females rely heavily on capital, rather than income, for their first clutch of the season at least. This is supported by the lack of difference between clutch characteristics for the two feeding groups. Furthermore, the strong correlation between clutch size and postpartum mass in the high feeding group, but not in the low (Table 2.1) suggests that income while gravid goes to the female and not the offspring (Gregory and Skebo 1998). At first sight, the higher hatchling mass for the high feeding treatment (Fig. 2.5) contradicts this, but the lack of data for the high incubation treatment leaves this interaction untestable.

Kwiat and Gist (1987) found that ovulation in female *Podarcis muralis* in Cincinnati, Ohio occurred between mid-April and late July, whereas maximum sperm production in males occurred between mid-March and mid-June. In Spain, female *Podarcis muralis* were observed to lay eggs from late April to early July (Ji and Braña 2000). This cycle indicates that in late summer and fall, *Podarcis muralis* can dedicate themselves to gathering food and developing fat stores, allowing their first reproductive event to occur shortly after emergence from the overwintering dens the next spring. In the spring, food supplies (i.e. insects) may not yet be readily available and abundant, so capital or fat stores are relied upon to facilitate egg development. Conversely, in early and mid summer, when insect populations are increasing and fruit production is occurring, *Podarcis muralis* might rely more on the energy collected daily (income) to facilitate second and third reproductive events.

Although there were no differences in the number or size of eggs deposited by females in each experimental group, low feeders deposited their eggs more than a week earlier than high feeders. Based on the above discussion, which suggests that the initial clutch of a season is produced through capital breeding and subsequent clutches might depend more on income, the dates of egg deposition could represent a trade-off between reproduction and growth. Gravid females of the oviparous lizard *Sceloporus undulates* were found to have metabolic rates 122% of non-gravid females (Angilletta and Sears 2000). Reduced food availability could stimulate earlier egg deposition, allowing resources to be directed to physical maintenance and growth, thereby relieving the body of the added burden of eggs.

Correlations between female morphological measurements and clutch characteristics indicate a link between egg shape and mass, between the number and length of eggs in a clutch and between body condition and clutch size (Table 2.1). The negative correlation between egg length and number of eggs in a clutch is evidence of a trade-off between size at birth and number of offspring. Since females likely were already gravid when collected, the number of developing eggs had already been determined. Hence the observed positive correlation between body condition and number of eggs in a clutch cannot be attributed to the different feeding regimes of this experiment, but does provide further support for use of capital in breeding *Podarcis muralis*.

Although there were no differences in clutch characteristics (e.g. egg size and mass) between maternal feeding regimes, there was a posthatching effect on hatchling mass. Eggs from the maternal high feeding treatment produced heavier hatchlings compared to eggs from the low feeding treatment (Fig. 2.5). This result might be linked to the nutritional contents of the eggs. Ji et al. (2002) dissected and dried freshly laid eggs of *Calotes versicolor*, reducing them to three main components: dry material, energy and nonpolar lipids. Different percentages of each component (50.8-60.6 % of dry material, 43.9-50.8 % of energy and 21.2-29.2 % of nonpolar lipids) were transferred from yolk to hatchlings (Ji et al. 2002). Potentially, in my experiment, lower amounts of energy and other nutritional components, relative to water, were passed to the developing embryos of low-feeding females compared to the eggs of females in the high feeding treatment. However, this argument is inconsistent with the previously supported notion of capital breeding, in which yolk has already been committed to eggs. Perhaps lower mass of hatchlings from low-feeding lizards is instead related to the earlier oviposition dates in this group. That is, overall shorter development periods (in mother plus incubation) might influence transfer of nutrients from yolk to embryo (see below). Alternatively, the effect was due to incubation temperature; however, because the sample size in the high incubation temperature treatment was too small for analysis, additional study is required before conclusions can be reached on this point.

Hatchling size and incubation period were both affected by incubation temperature. Lower incubation temperature resulted in larger hatchlings (SVL and mass), higher hatching success and longer incubation periods. Similar results have been recorded for various species of reptiles (Webb and Cooper-Preston 1989, Janzen 1993, Steyermark and Spotila 2001, Ji et al. 2002, Pina et al. 2003), including *Podarcis muralis* (Van Damme et al. 1992, Braña and Ji 2000). These three measurements are linked through their relationship to residual yolk. Lower incubation temperatures lead to longer incubation periods (in days), which provides more time for yolk absorption to occur, resulting in heavier hatchlings (Webb and Cooper-Preston 1989).

In addition to larger hatchlings, I observed greater hatching success at the lower temperature. Van Damme et al. (1992) incubated *Podarcis muralis* eggs at temperatures of 24, 28, 32 and 35°C and found 28°C to provide optimal results. A similar pattern of variation in hatchling success, and occurrence of abnormalities over a range of incubation temperatures, was observed for the oriental garden lizard (*Calotes versicolor*; Ji et al. 2002). These observed differences in hatchling morphology and success suggest the presence of reaction norms. Further study, including measurement of phenotype over many more temperature increments, would provide stronger evidence for continuous variation of hatchling characteristics.

The problems I encountered with this experiment and the resultant incompleteness of the data make it difficult to infer the influence of life-history variation on population ecology of *Podarcis muralis* and hence to make relevant recommendations for management and conservation. That said, my limited data do not support the hypothesis that success of *Podarcis muralis* as an invasive species is attributable either to a largely income-dependent reproductive strategy or to a relative insensitivity of hatchling phenotypes to incubation temperature. Thus, the life-history advantages, if any, enjoyed by *Podarcis muralis* presumably lie elsewhere. Only further, more rigorous, experimentation will allow this question to be addressed.

Chapter 3

Locomotor Performance of *Podarcis muralis* and *Elgaria coerulea*

Introduction

Podarcis muralis, a European lizard species, has been introduced into two US states (Ohio and Kentucky) and one Canadian province (British Columbia). In the latter case, twelve *Podarcis muralis* were released on the Saanich Peninsula of Vancouver Island, British Columbia in 1970 and a large population has since become established. Although we do not know the extent to which *Podarcis muralis* is a threat to native species (especially *Elgaria coerulea*), in order to anticipate possible problems, and be ready with solutions, we need to have a good understanding of the ecology of this introduced species, particularly in comparison with relevant native species. One key potential limiting factor on lizards is climate, particularily temperature.

Climate is critical to ectotherms such as lizards, since environmental temperatures directly affect activity patterns (Foa and Bertolucci 2001, Whitaker and Shine 2002, Braña 1993), growth (Litzgus and Brooks 1998) and development (Webb et al. 2001, Wapstra 2000) of these organisms. In temperate-zone regions, where temperatures vary annually and daily, the ability to perform or be active over a range of temperatures is advantageous.

One way of quantifying lizard performance over a range of temperatures is the measurement of sprint speeds (Zhang and Ji 2004, Pinch and Claussen 2003). Sprint speeds achieved over a range of temperatures highlight the temperatures at which maximum performance occurs, as well as the temperatures at which performance is hindered or prevented. Invasive species that can maintain activity levels over a wide range of temperatures have more opportunities to engage in activities that increase growth and reproduction; hence, their potential to become established is increased.

Podarcis muralis apparently is well adapted to cool temperate climates; for example, it has been shown to be freeze-tolerant (Claussen et al. 1990). In the context of invasiveness, a species that can withstand temperature declines, whether they are sudden and unexpected (e.g. during the active season) or gradual and extreme (e.g. during the overwintering period), is placed at a survival advantage compared to species that are not cold-tolerant. Thus, cold weather events may have a detrimental, but not devastating, effect on populations of such species.

The objectives of this chapter are: (a) to determine how sprint speeds of *Podarcis muralis* vary with temperatures within the normal activity range; (b) to compare sprint speeds of *Podarcis muralis* at each temperature with those of *Elgaria coerulea*. I predict that sprint speed in each species will be positively correlated with temperature, and based on the hypothesis of higher cold-tolerance of *Podarcis muralis,* this lizard will perform faster at lower temperatures than *Elgaria coerulea.*

Methods

Between 18 April – 10 May 2002, I collected *Podarcis muralis* from a powerline adjacent to the original release site of *Podarcis muralis* on Vancouver Island. I placed pairs of males and females in separate 45 X 25 X 30 cm plastic cages with mesh lids. Each cage included substrate of approximately 2 inches of sterilized soil and pebbles, a water dish and 1-2 pieces of bark for cover. A 10 watt bulb provided heat and light on a 12 light:12 dark cycle. As part of a reproductive experiment (see Chapter 2), two feeding groups (17 pairs each) were established. Feeding occurred approximately every second day (3-4 days per week); each 'high feeding' pair received ~3 grams of crickets per week while the 'low feeding' pairs received ~1 gram per week. The feeding experiment ended in September, after which time the lizards were fed ad lib.

Between 18 September – October 9 2002, *Elgaria coerulea* were collected from a disused quarry near Shawnigan Lake. I housed them in similar cages and with the same substrate, light and heat as *Podarcis muralis*. For food, I maintained several mealworms in the cages at all times and provided crickets every second day. The *Elgaria coerulea* were released in spring 2004 at their original capture locations.

On 1 November 2002, I measured the mass and SVL of each lizard. Residual values from a regression of mass and SVL were calculated and used as measures of body condition. Measurement of sprint speed took place November 3 – 23. Lizards were chased down a 1.1m x 15cm x 20cm fiber-board 'race track' into a darkened container. A digital unit attached to the track was activated by a lizard breaking a beam of light at the start and end of 1m; the digital unit measured and displayed time to run 1m (s) and calculated and displayed velocity (ms^{-1}). Sprint speed temperature trials occurred first at room temperature (22°C), then high temperature (33°C), then low temperature (11°C), and were separated by a minimum of 2 days (maximum 15). I completed three measurements of sprint speed for each lizard (72 *Podarcis muralis*, 11 *Elgaria coerulea*), with a minimum of 30 minutes and a maximum of 1 hour between measurements of the same individual lizards. In several cases, sprint speed measurements were missing from the data set (e.g. due to recording errors); these individuals were removed from the analysis, leaving 65 *Podarcis muralis* and 11 *Elgaria coeurlea*. For each lizard, I chose the fastest of its three measurements at a given temperature as a measure of maximum sprint speed for analysis.

A refrigerator and incubator were used to achieve the required body temperatures in the low and high temperature trials, respectively. I placed lizards in separate plastic containers in the refrigerator or incubator until the air temperature in the container was close (± 2°C) to the desired test temperature (15-30 minutes). On the day of the room temperature trial, heat lamps on the lizard cages were not turned on in the morning, ensuring that the lizards were at room temperature. Between successive sprint speed measurements, I kept the lizards at room temperature (30 minutes to 1 hour) until 15-30 minutes before the trial, when I placed them back in the refrigerator or incubator to assume the appropriate test temperature.

I analyzed performance differences between species and temperatures using SPSS 11.0 and SAS 8.0. I employed a two-way (species*temperature) repeated measures ANOVA, in which individual lizards were nested within species and treated as a random factor (species, temperature = fixed factors). Appropriate F-tests were determined using the RANDOM/ TEST option in PROC GLM of SAS. I then ran one-way ANOVAs comparing maximum velocity between species at each temperature and two-way ANOVAs (temperature*individual lizard, with no replication) between temperatures for each species. Differences in male and female performance were analyzed using one-way ANOVA separately for each species at each temperature.

Results

Maximum sprint speed was not related to body size in either species (Figs. 3.1, 3.2). Thus, I did not correct the data in the remaining analyses for differences in SVL. Two-way repeated measures ANOVA indicated no significant interaction between species and temperature ($F_{2,\,146} = 2.17$, $P = .1177$; Table 3.1). The analysis indicated no significant difference in maximum velocity between species ($F_{1,\,73} = 2.91$, $P = .0922$; Table 3.1), but a highly significant difference in maximum velocity among temperatures ($F_{2,\,146} = 99.34$, $P = <.0001$; Table 3.1). One-way ANOVA indicated significant differences in maximum velocity among all temperatures for both species and between the species at room temperature only (Fig. 3.3, Table 3.2).

Males from both species were found to achieve significantly higher velocities at room temperature than females (*Podarcis muralis*: $F_{1,\,62} = 7.49$, $P = .0081$; Fig. 3.4; *Elgaria coerulea*: $F_{1,\,9} = 6.5$, $P = .0317$; Fig. 3.5). Males also were faster than females at the other two temperatures, but the differences were not significant (*Podarcis muralis* – cold: $F_{1,62} = .063$, $P = .803$; warm: $F_{1,62} = 1.136$, $P = .291$; *Elgaria coerulea* – cold: $F_{1,9} = .706$, $P = .422$; warm: $F_{1,9} = .956$, $P = .354$). Snout-vent lengths of male and female *Podarcis muralis* were not significantly different, but males did have superior body condition ($t_{62} = 1.05$, $P = .299$ and $t_{62} = 4.69$, $P < .0001$, respectively). Snout-vent length and body condition of male and female *Elgaria coerulea* were not different ($t_9 = .853$, $P = .416$ and $t_9 = .468$, $P = .651$, respectively).

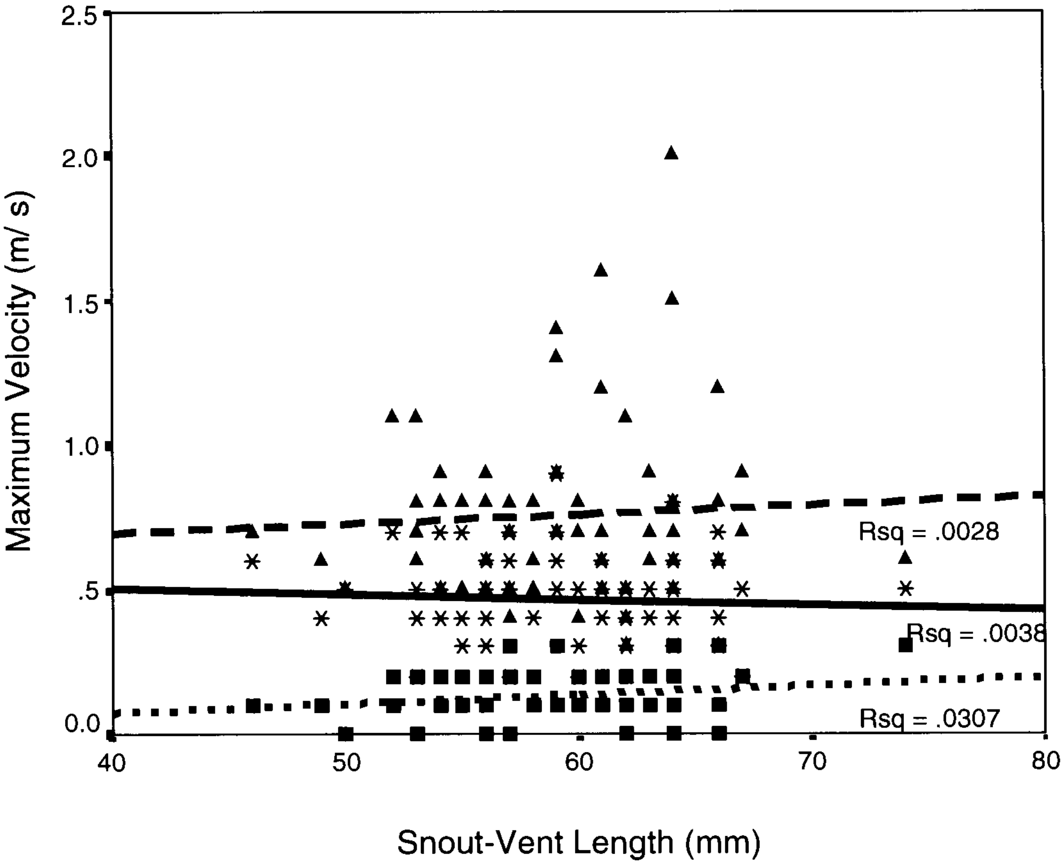


Fig. 3.1 Linear regression of *Podarcis muralis* snout-vent length (mm) versus maximum velocity (m/ s) with coefficients of determination (Rsq). Three temperature treatments were analyzed: low (squares; short dashes; *P* = .1658), room (asterisks; solid line; *P* = .6299) and high (triangles; long dashes; *P* = .6796).

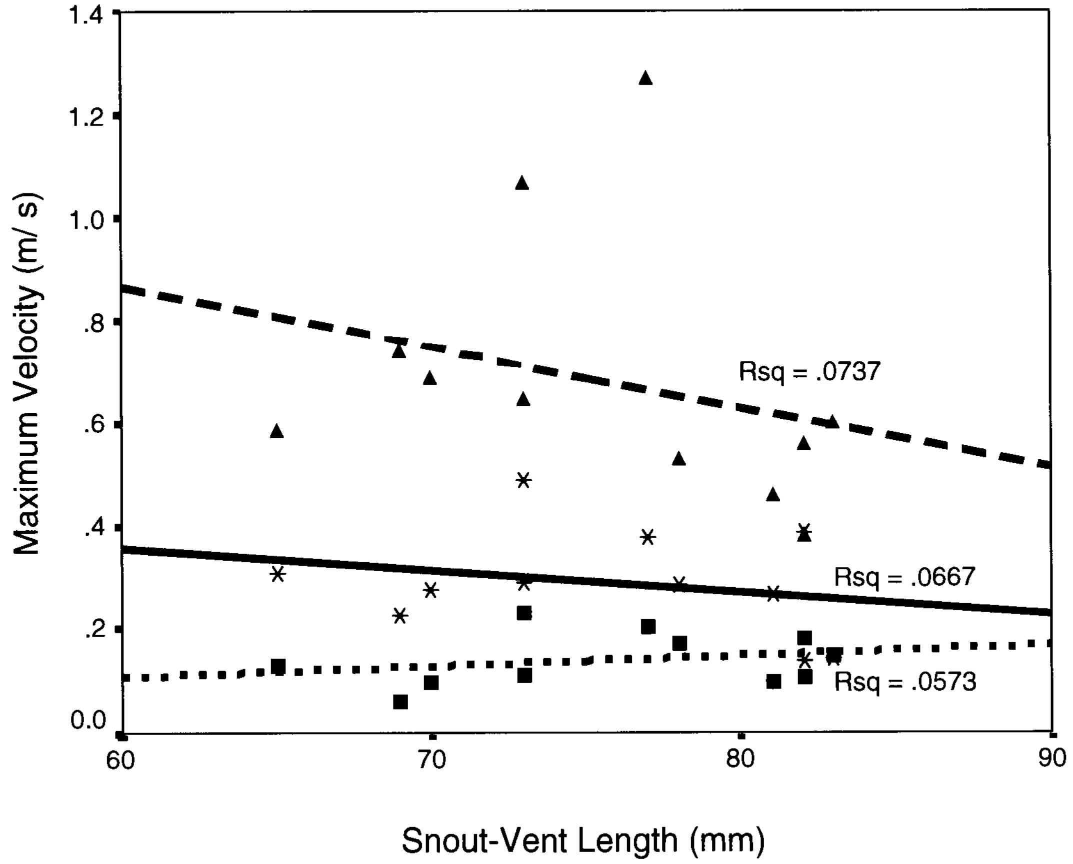


Fig. 3.2 Linear regression of *Elgaria coerulea* snout-vent length (mm) versus maximum velocity (m/ s) with coefficients of determination (Rsq). Three temperature treatments were analyzed: low (squares; short dashes; *P* = .4782), room (asterisks; solid line; *P* = .4434) and high (triangles; long dashes; *P* = .4193).

Table 3.1 Results of repeated measures ANOVA comparing maximum velocity of *Podarcis muralis* and *Elgaria coerulea* at three temperatures (high = 33°C; room = 22°C; low = 11°C).

Source of Variation	*F*	df, Error df	*P*
Species	2.91	1, 73	.0922
Individual nested within Species	1.88	73, 146	.0007
Temperature	99.34	2, 146	<.0001
Species * Temperature	2.17	2, 146	.1177

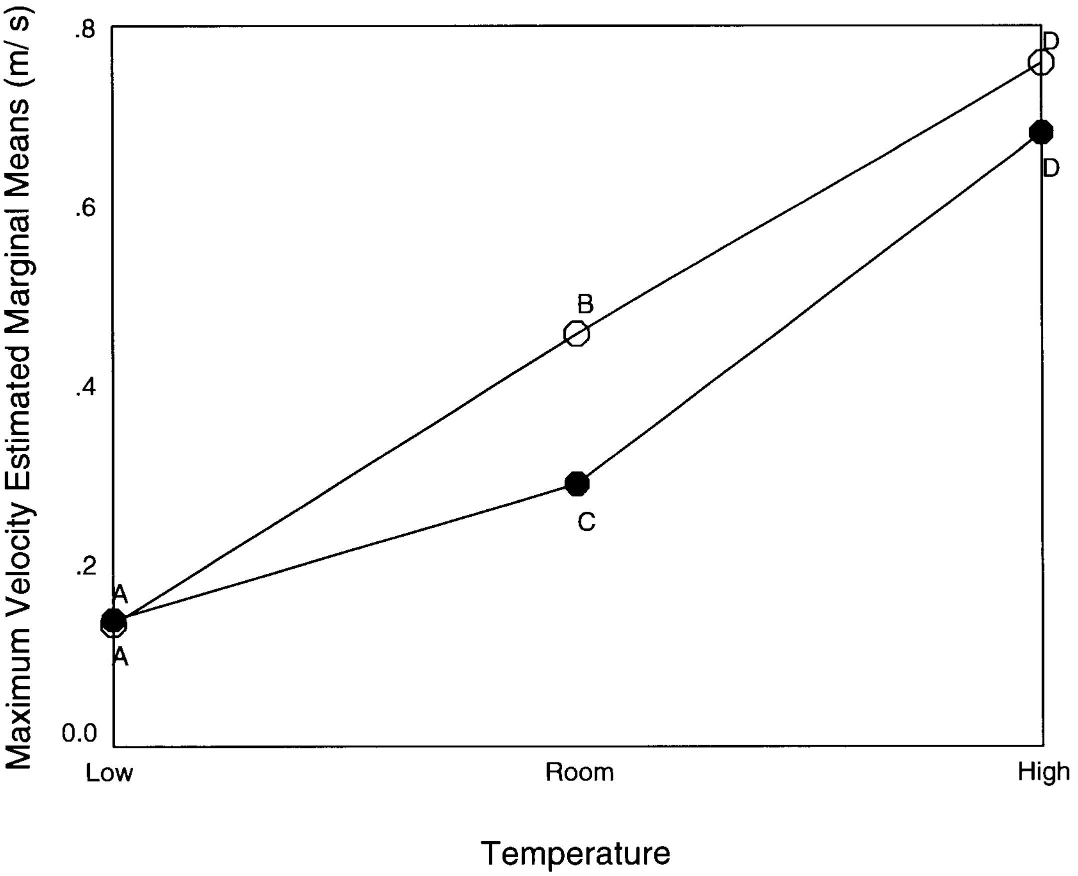


Fig. 3.3 Estimated marginal means velocity for each lizard species (*Podarcis muralis* - open circles; *Elgaria coerulea* - closed circles) at three temperatures (low = 11°C, room = 22°C, high = 33°C). Means labeled with the same letter are not statistically different, while those with different labels are.

Table 3.2 Results of one-way ANOVA comparisons of maximum velocity between species at low (11°C), room (22°C) and high (33°C) temperatures and between temperatures for each species (Pm = *Podarcis muralis*, Ec = *Elgaria coerulea*).

Comparison	*F*	df, Error df	*P*
Pm low vs. Pm room	8.75	1, 63	<.0001
Pm low vs. Pm high	16.77	1, 63	<.0001
Pm room vs. Pm high	8.02	1, 63	<.0001
Ec low vs. Ec room	2.15	1, 10	.0394
Ec low vs. Ec high	7.67	1, 10	<.0001
Ec room vs. Ec high	5.52	1, 10	<.0001
Pm low vs. Ec low	.05	1, 73	.8301
Pm room vs. Ec room	11.3	1, 73	.0012
Pm high vs. Ec high	.56	1, 73	.4558

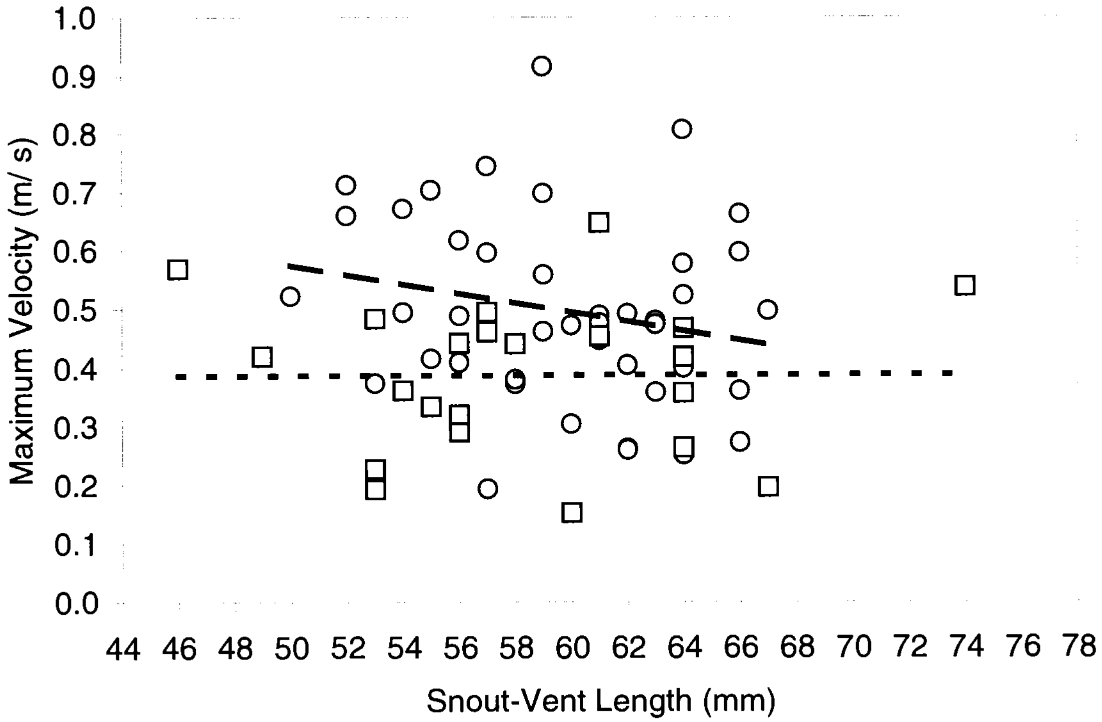


Fig. 3.4 Maximum velocity (m/s) versus snout-vent length (mm) at room temperature (22°C) for *Podarcis muralis* male (circles; long dash) and female (squares; short dash).

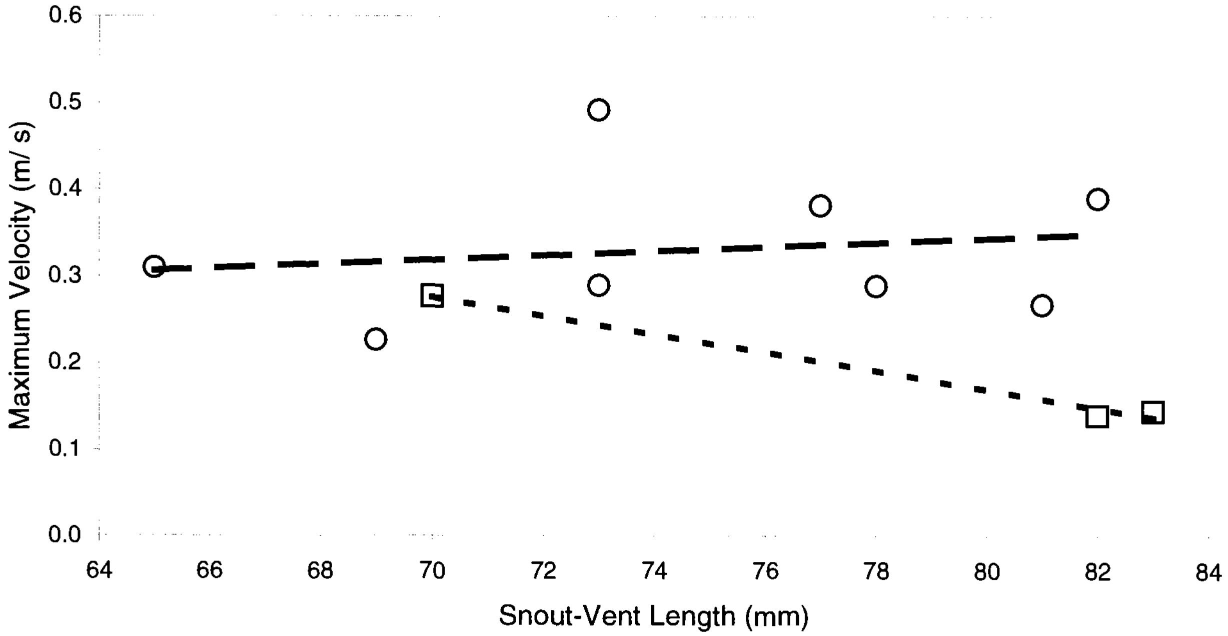


Fig. 3.5 Maximum velocity (m/s) versus snout-vent length (mm) at room temperature (22°C) for *Elgaria coerulea* males (circles; long dashes) and females (squares; short dashes).

Discussion

As predicted, maximum velocities of both *Podarcis muralis* and *Elgaria coerulea* increased with temperature. These patterns are consistent with data for other species (Chen et al. 2003, Pinch and Claussen 2003, Claussen et al. 2002). At room temperature (22°C), *Podarcis muralis* reached significantly higher maximum velocities than *Elgaria coerulea,* while similar performance was observed between species at the other temperatures. Most notably, despite the presumed cold tolerance of *Podarcis muralis, Elgaria coerulea* performed equally well at the lowest temperature I tested. Although no aspect of cold-tolerance has been assessed for *Elgaria coerulea*, my study site is near the northern limits of this species' range; hence, some form of resistance and/or adaptation to cold is expected. The evolution of both species in temperate northern climates may be responsible for the observed similarities in their locomotor performance at low temperatures.

The apparent ability of *Podarcis muralis* to perform better at moderate temperatures than *Elgaria coerulea* (Fig. 3.3), however, may have implications for its success as an introduced species. The apparently less temperature-sensitive performance curve of *Podarcis muralis* would allow biological activities to occur more efficiently over a greater range of temperatures, thereby providing a longer active season. The ability to forage in cooler weather, while retaining the ability to escape predators, means increased opportunity for growth and reproduction, leading to higher population growth and range expansion. However, whether these differences in maximum velocity actually translate into fitness differences remains to be tested.

In this study, all of the significant differences detected between species and sexes occurred at room temperature, suggesting that this is where we might expect potential fitness differentials to manifest themselves in temperate-zone lizards. At low temperatures, lizard locomotor performance is hindered to the point where normal activities (e.g. fleeing from predators, catching prey) are compromised; therefore lizards remain hidden. Hence, the influence of low temperatures on the thermal niche (determined by the frequency distribution of body temperatures obtained in the field) of reptiles is minimal (Davies et al. 1981). Conversely, at high temperatures, maximum locomotor performance (as measured in the laboratory) exceeds routine field locomotor requirements (Braña 2003). If the maximum speeds achieved at high temperatures are beyond those required in the field, the competitive advantage of such speeds is negated.

Since low and high temperatures have less relevance to thermal niches of reptiles, mid temperatures define this niche and the ability to out- perform sympatric species at mid temperatures emerges as a potential competitive advantage. *Podarcis muralis* performed significantly faster than *Elgaria coerulea* at the mid temperature tested. The ability of *Podarcis muralis* to reach higher velocities at this range of temperatures suggests that it could have an advantage in terms of food acquisition, predator avoidance, and other key activities requiring movement.

Performance differences were not attributable solely to species and temperature, but also to sex, with males being faster than females. The higher velocities achieved by males were not a function of higher SVL values since I found no significant difference between male and female SVL for either species. However, body condition of male *Podarcis muralis* was significantly higher than that of females. Higher body condition values indicate greater fat stores; hence males were in better physical condition and able to perform at a higher level. Reduced body condition in females may be a result of male dominance and competition for food. Aggressive interactions were often observed during feeding when certain individuals would actively steal food (crickets) from presumably less dominant individuals. Due to costs of reproduction, the reproductive experiment described in Chapter 2 also may have put females at a disadvantage in terms of growth. Gravid females experience thermoregulatory constraints, increased retreat behaviour and reduced foraging (Braña 1993). These factors may have limited the ability of gravid females to efficiently acquire and assimilate food, allowing males to dominate the food supply and achieve superior body condition.

Neither SVL or body condition differed between male and female *Elgaria coerulea*; however, males still performed better at room temperature. Potentially, an unmeasured factor (e.g. tail length, leg length) may be responsible for the observed difference in performance. For example, lizards with recently autotomized tails are shown to perform faster than those with regenerated or original tails (Brown et al. 1995). The SVLs of *Elgaria coerulea* females in this analysis are consistent with those of females considered mature and able to reproduce (Stewart 1985). Assuming these females all reproduced during the preceding summer, they would incur costs of reproduction that males would not, potentially placing males at an energetic advantage. For example, Olsson et al. (2000), suggest physiological factors rather than physical burden are the cause of reduced locomotor performance in gravid females, since locomotor impairment was observed to persist after parturition. Further analysis using larger sample sizes and more factors might clarify these relationships between male and female performance.

Chapter 4

Habitat Use of *Podarcis muralis* and *Elgaria coerulea*

Introduction

The European wall lizard, *Podarcis muralis*, a species native to Europe and introduced in North America, is currently found in Ohio (Vigle 1977, Hedeen 1984), Kentucky (Draud and Ferner 1994), and southern Vancouver Island (Allan et al. 1993). In Kentucky, interactions, or lack thereof, with other lizard species have not been described, and none of the three lizard species native to the Cincinnati, Ohio area are found where *Podarcis muralis* has become established, so that interspecific competition between *Podarcis muralis* and native lizards has not been observed (Hedeen 1984). On Vancouver Island, *Podarcis muralis* has been introduced into areas occupied by the native alligator lizard (*Elgaria coerulea*), raising the possibility of competitive interactions.

These two species share space on a large scale, but what habitat selection choices do they make on a small scale? Partitioning of habitat and resource use has been shown to mitigate the effects of competition within and between species (Angert et al. 2002, Gabor et al. 2001, Munday et al. 2001, Vanhooydonck et al. 2000, Capula et al. 1993). Detection of microhabitat use overlap serves to identify a potential for competitive interactions; however, other factors such as behaviour and resource partitioning still might prevent high levels of competition. Nonetheless, a comparative analysis of the habitats used by these two species should serve as an initial indicator of the potential for negative competitive effects of *Podarcis muralis* on *Elgaria coerulea.*

Data on the habitat characteristics of sites where *Podarcis muralis* occurs also are important for making predictions about where this species will spread in the future. In its native habitat and in North America, *Podarcis muralis* typically is associated with human developments (Arnold and Burton 1978, Hedeen 1984, Brown et al. 1995, Hedeen and Hedeen 1999). Diffusion along manmade corridors (e.g. railways) has been observed for this species (Hedeen and Hedeen 1999) and should be expected on Vancouver Island.

The objectives of this study were: (a) to compare habitats used by *Podarcis muralis* and *Elgaria coerulea*, in order to assess potential for small scale co-occurrence and competition; (b) to quantify habitat used by *Podarcis muralis*, in order to facilitate prediction of future patterns of dispersal. These objectives were achieved through collection and analysis of small-scale habitat data obtained from individual lizard locations (both species), coupled with documentation of locations of populations of *Podarcis muralis* and apparent diffusion patterns on Vancouver Island.

Methods

I collected habitat data from April 28 - May 16, 2003. I completed plots both at locations where individual *Podarcis muralis* and *Elgaria coerulea* were found and at random locations. Random plots were located a 2-minute walk in a randomly chosen direction from each lizard plot. Plots were 1m x 1m square, the centre point being where the lizard was first seen (lizard plots) and the location where 2-minutes ended (random plots). To prevent bias during positioning of the square, one side always pointed north. If more than one lizard was seen at a location, only one plot was completed, based on the first lizard observed.

I recorded the following habitat variables for each plot: aspect (0-360°); slope (%); distance to nearest rock (cm), shrub (cm), forest edge (m), road or powerline (m); percent cover of gravel, moss, leaves, soil, solid rock, loose rock, vegetation, shrub, coarse woody debris, tree canopy. I also recorded the substrate on which the lizard was found (on log, on rock, on cement, on dirt, on moss, on wood, on dirt/rock, in dead vegetation, in vegetation, under rock) and the mesoslope of the location (crest, upper, middle, lower, toe, level).

Habitat characteristics from *Podarcis muralis* and *Elgaria coerulea* locations (both lizard sites and associated random sites) were compared using an independent sample t-test. Chi-square tests were used to compare relative frequencies of substrate and mesoslope variables. To ensure expected values of greater than two in the Chi-square test, the categories (see paragraph above) were grouped together based on similarity to form three categories per variable. I used paired t-tests to compare the habitat characteristics of individuals of each species with the corresponding random location data.

Results

Podarcis muralis were restricted to human-altered habitats, specifically roadsides, fence lines, powerlines, cement foundations, and houses. *Elgaria coerulea* were found at two types of sites, natural (e.g. regional and city parks) and powerlines. Although I considered parks to be natural sites, I also accounted for proximity of lizards to manmade features within the parks such as roads and major trails.

Mean values for aspect ($t = 3.295$, df = 41, $P = .002$), distance to nearest powerline or road ($t = 3.965$, df = 41, $P < .0001$), distance to forest edge ($t = 2.260$, df = 41, $P = .029$) and percent cover of moss ($t = 2.761$, df = 41, $P = .009$) were significantly different between locations where *Podarcis muralis* and *Elgaria coerulea* were found (Table 4.1). Although *Podarcis muralis*, on average, were found much farther from rocks

Table 4.1 Mean values and standard deviations for habitat variables collected at *Podarcis muralis* (Pm), *Elgaria coerulea* (Ec) and associated random locations. Significant comparisons between Pm and Ec sites (independent samples t-test, $P < .05$; superscript circle), Pm and Pm random locations (paired t-test, $P < .05$; superscript triangle), and Ec and Ec random locations (paired t-test, $P < .05$; superscript square) are summarized.

	P. muralis		*E. coerulea*		Pm Random		Ec Random	
	(n = 21)		(n = 22)		(n = 21)		(n = 22)	
Habitat Variable	Mean	SD	mean	SD	mean	SD	mean	SD
aspect (°)	$109.8^{\bullet}$	111.7	$210.3^{\bullet}$	87.5	107.5	127.7	198.6	108.4
slope (%)	24.1	30.7	31.6	22.6	16.3	17.4	22.6	22.6
distance to:								
rock (cm)	$14.9^{\blacktriangle}$	35.7	0.1	0.2	$72.7^{\blacktriangle}$	44.4	10.5	29.0
shrub (cm)	$2.1^{\blacktriangle}$	3.5	2.5	3.8	$6.1^{\blacktriangle}$	9.3	2.3	3.3
forest edge (m)	$73.1^{\bullet}$	79.3	$31.7^{\bullet}$	32.5	67.0	85.0	28.7	41.4
powerline/road (m)	$0.1^{\blacktriangle\bullet}$	0.2	$40.9^{\bullet}$	47.2	$3.1^{\blacktriangle}$	5.1	43.2	49.5
% cover:								
shrub	$15.6^{\blacktriangle}$	21.3	$11.2^{\blacksquare}$	18.3	$47.4^{\blacktriangle}$	42.9	$30.8^{\blacksquare}$	40.1
coarse woody debris	6.9	11.8	4.8	13.5	6.4	16.5	4.9	6.9
tree canopy	11.7	28.1	6.8	23.4	31.3	43.6	25.2	38.2
gravel	5.5	13.6	0.1	0.6	0.05	0.2	0.0	0.0
moss	$7.3^{\blacktriangle\bullet}$	22.3	$30.1^{\bullet\blacksquare}$	31.1	$51.4^{\blacktriangle}$	49.5	$47.4^{\blacksquare}$	46.4
leaves	1.4	2.7	1.8	2.5	2.2	3.5	14.4	30.5
soil	2.7	6.2	2.6	10.7	3.0	13.1	1.1	4.3
solid rock	$9.3^{\blacktriangle}$	18.6	8.0	14.0	$0.0^{\blacktriangle}$	0.0	7.0	21.6
loose rock	$20.1^{\blacktriangle}$	31.7	$22.3^{\blacksquare}$	26.5	$0.8^{\blacktriangle}$	2.5	$1.0^{\blacksquare}$	2.9
vegetation	40.2	39.1	48.3	35.0	40.7	45.7	37.3	33.8

than *Elgaria coerulea* (Table 4.1), this difference was not significant; because there was an obvious problem of high heterogeneity of variance in this comparison, I also tested it using a non-parametric Mann-Whitney test, but obtained the same result. These two species also were found on different types of substrates ($\chi^2 = 29.6$, df = 2, $P < .0001$; Fig. 4.1) and different mesoslopes ($\chi^2 = 21.9$, df = 2, $P < .0001$; Fig. 4.2). *Podarcis muralis* were found mainly on rock or cement on level areas with ESE (109.8°) aspects, whereas *Elgaria coerulea* were mainly located in vegetation or under rocks in the middle of SSW (210.3°) slopes (Table 4.1, Figs. 4.1, 4.2).

Several of the habitat characteristics of each species differed from their corresponding random plot characteristics (Table 4.1). *Podarcis muralis* were significantly closer to rocks ($t = 4.504$, df = 20, $P < .0001$), shrubs ($t = 2.214$, df = 20, $P = .039$) and powerlines/ roads ($t = 2.804$, df = 20, $P = .011$) than their associated random locations. I found less percent cover of moss ($t = 4.017$, df = 20, $P = .001$) and shrub ($t = 3.075$, df = 20, $P = .006$), and greater percent cover of loose rock ($t = 2.870$, df = 20, $P = .009$) and solid rock ($t = 2.297$, df = 20, $P = .033$) at *Podarcis muralis* sites, compared to associated random sites. *Elgaria coerulea* sites had less percent cover of shrub ($t = 2.902$, df = 21, $P = .009$) and moss ($t = 2.116$, df = 21, $P = .046$), and higher percent cover of loose rock ($t = 3.784$, df = 21, $P = .001$) than associated random sites.

Discussion

Likely the most distinguishing feature between *Podarcis muralis* and *Elgaria coerulea* locations was the close proximity of *Podarcis muralis* to roads and/or powerlines. Since this habitat variable appears to be one of the primary predictors of

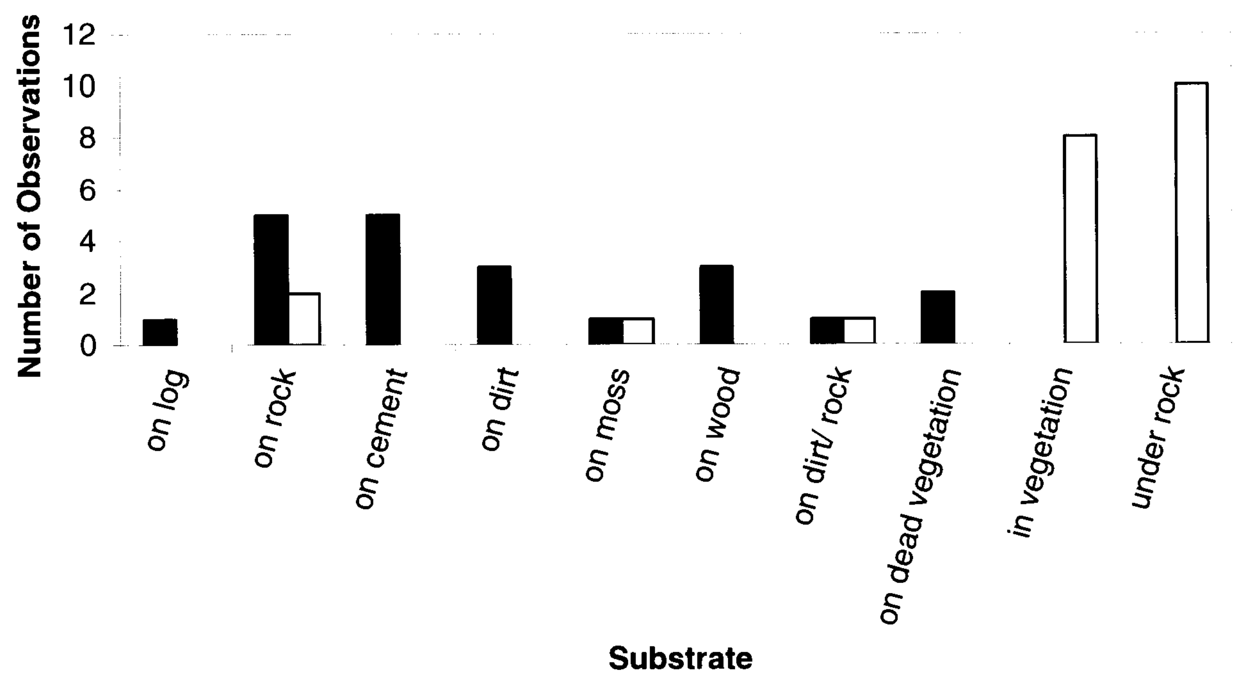


Fig. 4.1 Number of *Podarcis muralis* (Pm; black bars) and *Elgaria coerulea* (Ec; white bars) sightings at various locations (on log, on rock, on cement, on dirt, on moss, on wood, on dirt/rock, in dead vegetation, in vegetation, under rock). Chi-square tests analyzed three categories created by grouping similar substrate categories. These groupings were: 1)on log, on rock, on cement, on moss, on wood, 2) on dirt, on dirt/ rock, on dead vegetation and 3) in vegetation, under rock.

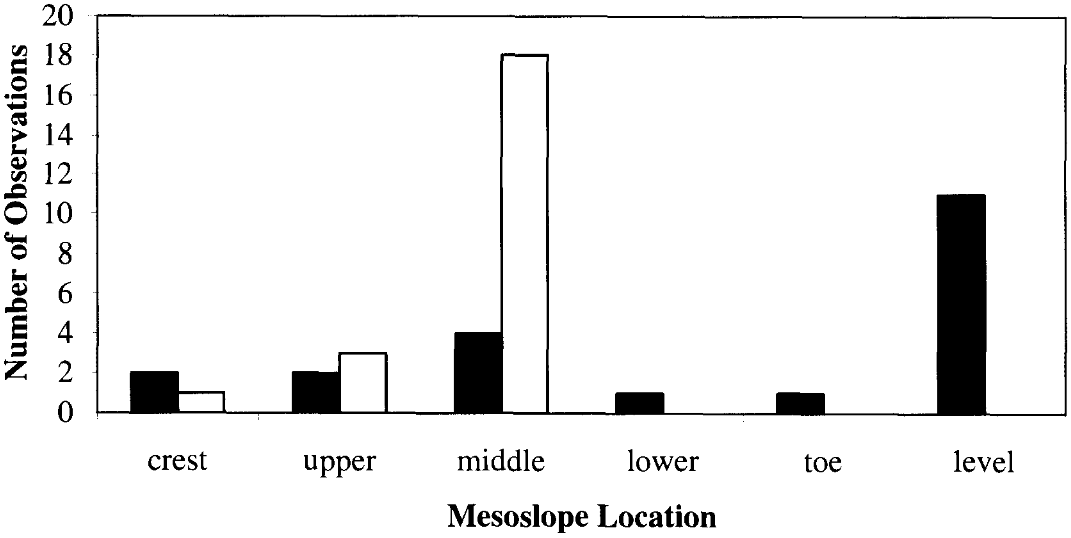


Fig. 4.2 Number of *Podarcis muralis* (Pm; black bars) and *Elgaria coerulea* (Ec; white bars) sightings at various mesoslope locations (crest, upper, middle, lower, toe, level). Chi-square tests analyzed three categories created by grouping similar mesoslope categories. These groupings were: 1) crest, upper, 2) middle and 3) lower, toe, level.

Podarcis muralis habitat use, we can predict that further expansion along roads and powerlines will occur. However, when these corridors intersect human developments, (e.g. residential and commercial areas), the rate of diffusion may change. Roadsides and powerlines are generally uniform in structure, compared to areas with features such as buildings and parking lots, where suitable habitat is separated by inhospitable areas (Hedeen and Hedeen 1999). This raises an opportunity for future investigation, the prediction being a diffusion pattern of rapid expansion along roads/powerlines and relatively slower expansion rates through residential/commercial areas.

Currently, the spread of *Podarcis muralis* along roads and powerlines also is bringing the lizards to recreation (Gowland-Tod Provincial Park) and industrial areas (Hartland Road Landfill), which contain features (e.g. disturbed soils, wood piles, rock and concrete walls etc.) that these lizards find hospitable. The potential for interactions with members of the public also is increased at these types of areas. Movement of *Podarcis muralis* by humans over long distances, resulting in satellite populations, is documented in Kentucky (Draud and Ferner 1994), Ohio (Deichsel and Gist 2001) and Vancouver Island (see Chapter 1). These satellite populations bring *Podarcis muralis* into new areas exposing them to new corridors of range expansion.

I found that *Podarcis muralis* were most often on the surface, while *Elgaria coerulea* were usually in vegetation or under rocks (Fig. 4.1). *Elgaria coerulea* are diurnal (Vitt 1973) and most likely to be found in the open between 1 and 4pm (Rutherford and Gregory 2003). Aside from mating behaviour (Vitt 1973) and basking (Vitt 1973, Rutherford and Gregory 2003), *Elgaria coerulea* are rarely observed in the open. By contrast, *Podarcis muralis* were observed exclusively in the open during this study. Given suitably warm weather, there was no need to look under rocks or other cover objects because *Podarcis muralis* were commonly observed moving or basking in the habitat. Searching in this study occurred primarily during warm weather; however, if searching was expanded to cooler weather, for example during early spring, late fall, or early and late in the day, *Podarcis muralis* would likely be found more often under cover.

Both species of lizards are found on powerlines, and I recorded their co-occurrence at one such site that I examined (adjacent to original release site). Since *Elgaria coerulea* are found on at least one other powerline (intersects Prospect Lake Road approximately 2km south of Prospect Lake Golf Course) that has not yet been invaded by *Podarcis muralis,* the potential for further contact is high at these types of sites. Proximity of *Elgaria coerulea* to cover varies with time of day and age class, but individuals generally stay within 1m of cover objects or retreat sites (Rutherford and Gregory 2003). *Podarcis muralis* are known to use territories where they maintain preferred sunning and retreat areas linked by specific routes of travel (Boag 1973, Brown et al. 1995). Although *Elgaria coerulea* typically were found much nearer rocks than were *Podarcis muralis* (Table 4.1), this difference fell short of statistical significance. However, assuming that both species use rocks as retreat sites, individuals of both species could depend on the same rock as cover in some cases. Whether interspecific interactions occur under cover objects, if or when both species share this space, emerges as an important research question.

Sites where both lizards were found had less percent cover of moss and shrub, and greater percent cover of loose rock, than nearby random sites. Both species appear to be selecting microhabitat sites that provide sufficient sunlight, substrate suitable for thermoregulation and convenient cover/ retreat sites. A pattern of non-uniform distribution in the habitat, whereby pockets of habitat such as rock outcrops and stone walls, are preferred, while areas of surrounding forest or dense shrub are avoided, is observed for both *Podarcis muralis* (Allen et al. 1992, Brown et al. 1995) and *Elgaria coerulea* (P. Rutherford *pers. comm.*, Stewart 1985).

Although this study provides a starting point for comparing habitat use of these two lizards species, certain deficiencies exist due to the small number of sites where data collection occurred. Interpretation is somewhat confounded by the inherent differences of these sites. For example, in this study, *Podarcis muralis* were found on level mesoslopes while *Elgaria coerulea* were found in the middle of slopes. Is this difference due to variation in the two species' habitat preferences or simply due to the fact that many of the *Podarcis muralis* were found on roadsides which are generally level and *Elgaria coerulea* were located in parks (e.g. Mount Douglas) which contain slopes? This would be remedied by examining many more sites, for example, several sites with both species (for direct comparison with each other) and several with one or the other species (for comparison with the sites at which they co-occur to detect habitat shifts due to interspecific competition).

Chapter 5

Behaviour of *Elgaria coerulea* and *Podarcis muralis* in Paired Encounters

Introduction

The evolution of species assemblages in nature produces a complex system of resource use and niche partitioning. The introduction of a non-native species inevitably alters the balance on some level (Davis 2003). If habitat overlap occurs between ecologically similar introduced and native species, certain sites may be important for both species, resulting in interspecific competition and potential negative effects on the native species. The European Wall Lizard, *Podarcis muralis*, was introduced to the Saanich Peninsula of Vancouver Island in 1970 and is established and spreading. One native lizard species, the Northern Alligator Lizard (*Elgaria coerulea*), also is found on Vancouver Island (Gregory and Campbell 1984). Although the two species apparently have different habitat preferences, those preferences overlap to varying degrees and both species therefore coexist at some sites (Chapter 4). Thus, any study of the impact of one species on the other requires study of their interactions at the level of individual lizards.

Cover plays an important role in many aspects of reptile ecology, influencing, for example, thermoregulation (Kearney 2002), predator avoidance (Reaney and Whiting 2003), and reproduction (Shine 1999). Lizards exhibit behaviours ranging from aggregation under a common cover object (Shah et al. 2003) to interference competition for preferred basking sites (Downes and Bauwens 2002). In situations where common use of cover objects is not observed, avoidance or exclusion by one species or the other may be occurring.

Avoidance of specific sites may be aided by chemosensory and/or scent cues. Lizards are known to use scents to facilitate activities such as predator avoidance (Stapley 2003), prey identification (Cooper and Perez-Mellado 2002) and conspecific identification (Cooper and Perez-Mellado 2002). In terms of conspecific identification, faecal pellets (Aragon et al. 2000) and pheromones (Cooper and Perez-Mellado 2002, Font and Desfilis 2002) both contain chemicals that are detected and interpreted by lizard chemosensory organs. Hence, chemical odours of one species could affect behaviour of individuals of another species, without actual physical interaction between lizards.

Exclusion from habitat features, such as cover objects, might also occur through interference competition. Lizards interact in several ways, for example, via signalling body postures (Peters and Ord 2003) and via chasing and biting (Sheldahl and Martins 2000). These interactions range from subtle to overt and may be associated with territoriality, mating, etc. Individuals that win or dominate during encounters are rewarded with a superior breeding territory, mate, or foraging area.

I undertook three experiments to explore the outcome of interactions between *Podarcis muralis* and *Elgaria coerulea* in close quarters. The objectives of these experiments were: 1) determine the effect of *Podarcis muralis* scent on *Elgaria coerulea* behaviour; 2) quantify the nature and outcome of paired encounters between these two lizards; and 3) determine if *Elgaria coerulea* avoid sharing cover objects with *Podarcis muralis*.

Methods

All three experiments took place in a quiet laboratory with restricted access. In order to minimize stress due to transportation, the cages containing *Elgaria coerulea* (home cages) were moved to the laboratory 24 hours before each experiment. *Podarcis muralis* were maintained in an adjacent laboratory; it took less than 2 minutes to transport them to the experimental laboratory. I fed all lizards 24 hours before each experiment and immediately after each experiment. Water dishes were placed in all experimental cages in which a lizard was contained for more than 20 minutes. I used soap and water to thoroughly clean nine 45 X 25 X 30 cm plastic cages for each experiment; all cover objects and water dishes placed in experimental cages also were washed in the same manner before each experiment.

Experiment 1

The odour experiment took place 10 December 2002. I covered all four sides of the cages with white paper to prevent visual distractions during the experiment. Half of the bottom of each cage was covered with a clean piece of absorbent cage liner, while the other half was covered with a piece soiled with *Podarcis muralis* odour. The soiled pieces were obtained by placing two randomly chosen male and two randomly chosen female *Podarcis muralis* in a 15 X 25 X 2 cm container with cage liner for 24 hours before the experiment. The wall lizards had been fed just prior to being placed in the containers. On the morning of the experiment heat lamps were not turned on to ensure all *Elgaria coerulea* had body temperature similar to room temperature during the experiment. The temperatures of each side of the cage were measured before and after the experiment.

Using a camera stand, I set up a video camera to record the cages from overhead; the camera was placed high enough to record the entire floor area of the cage. I randomly selected an *Elgaria coerulea* and placed it in the middle of the experimental cage. After 15 seconds, I started video recording. After 20 minutes of recording, I stopped the camera and placed the *Elgaria coerulea* back in its home cage. I watched the videotapes, recording the amount of time each lizard spent on the clean and odour-soiled sides of the cage.

Experiment 2

I undertook the paired-encounter experiment on December 11-12, 2002. I placed a clean piece of absorbent cage liner over the bottom of each cage and covered both ends and one side with white paper. A cover object, with an opening on one side, was placed in the middle of the cage, positioned with the closed end touching the covered side of the cage and the open end facing the uncovered side. I set up a video camera to record through the uncovered side of the cage, facing into the open end of the cover object.

The largest *Podarcis muralis* were identified, in an attempt to size match the two species, since interactions between similarly sized *Podarcis muralis* are more aggressive (Boag 1973). Individuals from this group were randomly selected and paired with randomly selected *Elgaria coerulea. Podarcis muralis* were placed on a randomly selected side of the experimental cage under a plastic container; I placed *Elgaria coerulea* at the opposite side of the cage, uncovered. After measuring the temperature of the cage bottom, I released the *Podarcis muralis* and started video recording. After 60 minutes, recording was stopped and the lizards were returned to their home cages. I watched the videotapes, recording the number of times each species approached the other while in the open (approaches that occurred when a lizard was under cover were not included), the number of times each species retreated from such an approach, and the amount of time each species spent under the cover object. I defined an approach as one lizard moving towards the other (from the front or from behind) in a deliberate way. This was usually characterized by a slow, steady approach where the approaching lizard appeared to be interested in investigating the other lizard. Retreats ranged from fast to slow in speed (e.g. quick jerk to slow reverse movement), but were defined by either lizard in the encounter changing its focus from the other lizard to some other acitivity (e.g. investigating the cage, trying to escape).

Experiment 3

The final experiment tested differences in proximity of *Elgaria coerulea* to cover objects with captive *Podarcis muralis* (10 May 2003) or empty controls (17 May 2003). The experimental cage setup included two cover objects, a water dish and a heat lamp (Fig. 5.1). Twenty-four hours before commencement of the experiment, an *Elgaria coerulea* was placed in each cage to establish residency. A cardboard tube with holes punched in it and screens at each end held the *Podarcis muralis* captive. The experiment began at 8 am, at which time I placed the tube under the cover object that the resident *Elgaria coerulea* was under or closest to. Every hour for the next 12 hours the location of *Elgaria coerulea* with respect to the captive *Podarcis muralis* was recorded. Three positions were used to describe *Elgaria coerulea* location: 1) under the same cover object as *Podarcis muralis* or in the immediate vicinity (within

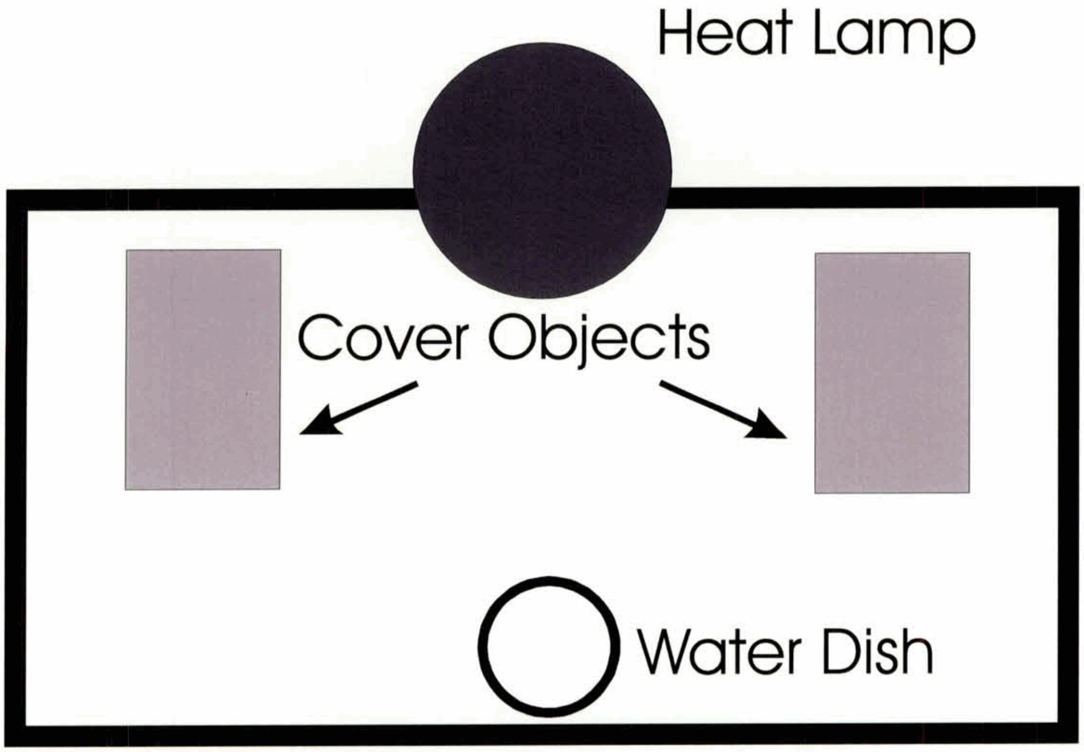


Fig. 5.1 Experiment 3 cage set up. A *Podarcis muralis* held captive in a tube, or a control tube (empty tube), was placed under one of the two cover objects.

5cm) of this cover object, 2) basking directly under the heat lamp and 3) under or in the immediate vicinity of the cover object where *Podarcis muralis* was not located. I repeated the experiment the next week, replacing the *Podarcis muralis* tube with a clean empty tube.

The statistical methods I used are described separately for each experiment in Results.

Results

Experiment 1

Because *Elgaria coerulea* spent some time exploring the walls of the cage and attempting to escape, I deducted time engaged in such activity from the total time in each experimental trial. I then used paired-sample t-tests to compare the mean proportion of time spent on the *Podarcis muralis*-scented side of the cage versus the clean, unscented side. I found no difference in the mean proportion of total time that *Elgaria coerulea* spent on the clean or scented side of the cage (t = .887, df = 8, P = .401; Fig. 5.2).

Experiment 2

The number of times each species approached the other, and the number times each species or neither species retreated from an encounter were calculated as a proportion of the total number of approaches. Only encounters that occurred when both species were in the open were used. The overall variance of the estimated

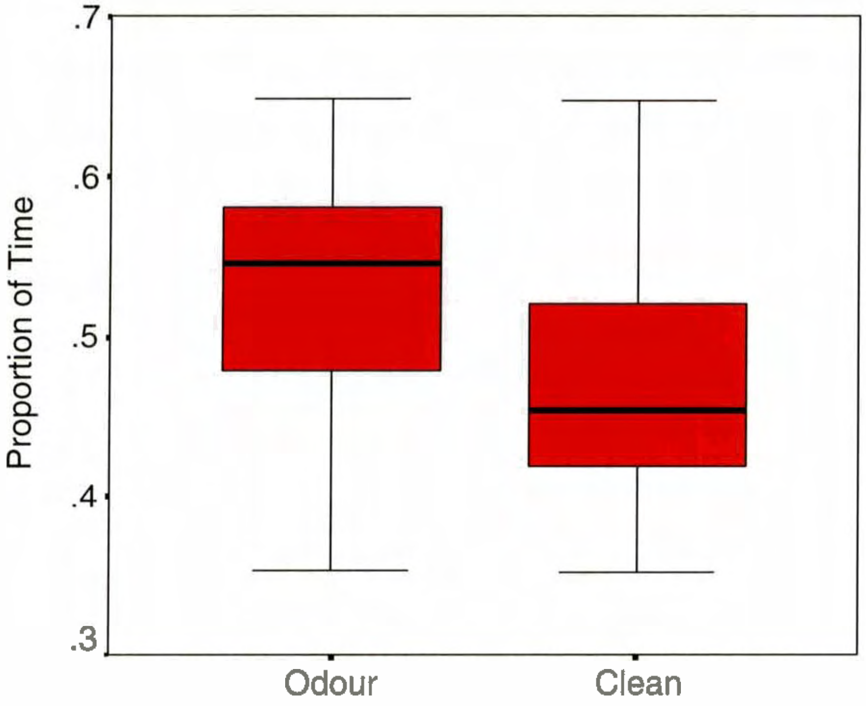


Fig. 5.2 Proportion of time (total time minus time spent trying to escape) that *Elgaria coerulea* spent on areas scented with *Podarcis muralis* odour vs. unscented. Boxes represent the interquartile range, the vertical lines extend to the highest and lowest values and the horizontal black lines indicate the median (n = 9).

proportion was calculated for each species by pooling encounter data from eight trials (the ninth trial was omitted from the analysis because no encounters occurred in the open). The formula used follows Waye and Gregory (1993):

$$p\ (\text{approach, retreat}) = \frac{\Sigma\ a_{i,j,k}}{\Sigma\ m}$$

where a = the number of retreats or approaches made by *Podarcis muralis* (i) and *Elgaria coeruela* (j), or number of retreats by neither species (k), m = total number of approaches. Again, following Waye and Gregory (1993) I calculated variance with:

$$V\ (p) = \frac{1}{ns^2}\ \frac{[\ \Sigma a^2 - 2p\ \Sigma am + p^2\ \Sigma m^2\ ]}{n - 1}$$

where n = number of lizards in the sample and s = the average number of approaches. Approximate 95% confidence intervals were calculated as 2 V(p).

I found no difference between the proportion of retreats observed for *Podarcis muralis*, *Elgaria coerulea* or neither species (Fig. 5.3). *Podarcis muralis* approached *Elgaria coerulea* significantly more often than vice versa (Fig. 5.4). I observed only one example of overtly aggressive behaviour, when an *Elgaria coerulea* briefly chased and bit an approaching *Podarcis muralis*. Paired-sample t-tests were used to compare the amount of time each species spent under cover; *Elgaria coerulea* spent a significantly greater amount of time under the cover object than did *Podarcis muralis* (t = 3.681, df = 8, P = .006; Fig. 5.5).

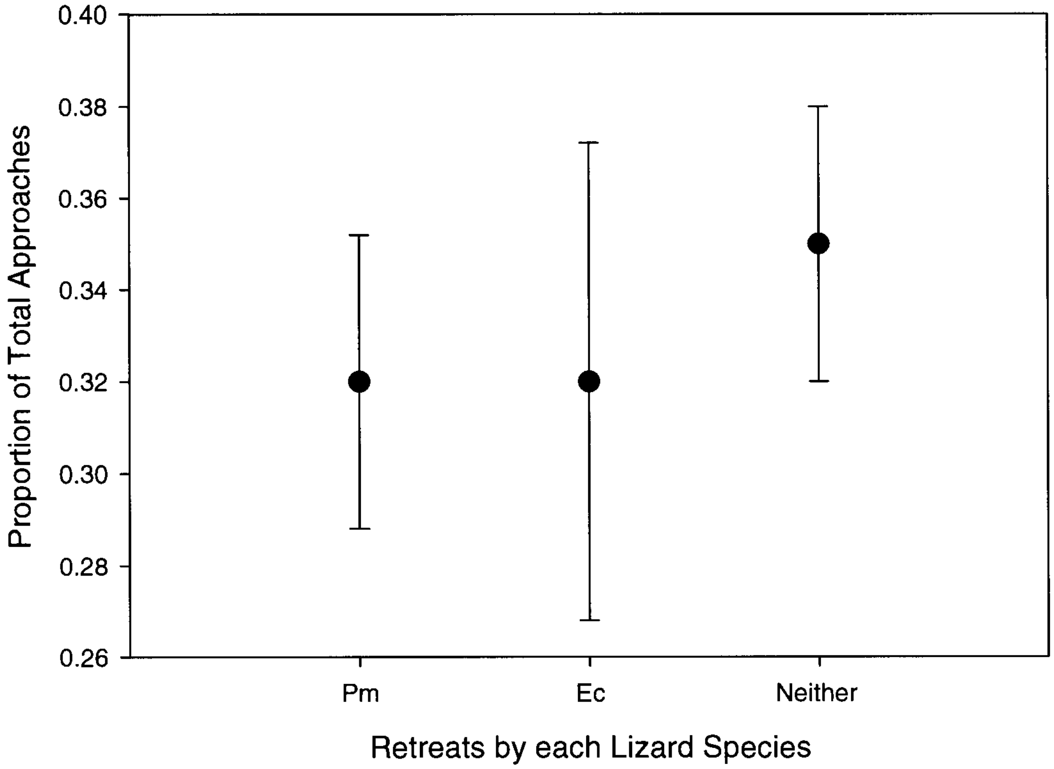


Fig. 5.3 Retreats as a proportion of total approaches for each species (Pm = *Podarcis muralis*, Ec = *Elgaria coerulea*, neither = neither species retreated). Vertical lines are approximate 95% confidence limits.

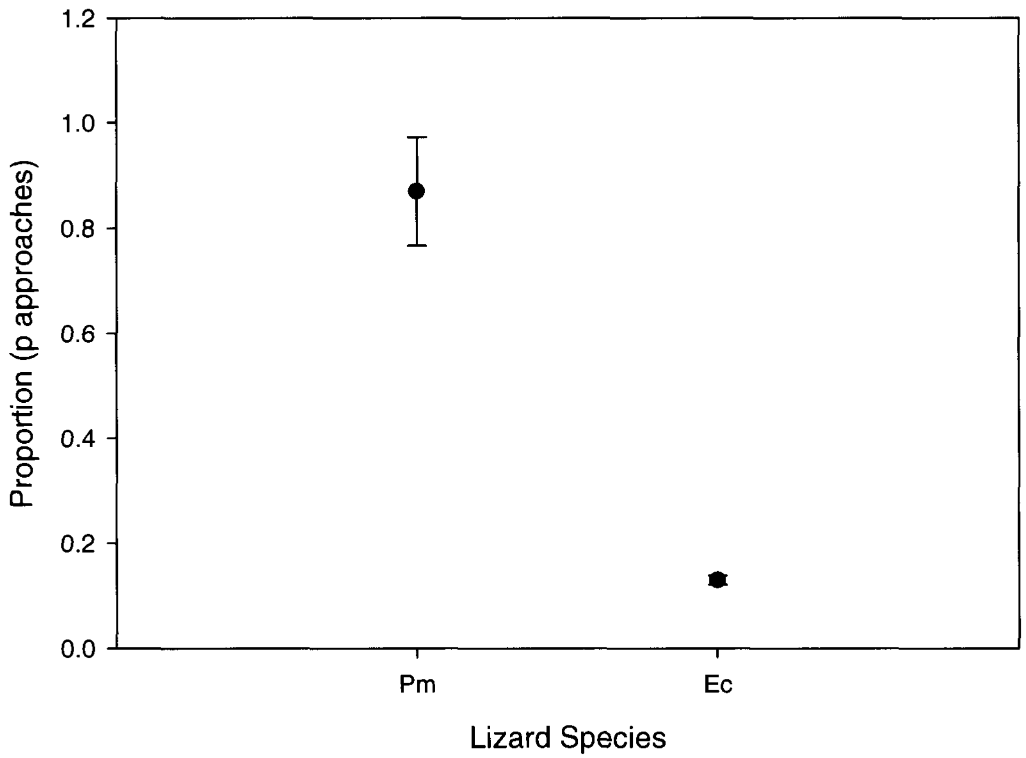


Fig. 5.4 Approaches by each species as a proportion of total approaches (Pm = *Podarcis muralis*, Ec = *Elgaria coerulea*). Vertical lines are approximate 95% confidence limits.

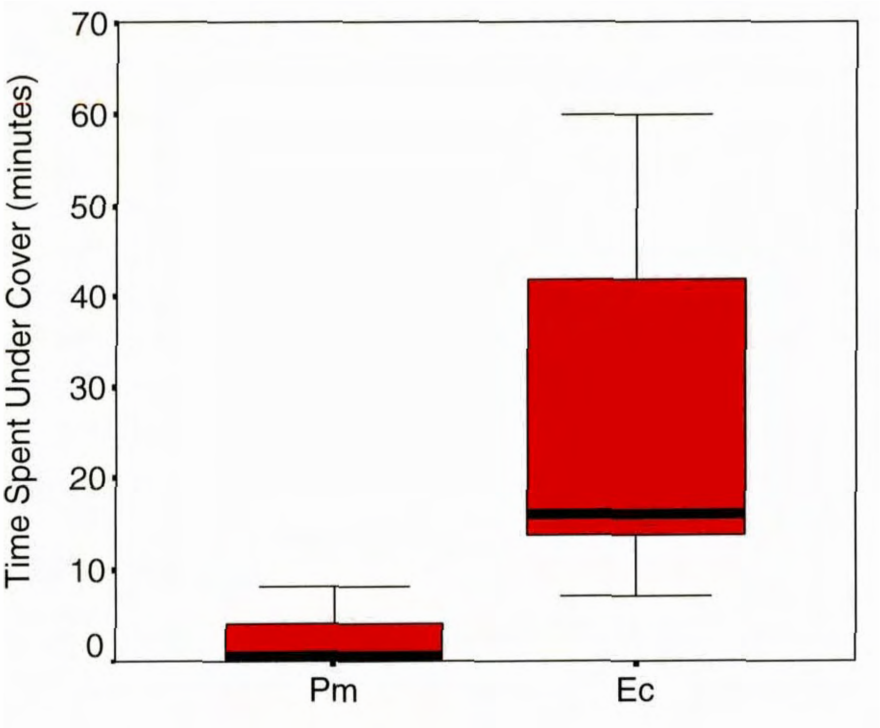


Fig. 5.5 Total time that each *Podarcis muralis* (Pm) and *Elgaria coerulea* (Ec) spent under cover. Boxes represent the interquartile range, the vertical lines extend to the highest and lowest values and the horizontal black lines indicate the median (n = 9).

Experiment 3

I used chi-square tests to analyze differences between the position of *Elgaria coerulea* (see Methods), when *Podarcis muralis* were, and were not, held captive under a cover object. When a tube containing *Podarcis muralis* was under a cover object, *Elgaria coerulea* were observed far from this cover object a significantly greater number of times ($\chi^2 = 16.0$, df = 8, $P = .042$; Fig. 5.6) than when the tube was empty. The proportion of observations of *Elgaria coerulea* close to the experimental tube, or basking, did not differ between the two experiments ($\chi^2 = 10.67$, df = 9, $P =$ .299 and $\chi^2 = 2.53$, df = 4, $P = .639$, respectively; Fig. 5.6).

Discussion

Collectively, these experiments suggest that interactions between *Podarcis muralis* and *Elgaria coerulea* may be fairly complex. *Podarcis muralis* initiated approaches more often than *Elgaria coerulea*, but both species retreated from encounters equally as often. This, plus the small number of observations of overt aggression, suggests that the interaction between these two species is a neutral one. On the other hand, choice of cover object by *Elgaria coerulea* apparently was negatively affected by the presence of *Podarcis muralis*, suggesting possible competition for retreat sites. If *Elgaria coerulea* do avoid *Podarcis muralis*, however, the cue used apparently is not chemical.

This latter result is perhaps surprising. Recognition of, and behavioural response to, odours is well documented in squamate reptiles (Halpern 1992, Mason

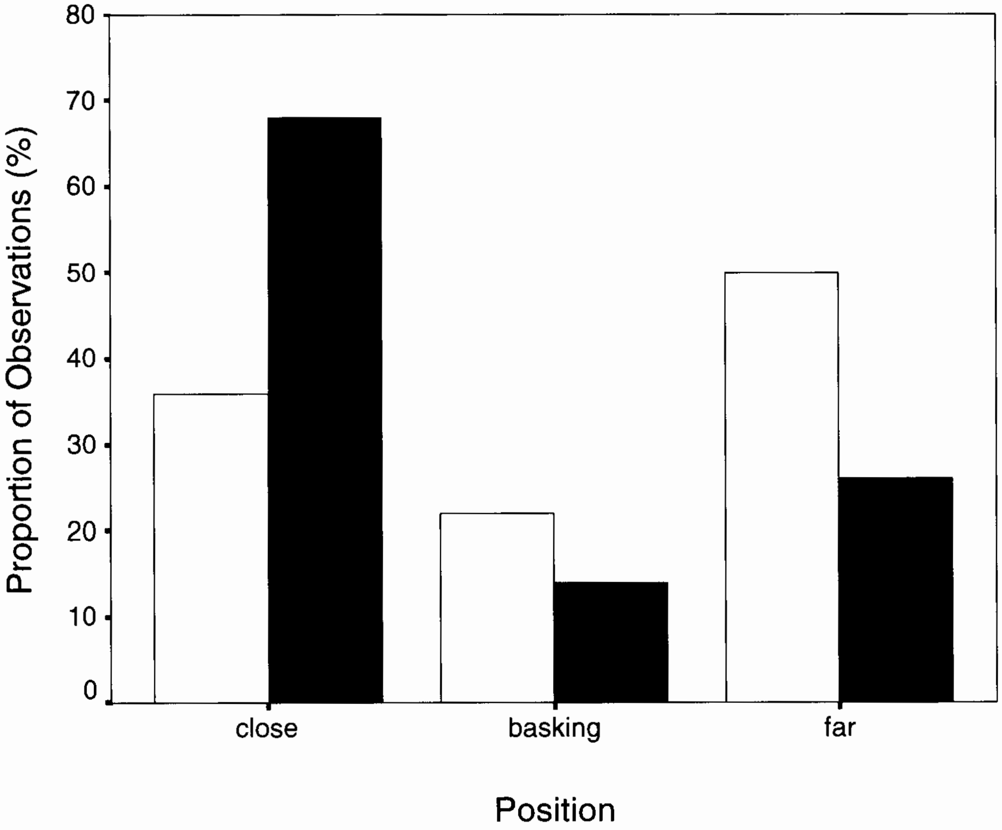


Fig. 5.6 Proportion of observations of *Elgaria coerulea*, relatively close to, or far from, a *Podarcis muralis* individual held captive in a tube (white bars) or an empty tube (black bars). Observations of basking are also shown (n = 9).

1992). For example, faecal pellets are used to delineate territories by some lizard species (Aragon et al. 2003, Carpenter and Duvall 1995). Memory and familiarity of neighboring lizards (the “dear enemy” hypothesis) is a possible means of minimizing the costs of aggressive encounters (Trigosso-Venario et al. 2002, Paterson 2002, Whiting 1999) and conspecific odour recognition has been suggested as a means of identifying such familiar individuals (Aragon et al. 2002).

Nonetheless, despite the apparent importance of chemical cues to squamates (especially scleroglossans, which include *Elgaria coerulea*), I found *Podarcis muralis* scent (primarily feces and urine) to have no detectable effect on behaviour of *Elgaria coerulea*. This might have been because test papers had been inadequately scented. More likely, though, it was due to inadequate features of my experimental design (very artificial environment, insufficient time for *Elgaria coerulea* to “settle”, inadequate length of observation period). Furthermore, the scent of *Podarcis muralis* presumably was completely novel to the *Elgaria coerulea* I used in this experiment because they came from a site that *Podarcis muralis* is not known to have invaded. The experimental conditions simply may have provided a safe opportunity to investigate the scent.

In paired encounter experiments, more encounters were initiated by *Podarcis muralis*. I predicted the more aggressive or dominant species to initiate and/ or ‘win’ a higher percentage of encounters. In fact, very few of the encounters appeared aggressive in nature and there was no statistical difference between the proportion of retreats exhibited by each species.

In nature, *Podarcis muralis* maintain territories, and patrol these areas in the open on a regular basis (Boag 1973, Brown et al. 1995), although their activity pattern in summer is bimodal, with reduced activity during the warmest times of the day (Braña 1991). Conversely, Rutherford and Gregory (2003a) found 62% of approximately 240 *Elgaria coerulea* under cover. Observations from this study are in agreement with these observations. In my study of habitat preferences (Chapter 4), I observed *Podarcis muralis* exclusively in the open, but found the majority of *Elgaria coerulea* by lifting rocks. Similarly, in these experiments, *Elgaria coerulea* used cover much more of the time than did *Podarcis muralis.* Thus, differences in activity levels, rather than dominance or aggression, might explain the higher percentage of encounters initiated by *Podarcis muralis.*

I found that *Elgaria coerulea* avoided a cover object with a *Podarcis muralis* held captive in a tube under it, versus a control (clean, empty tube). A study examining habitat use and movement patterns of *Elgaria coerulea* and Western Skinks (*Eumeces skiltonianus*) found the two species to use the same cover objects, but never at the same time; only copulating pairs and newborns from the same litter were found under a cover object at the same time (Rutherford and Gregory 2003b). These results, combined with observations from the odour experiment, suggest the physical presence of another lizard, not their scent alone, deters *Elgaria coerulea* from simultaneously using a cover object with another lizard. In snakes, by contrast, instances of multiple individuals, and often multiple species, using the same cover object are common (Gregory 2004).

These experiments represent a preliminary investigation into the interactions between *Elgaria coerulea* and *Podarcis muralis*. Further experimentation should focus on increasing the complexity of the experimental arena (e.g. paired encounters in a larger, more natural environment). Longer-term experiments in such conditions would determine if patterns of habitat use (e.g. temporal) are contributing to or mitigating competition. Staging encounters where a resource (e.g. basking site, food or cover object) is in limited supply may have an effect on the level of aggression, and would provide further insight into the nature and potential for competition between these two species.

Conclusions

The introduction of non-native species and its subsequent effects is one of the leading practical issues facing ecologists today. The modern 'global' community and associated human activities (e.g. trade, tourism) are the primary cause of such introductions. Collecting information on the ecology of these introduced species in their new habitat is key to understanding both their patterns of spread and effects on other species. The European Wall lizard (*Podarcis muralis*) was introduced to Vancouver Island in 1970, but its effects, if any, on native fauna have not been documented. This study addressed the pattern of spread, and aspects of the life history and ecology of *Podarcis muralis* that might contribute to negative effects on the native Northern Alligator lizard (*Elgaria coerulea*). Major conclusions of this study are:

- the spread of *Podarcis muralis* is occurring primarily through diffusion along roads and powerlines; however, 'jump dispersal' facilitated by humans also has produced at least two satellite populations
- *Podarcis muralis* on Vancouver Island are primarily associated with habitats altered by humans in some way; although *Elgaria coerulea* also can occur in such habitats, there were significant overall differences in characteristics of habitats in which I found the two species; both species seem to require habitats with rocks or other cover, but *Podarcis muralis* are usually seen in the open during the day, whereas *Elgaria coerulea* are usually found under cover
- co-occurrence of *Podarcis muralis* and *Elgaria coerulea* has been documented at one site at least; as *Podarcis muralis* spreads there is potential for higher incidence of co-occurrence

- *Podarcis muralis* and *Elgaria coerulea* differ substantially in key life-history characteristics; the former is oviparous and capable of multiple clutches per year, whereas the latter is viviparous and produces a single litter annually; the life history of *Podarcis muralis* is likely a key factor contributing to its explosive population growth in areas where it has been introduced in North America
- I found evidence that *Podarcis muralis*, at least with respect to its first clutch of the season, is primarily a capital breeder, relying on previously acquired, stored resources; thus, the apparently rapid population growth of *Podarcis muralis* likely is not attributable to an ability to take advantage of immediately available resources as income; as in other species of squamates, incubation temperature had significant effects on both incubation time and offspring phenotype (mass)
- there were significant locomotory performance differences between *Podarcis muralis* and *Elgaria coerulea*, but only at room temperature, at which *Podarcis muralis* sprinted faster than *Elgaria coerulea*; the ability of *Podarcis muralis* to perform well over a relatively wide range of temperatures may be a significant factor in its success as an invading species, especially if such relative temperature-insensitivity allows it to extend the length of its annual season of activity
- behavioural experiments in the laboratory suggested that *Elgaria coerulea* do not avoid areas scented with the odour of *Podarcis muralis*, but do avoid sharing cover objects with *Podarcis muralis*; paired encounters showed that *Podarcis muralis* initiated more approaches than *Elgaria coerulea*, but there was little

evidence of aggressive behaviour and both species retreated from encounters equally often

- overall, my data suggest that there is potential for negative competitive effects of *Podarcis muralis* on *Elgaria coerulea* on Vancouver Island; however, testing the population-level consequences of invasion by *Podarcis muralis* on *Elgaria coerulea* will require carefully designed and replicated field experiments and longer-term field work

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