Population profile of an introduced species, the common wall lizard (*Podarcis muralis*), on Vancouver Island, Canada

G. Michael Allan, Christopher J. Prelypchan, and Patrick T. Gregory

Abstract: Introduced species represent one of the greatest potential threats to persistence of native species. Therefore, it is important to understand the ecology of introduced species in order to develop appropriate mitigation strategies if required. In this study, using data collected in 1992–1993, we describe some fundamental population attributes of common wall lizards, *Podarcis muralis* (Laurenti, 1768), of Italian origin, introduced near Victoria, British Columbia, in the early 1970s. Male and female wall lizards reached similar snout–vent lengths, but males had relatively longer tails and were heavier. However, when gravid, females attained a body mass similar to that of males of equal snout–vent length. We found gravid females in all months from May to July, inclusive, but hatchlings did not appear in the field before late July. Growth rate was inversely related to body size, and lizards probably reached maturity in their second full summer. Larger lizards were more likely than smaller lizards to have experienced tail loss prior to capture, but the probability of tail loss upon capture was higher for smaller lizards than for adults. Our results suggest no fundamental differences in population characteristics between *P. muralis* on southern Vancouver Island and populations at sites within the species' natural range in Europe. Whether *P. muralis* on Vancouver Island is a threat to the native northern alligator lizard, *Elgaria coerulea* (Wiegmann, 1828), remains an open question.

Résumé : Les espèces introduites représentent une des menaces potentielles les plus importantes à la persistance des espèces indigènes. Il est donc essentiel de comprendre l'écologie des espèces introduites afin de mettre au point, s'il y a lieu, des stratégies appropriées de mitigation. À partir de données récoltées en 1992–1993, nous décrivons certaines caractéristiques démographiques fondamentales du lézard des murailles, *Podarcis muralis* (Laurenti, 1768), d'origine italienne qui a été introduit près de Victoria, Colombie-Britannique, au début des années 1970. Les lézards des murailles mâles et femelles atteignent des longueurs museau–cloaque semblables, mais les mâles possèdent des queues relativement plus longues et sont plus lourds. Cependant, les femelles gravides atteignent une masse corporelle semblable à celle des mâles de longueur museau–cloaque similaire. Il y a des femelles gravides durant tous les mois, de mai à la fin de juillet, mais les nouveau-nés n'apparaissent pas en nature avant la fin de juillet. Le taux de croissance est en relation inverse avec la taille du corps et les lézards atteignent probablement leur maturité sexuelle durant leur second été complet. Les grands lézards sont plus susceptibles que les petits d'avoir perdu leur queue avant la capture, mais il y a une plus forte probabilité de perte de la queue lors de la capture chez les petits lézards que chez les adultes. Nos résultats indiquent qu'il n'y a pas de différence fondamentale entre les caractéristiques démographiques de *P. muralis* dans sud de l'île de Vancouver et celles de l'espèce dans des sites de son aire naturelle de répartition en Europe. La question à savoir si *P. muralis* sur l'île de Vancouver est une menace au lézard-alligator boréal, *Elgaria coerulea* (Wiegmann, 1828), indigène reste encore sans réponse.

[Traduit par la Rédaction]

Introduction

One of the major consequences of geographic patterns of human movement and transport is the frequent relocation, either accidental or deliberate, of organisms from their native environments to foreign ones. Such alien species often fail to become established and, even if they do, may be innocuous. However, alien species can also become invasive and have negative effects on natural communities. In fact, in North America, invasive species may be the second greatest threat, after habitat destruction, to native species (Wilcove et al. 1998). Thus, the establishment of an exotic species in a new area usually raises concerns about possible influences of that species on native animals and plants.

The common wall lizard, *Podarcis muralis* (Laurenti, 1768), has a native range that encompasses much of Europe,

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G.M. Allan,[1] C.J. Prelypchan,[2] and P.T. Gregory.[3] Department of Biology, University of Victoria, P.O. Box 3020, Victoria, BC V8W 3N5, Canada.

[1] Present address: Department of Family Medicine, 205 College Plaza, University of Alberta, Edmonton, AB T6G 2C8, Canada.
[2] Present address: 15 Thor Drive, Kamloops, BC V2C 6P8, Canada.
[3] Corresponding author (e-mail: viper@uvic.ca).

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extending as far north as 50°N (Arnold and Burton 1978). This species and its congener, the Italian wall lizard, *Podarcis sicula* (Rafinesque, 1810), have also been introduced into several localities in the United States and have established persistent populations (summarized by Bertram 2004). Evidently, once dispersed, wall lizards establish themselves fairly readily. In Cincinnati, Ohio, the introduction of 2–10 *P. muralis* in 1951 was sufficient to establish a population, which has grown to 607 individuals·ha^{-1} in some areas (Hedeen 1984; Kwiat and Gist 1987; Deichsel and Gist 2001). Wall lizards have also been introduced several times in southern England, with populations persisting for varying periods of time (Smith 1973; Arnold and Burton 1978). Beebee and Griffiths (2000) review the current status of *P. muralis* in England.

In 1970, a small number of *P. muralis*, apparently of Italian origin (Gregory and Gregory 1999; Deichsel and Schweiger 2004), were released in west Saanich near Victoria, on Vancouver Island, British Columbia (lat. 48°26′N, long. 123°22′W), when a small private zoo closed (Deichsel and Schweiger 2004). Since then, *P. muralis* has become firmly established in the area near its point of release and has spread to surrounding areas on southern Vancouver Island (Bertram 2004).

The occurrence of nonnative species in an area must be taken seriously; we need to study such cases to determine the extent, if any, of impacts on native species so that mitigative action can be planned where necessary and feasible. Introduced wall lizards might compete with, and therefore negatively influence, the native northern alligator lizard, *Elgaria coerulea* (Wiegmann, 1828). Some behavioural aspects of that interaction have been studied by Bertram (2004), but knowledge of population ecology also is pertinent to both further study of interspecific competition and development of any plans to control the invading species. In this paper, we report on early work on *P. muralis* on Vancouver Island that focused on determining basic population characteristics of these lizards.

Methods

Our main study site was at the dead end of a road in the Highlands district near Victoria, but we also searched nearby areas. The main site had an open parking and turn-round area inhabited by numerous wall lizards. From there a path led through woods to other open habitats, including a hydroelectric line. We visited the main site and the surrounding area frequently (at times, daily) from May to August 1992 to capture and mark lizards. This fieldwork continued at a reduced level from May to July 1993. Since we completed this work, the site has been developed for housing and we no longer have access to it.

We used a variety of methods to capture lizards. The most reliable technique for capturing adults was “noosing”, using a dental floss noose at the end of a long, thin stick or fishing pole. We also sometimes captured adult lizards by hand (most often in rubble or piles of small rocks), but hand capture was much more successful with hatchlings and other young lizards. Finally, a few lizards were caught in traps, either a simple pit trap, consisting of a can buried in the ground with its top flush with the surface of the ground and partly covered by a board to provide shade, or the “habitat trap” described by Allan et al. (2000).

We processed most captured lizards on the spot at the field site. We determined their sex, measured (snout–vent length (SVL) and total length; tail length was obtained by subtraction) and weighed them, and then marked and released them. We determined the sex of animals by applying pressure to the base of the tail to force eversion of hemipenes of males. This method was especially helpful in identifying the sex of very young animals (Gregory 1983). The sex of adults could also be determined readily by secondary sex characters (e.g., femoral pores in males, gravid condition in females). We marked all captured animals with toe clips, using the scheme described by Waichman (1992). In addition, we painted marks on the backs of adults, using both red and white paint in dots, lines, or crosses. This was done to avoid unnecessarily frequent recapture of the same animals. The paint was lost within 2 days to approximately 2 weeks.

Sampling times varied throughout the summer, depending on activity patterns of lizards. Early in the season, lizards seemed to be most plentiful in midmorning (although this varied somewhat with weather conditions). However, later in the summer, animals were either less plentiful or less active at midmorning, so sampling times were regularly alternated between dawn and sunset (a few sampling times lasted until complete darkness). Sampling periods usually lasted as long as lizards could be caught.

We brought all gravid females that we captured back to the laboratory, where they were maintained until oviposition, whereupon we recorded clutch sizes.

Statistical methods used to analyze data are described as necessary in the Results. To maintain independence of data, no individual appeared more than once in any analysis; in most cases, this meant restricting the analysis to original captures only (i.e., excluding recaptures). We analyzed the data with SAS® Version 8.0 (SAS Institute Inc., Cary, North Carolina) using a nominal rejection level of $\alpha = 0.05$. Because of non-orthogonality of data in some cases, we used Type III sums of squares in tests of significance, where appropriate.

This study was done in accordance with guidelines laid out by the Canadian Council on Animal Care and under the approval of the University of Victoria Animal Care Committee.

Results

Wall lizards were abundant and conspicuous where found. Adults and subadults were seen almost exclusively around large cover objects (piles of logs and rocks, especially the latter) in open areas, but juvenile lizards were seen most often in lightly vegetated areas, particularly tall, thin grass, and were found out in the open away from cover much more frequently than adults. We almost never saw wall lizards in forests or dense bush.

We found no evidence of sexual dimorphism in SVL of wall lizards (ANOVA, $F_{[1,490]} = 2.52$, $P = 0.11$). SVL of males averaged 45.1 mm ($N = 219$, range 23–75 mm), and that of females averaged 47.5 mm ($N = 273$, range 23–71 mm). This lack of size dimorphism is also apparent in plots of SVL versus time (Fig. 1).

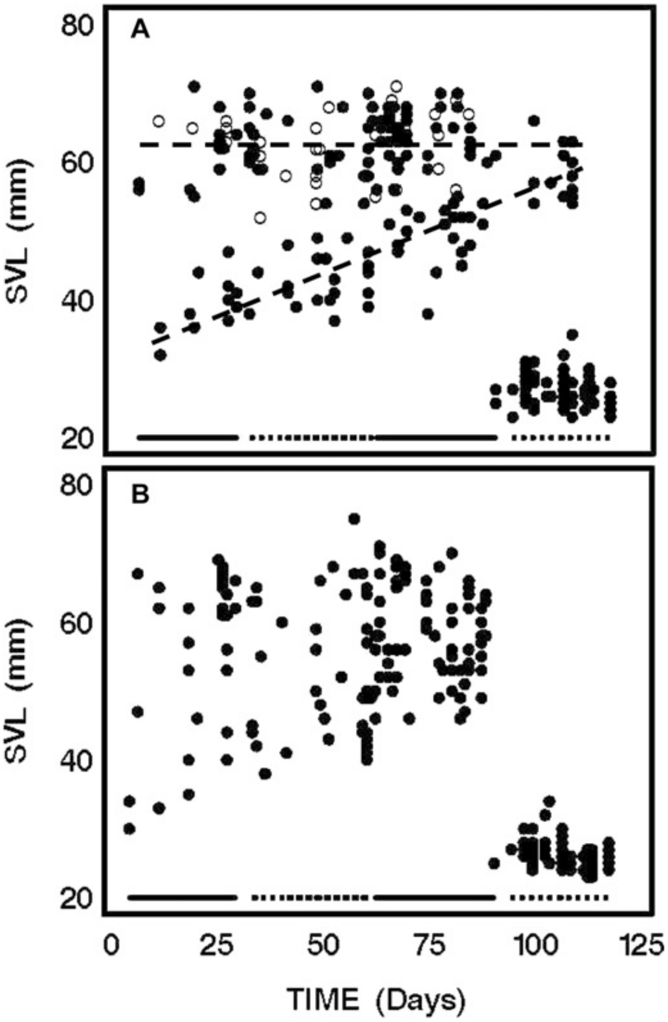
Both body mass and tail length were highly correlated with SVL overall. Therefore, to test for sexual dimorphism in body mass and tail length, we used ANCOVA with SVL as a covariate. However, because of possible allometric relationships, we log-transformed (base e) the data before analysis (Gregory 2004). To quantify sexual dimorphism, we calculated least squares means of the relevant variable, adjusted for SVL, for each sex; we used the ratio of the larger to the smaller value, calculated as the back-transformation of the difference between the least squares means of the log-transformed variables (Gregory 2004).

Because gravid females were expected to be heavier than non-gravid females of the same SVL, we treated them as a separate group for analysis of body mass. We first compared males and non-gravid females and found that there was significant heterogeneity between slopes ($F_{[1,456]} = 7.83$, $P = 0.005$; steeper slope in males). We then divided lizards into juveniles (<50 mm SVL) and adults, based on the smallest gravid female we found (52 mm), and analyzed them separately. Among juveniles, males were significantly heavier than females ($F_{[1,238]} = 4.75$, $P = 0.03$, dimorphism ratio = 1.044; slopes homogeneous). There were also highly significant differences in mass among adults ($F_{[2,245]} = 20.81$, $P < 0.0001$, dimorphism ratio between males and non-gravid females = 1.131; slopes homogeneous); comparisons between groups showed that there was no difference between males and gravid females, but that both were significantly heavier than non-gravid females at a given SVL.

To compare tail lengths between the sexes, we used only lizards that had an intact tail at the time of capture. When we compared all lizards, we again found significant heterogeneity of slopes between the sexes ($F_{[1,297]} = 18.52$, $P < 0.0001$; slope steeper in males). We then divided lizards into juveniles and adults, as above, and compared the sexes within each group. In both cases, slopes were homogeneous between the sexes, but males had relatively longer tails in each case, with the difference being strongest in adults (juveniles: $F_{[1,188]} = 5.17$, $P = 0.02$, dimorphism ratio = 1.025; adults: $F_{[1,107]} = 56.07$, $P < 0.0001$, dimorphism ratio = 1.127).

Although we saw no copulations in the field, we observed several instances of males apparently following females in May, as well as fighting between lizards (presumably males). In 1992 we found gravid females in June and July only, but in 1993 we also found them in May (Fig. 1). We recorded a total of 33 gravid females. Two of these had been captured on another occasion in the same summer, but they had been non-gravid (one had been immature when first caught in May). Another two of these lizards were caught in both summers. One was gravid in 1992 but not in 1993, whereas the other was gravid in both years. The latter female was the same size in each year and produced the same number of eggs each year (in July 1992 and June 1993); we used only one of these clutches in our analysis. Clutch size in our study ranged from 3 to 8 (mean = 4.9, $N = 29$) and was significantly correlated with SVL of females ($r = 0.50$, $P = 0.0006$, $N = 29$). Among original captures only (May–July, both years combined), 31 of 131 (24%) adult females (≥50 mm SVL) were gravid when captured. The percentage of these females that were gravid increased with SVL and declined over the 3-month period, but neither of these trends was significant (logistic regressions: SVL, Wald $\chi^2_1 = 2.38$, $P = 0.12$; time, Wald $\chi^2_1 = 2.33$, $P = 0.13$; Homer and Lemeshow test nonsignificant in each case).

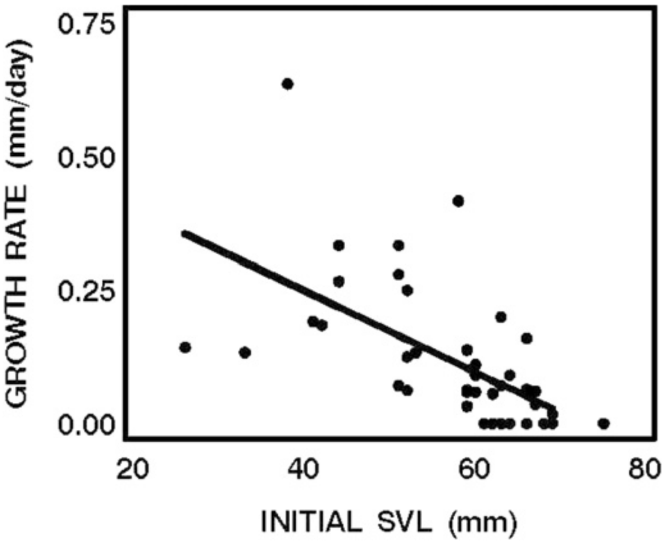
Fig. 1. Plots of snout–vent length (SVL) versus time (days into the active season; day 1 = 1 May) for (A) female and (B) male common wall lizards, *Podarcis muralis* (original captures only, for both years (1992 and 1993) combined). Open symbols in (A) indicate gravid females and dashed lines (fitted by eye) show the change in SVL over the season for juvenile or subadult (lower line) and adult (upper line) lizards. Alternating solid and dashed lines at the bottom of each panel represent May, June, July, and August, respectively.



Oviposition in the laboratory occurred only in June and July in both years (7 June – 30 July). We found only three nests in the field. One, under a rock in mid-July 1993, held what was possibly a single clutch of 6 eggs, but the other two nests clearly represented communal nesting. We found 65 eggs (all in good condition) in a depression in the soil under a large slab of concrete in late July 1992 and approximately 40 eggs in the same place in mid-July 1993. Eggs found in this second communal nest (i.e., in 1993) were either dried out or empty, indicating that they had already hatched.

We analyzed within-year growth via multiple regression using combined 1992 and 1993 data. Because very short recapture intervals may not reveal any growth, we chose the

Fig. 2. Within-season growth rate of wall lizards versus snout–vent length (SVL) at the beginning of the growth interval (no duplicate records for any individual; interval lengths variable; both years (1992 and 1993) combined). In the multiple regression analysis (see text), the dependent variable was simply the change in SVL over an interval, and interval length was one of the independent variables. Here, however, for ease of illustration, the two variables are incorporated into a single variable, growth rate. The solid line is the predicted ordinary least squares regression line.

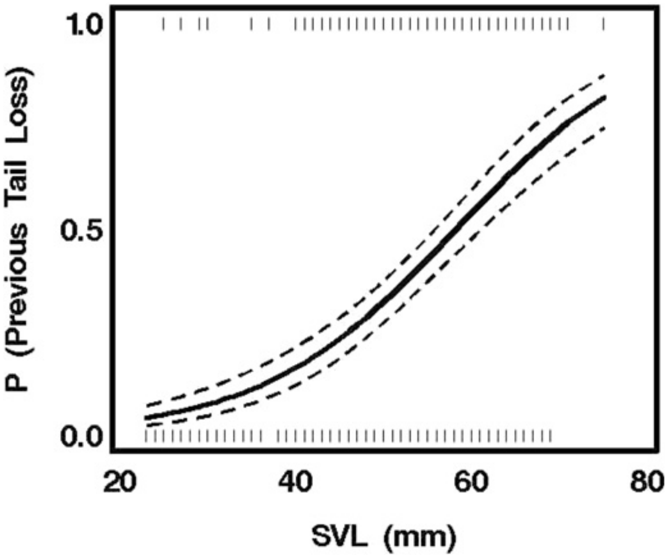


longest within-year recapture interval for each lizard that had been caught at least twice in the same year. We also dropped from the analysis any intervals of fewer than 10 days. The independent variables used in the regression were as follows: initial SVL (i.e., SVL at the beginning of the interval), length of interval, day of initial capture (recorded as the number of days since 30 April), and the squared value of day of initial capture (i.e., quadratic term, to account for the possibility of nonlinear seasonal variation in growth).

We used change in SVL over the recapture interval (set to 0 in a few cases where measurement error suggested slight negative growth) as the dependent variable. Both initial SVL and interval length had significant partial effects on the amount of change in SVL (SVL, $F_{[1,38]} = 33.25$, $P < 0.0001$, negative effect; interval, $F_{[1,38]} = 3.99$, $P = 0.05$, positive effect). Day of initial capture had a nonsignificant positive effect on the amount of growth ($F_{[1,38]} = 3.04$, $P = 0.09$), but the second-order term (day^2) had a significant negative effect ($F_{[1,38]} = 4.27$, $P = 0.05$). Thus, the greatest growth was seen in small lizards, especially those recaptured over long intervals, and the largest lizards did not grow at all (Fig. 2). Moreover, with SVL and interval length held constant, there was also some evidence for a seasonal effect: the amount grown increased slightly from early in the season to mid-June, then declined thereafter. We found no differences in growth between the sexes.

Tail autotomy is a common anti-predator strategy in lizards (Arnold 1988). For various reasons, but especially because older animals have simply had more opportunity to encounter and escape from predators, the frequency of tail loss should increase with age (or size) of lizards (see Gregory and Isaac (2005) for more detailed arguments regarding injuries in snakes). We scored each lizard as to whether its tail was intact or had suffered at least one break prior to capture (indicated by a stump tail or a regenerating or regenerated tail). We tested the relationship between tail-break frequency and SVL using logistic regression, which was a good fit to the data (Homer and Lemeshow $\chi^2_8 = 12.04$, $P = 0.15$); as predicted, there was a strong positive relationship (Wald $\chi^2_1 = 96.67$, $P < 0.0001$, $N = 481$; Fig. 3). When we added sex as a predictor variable, we found no significant effect due to that factor. Thus, SVL was sufficient for predicting the probability of previous tail break.

Fig. 3. Logistic regression of the probability that a wall lizard had lost part of its tail prior to capture versus snout–vent length (SVL) at capture (original captures only, for both years (1992 and 1993) combined). Vertical lines at the top and bottom are data points (0, intact tail; 1, previously broken tail); note that numerous points are hidden because of overlaps. The solid line is the predicted regression line and dashed lines are 95% confidence limits.



Tail loss during capture of either adults or juveniles was uncommon, but it occurred more frequently with hand capture than with other methods. Thus, the higher probability of tail break upon capture in smaller lizards compared with larger lizards (logistic regression: Wald $\chi^2_1 = 14.38$, $P = 0.0001$) was likely attributable mainly to capture method. However, the probability of tail break upon capture was only about 0.15 for the smallest lizards, and the logistic regression was a questionable model for the data (Homer and Lemeshow $\chi^2_7 = 18.31$, $P = 0.01$).

Discussion

The results of our study are important in three ways. First, they reveal that the population biology of *P. muralis* on southern Vancouver Island is similar in several respects to that of populations of this species elsewhere, both native and introduced; thus, data from other populations may be directly relevant to management of the species on Vancouver Island. Second, our study and studies of *P. muralis* elsewhere collectively point to traits that may make this species a successful invader. Third, our data provide a starting point for more intensive study of the population ecology of this species on Vancouver Island; such study will be essential to any future plans for population control.

Although SVL in our study was similar between the sexes, males increased in mass and tail length more rapidly, relative to SVL, than females. Sexual dimorphism in these characters was evident in small lizards but was more pronounced in adults, consistent with the differential growth rates implied by the heterogeneous slopes in the combined analyses of young and adults. Adult females achieved relative masses similar to those of males only when gravid.

Strijbosch et al. (1980), Barbault and Mou (1988), and Braña (1996) found no significant difference in SVL between adults of the two sexes, although males were longer than females in Strijbosch et al.'s study. Males were also longer than females in Boag's (1973) and Edsman's (1990) studies. Edsman attributed this difference to a faster growth rate of males and not to differential survival between sexes; he also found that males had larger heads than females of similar body size. In another study, male *P. muralis* had significantly larger relative head sizes, but significantly shorter relative abdomen lengths, than females (Braña 1996). Like us, Strijbosch et al. (1980) found that males had significantly greater relative tail lengths than females.

Not surprisingly, given the wide geographical range occupied by *P. muralis*, there is inter-population variation in body size. For example, the northern population studied by Strijbosch et al. (1980) in Holland consisted of lizards somewhat shorter than those found elsewhere (e.g., Italy; Boag 1973). In general, SVLs of the adult lizards we measured were similar to those reported by Strijbosch et al. (1980) and Barbault and Mou (1988).

Although we found gravid females throughout much of the summer, the percentage of adult females that were gravid was low. The percentage was probably underestimated because "non-gravid" females could include reproductive females not yet obviously gravid, females that had already produced a clutch, and females just reaching mature size. In addition, only one female was found gravid on two occasions, and then in different years. Thus, we have no evidence that females in this population produce multiple clutches in the same year, but the data set was small. Multiple clutches per year have been observed in the field in other studies (e.g., Kwiat and Gist 1987; Barbault and Mou 1988; Ji and Braña 2000) and we cannot rule out this possibility for Vancouver Island wall lizards, especially given that the timing of first appearance of hatchlings in late July (Fig. 1) was similar to that observed by Barbault and Mou (1988). Strijbosch et al. (1980), by contrast, did not see hatchlings until mid-October. Frequency of oviposition by wall lizards on Vancouver Island merits further study.

Clutch size in our study was similar to values reported by Barbault and Mou (1988) and Ji and Braña (2000), who, along with Braña (1996), also found that clutch size depended on the size of the female. Bertram (2004) found that SVL of hatchling *P. muralis* on Vancouver Island ranged from 19 to 25 mm, similar to that of the smallest lizards we saw in the field (Fig. 1). SVL of Cooper's (1958) hatchlings ranged from 24 to 26 mm, and the smallest hatchlings in Barbault and Mou's (1988) study had an SVL of 22 mm.

Presumably, our increased attention to hatchlings explains the smaller number of adult lizards we caught in late summer, but the abrupt disappearance of adult males from our samples (Fig. 1) is surprising. Perhaps males have different seasonal activity patterns than females, similar to the teiid *Cnemidophorus tigris* Baird and Girard, 1852, in which males begin hibernation in late summer, before other members of the population (Gaffney and Fitzpatrick 1973). Presumably, for males in such cases, the costs of continued activity outweigh the benefits, whereas juveniles and adult females can continue to acquire resources for growth and future reproduction, respectively. More intensive study is required to determine whether these apparent differences in activity patterns of wall lizards are real or artifactual.

Our mark–recapture data indicate that growth of Vancouver Island wall lizards is fastest in young animals and declines effectively to zero in adults. Faster growth in subadult lizards is also evident from plots of SVL versus time, in which three size groups are apparent for each sex: hatchlings, appearing at the end of the summer; subadults, growing from near-hatchling size at the beginning of summer to near-adult size by the end of summer; and adults, showing no obvious change in size over the summer (Fig. 1). From recaptures of adults between years, we surmise that the adult size group includes more than one age group, but we were unable to distinguish them. Authors of other studies also have been able to distinguish size classes of wall lizards representing subadult and adult lizards (Barbault and Mou 1988). In Holland, Strijbosch et al. (1980) found that subadults, young adults, and older adults exhibited monthly size increases of 3.6, 1.5–2, and 1 mm, respectively. In Barbault and Mou's (1988) study, subadults grew an average of about 3 $\text{mm}\cdot\text{month}^{-1}$ and adults grew more slowly. Our data suggest somewhat higher growth rates for Vancouver Island lizards, although the average is biased by one very fast-growing individual (Fig. 2). Based on Fig. 1, we conclude that wall lizards on Vancouver Island likely reach maturity in their second full summer, consistent with Barbault and Mou's (1988) conclusion that wall lizards in France reach maturity in 2 years. Size at maturity for females in this study was similar to values reported by Barbault and Mou (1988) and Ji and Braña (2000).

Because tail loss rates did not vary by sex, we conclude that such injuries are not due to sex-specific activities, such as aggressive interactions between males during the mating season, but are more likely due to attempted predation on lizards. Strijbosch et al. (1980) also found no difference between the sexes in frequency of tail loss, but frequency of tail loss apparently varies among populations (e.g., 1/2 in Boag 1973; 2/3 in Strijbosch et al. 1980) and over time (Boag 1973). However, given our results, it is difficult to ascertain whether these comparisons are meaningful without adjusting for possible differences in body size (or age) of lizards. Boag (1973) attributed inter-year variation in frequency of tail loss to variation in predation rate, but the percentage of animals with injuries might reflect predator inefficiency rather than effectiveness (Jaksić and Greene 1984). Nonetheless, the high rates of tail loss we observed for large adults suggest that wall lizards on Vancouver Island are not free of predation risk and predators might be a limiting factor for the population size of wall lizards. Furthermore, tail autotomy itself has potential fitness consequences. For example, Brown et al. (1995) found that tail loss in *P. muralis* affected subsequent locomotor performance, but in complex ways depending on the type of locomotion and whether the lizard had previously experienced autotomy. Tail loss also can affect viability in other ways and can negatively affect reproductive output in females (Arnold 1988).

What characteristics make *P. muralis* a successful invader? Identifying such traits in introduced species has proven difficult, but significant progress has been made for some taxa (Duncan et al. 2001). Obviously, suitable habitat and climate are necessities, but presumably demographic and life-history traits also play a role in determining whether an introduction will succeed. All else being equal, species with rapid population growth (high r_m) should establish themselves most readily (Duncan et al. 2001). We have not measured the population density of wall lizards on Vancouver Island, but there and elsewhere (Hedeen 1984) these lizards clearly have reached high numbers fairly quickly from very small founding populations. We lack data on key components of r_m for wall lizards on Vancouver Island (e.g., frequency of reproduction, survivorship), but rapid growth and short time to maturity both clearly are important contributors.

Is *P. muralis* a threat to the native *E. coerulea* on Vancouver Island? Deichsel and Schweiger (2004) anecdotally mentioned the "expulsion" of alligator lizards by wall lizards at another site on southern Vancouver Island, but provided no supporting data. The two species co-occur in some habitats (Bertram 2004), including our study site, so interspecific competition is certainly possible. Wall lizards are known to be aggressive, but experiments so far have yielded no evidence of aggressive behaviour of wall lizards towards alligator lizards (Bertram 2004). However, alligator lizards apparently avoid cover objects that are used by wall lizards (Bertram 2004), suggesting some potential for a negative influence of wall lizards on alligator lizards.

That said, at least two factors may help to mitigate any threat posed by *P. muralis*. First, the alligator lizard is still far more widespread on Vancouver Island than the wall lizard, so if the further spread of the latter can be limited, so will any threat it poses. Despite the limited distribution of wall lizards on Vancouver Island, extirpation of them is probably impractical because of their high density and the fact that many of them live on private property, whose owners often value the lizards. Second, unlike the oviparous wall lizard, the alligator lizard is viviparous and, as a consequence, may be more successful in producing clutches in cooler parts of its range (Shine 1985), thereby shifting any competitive advantage enjoyed by the wall lizard. This and other aspects of the comparative ecology of these two species of lizards merit further study.

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