## Do demographic aspects of neighbouring lizard populations differ? A case study with the common wall lizard, *Podarcis muralis*

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Abstract. Demographic and morphological aspects of two nearby subpopulations of the common wall lizard (*Podarcis muralis*) were studied, by a capture-mark-recapture procedure, at an archaeological site in the surroundings of Rome, central Italy. In both sites, the births peak was observed in September. Adult sex-ratio was skewed towards males in one subpopulation, but was close to equality in the other. Morphological characteristics were consistent in the two sites, with males always exhibiting larger snout-vent-length and head size. Population size and density, computed by a Jolly-Seber index applied by using POPAN model revealed differences between subpopulations, with lizard density being much higher in the site with higher habitat heterogeneity and shelter availability. Tail condition was similar between sites. The general implications of these data are discussed.

Keywords: Demography, population structure, habitat heterogenity, common wall lizard.

## Introduction

Studying population structure and determining aspects and properties of demography are among the main goals of population ecology studies (e.g., Schoener and Schoener, 1980; Galan, 2004). However, despite lizards are among the most intensely studied ectotherms, studies dealing with their demographic characteristics are still rare, even for common and widespread species (Barbault and Mou, 1988; Cavin, 1993; Roytberg and Smirina, 1995). For instance, several studies on the demography of a single lizard population have been used as indicative of more general demographic properties for that given species (e.g., Barbault and Mou, 1988; Lecomte and Clobert, 1996). However, there is no test of similarities and differences in terms of demographic characteristics between adjacent population subgroups within the same lacertid species (e.g., see Galan, 2004). In this paper we analyse several demographic

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parameters (population size, density and sexratio, as well as morphological traits and tail condition) of two nearby sub-populations of the common wall lizard (*Podarcis muralis* Laurenti, 1768) inhabiting an area characterized by Roman age ruins in Mediterranean central Italy.

Study area. — The field study was carried out at the archeological area of Ancient Ostia, about 23 km south-west of Roma (Bagnasco, 1998). The climate of the study area is meso-Mediterranean (Blasi, 1994), with low rainfall (593-811 mm), and mean annual temperature of  $15.5^{\circ}$ C. The study area is characterized by a mosaic landscape with ruderal vegetation dominated by *Hedera helix*, and several trees and bush species such as *Pinus pinea*, *Eucaliptus* spp., *Cupressus sempervirens*, *Laurus nobilis*, *Robinia pseudoacacia*, *Ficus carica*, *Populus alba*, *Salix* spp., and *Rubus* spp. (Bagnasco, 1998).

Two study sites, denoted A and B in the following text, were selected for the field research. The two sites were separated from each other by approximately 500 m of herbaceous matrix, unsuitable for the study species. Site A ('Palazzo Imperiale') was 1680 m<sup>2</sup> surface area, and site B ('Terme di Porta Marina') was 1620 m<sup>2</sup> surface area. Both sites were characterized by bricks and tuffaceous ruins of Roman age. Although globally similar, the two sites differed in that (1) the vegetation cover of both climbing plants on ruins and of herbs on ground was much higher in site A ( $60 \pm 12\%$  versus  $22 \pm 7\%$ ), and (2) the ruined walls had a considerably higher mean height in site B ( $2.70 \pm 0.8$  m versus  $1.60 \pm 1.2$  m, for more details, see Gracceva, 2007).

*Protocol.* — The field study was carried out from March to October 2006 (Gracceva, 2007). Four sampling periods were performed: in March (S1), May (S2), June (S3), and September (S4). In total, sixteen days (two days per sampling period per site) of research were spent in the field,

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Figure 1. Gular patterns of two different individuals (A17 left; B21 right) of *Podarcis muralis* from the study area. Note the differences.

with a daily effort of approximately 6-7 hours. Recaptures were entered in the analyses starting with the second sampling period (May). In the following text the recaptures are relative to individuals marked during previous sampling periods. Lizards were captured by hand or noosed during random routes through the study sites. Altogether, up to 7 people were employed to catch lizards on a daily basis. However, only three people simultaneously were alternatively employed to search for lizards within the sites. This was done to avoid biases in density calculations with Jolly-Seber index that obviously assumes that there should be equal probability of capture. Since lizards from the population were identifiable by their gular coloration patterns (Gracceva, 2007), we identified each individual by recording their gular patterns with a digital photo (fig. 1). Males were distinguished from females by their secondary sexual characters, i.e. enlarged triangular head shape and femoral pores in males (Bruno and Maugeri, 1977). Smaller specimens that remained unidentified to sex were classified as juveniles. Each individual was weighed with an electronic balance (precision: 0.01 g), and was measured with a calliper (to the nearest 0.01 mm) for snout-vent-length (SVL), headwidth (HW), shield-width (SL), and shield-length (SLE), and then released unharmed to the exact place of capture.

Statistical analyses. - In order to estimate the population size, we used the Jolly-Seber open population model using the POPAN procedure, and calculated by the program Mark (version 4.3). The POPAN method allows the estimation of four parameters: apparent survival rate ( $\varphi$ ), recapture rate (p), immigration/natality rate (pent), and population size (N), all being assessed either time-dependent or time-independent. Schwarz and Arnason (1996) parameterized the Jolly-Seber model in terms of a super population (N), and the probability of entry ( $\beta$  in the original paper, pent in MARK). The MLogit link function provides a constraint that makes the sum of the pent parameters  $\leq 1$ , with the probability of occurring in the population on the first occasion as 1 - sum(pent(t)). Four parameter matrices are created for each group (i.e., young, males, females):  $\varphi$  (apparent survival), p (capture probability given the animal is alive and on the study area, i.e., available for capture), pent (or  $\beta$ , probability of entry into the population for this occasion), and N (super-population size). For t occasions, there are  $t - 1 \varphi$  estimates,  $t \times p$  estimates, t - 1 pent estimates, and 1 N estimate. The t - 1 pent estimates correspond to the probability of entry for occasions  $2, 3, \ldots, t$ . The probability of being in the population on the first occasion is equal

to pent(0) = 1 - sum(pent(i)). The *MLogit* link function provides a constraint that makes the sum of the pent parameters  $\leq 1$ , with the probability of occurring in the population on the first occasion as 1 - sum(pent(t)). Convergence of this model is problematic unless the MLogit link function is used with the pent parameters. The Mlogit link function is the function that links the linear model specified in the design matrix, where columns represent the  $\beta$  parameters and rows the real parameters. Real parameters are the parameters of interest, e.g., the survival, recapture, fidelity or population size parameters, that are defined in the parameter matrices.  $\beta$  parameters are parameters that are estimated directly in the likelihood function based on the columns of the design matrix. The number of animals in the population on occasion 1 is  $N(1) = pent(0) \times N$ . The number of new animals (births, B) entering the population prior to occasions  $i = 2, 3, \dots, t$  is  $B(i) = pent(i - 1) \times N$ . The population size on occasion i = 2, 3, ..., t is N(i) = $(N(i-1) - losses on capture) \times \varphi(i-1) + B(i)$ . One limitation of the POPAN model is with the use of individual covariates. Because the super-population size (N) estimates the number of animals never captured, this parameter includes animals for which the individual covariate is not known. Thus, modelling N as a function of individual covariates is inappropriate. Further, the B(i) and N(i) parameters are functions of N, as well at the *pent*(i) and  $\varphi(i)$ . Thus, if the pent(i) or  $\varphi(i)$  are modelled as functions of individual covariates, the derived parameters will also be functions of these individual covariates, creating a illogical estimate. The best strategy for use of individual covariates with the POPAN data type is to use the mean values of the individual covariates for providing the estimates of the real and derived parameters, and this solution has been used for this study. The best model was then selected based on Akaike Information Criterion corrected for small samples (AICc), and then the model with the lower AICc was retained as the best model (Akaike, 1974; Mazerolle, 2006). Population density was calculated by dividing the N estimates by the site surfaces.

Statistics were performed using STATISTICA (version 7.0) PC package, with all tests being two-tailed and alpha set at 5%. Variables that were non-normally distributed were (log) transformed in order to achieve normality and homoscedasticity. In the text, the means are followed by  $\pm 1$  Standard Deviation.

## *Total number of captures and sex-ratio.* — A total of 179 capture events (100 in site A and

79 in site B; including both captures and recaptures in this count) were done (table 1), out of which 143 were different individuals (87 in site A [36 males, 27 females, 24 juveniles], and 56 in site B [28 males, 15 females, 13 juveniles]). Since no significant differences between study sites were observed in terms of population cohorts ( $\chi^2$  test, N.S.), we pooled data from both sites in the following analyses. The frequency of occurrence of juveniles was significantly higher in S4 than in other periods ( $\chi^2 = 28.9$ ; df = 1; P < 0.0001). On the other hand, during S3, the frequency of occurrence of juveniles was significantly lower than in the other months ( $\chi^2 =$ 4.9; df = 1; P < 0.05).

Pooling the two study sites, the adult sexratio (male: female, 1.52:1) was significantly skewed towards males ( $\chi^2 = 4.566$ ; df = 1; P < 0.03). Adult sex-ratio was significantly skewed to males in site B, but not in site A (site A: 1.33:1,  $\chi^2 = 1.286$ , df = 1, P = 0.257; site B: 1.87:1,  $\chi^2 = 3.93$ , df = 1, P < 0.05).

Population estimate and density. — The competing models used for population size analysis, including the number of estimated parameters for each model, are shown in table 2. For site A, the best model was time-dependent recapture rate ( $\varphi$ ), time-independent apparent survival rate (p), and time-dependent immigra-

 Table 1. Total number of capture events for both subpopulations of *Podarcis muralis* at the two study sites during the research period.

|          | Site A     |    |            |            | Site B     |    |            |    |
|----------|------------|----|------------|------------|------------|----|------------|----|
|          | <b>S</b> 1 | S2 | <b>S</b> 3 | <b>S</b> 4 | <b>S</b> 1 | S2 | <b>S</b> 3 | S4 |
| Male     | 17         | 12 | 8          | 5          | 16         | 16 | 7          | 5  |
| Female   | 13         | 6  | 6          | 6          | 5          | 10 | 5          | 2  |
| Juvenile | 3          | 5  | 2          | 17         | 2          | 0  | 1          | 10 |

Table 2. Models for the population parameters estimate, including their Akaike information criterion score for small samples.

|                                     | Site A |               | Site B                              |        |               |  |  |
|-------------------------------------|--------|---------------|-------------------------------------|--------|---------------|--|--|
| Model                               | AICc   | N° parameters | Model                               | AICc   | N° parameters |  |  |
| $\{\varphi(t)p(\cdot)pent(t)\}$     | 115.10 | 7             | $\{\varphi(\cdot)p(t)pent(t)\}$     | 114.79 | 7             |  |  |
| $\{\varphi(\cdot)p(\cdot)pent(t)\}$ | 115.29 | 6             | $\{\varphi(t) p(t) p(t) pent(t)\}$  | 116.79 | 8             |  |  |
| $\{\varphi(\cdot) p(t) pent(t)\}$   | 117.78 | 8             | $\{\varphi(\cdot)p(\cdot)pent(t)\}$ | 117.45 | 6             |  |  |
| $\{\varphi(t)p(t)pent(t)\}$         | 119.34 | 9             | $\{\varphi(t)p(\cdot)pent(t)\}$     | 118.40 | 8             |  |  |

| Parameter    | Site A   |          |               |               | Site B   |                 |               |        |
|--------------|----------|----------|---------------|---------------|----------|-----------------|---------------|--------|
|              | Estimate | Err. St. | Bound<br>inf. | Bound<br>sup. | Estimate | Err. St.<br>inf | Bound<br>sup. | Bound  |
| $\varphi(1)$ | 0.72     | 0.16     | 0.35          | 0.92          | 0.51     | 0.10            | 0.32          | 0.69   |
| $\varphi(2)$ | 0.47     | 0.23     | 0.13          | 0.84          | 1.00     | 0.00            | 1.00          | 100    |
| P            | 0.26     | 0.08     | 0.12          | 0.45          | 0.60     | 0.20            | 0.23          | 0.89   |
| pent(2)      | 0.08     | 0.07     | 0.01          | 0.40          | 0.10     | 0.06            | 0.03          | 0.27   |
| N            | 235.41   | 63.15    | 153.71        | 417.15        | 81.01    | 25.86           | 60.70         | 189.04 |

**Table 3.** Population data estimate for sites A (Model:  $\{\varphi(t)p(\cdot)pent(t)\}\)$  and B (Model:  $\{\varphi(\cdot)p(t)pent(t)\}\)$ . In both cases, confidence interval = 95%.

tion rate (*pent*). Instead, for site B the best model selected was time-independent  $\varphi$  and time-dependent *p* and time-dependent *pent*.

Population estimates for the two sites are given in table 3. These models indicated that population B was considerably smaller than population A (table 3). The overall density was  $0.14 \pm 0.038$  individuals per m<sup>2</sup> in site A, and  $0.05 \pm 0.016$  individuals per m<sup>2</sup> in site B.

Body size measurements. — In terms of body mass, and after inclusion of only adults in the analysis, the males weighted more than the females in both site A (males:  $5.28 \pm 1.65$  g, n = 36; females:  $4.28 \pm 1.04$  g, n = 27) and site B (males:  $5.96 \pm 1.89$  g, n = 28; females:  $4.97 \pm 1.74$  g, n = 15). Overall, these intersexual differences were statistically significant (one-way ANOVA, F = 72.801; P < 0.0001). Lizards body mass varied significantly between plots (F = 5.135; P < 0.03). In particular, the lizards from site B were heavier than those from site A. However, the interactive effect between sex and study site was not significant (F = 0.896; P = 0.411).

In terms of SVL, adult males were larger than females in both sites (site A, males:  $59.9 \pm 6.1$ mm, n = 36; females:  $58.0 \pm 5.5$  mm, n = 27; site B, males:  $61.7 \pm 6.6$  mm, n = 28; females:  $61.0 \pm 4.5$  mm, n = 15), and the intersexual difference was statistically significant (F = 66.24; P < 0.0001), with no effect of site on SVL measurements (F = 0.29; P =0.748), when juveniles were also considered in the analysis.

These intersexual differences were also mirrored by head size parameters (data not shown for brevity), with males being larger than females in terms of HW (males:  $10.61 \pm 0.34$ mm; females:  $8.83 \pm 0.4$  mm; F = 67.241; P = 0.00001), SL (males:  $15.27 \pm 1.67$  mm; females:  $13.22 \pm 0.96$  mm; F = 52.28; P = 0.00001), and SLE (males:  $7.45 \pm 0.97$  mm; females:  $6.39 \pm 0.56$  mm; F = 55.39; P = 0.00001). Overall head size measurements did not differ between study sites (P = 0.438, oneway ANOVA).

*Tail condition.* — The number of lizards with damaged tail was not significantly different between sites A (49.4%, n = 87) and B (58%, n = 50) ( $\chi^2 = 2.722$ ; df = 1; P = 0.097). Furthermore, males, females and juveniles had similar damaged tail frequency in either site A (males 55.6%, females 48.1%, juveniles 34.5%;  $\chi^2 = 3.683$ ; df = 2; P = 0.159) or in site B (males 59.1%, females 66.7%, juveniles 26.3%,  $\chi^2 = 3.501$ ; df = 2; P = 0.174).

Overall, our study showed both similarities and differences in terms of demographic traits between the two nearby subpopulations of *Podarcis muralis*. The two subpopulations did not differ in terms of morphological characteristics (males being larger than females in either SVL and head size), and tail condition, although they differed in body mass. However, the two subpopulations differed in other aspects, including the adult sex-ratio (that was skewed to males in one of the two subpopulations), subpopulation size and density.

Generally the morphological similarities between subpopulations were expected, since a larger-male sexual dimorphism is a general pattern in *Podarcis muralis* and in other lacertid lizards as well (e.g., see Gruschwitz and Böhme, 1986). Similarity among subpopulations in terms of percent of lizards with damaged tail could reflect an overall similarity in terms of predation pressure exposure between sites (e.g., see Arnold, 1988; Martin and Lopez, 2003; Luiselli et al., 2005), that is indeed very likely considering that the two sites are close each another and are relatively uniform in terms of habitat characteristics. The only potential predators for lizards at both study sites were the snake Hierophis viridiflavus (Lacépède, 1789), (Capizzi and Luiselli, 1996) and the kestrel, Falco tinnunculus Linnaeus, 1758 (Costantini et al., 2007). On the other hand, the differences between subpopulations in terms of sex-ratio are not easily resolved. Indeed, available literature data on lacertid lizards in general, and P. muralis in particular, indicate that the number of adult males often exceed that of adult females in field populations (e.g., see Barbault and Mou, 1988) with some cases of female-skewed sex-ratios being known (e.g., Galan, 1994). In our study case the trend of a sex-ratio skewed towards males is true for both subpopulations, although not at a statistically significant level. This latter is in agreement with Vogrin's (1998) observations in Slovenian P. muralis. When in lizard populations adult sex-ratio differs from 1:1. this pattern may depend on mortality and/or emigration different between sexes (Le Galliard et al., 2005), or on a temperature-dependent sex determination (Stamps, 1983; Crews et al., 1994; M'Closkey et al., 1998). In our study case, the ultimate reasons for this observed difference should be inspected by ad-hoc experiments, and is still unknown at the present level of our research.

Concerning subpopulation size and density, the observed values are congruent with the range proposed in previous literature (Barbault and Mou, 1988; Vogrin, 1998). However the higher density of subpopulation A may be due to the higher microhabitat heterogeneity and shelter availability of site A compared to site B (see Gracceva, 2007 for more details of the site characteristics). Thus, site A seems to be a more suitable area for the ecological requirements of *P. muralis*.

In conclusion, this study shows that research conducted on nearby populations of lizards, even applying identical field protocols, may evidence some demographic differences that are likely linked to the very proximate microhabitat characteristics of the study sites inhabited by lizards. Therefore, we urge for some caution in addressing general trends from datasets extrapolated from single populations.

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