



Population density of syntopic, differently sized lizards in three fragmented woodlands from Mediterranean Central Italy

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Abstract: The population density of three lacertid lizards (*Podarcis sicula*, *Podarcis muralis*, *Lacerta viridis*) was studied along several transects crossing agro-forest habitats in Mediterranean central Italy. Overall, seven transects, in three different wooded patches, were walked for lizards. Distance sampling (with uniform model design) was applied to the dataset in order to calculate population size, dispersion, and coefficient of variation at each site. In order to detect which factors may influence lizard density, a Generalized Linear Model (GLZ; multinomial distribution and cumulative log link function) was built, with environmental variables and density of predators' variables being included in the model as covariates (scale predictor). Density of the three lizard species differed significantly among study sites, evidencing species-specific responses to local patch conditions. None of the environmental variables taken separately in the GLZ model influenced significantly the lizard densities, whereas lizards densities showed species-specific response to the considered environmental variables. The largest species (*L. viridis*) showed the highest density in the fragment with the most irregular shape and largest wood size, whereas the two smaller *Podarcis* species presented their highest population density in the site with the smallest wood patch and with a very low snake density. Density of *P. sicula* was negatively correlated with both the woodland area and Colubridae density, and was positively correlated with woodland shape (i.e. with circularity).

Abbreviations: MARCIG – Marcigliana; VALLEC – Valle Cavallara; MONTES – Monte S. Biagio; AIC – Akaike Information criterion; AICc – second-order Akaike Information Criterion; D – Density; GLZ – Generalized Linear Model.

Introduction

Over the past decades, considerable effort has been spent by ecologists in order to establish which factors may determine animal distribution in habitat patches (Connor and McCoy 1979, Matter 1997, 1999, Connor et al. 2000, Brotons et al. 2003, Tischendorf et al. 2005, Hämbäck et al. 2006). Habitat heterogeneity and quality, patch size and shape, matrix quality, isolation and connectivity, density of predators, and density of prey have been considered among the main factors affecting species distribution in fragmented habitats (e.g., Wiens 1976, Kotliar and Wiens 1990).

Species occurring in patchy environments usually exhibit a metapopulation demographic structure (Laan and Verboom 1990, Hanski 1991, 1999, Joyal et al. 2001, Tischendorf et al. 2005). In these species, it is expected that those with larger body size, greater home range and higher dispersal capability may be more prone to extinction risks at the local scale (Belovsky 1987, Gaston and Blackburn 1995, 1996, Owens and Bennett 2000, Kjøss and Litvaitis 2001). This is especially due to the widely accepted inverse relationships existing between body size and abundance in most animals (Damuth 1981, 1987, Peters and Raelson 1984, Blackburn et al. 1993, Luiselli et al. 2005a, Luiselli 2006). In

addition, the eventual elimination of large predators occurring in small remnant patches may allow population density of smaller predators to increase after being released from intraguild predation and competition (Mesopredator release theory: Soulé et al. 1988, Crooks and Soulé 1999), thus causing negative cascade effects on trophic networks at every ecological level.

Because of the above-mentioned issues, predators situated at intermediate levels of trophic chains, such as lizards, may be particularly instrumental for studying factors influencing population density in patchy environments. In addition, with regards to agro-forest ecosystems, lizards show remarkable sensibility to both their prey and predator density perturbations (Pilorge 1988), and are easily observable in the field.

The distribution pattern of lizards across patchy habitats is determined by a suite of factors associated to both patch features (i.e., abundance and diversity of resources, habitat heterogeneity, Jellinek et al. 2004, Buckley and Rougharden 2006) and matrix characteristics (Lehtinen et al. 2003, Urbina Cardona et al. 2006, Venugopal 2010). In addition, Rugiero and Luiselli (2007) showed that lizard communities occurring in remnant green areas of Rome (Central Italy) were non-randomly structured across the suite of habitat

types available, thus indicating that each lizard species may respond differently to local conditions. Moreover, different responses to habitat patch features have been described among the two *Podarcis* spp. and *Lacerta viridis*: the former being randomly distributed across the green fragments due to their generalist habits and the latter being widespread in the fragment with irregular shaped woods (Vignoli et al. 2009).

For this study, we analyzed the effects of (i) habitat heterogeneity, (ii) size and shape of wooded patches, and (iii) density of selected predators (snakes) on the densities of three lizard species (Lacertidae: *L. viridis*, *Podarcis muralis* and *P. sicula*) in Central Italy. All these lizard species are well-known to be (a) sympatric in several microhabitats in Central Italy (Rugiero and Luiselli 2007), (b) generalist in both habitat use and prey selection (Capula et al. 1993, Rugiero and Luiselli 2007), and (c) characterized by different body sizes (*L. viridis* being considerably bigger than the other two species; Vollono and Guarino 2002).

More explicitly, based on the previous studies of lizard density and distribution in remnant woodland fragments (Pilorge 1988, Rugiero and Luiselli 2007, Vignoli et al. 2009) we predict that: (1) area and shape of the wooded patch and habitat heterogeneity should be the main factors determining lizard relative abundances; and (2) the population density of the lizard species should be directly influenced by the presence and the abundance of their specialized predators (i.e. snakes).

Materials and methods

Study species

We studied the wall lizard, *Podarcis muralis* (Laurenti, 1768), the ruin lizard, *Podarcis sicula* (Laurenti, 1768), and the Italian green lizard, *Lacerta viridis bilineata* (Laurenti, 1768), three invertebrate-eating, oviparous lacertid lizards with a wide distribution in Mediterranean Central Italy (Sindaco et al. 2006). Both *P. muralis* and *P. sicula* are considerably smaller (respectively, snout vent-length of 5-7 cm and 5-8 cm) than *L. viridis* (8-12 cm; Vollono and Guarino 2002).

Study areas

Surveys were carried out at two protected natural reserves of Latium (Central Italy), namely the Marcigliana and Nomentum Nature Reserves, on the North-East periphery of Rome. Both reserves are characterized by Mediterranean climate, with mild-rainy winter and hot summer, and annual rainfall ranging from 810 to 940 mm (Blasi 1994). The vegetation is mainly composed of mixed oak woodlands (*Quercus cerris*, *Q. pubescens*, *Q. ilex*, *Q. suber*, *Acer campestre*, *Ulmus minor*) and shrubberies (*Spartium junceum*, *Rosa sempervirens*, *R. gallica*, *R. canina*, *Arundo plinii*, *Rubus ulmifolius*, *R. caesius*, *Prunus spinosa*, *Crataegus monogyna*, *Euonymus europaeus* and *Sambucus nigra*; Blasi 1994, Macchiolo and Sauli 2006). The two protected areas differ in terms of area and relative abundance of woods, shrubs, cul-

tivated fields, pastures, and urban areas. The Marcigliana Nature Reserve, 4696 ha surface, mainly consists of large patches with monocultivations, pastures and residual woodlands, delimiting valleys in the hilliest part of the reserve (Cazzola 2004). The Nomentum Nature Reserve, 850 ha area, is composed of remnant woodlands, cultivation fields, an archaeological area, and a part of the town 'Mentana'. This latter reserve is surrounded by a very disturbed environment (Guidi and Battisti 2002).

Three wooded patches, separated by at least 3 km air distance and isolated from each other by an impermeable urban-agricultural matrix, were explored for lizards. These patches were: (i) Marcigliana (MARCIG), situated in the central-eastern side of Marcigliana Nature Reserve (42° 0'56.97"N, 12°32'4.48"E), with a large (over 128 ha) remnant wood of irregular shape, and surrounded by an agricultural matrix; (ii) Valle Cavallara (VALLEC), situated in the eastern part of Nomentum Nature Reserve (42°0'38.88"N, 12°38'45.53"E), with a remnant wood of medium size (over 43 ha) and a regular shape, surrounded by a suburban matrix; and (iii) Monte S. Biagio (MONTES), situated in the southern part of Nomentum Nature Reserve (41°59'12.94"N, 12°39'12.54"E), with a small (less than 33 ha) remnant wood size with a regular shape, and surrounded by a suburban matrix. Summarized information on the structural variables of each study area is given in Table 1.

Protocol

Lizard surveys. Surveys for lizards were carried out in March-November 2007, with 42 field days. Several transects were walked in each study patch. Transects were laid at the forest edges in order to maximize the probability of encounter with lizards, thus making a better estimation of the population density (e.g., Schroder 1981, Connor et al. 2000). If otherwise transects were laid in the internal portion of the forests, the number of encountered lizards would have been much lower because of a minor detectability, thus biasing our estimates of population sizes (Caughley and Sinclair 1994). Four transects were walked in MARCIG (total length 1688 m), one in VALLEC (total length 962 m) and two in MONTES (total length 714 m; Table 1). The four transects in MARCIG were very close from each other (< 20 meters). Hence, we considered them as non-independent, thus pooling the relative datasets. The same was true also for the two transects in MONTES. Total transect lengths differed among patches (Table 1). This was due simply to the fact that we selected transects where the detectability of lizards was high because of easy access and freedom of walking, minimum disturbance associated with our passage, etc; and the available transects with these characteristics were simply different in length among sites. In any case, as our analyses took into consideration differences in relative transect length (see below), this would have not been a problem in our study. Conversely, the distance among the three study areas (over 3 km) and the type of matrix occurring in-between them clearly prevented from dispersal of lizard individuals across patches.

Table 1. Surface and shape of the wood patch in each studied site and number, length, total length and replicates of each transect are indicated.

Site	Wood area (ha)	Wood Perimeter (m)	Wood shape (Cs)	Transects (T)	T Length (m)	Total T Length (m)	N° replicates
MARCIG	128.03	23641.15	0.05	M1	333.48	1688.48	16
				M2	254.73		12
				M3	780.15		16
				M4	320.12		12
VALLEC	43.41	5588.24	0.13	VC	962	962	17
MONTES	32.74	3191.90	0.20	MSB1	191.73	714.21	20
				MSB2	522.48		17

Thus, we are sure that the three study patches were independent from each other.

Each transect was slowly walked (100 m/10 min) in each day of survey. The orthogonal distance from each sighting site to the transect was recorded. If the species of a sighted individual was not determined, the record was assigned to a superior taxa such as 'Lacertidae' or '*Podarcis*'. Undetermined data were not used in the analyses. Pseudoreplication (sensu Hurlbert 1984) was avoided by walking all transects in a single direction within each field day. Since (i) we are sure we did not count multiple times any lizard (or snake) individual within each day of sampling, and (ii) DISTANCE software analyses the daily transects as independent and then averages the estimated densities for the total number of days by each transect, we can be sure that pseudoreplication biases would have not affected our analyses.

Snake surveys. Snakes were searched for throughout the same transects as lizards, but for a higher number of field days (50). A higher field effort was devoted to search for snakes because they are more secretive than lizards and their density is lower. The same above-mentioned specifications on lizard surveys also apply to snakes. In this study, we considered *Vipera aspis* (Viperidae), *Hierophis viridiflavus*, *Zamenis longissimus*, and *Elaphe quatuorlineata* (Colubridae) because all of these species are known to forage intensively on lizards (at adult and/or juvenile stages) at the study areas (Capizzi and Luiselli 1996). Another snake species occurring at the study area (*Natrix natrix*) does not feed habitually on lizards (Luiselli et al. 2005b), and was hence excluded from our analyses.

Distance analyses. We calculated the estimated population density of each population by the program DISTANCE 5.0 (Buckland et al. 2001). In this program, a detection function ($g(x)$) described the probability of detecting an object (a lizard in our study case) given that it is at distance x from the line transect under survey. Spatial line transect models in

comparison with conventional line transect methods permit to extract more than just an abundance estimate from sighting surveys. In fact, they estimate the abundance in relation to spatial variables reflecting topography, habitat, and other factors that affect animals' environment (Hedley and Buckland 2004). For instance, DISTANCE can estimate abundance for different subset of the survey region and compare different data distribution models, suggesting which is the model that best fits the data collected.

We explored the distribution across transects of lizards and of their potential snake predators in the study areas, in order to detect if animals were recorded in all the sections of our transects (homogeneous distribution) or not (e.g. aggregated, weakly increasing etc), by geo-referencing all sightings using ESRI Arcview (version 3.2) GIS software. Because lizards showed a clear homogeneous distribution along transects, we analyzed lizard data using the uniform model ('strictly monotonically non-increasing'/estimate variance empirically') as detection function. This detection function has been considered an 'omnibus' function for cases such as ours (Buckland et al. 1993, Hein 1997). On the contrary, snakes exhibited a non-homogeneous distribution in our study transects with a tendency to a kind of aggregated distribution. In order to understand which distribution model better fitted with these data, we tested nine different models combining three detection functions of the object distribution (e.g. uniform, weakly increasing and aggregate distribution) with three detection functions of the variance distribution (e.g. no assumption, Poisson, and over-dispersed variance distribution), as follows: "Ψ1 = strictly monotonically non-increasing and estimate variance empirically"; "Ψ2 = weakly monotonically non-increasing and estimate variance empirically"; "Ψ3 = no constraints and estimate variance empirically"; "Ψ4 = strictly monotonically non-increasing and assumption of Poisson distribution"; "Ψ5 = strictly monotonically non-increasing and assumption of Poisson distribution with an over-dispersion factor 3 (m)"; "Ψ6 = weakly

Table 2. Distribution of the vegetation type abundances across transects at the study sites. Symbols: SST = shrubland with scattered trees (*Ulmus minor*, *Quercus cerris*, *Q. pubescens*, *Q. ilex* and *Acer campestre*); TOS = Thorny open shrubland (dominated by *Rosa* spp, *Prunus spinosa*, *Crataegus monogyna*, *Smilax aspera*); TCS = Thorny close shrubland (dominated by *Rubus ulmifolius*); OS= open shrubland (dominated by *Spartium junceum*); TG = tall grasses (*Arundo plinii* stands); H = Simpson's heterogeneity index; Hmean = mean of the Simpson's H calculated for each study site.

Site	Transects (T)	SST	TOS	TCS	OS	TG	H	Hmean
MARCIG	M1	0%	7%	93%	0%	0%	1.15	2.11
	M2	8%	23%	69%	0%	0%	1.87	
	M3	52%	25%	23%	0%	0%	2.59	
	M4	22%	36%	42%	0%	0%	2.82	
VALLEC	VC	26%	35%	4%	3%	32%	3.39	3.39
MONTES	MSB1	63%	33%	4%	0%	0%	1.97	2.41
	MSB2	52%	16%	2%	8%	22%	2.85	

monotonically non-increasing and assumption of Poisson distribution"; "Ψ7 = weakly monotonically non-increasing and assumption of Poisson distribution with an over-dispersion factor 3 (m)"; "Ψ8 = no constraints and assumption of Poisson distribution"; "Ψ9 = no constraints and assumption of Poisson distribution with an over-dispersion factor 3 (m)". Model selection was based on information-theoretic methods (Akaike Information Criterion, AIC), and more precisely on the second-order AIC for small samples (AICc; Burnham and Anderson 2002). The formula for AICc is as follows:

$$\text{AICc} = -2 \log \text{Likelihood} + 2K + 2K(K + 1)/(n - \text{ess} - K - 1)$$

In the above formula, $n - \text{ess}$ is the sample size and K corresponds to the number of model parameters plus one. The best model was that with lowest AICc, lowest K and lowest coefficient of density variance (CV), that corresponds to the error of the density value obtained. All together, the AICc, K and CV provide a measure to the fit of the model to the data (based on the likelihood) (Burnham and Anderson 2002).

A key assumption regarding the use of Distance sampling is that all animals on the line (i.e., at 0 m) are detected. We did not test this empirically (Young et al. 2008) but we made every possible effort to locate lizards and snakes through careful searching of the vegetation occurring on the transect line. In addition, these reptiles typically do not escape silently when running through the vegetation (Martin and Lopez 2001); hence, we are confident that this assumption was surely respected in our study case.

In order to verify inter-specific differences in lizard density at each study site and intra-specific differences in lizard density among study sites, two independent χ^2 tests were calculated by using the software EcoSim 7.0 (Gotelli and Entsminger 2001). The software calculates the expected values, randomizes the matrix and calculates a χ^2 deviation statistic for both the observed and simulated data. Because our matrix consisted of a single column of data, we selected the option 'randomize columns' (that randomly reshuffles the observed values within each column of the matrix) and we inserted the values of the expected matrix. By means of the EcoSim package, Monte Carlo simulations (5000 iterations) were performed and in order to test our hypothesis, χ^2 deviation statistic for both the observed and simulated data were compared. Instead of a conventional χ^2 test, the randomiza-

tion test has some advantages such as the chance to use small expected values and to not specify the degrees of freedom associated to the test (see Gotelli and Entsminger 2001, for more details). In order to verify intra- and inter-specific differences in density among Viperidae and Colubridae at each study site, Fisher exact tests were performed.

Environmental variables. As environmental variables, we analyzed: (i) wooded patch size, (ii) wooded patch shape, and (iii) habitat heterogeneity along the study transects.

The wooded patch area, and transect lengths of each fragment were recorded and evaluated by using ESRI Arcview 3.2 (Table 1). The wooded patch shape (C_s) was estimated by applying a shape index, ranging from 0 to 1, calculated as follows:

$$C_s = (A/P)x / (A/P)c$$

where $(A/P)x$ is the surface/perimeter ratio of the wooded patch x and $(A/P)c$ is the surface/perimeter ratio of the circle of equal surface to patch x (Vignoli et al. 2009). With this formula, the more the patch surface approximates that of a circle, the more the index tends to 1 (Table 1).

Habitat heterogeneity was evaluated by distinguishing main vegetation categories within each transect. The vegetation categories were: shrubland with scattered trees (*Ulmus minor*, *Quercus cerris*, *Q. pubescens*, *Q. ilex* and *Acer campestre*); thorny open shrubland (dominated by *Rosa* spp, *Prunus spinosa*, *Crataegus monogyna*, *Smilax aspera*); thorny close shrubland (dominated by *Rubus ulmifolius*); open shrubland (dominated by *Spartium junceum*); tall grasses (*Arundo plinii* stands) (Table 2). A boundary strip of five metres on either side of the ecotonal transect was characterized on the basis of its vegetation category relative abundance. Habitat heterogeneity was explored by calculating a Simpson's (1949) diversity index of the percent availabilities of the various vegetation types for each transect, and then calculating the means of Simpson's index for the transects of each study site. Based on environmental variables summarized in Tables 1 and 2, MARCIG was the site biggest in size with the lowest shape coefficient (i.e.: high shape irregularity), with the highest transect total length and with the lowest heterogeneity index (Hmean). MONTES was the smallest site, with the highest shape coefficient (high shape regular-

Table 3. Spearman’s rank correlation coefficients among lizard density (D_L) and the selected patch features (D_COL= colubrid density; D_VIP = viperid density; HETEROG = Simpson’s heterogeneity index; Wa = Wooded patch area; Wsh = wooded patch shape; TransLength = transect length). Significant coefficients ($p < 0.05$) are given in bold with ‘-’ and ‘+’ designating respectively negative and positive correlations.

	D_L	D_COL	D_VIP	HETEROG	Wa	Wsh	TransLength
D_L	1	0.012	-0.103	-0.051	-0.042	0.042	0.193
D_COL		1	0.771	-0.607	0.837	-0.837	-0.071
D_VIP			1	-0.143	0.926	-0.926	0.028
HETEROG				1	-0.458	0.458	0.607
Wa					1	-1	0.020
Wsh						1	-0.020
TransLength							1

ity), the lowest transect total length, and with an intermediate heterogeneity index value among the three sites. VALLEC had an intermediate patch shape and total transect length, but the highest heterogeneity index.

The pattern of lizard density among the study sites and throughout all the analysed transects was modelled by means of Generalized Linear Models procedure. One model was built selecting as dependent variable the lizard density (multinomial distribution and cumulative log link function). The variable ‘species’ was introduced in the model as factor (categorical predictor), whilst the variables ‘wooded patch size’, ‘wooded patch shape’, ‘habitat heterogeneity’, as well as the variable ‘density of predators’, were included in the model as covariates (scale predictor); the model design included the main effects for each variable, and all 2-way interactions between the factor and the covariates (fractional factorial design) (McCullagh and Nelder 1989). We considered for the analyses only the autocorrelated covariates with a stronger biological meaning (density of colubrid snakes, wooded patch shape, and habitat heterogeneity). We excluded from the model the density of viperids because they are lacertophagous only in the first years of life (Capizzi and Luiselli 1996). Sample size was large enough for this type of analysis, which is robust also with autocorrelated variables design (Nelder and Wedderburn 1972, Hardin and Hilbe 2003) as is the present study case (Table 3). Analyses were performed using STATISTICA (version 7.0) PC package and Minitab version 16.0 software, with all tests being two-tailed and alpha set at 5%.

Results

Lizards. Overall, we recorded a total of 886 lizards. The number of lizard sightings were clearly uneven by site and by species (Figure 1). Indeed, the number of observed individuals of both *P. muralis* and *P. sicula* increased at MONTES, whereas the number of *L. viridis* was much higher at MARCIG than at the two other sites.

The estimated population density for the three lizard species in the three study areas and in each of the transects, including details of dispersion measures and coefficients of variation, are presented respectively in Table 4 and 6.

There were significant intra-specific density variations among study sites in all the three lizard species: *L. viridis* (observed index = 36.75000, mean of simulated indices = 1.99347 ± 4.20280 , $P_{obs \leq exp} = 1.00000$, $P_{obs < exp} = 0.00000$); *P. muralis* (Observed index = 14.17345, mean of simulated indices = 1.99945 ± 4.03793 , $P_{obs \leq exp} = 0.99900$, $P_{obs < exp} = 0.00100$); and *P. sicula* (observed index = 19.61122, mean of simulated indices = 2.00237 ± 3.68370 , $P_{obs \leq exp} = 1.00000$, $P_{obs < exp} = 0.00000$).

Interspecifically, there were significant density differences among *P. muralis*, *P. sicula*, and *L. viridis* in MARCIG (observed index = 41.11018, mean of simulated indices = 1.96793 ± 3.78766 , $P_{obs \leq exp} = 1.00000$, $P_{obs < exp} = 0.00000$) and MONTES (observed index = 17.77966, mean of simulated indices = 2.01513 ± 4.06061 , $P_{obs \leq exp} = 1.00000$, $P_{obs < exp} = 0.00000$) but not in VALLEC (observed index = 4.17383, mean of simulated indices = 1.9926 ± 3.73013 , $P_{obs \leq exp} = 0.88400$, $P_{obs < exp} = 0.12900$). Density of *L. viridis* (D= 48.25 individuals/ha, coefficient of variation 0.20) was significantly higher than that of *P. muralis* (D= 18.20 individuals/ha, coefficient of variation 0.21) and *P. sicula* (D= 5.10 individuals/ha, coefficient of variation 0.28) in the largest site (MARCIG). On the other hand, the densities of the two *Podarcis* species (*P. muralis*, D= 37.99 individuals/ha, coefficient of variation 0.20; *P. sicula*, D= 24.35 individuals/ha, coefficient of variation 1.93) were significantly higher than that of *L. viridis* (D= 9.35 individuals/ha, coefficient of variation 0.37) in MONTES, the smallest site.

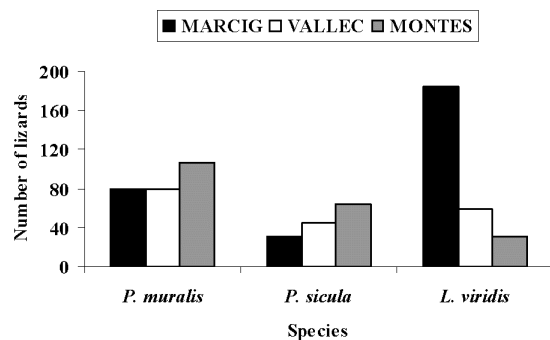


Figure 1. Number of lizard sightings by species and by site in the three study areas. For the symbols, see the text.

Table 4. Population densities (D), lower D value (DLCL), higher D value (DUCL) and D variation coefficient (DCV) of *L. viridis*, *P. muralis* and *P. sicula* in each study area, estimated using the DISTANCE method.

Taxa	D (N/ha)	DLCL	DUCL	DCV
MARCIG				
<i>Lacerta viridis</i>	48.25	32.71	71.17	0.20
<i>Podarcis muralis</i>	18.20	12.08	27.42	0.21
<i>Podarcis sicula</i>	5.10	2.97	8.75	0.28
VALLEC				
<i>Lacerta viridis</i>	14.67	7.90	27.24	0.32
<i>Podarcis muralis</i>	13.56	8.34	22.05	0.24
<i>Podarcis sicula</i>	5.82	3.53	9.59	0.25
MONTES				
<i>Lacerta viridis</i>	9.35	4.57	19.13	0.37
<i>Podarcis muralis</i>	37.99	25.57	56.45	0.20
<i>Podarcis sicula</i>	24.35	1.95	304.82	1.93

Snakes. Density estimates for snakes in the three study areas, based on alternative Distance models ordinated by the lowest AICc, lowest K and lowest coefficient of density variance are given in Table 5. Density estimates for snakes in each transects are shown in Table 6. In this case, the Distance alternative models have not been shown for brevity and only the value of the best model was reported. As regards the density estimates in the three study sites and according to the most likelihood model, Colubridae and Viperidae highest densities were found in MARCIG (Colubridae, D= 2.883 individuals/ha, coefficient of variation 0.242; Viperidae, D = 2.72 individuals/ha, coefficient of variation 0.23) whereas the lowest density was found in MONTES for Viperidae (D= 0.31 individuals/ha, coefficient of variation 0.55) and in VALLEC for Colubridae (D= 0.84 individuals/ha, coefficient of variation 0.26).

Viperidae density differed significantly among study sites: MARCIG – VALLEC ($p < 0.001$), MARCIG – MONTES ($p < 0.001$) and VALLEC – MONTES ($p < 0.05$). Colubridae density differed significantly between sites for MARCIG – VALLEC ($p < 0.001$) and MARCIG – MONTES ($p < 0.01$), but not for VALLEC – MONTES ($p = 0.08$). Density comparisons among Viperidae and Colubridae showed significant differences only in MONTES ($p < 0.05$), but not in MARCIG ($p = 0.096$) and VALLEC ($p = 0.083$).

Generalized Linear Model. Results of our GLZ model showed that (i) the species factor significantly had an effect on the model (i.e. showing species specific response patterns to the considered variables), (ii) none of the covariates showed a main effect influencing lizard density, and (iii) all the between-effects obtained from the model had an effect on the independent variable: the interaction between species \times patch shape was particularly significant, although also those of species \times heterogeneity and species \times density of Colubridae were also significant (Table 7). Pairwise multiple comparisons post-hoc tests showed that density of *P. sicula* was positively influenced by patch shape ($p < 0.001$), and that of

Table 5. Density estimates (D) for snakes (Colubridae and Viperidae), based on alternative Distance models ordinated by the lowest Akaike Information criterion on the small-sample-size correction (AICc), the lowest number of parameters (K) and the lowest coefficient of density variance (CV).

MODEL	AICc	K	D	DCV	Δ AICc	Δ DCV
COLUBRIDAE						
MARCIG						
ψ 6	43.8	3	2.883	0.242	0	0.03
ψ 8	43.8	3	2.883	0.242	0	0.03
ψ 2	43.8	3	2.883	0.256	0	0.03
ψ 3	43.8	3	2.883	0.256	0	0.03
ψ 7	43.8	3	2.883	0.34	0	0.04
ψ 9	43.8	3	2.883	0.34	0	0.04
ψ 4	45.41	2	3.063	0.239	0	0.03
ψ 1	45.41	2	3.063	0.254	0	0.03
ψ 5	45.41	2	3.063	0.338	0	0.04
VALLEC						
ψ 4	70.05	1	0.93	0.27	0	0
ψ 6	70.05	1	0.93	0.27	0	0
ψ 7	70.05	1	0.93	0.27	0	0
ψ 8	70.05	1	0.93	0.27	0	0
ψ 9	70.05	1	0.93	0.27	0	0
ψ 1	70.05	1	0.93	0.31	0	0.03
ψ 2	70.05	1	0.93	0.31	0	0.03
ψ 3	70.05	1	0.93	0.31	0	0.03
ψ 5	70.05	1	0.93	0.41	0	0.14
MONTES						
ψ 1	58.43	1	1.75	0.25	0	0
ψ 2	58.43	1	1.75	0.25	0	0
ψ 3	58.43	1	1.75	0.25	0	0
ψ 4	58.43	1	1.75	0.28	0	0.03
ψ 6	58.43	1	1.75	0.28	0	0.03
ψ 8	58.43	1	1.75	0.28	0	0.03
ψ 5	58.43	1	1.75	0.42	0	0.17
ψ 7	58.43	1	1.75	0.42	0	0.17
ψ 9	58.43	1	1.75	0.42	0	0.17
VIPERIDAE						
MARCIG						
ψ 6	50.49	2	2.72	0.23	0	0
ψ 8	50.49	2	2.72	0.23	0	0
ψ 2	50.49	2	2.72	0.25	0	0.02
ψ 3	50.49	2	2.72	0.25	0	0.02
ψ 7	50.49	2	2.72	0.33	0	0.1
ψ 9	50.49	2	2.72	0.33	0	0.1
ψ 4	55.27	2	2.38	0.26	4.78	0
ψ 1	55.27	2	2.38	0.28	4.78	0.02
ψ 5	55.27	2	2.38	0.35	4.78	0.09
VALLEC						
ψ 1	67.85	1	0.84	0.26	0	0
ψ 2	67.85	1	0.84	0.26	0	0
ψ 3	67.85	1	0.84	0.26	0	0
ψ 4	67.85	1	0.84	0.28	0	0.03
ψ 6	67.85	1	0.84	0.28	0	0.03
ψ 8	67.85	1	0.84	0.28	0	0.03
ψ 5	67.85	1	0.84	0.42	0	0.16
ψ 7	67.85	1	0.84	0.42	0	0.16
ψ 9	67.85	1	0.84	0.42	0	0.16
MONTES						
ψ 1	15.84	1	0.31	0.55	0	0
ψ 2	15.84	1	0.31	0.55	0	0
ψ 3	15.84	1	0.31	0.55	0	0
ψ 4	15.84	1	0.31	0.6	0	0.05
ψ 6	15.84	1	0.31	0.6	0	0.05
ψ 8	15.84	1	0.31	0.6	0	0.05
ψ 5	15.84	1	0.31	0.87	0	0.32
ψ 7	15.84	1	0.31	0.87	0	0.32
ψ 9	15.84	1	0.31	0.87	0	0.32

L. viridis was negatively correlated by patch shape ($p < 0.001$), whereas density of *P. muralis* was not influenced by this variable ($p = 0.441$). Habitat heterogeneity negatively influenced *L. viridis* density ($p < 0.001$), whereas it was irrelevant for the two *Podarcis* species (at least $p = 0.137$ in pairwise multiple comparisons post-hoc test). Density of Colubridae negatively influenced *P. sicula* density ($p < 0.030$) and *P. muralis* density ($p < 0.022$).

Table 6. Population densities (D), lower D value (DLCL), higher D value (DUCL) and D variation coefficient (DCV) of *L. viridis*, *P. muralis*, *P. sicula*, Colubridae and Viperidae in each transect, estimated using the DISTANCE method.

Taxon	Transect	D (N/ha)	DLCL	DUCL	DCV
<i>Lacerta viridis</i>	M1	111.23	67.80	182.50	0.24
	M2	94.12	56.55	156.63	0.25
	M3	7.41	4.39	12.49	0.26
	M4	49.76	29.11	85.05	0.25
	VC	14.67	7.90	27.24	0.32
	MSB1	7.61	2.24	25.84	0.62
	MSB2	6.62	2.35	18.63	0.53
<i>Podarcis muralis</i>	M1	20.65	10.58	40.30	0.33
	M2	4.91	0.99	24.40	0.84
	M3	19.44	10.16	37.21	0.32
	M4	8.09	2.26	28.97	0.66
	VC	13.56	8.34	22.05	0.24
	MSB1	30.70	14.52	64.92	0.38
	MSB2	41.11	24.48	69.05	0.26
<i>Podarcis sicula</i>	M1	0.00	-	-	-
	M2	5.45	0.87	34.07	1.00
	M3	8.25	4.43	15.35	0.31
	M4	4.81	0.73	31.46	1.06
	VC	5.82	3.53	9.59	0.25
	MSB1	19.80	8.45	46.38	0.43
	MSB2	8.47	4.60	15.61	0.29
Colubridae	M1	5.10	1.63	15.99	0.49
	M2	15.69	3.54	69.54	0.58
	M3	2.87	1.43	5.74	0.34
	M4	2.08	0.31	14.07	0.66
	VC	0.93	0.53	1.62	0.27
	MSB1	0.55	-	-	1.32
	MSB2	0.94	0.19	4.62	0.87
Viperidae	M1	2.81	0.90	8.72	0.53
	M2	unapplicable	-	-	-
	M3	1.50	0.38	5.89	0.63
	M4	4.25	1.86	9.74	0.43
	VC	0.84	0.36	1.93	0.42
	MSB1	0.00	-	-	-
	MSB2	0.38	0.12	1.17	0.56

Table 7. Results of a Generalized Linear Model with lizard density as dependent variables, and the various environmental variables

Source	Wald Chi ² (df)	P
Species	12.563 (2)	0.002
Density Colubridae	0.567 (1)	0.461
Heterogeneity	1.620 (1)	0.203
Patch shape	0.040 (1)	0.841
Species x Density Colubridae	7.509 (2)	0.023
Species x Heterogeneity	7.147 (2)	0.028
Species x Patch shape	9.888 (2)	0.007

Discussion

Correlates of population density by species.

In this study, we documented the following three non-random patterns: (1) density of the three lizard species differed in each study site; (2) none of the environmental variables taken separately influenced significantly the lizard densities; (3) lizards showed species specific response to the considered environmental variables. As concerns environmental correlates by species, our results evidenced that: (i) the density of *L. viridis* was negatively influenced by both patch shape coefficient and habitat heterogeneity, this species preferring wooded patches with high shape irregularity (i.e. high development of edge line with respect to the surface), and habitat heterogeneity, evidencing for this species a degree of specialization in microhabitat selection; green lizards were not affected by density of lacertophagous predators (Colubridae snakes) and this fact could be in part due to the big size of *L. viridis* that reduces the potential risk of predation (at least at the adult stage), although at least *H. viridiflavus* is a well known predator for adults of this species (Capizzi and Luiselli 1996); (ii) the density of *P. muralis* was not influenced by any of the investigated variables but negatively by density of Colubridae; (iii) the density of *P. sicula*

was positively influenced by patch shape coefficient and negatively by colubrid snake density.

Concerning issue (1), our result suggests that lizard densities may vary considerably also according to very local conditions, thus exhibiting strong among-site variations despite closeness of sites and environmental similarities. This pattern mirrors data obtained by Rugiero and Luiselli (2007) on lizard communities from Rome, despite these authors used an entirely different statistical tool (null model analysis) to achieve their results. Hence, the habitat-related variations in local density of these lizards are susceptible to many factors and their prediction is complicated because of the considerable inter-population differences of this parameter (see also Rugiero and Luiselli 2007). In general, considering the known and considerably different microhabitat-selection preferences of the three species (see also Rugiero and Luiselli 2007), the inclusion in the analyses of other variables characterizing the micro-habitats, such as composition of ligneous and grass-type vegetation or density of rocky outcrops, would have had an higher effect on the observed population densities.

The lack of significance of the individual variables for lizard densities (issue 2) suggests that these reptiles respond to a suite of different ecological determinants which regulate

their population densities, and hence it is unlikely to predict whether a lizard species may reach high population densities based on single environmental variables.

As regards *L. viridis* (issue 3), the fact that its density was positively influenced by woodland patch irregularity and the highest number of individuals was found at the site biggest in size (MARCIG) and with the lowest habitat heterogeneity could be due to the wide home ranges of this large lizard (Saint Girons and Bradshaw 1989), which requires larger patches of suitable habitats (i.e., homogeneous woodland habitats) than smaller species with narrower home ranges. Home ranges of *L. viridis* are indeed much wider than those documented for *Podarcis* species (e.g., Brown et al. 1995). The intriguing negative effect of habitat heterogeneity on *L. viridis* density could be explained by the association of this species to *Rubus* bushes (Rugiero and Luiselli 2007), which is the dominant vegetation type along the ecotones at the least heterogeneous study area (MARCIG). The inverse relationship of *L. viridis* density with patch shape is consistent with the fact that this species is usually linked to ecotones and wooded corridors, thus becoming more abundant in elongated rather than circular fragments (Vignoli et al. 2009).

Our study did not reveal any significant correlates to density of *P. muralis* (issue 3) apart from a negative association with their colubrid predators. This is due to the fact that this species was nearly omnipresent across our study transects. Indeed, this species is well known to be the dominant lizard species within wooded habitats in Central Italy (Rugiero and Luiselli 2007, Vignoli et al. 2009).

With regards to *P. sicula* density (issue 3), its positive association with (circular) fragment shape can be explained by the higher area of grassy matrix surrounding the wooded fragments tending to circular shape than in those with irregular profile. Indeed, *P. sicula* is very well known to be an inhabitant of open grassy and altered lands (Capula et al. 1993, Marsili et al. 2009), and in general avoids wooded habitats (Rugiero and Luiselli 2007), thus showing interspecific ecological differences at a microhabitat scale in respect to the other species investigated. The negative association between *Podarcis* species and colubrid snakes is clearly interpretable as predator pressure avoidance.

Interspecific comparisons vs. environmental variables and predator density

We investigated the patch size and shape, the habitat heterogeneity and the selected potential predator densities of each patch in order to detect if in our study case, lizard density patterns can be explained by the above factors. We found that: *L. viridis* density was significantly higher than that of the two *Podarcis* spp. in MARCIG, the opposite being true for MONTES; comparable densities were estimated in VALLEC.

The higher density of *L. viridis* compared to *Podarcis* spp. in MARCIG is apparently counterintuitive with the general trends for bigger organisms to exhibit lower population

densities compared to smaller closely related species (MacArthur and Pianka 1966). We suggest two possible explanations of this unexpected pattern. Firstly, this pattern may be due to the very irregular shape and large patch size of MARCIG; this would be consistent with our above-presented results about the influences of patch shape and size on distribution patterns of this species, and also with previous literature (Vignoli et al. 2009). Secondly, this pattern may also be due to the abundance of *Rubus* bushes at MARCIG. Also, this explanation mirrors evidence from a previous study (Rugiero and Luiselli 2007) demonstrating a strong correlation of *L. viridis* density with *Rubus* bushes.

In MONTES, the predicted density relationships among species (smaller taxa being more dense) were indeed confirmed. Incidentally, this patch was also that in which snake density reached the lowest values, hence suggesting that the high density of small-sized *Podarcis* lizards may in part be aided also by a possible release in the predation pressure (*Mesopredator release theory*: Soulé et al. 1988, Crooks and Soulé 1999). In particular, this can be true for *P. sicula*, that in MONTES resulted to be one of the favorite prey of *Hierophis viridiflavus* (Capizzi and Luiselli 1996).

Reasons behind the similar densities reached by the three lizard species in VALLEC may be due to the complex interaction of all the factors above mentioned (predator density, shape, total transect length, habitat heterogeneity), but our data are insufficient to disentangle this complex scenario.

Overall, the main shortcoming of the present study is that we do not have a sufficient number of independent study sites (replicates) for testing the above-mentioned patterns and hypotheses carefully. Therefore, further ad-hoc studies should be planned in order to confirm the evidences presented in this study.

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