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Population density in *Podarcis lilfordi* (Squamata, Lacertidae), a lizard species endemic to small islets in the Balearic Islands (Spain)

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Abstract. The Balearic lizard, *Podarcis lilfordi*, is present in 43 insular populations in the Cabrera archipelago and around the coasts of Mallorca and Menorca islands (Spain). We studied lizard densities over the entire range of distribution, analyzing observed differences of density in relation to island area, habitat diversity, availability of resources, presence of predators, competitors and human disturbances. The density of the Balearic lizard varies from less than 35 to almost 8000 lizards ha^{-1}, with an average of around 1500 lizards ha^{-1}. In some very small islets we detected no more than 10 individuals. Using a subsample of nine coastal islets (Menorca) we did not find any significant correlation between ground arthropod biomass and lizard density. The combination of island area and its maximal altitude, its so-called biotic capacity, was also uncorrelated with lizard density. In addition, neither degree of island accessibility nor presence/absence of seagull breeding colonies, were able to explain lizard densities.

Islands without ship rats (*Rattus rattus*) showed a significantly higher lizard density, but islands in which rat eradication programs were launched during the study period, showed lower densities than those with rats but no eradication actions. Genetic variability was significantly higher on bigger lizard populations, lacking a correlation with lizard densities. No single independent variable can explain density differences among populations under study. Our results are discussed in the light of available hypotheses on factors affecting population densities.

Keywords: Balearic Islands, genetic variability, Lacertidae, lizard density, *Podarcis lilfordi*.

Introduction

In many islands, lizards represent important elements within food webs and have consequently been used as model organisms in several areas of ecology and evolution, but the number of studies of population density is still relatively low (Rodda et al., 2001). Within the Mediterranean basin, the Balearic Islands (Spain) are one of the regions in which endemic lizards attain very high densities (Salvador, 1986; Pérez-Mellado, 1989, 1998). At the same time, population sizes on some coastal islets are extremely small, with less than 50, 250 or 1000 individuals and so considered as critically endangered, endangered and vulnerable, respectively, according to the IUCN system (IUCN, 2001). The Balearic lizard is one of three terrestrial vertebrates endemic to the Islands that survived human colonization. The introduction of several predators and potential competitors in the archipelago led to a massive extinction of pre-human vertebrates and only the Majorcan midwife toad, *Alytes muletensis*, the Pityusic lizard, *Podarcis pityusensis* and the Balearic lizard, *P. lilfordi*, have survived to the present day. The Balearic lizard lives only in Cabrera archipelago and coastal islets of Mallorca and Menorca, where predators and competitors were absent.

The conservation status of the Balearic lizard has been recently assessed for the whole species (Pérez-Mellado, 2005; Viada, 2006), but without an analysis of different population sizes, their genetic variability and the relation of lizard abundance with island area, habitat type and

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human pressure. Several factors are known to influence lizard densities, including vegetation cover, presence of competitors and predators, degree of human disturbance and the abundance of food resources (Case and Bolger, 1991a; Rodda et al., 2001).

Here we examine the current status of Balearic lizard populations over the entire species range, discussing the available information on population density, genetic variability, predation pressure and other characteristics. We analyse how lizard abundance varies with island area and some of its correlates such as habitat heterogeneity, topographic diversity and resource availability. The particular distribution pattern of the Balearic lizard provides an excellent opportunity to test different hypotheses based on density-determining factors, because some populations live in large islands with some predators and a continuous human presence, while others live in very small islets as the only terrestrial vertebrate.

Material and methods

Species under study

The Balearic lizard, *Podarcis lilfordi* (Günther, 1874) (Squamata, Lacertidae) is a medium-sized lizard endemic to coastal islets of Mallorca, Menorca and the Cabrera archipelago (Balearic Islands). It is considered an Endangered species (EN) at a national level (Pérez-Mellado, 2002a) and by the IUCN (Cox, Chanson and Stuart, 2006; Pérez-Mellado, 2005), while it was classified as Vulnerable at the regional level of Balearic Islands in its recent Red Book of Vertebrates (Viada, 2006).

Study area

We studied the Balearic lizard covering its entire range (fig. 1), including the archipelago of Cabrera and the islands of Mallorca and Menorca where it is only present on coastal islets around the two main islands (Salvador, 1986; Pérez-Mellado and Salvador, 1988; Pérez-Mellado, 1989; Esteban et al., 1994; Pérez-Mellado, 1998). All populations were visited, although in two of them, En Carabassot de l'Estell den Terra and Illot des Fonoll (Cabrera archipelago), we did not obtain data on lizard abundance nor genetic variability. Due to the assumptions of the method employed (see below), we were unable to obtain density estimates for the following populations: Binicodrell Petit, Rovells, Mel, Ses Aguiles (Menorca), El Toro, Es Colomer (Mallorca) and Esponja (Cabrera).

Density estimation

We employed the line transect method (Buckland et al., 2001), where an observer travels along a line of variable length and records the perpendicular distance from the object to the line for all objects seen. The accuracy of the method primarily depends on the detection of all animals situated on the line of transect. We used ungrouped data, avoiding the inaccuracies of grouping (Southwell and Weaver, 1993). When replicate transects were available, we obtained population densities and associated variances combining them by means of a jackknife procedure. We employed the most recent estimations for each population. In all of them, from line transects done during the period of peak lizard's activity (spring and early summer, from 07.00 to 11.00 GMT). All transects were performed by the same observer (VPM) with the exception of two islets, Na Redona and Ses Rates (Cabrera archipelago), in which we employed density estimations made previously (Sáez, 1994 and unpub. data). Transects were performed during the period 2001-2006, except for Bledas and Porros (Menorca), where we had only density estimates from 1997 and those made by Sáez (1994). Thus, all transect densities correspond only to adult lizards. Line transects were analysed with DISTANCE 5.0 (release Beta 5, Thomas et al., 2005), following the criteria of Buckland et al. (2001) to select the best model for each analysis (additional information concerning number of line transects, lengths and other details for each population is available upon request to the first author).

Population size was estimated as the total number of adult lizards present in each population using the density and the available surface area of each islet. Finally, we employed average body mass of adult lizards from each population (VPM, unpub. data) to calculate the approximate biomass ha^{-1} of lizards on each islet (table 1).

Population characteristics

Due to discordances among different published sources concerning the surface of coastal islets, for each islet we computed its surface, estimated with Sigpac package (http://sigpac.mapa.es), a GIS utility that allows accurate measurements of land surface. We also recorded the maximum altitude of the islet and, as an estimation of the habitat and topographic diversity of the island, the so-called index D of "biotic capacity" (Cheylan, 1992 and references therein) with the formula: $\mathbf{D} = \log(\mathbf{S} \times \mathbf{a})$, where $\mathbf{S}$ is the surface of the island and $\mathbf{a}$ its maximal altitude (Cheylan, 1992; see also Parlanti et al., 1988). To compare islets with and without lizards, biotic capacity was calculated for 26 additional coastal islets from Mallorca, Menorca and Cabrera with surface areas of at least, 0.01 ha and with some shrub vegetation cover. Lizards were absent on those additional coastal islets (pers. obs.).

The presence on each islet of the Ship rat, *Rattus rattus*, was recorded as well as the presence of breeding colonies of the Yellow-legged Gull, *Larus michaellis* and Audouin's Gull, *Larus audouinii*. When available (from official censuses of the Conselleria de Medi Ambient, Govern de les Illes Balears), we included in the analyses the most recent

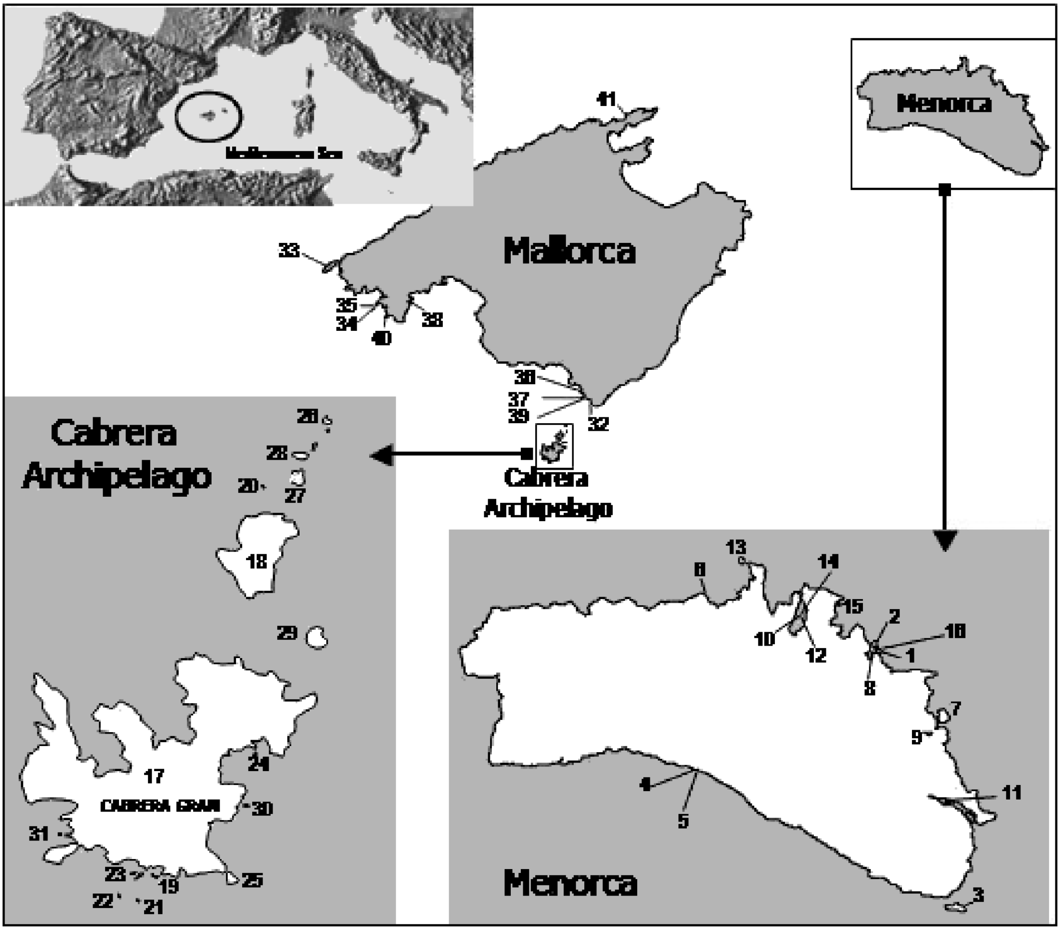


Figure 1. Location of Balearic Islands, the main islands of Mallorca, Menorca and Cabrera archipelago and coastal islets inhabited by the Balearic lizard. Numbers correspond to populations listed in table 1.

estimations of the number of breeding pairs for both seagull species and we calculated a seagull abundance index, as the total number of breeding pairs divided by island area.

The number of vascular plants at each population was obtained from several sources (Bibiloni, Alomar and Rita, 1993 for Cabrera archipelago and unpublished lists). In addition, on 20 populations (see table 1) we performed 2-10 line transects of 25 m length, estimating the percentage cover of different substrates (rocks under 50 cm height, rocks above 50 cm, open ground and grass and the cover by 52 different shrubs and vascular plants that are suitable for lizards as refuges, foraging sites or thermoregulation perches). From these transects, we estimated the diversity of available substrates at each islet with Levins' niche breadth index (Levins, 1968). We also calculated the total percentage of area without vegetation cover from line transects. Arthropod biomass was estimated on 9 coastal islets of Menorca during July 2003. We sampled each islet with a biocenometer, a 1 m^3 mesh tent. Its open bottom was randomly placed on different substrates of each islet and all epigeal arthropods collected. These were identified to family level, measured and dried on furnace at 65°C to constant weight. Weight was obtained with an electronic balance (Mettler®, model H20). For each islet we computed the average arthropod biomass (grams/m^3).

According to potential human disturbance, we grouped islets into four different accessibility groups (0: islets with cliffy coast, no landing areas and very rare human visits, 1: islets with a difficult access, far from any port and only with sporadic human visits, 2: islets of easy access, close to coast and frequent visits, at least during summer and 3: very easy access, very close to coast and/or presence of a jetty, frequent visits during the whole year).

Genetic variability

A total of 250 individuals were sampled, two to five individuals of *P. lilfordi* from 41 insular populations (from Cabrera Island we sampled lizards from three different localities, fig. 1). The tail tip of each individual was clipped off and stored in 100% ethanol. Live animals were released

Table 1. S: island area (in hectares), rats: presence (+) or absence (−) of the ship rat, *Rattus rattus*; seagulls: presence (+) or absence (−) of seagull breeding colonies; H: maximum altitude of the island, D: Biotic capacity index (see Material and Methods), B: niche breath index of vegetation and substrate cover, lizard density (mean ± SE lizards ha^{-1}, excepting for estimation at Na Redona and Ses Rates, see Sáez, 1994), PS: adult population size calculated with the average lizard density and the area of each islet, Biom: lizard's biomass (kg ha^{-1}), NPS: total number of polymorphic sites, P_i: nucleotide diversity, k: average number of nucleotide differences.

Population	S	rats	seagulls	H	D	B	density	±SE	PS	Biom	NPS	P_i	k
MENORCA													
1. Addaia Gran	5.55	−	+	22.1	4.81	5.47	1062.40	391.81	5896	5.79	3	0.000775	1.60
2. Addaia Petita	3.29	+	+	7.8	3.24	3.33	412.57	113.35	1357	2.74	3	0.000550	1.20
3. Aire	29.80	−	+	15	6.10	5.58	4098.60	586.60	122 138	32.54	1	0.000200	0.50
4. Binicodrell Gros	0.29	−	−	6.1	0.57	3.84	1180.50	264.45	341	7.59	0	0.000000	0.00
5. Binicodrell Petit	0.01	−	−	6.1	−2.67						1	0.000250	0.60
6. Bledes	2.32	+	+	61.5	4.96		1060.80	248.07	2461	5.37	1	0.000500	0.60
7. Colom	51.14	+	+	40	7.62	9.38	1615.50	294.93	82 616	11.02	4	0.000950	2.07
8. En Carbó	0.14	−	−	3.6	−0.71	4.90	475.33	261.43	65	2.61	6	0.001775	3.47
9. Mel	0.20	−	−		−0.93						5	0.001675	3.00
10. Porros de Fornells	0.05	−	−	1.4	−2.64	5.18	1676.00	599.31	86	12.07	1	0.000275	0.67
11. Rei	4.08	+	−	14.5	4.08	4.43	402.66	75.65	1643	3.14	5	0.001500	2.94
12. Rovells	0.24	−	−	6.3	0.43	3.35					4	0.001225	2.00
13. Sanitja	5.15	−	+	18.5	4.56	4.71	1541.80	424.86	7940	10.07	4	0.000875	1.60
14. Sargantana	2.30	−	−	14.5	3.51	2.40	687.66	155.99	1582	4.40	3	0.000675	1.40
15. En Tosqueta	0.29	+	−	6.1	0.57	4.91	1703.00	501.41	492	11.29	0	0.000000	0.00
16. Ses Aguiles	0.14	−	+	13.3	0.65						0	0.000000	0.00
CABRERA													
17. Cabrera Gran	1147.84	+	+	172	12.19		329.59	80.15	378 316	2.30	24	0.004100	7.13
18. Sa Conillera	139.81	+	+	100	9.54		633.85	230.04	88 618	5.74	14	0.004725	8.17
19. Esclata-sang	0.39	−	+	35	2.61	6.34	3117.40	676.28	1213	32.67	8	0.003333	4.53
20. Esponja	0.15	−	+	23	1.23						0	0.000000	0.00
21. Estell de Fora	0.16	−	−	24	1.31	2.65					0	0.000000	0.00
22. Estell des Coll	0.50	−	−	35	2.86						2	0.000400	0.80
23. Estell Xapat	1.491	+	−	44	4.18	3.09	2006.70	562.04	2990	19.76	1	0.000325	0.67
24. Fonoll	0.27	−	−	13	1.25	6.12	7815.50	2398.20	2101	79.25	1	0.000325	0.60
25. Imperial	2.12	+	+	70	5.00		1483.70	379.87	3145	12.82	0	0.000000	0.00
26. Na Foradada	1.61	−	+	27	3.77	2.93	2595.40	336.60	4178	25.17	0	0.000000	0.00
27. Na Plana	3.93	−	−	22	4.46	3.00	2021.60	300.84	7945	18.50	10	0.003025	5.00
28. Na Pobra	2.07	−	−	24	3.90	4.19	2361.10	477.45	4887	24.20	0	0.000000	0.00
29. Na Redona	9.98	+	+	56	6.32		212.20		2118	2.08	6	0.001475	3.00
30. Ses Bledes	0.57	−	−	9	1.63	3.95	2852.80	783.59	1623	39.51	0	0.000000	0.00
31. Ses Rates	0.33	+	+	8.5	1.03		32.00		11	0.27	0	0.000000	0.00
MALLORCA													
32. Es Caragol	0.38	−	+	5	0.63		845.00	429.96	317	6.08	0	0.000000	0.00
33. Dragonera	267.81	+	+	300	11.29		729.42	124.15	195 346	5.60	9	0.002925	4.33
34. Malgrat gran	8.62	+	+	62	6.28		235.42	92.43	2029	1.84	0	0.000000	0.00
35. Malgrat petit	0.91	+	+	29	3.27		1201.90	331.85	1095	9.13	1	0.000275	0.40
36. Na Guardia	1.66	−	+	7	2.45		1700.90	341.75	2823	11.77	0	0.000000	0.00
37. Na Moltona	4.00	−	−	9	3.58		2515.40	746.90	10 061	18.89	9	0.002550	5.00
38. Na Porrassa	4.10	−	+	38	5.05		334.01	100.26	1369	2.77	0	0.000000	0.00
39. Na Pelada	1.05	−	−	3	1.15		73.42	33.57	77	0.52	0	0.000000	0.00
40. El Toro	0.47	+	+	28.9	2.61						0	0.000000	0.00
41. Es Colomer	3.05	−	+	102	5.74						16	0.004550	8.09

again in the same capture site. Total genomic DNA was extracted following standard protocols (González et al., 1996) with minor modifications. Four mitochondrial partial genes, 12S RNA, cytochrome *b* (two regions obtained separately), ND2, partial control region and nuclear gene C-mos were studied. For each fragment amplifications were done using specific primers and PCR conditions (Terrasa et al., in prep.). PCR products were purified and sequenced using the ABI Prism BigDye Perminator Cycle sequencing protocol in an ABI Prism 3100 automated sequencer (Applied Biosystems®). Sequences were aligned by eye with BIOEDIT program. The total length of mitochondrial sequence obtained for each individual was 2388 bp.

Sequences variability was estimated for each fragment and population. The number of polymorphic sites (NPS), the nucleotide diversity (P_i) and the average number of nucleotide differences between two sequences (k) were estimated using MEGA 3.1 (Kumar, Tamura and Nei, 2004) and DnaSP 4.0 (Rozas et al., 2003).

Statistical analyses

Results are expressed as mean ± standard error, unless otherwise stated. We performed linear and second-order polynomial regressions to determine the variance in the density variable accounted for by the following explanatory variables: Biotic capacity, abundance of vascular plants (log-transformed), diversity of available substrates estimated with niche breath index (log transformed) and the proportion of open areas uncovered by vegetation. The criterion used to select model is the change in the error sum of squares produced by the inclusion or exclusion of variable or subset of variables (Neter, Wasserman and Kutner, 1985). The groups of islets and different conditions were compared with ANOVA analyses, providing that data meet the assumptions of normality and variance homogeneity (Zar, 1999).

We applied the regression trees to explore the structure of islands in terms of density. Regression trees are based on the AID method (Automatic Interaction Detection) proposed by Morgan and Sonquist (1963). The algorithm performs stepwise splitting. It begins with a single cluster of cases and searches a candidate set of predictor variables as a way to split this cluster into two further clusters. The criterion to split the cluster is based on the sums of squares which most significantly separate the means. P-values were adjusted in a complex manner that takes into account the number of different splits that can occur. A sample size of 5 was chosen as the total sample size which becomes the minimum size splitting allowed. The explanatory variables included in this analysis were: Biotic capacity, vascular plants abundance, the diversity of available substrates estimated with niche breath index and the proportion of open areas uncovered by vegetation), rats (presence/absence), seagull breeding colonies (presence/absence) and presence/absence of a rat eradication program. In addition, we computed non parametric correlations (Spearman rank correlation test) between density and estimators of genetic variability as well as between density and arthropod availability, from which we only had data from nine populations. All analyses were done with the packages Statistica (ver. 6.0) and JMP (ver. 5.01).

Results

Density and habitat characteristics

The Balearic lizard is present in 43 insular populations in Mallorca, Menorca and the Cabrera archipelago (fig. 1). Coastal islets with lizard populations have a significantly higher biotic capacity than those without lizard populations (one-way ANOVA $F_{1,63} = 4.02$, $P = 0.04$; homogeneous variances, Levene test: $F = 0.28$, $P = 0.60$; islets with lizards: mean $= 3.35 \pm 0.50$, range: -2.67-12.19, $n = 41$; islets without lizards: mean $= 1.79 \pm 0.34$, range: -0.64-6.20, $n = 26$).

We were unable to estimate densities in some of the smaller islets. In Ses Aguiles (Menorca) we detected no more than 10 different lizards during five surveys between 2001-2006. This was similar to the situation in Binicodrell Petit (Menorca), very close but fully isolated from Binicodrell Gros. In Mel and Rovells (Menorca) we detected abundant lizard populations, but could not estimate respective densities because of the very dense shrub cover. The density is extremely low on Esponja islet (Cabrera), where we observed only three individuals during a survey of more than two hours in September 2004 (under excellent weather conditions). On Estell de dos Colls and Estell de Fora (Cabrera), lizard densities appeared high but the cliffy nature of the islets precluded reliable estimations. In Mallorca, lizard density is extremely low at El Toro islet, where we detected no more than 10 individuals during a three hours survey in July 2006. Finally, Es Colomer islet probably has a very abundant lizard population, according to observations made during June 2006, but we were only able to visit the more stepped areas of the islet, in which a line transect estimation was impractical.

For line transects from the remaining populations ($n = 33$), the average lizard density was: mean $= 1529.24 \pm 252.09$ lizards ha^{-1} (range: 32.0-7815.5). Most lizard densities estimates are under 1000 lizards ha^{-1} (table 1). In spite of large differences between islets and differences

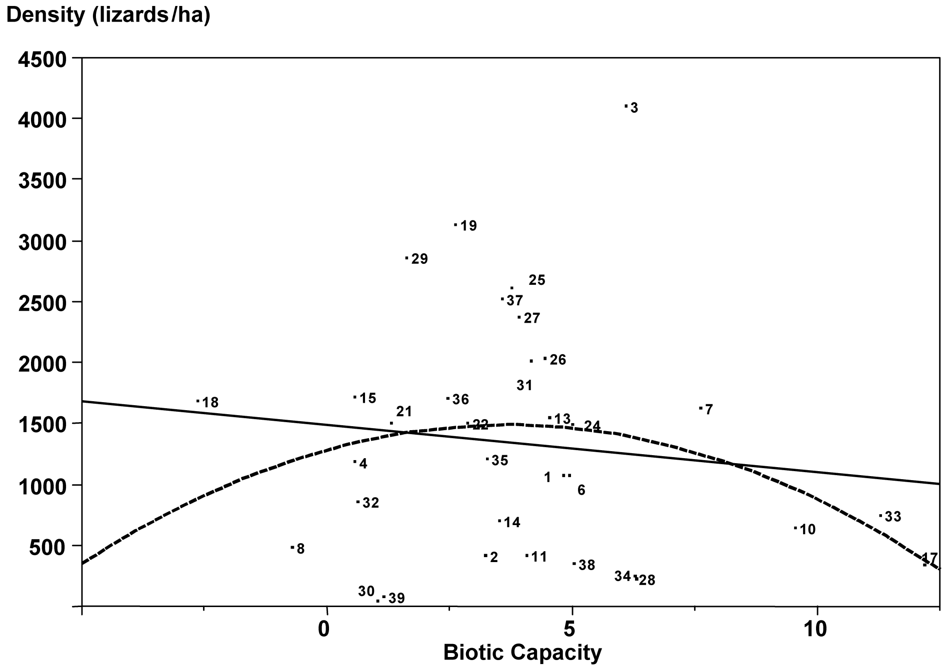


Figure 2. Regression analyses for density (y-axis) versus biotic capacity (BC). Linear regression ($\text{Density} = 1491.66 - 39.06 \times \text{BC}$) and quadratic regression ($\text{Density} = 1283.54 + 111.145\text{BC} - 15.16\text{BC}^2$) models are represented by continuous and dashed lines, respectively.

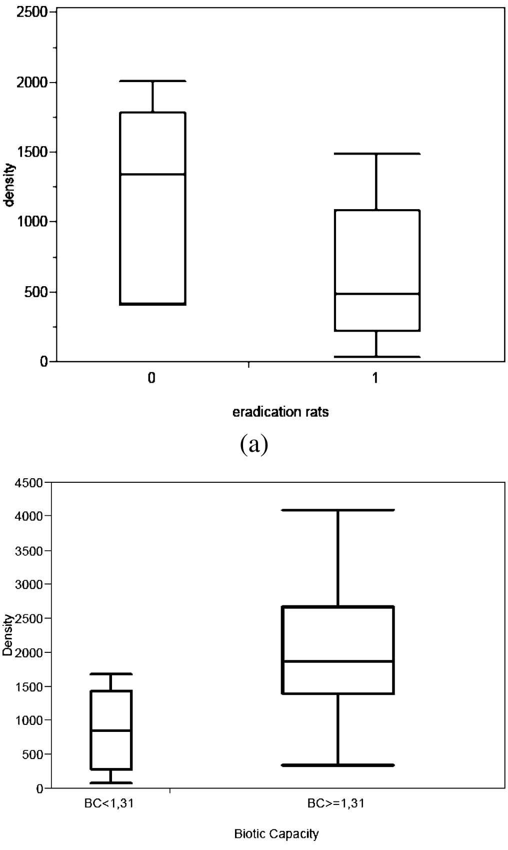
observed between mean densities, we did not detect significant differences among the three groups of populations, from Mallorca, Cabrera and Menorca (one-way ANOVA, $F_{2,31} = 1.59$, $P = 0.22$, Levene test, $F = 1.19$, $P = 0.32$; Mallorca: mean $= 954.43 \pm 292.64$ ha^{-1}, $n = 8$, range: 73.42-2515.40; Cabrera: mean $= 2031.56 \pm 517.71$ ha^{-1}, $n = 14$, range: 32-7815.5; Menorca: mean $= 1326.40 \pm 289.48$ ha^{-1}, $n = 12$, range: 402.66-4098.60). In addition, we did not detect any significant difference in the average surface of islets with lizards from Mallorca, Cabrera and Menorca (one-way ANOVA, $F_{2,31} = 0.59$, $P = 0.56$, Levene test, $F = 2.48$, $P = 0.10$). Hence, for the remaining comparisons, we pooled the data from the three island groups. From the nine coastal islet of Menorca (Addaia Gran, Aire, Binicodrell Gros, En Carbó, Porros de Fornells, Rei, Sanitja, Sargantana and En Tosqueta, see table 1) from which we have information on arthropod availability, we did not find any significant correlation of available arthropod biomass and lizard density (Spearman rank correlation, $R_s = 0.25$, $t = 0.68$, $P = 0.52$, $n = 9$).

We did not find significant linear ($F_{1,31} = 0.50$, $P = 0.48$) nor quadratic ($F_{1,31} = 1.14$, $P = 0.33$) relationships between lizard density and biotic capacity (fig. 2). The proportion of variance of the density explained by biotic capacity is very low in both models ($R^2 = 1.6\%$ for the linear model and $R^2 = 7.1\%$ for second-order polynomial model). The change in the error sum produced when we include the quadratic term was non-significant ($F_{1,30} = 1.67$, $P = 0.20$). The densities of lizards in Aire Island could be an influential point for linear and polynomial models (fig. 2). However, when it is removed, the results are quite similar for both models ($R^2 = 4.8\%$; $F_{1,30} = 1.54$, $P = 0.22$; $R^2 = 9.0\%$, $F_{1,30} = 1.44$, $P = 0.25$, respectively). In the same way, the remaining explanatory variables were not significant for linear and quadratic models. The multiple regression model with all variables was also not significant ($F_{4,14} = 0.62$, $P = 0.66$, $R^2 = 19\%$).

Density, humans, seagulls and rats

The degree of accessibility to islets is a negligible factor to explain lizard densities (one-way ANOVA, $F_{3,30} = 0.70$, $P = 0.56$, Levene test, $F = 0.95$, $P = 0.43$). Islets with seagull breeding colonies have similar densities than those without seagulls (one-way ANOVA, $F_{1,32} = 0.42$, $P = 0.52$, Levene test, $F = 0.11$, $P = 0.74$).

We compared lizard densities on islands with and without rats and we found significantly higher densities on islands without ship rats (ANOVA analysis, $F_{1,31} = 5.60$, $P = 0.02$, fig. 4). In several islets with ship rats, an eradication program was launched by the Nature Conservation Agency of the Balearic Government (Conselleria de Medi Ambient, Govern de les Illes Balears). We compared, within the subset of islets with ship rats, those populations where an eradication action took place with those without any eradication program during the study period. We detected a marginally significant lower density on islets with an eradication program (one-way ANOVA, $F_{1,12} = 3.45$, $P = 0.09$; Levene test, $F = 1.32$, $P = 0.27$; islets with rats and no eradication program: mean $= 1200.20 \pm 279.79$ ha^{-1}, range: 402.66-2006.7, $n = 6$; islets with rats and eradication program: mean $= 607.26 \pm 181.25$ ha^{-1}, range: 32-1483.7, $n = 8$). Moreover, if we compare islets with and without ship rats, but excluding those where an eradication program took place, we did not find any significant difference on lizard density (one-way ANOVA, $F_{1,22} = 0.87$, $P = 0.36$; Levene test, $F = 0.59$, $P = 0.45$).



(a)

(b)

Figure 3. Box-plots of lizard densities for the four terminal groups found in the regression tree analysis (see fig. 4): A) Island with rats and eradication program (0), Island with rats without eradication program (1). B) Island without rats and biotic capacity <1.13, Island without rats and biotic capacity >1.13.

Moreover, in the AID analysis, habitat, presence/absence of rats, seagulls and eradication action were the predictor variables. The first partition was due to presence/absence of rats. This variable created splits with the largest separation of the means by the sums of squares (adjusted P-value $= 0.01$, fig. 3). The second partition, within the islands with rats, was due to the presence/absence of an eradication program as we previously showed. These clusters did not split further because subsequent groups were under the minimum splitting size allowed (see above). The partition within islands without rats cluster is due to biotic capacity index. Biotic capacity <1.31 and biotic capacity $\geqslant$1.31 was the splitting threshold which computes the highest difference between means of all possible ways to divide this cluster into two groups. Although the adjusted P-value is large ($P = 0.26$) the difference between means is substantial (biotic bapacity <1.31, mean $= 850.05 \pm 123.89$ ha^{-1}, $n = 5$; Biotic capacity $\geqslant$1.31, mean $= 1990.65 \pm 72.32$ ha^{-1}, $n = 14$). The next partition of the cluster, biotic capacity $\geqslant$1.31, was rejected because the adjusted P-value was very large (0.44). Thus, we found four final groups

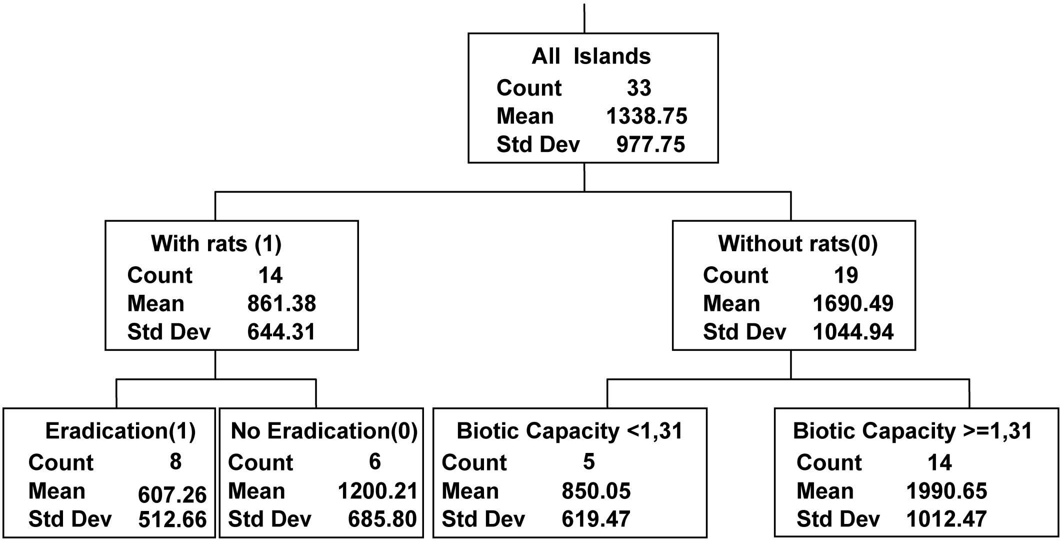


Figure 4. Classification tree of average densities calculated from the following explanatory variables: Biotic capacity, vascular plants abundance, diversity of available substrates estimated with niche breath index and the proportion of open areas uncovered by vegetation, presence/absence of ship rats, presence/absence of seagull breeding colonies and the launching of a rat eradication program during the study period. Each split is defined by adjusted P-values (see more details in the text).

defined by the presence or absence of ship rats, the existence of an eradication program and the biotic capacity index (fig. 4).

Lizard abundance and genetic variability

We do not detect any significant correlation between lizard density and the three different estimators of genetic variability, that is, the total number of polymorphic sites ($R_s = -0.07$, $t = -0.39$, $P = 0.70$, $n = 34$), the average nucleotide diversity ($R_s = -0.07$, $t = -0.38$, $P = 0.71$) or the average of nucleotide differences ($R_s = -0.05$, $t = -0.30$, $P = 0.76$). On the other hand, population size was significantly correlated with the total number of polymorphic sites ($R_s = 0.48$, $t = 3.07$, $P = 0.004$, $n = 34$), average nucleotide diversity ($R_s = 0.48$, $t = 3.43$, $P = 0.001$) and average nucleotide differences ($R_s = 0.46$, $t = 2.95$, $P = 0.006$).

Discussion

Amphibians and reptiles generally reach much higher densities than endothermic vertebrates (birds, mammals). Lizards are particularly abundant on islands where densities above 4000 individuals/ha are frequently reported (Bennett and Gorman, 1979; Brown and Pérez-Mellado, 1994), with extreme estimates of 20 000 animals/ha in some *Anolis* species (Gorman and Harwood, 1977; Rodda et al., 2001). The highest value recorded for a non-aggregated lizard was for *Sphaerodactylus macrolepis* at some study plots in the Virgin Islands, where Rodda et al. (2001) estimated an average lizard density of 52 800 ha^{-1} (with a maximum of 67 600 ha^{-1}).

In spite of a rather difficult comparison, due to the wide range of estimation methods employed by different authors, densities reported for Balearic Islands are similar to those previously known from several islands. In Corsica Island, a density of 700 to 870 lizards ha^{-1} is common in *Podarcis tiliguerta*, while on small coastal islets around Corsica (Lavezzi archipelago), densities of 1700-2180 lizards ha^{-1} were recorded (Delaugerre and Cheylan, 1992).

In Cabrera archipelago, Martínez-Rica and Castilla (1987) reported a density of *Podarcis lilfordi* of 492 ha^{-1} in the islet of Sa Conillera and 1080 ha^{-1} from Na Foradada islet, although Salvador (1993) later suggested that these values probably underestimated true densities on these islets, as we can confirm in our results (table 1). In a more detailed study, Sáez (1994) estimated densities ranging from 13.6 to 225.7 lizards ha^{-1} on the main island of Cabrera, to 2569 lizards ha^{-1} in Na Foradada islet. It is interesting to note that the density of Na Foradada is practically identical to our estimate despite a ten years interval (Sáez, 1994 and table 1).

We were unable to find a significant relationship (fig. 2) between lizard density and island area, employing linear and polynomial regressions. In addition, we were also unable to demonstrate a clear relationship between lizard density and habitat characteristics or human pressure. The density of the Balearic lizard seems to be subject to a host of factors that do not vary uniformly from island to island.

Several hypotheses could explain the high densities of the Balearic lizard in some of the populations under study. The resource-concentration hypothesis predicts that density will increase with increasing area. According to Root (1973), the density will increase as the diversity and concentration of resources in larger areas increases carrying capacities. Hence, increases in the abundance and diversity of resources with area will increase the density of individuals (Connor et al., 2000; Buckley and Roughgarden, 2006). But, searching for this density-area relationship, Connor et al. (2000) reported conflicting shapes of graphical models relating these factors (Buckley and Roughgarden, 2006). The density compensation effect (MacArthur, Diamond and Karr, 1972) is one of these general explanations. Giving a simplified community in islands, resident species compensate for the lack of interspecific competitors reaching a similar density than the overall density of a continental guild of potential competitors. In other words, the density compensation hypothesis predicts that density will decrease with increasing area. That is, species are predicted to expand their ecological niches on small islands when released from competition and predation (MacArthur, Diamond and Karr, 1972). In the case of the Balearic lizard, density compensation would be enabled by a release from most of the terrestrial predators and the competition by insectivorous birds, practically absent in most of the islets (pers. obs.). The second explanation is based on lower predation regimes on islands in comparison with continental areas (Case, 1975); the lack of specialized predators on the small Mediterranean islets like in other ecosystems, explains the high densities (Case, 1983; Barbault, 1991; Case and Bolger, 1991a, b; Brown et al., 1992). Brown and Pérez-Mellado (1994) showed that high lizard densities in two coastal islets of Menorca (Sanitja and Aire) accord well with the hypothesis of predation relaxation. Densities should be higher in smaller, less heterogeneous islands with fewer predators. Krebs, Keller and Tamarin (1969) and MacArthur, Diamond and Karr (1972) also proposed an explanation based on the "fence effect". That is, the existence of a physical barrier for dispersal and the occupation of marginal habitats would allow high densities.

A final hypothesis deserves particular attention. According to Emlen (1978, 1979), the restrained or null genetic flux between different insular populations promoted a rapid and widespread transmission of adaptive characteristics among individuals within the same population, a consequent increase in their fitness and, finally, a higher population density. Obviously, this last cause could act in combination with any of the other causes above mentioned, amplifying their effects. However, in the case of Balearic Islands, we are more prone to explain high densities of several populations as a response to low or even non-existent levels of predation.

Values of genetic variability detected at the populations of the Balearic lizard are lower than those described in other insular lizards, as the Columbretes Wall Lizard, *Podarcis atrata*, an endemic lacertid lizard inhabiting Columbretes archipelago, close to the eastern Spanish coast. In *P. atrata*, nucleotide diversity ranges from 0.02176 ± 0.004 to 0.07068 ± 0.029 (Castilla et al., 1998). We detected a clear relation between the size of lizard populations and genetic variability in terms of total number of polymorphic sites. This result agrees with those obtained from other vertebrate populations (Frankham, 1996; Frankham, Ballou and Briscoe, 2002) and indicates the importance of population size as a conservation factor. Those populations of small islets with a very small size exhibited a very low genetic variability, probably as the consequence of the bottleneck during the early isolation of the islet. Supposedly, this reduction of genetic variability would produce a decrease of individual fitness (see, for example, O'Brien et al., 1985 and Ledig, 1986). But, surprisingly, some lizard populations from Balearic Islands maintain very small sizes, below 100 adult lizards, seem to have survived for long periods despite extremely low genetic variability. Perhaps the random distribution of deleterious alleles in gametes implies a lower probability of their transmission by population founders on these small demes (Soulé, 1987).

Concerning the relation between lizard density and rat presence, the role of introduced rodents at insular ecosystems still remains controversial (Pérez-Mellado, 2002b; Ganzhorn, 2003). Palmer and Pons (1996) documented a sharp effect of introduced rats on terrestrial invertebrates from Balearic coastal islets. Thus, we could expect an indirect effect on an omnivorous vertebrate as the Balearic lizard that consumes a wide range of arthropods and plant species (Pérez-Mellado and Corti, 1993). In Seychelles and Comoros Islands, rat-free islands have lower lizard densities than those with introduced rats (Brooke and Houston, 1983; Cheke, 1984).

Data on Ship rat densities at Balearic Islands are not available (Zamorano and Palomo, 2002), but in Colom, Dragonera and Cabrera Gran, rat densities are very high (pers. obs.). In fact, the presence of ship rats is also evident in some islets not included in density analyses, because we lack density estimations from them, e.g., El Toro islet, where lizard density is very low. However, if we exclude islets without an eradication program, lizard densities are not different on islets with or without rats. Thus, is it the result of a smaller sample size on the ANOVA analyses or do the eradication programs themselves really affect the lizards? We do not have a clear answer, although in some islets such as Ses Rates (Cabrera) almost 100% of faecal samples from lizards contained evidence of rat venom (VPM, pers. obs.). Thus, we cannot rule out the possibility that eradication programs have a negative effect on lizard populations.

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