Acta Oecologica **19** (2) (1998) 107-114 / © Elsevier, Paris

Predation and spatial distribution of the lizard *Podarcis hispanica atrata*: an experimental approach

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Received April 4 1997; accepted August 27 1997

Abstract – This study reports on an experiment designed to quantify potential predation by birds on the lizard *Podarcis hispanica atrata* in the Columbretes islands (Castellón, Spain). We used plasticine replicas to examine predation risk of replicas as a function of proximity to vegetation and to potential predators, and to investigate the seasonal variation in patterns of predation. Predation on replicas was very high and intensive within only four days, and differed between study areas and seasons. Predation was more intense when replicas were closer to nests of gulls and far from vegetation. The Yellow-legged Gull (*Larus cachinnans michaellis*) was identified as the major species responsible for predation on lizard replicas.

Mediterranean islands / Spain / lizard / *Podarcis hispanica atrata* / predation / plasticine replicas

1. INTRODUCTION

Predation is one of the most important factors that determine patterns of mortality rates [32] and distribution [4] in animals. This selective pressure can determine demographic parameters, population structure and life history traits in prey populations [37]. The major problem associated with studies of predation is that encounters between predators and prey are only rarely observed in nature. Consequently, some studies employ long-term predator exclusion experiments to evaluate the effect of predation [e.g. 21, 26], whereas others use indirect evidence such as injury (e.g. tail-breaks in lizards) frequencies as an index of predation intensity [e.g. 35]. An alternative approach used in short-term studies consists of recording predatory attacks on soft replicas of the prey species of interest. The use of soft replicas is particularly useful, because it allows identification of predators through examination of the imprints on the replica surface [refs. in 28]. This methodology has provided very interesting and successful results in studies of predation on bird nests [11, 31] and on reptiles [8, 9].

In this study, we estimated the potential predatory intensity on the lizard *Podarcis hispanica atrata* in different areas within a small (13 ha) Mediterranean island. We used soft replicas to determine which bird species were responsible for predation. By locating lizard replicas at sites that differed in vegetation structure and densities of potential predators, we examined the extent of inter-site variation in potential predation rates. A main goal of this study was to evaluate whether microgeographic variation in attack frequency on lizard replicas is correlated with variation in lizard densities, and can help to explain patterns of lizard distribution in Mediterranean islands.

2. MATERIAL AND METHODS

2.1. Study site and animal

The Columbretes islands (39 × 54' N, 0° 41' E; *figure 1*) are an archipelago of small islets of volcanic origin situated in the Mediterranean sea *c.* 50 km off the coast of Castellón (province of Castellón, Spain: see [13]; *figure 1*). The vegetation consists mainly of perennial scrubs (*Suaeda vera*), patches of herbs (*Lobularia maritima*, *Lavatera mauritanica*, *Malva parviflora*) and grasses.

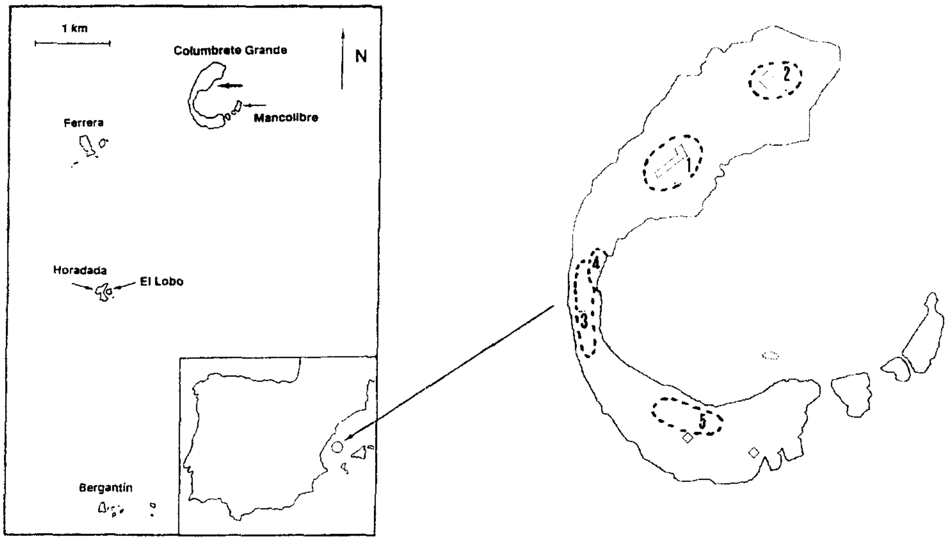

Figure 1. Location of the 5 study areas on Columbrete Grande island (Castellón, Spain).

The islands are inhabited by the endemic and endangered lacertid lizard *Podarcis hispanica atrata,* whose entire geographic range is restricted to *c.* 20 ha. It is a small (adult snout-vent length (SVL), 52-74 mm; mass, 3-7 g) heliothermic lizard that spends most of its time on the ground in semi-open habitats. Bushes, burrows, rocks, bricks and rock crevices serve as diurnal refugia from avian predators. Adult lizards typically capture invertebrates and conspecific juveniles through foraging widely [13, 16].

Besides lizards, the only vertebrates that breed on the islands are seabirds and falcons: mammals are absent [13]. As the islands are situated along a major migratory route for birds, several bird species were temporarily present during the course of this study.

2.2. Replica construction and placement

Lizard replicas were constructed using precoloured, non-toxic plasticine. We used a plastic mould to obtain replicas similar in size and body shape to adult *Podarcis* lizards. Replicas were one of three colours, which mimicked the main colouration of the lizards' back (green and brownish) and of their vent and throat (orange).

The study was conducted during May (spring) and September (autumn) 1991 on 'Columbrete Grande' (13 ha). Five study areas (*figure 1*) differing in habitat structure [12], lizard density [13, 14] and abundance of predators (pers. obs.), were chosen for the experiments. Area 1 is a well-vegetated site with a fine-grained mosaic of patches covered by scrubs, herbs, grasses, bare sand, or piles of volcanic stones. Lizard density is high (*c.* 1 000 ind · ha^{-1}). Gulls do not breed in this area, although solitary Yellow-legged Gulls occasionally approach the site to search for human discards. Area 2 is mainly covered by loose rocks, stones and debris of abandoned human constructions, and rather sparsely vegetated by scrubs and herbs. Lizards density is high (*c.* 800 ind · ha^{-1}). Yellow-legged Gulls have established a small breeding colony in this area. Area 3 includes an area covered by bare volcanic rocks with sparse, low herbs (***Mesembryanteum nodiflorum***), and a smaller area with patches covered by sand, rocky soil, herbs and scrubs. Lizard density is very low (< 200 ind · ha^{-1}). Yellow-legged Gulls used this area as a major breeding site during May and as a roosting area during September. Area 4 is almost completely covered by bare volcanic rocks; vegetation is virtually absent with the exception of some small herbs (*Mesembryantemum nodiflorum*). Lizard density is low (< 100 ind · ha^{-1}) and a few nests of Yellow-legged Gulls were present during May. Area 5 is entirely covered by rocks with no vegetation. Lizards are virtually absent; Yellow-legged Gulls used this site as a major roosting area during September.

Within each area, we positioned replicas every 5 m at both sites of a transect line, selecting replica colour at random. All replicas were located at ground level, in a position that simulated an immobile 'basking' lizard. Replicas were loosely fixed on rocks or on the ground to prevent being blown away by the wind. For each replica positioned during May, we recorded: area, replica colour, type and height of the nearest vegetation, distance to nearest vegetation, and distance to the nearest nest of the Yellow-legged Gull. To facilitate recovery and control of the replicas, we placed a numbered flag (15 × 3 cm) 20 cm from each replica. Because all flags were identical in size, colour (beige) and distance to the replica, differences among areas in predation rates over replicas cannot be attributed to the flags, even if their presence would have attracted the predators' attention. All replicas in both seasons were placed during a single day and subsequently censused every other day (trials). During each census, we recorded whether a replica was intact, had small or intermediate bill-marking, was smashed (i.e. totally broken due to intense predation), or was missing. For each replica, we estimated the intensity of mutilation as the percentage of the replica's surface that bore bill markings. A 100 % mutilation intensity was assigned to missing replicas. On every census, we replaced attacked or missing replicas with a new one of the same colour. Based on the size and shape of the bill markings (similar to those left on cutterfish bone), predatory attempts by gulls could easily be distinguished from those by other birds. Different species of resident and migratory birds during both study periods were recorded using a binocular (8 × 40) or telescope (30 ×).

2.3. Data analysis

Replicas were exposed to predators during two consecutive 2-day periods. However, results obtained during different trials for the same replica in the same location cannot be considered as statistically independent. We therefore estimated rates of predation as the proportion of replicas that were predated at least once during the two trials. We used logistic regression [24] to examine whether the predation rate of a replica in May was related to several continuous (distance to nest, distance to vegetation, height of vegetation) and categorical (replica colour, type of vegetation) variables. Analyses were performed with SPSS/PC+ V5.0

3. RESULTS

Predation rates on lizard replicas differed significantly between study areas during May ($\chi^2 = 64.79_{\text{d.f.} = 3}$, $P < 0.001$; *table I*). Predation occurred in all areas within only 4 days of exposure to predators. In area 3, where Yellow-legged Gulls established their major breeding colony, most replicas (93 %) were attacked by predators, whereas only 9 % of the replicas placed in area 1 (near human settlements) were predated. During September, predation rates on replicas also varied significantly among areas ($\chi^2_{\text{d.f.} = 4}$ =

Table I. Predation rates in different study areas during May and September 1991. Percentage of replicas that were predated during the first and second trials, and percentage predated at least once during the two first trials (1+2) are indicated. Numbers indicate percentages, number of replicas in paranthesis.

	May			September		
Area	Trial 1	Trial 2	Trial 1+2	Trial 1	Trial 2	Trial 1+2
1	5	5	9	0	0	0
	(42)	(42)	(42)	(34)	(34)	(34)
2	20	7	27	0	0	0
	(30)	(30)	(30)	(34)	(34)	(34)
3	66	77	93	0	27	27
	(41)	(41)	(41)	(34)	(34)	(34)
4	12	25	31	0	0	0
	(16)	(16)	(16)	(16)	(16)	(16)
5	-	-	-	35	49	49
	-	-	-	(74)	(74)	(74)

Table II. Summary statistics (mean ± 1 S.E.; in cm) of habitat characteristics at different study areas (1-4) and results of inter-area comparisons. Sample sizes are shown in parentheses.

	1	2	3	4	Kruskal-Wallis
	(42)	(30)	(41)	(16)	*P*
Distance to nest	1530 ± 2	750 ± 45	445 ± 45	930 ± 43	< 0.001
Distance to vegetation	21 ± 5	26 ± 7	42 ± 20	532 ± 111	< 0.001
Vegetation height	33 ± 5	31 ± 5	23 ± 3	8 ± 2	< 0.001

52.09, $P < 0.001$; *table I*), and was only evident in areas 3 and 5. The highest predation rate (49 %) in September was encountered in area 5, where Yellow-legged Gulls had a large roosting area. In area 3, where these gulls established a smaller roost, predation on replicas was lower (27 %) than in May (93 %). Overall predation rates were lower in September than in May (*table I*).

What factors cause the inter-area difference in predation rates over lizard replicas? Replicas of different colours were uniformly distributed over the study areas (May: $\chi^2_{d.f. = 6} = 3.92$, $P > 0.60$; September: $\chi^2_{d.f. = 8} = 1.45$, $P > 0.20$). Hence, differences in predation rates among areas are unlikely to be biased by replica colour. The study areas differed considerably in vegetation type and cover (*table II*). Plant species near replicas (grouped in 4 categories) also differed between the 4 study areas ($\chi^2_{d.f. = 9} = 89.37$, $P < 0.001$). Vegetation was especially sparse and low in areas 3 and 4. Thus, both vegetation height and the distance between the replica and the nearest patch of vegetation varied significantly among study areas (*table II*). The distance of replicas to the nearest nest of gull differed among areas (*table II*).

The global, forward and backward logistic regression models provided identical results. All variables were removed from the model except 'area'($\chi^2_{d.f. = 3} = 18.33$, $P < 0.001$) and distance from the replica to the nearest nest ($\chi^2_{d.f. = 1} = 3.19$, $P = 0.07$). Results indicated that 83 % of the replicas were correctly classified as either being attacked by predators or not. Given that variables indexing vegetation structure and presence of gulls differed significantly among study areas (*table II*), the variable 'area' somehow represents a combination of all these differences. Therefore, we excluded the variable 'area' from the analysis in order to examine which of the remaining variables was most closely associated with the incidence of predatory attacks on the replicas. The new stepwise backward analysis removed all the variables, except the distance to the nearest gull nest ($P < 0.001$) and distance to vegetation ($P = 0.04$). The probability of a predatory attack on a replica increased with decreasing distance to the nearest gull nest (*figure 2*) and to the nearest patch of vegetation. The elimination of all other variables from the analysis indicates that predation rates on replicas were not clearly related to replica colour or to vegetation cover.

The inter-area differences in predation rates over replicas was negatively rank correlated with lizard density in both seasons (May: $r_s = -0.80$, $P = 0.10$; September: $r_s = -0.67$, $P = 0.11$; Fisher's combined probability test: $\chi^2 = 9.132$, $P = 0.05$). Thus, lizards tended to be more abundant in areas with a more relaxed predatory intensity on replicas.

3.1. Mutilation rates on replicas and identity of predators

During May, the intensity of mutilation on replicas showed significant differences between areas ($\chi^2_{d.f. = 9}$

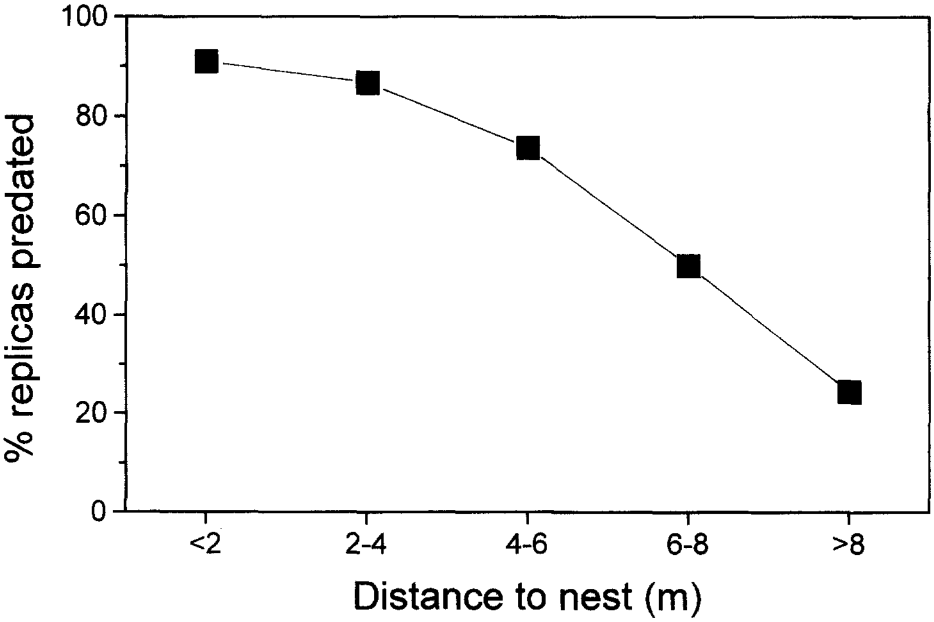

Figure 2. Relationship between the percentage of lizard replicas that were predated and distance to the nearest nest of the gull *Larus cachinnans michaellis* during May 1991.

= 20.75; $P = 0.01$). Mutilation on replicas was more intense in areas where a higher proportion of the replicas had been attacked. In areas 1 and 2 where predation was not intense, most attacked replicas were slightly picked (68 % and 95 % respectively), none were smashed and very few were missing (25 % and 7 % respectively) (*figure 3*). By contrast, in areas 3 and 4 many replicas were smashed (30 % and 25 % respectively) or missing (20 % and 10 %). In September, mutilation rate was very intense in the only two areas (3 and 5) where predation took place (73 % and 91 % respectively).

By examining bill impressions on the plasticine we were able to identify two groups of predators in May: gulls (47 %) and small passserine birds (6 %). The remaining replicas bore bill markings of birds that could not be identified (14 %) (*table III*), or were smashed or missing (33 %). In September, bill markings of gulls were detected in 63 % of the replicas, 6 % had unrecognisable bird markings and 31 % were smashed or missing.

4. DISCUSION

In this study we evaluated whether predation rates on lizard replicas might help to explain microgeographic distribution and variation in lizard densities within a small island. We considered 'Columbrete Grande' a suitable island to perform this study because birds are the only potential lizard predators present, and because the lizard *P. hispanica atrata* lives in a system that is free of any other reptilian or mammalian competitors [13]. The latter is especially worth noting,

Table III. Number of bird species within different families that were seen in the island of Columbrete Grande during both study periods, and number known to be lizard predators.

	May	September	Predators
Passerine	39	24	2
Apodidae	1	1	0
Picidae	0	1	0
Columbidae	1	1	0
Coraciidae	2	1	0
Caprimulgidae	2	0	0
Charadriidae	4	5	1
Procellariidae	3	3	0
Pelecanidae	2	1	0
Podicipedidae	1	0	0
Ciconiidae	3	5	4
Accipitridae	8	7	10
Strigidae	1	0	1
Total	67	49	18

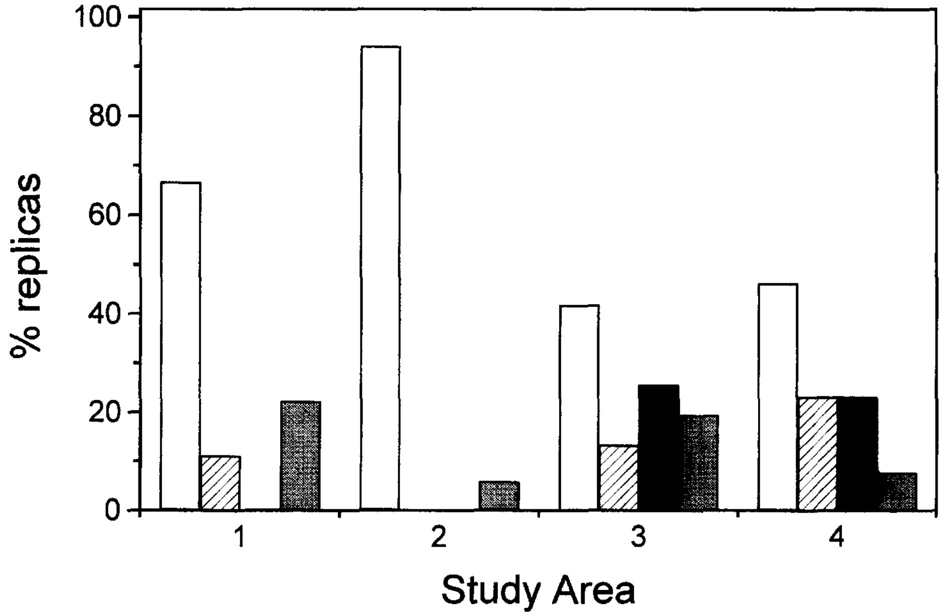

Figure 3. Percentage of lizard replicas that had small bill markings (white), intermediate bill marking (lines), that were smashed (black) or missing (dots) in 4 study areas during May 1991.

because interspecific competition may affect patterns of animal distribution [4].

The use of replicas to measure rates of predation has an obvious and important drawback: replicas do not exhibit antipredator behaviour. Thus, our procedures index variation in predation on immobile lizards only. Lizards of this species remain immobile for considerable amounts of time during the early morning and late afternoon warming-up periods [2]. While basking, these lizards expose their entire body surface to the sun, and hence also to potential predators. Hence, we constructed and located the replicas such that they simulated real lizards in a basking position. However, given that basking lizards–unlike our replicas–may actively flee from an attacking predator, our results can only be considered as estimates of the potential rate of predation on immobile lizards. Nevertheless, as a similar experiment design was used in all areas, the observed microgeographic differences in attack rates can be considered as estimates of the relative differences in potential predation rates.

4.1. Predation rates and predators

Predation on replicas, which was mainly caused by the Yellow-legged Gull, was intense overall but differed among areas and seasons. Parallel microgeographic differences within the same island were found during the course of other experiments in May 1995 [Castilla, unpubl. data]. Thus, the inter-area differences observed during this study appear to be stable over a period of several years. Variation in the intensity of predation was mainly explained by the proximity of replicas to the nests of gulls, and by their proximity to the vegetation. This is in agreement with Branch and Els [7] who attributed increasing intensity of predation by gulls (*Larus dominicanus*) on the angulate tortoise (*Chersina angulata*) on the Dassen Islands to the greater conspicuousness of tortoises when vegetation dies back, the opportunistic feeding behaviour of gulls during the breeding season, and a high density of gulls.

Overall predation rates were higher in May than in September. This result was somewhat surprising, considering that higher numbers of Yellow-legged Gulls were present in September (*c.* 3 000 roosting individuals; Natural Reserve, unpubl. obs.) compared to May (*c.* 700 breeding individuals). Several factors may explain the higher intensity of predation in May. First, breeding gulls (May) spend relatively long periods of time on the ground, a condition that may have increased the chances of observing and predating lizard replicas. Second, the banning of fishery activities around Columbretes in May [15] may have reduced the amount of waste food from fishing vessels available to the gulls and forced them to search for other types of food. In September, when breeding was finished and fishery activities restored [33], a decrease in energy demands and an increase in food availability may have induced a decrease in the predation rate on lizard replicas.

4.2. Relation between predation rates on replicas and lizard densities

We found a negative, marginally significant rank correlation between the proportion of predated replicas and actual lizard density in the different areas. Given the small sample size (five study areas), and hence the poor statistical power of the analyses, we assume that this reflects a strong trend. Thus, areas with a high potential predation rate should be considered unfavourable for the establishment of dense lizard populations and their survival [see similar examples in 1, 27, 34]. It is important to remark that our study areas differed not only in abundance of predators (e.g. gulls), but also in habitat structure and levels of food availability (direct observations). These factors may have a direct effect on the local abundance and distribution of reptile populations [2, 19, 23], and as such we cannot assert that the relation between predation rate and density is a direct and causal one.

4.3. The Yellow-legged Gull as a lizard predator

Several species of Gulls are considered as predators of reptiles [7, 18, 29]. The Yellow-legged Gull is an opportunistic species that feeds mainly on fish and makes extensive use of human-derived food sources such as discard and garbage from fishing vessels [18]. This gull species has previously been identified as an occasional predator of lizards [18, 29] particularly on islands [10, 17, 30]. Nevertheless, even occasional predators may have dramatic effects on small, isolated populations. If individual gulls would accidentally (e.g. only once a year) capture a lizard, large gull colonies may still have dramatic effects on small isolated lizard populations. In addition to the direct mortality effect, the presence of large numbers of potential predators may interfere with the lizards' normal thermoregulatory activities, and thereby negatively affect other biological functions that are temperature dependent [20, 25, 36], and ultimately limit or reduce population growth.

Despite the potential impact of the Yellow-legged Gull on lizard populations, data on the actual intensity of predation is rare and fragmentary, often based on anecdotal and casual observations. Our experimental data provide quantitative support for the putative predatory impact of Gulls on lizard populations and suggest that the Yellow-legged Gull may have an important effect on the demography and evolution of Mediterranean lacertids. Given that the Yellow-legged Gull is the most common seabird in the Mediterranean

[3] and that Gull populations in Europe are continuously increasing [5, 22], it should be advisable to evaluate their effect on lizard populations, especially those that inhabit small islands. As some breeding colonies of Gulls are being controlled and culled [6], this situation offers a unique opportunity to assess the effect of 'experimental' reductions in Gull numbers on lizard population densities.

Acknowledgements

We thank the ConsellerÌa de Medio Ambiente of the Generalitat Valenciana and the DirecciÛn General de Puertos of Castellón for permission and transportation. We acknowledge the co-operation, help and company in the island of J. JimÈnez, director of the Natural Reserve Illes Columbretes, the wardens ValentÌn, Tony, Santi, Xavi, Capy and especially of M. AlÌ for helping with the construction and monitoring of lizard replicas in the field. We are grateful to V. Cambiazo, F. Labra, M. Mendez, D. Bauwens and especially to S. Adolph for useful comments on the manuscript. This work was supported by a contract of the Spanish National Science Foundation (C.S.I.C.) and funds from the Exmo. Ayuntamiento de CastellÛn (to AMC), and by FONDECYT no. 4960001 and no. 2950015 (to AL).

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