Research

Differences in morphology, performance and behaviour between recently diverged populations of *Podarcis sicula* mirror differences in predation pressure

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We investigated the possible role of variation in predation pressure in the phenotypic divergence of two island populations of the Italian wall lizard, *Podarcis sicula*. In 1971, ten adult specimens from the island of Pod Kopište (Adriatic Sea, Croatia) were transported to the island of Pod Mrčaru, 3.5 km east, where they founded a new population. Although the two islands resemble each other in general physiognomy (size, elevation, microclimate) and in the absence of terrestrial predators, lizards from the newly established population are now on average larger and have shorter hind limbs. They also exhibit lower maximal sprint speed as measured on a racetrack, and fatigue faster when chased in a torus track. In the field, lizards from the original population of Pod Kopište respond to a simulated predatory attack by fleeing at larger approach distances and by running further from the predator than lizards from Pod Mrčaru. These changes in morphology, behaviour and performance may result from the relaxed predation intensity on the latter island. Our analysis of the structural features of the microhabitats suggests that the vegetation on Pod Mrčaru offers more protection to lizards. Also, plasticine models of lizards, laid out on the islands, less often exhibited signs of being attacked by birds on Pod Mrčaru than on Pod Kopište. Our findings provide an example of how changes in (possibly a single) environmental factor may simultaneously produce responses in behaviour, morphology and whole-animal physiology, and this on a surprisingly small spatial and temporal scale.

Predation is often considered an important selective force that can shape the morphological, physiological, behavioural, and life-history characteristics of prey. Although a few important studies have documented temporal changes in prey populations following the (experimental) introduction of a predator species (Trussell and Smith 2000, Losos et al. 2004), the effects of predation on prey characteristics have generally been inferred from comparisons of geographically distinct, contemporary populations with varying degrees of predation intensity (reviewed by Strauss et al. 2006). Several issues may thwart the interpretation of the latter kind of evidence. First, because direct observations of predatory attacks in the field are usually rare, obtaining reliable estimates of actual predation pressure is difficult. Typically, authors assume that localities differ in predation risk because they differ in predator density or community (McLaughlin and Roughgarden 1989, Van Damme and Castilla 1996), or in the availability of protective cover (Snell et al. 1988). However, the relationship between the number and nature of potential predators, and the amount of cover on the one hand, and predation risk on the other, is seldom tested. Others have used the frequency of injuries in prey animals (e.g. tail loss in lizards, beak marks on butterfly wings) to infer variation in predation pressure, although there is good evidence that injury frequency reflects the inefficiency of predators, rather than the intensity of predation (Jaksic and Greene 1984, Ide 2006). Second, geographically distinct locations are likely to differ in more aspects of the environment than in predation pressure alone. For

instance, in comparison to mainland conditions, island populations may enjoy relaxed predation pressure, but they are also likely to experience reduced prey availability, different thermal conditions etcetera. Few studies have controlled for these possibly confounding factors. Finally, the time elapsed since the isolation between the populations considered is usually considerable and often unknown (Strauss et al. 2006 for a few notable exceptions). Therefore, information on the rate of evolutionary change due to predation pressure is scarce. This is unfortunate because there is some evidence that changes in predation intensity may cause extremely rapid phenotypic change (Losos et al. 2004). Data from populations that are known to have diverged recently, would allow to test ideas on the relative importance and the timing of behavioural, morphological and life history adaptations (Losos et al. 2004).

We take here advantage of an exceptional opportunity offered by a historical introduction experiment to circumvent some of the problems mentioned above. We examine predation pressure, escape behaviour, locomotor performance capacity and morphology in two Croatian island populations of the lacertid lizard, *Podarcis sicula*. One population, on the island Pod Mrčaru, consists of the descendants of 10 individuals (5 males, 5 females) that were introduced into the island in August 1971 by Nevo and co-workers, as part of a competitive exclusion experiment (Nevo et al. 1972). The other population is situated on the nearby island of Pod Kopište, from which the 10 founders were originally taken. Both islands are tiny (Pod Mrčaru: 0.3 km^2; Pod Kopište: 0.9 km^2), are highly similar in general physiognomy, exposure and elevation and only 4.5 km apart. Therefore, the two islands probably resemble each other closely in their abiotic environments. The only other ground-dwelling vertebrate on the islands is the lizard *Lacerta oxycephala*. This species occurs at very low densities on the outer reaches of the islands, where densities of *P. sicula* are low. Birds are probably the only significant predators in these populations. At first sight, the two islands do differ in vegetation structure. Both consist of an outer girdle of rocks with little or no vegetation, and a central part containing more lush vegetation. However, possibly due to the presence of a small number (<5) of sheep, the vegetation on Pod Kopište is lower and less dense and may provide less cover from aerial attacks.

In this study, we estimated relative predation intensity by using painted plasticine models of lizards on both islands and counting the number of beak marks in these models. This method has proved useful in earlier studies assessing the predation risk in different habitats (Castilla and Labra 1998) or on different animal phenotypes (Brodie 1993, Husak et al. 2006). We also measured aspects of the lizard's morphology, physiological performance and behaviour that may be relevant in a predatory context, and test whether differences between populations are as predicted if predation pressure (or relaxation thereof) acts as the main selective agent. More specifically, we hypothesized that lizards from the population at higher risk would flee sooner and further in response to a simulated attack, that they would have greater locomotor abilities (maximal sprint speed, exertion), and would have longer limbs relative to body length.

Material and methods

Study animals and study sites

The Italian wall lizard *Podarcis sicula* is a robust, ground-dwelling, heliothermic, actively foraging lacertid lizard (adult snout−vent length [SVL] 55−70 mm) that occupies a variety of semi-open habitats in the Mediterranean. In the field, most animals reach maturity after one year. Females produce up to 5 clutches of 2−7 eggs per year. Adult males have larger heads, longer hind limbs and better-developed femoral pores than females. A review of the general biology of *P. sicula* can be found in Henle and Klaver (1986).

The islets of Pod Mrčaru (42°46′N, 16°46 E) and Pod Kopište (42°45′N, 16°43′E) are situated 4.5 km apart in the Adriatic Sea, northwest of the larger island of Lastovo. The islands resemble each other in general aspects. Both consist of organic limestone and have a central, vegetated zone (rising up to 20 m on Pod Mrčaru and 30 m on Pod Kopište), encircled by more barren rocky belt. Plant cover on Pod Mrčaru (Fig. 2b) consists mainly of annuals: *Lavatera arborea*, *Lotus edulis*, *Portulacea oleracea*, *Allium ampeloprasum* and *Cynodon dactylon* in the centre, and *Crithmum maritimum* in the periphery. Pod Kopište (Fig. 2a) has some low bushes of *Pistacia lenticus* and *Juniperus excelsa*; the central part is covered mainly by *Chenopodium murale*, *Cynodon dactylon* and *Aspargus officinalis*; *Crithmum maritimum* is the dominant species on the rocky fringes. We noticed a few specimens of the sharp-snouted rock lizard, *Lacerta oxycephala*, climbing rocks in the outer fringes on both islands. Except for a small number of breeding yellow-legged seagulls (*Larus michahellis*), no other vertebrates likely inhabit the islands.

Microhabitats

To examine differences in microhabitats available to lizards on the two islands, we estimated the percentage of the surface covered by soil, rocks, dead plant material and different plant species in 80 randomly chosen one m^2 plots (20 plots per zone and per island). Since

we were interested in the structural aspects of the vegetation, rather than in its taxonomical composition, we assigned each plant species to one of four structural classes, depending on its putative usefulness as a hiding place from aerial attacks. Plants with woody stems, hard leaves, dense foliage or spines were given a higher ranking than soft, resilient species that offer little or no cover. The structural class 1 was assigned to *Cynodon dactylon*, class 2 to *Allium ampeloprasum*, *Asparagus officinalis* and *Atriplex littoralis*. *Chenopodium murale*, *Crithmum maritimum*, *Lotus cystoides*, *L. edulis*, *Othantus maritime*, *Portulaca oleacea*, *Salsoli kali*, *Silene inflata* and *Spergularia marina* were assigned to structural class 3 and *Lavatera arborea* to class 4. For each plot, we also noted the average height of the vegetation and the distance to the nearest rock or stone under which a lizard could hide.

We used principal component analysis (PCA) to summarize variation in structural microhabitat features between islands and zones. Since the sum of the % coverage variables by rocks, soil, dead plant material or living plants from different structural classes equals 100% in each plot, our data suffer from the "constant sum constraint" (Aitchison 1983, Jackson 1993). To avoid problems associated with the analysis of compositional data, we followed the procedure outlined by Aitchison (1983) and performed the PCA on the covariance matrix γ where

$$\gamma_{ij} = \text{cov} \; (\log[x_i/g(x)]), \; \log[x_j/g(x)]; \; \text{with i, j} = 1\text{-}7$$

and g(x) is the geometric mean of the raw variables. Differences among the scores on the first three axes, average vegetation heights and distances to rocky hides were examined using two-way ANOVAs.

Morphometrics and locomotor performance

Lizards were caught by noose, individually stored in cloth bags and transported to the field station on the nearby island of Lastovo. There we measured SVL and hind limb length (sum of femur, tibia and metatarsus length) to the nearest 0.01 mm using electronic callipers.

Prior to each performance trial, lizards were allowed to rest for at least one hour in large outdoor terraria wherein they could thermoregulate freely. Before each measurement, we tested if the lizard's body temperature was within the optimal range for sprinting (~36°C, Van Damme et al. 1990), using a thermocouple connected to an electronic thermometer. Maximal sprint speed was measured by chasing lizards three times along a horizontal 2 m racetrack with a cork substrate. The fastest time over any 25 cm interval (as recorded by photocells placed alongside the track) was considered an estimate of an individual's maximal sprint performance. We scored

each trial as "good" or "bad" (Tsuji et al. 1989). Occasional "bad" trials (<5%) were eliminated from further analysis. Exertion was estimated by chasing lizards along a horizontal torus track (1 m diameter), until they reached exhaustion (Bennett 1980). We considered lizards "exhausted" when they no longer responded to ten consecutive (gentle) taps on the dorsum. The time elapsed between the start and the end of the run was taken as a measure of exertion. Because this procedure is demanding (for the lizard and the experimenter), each individual was tested only once. However, earlier measurements on a smaller sample of specimens proved that the procedure yields very repeatable results (Vervust unpubl.). Upon completion of the measurements, the lizards were marked using individual toe clip codes and released at the exact site of capture. This was always within two days.

We used analysis of (co-) variance (SVL as covariate) to examine differences in $\log_{10}$-transformed performance and morphometric variables between islands and sexes.

Estimates of predation pressure

We produced 569 realistic models of an adult *P. sicula* by pouring non-toxic plasticine into a flexible mould that was constructed using a preserved museum specimen of *P. sicula*. The models were painted to resemble the colours of live animals. In April and September 2006, we placed at least 100 replicas in both zones of the two islands. The models were placed in rows, with about two meters between consecutive models. We placed each replica in approximately the same position as the real lizard last observed before putting the model. We then left the island in order not to disturb potential predators. For similar reasons, we did not use flags or other signs to facilitate the recovery of the models. Between 48 and 52 h later, we returned to the islands and noted the number and location (head, body, tail, limbs) of beak marks on each plasticine model. We considered a replica as "attacked" when it exhibited at least one clear beak mark, or when it had disappeared. We used generalized linear models (GENMOD procedure, SAS v9.1) to examine the effects of season, island and zone on the probability that a model was attacked (binomial distribution, logit link function) and on the number of marks per attacked model (Poisson distribution, log link function). Throughout our visits to the islands, we also noted all resident and migratory birds observed, using binoculars.

Quantifying anti-predator behaviour

We quantified the anti-predatory behaviour of field-active lizards by slowly (walking speed, ca 2 km h^{-1}) approaching them and noting the approach distance,

the running distance and the flight distance (Rand 1964, Bulova 1994). All experiments were performed by one of us (BV), dressed in the same clothes, to keep the procedure as standardized as possible (Burger and Gochfeld 1993). We also noted the sex and age class of the lizard, its behaviour prior to the escape (perching, basking, moving, fighting), the island zone where it was observed (rocky/vegetated), and the weather conditions (cloudy/sunny). Only lizards that had not been disturbed by our presence prior to the onset of the experiment were approached. All observations were performed during the lizards' peak activity hours (10:00–16:00). We used multivariate analysis of variance on $\log_{10}$-transformed distance measures to test for differences in overall escape behaviour between islands, zones and sexes.

Results

Microhabitat structure

Principal component analysis on the covariance matrix of the 7 log-ratio transformed habitat variables produced three composite axes that together explained 66% of the variation among individual plots. The first axis was correlated positively with % coverage by soil ($r = +0.59$), and % coverage by plants that offer little cover (class 1, $r = +0.84$); and negatively with % coverage by highly protective plants (class 4,

$r = -0.65$). The mean scores of the individual plots on this first axis showed a significant island × zone interaction effect ($F_{1,76} = 5.38$, $p = 0.023$). For both islands, scores for plots from the rocky zone are higher than those from the vegetated zone, but the difference is much more pronounced on Pod Kopište. Plots from the vegetated zone on Pod Kopište have much higher scores than those from Pod Mrčaru (Fig. 1). The second PCA correlated positively with % coverage by rocks ($r = +0.66$) and plants of class 2 ($r = +0.80$); it associated negatively with % coverage by dead plant material ($r = -0.59$). This axis separated zones ($F_{1,76} = 47.69$, $p < 0.001$), with plots from the rocky zone scoring high and plots from the vegetated zone scoring low. The interaction and island main effect were not significant (both $p > 0.21$). Finally, the third axis correlated with % coverage by plants of class 3 ($r = +0.89$) and of class 4 ($r = -0.67$). Plots from Pod Mrčaru scored low on this axis, those from Pod Kopište scored high ($F_{1,76} = 4.44$, $p = 0.04$). No zone or interaction effects were found (both $p > 0.3$).

The average height of the vegetation on Pod Kopište ($x \pm SE = 15.5 \pm 1.6$ cm) is low compared to that on Pod Mrčaru (24.1 ± 1.7 cm) (vegetated zones only, t-test, $t_{78} = 3.35$, $p = 0.001$).

The difference in the availability of hiding places between island zones differs between the islands (zone × island interaction effect, $F_{1,76} = 8.38$, $p = 0.005$). On Pod Mrčaru, the distance to the nearest hide is equally low in the rocky zone ($x \pm SE = 33.7 \pm 8.8$ cm) as in the
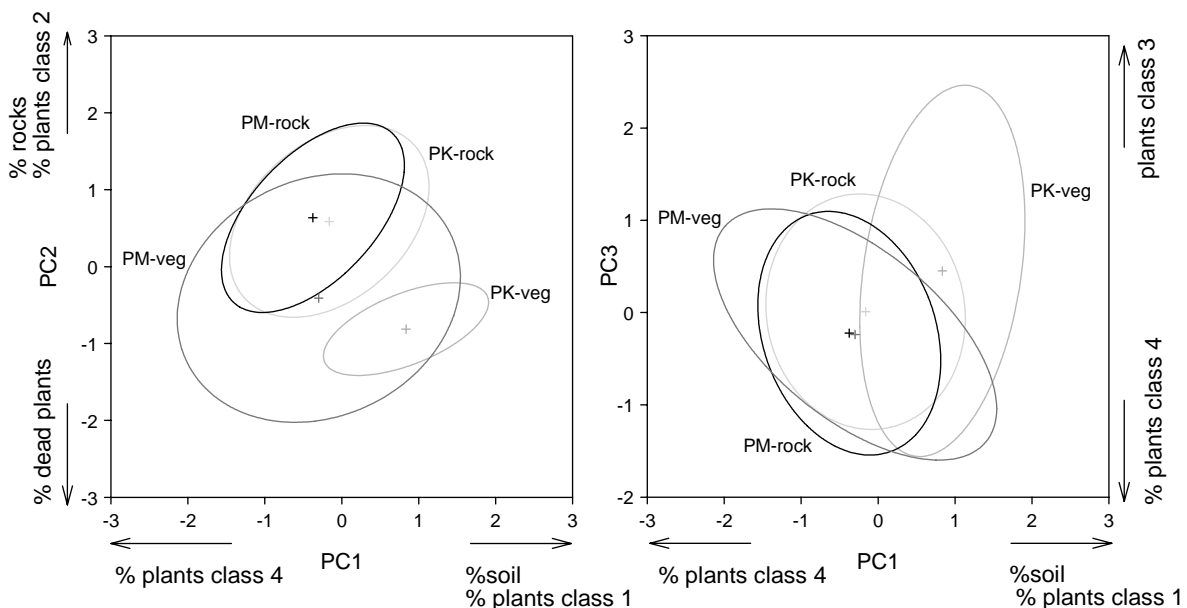

Fig. 1. Differences in the structural features of the micro-habitat on the rocky (rock) and vegetated (veg) zones of the islands Pod Kopiste (PK) and Pod Mrcaru (PM), as revealed by principal component analysis. Indicated are mean scores and 95% confidence ellipses. See text for the definition of the PC axes.
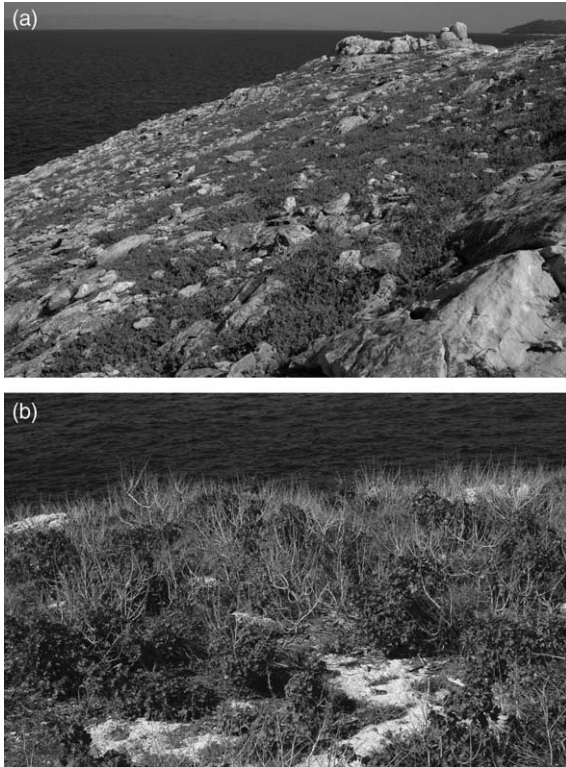
Fig. 2. (a) Vegetative cover of Pod Kopište, during summer. Vegetation consists mainly of *Cynodon dactylon* and *Chenopodium murale*. (b) Vegetative cover of Pod Mrčaru, during summer. Vegetation consists mainly of *Lavatera arborea* and *Portulacea oleracea*.

vegetated zone (37.2 ± 8.3 cm). On Pod Kopište, hiding places tend to be much further away in the vegetated zone (103.7 ± 13.6 cm) than in the rocky zone (35 ± 8.7 cm).

Predation intensity

Lizard models in open and vegetated zones were attacked at similar rates (zone-effect: $\chi_1^2 = 0.17$, p = 0.68) and none of the interaction terms involving zone were significant (all p > 0.15). We therefore pooled the data for both zones. The effect of season on the proportion of models attacked differed between islands (Fig. 3, $\chi_1^2 = 4.68$, p = 0.03). In both seasons, the attack rate was higher on Pod Kopište than on Pod Mrčaru, but the difference was more pronounced in September (58% vs 9%, p < 0.0001) than in April (79% vs 48%, p = 0.006).

The number of bill marks per attacked model varied in a complex way between zones, islands and seasons (Fig. 4, three-way interaction effect: $\chi_1^2 = 21.27$, p < 0.0001). In September, the mean number was higher on Pod Kopište than on Pod Mrčaru ($\chi_1^2 = 38.56$, p < 0.0001) and higher in the vegetated zone than in
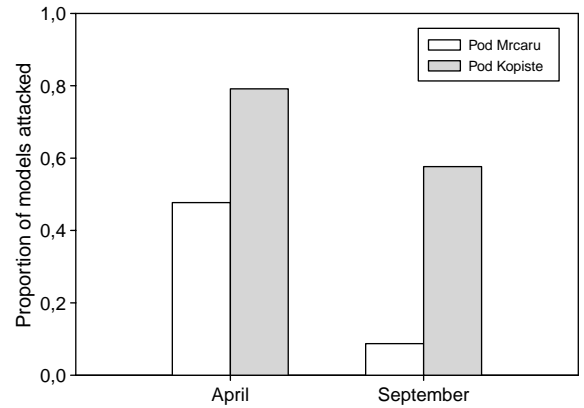

Fig. 3. Differences in predation pressure between Pod Mrčaru and Pod Kopište during both seasons.

the open zone ($\chi_1^2 = 8.64$, p = 0.003). The island × zone interaction was not significant in September ($\chi_1^2 = 0.10$, p = 0.76). In April, the effect of zone differed between islands ($\chi_1^2 = 40.64$, p < 0.0001). On Pod Kopište, more impressions were found in models attacked in the open zone; on Pod Mrčaru, more marks were seen in models attacked in the vegetated zone. For both zones, the difference between the islands was significant (both p < 0.0002).

During our visits to the islands, we observed several bird species that are considered (occasional) predators of lacertid lizards (Martin and Lopez 1990): common raven, *Corvus corax;* common kestrel, *Falco tinnunculus;* Eleonora's falcon, *Falco eleonorae;* peregrine falcon, *Falco peregrinus;*, common buzzard, *Buteo buteo;*, short-toed eagle, *Circaetus gallicus;* honey-buzzard, *Pernis apivorus;* common crane, *Grus grus;*, yellow-legged gull, *Larus michahellis;* shag, *Phalacrocorax aristotelis;* squacco heron, *Ardeola ralloides;* little egret, *Egretta*
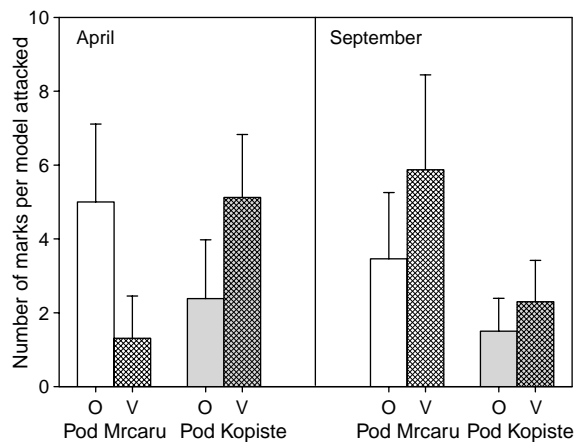

Fig. 4. Number of marks per model attacked. During both seasons (April, September) and in the different zones (O = open, V = vegetated).

egretta; grey heron, *Ardea cinerea,* and purple heron, *Ardea purpurea*.

Lizard morphometrics and performance

Table 1 lists the data and statistics on performance measurements. Lizards from Pod Kopište attained higher maximal sprint speeds and had superior stamina than lizards from Pod Mrčaru. Sexes did not differ in sprint speed and males and females had equally high endurance on Pod Kopište. Male and female lizards of Pod Mrčaru were on average larger than members of the corresponding sex on Pod Kopište (Table 1). The sexual size dimorphism (males being larger than females) is more pronounced on Pod Mrčaru. Hind limb length scaled similar with SVL in males and females of both islands (ANCOVA, all interaction effects with SVL p > 0.38). Males have longer hind limbs relative to their SVL than do females ($F_{1,497} = 334.55$, p < 0.001). Lizards from Pod Kopište have longer hind limbs than lizards from Pod Mrčaru ($F_{1,497} = 7.12$, p = 0.008).

Lizard behaviour

Responses to simulated attacks differed in a complex way between islands and between zones within islands (Fig. 5, MANOVA, island × zone interaction effect: Pillai's trace = 0.069, $F_{3,208} = 5.1$, P = 0.002). The island × zone interaction proved significant for all three behavioural variables (approach distance: $F_{1,210} = 14.35$, p < 0.001; flight distance: $F_{1,210} = 6.97$, = 0.009; final distance: $F_{1,210} = 13.29$, p < 0.001). On Pod Kopište, we saw no difference in approach distance (t-test, $t_{109} = 1.09$, p = 0.28) or final distance ($t_{109} = 1.33$, p = 0.18) between the zones, but lizards fled over somewhat smaller distances when approached in the
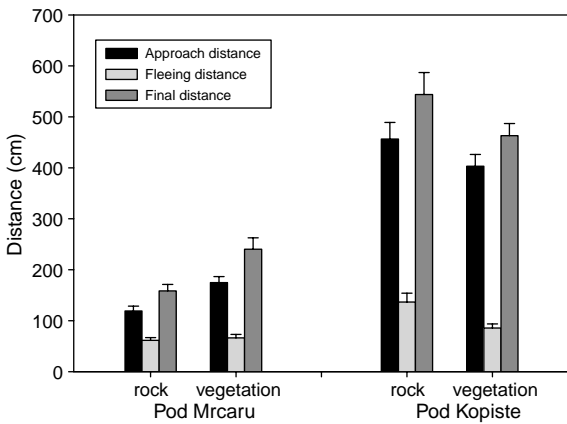
Fig. 5. Differences observed in anti-predator behaviour between the different islands and zones.

Table 1. Mean morphometric and performance measurements for adult male and female *Podarcis sicula* from Pod Mrčaru and Pod Kopište. F-statistics and p-values derive from ANOVAs on log-transformed variables. In the analyses of hind limb length, SVL was introduced as a covariate.

	SVL (mm)			Hind limb length (%SVL)			Speed (cm s⁻¹)			Exertion (s)		
	x̄	SE	n	x̄	SE	n	x̄	SE	n	x̄	SE	n
Males												
Pod Mrčaru	69.32	0.3	133	48.47	0.4	126	175.6	5.1	94	45.55	0.9	101
Pod Kopište	64.12	0.3	76	50.24	0.3	76	184.9	4.8	76	54.34	1.7	71
Females												
Pod Mrčaru	63.24	0.3	152	44.82	0.4	149	173	3.9	120	39.41	0.9	120
Pod Kopište	60.78	0.3	146	45.54	0.3	146	182.8	4.7	138	53.59	1.1	135
	F	P		F	P		F	P		F	P	
Sex	219.95	<0.001		334.55	<0.001		0.24	0.63		11.4	0.001	
Island	137.67	<0.001		7.11	0.008		3.96	0.047		96.21	<0.001	
Sex × island	14.96	<0.001		0.6	0.44		0.003	0.96		8.64	0.003	

vegetation ($t_{109} = 2.34$, $p = 0.02$). On Pod Mrčaru, lizards that were approached in the rocky zone fled sooner ($t_{101} = -4.33$, $p < 0.001$) and stopped farther from the predator ($t_{101} = 3.65$, $p < 0.001$); fleeing distance did not differ between zones ($t_{101} = 0.23$, $p = 0.82$). Most pronounced, however, were the differences between islands, with lizards from Pod Kopište fleeing much sooner ($F_{1,210} = 250.8$, $p < 0.001$), over larger distances ($F_{1,210} = 20.01$, $p < 0.001$) and stopping farther ($F_{1,210} = 206.98$, $p < 0.001$) than lizards on Pod Mrčaru.

Discussion

Our data suggest that predation pressure on island populations of lizards may vary considerably, on a surprisingly small geographical scale, and that this variation may affect the morphology, performance and behaviour of prey populations.

Differences in predation pressure

The exact reason for the differences in predation intensity in our study system is not immediately clear. Although the frequency and intensity with which our plasticine lizard models were attacked was higher on the less vegetated island of Pod Kopište, the difference in predation intensity does not seem associated with the degree of exposure (absence of cover) directly, since we found no differences in attack rates on models in the vegetated versus the rocky zones of the islands. For some reason, bird predators seem less keen to attack lizards on Pod Mrčaru than on Pod Kopište. It may be that foraging birds visit Pod Mrčaru (as a whole) less frequently because they have experienced difficulties in capturing lizards there in the past. In this case, the more lush vegetation in the centre of the island would make the island (including its barren fringes) a safer place than Pod Kopište. Paradoxically, the higher densities of breeding gulls on Pod Mrčaru may provide an alternative explanation. Pod Mrčaru has long been known as a brooding place for yellow-legged seagulls (Radovanović 1956) and also during our visits, we found many more occupied nests on this island (n = 38, 29.23 nest hect^{-1}) than on Pod Kopište (n = 8, 1.6 nest hect^{-1}). Sea gulls may prefer Pod Mrčaru as a brooding place because its vegetation offers more protection to their eggs and young (Martinez-Abrain et al. 2004), or conversely, their presence may have changed the aboveground biomass of plants and community composition (Ellis 2005). The presence of gulls may relax predation pressure on lizards because gulls tend to chase away other, perhaps more dangerous bird predators (such as crows and falcons), and this benefit may outweigh the

putative greater risk of predation by the gulls themselves (Wheelwright et al. 1997). Kammerer (1926) has even suggested a mutualistic relationship between breeding seagulls and lacertid lizards, in which the gulls would refrain from attacking lizards near their nest because they would help reduce the chicks' ectoparasite load (Gruber 1986, Salvador 1986). This is contradicted by the experimental study of Castilla and Labra (1998), who showed that the predation intensity on *Podarcis atrata* increased near a gull colony. Overall, the importance of gulls as predators of lizards is debated (Martinez-Rica and Cirer 1982, Pérez-Mellado et al. 1997). However, as noted by Castilla and Labra (1998), even occasional predators may have dramatic effects on small, isolated populations.

Although coloured plasticine or clay models have been used successfully in studies comparing predation risk among localities (Castilla and Labra 1998) or between prey phenotypes (Olsson 1993, Husak et al. 2006), they obviously fall short in not exhibiting antipredator behaviour such as running or fighting back. Also, we did not obtain photometric readings of the models, nor do we have data on the predators' sensitivity to light of different wavelengths. Therefore, we can only assume that the frequency of attacks on the models genuinely indexes predation risk. However, the combination of a higher attack rate and lower hiding opportunities on Pod Kopište does strongly suggest that predation intensity on this island is high compared to that on Pod Mrčaru.

Possible causes of phenotypic change

Our behavioural, morphometric and performance measurements demonstrate considerable phenotypic difference between the two island populations, despite their recent divergence. Although our study system clearly suffers from the problems associated with inferring adaptation from two-populations comparisons (Garland and Adolph 1991), two considerations suggest that these phenotypic changes may be causally related to the difference in predation pressure. First, all changes are in line with predictions based on predation driven selection: lizards from the more perilous island have longer limbs, have higher stamina and sprint speed capacity, and flee faster and farther than lizards from the safer island. Maximal sprint speed is generally considered an important determinant of survival in lizards (Warner and Andrews 2002, Miles 2004, Husak et al. 2006, but see Bennett and Huey 1990), and relative hind limb length is by far the best documented morphological correlate of sprint capacity (Sinervo and Losos 1991, Miles et al. 1995, Melville and Swain 2000, but see Garland 1984). Although the direct evidence for a survival value of endurance capacity is

mixed (Le Galliard et al. 2004, but see Clobert et al. 2000), it seems logical to assume that good exertion abilities would benefit lizards that are being chased in relatively open habitats. Second, given the proximity and similarity of the two study sites, we see few other aspects of the biotic or abiotic environment that may have driven the observed phenotypic changes. There are no competitors on the islands, and preliminary measurements suggest no consistent differences in food availability or thermal environmental quality (Vervust unpubl.). One factor that requires further attention is the difference in lizard density, with the density of Pod Mrčaru being about three times as high as that on Pod Kopište (Vervust unpubl.). Lizards on the former island are seen more often engaging in intraspecific aggressive behaviour, and also more frequently bear signs of previous fighting (scars, missing toes). However, it seems unlikely that increased levels of intraspecific aggression would select for lower sprint capacities or lower exertion abilities, as both performance measures in general correlate positively with fighting capacity and dominance status in lizards (Garland et al. 1990, Robson and Miles 2000, Perry et al. 2004). Possibly, lizards must tradeoff locomotory abilities (allocation towards appendicular musculoskeletal system) against fighting capacity (larger heads for increased bite capacity), as suggested in *Lacerta monticola* (Lopez and Martin 2002).

It could also be argued that the phenotypic differences between the populations reflect adaptation to peculiarities of the respective environments that existed in the recent past, but that have now disappeared (the so-called "ghost of competition/predation past" argument, Connell 1980). This explanation seems unlikely here, because descriptions of the islands in papers predating the divergence of the population (Kammerer 1926, Nevo et al. 1972) suggest no substantial changes in the abiotic environment or the vegetation structure. Also, although the Pod Mrčaru population must have dealt with the original *Podarcis melisellensis* population after its introduction, it seems unlikely that interspecific competition would select for decreased locomotor abilities. An alternative idea, that the observed differences are examples of the founder effect, may seem more likely; especially because the founder population consisted of 10 individuals only, and therefore has gone through a severe bottleneck. On the other hand, characteristics studied are most likely polygenic, ecologically relevant traits, and therefore more likely to evolve through natural selection than under genetic drift (Merilä and Crnokrak 2001). We plan to evaluate the effects of the introduction on the genetic variation in this system in the future to further explore the idea. Yet another possibility is that the variation in morphology, behavior and performance constitutes a plastic response, rather than genetic

adaptation. The possible role of phenotypic plasticity has been largely neglected in studies of interpopulational variation, and recent findings suggest that this may be unwarranted (Losos et al. 2000, 2001, Aubret et al. 2004, Kolbe and Losos 2005). We plan to investigate this possibility, using a common garden approach. However, even if the phenotypic differences are plastic, rather than genetic (or a combination of both), predation pressure seems the most likely driving force.

Our findings present a new example of how changes in predation pressure may cause extremely rapid changes in phenotypic traits (Losos et al. 2004, Phillips and Shine 2004). Surprisingly however, in this study system, the changes seem a consequence of predation relaxation, rather than intensification. This would suggest that maintaining a behavioural and morphological phenotype adept to escape predatory attacks is costly, and therefore strongly selected against in relaxed environments. We can only speculate on the nature of these costs. Excessive vigilance is likely to be costly in terms of time and energy, and may also jeopardize an individual's territorial claims; developing long limbs may interfere with the development of other structures (Lopez and Martin 2002); and walking or running on long limbs is probably energetically less favourable.

Although further study is necessary to unravel the exact mechanisms of the phenotypic divergence of these two populations, it is clear that *Podarcis sicula* is able to respond rapidly to changes in its environment. This observation may raise hope for the survival of populations of many other (lizard) species that are increasingly confronted with anthropogenic alterations of their environment. However, it is highly unsure whether other species (even closely related ones) would be capable of similar responses. Perhaps it is not a coincidence that many examples of fast phenotypic evolution have been reported in ruderal, colonizing species (Losos et al. 2004). *Podarcis sicula* is not an exception in this regard; among lacertid lizards, it is probably one of the species that has most successfully invaded new territories, including locations well outside its natural range of distribution (Henle and Klaver 1986). It would be informative to study whether less invasive species (e.g. the closely related and largely sympatric *P. melisellensis*) exhibits similar powers of adaptability.Unlinked Reference   Phillips and Shine, 2005.

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