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The mystery of the missing toes: extreme levels of natural mutilation in island lizard populations

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Summary

1. Ecological interactions that involve aggressive confrontations between animals are important in shaping the evolution of morphology, behaviour and life history. However, as such confrontations are rarely witnessed, direct quantification of the intensity of these processes in natural populations is notoriously difficult. While the utilization of the frequency of non-lethal injuries is fraught with difficulties, it may provide information concerning different types of interaction, such as predation, intraspecific aggression and interspecific interference competition.

2. In this paper, we report on an exceptionally large difference in toe loss incidence between two populations of *Podarcis sicula* lizards living on small, neighbouring islands in the Adriatic Sea. We caught 900 lizards and recorded the number and location of missing toes. Subsequently, we investigated five non-mutually exclusive hypotheses concerning differences in bite force capacity, bone strength, predation intensity, average age and intraspecific aggression that may provide proximate explanations for the observed differences in injury frequencies.

3. Bite force differences differed considerably between the populations, but bone strength was found to be stronger in the populations with a higher frequency of natural scars. Predation pressure clearly differed between the populations, but we found higher injury rates under predation relaxation.

4. Our results indicate that density and consequently an increased intraspecific competition is the most likely explanation for the observed high frequencies of injuries. We suggest that the intensity of toe amputation between lizard populations may be a useable indirect indication for the intensity of intraspecific competition.

5. This study shows how a combination of morphological, physiological, behavioural and ecological measurements can be used to test assumptions implicit to alternative explanations of an observed phenomenon. Such tests can reveal how likely each of these explanations is, even if the processes leading to the phenomenon are difficult to observe directly.

Key-words: intraspecific competition, injury frequency, density, sex ratio, *Podarcis sicula*, social behaviour, aggression

Introduction

Ecological interactions that involve aggressive confrontations are important in shaping the evolution of morphology, physiological performance, behaviour and life history of organisms. These interactions have led to the evolution of weapons (horns, antlers), other functional, chemical defences and autotomy, in a wide array of taxonomic groups, but may also provide information about the ecological pressures on organisms. Because such aggressive confrontations are rarely witnessed, direct quantification of the intensity of predation and intraspecific interactions in natural populations is notoriously difficult. Therefore, many investigators have resorted to indirect measures of interaction intensity (Abrams 2001). One of the most widely used examples of such measures is the frequency of non-lethal injuries (e.g. Rand 1954; Raffaelli 1978; Schoener 1979; Semlitsch & Reichling 1989; Heithaus *et al*. 2002).

It has long been recognized that utilizing the frequency of non-lethal injuries is fraught with difficulties (Schoener 1979). (i) The exact origin of the damage is not always clear. Various studies have used the same types of injuries as an index for different kinds of interaction, such as predation (e.g. Pianka 1967; Schoener & Schoener 1980; Arnold 1988; Pianka & Vitt

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2003), intraspecific aggression (e.g. Kramer 1951; Blair 1960; Tinkle 1967; Pianka 1973) or interspecific interference competition (e.g. Chadwick 1991; Soederbaeck 1995). (ii) High rates of predator-inflicted injuries may reflect predator inefficiency, rather than predation pressure (Schoener 1979; Arnold 1988; Medel *et al.* 1988): a population suffering predation by a 100% effective predator will have zero per cent injured members. (iii) In systems with inefficient predators, injury frequency will echo the average age of individuals in the population more than predator load (Brown & Ruby 1977; Schoener 1979). (iv) Perhaps less well recognized; animals may vary in their ability to inflict injuries and in the likeliness to carry the visible consequences. For instance, aggressive interactions may go unnoticed if the aggressor lacks the morphology (e.g. teeth, claws) to inflict manifest damage to his opponent. In the case of autotomous mutilations, individuals (or populations) may vary in their tendency to sacrifice body parts (Congdon *et al.* 1974; Vitt *et al.* 1977; Pafilis & Valakos 2008). (v) Finally, the differential mortality of injured individuals may obscure differences in interaction intensity among individuals or populations. Toes are important in both forms of locomotion (terrestrial, arboreal), but toe loss has a greater effect on arboreal lizards (Bloch & Irschick 2004). Therefore, individuals with missing toes are more likely to be eliminated from arboreal or saxicolous populations than from ground-dwelling populations, and thus the injury rate will appear higher in the latter.

In this paper, we report on an exceptionally large difference in toe loss incidence and tail break frequency between two populations of *Podarcis sicula* lizards living on small, neighbouring islands in the Adriatic Sea. Toe loss in lizards is generally attributed to aggressive encounters with conspecifics or competitors (Zweifel & Lowe 1966; Gvozdik 2000), but may also result from predation attempts (Schoener & Schoener 1980; Hudson 1996; Nemes 2005), or may even represent a pathological condition (e.g. progressive digital necrosis, Hazell *et al.* 1985).

The incidence of tail breaks and proportion of regenerated tails in lizards is typically associated with predation intensity (Rand 1954; Blair 1960; Tinkle & Ballinger 1972; Arnold 1988) or inefficiency (Jaksic & Fuentes 1980; Jaksic & Greene 1984; Arnold 1988) but has also been coupled to inter- and intraspecific agonistic encounters (Vitt *et al.* 1974; Brown & Ruby 1977; Jaksic & Busack 1984).

We consider the evidence favouring and disfavouring the following hypotheses.

1. The difference in toe loss incidence between the two island populations merely reflects a difference in average age. If this is the case, we expect that the relationship between age and toe loss incidence will be the same for the two populations, and that the populations differ in age structure.
2. Individuals from the two populations differ in bite force, and therefore antagonistic bites in one population have a higher probability of inflicting toe loss. We determine the bite force capacity of lizards from both populations and compare it to the minimal force required to sever toes. This hypothesis should be considered in concert with hypothesis (3).
3. Individuals from the two populations differ in toe bone strength, and therefore agonistic bites in one population are more likely to result in toe loss than in the other. We compare the forces required to cut the digits of lizards from both populations.
4. Differences in toe injury rates mirror differences in predation intensity. We evaluate this hypothesis using independent estimates of predation pressure using plasticine models (Vervust *et al.* 2007).
5. Differences in toe loss reflect differences in intraspecific aggression. We appraise this idea using population density data, adult sex ratio (ASR) and direct observations of social behaviour.

Materials and methods

STUDY ORGANISM AND AREA

The Italian wall lizard (*Podarcis sicula* Rafinesque-Schmaltz, 1810, Fig. 1) is a medium-sized [adult snout vent length (SVL) 55–70 mm], diurnal, heliothermic lacertid inhabiting Italy, coastal Slovenia and Croatia and a large number of major and minor islands in the Mediterranean. The species is dimorphic, with adult males having more robust heads, enlarged femoral pores and longer hind limbs than females (Henle & Klaver 1989). It occupies a variety of semi-open habitats, but climbs less than most other *Podarcis* species. Both males and females occupy slightly overlapping territories with preferred basking spots that they defend against other members of the same sex. Subordinate individuals do not hold territories and, therefore, probably suffer higher predation rates (Boag 1973).

The populations of *P. sicula* in this study occupy two small islands, Pod Mrčaru (42°46N, 16°46·7E) and Pod Kopište (42°45N, 16°43·7E) in the Croatian Adriatic Sea, west of the larger island Lastovo. The two islands closely resemble each other in general abiotic, but differ considerably in biotic conditions (see details in Vervust *et al.* 2007). The islands are separated by a water gap of 4·5 km. The population on Pod Mrčaru consists of the descendants of 10 founding animals, experimentally transplanted from Pod Kopište in 1971 (Nevo *et al.* 1972). The only other lacertid species on the islands is *Dalmatolacerta oxycephala* (Vervust *et al.* 2007).

FIELD METHODS AND BIOMETRICS

Lizards were caught by noose, by hand or in traps (plastic bottles with reversed necks) baited with soft fruits (peach or grapes). There are no

Fig. 1. Picture of an adult male *Podarcis sicula*.

statistically significant differences in the lizards' phenotype (speed of locomotion, toe loss rate, etc.) caught by different techniques (Bart Vervust, unpublished data). Upon capture, we determined a lizard's SVL (to the nearest 0·1 mm, using electronic callipers, CD-20PP; Mitutoyo Corporation, Kawasaki, Japan), body mass (to the nearest 0·01 g, using an electronic balance, Scout Pro SPU202; Ohaus Corporation, New Jersey, USA) and noted the number and location of missing toes. We included cases where all or part of the toe was missing, but did not include those where the toe was damaged but essentially intact. In a subset of 50 individuals with undamaged toes, we measured the length of each toe separately. Toes were conventionally numbered from 1 to 5, anterior to posterior on the manus and posterior to anterior on the pes. Some of the lizards had been previously toe-clipped for individual identification. These animals could be readily recognized because we had also given them a unique mark by burning a small scar into a specific combination of ventral scales (Vervust and Van Damme 2009) with a portable cautery (type H104; Aaron Medical, St. Petersburg, FL). These recaptures were not considered in our analyses of missing toe frequencies. All lizards were released at the exact site of capture.

AGONISTIC ENCOUNTERS

To index levels of intraspecific aggressiveness, we delineated 96 areas (49 on Pod Mrčaru and 47 on Pod Kopište) of 4 × 4 m using a 16-m rope. These plots were observed continuously over a period of 20 min each, from a distance of 5 m. We noted the number and type of interactions (fight/chase/mating/unknown), the age class (juvenile/sub adult/adult) and sex (male/female/unknown) of the interacting animals. Age classes are defined as; juveniles – animals from the first calendar year; sub adults – animals in their second calendar year, recognizable as animals of a moderate size with an absence of bite marks (females) and underdeveloped femoral pores (males); adults – specimens with bite marks (females) and clearly developed femoral pores (males). We define fighting as an interaction in which both animals showing aggression and chasing as the unidirectional aggressive action of an individual. However, those interactions are often combined and we therefore consider them as aggressive interactions. Sometimes, however, chasing resulted from fighting, but this was not always the case, as observed especially between immature and mature individuals. In some cases, we define an interaction as not known. In these cases, animals were interacting (chasing, fighting, mating), but the exact provocation of interaction was not visible (due to rocks, vegetation, etc.). Local density at each plot was estimated by counting the number of individuals seen in the quadrant. All observations were carried out during good weather conditions when the lizards were fully active, in areas where lizard density is the highest (i.e. on the higher altitudinal centre of the islands, Vervust *et al.* 2007). All measurements were conducted by the same person (B.V.).

DENSITY ESTIMATION

We used line transect counts (Overton 1971) to estimate population density on both islands. Transects were on average 65 m (range: 45–115 m) long and traversed the centre of the islands. We performed 18 transect counts on Pod Mrčaru and 20 on Pod Kopište. Transect length was calculated using a GPS (Garmin 60S, Garmin International, Olathe, Kansas, USA) with the software program Trip and Waypoints Manager V2 (MAPSOURCE, Version 6.0; Garmin). We monitored transects during periods of maximal lizard activity and noted the number of lizards observed, and their distance perpendicular to the transect line. The data were used to calculate population densities using the DISTANCE software (Harris & Burnham 2002).

PREDATION PRESSURE ESTIMATION

Relative estimates of predation pressure were obtained from Vervust *et al.* (2007). Briefly, we placed 569 plasticine lizard models randomly on both islands and collected them *c.* 48–52 h later. A model was considered to have been 'attacked' when it exhibited at least one beak mark. The proportion of lizard replicas attacked was regarded as a measure of relative predation pressure.

BITE FORCE CAPACITY

To test the hypothesis that lizards from one population are more likely to inflict toe injuries on conspecifics than lizards from the other population, we measured bite forces of individuals from both islands. Lizards were transported to the island of Lastovo and kept in large indoor terraria where they were free to thermoregulate. Bite force was assessed within 1 day following capture. Prior to each measurement, we checked the cloacal body temperature of the lizard using a thermocouple connected to an electronic thermometer (APPA 51, APPA Technology Corporation, Shin-Tien City, Taipei, Taiwan). Only lizards with body temperatures in the range of 35–37 °C were used (Van Damme *et al.* 1990). Bite force was measured using an isometric Kistler force transducer (type 9203; Kistler Inc. Wintherthur, Switzerland), mounted on a purpose-built holder and connected to a Kistler charge amplifier (type 5058A). All animals were induced to bite on two parallel plates, fixed at a distance of 3·65 mm. Bite forces were recorded using a portable computer equipped with an A/D converter (PC-Scope T512; Imtec GmbH, Backnang, Germany). For a full description of the measuring device, see Herrel *et al.* (2001a,b). Each individual lizard was tested five times, with at least 1 h between consecutive trials. The highest bite force registered was considered an estimate of individual's maximal bite capacity.

TOE BONE STRENGTH

The same equipment of the bite force measurements was used to obtain an estimate of bone strength (Herrel *et al.* 2001a,b). The force transducer was mounted on a complete head of a preserved *P. sicula* specimen (Fig. 2). We placed a toe between the upper and lower jaw of the lizard head and then slowly increased the pressure on the head, until the bone broke. The maximal force registered by the transducer was considered an estimate of toe bone strength. All measurements were conducted by the same person (B.V.). We used toes that had been clipped for identification and DNA-collecting purposes. These toes had been stored in 70% ethanol. Ethanol does not decalcify bones (Sturgess & Nicola 1975), so the effect on bone strength would be minimal. Toes of both populations had been stored for 1 year prior to the experiment. During the breakage experiment, toes obtained from individuals of Pod Mrčaru and Pod Kopište were tested alternately to prevent possible confounding effects due to wearing of the skull.

STATISTICAL ANALYSES

Analyses of injuries

To analyse variation in the occurrence of amputated toes, we used a Generalized Linear Model with logit link and binomial error. Population, sex, age, fore/hind limb, side (left/right), toe position

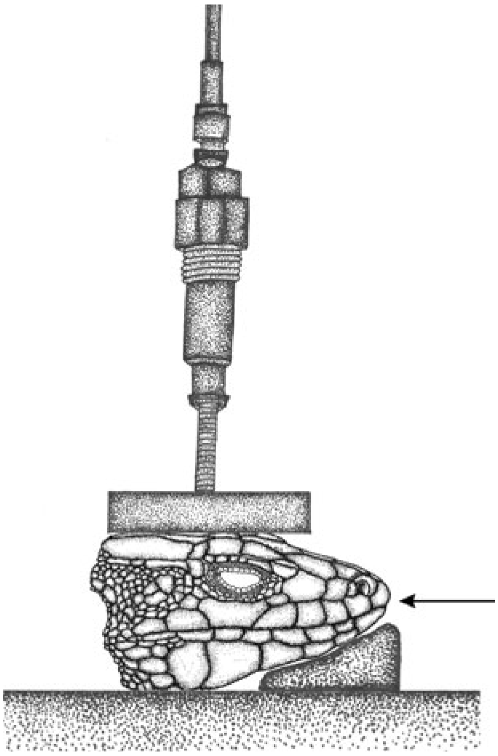

Fig. 2. Device for measuring bite force needed for breaking a toe. Location where toe was placed in the mouth before pressure is indicated with an arrow.

number (1–5) and SVL were added to the model as fixed effects to test their associations with the probability of toe amputation. Significance tests were based on Wald tests. Because the data consisted of repeated measurements (i.e. counts on the four limbs), tests and parameter estimates we obtained robust estimates using General Estimation Equations with a compound symmetry correlation structure as working correlation matrix (modelled in GENMOD procedure in SAS version 9.1). Based on the above model and analysis, we anticipate that the probability of toe amputation would be related to toe length. Therefore we tested whether the length of toes differed between toe positions using a repeated-measure ANOVA. We then tested for an association between average toe length and overall probability of amputation using a spearman rank correlation. Finally, the probability of tail injuries was compared between populations and between males and females using a logistic model with logit link and binomial error.

Population densities, sex ratios and social interactions

Sex ratios were compared in the populations using a log-linear model with log link and Poisson error. We related frequency of interactions to local population density and compared the populations using an ANCOVA model with number of interactions as dependent variable and local density, population and the two-way interaction as factors of the model. Because densities differ between populations, we also repeated this ANCOVA analyses for a range of local densities that is comparable between the two populations.

Bite force and bone strength

Bite force and bone strength were compared in the populations and sexes using two-way ANCOVA models, with SVL as covariable.

Results

INJURY STATISTICS

The incidence of naturally missing toes was extremely high (Table 1), especially on the island of Pod Mrčaru. Of 465 lizards caught on Pod Mrčaru, 258 lizards (55·48%) had at least one injured toe; on Pod Kopište, this percentage was 12·87% (56 of 435). This difference is highly significant (Generalized Linear Model, island effect: χ^2 = 96·67, P < 0·001). The population on Pod Mrčaru also showed a significant sex difference in injury frequency, with males more frequently exhibiting damage than females (69·3% vs. 49·7%, χ^2 = 23·79, P = 0·008), an effect which was not found in the Pod Kopište population (χ^2 = 5·37, P = 0·25).

The proportion of injuries (number of amputated toes) increased with SVL (Spearman's correlation coefficient, σ_{898} = 0·492, P < 0·001). Therefore, we added SVL as covariable in all analyses. Our analyses indicate that for a given SVL, lizards from Pod Mrčaru have more toe amputations than lizards from Pod Kopište. This can only reflect differences in average age between the populations if lizards on Pod Mrčaru are initially smaller than those on Pod Kopište (or grow more slowly in their first year), but then survive longer. We have no indication that this is the case; on the contrary, juvenile and sub adult lizards have larger SVLs on Pod Mrčaru than on Pod Kopište (t_{131} = 2·42, P = 0·017). In addition, females on Pod Mrčaru produce larger eggs than females on Pod Kopište (Bart Vervust, unpublished data). Hence, although a (putative) difference in average age between the two populations may contribute to the higher absolute number of toe amputations, it cannot explain the difference in SVL-corrected amputation load.

We found no sign of laterality in the number of injured toes (left vs. right side; $\chi2$ = 0·26, P = 0·61; Front-hind × Side; χ^2 = 0·03, P = 0·86), but more toes were damaged on the hind limbs than on the fore limbs (Fig. 2, χ^2 = 5·49, P = 0·02). We also found a significant interaction (χ^2 = 45·95, P < 0·001) between toe position number (1–5) and location (fore limb/hind limb). Toes from the fore- and hind limbs have a different amputation load considering their position. Populations did not differ in their number of amputations between front and hind limbs (χ^2 = 0·44, P = 0·51; nor in the interaction Population × Number; χ^2 = 6·14, P = 0·18). Our data set on intact digits shows obvious differences in length among the digits at different positions

Table 1. Frequency of amputated toes of lizards from the two islands. Data are shown in the form of counts of lizards with number of missing toes

Number of toes amputated	0	1	2	3	4	5	6	7	8	9	11	SUM
Pod Mrčaru	207	92	60	40	22	22	14	1	3	3	1	465
Pod Kopište	379	43	7	3	3	0	0	0	0	0	0	435

($F_{18,400}$ = 64·12, P < 0·001). Longer digits are more likely to be missing or to be cut (r_S = 0·91, P < 0·001; Fig. 3).

The proportion of lizards with a broken tail is significantly higher on Pod Kopište (181 of 441, or 41%) than on Pod Mrčaru (122 of 477, or 25·5%) (χ^2 = 17·62, P < 0·001). Tail injury is significantly higher in males than in females on Pod Mrčaru (χ^2 = 6·26, P = 0·045) but not on Pod Kopište (χ^2 = 1·78, P = 0·18). Compared to adult animals, juveniles have lower frequencies of broken tails (χ^2 = 14·5, P < 0·001).

POPULATION DENSITIES, SEX RATIOS AND SOCIAL INTERACTIONS

We obtained population density estimates of 3082 lizards ha^{-1} for Pod Mrčaru and 1045 lizards ha^{-1} for Pod Kopište. Sex ratios were female-biased (n = 235, χ^2 = 51·38, P < 0·001) on both islands (Pod Mrčaru: 33 males/88 females, 27·27–72·72%; Pod Kopište: 43 males/71 females, 37·72–62·28%). The difference between the islands was significant (Island × Sex effect; n = 235, χ^2 = 2·93; P = 0·007).

The number of interactions scored during 20 min observations of the experimental plots was positively correlated with local density at the plot (r_S = 0·93, n = 96, P < 0·001; Fig. 4). When correcting for this local density effect, lizards on Pod Mrčaru are not more aggressive than those on Pod Kopište (ANCOVA with local density as covariable, $F_{1,73}$ = 0·78, P = 0·38). This analysis was conducted with densities in the same range only. The most common form of social interaction is aggression (67·79%), followed by not known (30·51%). Mating was observed only 13 times of 201 interactions (0·06%). In 28·57% of the cases an adult chased a juvenile or sub adult; this occurs not more often than expected by juvenile abundance (χ^2_{25} = 30·5, P = 0·205).

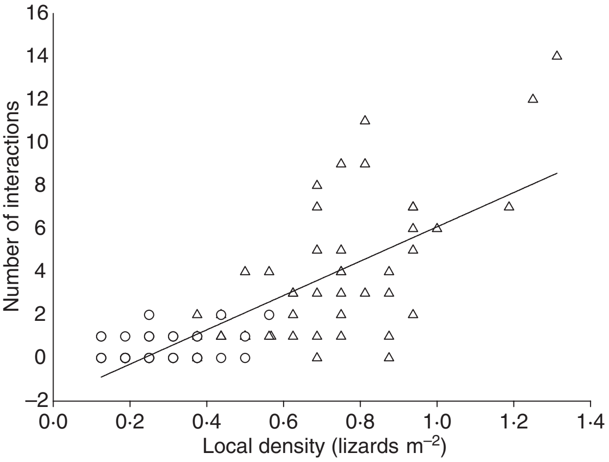

Fig. 3. Relationships between the numbers of interactions scored during 20 min and local density in experimental plots. Triangles represent observations on Pod Mrčaru, circles on Pod Kopište.

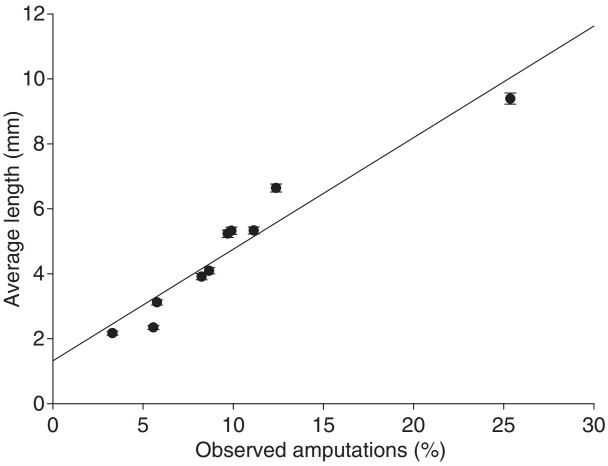

Fig. 4. Correlation with the observed amputations in percentage, and average length of toes and fingers of *Podarcis sicula* on Pod Kopište and Pod Mrčaru (pooled data).

BITE FORCE AND BONE STRENGTH

Maximal bite force differed significantly between populations (ANCOVA with SVL as covariable, $F_{1,318}$ = 258·05, P < 0·001) and between sexes ($F_{1,318}$ = 1089·1, P < 0·001). The interaction between population and sex was not significant ($F_{1,318}$ = 0·206, P = 0·65). Males in both populations bit harder than females, and lizards from Pod Mrčaru bit harder than those from Pod Kopište (Table 2). Forces required to break the bones also differed between populations ($F_{1,328}$ = 35·2, P < 0·001), but were similar for toes originating from males or females ($F_{1,328}$ = 2·62, P = 0·1). Lizards from Pod Mrčaru had stronger toes than those from Pod Kopište (Table 2). We found no effect of SVL on bone strength ($F_{1,328}$ = 2·43, P = 0·12).

Discussion

The potential use of non-lethal injuries has received substantial attention from evolutionary ecologists (Pianka 1967; Schoener 1979; Schoener & Schoener 1980; Arnold 1988; Pianka & Vitt 2003). While the utilization of non-lethal injuries to indirectly index levels of interaction intensity is often fraught with difficulties (Schoener 1979), our study examined several non-mutually exclusive hypotheses providing a proximate explanation for the observed differences in injury frequencies. Many ecological interactions have been put forward to explain toe loss in lizards, and they may provide a valuable tool for evolutionary-ecological studies.

The reported incidence of naturally missing toes differs considerably among lizard species, varying from zero in geckoes such as *Oedura ocellata* (Bustard 1971), *Gehyra variegata* (Bustard 1968a) and *Heteronotia binoei* (Bustard 1968b), over 3·6% and 10% in populations of *Zootoca vivipara* (Middelburg & Strijbosh 1988; Gvozdik 2000), up to 11·2% in the skink *Egernia whitii* (Bellamy 2006) and 34·3% in *Pseudemoia entrecasteauxii* (Hudson 1996). In comparison with these species, toe loss in both our island populations of *P. sicula* is

Table 2. Maximal bite force capacity and strength of toe bones (mean ± SE) of lizards from the two islands

	Pod Mrčaru		Pod Kopište	
	♂♂	♀♀	♂♂	♀♀
Bite force (N)	11·923 ± 0·24	7·20 ± 0·46	9·05 ± 0·32	5·08 ± 0·21
Toe bone strength (N)	17·51 ± 0·56	15·94 ± 0·35	8·65 ± 0·65	9·23 ± 0·44

exceptionally high, the incidence on Pod Mrčaru is almost double that of the highest reported. Both the aetiology of missing toes and why the incidence varies so widely among species and populations remain unclear.

The most logical and straightforward explanation would be that differences in toe loss incidence between the two island populations merely reflect a difference in average age. In systems with unsuccessful predators, older prey animals are more likely to have experienced attacks and, therefore, will show higher frequencies of scars and mutilations (Schoener 1979). Similarly, older individuals are more likely to bear the consequences of intra- or interspecific fights. In accordance with this hypothesis, our results show a higher number of injured toes in adults compared with juveniles. On the other hand, our analyses indicate that for a given SVL, lizards from Pod Mrčaru have more toe amputations than lizards from Pod Kopište. Like suggested before, this might be an artefact if lizards in Pod Mrčaru are initially smaller than those on Pod Kopište. Alternatively, lizards from Pod Mrčaru may grow more slowly and survive longer as it is known that lizards keep on growing throughout their life. Contrary to this prediction, lizards on Pod Mrčaru are larger at birth than those on Pod Kopište, possibly induced by the initial larger egg size on Pod Mrčaru compared with Pod Kopište (Bart Vervust, unpublished data). Hence, although a (putative) difference in average age between the two populations may contribute to the higher absolute number of toe amputations, it cannot explain the difference in SVL-corrected amputation load.

Alternatively, differences in injury frequencies may be caused by a difference in offensive power between the two island populations. Individuals from one island are, because of their bite force capacities, more likely to inflict injuries on conspecifics than on individuals from the other island. The fact that lizards from Pod Mrčaru bit with more force than those from Pod Kopište conforms with this hypothesis. The observation that both males and females from Pod Mrčaru bite with considerably more strength than their counterparts on Pod Kopište corroborate this idea. Although the bite forces listed in Table 1 are somewhat lower than the forces required to break toes, we still believe that lizards from both islands are capable of severing toes of conspecifics. In our experimental bone failure assessments, we primarily apply a transverse force to the digits. However, in reality, and especially during violent interactions, bones probably experience considerable torsion and/or bending, resulting in shear. Bone is weakest in shear, followed by tension and then compression (McGee *et al.* 2004). If lizards can generate (almost) sufficient bite force to inflict transverse fractures, they should be capable of producing torsional fractures. Moreover, bites may result in toe loss without actual fracture of the toe bone, e.g. by progressive necrosis following infection (Hazell *et al.* 1985). In concert with the previous idea, we tested whether individuals of one population may be more predisposed to lose digits, because their bones are weaker. This idea is not supported by our data. The two populations differ in mean bone strength, but contrary to what was expected: lizards from the island with higher toe loss incidence have, on average, stronger bones than the other population. It is unknown which proximate factors are responsible for this interpopulation difference. Structural bone strength is known to be influenced by both tissue material properties and the distribution of that material in the bone (Van der Meulen *et al.* 2001), variables that are, in turn, affected by a multitude of internal and external conditions, including diet, exercise and hormone levels. Interestingly, androgens maintain cancellous bone mass and integrity (Vanderschueren *et al.* 2004), so bone strength can be expected to be higher in populations that sustain high levels of sex hormones.

Several investigators have suggested that differences in predation pressure may induce a different rate of injuries among populations due to inefficient predators. Toe loss results from predatory attempts and differences in toe loss incidence reflect differences in predation pressure. This is not supported by our data. In an earlier study (Vervust *et al.* 2007), we showed that predation rate, as estimated from the number of peck marks on plasticine lizard models, is higher on Pod Kopište, the island with the lower toe loss incidence. Most attacks are assumed to come from yellow-legged gulls (*Larus michahellis*) or other non-specialized avian predators. In addition, Pod Kopište offers fewer hiding opportunities (rocks, protective vegetation), probably making it a more dangerous place to live (Vervust *et al.* 2007). In contrast to toe loss incidences, tail break frequencies follow the difference in estimated predation pressure. This is to be expected in a system with relatively inefficient predators (Schoener 1979).

On the other hand, toe loss might result from intraspecific fights and differences in toe loss incidence reflect differences in the frequency (or intensity) of aggressive encounters. One assumption of this hypothesis, lizards are capable of severing toes, seems to be correct. The hypothesis is also consistent with the observations that population density and the frequency of intraspecific interactions are higher on the island with high toe loss incidence. Our density estimate for the population on Pod Mrčaru is among the highest recorded for any lizard species (cf. Buckley & Jetz 2007). Further support comes from the fact that on Pod Mrčaru, males more frequently miss toes than females. Although both sexes in

P. sicula defend territories against members of the same sex, males are much more antagonistic towards other adult males than adult females (Boag 1973). Moreover, as most battles occur between members of the same sex, males will be more often confronted by an opponent with a high biting capacity. The observed high population density is a key parameter in the demography and proximate factor driving intraspecific competition of animal populations, resulting in more aggressive interactions. Also the ASR may be important in driving intraspecific competition. ASR is often found equal in lizard populations (Castilla & Bauwens 1992; Pérez-Mellado *et al.* 1997) but sometimes female biased (Strijbosch & Creemers 1988; Diego-Rasilla & Pérez-Mellado 2003). Diego-Rasilla & Pérez-Mellado (2003) interpreted the skewed sex ratios as the result of different survival rates for males and females, as is shown for some lizard species, where females enjoy better survivorship than males throughout their lifetime (Blair 1960; Tinkle 1967; Strijbosch & Creemers 1988; but see Le Gaillard *et al.* 2005). The significant interaction between island and sex in ASR shows that the female-biased pattern is stronger on Pod Mrčaru; therefore, competition for females on Pod Kopište should be stronger; however, only the population of Pod Mrčaru showed a significant sex difference in injury frequency. This reduction in males on Pod Kopište may result from the increased predation pressure. In general, Pod Mrčaru is more complex in microhabitat (rocks, vegetation, etc.) than Pod Kopište (Vervust *et al.* 2007), which may be an alternative cause of toe damage. Regarding the recently founded origin of this population it would be worthwhile investigating whether this high population density would remain stable over time or if the population would crash. Alternatively, lizards on Pod Kopište may have a different activity level (short periods of activity and long periods of latency), which may bias density estimations.

Alternatively, the difference in the frequency of individuals with missing toes between islands results from differential selection against injured animals. Several authors have investigated the effect of missing toes on locomotor performance of lizards, with conflicting results. Toe amputation (usually by toe clipping) had no effect on sprint speed in the lizards *Sceloporus merriami* (Huey *et al.* 1990), *Cnemidophorus sexlineatus* (Dodd 1993), *Hemidactylus turcicus* (Paulissen & Meyer 2000) and *Eulamprus quoyii* (Borges-Landaez & Shine 2003), but drastically reduced clinging performance in the arboreal *Anolis carolinensis* (Bloch & Irschick 2004). Our own results using *P. sicula* lizards from these islands suggest little, but existing effect of amputations on maximal running speed (Bart Vervust *et al.* unpublished data). And it is worthwhile questioning whether those differences are reflected in a different survival between severely amputated and non-amputated individuals. We did not find any difference in laterality (left, right) as shown by Seligmann *et al.* (2003), and found that longer toes are more likely to be amputated.

Differences in toe injury frequencies are best explained by differences in the intensity of intraspecific competition. In addition, autotomy frequency correlates with the difference in predation pressure as expected in a system (Vervust *et al.* 2007) with relatively inefficient predators (Schoener 1979). Our results also suggest that males are more likely to suffer injuries than females, in accordance with previous data on other species (Tinkle 1967; Schoener & Schoener 1980; Pérez-Mellado *et al.* 1997; Gvozdik 2000; Mayol 2004) with the exception of the study of Middelburg & Strijbosh (1988), who studied *Zootoca vivipara* populations in which females suffered more injuries. Lizards on Pod Mrčaru do not seem to be more intrinsically aggressive, but higher densities result in an increased number of interactions. This is possibly an important factor in phenotypic differentiation of this species in the Mediterranean. We suggest that the amount of toe amputation load may present an indirect estimation of the frequency of intraspecific competition.

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References

Abrams, P.A. (2001) Describing and quantifying interspecific interactions: a commentary on recent approaches. *Oikos*, **94**, 209–218.

Arnold, E.N. (1988) Caudal autotomy as a defense. *Biology of the Reptilia*, Vol. 16 (eds C. Gans & R. B. Huey), pp. 235–273. Alan R. Liss, New York.

Bellamy, S. (2006) *Resource partitioning between two sympatric Australian skinks, Egernia multiscutata and Egernia whitii*. PhD thesis, School of Biological Sciences, Flinders University, Adelaide, Australia.

Blair, W.F. (1960) *The rusty lizard, a population study*. University of Texas Press, Austria , 185 pp.

Bloch, N. & Irschick, D.J. (2004) Toe-clipping dramatically reduces clinging performance in a pad-bearing lizard (*Anolis carolinensis*). *Journal of Herpetology*, **37**, 293–298.

Boag, D.A. (1973) Spatial relationships among members of a population of wall lizards. *Oecologia*, **12**, 1–13.

Borges-Landaez, P.A. & Shine, R. (2003) Influence of toe-clipping on running speed in *Eulamprus quoyii*, an Australian scincid lizard. *Journal of Herpetology*, **37**, 592–595.

Brown, C.K. & Ruby, D.E. (1977) Sex-associated variation in the frequencies of tail autotomy in *Sceloporus jarrovi* (Sauria: Iguanidae) at different elevations. *Herpetologica*, **33**, 380–387.

Buckley, L.B. & Jetz, W. (2007) Insularity and the determinants of lizard population density. *Ecological Letters*, **10**, 481–489.

Bustard, H.R. (1968a) The ecology of the Australian gecko *Gehydra variegata* in northern New South Wales. *Journal of Zoology*, **154**, 113–138.

Bustard, H.R. (1968b) The ecology of the Australian gecko *Heteronotia binouri* in northern New South Wales. *Journal of Zoology*, **156**, 483–497.

Bustard, H.R. (1971) A population study of the Eyed Gecko, *Oedura ocellata*, in northern New South Wales. *Copeia*, **4**, 658–669.

Castilla, A.M. & Bauwens, D. (1992) Habitat selection by the lizard *Lacerta lepida* in a Mediterranean oak forest. *Herpetological Journal*, **2**, 27–30.

Chadwick, N.E. (1991) Spatial distribution and the effects of competition on some temperate Scleractinia and Corallimorpharia. *Marine Ecology Progress Series*, **70**, 39–48.

Congdon, J.D., Vitt, L. & King, W.W. (1974) Geckoes: adaptive significance and energetics of tail autotomy. *Science*, **184**, 1379–1380.

Diego-Rasilla, F.J. & Pérez-Mellado, V. (2003) Home range and habitat selection by *Podarcis hispanica* (Squamata, Lacertidae) in Western Spain. *Folia Zoologica*, **52**, 87–98.

Dodd, C.K. (1993) The effects of toe-clipping on sprint performance of the lizard *Cnemidophorus sexlineatus*. *Journal of Herpetology*, **27**, 209–213.

Gvozdik, L. (2000) Intrapopulation variation in injury frequencies in the sand lizard, *Lacerta agilis* (Squamata, Lacertidae). *Biologica*, **55**, 557–561.

Harris, R.B. & Burnham, K.P. (2002) On estimating wildlife densities from line transect data. *Acta Zoological Sinica*, **48**, 812–818.

Hazell, S.L., Eamens, G.J. & Perry, R.A. (1985) Progressive digital necrosis in the Eastern Bluetonged skink, *Tiliqua scincoides* (Shaw). *Journal of Wildlife Diseases*, **21**, 186–188.

Heithaus, M.R., Frid, A. & Dill, L.M. (2002) Shark-inflicted injury frequencies, escape ability, and habitat use of green and loggerhead turtles. *Marine Biology*, **140**, 229–236.

Henle, K. & Klaver, C.J.J. (1989) *Podarcis sicula* (Rafinesque-Schmaltz, 1810) – Ruineneidechse. *Handbuch der Reptielen und Amphibien Europas* (ed. W. Böhme), pp. 254–342. Aula-Verlag, Wiesbaden.

Herrel, A., De Grauw, F. & Lemos – Espinol, J.A. (2001a) Head shape and bite performance in xenosaurid lizards. *Journal of Experimental Zoology*, **290**, 101–107.

Herrel, A., Van Damme, R., Vanhooydonck, B. & De Vree, F. (2001b) The implications of bite performance for diet in two species of lacertid lizards. *Canadian Journal of Zoology*, **79**, 662–670.

Hudson, S. (1996) Natural toe loss in southeastern Australian skinks: implications for marking lizards by toe-clipping. *Journal of Herpetology*, **30**, 106–110.

Huey, R.B., Dunham, A.E., Overall, K.L. & Newman, R.A. (1990) Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami*. *Physiological Zoology*, **63**, 845–872.

Jaksic, F.M. & Busack, S.D. (1984) Apparent inadequacy of tail-loss figures as estimates of predation upon lizards. *Amphibia-Reptilia*, **5**, 177–179.

Jaksic, F.M. & Fuentes, E.R. (1980) Correlates of tail losses in twelve species of *Liolaemus* lizards. *Journal of Herpetology*, **14**, 137–141.

Jaksic, F.M. & Greene, H.W. (1984) Empirical evidence of non-correlation between tail loss frequency and predation intensity on lizards. *Oikos*, **42**, 407–411.

Kramer, G. (1951) Body proportions of mainland and island lizards. *Evolution*, **5**, 193–206.

Le Gaillard, J.-F., Fitze, P.S., Ferrière, R. & Clobert, J. (2005) Sex ratio bias, male aggression, and population collapse in lizards. *Proceedings of the National Academy of Sciences of the United States of America*, **120**, 18231–18236.

Mayol, J. (2004) *A conservation proposal for most endangered insular lizards in the Balearics. The Biology of Lacertid Lizards. Evolutionary and Ecological Perspectives* (eds V. Pérez-Mellado, N. Riera & A. Perera), pp. 231–238. Institut Menorqui d'Estudis, Menorca.

McGee, A.M., Qureshi, A.A. & Porter, K.M. (2004) Review of the biomechanics and patterns of limb fractures. *Trauma*, **6**, 29–40.

Medel, R.G., Jimenez, J.E., Fox, S.F. & Jaksic, F.M. (1988) Experimental evidence that high population frequencies of lizard tail autotomy indicate inefficient predation. *Oikos*, **53**, 321–324.

Middelburg, J.J.M. & Strijbosh, H. (1988) The reliability of the toe-clipping method with the common lizard (*Lacerta vivipara*). *Herpetological Journal*, **1**, 291–293.

Nemes, S. (2005) Comparative morphometric analysis of injured and uninjured newly metamorphosed smooth newts (*Triturus vulgaris*). *North-Western Journal of Zoology*, **1**, 61–63.

Nevo, E., Gorman, G., Soulé, M., Yang, S.Y., Clover, R. & Jovanović, V. (1972) Competitive exclusion between Insular *Lacerta* species (Sauria, Lacertidae). *Oecologia*, **10**, 183–190.

Overton, W.C. (1971) Estimating the numbers of animals in wildlife populations. *Wildlife Management Techniques* (ed. R. H. Giles), pp. 403–456. The Wildlife Society, Washington, DC.

Pafilis, P. & Valakos, E.D. (2008) Loss of caudal autotomy during ontogeny of Balkan Green lizard, *Lacerta trilineata*. *Journal of Natural History*, **42**, 409–419.

Paulissen, M.A. & Meyer, H.A. (2000) The effect of toe-clipping on the gecko *Hemidactylus turcicus*. *Journal of Herpetology*, **34**, 282–285.

Pérez-Mellado, V., Corti, C. & LoCascio, P. (1997) Tail autotomy and extinction in Mediterranean lizards: a preliminary study of continental and insular populations. *Journal of Zoology*, **243**, 533–541.

Pianka, E.R. (1967) Lizard species diversity. *Ecology*, **48**, 333–351.

Pianka, E.R. (1973) The structure of lizard communities. *Annual Review of Ecology and Systematics*, **4**, 53–74 (doi: 10.1146/annurev.es.04.110173.000413).

Pianka, E.R. & Vitt, L.J. (2003) *Lizards: Windows to the Evolution of Diversity*. University of California Press, Berkeley, 346 pp.

Raffaelli, D.G. (1978) The relationship between shell injuries, shell thickness and habitat characteristics on the intertidal snail *Littorina rudis* Maton. *Journal of Molluscan Studies*, **44**, 166–170.

Rand, A.S. (1954) Variation and predation pressure in an island and mainland population of lizards. *Copeia*, **1954**, 260–262.

Schoener, T.W. (1979) Inferring the properties of predation and other injury-producing agents from injury frequencies. *Ecology*, **60**, 1110–1115.

Schoener, T.W. & Schoener, A. (1980) Ecological and demographic correlates of injury rates in some Bahamian *Anolis* lizards. *Copeia*, **1980**, 839–850.

Seligmann, H., Beiles, A. & Werner, Y.L. (2003) More injuries in left-footed individual lizards and *Sphenodon*. *Journal of Zoology*, **260**, 129–144.

Semlitsch, R.D. & Reichling, S.B. (1989) Density-dependent injury in larval salamanders. *Oecologia*, **81**, 100–103 (doi: 10.1007/BF00377017).

Soederbaeck, B. (1995) Replacement of the native crayfish *Astacus astacus* by the introduced species *Pacifastacus leniusculus* in a Swedish lake: possible causes and mechanisms. *Freshwater Biology*, **33**, 291–304.

Strijbosch, H. & Creemers, R.C.M. (1988) Comparative demography of sympatric populations of *Lacerta vivipara* and *Lacerta agilis*. *Oecologia*, **76**, 20–26.

Sturgess, J.A. & Nicola, S.J. (1975) *Preparation of Fish for Identification and Preservation as Museum Specimens*. Department of Fish and Game, Inland Fisheries Informational Leaflet 29. The Resources Agency of California, Sacramento.

Tinkle, D.W. (1967) The life and demography of the side-blotched lizard, *Uta stansburiana*. *Misc. Publi. Mus. Zool. University of Michigan*, **132**, 1–182.

Tinkle, D.W. & Ballinger, R.E. (1972) *Sceloporus undulatus*: a study of the intraspecific competitive demography of a lizard. *Ecology*, **53**, 570–584.

Van Damme, R., Bauwens, D., Castilla, A.M. & Verheyen, R.F. (1990) Comparative thermal ecology of the sympatric lizards *Podarcis tiliguerta* and *Podarcis sicula*. *Acta Oecologica*, **11**, 503–512.

Van der Meulen, M.C.H., Jespen, K.J. & Mikic, B. (2001) Understanding bone strength: size isn't everything. *Bone*, **29**, 101–104.

Vanderschueren, D., Vandenput, L., Boonen, S., Lindberg, M.K., Bouillon, R. & Ohlsson, C. (2004) Androgens and bone. *Endocrine Reviews*, **25**, 389–425.

Vervust, B. & Van Damme, R. (2009) Marking lizards by heat branding. *Herpetological Review*, in press.

Vervust, B., Grbac, I. & Van Damme, R. (2007) Differences in morphology, performance and behaviour between recently diverged populations of *Podarcis sicula* mirror differences in predation pressure. *Oikos*, **116**, 1343–1352.

Vitt, L.J., Congdon, J.D., Hulse, A.C. & Platz, J.R. (1974) Territorial aggressive encounters and tail breaks in lizard *Sceloporus magister*. *Copeia*, **1974**, 990–992.

Vitt, L.J., Congdon, J.D. & Dickson, N.A. (1977) Adaptive strategies and energetics of tail autotomy in lizards. *Ecology*, **58**, 326–337.

Zweifel, R.G. & Lowe, C.H. (1966) The ecology of a population of *Xantusia vigilis*. *American Museum Novitates*, **2247**, 1–57.

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