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Feed or fight: testing the impact of food availability and intraspecific aggression on the functional ecology of an island lizard

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Summary

1. Body size often varies among insular populations relative to continental conspecifics – the 'island rule' – and functional, context-dependent morphological differences tend to track this body size variation on islands.

2. Two hypotheses are often proposed as potential drivers of insular population differences in morphology: one relating to diet and the other involving intraspecific competition and aggression. We directly tested whether differences in morphology and maximum bite capacity were explained by interisland changes in hardness of both available and consumed prey, and levels of lizard-to-lizard aggression among small-island populations.

3. Our study included 11 islands in the Greek Cyclades and made use of a gradient in island area spanning five orders of magnitude. We focused on the widespread lizard *Podarcis erhardii*.

4. We found that on smaller islands, *P. erhardii* body size was larger, head height was larger relative to body size, and maximum bite capacity became proportionally stronger.

5. This pattern in morphology and performance was not related to differences in diet, but was highly correlated with proxies of intraspecific aggression – bite scars and missing toes.

6. Our findings suggest that critical functional traits such as body size and bite force in *P. erhardii* follow the predictions of the island rule and are changing in response to changes in the competitive landscape across islands of different sizes.

Key-words: bite force, Cyclade islands, diet, Greece, intraspecific aggression, island rule, *Podarcis erhardii*

Introduction

Extreme body size, shape, and performance differences among insular populations relative to continental populations of the same species have been documented in a number of cases – pygmy pachyderms in the Mediterranean and gigantic Galapagos tortoises among them (Case 1978; Lomolino 1985; Sondaar 1986; Hayes *et al.* 1988; Jaffe, Slater & Alfaro 2011; Sagonas *et al.* 2014). However, whether this 'island rule' can be generalized across taxa and conditions is very much in question (Lomolino 2005; Meiri, Cooper & Purvis 2008), particularly for reptiles (Meiri, Dayan & Simberloff 2006; Meiri 2008; Itescu *et al.* 2014).

Studies testing the island rule typically invoke a trophic explanation (energetics and diet selection) as the basis for changes in body morphology following a species' arrival to an island (Van Valen 1965; Roughgarden 1972; Lister 1976; Case 1978; Lomolino 1985). The rationale is that selection will favour convergence on a new optimal phenotype for efficient resource acquisition in the new insular environment (Lomolino 1985). Thus, relative to mainland populations of the same or closely related species, small- to medium-sized vertebrate species will tend to become larger on islands to benefit from metabolic efficiencies, while large vertebrate species will tend to become smaller to capitalize on limited food resources (Case 1978; Lomolino 1985). This pattern has been demonstrated, for example, among species of nonvolant mammals (Lomolino 1985), snakes (Boback & Guyer 2003) and birds (Clegg & Owens 2002).

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Yet, alternative, non-trophic explanations for the island rule pattern have also been advanced. Larger body size of some island populations may reflect the island colonizer's need for robust morphology to reach the island in the first place (Lomolino 2005). Or, insular populations may experience a shift in the nature of the interactions that determine selection for different body morphologies, such as a release from predation or a shift from predominantly interspecific competition on mainland to intraspecific pressure on islands (Case 1978; Lomolino 1985, 2005; Pafilis *et al.* 2009). However, to our knowledge, these alternative trophic and non-trophic explanations have never been simultaneously tested. Our study examines the relative contribution of these two mechanisms to variability in morphology and performance in the lizard *Podarcis erhardii* (Werner 1930), making use of the Greek Cyclades as a natural experimental laboratory.

Archipelagos provide unique settings for natural experiments aimed at comparing the relative impacts of ecological contexts on a species' traits. Biogeography theory predicts that as islands get smaller, and more remote, species diversity and overall biomass will decrease (MacArthur & Wilson 1967). Large vertebrates, particularly carnivores, are lost first as island area decreases (MacArthur & Wilson 1967). The lack of top predators on small islands is known to release meso-predators (Blumstein 2002) – including lizards – enabling higher densities on small predator-free islands (Pérez-Mellado & Corti 1993; Buckley & Jetz 2007; Pafilis *et al.* 2009). Agonistic behaviour in lizards is correlated with increased competition for food, territory, mates and other resources (Diego-Rasilla & Pérez-Mellado 2000; Vervust *et al.* 2009). Thus, life on small islands can drive high rates of intraspecific aggression (Pafilis *et al.* 2009; Brock *et al.* 2014), resulting in bite scars (Vitt & Cooper 1985; Gillingham, Carmichael & Miller 1995; Jennings & Thompson 1999), amputation of toes (Vervust *et al.* 2009), tail shedding (Brock *et al.* 2014) and even cannibalism (Pafilis *et al.* 2009; Cooper, Dimopoulos & Pafilis 2014; Deem & Hedman 2014).

Mediterranean islands – many smaller than 1 km^2 – with very little food or shelter from the hot, dry and windy summers, can be harsh environments for lizards. We then expect that lizards living in different island contexts would be locally adapted to maximize their fitness in those conditions. Indeed, numerous studies have shown that lizards living on islands display a host of morphological (Huyghe, Vanhooydonck & Scheers 2005; Sagonas *et al.* 2014), performance (Pafilis, Foufopoulos & Poulakakis 2007; Vervust, Grbac & Van Damme 2007; Pafilis *et al.* 2009), and behavioural (Cooper & Pérez-Mellado 2012; Cooper, Dimopoulos & Pafilis 2014) differences relative to mainland populations, and even populations on larger islands (Runemark *et al.* 2010; Pafilis *et al.* 2011; Brock *et al.* 2014).

Body size differences between island populations are one of the most cited island effects on lizard morphology; larger bodies among small-island lizards often enable herbivory (Van Damme 1999; Cooper & Vitt 2002; Herrel *et al.* 2008), critically broadening the niche of these insular species. Head morphology is also known to change on small islands, often getting larger with body size, and at times changing shape altogether (Herrel, Vanhooydonck & Van Damme 2004; Huyghe *et al.* 2009). Moreover, with head morphology changes, concomitant changes in bite force are often observed (Herrel *et al.* 1999; Huyghe *et al.* 2009).

A lizard's bite capacity is directly related to its ability to acquire and protect valuable resources – food, shelter and mates (Verwaijen, Van Damme & Herrel 2002; Lailvaux *et al.* 2004; Huyghe, Vanhooydonck & Scheers 2005). Maximum bite force varies considerably between lizard species (Herrel *et al.* 2001; Herrel, Vanhooydonck & Van Damme 2004), but can also vary within a species (Huyghe, Vanhooydonck & Scheers 2005; Brecko *et al.* 2008), and in different ecological contexts (Sagonas *et al.* 2014). This intraspecific variation in bite force is often attributed either to dietary (trophic) or behavioural (non-trophic) differences between populations. Proportionally stronger bite forces on small islands, for example, may enable a more herbivorous diet (Herrel, Vanhooydonck & Van Damme 2004; Herrel *et al.* 2008; Herrel & De Vree 2009), or access to heavily defended (hard body) prey items like beetles with strong elytra or snails with shells (Herrel *et al.* 1999, 2001; Verwaijen, Van Damme & Herrel 2002). Alternatively, stronger bite forces on small islands may correspond to higher intraspecific aggression and competition (Lailvaux *et al.* 2004; Huyghe, Vanhooydonck & Scheers 2005; Lailvaux & Irschick 2007).

We found that *P. erhardii* bite force was stronger on small islands and investigated whether diet or intraspecific interactions explain this pattern. If diet is an important driver of differences in bite force, lizards on small islands would ingest a significantly higher proportion of hard prey items or plant material. If intraspecific interactions drive differences in bite force, then we would expect proxies of aggression, like bite scars, amputation of toes and tail shedding, to increase in frequency on smaller islands. Moreover, we predicted that the body size of *P. erhardii* individuals would be inversely related to island size and individuals should have larger heads, relative to body size, on the smallest islands. These larger heads should translate into proportionally harder bites.

Materials and methods

STUDY SITES AND SPECIES

We conducted our study on 11 islands in the Greek Cyclades ranging in size from 0·004 km^2 to over 400 km^2 (Fig. 1a). During the last glacial maximum, these islands were connected in a large cluster – 'Cycladia' – and in the ensuing 10 000 years have become isolated in a known fragmentation sequence calculated using bathymetry data and historical sea-level rise (Foufopoulos & Ives 1999). All islands in the study are within 50 km of each other and experience very similar climate conditions: warm, dry summers

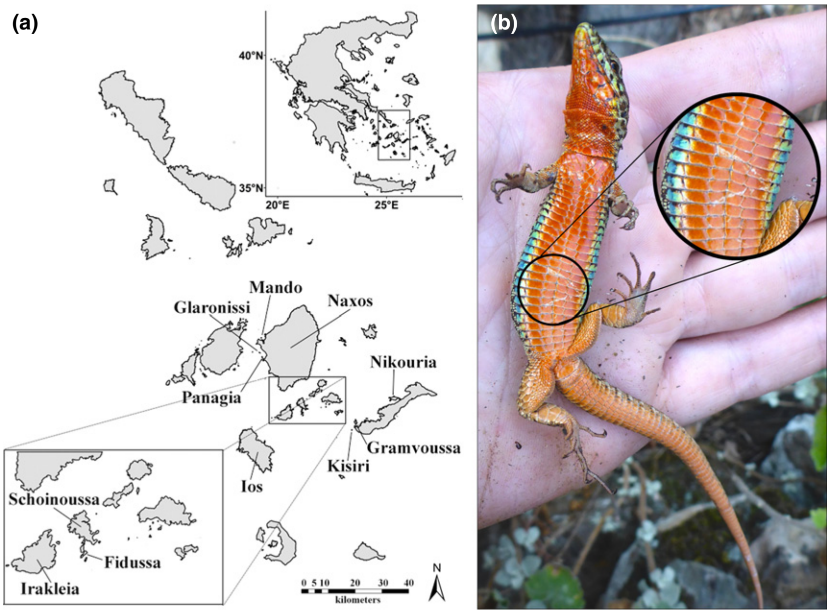

Fig. 1. (a) A map of Greece (top right inset), the Greek Cyclades and the small Cyclade islands (bottom left inset), where this research was conducted. In all, 11 islands were sampled: Fidussa, Glaronissi, Gramvoussa, Ios, Irakleia, Kisiri, Mando, Naxos, Nikouria, Panagia and Schoinoussa. (b) A male *P. erhardii* with a characteristic ventral bite scar caused by intraspecific aggression. This individual is also missing a toe on its front right foot.

and mild, wet winters. Human land use has left an indelible mark on the large islands with a widespread network of drystone walls and terraces dominating landscape structure. Free-ranging goats and sheep also significantly impact the characteristic Mediterranean phrygana/maquis vegetation: evergreen or summer-deciduous, dwarf, spinose, scrub with additional aromatic forbs. Smaller islands less frequently have built structures, but often host small populations of goats left unattended by local landowners, causing vegetation communities to resemble other heavily grazed areas on larger islands (Pafilis *et al.* 2013).

Podarcis erhardii (Fig. 1b) is a medium-sized [snout-to-vent length (SVL) 49–78 mm] lizard that is widely distributed in the southern Balkan Peninsula (Valakos *et al.* 2008). *Podarcis erhardii* is a generalist predator of arthropods, most often consuming prey around 5 mm in length (Valakos 1986), but it is also known to eat snails and insect larvae (Adamopoulou, Valakos & Pafilis 1999). Previous studies have suggested its diet is largely devoid of plant material (Valakos 1986; Adamopoulou, Valakos & Pafilis 1999) in contrast to other Mediterranean *Podarcis* species, though some frugivory has previously been observed (Brock, Donihue & Pafilis 2014).

MORPHOLOGICAL AND PERFORMANCE ANALYSES

During the summer of 2014 (20 May through 10 June), we captured at least eight males and females from each of the study's 11 islands (Fig. 1a, Table A1, Supporting information). We measured lizard mass, body size (snout-to-vent length), head length (snout tip to back of parietal scale), width (at widest point, including soft tissue), height (at back of parietal scale) and jaw length (between tip of the lower jaw to the point of articulation between jaws). All length measures were taken using digital calipers (Frankford Arsenal Electronic Dial Calipers) and mass measurements with a spring scale (Pesola LightLine 50 g × 0·5 g). Additionally, we counted the number of bite scars on the body of the lizard, the number of toes missing and the condition of the tail. Intraspecific bite scars are easily distinguishable from scars inflicted by predators due to their shape and size (Fig. 1b). We counted the number of bite scars on the entire body from head to tail and all four legs, and disregarded any scarring that was not obviously caused by a conspecific. Aggressive encounters between lizards can also result in toe amputation (Vervust *et al.* 2009). We counted a toe as 'missing' if any part of the digit was fully amputated, but did not count toes that were intact, albeit damaged or scarred. Tail breaks, while usually studied in relation to predation (Pafilis *et al.* 2009; Brock *et al.* 2014; Li *et al.* 2014), can also occur in skirmishes between lizards (Bateman & Fleming 2009; Deem & Hedman 2014), and so, in tandem with bite scars and toe amputation rates can give a sense of the competitive landscape experienced by the lizard, particularly on predator-free islands. Because frequency of these physical scars can also be related to age (Brown & Ruby 1977), only adult (>50 mm SVL) males and females were used.

Using a purpose-built bite force metre composed of metal biting plates connected to a Kistler force transducer (type 9203; Kistler Inc., Switzerland), and pivoting over a microcaliper fulcrum (see Herrel *et al.* 1999 for full description), we recorded bite force of each lizard in three repeated trials. The metal bite plates were always placed in the lizards' mouth in-line with the lizard, visually standardizing the bite position on the plate. Thus, the lizard consistently bit with the front of its mouth as plate positioning can affect bite performance (Lappin & Jones 2014). The distance between the bite plates was set to 3·5 mm, but this distance varied by as much as 0·2 mm following routine reassembly of the apparatus or particularly strong bites. Because bite plate distance can significantly affect the force the lizard can exert (Herrel *et al.* 1999), we recorded this distance before each trial and used this measurement as a covariate in all bite force analyses. Additionally, within 3 h of capture, each lizard's stomach was flushed with water through a ball-tipped syringe until the contents of the stomach were regurgitated (Herrel *et al.* 2006). These stomach contents were saved in individual tubes of ethanol for subsequent identification and analysis.

ECOLOGICAL COMMUNITY MEASURES

We conducted four line transects on the apex of each study island in cardinal directions to estimate lizard population density. Each transect was 50 m long and was walked by the same investigator (KMB) to control for biases in searching speed. All lizards within 3 m of either side of the transect line were counted, and in this way, a comparable approximate measure of density within a 1200 m^2 area was calculated. On our smallest island, Panagia, repeated transects risked double-counting individuals, and so only three transects were used. Transect counts were performed at the same time as lizard capture within the regular morning lizard activity period (09.00–11.00 h) and during good weather conditions (27–29 °C, sunny and no clouds) with minimal wind (<2 Beaufort).

Additionally, on each island, eight pitfall and sticky insect trap pairs were arrayed within the area we were capturing lizards. Pitfall traps were approximately 5 cm in diameter and 10 cm deep, and filled with 2 cm of antifreeze. Sticky traps were 7·6 cm by 12·7 cm and were set on 30-cm stakes over the pitfall traps. These traps were left for 48 h to sample the insect community available to the lizards. All insects collected in sticky traps or pitfall traps were assigned a hardness index (hard, medium, soft) according to Herrel *et al.* (1999, 2006; see Table C1 for assignations). Using the hardness indices for each trap, we then calculated the proportion of each prey category for each island in order to control for anticipated differences in insect abundance relative to island size or to minor variations in weather conditions during trapping.

The lizard stomach contents were identified with the aid of a dissecting microscope in October and November 2014. Each bolus was searched, and every component was identified to insect order, invertebrate type (gastropod, pseudoscorpion, tick, etc.) or plant structure (stem, leaf, flower, etc.; see Table C1 for complete list of found stomach contents).

STATISTICAL ANALYSES

Because island size varied over five orders of magnitude, island area was natural log-transformed for all analyses. Direct interisland comparisons of body size were calculated by regressing the island population's mean (to avoid pseudoreplication), against the transformed island area. Variability in head morphological traits and bite force was tested using generalized linear models (GLMs). For each model, all interactions were initially tested and non-significant terms were iteratively removed until the final model contained only significant predictors of the response variable. Diet analyses were conducted on summed hardness indexes calculated both for each individual and averaged among a population. We arcsin-transformed the diet proportion data before analysing them. The same assignations, transformations and analyses were performed on the sticky and pitfall trap data to calculate the availability of different prey hardness types across islands of different sizes. Individual plant parts were sometimes difficult to distinguish and count in the lizard stomach contents, and so we analysed herbivory using logistic regression on the presence or absence of plant material in the gut. All analyses of aggressive proxies were calculated with simple linear regressions using island area or lizard density as independent variables. All analyses were conducted in JMP 10.0.0 (© 2012; SAS Institute Inc., Cary, NC, USA).

Results

MORPHOLOGY AND PERFORMANCE ACROSS THE CYCLADES

We found a significant relationship between mean adult lizard body size and island area; on average, lizards were larger on smaller islands (R^2 adj: 0·34, P = 0·036, n = 11, d.f. = 9). When we analysed this relationship for each sex independently (Fig. 2), we found females were larger on small islands (R^2 adj: 0·40, P = 0·022, n = 11, d.f. = 9), while males trended in the same direction (R^2 adj: 0·25, P = 0·067, n = 11, d.f. = 9).

This pattern in body size was mirrored by head morphology. Generalized linear models incorporating sex and island area explained significant variation in lizard head length (R^2 adj: 0·62, P < 0·0001, n = 345, d.f. = 342), head width (R^2 adj: 0·54, P < 0·0001, n = 345, d.f. = 342), head height (R^2 adj: 0·50, P < 0·0001, n = 345, d.f. = 342) and jaw length (R^2 adj: 0·48, P < 0·0001, n = 345, d.f. = 342; Table B1). All head metrics were larger among small-island populations. We then asked whether lizard head shape differed between islands, that is lizard head size standardized by incorporating body size in the GLM. We found that only head height varied proportionally with island area – lizards had relatively taller heads on small islands (R^2 adj: 0·70, P < 0·0001, n = 345, d.f. = 340; Table B2).

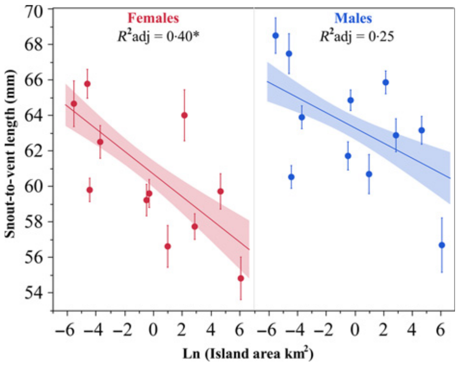

Fig. 2. The relationship between lizard body size and island area for both females (red) and males (blue). Each point represents a population average with standard error bars. Line of best fit added with 95% confidence shaded in same colour, and adjusted R^2 displayed for each relationship. Generally, both males and females are larger on small islands and the female relationship was significant at the P < 0·05 threshold, denoted by '*'.

Head shape significantly affected bite force in these lizards. In GLMs incorporating head morphometric, sex, SVL and bite plate distance, all four head measurements significantly informed variability in maximum bite force (Table B3). Furthermore, maximum bite capacity significantly increased among small-island populations even accounting for interisland variability in SVL (R^2 adj: 0·723, P < 0·0001, n = 339, d.f. = 331; Table 1). While bite plate distance did not itself significantly inform variability in bite force, we did find bite force was significantly related through interactions between SVL and bite plate distance and island area and bite plate distance (Table 1).

BITE FORCE AND DIET

One of our hypothesized drivers of bite force is diet. After categorizing the flushed contents of lizard stomachs from all islands, we found lizards with a harder bite force generally had consumed a higher proportion of hard diet items (P = 0·0037, d.f. = 246) and lower proportion of soft items (P = 0·032, d.f. = 246). However, bite force explained very little of the variability in these prey types between individuals (hard: R^2 adj: 0·029; soft: R^2 adj: 0·015). Bite force was not related to the per cent of medium-hardness diet items (R^2 adj: 0·002, P = 0·223, d.f. = 246). We discovered

Table 1. Factors affecting maximum bite force across islands

	Estimate	*t* Ratio	$P > \|t\|$
Intercept	−13·753	−6·8	<0·0001
Sex (F)	−2·283	−21·19	<0·0001
SVL	0·322	13·32	<0·0001
Ln (Island area)	−0·069	2·25	0·0249
Bite plate distance	0·669	1·26	0·2082
Sex (F) × SVL	−0·127	−5·96	<0·0001
Ln (Island area) × bite plate distance	0·348	2·23	0·0266
SVL × bite plate distance	−0·149	−2·18	0·0299

Maximum bite force in *P. erhardii* varies with island area, even when taking into account differences in body size between islands. We also found significant interactions between sex and body size, reflecting relative differences in the bite capacity of the two sexes; island area and bite plate distances that reflect differences in the metre between sampling days (see Discussion); and between body size and bite plate distance reflecting the bite force advantage of larger-bodied individuals. The total R^2 of the model was 0·723, incorporating 339 observations with 331 degrees of freedom.
SVL, snout-to-vent length.

a significant negative relationship between per cent of medium-hardness prey items and SVL (R^2 adj: 0·0135, P = 0·0369, d.f. = 246); however, once again body size explained relatively little of the variation in diet. Per cent hard or soft prey items were not related to lizard body size (hard: R^2 adj:−0·001, P = 0·41, d.f. = 246; soft: R^2 adj:−0·0003, P = 0·33, d.f. = 246).

Comparing populations between islands, we discovered significant differences in the average proportion of hard (P < 0·0001, d.f. = 9), medium (P = 0·0003, d.f. = 9) and soft (P < 0·0001, d.f. = 9) prey items consumed by lizards on different islands and by the two sexes. These differences were confirmed using Tukey's HSD test for multiple comparisons (Table C2). However, these population-specific differences in diet hardness were not explained by island area in a simple linear regression (%hard prey: R^2 adj: −0·07, P = 0·53, n = 10, d.f. = 8; %medium prey: R^2 adj: −0·08, P = 0·60, n = 10, d.f. = 8; %soft prey: R^2 adj: −0·07, P = 0·55, n = 10, d.f. = 8; Fig. 3). Finally, we found no relationship between island area and likelihood of plant material in the lizards' stomach contents (R^2 adj: −0·0004, P = 0·34, n = 248, d.f. = 246). However, in contrast to previous studies of this species, we did find higher than expected incidence of herbivory; there was plant material in the stomachs of 40 (approximately 16%) of our study lizards.

DIET AVAILABILITY BETWEEN ISLANDS

We also tested whether there were any differences in the hardness of the available prey between islands. The relative hardness of insects collected did not vary between islands of different sizes for either survey method – pitfall (%hard prey: R^2 adj: −0·11, P = 0·74, d.f. = 9; %medium prey: R^2 adj: −0·09, P = 0·61, d.f. = 9; %soft prey: R^2 adj: 0·07, P = 0·23, d.f. = 9) or sticky trap (%hard prey: R^2 adj: −0·03, P = 0·42, d.f. = 9; %medium prey: R^2 adj: 0·32, P = 0·051, d.f. = 9; %soft prey: R^2 adj: −0·02, P = 0·30, d.f. = 9). Furthermore, there was no relationship between the proportion of items belonging to each hardness class in the stomachs of the lizards and the average proportion of that hardness class found in pitfall (%hard prey: R^2 adj: 0·07, P = 0·23, d.f. = 246, %medium prey: R^2 adj: −0·08, P = 0·56, d.f. = 246; %soft prey: R^2 adj: −0·09, P = 0·65, d.f. = 246) or sticky traps (%hard prey: R^2 adj: 0·03, P = 0·29, d.f. = 246, %medium prey: R^2 adj: 0·06, P = 0·23, d.f. = 246; %soft prey: R^2 adj: 0·04, P = 0·28, d.f. = 246).

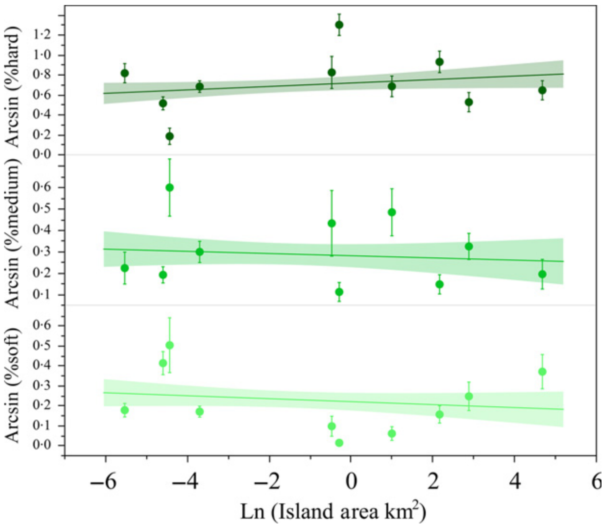

Fig. 3. The proportion of insects of each hardness class, arcsin-transformed, and related to island area with simple linear regression. Each point represents the average proportion of diet items of that hardness class in the stomachs of the lizards. Standard error bars have been added. Best-fit lines were added and shaded regions reflect 95% confidence intervals. Generally, we found no significant trends in the hardness of prey items across islands of different sizes. For more further analysis comparing the means for each island and each hardness category, see Appendix S3.

BITE FORCE AND INTRASPECIFIC INTERACTIONS

If intraspecific aggression and competition were more intense in small-island contexts, stronger bite forces would be advantageous. We tested whether several proxies of intraspecific aggression were more prevalent on smaller islands and whether any were related to bite force. First, we found a strong relationship between lizard density and island area; lizard densities were highest on small islands (R^2 adj: 0·39, P = 0·03, d.f. = 8; Fig. 4a). We also found that the average number of conspecific bite scars per individual was significantly higher on small islands (R^2 adj: 0·68, P = 0·002, d.f. = 8) and at high lizard densities (R^2 adj: 0·38, P = 0·045, d.f. = 8; Fig. 4b). The per cent of lizards with missing digits on each island followed the same trend: marginally higher rates on small islands (R^2 adj: 0·30, P = 0·058, d.f. = 8) and significantly higher rates on densely populated

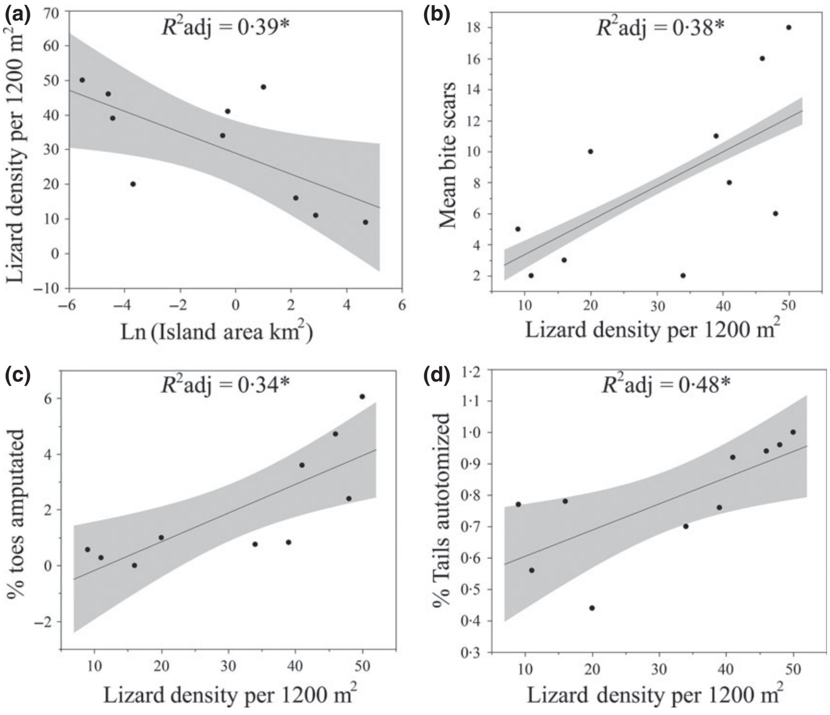

Fig. 4. A suite of linear regressions showing the relationships between (a) lizard density per 1200 m^2 and island area, (b) mean bite scars and lizard density, (c) per cent of the population's amputated toes and lizard density, and (d) broken tails and lizard density. Each point represents a population. For all figures, a line of best fit has been included with a 95% confidence interval shaded around it, and the adjusted R^2 value of the relationship has been presented. A '*' reflects significant relationships ($P < 0{\cdot}05$). We found that lizard density is significantly higher on small islands. Furthermore, we found that as lizard density increased, the mean number of bite scars and the per cent of the toes amputated and tails broken also increased significantly.

islands (R^2 adj: 0·34, $P = 0{\cdot}045$, d.f. = 8; Fig. 4c). Finally, while rates of tail loss were not explained by island area (R^2 adj: −0·08, $P = 0{\cdot}60$, d.f. = 8), they showed a strong positive relationship with lizard density (R^2 adj: 0·48, $P = 0{\cdot}016$, d.f. = 8; Fig. 4d).

We found that bite force was significantly related to a suite of these proxies of intraspecific aggression. The number of bite scars on an individual was positively related to its maximum bite capacity (R^2 adj: 0·251, $P < 0{\cdot}0001$, $n = 245$, d.f. = 236; Table 2). Similarly, the number of digits missing from a lizard increased significantly with the lizard's bite force (R^2 adj: 0·101, $P < 0{\cdot}0001$, $n = 245$, d.f. = 240; Table 2). We did not, however, find a relationship between bite force and the rates of tail breaks ($P = 0{\cdot}42$, d.f. = 240). We found a strong quadratic relationship between maximum bite force and lizard density. The maximum bite force of both males and females peaked at very low and very high lizard densities (males: R^2 adj: 0·178, $P < 0{\cdot}0001$, $n = 138$, d.f. = 136, females: R^2 adj: 0·04, $P < 0{\cdot}0364$, $n = 107$, d.f. = 105) though the significant relationship for females explained relatively little of the variability in bite force.

Finally, we directly tested whether intraspecific bite scars, toe amputations and tail breaks increased among individuals with high bite force on small islands. Specifically, in a GLM relating island area, bite force, bite plate distance and sex, we found that both bite scars and missing toes increased with bite force and decreasing island area (bite scars: R^2 adj: 0·47, $P < 0{\cdot}0001$, $n = 245$, d.f. = 240; missing toes: R^2 adj: 0·15, $P < 0{\cdot}0001$, $n = 245$, d.f. = 240; Table B4). Bite capacity, controlling for island

Table 2. Relationships between intraspecific competition proxies and lizard bite force

	Estimate	*t* Ratio	$P > \lvert t \rvert$	Model R^2	N (d.f.)
Bite scars				0·251	245 (236)
Intercept	52·8593	8·03	<0·0001		
Sex (F)	3·1533	5·27	<0·0001		
Bite force	0·8052	4·69	<0·0001		
Bite plate distance	−15·0161	−7·58	<0·0001		
Sex (F) × bite force	0·3395	1·98	0·0491		
Sex (F) × bite plate distance	−6·8195	−3·41	0·0008		
Bite force × bite plate distance	−1·6905	−3·47	0·0006		
Sex (F) × SVL	−0·0318	−4·95	<0·0001		
SVL	0·1204	18·71	<0·0001		
Missing digits				0·101	245 (240)
Intercept	2·2516	2·56	0·011		
Sex (F)	0·1523	2·08	0·0387		
Bite force	0·0974	4·75	<0·0001		
Bite plate distance	−0·8045	−3·03	0·0027		
Bite force × bite plate distance	−0·1409	−2·36	0·0193		

Both the number of bite scars and the number of missing toes were significantly related to the bite force of those individuals; generally, individuals with a stronger bite force had suffered more scars and amputated toes.

area effects, did not, however, significantly inform tail breaks ($P = 0{\cdot}22$, d.f. = 240; Table B4).

Discussion

We tested whether a suite of morphological traits and an associated performance trait, bite force, varied across islands of different sizes in the Greek Cyclades. We found that lizard body and head size were significantly larger among small-island populations than they were among lizards living on large islands. These small-island lizards had stronger bites, even after taking into account the significant differences in body size between populations on different islands. We then investigated two hypothesized drivers of these bite force differences. Contrary to predictions of a diet-driven hypothesis, we found no relationship between island area and the proportion of hard prey in the lizards' diet. Instead, we found that measures of intraspecific aggression dramatically increased on small islands and closely followed the observed pattern in bite force. This has led us to conclude that, while bite force does affect lizard diet, the interisland pattern in bite force observed in *P. erhardii* is more closely tied to the intense intraspecific aggression experienced on small Mediterranean islands.

MORPHOLOGY AND BITE FORCE VARIES WITH ISLAND AREA

Examples of body size differences among insular populations relative to continental conspecifics are well documented (Lomolino 1985, 2005). In accordance with the predictions of the island rule, we found that on smaller islands, the body size of *P. erhardii* was larger (Fig. 2). Closely tracking the body size trends, we found that head size also increased on small islands and that head height, when accounting for differences in body size, was proportionately larger on smaller islands. In accordance with a bite force study on the closely related *Podarcis melisellensis* (Huyghe *et al.* 2009), we found that head height was a good predictor of bite force in *P. erhardii* (Table B3). Overall, bite force was significantly stronger among small-island populations, even after accounting for differences in body size.

In our GLM analysis of bite force, we found two significant interaction effects that warrant specific discussion (Table 1). The bite force metre was routinely built and disassembled between sites, and so bite plate distance sometimes varied ($3{\cdot}5 \pm 0{\cdot}2$ mm). Larger animals can bite harder at larger bite plate distances due to their relatively lower gape angle (Herrel, Aerts & De Vree 1998; Dumont & Herrel 2003) and so had slightly harder bites when bite plate distance was larger. The bite plate distance also significantly varied with island area because it was disassembled between island visits and reassembled on each sampling day. Thus, the bite plate distance by island area interaction is actually a proxy for day-to-day changes in the tool, not an island area effect *per se*.

DIET CHANGES DO NOT EXPLAIN INTERISLAND DIFFERENCES IN BITE FORCE

The island rule would suggest that this trend towards larger bodies on small islands may be explained by the documented release of *P. erhardii* from predation by the primary snake and mammal predators of the lizard (Brock *et al.* 2014; Li *et al.* 2014) and the subsequent capitalization on food sources (Case 1978; Lomolino 1985, 2005; Pafilis *et al.* 2009). Lending further credence to this hypothesis, differences in lizard head size and maximum bite force are often associated with populations capitalizing on harder food items, including plants, in small-island systems (Herrel, Vanhooydonck & Van Damme 2004; Herrel *et al.* 2008; Herrel & De Vree 2009).

Our direct test of this hypothesis with investigation of the stomach contents of the study lizards, however, revealed no differences in the hardness of diet items along this island size gradient (Fig. 3). While we did find that lizard populations from different islands had significantly different proportions of hard, soft and intermediate prey items (Table C2), these differences were not explained by island area and did not track the interisland trend in bite force. We did find that lizards with harder bites tended to have more hard diet items in their stomachs; however, this relationship is weak (R^2 adj = $0{\cdot}0135$) reflecting high variability between individuals. Our test of whether the availability of different prey hardness classes varied between islands of different sizes also revealed no significant patterns for sticky or pitfall insect traps. Interestingly, there was very little relationship between the proportion of ingested insects of each hardness class and the availability of insects sampled with either pitfall or sticky traps. This suggests that the lizards are foraging selectively (Lo Cascio & Capula 2011), rather than being strict generalists as often assumed.

It is possible that because our diet analyses were conducted in the relatively productive season of the year, a bottleneck of hard prey at another point in the season could drive these patterns in bite force. We think, however, that this is not the case. While Valakos (1986) found *P. erhardii* diets do change month-to-month, the proportion of the hardest taxa, gastropods and coleopterans, remained consistent throughout the lizards' high-activity months, March through July, when nutritional quality is of most importance for mate competition and egg growth (Valakos 1986; Diego-Rasilla & Pérez-Mellado 2000).

INTRASPECIFIC AGGRESSION INCREASES ON SMALL ISLANDS, SO MAXIMIZING BITE FORCE IS ADVANTAGEOUS

Instead, our data suggest that the observed differences in morphology and performance are due to the necessity for aggressively defending valuable resources on small islands. While lizard bite force is often related to feeding ecology (Herrel *et al.* 1999, 2001; Verwaijen, Van Damme & Herrel

2002), it has also been linked to fighting ability (Lailvaux *et al*. 2004; Huyghe, Vanhooydonck & Scheers 2005; Lailvaux & Irschick 2007). While fully reciprocal fighting bouts to test aggression and dominance were not feasible for this study, we used a suite of proxies for the competitive environment that support the pattern found elsewhere that lizard aggression increases on insular systems (Pafilis *et al*. 2009; Vervust *et al*. 2009; Cooper, Dimopoulos & Pafilis 2014). We found that bite scars on the lizards increased dramatically on small islands and among lizards with stronger bites for both males and females. We also found rates of toe amputation were highest on these small islands and among lizards with the strongest bite force. Interestingly, the relationship between lizard density and bite force was quadratic with highest bite forces found among very low- and high-density populations. This trend may reflect the need at high population densities to protect resources and territories and at low densities to protect access to mates, though more specific experiments will be needed to test this prediction. Finally, rates of broken tails were by far highest in high-density populations, which tend to be small islands, in accordance with previously published data on the same trend (Brock *et al*. 2014). Because these small islands are lizard-predator-free, Brock *et al*. (2014) found a significantly lower proportion of lizards shed their tails when standardized force was applied. A stronger bite force would then be needed and advantageous for inflicting this kind of bout-ending damage. Furthermore, the potential for cannibalizing the tail (Deem & Hedman 2014) of a competitor could provide a secondary nutritional benefit to having a bite strong enough to remove the tail from a competitor. The relationship between tail breaks and island area was not significant (Fig. 4b) largely because of an outlier (−3·68, 0·44). This island, Mando, was previously sampled by Brock *et al*. (2014) and 80% of the lizards they sampled had broken tails. Their finding – twice our observed rate – was in line with the trend predicted and observed across the other 10 islands used in this study.

Using the occurrence of tail breaks as a metric of predation or competition pressure has been debated (reviewed in Bateman & Fleming 2009). Thus, we acknowledge that it is impossible to know the exact cause of the tail break – predator, intraspecific aggressor or otherwise. Nonetheless, because the small islands driving the pattern do not host any lizard predators (Brock *et al*. 2014), we are confident that most if not all of the broken tails are the result of intraspecific aggression. The accumulation of wounds and scars is also directly related to age of the individual (Brown & Ruby 1977). It is possible then that this trend for higher scarring rates is due to longer survival in predator-free island environments. While skeletal chronology (Patnaik & Behera 1981; El Mouden, Znari & Brown 1999) has not been conducted on these populations to conclusively determine their age structure, we have no reason to suspect our random sample of individuals from each population resulted in an age bias.

Conclusions

While island ecologies consistently differ from continental settings in predictable ways (MacArthur & Wilson 1967), this binary comparison is only part of the story; islands are highly variable in nutrients, productivity and species composition. Archipelagos provide valuable opportunities to test hypotheses on the relative impact different island contexts have on their inhabitants (Lomolino 2005). Because productivity and species composition are consistently related to island size (MacArthur & Wilson 1967; Losos & Ricklefs 2009), we used this gradient as a proxy for the different island conditions experienced by *P. erhardii* and driving differences in an important functional trait, maximum bite capacity. These two drivers are not mutually exclusive though and, likely, there are multiple benefits to stronger bites.

Our results suggest the intriguing possibility that the observed changes in this functional trait (*sensu* Violle *et al*. 2007; Schmitz *et al*. 2015) could feed back to influence the dynamics of the system as a whole. These eco-evolutionary feedbacks (Post & Palkovacs 2009; Schoener 2011) are largely undiscussed in island rule literature, but may play an important role in insular ecologies. Prime examples for study with this lens include the finch beaks in the Galapagos (Grant & Grant 1993, 1995) and *Anolis* lizards in the Caribbean (Spiller & Schoener 1994; Schoener & Spiller 1999). We believe more work along this line of inquiry will be productive in the future.

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Data accessibility

All data used for this work are archived and available on the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.65tt7 (Donihue *et al*. 2015).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Appendix S1. Island characteristics.

Table A1. Island area and lizards captured.

Appendix S2. Statistical output of inter-island morphometric analyses.

Table B1. Inter-island differences in head morphometrics.

Table B2. Proportional differences in head morphometrics across islands.

Table B3. Head shape predicts bite force.

Table B4. Competition proxies relative to bite force and island area.

Appendix S3. *Podarcis erhardii* stomach contents and their hardness.

Table C1. Animal and plant material found in *P. erhardii* stomachs.

Table C2. Diet hardness differences between islands.