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7 **Feed or fight: Testing the impact of food availability and intraspecific**
8 **aggression on the functional ecology of an island lizard**

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19
20 **Summary**

- 21 1. Body size often varies among insular populations relative to continental
22 conspecifics – the “island rule” – and functional, context-dependent
23 morphological differences tend to track this body size variation on islands.
24 2. Two hypotheses are often proposed as potential drivers of insular population
25 differences in morphology: one relating to diet, and the other involving intra-
26 specific competition and aggression. We directly tested whether differences in
27 morphology and maximum bite capacity were explained by inter-island changes

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28 in hardness of both available as well as consumed prey, and levels of lizard-to-
29 lizard aggression among small-island populations.

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

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

36 5. This pattern in morphology and performance was not related to differences in
37 diet, but was highly correlated with proxies of intra-specific aggression – bite
38 scars and missing toes.

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

42

43

44 **Key-words:** Greece, Cyclade islands, island rule, *Podarcis erhardii*, bite force, intra-
45 specific aggression, diet

46

47 **Introduction**

48 Extreme body size, shape, and performance differences among insular
49 populations relative to continental populations of the same species have been documented
50 in a number of cases – pygmy pachyderms in the Mediterranean and gigantic Galapagos
51 tortoises among them (Case 1978; Lomolino 1985; Sondaar 1986; Hayes et al. 1988;
52 Jaffe, Slater, & Alfaro 2011, Sagonas et al. 2014). However, whether this ‘island rule’
53 can be generalized across taxa and conditions is very much in question (Lomolino 2005;
54 Meiri, Cooper, & Purvis 2008), particularly for reptiles (Meiri, Dayan, & Simberloff
55 2006; Meiri 2008; Itescu et al. 2014).

56 Studies testing the island rule typically invoke a trophic explanation (energetics
57 and diet selection) as the basis for changes in body morphology following a species’
58 arrival to an island (Van Valen 1965; Roughgarden 1972; Lister 1976; Case 1978;

59 Lomolino 1985). The rationale is that selection will favor convergence on a new optimal
60 phenotype for efficient resource acquisition in the new insular environment (Lomolino
61 1985). Thus, relative to mainland populations of the same or closely related species,
62 small- to medium-sized vertebrate species will tend to become larger on islands to benefit
63 from metabolic efficiencies, while large vertebrate species will tend to become smaller to
64 capitalize on limited food resources (Case 1978; Lomolino 1985). This pattern has been
65 demonstrated, for example, among species of non-volant mammals (Lomolino 1985),
66 snakes (Boback and Guyer 2003), and birds (Clegg and Owens 2002).

67 Yet, alternative, non-trophic explanations for the island-rule pattern have also
68 been advanced. Larger body size of some island populations may reflect the island
69 colonizer's need for robust morphology to reach the island in the first place (Lomolino
70 2005). Or, insular populations may experience a shift in the nature of the interactions that
71 determine selection for different body morphologies, such as a release from predation or
72 a shift from predominantly inter-specific competition on mainland to intra-specific
73 pressure on islands (Case 1978; Lomolino 1985; Lomolino et al. 2005; Pafilis et al.
74 2009). However, to our knowledge these alternative trophic and non-trophic explanations
75 have never been simultaneously tested. Our study examines the relative contribution of
76 these two mechanisms to variability in morphology and performance in the lizard
77 *Podarcis erhardii* (Werner 1930), making use of the Greek Cyclades as a natural
78 experimental laboratory.

79 Archipelagos provide unique settings for natural experiments aimed at comparing
80 the relative impacts of ecological contexts on a species' traits. Biogeography theory
81 predicts that as islands get smaller, and more remote, species diversity and overall
82 biomass will decrease (McArthur & Wilson 1967). Large vertebrates, particularly
83 carnivores, are lost first as island area decreases (MacArthur & Wilson 1967). The lack of
84 top predators on small islands is known to release meso-predators (Blumstein 2002) –
85 including lizards – enabling higher densities on small predator-free islands (Perez-
86 Mellado & Corti 1993; Buckley & Jetz 2007; Pafilis et al. 2009). Agonistic behavior in
87 lizards is correlated with increased competition for food, territory, mates, and other
88 resources (Diego-Rasilla & Pérez-Mellado 2000; Vervust et al. 2009). Thus, life on small
89 islands can drive high rates of intra-specific aggression (Pafilis et al. 2009; Brock et al.

90 2014a), resulting in bite scars (Vitt & Cooper 1985; Gillingham, Carmichael, & Miller
91 1995; Jennings and Thompson 1999), amputation of toes (Vervust et al. 2009), tail
92 shedding (Brock et al. 2014a), and even cannibalism (Pafilis et al. 2009; Cooper Jr,
93 Dimopoulos, & Pafilis 2014; Deem & Hedman 2014).

94 Mediterranean islands – many smaller than 1 km² – with very little food or shelter
95 from the hot, dry, and windy summers, can be harsh environments for lizards. We then
96 expect that lizards living in different island contexts would be locally adapted to
97 maximize their fitness in those conditions. Indeed, numerous studies have shown that
98 lizards living on islands display a host of morphological (Huyghe, Vanhooydonck, &
99 Scheers 2005; Sagonas et al. 2014), performance (Vervust, Grbac, & Van Damme 2007;
100 Pafilis, Foufopoulos, & Poulakakis 2007; Pafilis et al. 2009), and behavioral (Cooper &
101 Perez-Mellado 2012; Cooper et al. 2014) differences relative to mainland populations,
102 and even populations on larger islands (Runemark et al. 2010; Pafilis et al. 2011; Brock
103 et al. 2014a).

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

112 A lizard's bite capacity is directly related to its ability to acquire and protect
113 valuable resources – food, shelter, and mates (Verwajen, Van Damme, & Herrel 2002;
114 Lailvaux et al. 2004; Huyghe et al. 2005). Maximum bite force varies considerably
115 between lizard species (Herrel et al. 2001; Herrel et al. 2004), but can also vary within a
116 species (Huyghe et al. 2005; Brecko et al. 2008), and in different ecological contexts
117 (Sagonas et al. 2014). This intra-specific variation in bite force is often attributed either to
118 dietary (trophic) or behavioral (non-trophic) differences between populations.

119 Proportionally stronger bite forces on small islands, for example, may enable a more
120 herbivorous diet (Herrel et al. 2004; Herrel et al. 2008; Herrel & DeVree 2009), or access

121 to heavily-defended (hard body) prey items like beetles with strong elytra or snails with
122 shells (Herrel et al. 1999; Herrel et al. 2001; Verwajen et al. 2002). Alternatively,
123 stronger bite forces on small islands may correspond to higher intra-specific aggression
124 and competition (Lailvaux et al. 2004; Huyghe et al. 2005; Lailvaux & Irschick 2007).

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

135

136 **Materials and methods**

137 *Study sites and species*

138 We conducted our study on 11 islands in the Greek Cyclades ranging in size from
139 0.004 km² to over 400 km² (Fig. 1A). During the last glacial maximum, these islands
140 were connected in a large cluster – ‘Cycladia’ – and in the ensuing 10,000 years have
141 become isolated in a known fragmentation sequence calculated using bathymetry data
142 and historical sea-level rise (Foufopoulos & Ives 1999). All islands in the study are
143 within 50 km of each other and experience very similar climate conditions: warm, dry
144 summers and mild, wet winters. Human land use has left an indelible mark on the large
145 islands with a widespread network of dry-stone walls and terraces dominating landscape
146 structure. Free-ranging goats and sheep also significantly impact the characteristic
147 Mediterranean phrygana/maquis vegetation: evergreen or summer-deciduous, dwarf,
148 spinose, scrub with additional aromatic forbs. Smaller islands less frequently have built
149 structures, but often host small populations of goats left unattended by local landowners,
150 causing vegetation communities to resemble other heavily-grazed areas on larger islands
151 (Pafilis et al. 2013).

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

160

161 *Morphological and performance analyses*

162 During the summer of 2014 (20 May through 10 June), we captured at least 8
163 males and females from each of the study's 11 islands (Fig. 1A, Table A1). We measured
164 lizard mass, body size (snout-to-vent length – SVL), head length (snout tip to back of
165 parietal scale), width (at widest point, including soft tissue), height (at back of parietal
166 scale), and jaw length (between tip of the lower jaw to the point of articulation between
167 jaws). All length measures were taken using digital calipers (Frankford Arsenal
168 Electronic Dial Calipers) and mass measurements with a spring scale (Pesola LightLine
169 50g x 0.5g). Additionally, we counted the number of bite scars on the body of the lizard,
170 the number of toes missing, and the condition of the tail. Intra-specific bite scars are
171 easily distinguishable from scars inflicted by predators due to their shape and size (Fig.
172 1B). We counted the number of bite scars on the entire body from head to tail and all four
173 legs, and disregarded any scarring that was not obviously caused by a conspecific.
174 Aggressive encounters between lizards can also result in toe amputation (Vervust et al.
175 2009). We counted a toe as “missing” if any part of the digit was fully amputated; but did
176 not count toes that were intact, albeit damaged or scarred. Tail breaks, while usually
177 studied in relation to predation (Pafilis et al. 2009; Li et al. 2014; Brock et al. 2014a), can
178 also occur in skirmishes between lizards (Bateman and Fleming 2009; Deem & Hedman
179 2014), and so, in tandem with bite scars and toe amputation rates can give a sense of the
180 competitive landscape experienced by the lizard, particularly on predator-free islands.
181 Because frequency of these physical scars can also be related to age (Brown & Ruby
182 1977), only adult (> 50 mm SVL) males and females were used.

183 Using a purpose-built bite force meter composed of metal biting plates connected
184 to a Kistler force transducer (type 9203, Kistler Inc., Switzerland), and pivoting over a
185 microcaliper fulcrum (see Herrel et al. 1999 for full description) we recorded bite force of
186 each lizard in three repeated trials. The metal bite plates were always placed in the
187 lizards' mouth in-line with the lizard, visually standardizing the bite position on the plate.
188 Thus, the lizard consistently bit with the front of its mouth as plate positioning can affect
189 bite performance (Lappin and Jones 2014). The distance between the bite plates was set
190 to 3.5 mm, but this distance varied by as much as 0.2 mm following routine re-assembly
191 of the apparatus or particularly strong bites. Because bite plate distance can significantly
192 affect the force the lizard can exert (Herrel et al. 1999), we recorded this distance before
193 each trial, and used this measurement as a covariate in all bite force analyses.
194 Additionally, within three hours of capture each lizard's stomach was flushed with water
195 through a ball-tipped syringe until the contents of the stomach were regurgitated (Herrel
196 et al. 2006). These stomach contents were saved in individual tubes of ethanol for
197 subsequent identification and analysis.

198

199 *Ecological community measures*

200 We conducted four line transects on the apex of each study island in cardinal directions to
201 estimate lizard population density. Each transect was 50 m long and was walked by the
202 same investigator (KMB) to control for biases in searching speed. All lizards within 3 m
203 of either side of the transect line were counted, and in this way a comparable approximate
204 measure of density within a 1200 m² area was calculated. On our smallest island,
205 Panagia, repeated transects risked double-counting individuals, and so only three
206 transects were used. Transect counts were performed at the same time as lizard capture
207 within the regular morning lizard activity period (0900-1100 hr) and during good weather
208 conditions (27-29 °C, sunny and no clouds) with minimal wind (< 2 Beaufort).

209 Additionally, on each island, eight pitfall and sticky insect trap pairs were arrayed
210 within the area we were capturing lizards. Pitfall traps were approximately 5 cm in
211 diameter and 10 cm deep, and filled with 2 cm of antifreeze. Sticky traps were 7.6 cm by
212 12.7 cm and were set on 30 cm stakes over the pitfall traps. These traps were left for 48
213 hours to sample the insect community available to the lizards. All insects collected in

214 sticky traps or pitfall traps were assigned a hardness index (hard, medium, soft) according
215 to Herrel et al. (1999; 2006; see supplemental Table C1 for assignments). Using the
216 hardness indices for each trap we then calculated the proportion of each prey category for
217 each island in order to control for anticipated differences in insect abundance relative to
218 island size or to minor variations in weather conditions during trapping.

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

224

225 *Statistical analyses*

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

243

244 **Results**

245 *Morphology and performance across the Cyclades*

246 We found a significant relationship between mean adult lizard body size and
247 island area; on average, lizards were larger on smaller islands (R^2 adj: 0.34, $p=0.036$,
248 $n=11$, $df=9$). When we analyzed this relationship for each sex independently (Fig. 2), we
249 found females were larger on small islands (R^2 adj: 0.40, $p=0.022$, $n=11$, $df=9$) while
250 males trended in the same direction (R^2 adj: 0.25, $p=0.067$, $n=11$, $df=9$).

251 ■ This pattern in body size was mirrored by head morphology. Generalized linear
252 models (GLMs) incorporating sex and island area explained significant variation in lizard
253 head length (R^2 adj: 0.62, $p<0.0001$, $n=345$, $df=342$), head width (R^2 adj: 0.54, $p<0.0001$,
254 $n=345$, $df=342$), head height (R^2 adj: 0.50, $p<0.0001$, $n=345$, $df=342$), and jaw length (R^2
255 adj: 0.48, $p<0.0001$, $n=345$, $df=342$; Table B1). All head metrics were larger among
256 small-island populations. We then asked whether lizard head shape differed between
257 islands, that is, lizard head size standardized by incorporating body size in the GLM. We
258 found that only head height varied proportionally with island area – lizards had relatively
259 taller heads on small islands (R^2 adj: 0.70, $p<0.0001$, $n=345$, $df=340$; Table B2).

260 Head shape significantly affected bite force in these lizards. In GLMs
261 incorporating head morphometric, sex, SVL, and bite plate distance, all four head
262 measurements significantly informed variability in maximum bite force (Table B3).
263 Furthermore, maximum bite capacity significantly increased among small-island
264 populations even accounting for inter-island variability in SVL (R^2 adj: 0.723, $p<0.0001$,
265 $n=339$, $df=331$; Table 1). While bite plate distance did not itself significantly inform
266 variability in bite force, we did find bite force was significantly related through
267 interactions between SVL and bite plate distance and island area and bite plate distance
268 (Table 1).

269

270 *Bite force and diet*

271 One of our hypothesized drivers of bite force is diet. After categorizing the flushed
272 contents of lizard stomachs from all islands, we found lizards with a harder bite force
273 generally had consumed a higher proportion of hard diet items ($p=0.0037$, $df=246$) and
274 lower proportion of soft items ($p=0.032$, $df=246$). However, bite force explained very
275 little of the variability in these prey types between individuals (hard: R^2 adj: 0.029; soft:

276 R^2 adj: 0.015). Bite force was not related to the percent of medium-hardness diet items
277 (R^2 adj: 0.002, $p=0.223$, $df=246$). We discovered a significant negative relationship
278 between percent of medium-hardness prey items and SVL (R^2 adj: 0.0135, $p=0.0369$,
279 $df=246$); however, once again body size explained relatively little of the variation in diet.
280 Percent hard or soft prey items were not related to lizard body size (hard: R^2 adj: -0.001,
281 $p=0.41$, $df=246$; soft: R^2 adj: -0.0003, $p=0.33$, $df=246$).

282 ■ Comparing populations between islands, we discovered significant differences in
283 the average proportion of hard ($p<0.0001$, $df=9$), medium ($p=0.0003$, $df=9$), and soft
284 ($p<0.0001$, $df=9$) prey items consumed by lizards on different islands and by the two
285 sexes. These differences were confirmed using Tukey's HSD test for multiple
286 comparisons (Table C2). However, these population-specific differences in diet hardness
287 were not explained by island area in a simple linear regression (%Hard Prey: R^2 adj: -
288 0.07, $p=0.53$, $n=10$, $df=8$; %Medium Prey: R^2 adj: -0.08, $p=0.60$, $n=10$, $df=8$; %Soft
289 Prey: R^2 adj: -0.07, $p=0.55$, $n=10$, $df=8$; Fig. 3). Finally, we found no relationship
290 between island area and likelihood of plant material in the lizards' stomach contents (R^2
291 adj: -0.0004, $p=0.34$, $n=248$, $df=246$). However, in contrast to previous studies of this
292 species we did find higher than expected incidence of herbivory; there was plant material
293 in the stomachs of 40 (approximately 16%) of our study lizards.

294

295 *Diet availability between islands*

296 We also tested whether there were any differences in the hardness of the available
297 prey between islands. The relative hardness of insects collected did not vary between
298 islands of different sizes for either survey method – pitfall (%Hard Prey: R^2 adj: -0.11,
299 $p=0.74$, $df=9$; %Medium Prey: R^2 adj: -0.09, $p=0.61$, $df=9$; %Soft Prey: R^2 adj: 0.07,
300 $p=0.23$, $df=9$) or sticky trap (%Hard Prey: R^2 adj: -0.03, $p=0.42$, $df=9$; %Medium Prey:
301 R^2 adj: 0.32, $p=0.051$, $df=9$; %Soft Prey: R^2 adj: -0.02, $p=0.30$, $df=9$). Furthermore, there
302 was no relationship between the proportion of items belonging to each hardness class in
303 the stomachs of the lizards and the average proportion of that hardness class found in
304 pitfall (%Hard Prey: R^2 adj: 0.07, $p=0.23$, $df=246$, %Medium Prey: R^2 adj: -0.08, $p=0.56$,
305 $df=246$; %Soft Prey: R^2 adj: -0.09, $p=0.65$, $df=246$) or sticky traps (%Hard Prey: R^2 adj:

306 0.03, $p=0.29$, $df=246$, %Medium Prey: R^2 adj: 0.06, $p=0.23$, $df=246$; %Soft Prey: R^2 adj:
307 0.04, $p=0.28$, $df=246$).

308

309 *Bite force and intra-specific interactions*

310 If intra-specific aggression and competition were more intense in small-island
311 contexts, stronger bite forces would be advantageous. We tested whether several proxies
312 of intra-specific aggression were more prevalent on smaller islands and whether any were
313 related to bite force. First, we found a strong relationship between lizard density and
314 island area; lizard densities were highest on small islands (R^2 adj: 0.39, $p=0.03$, $df=8$;
315 Fig. 4A). We also found that the average number of conspecific bite scars per individual
316 was significantly higher on small islands (R^2 adj: 0.68, $p=0.002$, $df=8$), and at high lizard
317 densities (R^2 adj: 0.38, $p=0.045$, $df=8$; Fig. 4B). The percent of lizards with missing
318 digits on each island followed the same trend: marginally higher rates on small islands
319 (R^2 adj: 0.30, $p=0.058$, $df=8$) and significantly higher rates on densely populated islands
320 (R^2 adj: 0.34, $p=0.045$, $df=8$; Fig. 4C). Finally, while rates of tail loss were not explained
321 by island area (R^2 adj: -0.08, $p=0.60$, $df=8$), they showed a strong positive relationship
322 with lizard density (R^2 adj: 0.48, $p=0.016$, $df=8$; Fig. 4D).

323 We found that bite force was significantly related to a suite of these proxies of
324 intra-specific aggression. The number of bite scars on an individual was positively related
325 to its maximum bite capacity (R^2 adj: 0.251, $p<0.0001$, $n=245$, $df=236$; Table 2).
326 Similarly, the number of digits missing from a lizard increased significantly with the
327 lizard's bite force (R^2 adj: 0.101, $p<0.0001$, $n=245$, $df=240$; Table 2). We did not,
328 however, find a relationship between bite force and the rates of tail breaks ($p=0.42$,
329 $df=240$). We found a strong quadratic relationship between maximum bite force and
330 lizard density. The maximum bite force of both males and females peaked at very low
331 and very high lizard densities (males: R^2 adj: 0.178, $p<0.0001$, $n=138$, $df=136$, females:
332 R^2 adj: 0.04, $p<0.0364$, $n=107$, $df=105$) though the significant relationship for females
333 explained relatively little of the variability in bite force.

334 Finally, we directly tested whether intraspecific bite scars, toe amputations, and
335 tail breaks increased among individuals with high bite force on small islands.

336 Specifically, in a GLM relating island area, bite force, bite plate distance, and sex, we

337 found that both bite scars and missing toes increased with bite force and decreasing island
338 area (bite scars: R^2 adj: 0.47, $p < 0.0001$, $n = 245$, $df = 240$; missing toes: R^2 adj: 0.15,
339 $p < 0.0001$, $n = 245$, $df = 240$; Table B4). Bite capacity, controlling for island area effects,
340 did not however significantly inform tail breaks ($p = 0.22$, $df = 240$; Table B4).

341

342 **Discussion**

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

356

357 *Morphology and bite force varies with island area*

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

368 In our GLM analysis of bite force, we found two significant interaction effects
369 that warrant specific discussion (Table 1). The bite force meter was routinely built and
370 disassembled between sites, and so bite plate distance sometimes varied (3.5 ± 0.2 mm).
371 Larger animals can bite harder at larger bite plate distances due to their relatively lower
372 gape angle (Herrel, Aerts & De Vree 1998; Dumont & Herrel 2003) and so had slightly
373 harder bites when bite plate distance was larger. The bite plate distance also significantly
374 varied with island area because it was disassembled between island visits and
375 reassembled on each sampling day. Thus the bite plate distance by island area interaction
376 is actually a proxy for day-to-day changes in the tool, not an island area effect *per se*.

377

378 *Diet changes do not explain inter-island differences in bite force*

379 The island rule would suggest that this trend toward larger bodies on small islands
380 may be explained by the documented release of *P. erhardii* from predation by the
381 primary snake and mammal predators of the lizard (Li et al. 2014; Brock et al. 2014a) and
382 the subsequent capitalization on food sources (Case 1978; Lomolino 1985; Lomolino
383 2005; Pafilis et al. 2009). Lending further credence to this hypothesis, differences in
384 lizard head size and maximum bite force are often associated with populations
385 capitalizing on harder food items, including plants, in small island systems (Herrel et al.
386 2004; Herrel et al. 2008; Herrel & DeVree 2009).

387 Our direct test of this hypothesis with investigation of the stomach contents of the
388 study lizards however revealed no differences in the hardness of diet items along this
389 island size gradient (Fig. 3). While we did find that lizard populations from different
390 islands had significantly different proportions of hard, soft, and intermediate prey items
391 (Table C2), these differences were not explained by island area, and did not track the
392 interisland trend in bite force. We did find that lizards with harder bites tended to have
393 more hard diet items in their stomachs, however this relationship is weak ($R^2_{\text{adj}} =$
394 0.0135) reflecting high variability between individuals. Our test of whether the
395 availability of different prey hardness classes varied between islands of different sizes
396 also revealed no significant patterns for sticky or pitfall insect traps. Interestingly, there
397 was very little relationship between the proportion of ingested insects of each hardness
398 class and the availability of insects sampled with either pitfall or sticky traps. This

399 suggests that the lizards are foraging selectively (Lo Cascio & Capula 2011), rather than
400 being strict generalists as often assumed.

401 It is possible that because our diet analyses were conducted in the relatively
402 productive season of the year, a bottleneck of hard prey at another point in the season
403 could drive these patterns in bite force. We think, however, that this is not the case. While
404 Valakos (1986) found *P. erhardii* diets do change month-to-month, the proportion of the
405 hardest taxa, gastropods and coleopterans, remained consistent throughout the lizards'
406 high-activity months, March through July, when nutritional quality is of most importance
407 for mate competition and egg growth (Valakos 1986; Diego-Rasilla & Pérez-Mellado
408 2000).

409

410 *Intra-specific aggression increases on small islands, so maximizing bite force is*
411 *advantageous*

412 Instead, our data suggest that the observed differences in morphology and
413 performance are due to the necessity for aggressively defending valuable resources on
414 small islands. While lizard bite force is often related to feeding ecology (Herrel et al.
415 1999; Herrel et al. 2001; Verwajen et al. 2002), it has also been linked to fighting ability
416 (Lailvaux et al. 2004; Huyghe et al. 2005; Lailvaux & Irschick 2007). While fully
417 reciprocal fighting bouts to test aggression and dominance were not feasible for this
418 study, we used a suite of proxies for the competitive environment that support the pattern
419 found elsewhere that lizard aggression increases on insular systems (Pafilis et al. 2009;
420 Vervust et al. 2009; Cooper et al. 2014). We found that bite scars on the lizards increased
421 dramatically on small islands and among lizards with stronger bites for both males and
422 females. We also found rates of toe amputation were highest on these small islands and
423 among lizards with the strongest bite force. Interestingly, the relationship between lizard
424 density and bite force was quadratic with highest bite forces found among very low- and
425 high-density populations. This trend may reflect the need at high population densities to
426 protect resources and territories, and at low densities to protect access to mates, though
427 more specific experiments will be needed to test this prediction. Finally, rates of broken
428 tails were by far highest in high-density populations, which tend to be small islands, in
429 accordance with previously published data on the same trend (Brock et al. 2014a).

430 Because these small islands are lizard-predator free, Brock et al. (2014a) found a
431 significantly lower proportion of lizards shed their tails when standardized force was
432 applied. A stronger bite force would then be needed and advantageous for inflicting this
433 kind of bout-ending damage. Furthermore, the potential for cannibalizing the tail (Deem
434 & Hedman 2014) of a competitor could provide a secondary nutritional benefit to having
435 a bite strong enough to remove the tail from a competitor. The relationship between tail
436 breaks and island area was not significant (Fig. 4b) largely because of an outlier (-3.68,
437 0.44). This island, Mando, was previously sampled by Brock et al. (2014a) and 80
438 percent of the lizards they sampled had broken tails. Their finding – twice our observed
439 rate – was in line with the trend predicted and observed across the other 10 islands used
440 in this study.

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

453

454 *Conclusions*

455 While island ecologies consistently differ from continental settings in predictable
456 ways (McArthur & Wilson 1967), this binary comparison is only part of the story; islands
457 are highly variable in nutrients, productivity, and species composition. Archipelagos
458 provide valuable opportunities to test hypotheses on the relative impact different island
459 contexts have on their inhabitants (Lomolino 2005). Because productivity and species
460 composition are consistently related to island size (McArthur & Wilson 1967; Losos &

461 Ricklefs 2009), we used this gradient as a proxy for the different island conditions
462 experienced by *P. erhardii* and driving differences in an important functional trait,
463 maximum bite capacity. These two drivers are not mutually exclusive though and, likely,
464 there are multiple benefits to stronger bites.

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

473

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487

488 **Data Accessibility**

489 All data used for this work is archived and available on the Dryad Digital Repository
490 doi:10.5061/dryad.65tt7 (Donihue et al, 2015)

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689
690

Table 1

FACTORS AFFECTING MAXIMUM BITE FORCE ACROSS ISLANDS

	Estimate	t Ratio	Prob> 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] x SVL	-0.127	-5.96	< 0.0001
Ln(Island Area) x Bite Plate Distance	0.348	2.23	0.0266
SVL x Bite Plate Distance	-0.149	-2.18	0.0299

691

692

693 NOTE. — Maximum bite force in *P. erhardii* varies with island area, even when taking
 694 into account differences in body size between islands. We also found significant
 695 interactions between sex and body size, reflecting relative differences in the bite capacity
 696 of the two sexes; island area and bite plate distances that reflect differences in the meter
 697 between sampling days (see discussion); and between body size and bite plate distance
 698 reflecting the bite force advantage of larger-bodied individuals. The total R^2 of the model
 699 was 0.723, incorporating 339 observations with 331 degrees of freedom.

700

701

Table 2

RELATIONSHIPS BETWEEN INTRA-SPECIFIC COMPETITION PROXIES AND LIZARD BITE FORCE

	Estimate	t Ratio	Prob> t	Model R^2	N (df)
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 x Bite Plate Distance	-1.6905	-3.47	0.0006		
Sex[F] x 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 x Bite Plate	-0.1409	-2.36	0.0193		

702

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

706

707

708 Figure Captions:

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

715

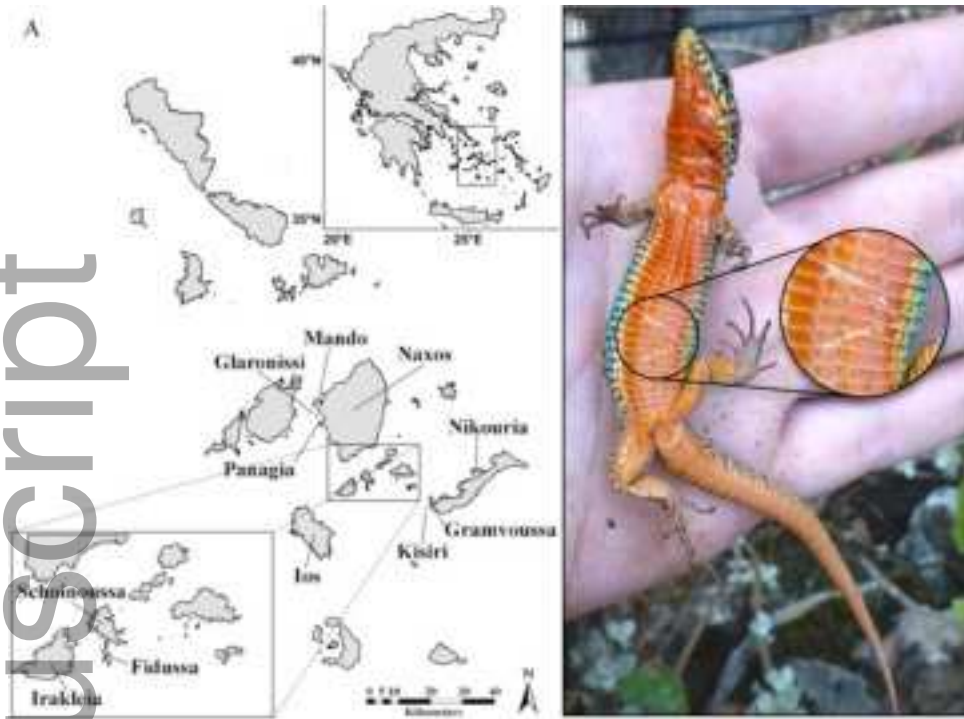
716 Figure 2: The relationship between lizard body size and island area for both females (red)
717 and males (blue). Each point represents a population average with standard error bars.
718 Line of best fit added with 95% confidence shaded in same color, and adjusted R^2
719 displayed for each relationship. Generally, both males and females are larger on small
720 islands and the female relationship was significant at the $p < 0.05$ threshold, denoted by
721 ‘*’.

722

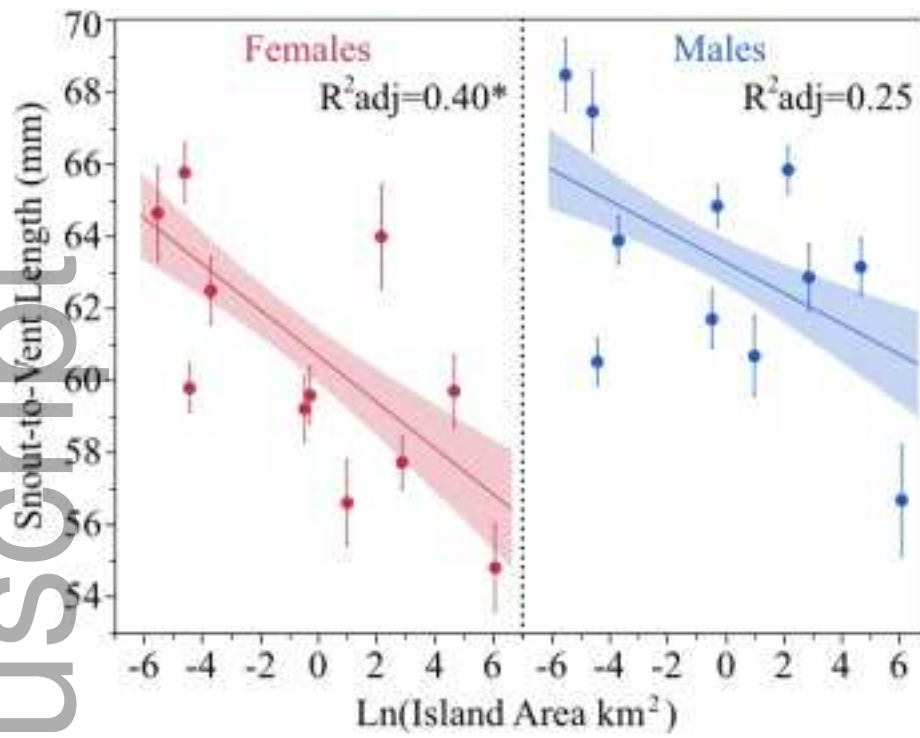
723 Figure 3: The proportion of insects of each hardness class, arcsin transformed, and related
724 to island area with simple linear regression. Each point represents the average proportion
725 of diet items of that hardness class in the stomachs of the lizards. Standard error bars
726 have been added.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

730

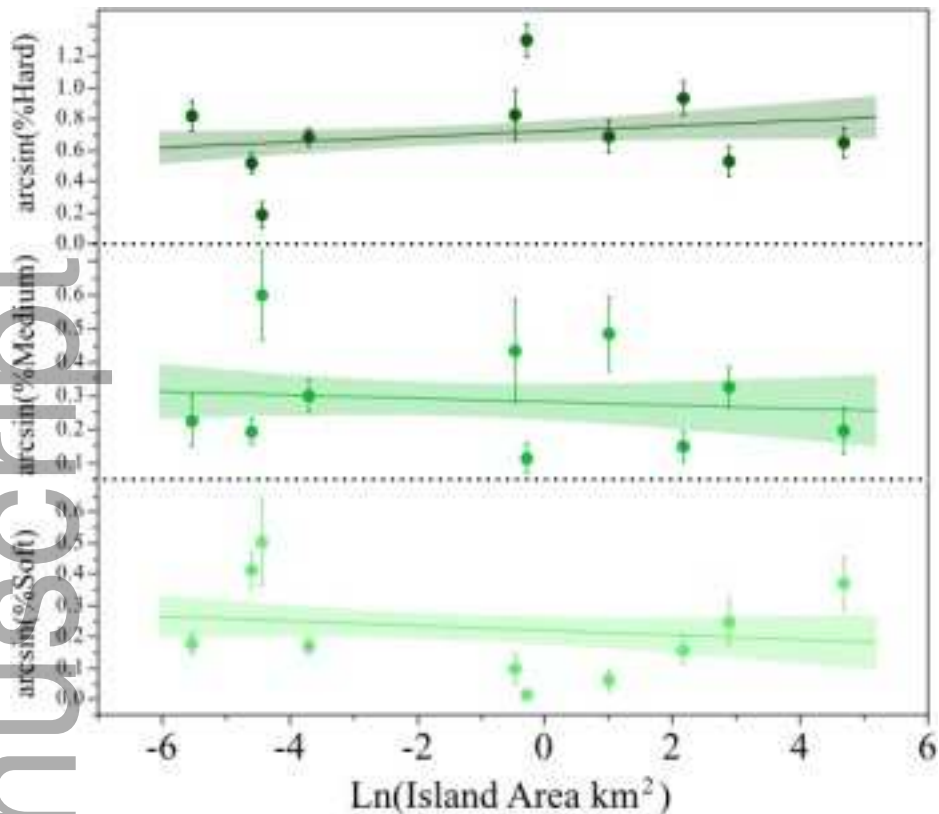
731 Figure 4: A suite of linear regressions showing the relationships between (A) lizard
732 density per 1200 m² and island area, (B) mean bite scars and lizard density, (C) percent of
733 the population's amputated toes and lizard density, and (D) broken tails and lizard
734 density. Each point represents a population. For all figures, a line of best fit has been
735 included with a 95% confidence interval shaded around it, and the adjusted R² value of
736 the relationship has been presented. A '*' reflects significant relationships ($p < 0.05$). We
737 found that lizard density is significantly higher on small islands. Furthermore, we found
738 that as lizard density increased, the mean number of bite scars and the percent of the toes
739 amputated and tails broken also increased significantly.



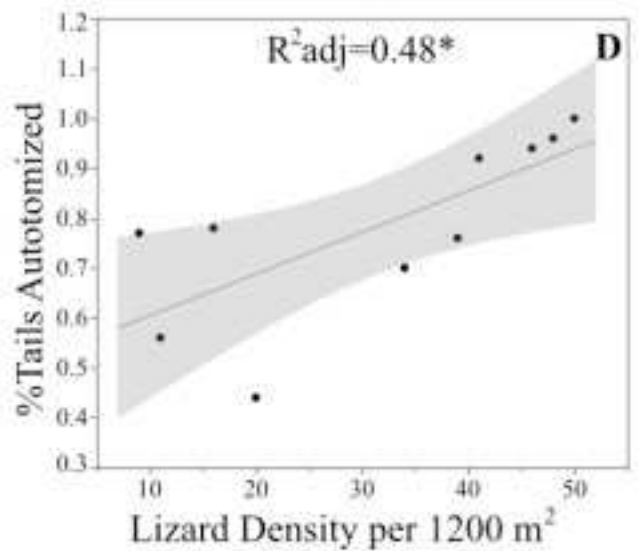
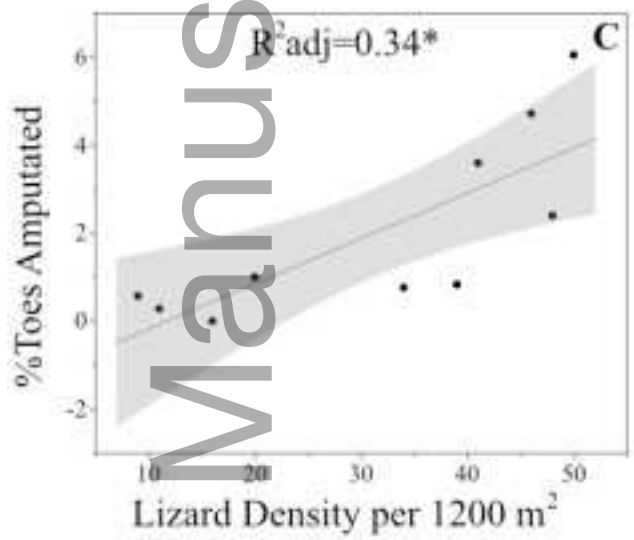
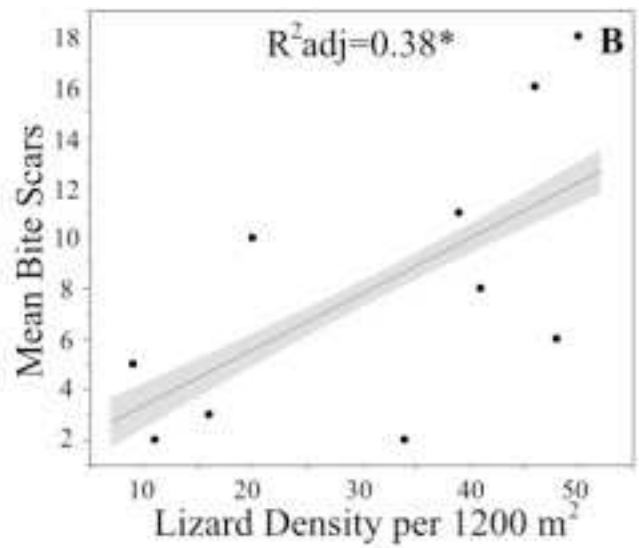
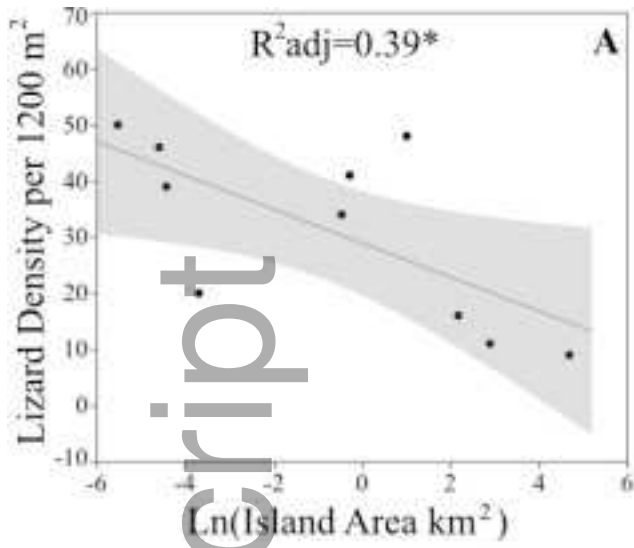
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