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11 **Rapid and Repeated Divergence of Animal Chemical Signals** 12 **in an Island Introduction Experiment**

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28 **Keywords:**

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29 Chemical Signal Design, Experimental Evolution, Phenotypic Plasticity, Lacertidae

30 **Abstract:**

- 31 1. Studies of animal communication have documented myriad rapid, context-dependent
32 changes in visual and acoustic signal design. In contrast, relatively little is known about
33 the capacity of vertebrate chemical signals to rapidly respond, either plastically or
34 deterministically, to changes in context.
- 35 2. Four years following an experimental introduction of lizards to replicate experimental
36 islets, we aimed to determine if chemical signal design of the experimental populations
37 differed from that of the source population.
- 38 3. In 2014, we translocated *Podarcis erhardii* lizards from a large, predator-rich island to
39 each of five replicate predator-free islets. Mean population densities increased five-fold
40 over the following four years and bite scars suggest significantly more intraspecific
41 fighting among these experimental populations. In 2018 we analyzed the chemical signal
42 design of males in each of the experimental populations and compared it to the chemical
43 signals of the source population.
- 44 4. We found that males consistently presented a significantly more complex chemical signal
45 compared to the source population. Moreover, their chemical signals were marked by
46 high proportions of octadecanoic acid, oleic acid, and α -tocopherol, three compounds that
47 are known to be associated with lizard territoriality and mate choice.
- 48 5. Our island introduction experiment thus suggests that the chemical signal design of
49 animals can shift rapidly and predictably in novel ecological contexts.

50

51

52 **Introduction**

53 Animal communication relies on signals that vary widely in form and function (Espmark
54 et al. 2000). While some of this variation arises due to stochastic forces, directional selection is
55 responsible for much of the animal kingdom's diversity in signal design (Espmark et al. 2000).
56 Sexual selection – selection on traits related to mating success – typically drives the evolution of
57 increasingly complex or novel signals that maximize information content and are often honest

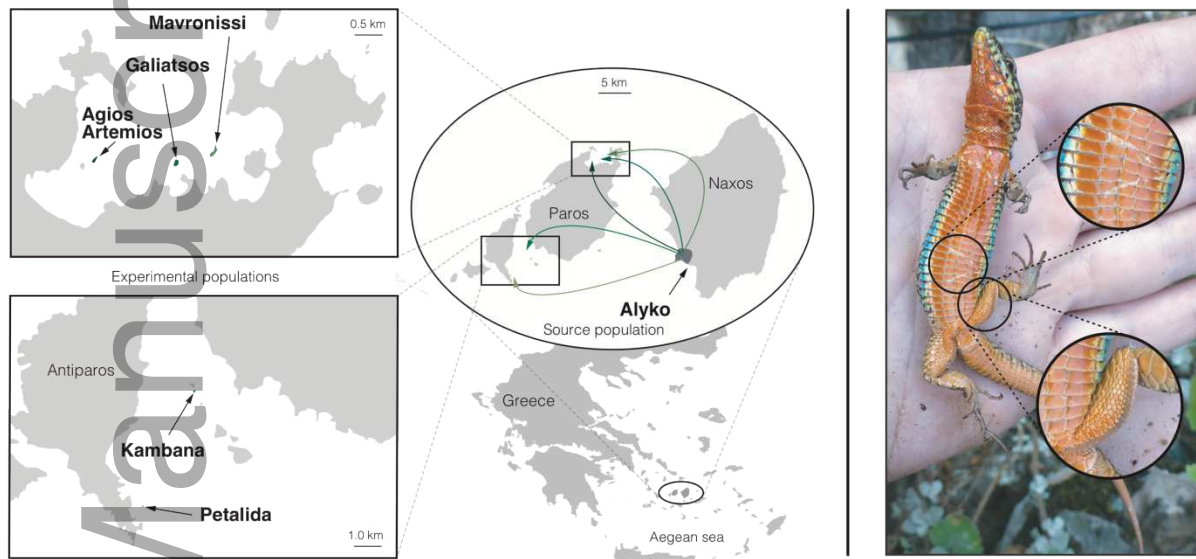
58 predictors of offspring fitness (Pomiankowski 1988; Steiger et al. 2011; Hunt et al. 2012). In
59 contrast, survival selection imposed by predators generally favors signal efficiency in a given
60 environment and the minimization of signal exposure to eavesdropping predators (Endler 1992,
61 1993). Ultimately, the interplay between these two selective forces – sometimes reinforcing,
62 sometimes opposed – shapes signal design (Endler and Basolo 1998, Eliason 2018).

63 There is growing empirical evidence that auditory and visual signals can shift quickly and
64 predictably according to ecological context (Zuk and Tinghitella 2008; Gordon et al. 2015; Zuk
65 et al. 2018). Relatively few studies, however, have investigated the speed and determinism of
66 context-dependent shifts in animal chemical signal design. Those that have – in crickets (Mullen
67 et al. 2007) and salamanders (Palmer et al. 2010) – have documented rapid and repeated
68 divergence in signal design between closely related species. Here, we investigated rapid within-
69 species chemical signal divergence in a lizard (*Podarcis erhardii*) four years after a replicated
70 experimental introduction of lizards from a large source island to five small islets.

71 Male lacertid lizards, including those of all *Podarcis* species, have specialized epidermal
72 glands on the underside of their hind legs that exude waxy secretions, which are deposited as
73 scent-marks in the environment when lizards move through the habitat (Mayer et al. 2015). Over
74 the last decade, extensive behavioral assays combined with studies of natural products chemistry
75 have revealed that the lipophilic compounds in these waxy secretions are important for lizard
76 communication (Khannoon et al. 2011; Heathcote et al. 2014; Pruett et al. 2016; MacGregor et
77 al. 2017; Zozaya et al. 2019). While an individual chemical compound can mediate social
78 interactions as varied as territorial behavior, male rival assessment, and mate choice (Wyatt
79 2014; Martín and López 2006, 2007; Kopena et al. 2011), in most cases the chemical signals of
80 lizards are composed of a species-specific mixture of multiple lipophilic compounds (Martín et
81 al. 2014; Martín and López 2015; Mayerl et al. 2015). While the signaling potential of *P.*
82 *erhardii*'s glandular secretions have not yet been investigated, preliminary data strongly suggest
83 that (as in all epidermal gland-bearing lizards species studied) femoral secretions of *P. erhardii*
84 males elicit chemoreceptive behavioral responses from conspecifics.

85 In 2014, we translocated 100 *P. erhardii* lizards from Naxos, the largest Cycladic island
86 in the Aegean Sea (Greece), to five small islets nearby (Fig. 1). These islets lacked both *P.*
87 *erhardii* and the predators experienced by the source population on Naxos—predominantly

88 snakes and cats (Brock et al. 2014; Li et al. 2014). Snakes in particular pose a threat to *P.*
 89 *erhardii*, since all six snake species living on Naxos are saurophagous (Brock et al. 2014), with
 90 most of them being chemically-oriented foragers that actively hunt their prey using chemical
 91 cues (Cooper et al. 1990; Baeckens et al. 2017a). Experimental lizard populations were not
 92 introduced to additional treatment islets hosting predators because no such islets exist in the
 93 Cyclades (Foufopoulos 1997).



94

95 **Fig. 1.** A map of Greece (bottom center) highlighting the Cycladic islands of Naxos and Paros
 96 (oval inset), along with the surrounding islets where this research was conducted (rectangular
 97 insets). The experimental *P. erhardii* populations originated from Alyko (a protected area in the
 98 southwest of Naxos) and were introduced to five small islets (Agios Artemios, Galiatsos,
 99 Kambana, Mavronissi, and Petalida). At right, a picture of a *P. erhardii* male with a conspecific
 100 bite scar (top inset picture) and femoral pores (bottom inset picture) with visible glandular
 101 secretions.

102

103 Small predator-free islets often reach high lizard population densities (Novosolov et al.
 104 2016) with lizards experiencing strong intraspecific competition and high rates of cannibalism
 105 (Castilla & Van Damme 1996; Vervust et al. 2009; Pafilis et al. 2009, Cooper et al. 2015).
 106 Therefore, we predict that due to the lack of predation, population densities and the degree of

107 intraspecific competition on the experimental islets will rapidly increase. With these changes in
108 ecological context, we hypothesize that the chemical signal design of lizards on the experimental
109 islets will be different from that of the source population. Furthermore, we predict this shift in
110 signal design will be rapid (i.e., over four generations) and convergent (i.e., similar for all five
111 populations).

112 **Methods:**

113 **The experimental system.** *Podarcis erhardii*, the Aegean Wall Lizard, is a common small-
114 bodied lizard that can be found throughout the Cyclades island group (Aegean Sea, Greece).
115 Adults range in body size between 40 and 75 mm (Valakos et al. 2008) and are largely
116 insectivorous (Adamopoulou et al. 1999; Donihue 2016), occasionally bolstering their diet with
117 fruits and conspecific eggs (Brock et al. 2014).

119 The Cyclades contain hundreds of islands ranging in size from Naxos, the largest with a
120 surface area of 440 km², to small rocky islets measuring less than 1 ha (Valakos et al. 2008). In
121 the spring of 2014, we surveyed many islands near Naxos and its neighbor Paros to identify any
122 islets lacking *Podarcis* lizards. For this experiment, we chose five small islets in the vicinity of
123 Paros that we predicted would support a small introduced lizard population, namely Agios
124 Artemios, Galiatsos, Kambana, Mavronissi, and Petalida (Fig. 1). All of these islets are small
125 with surface areas between 0.002 to 0.004 km². In addition, these islets are characterized by a
126 rocky limestone substrate with *Pistacea* shrubs, low flowering forbs, and grasses. Every year,
127 each islet is surveyed for predators and all of the experimental islets are and have been free off
128 terrestrial predators for the duration of the experiment (and birds of prey have never been
129 observed hunting on the islets). In contrast, the island of Naxos has a range of saurophagous
130 predators, including feral cats and snakes (Brock et al. 2014; Li et al. 2014). Specifically, three
131 saurophagous snake species (*Elaphe quatuorlineata*, *Vipera ammodytes*, and *Eryx jaculus*; Brock
132 et al. 2014) are found on Naxos and are known to be chemically-oriented predators (Schoener
133 1971; Baeckens et al. 2017a).

134 In June of 2014, we captured 100 adult *P. erhardii* from an undeveloped coastal area at
135 sea level on Naxos called Alyko, the “source” population. These lizards were captured
136 opportunistically, as they were observed. We then randomly distributed 20 lizards—eight males

137 and twelve females—to each of the five experimental islets (Fig. 1). We revisited the islets
138 annually over the following four years, each time censusing the populations by capturing all
139 lizards by hand or noose and marking all animals with implanted unique passive integrated
140 transponders (PIT tags; Loligo systems, #AB10320; 7 x 1.35 mm) placed subcutaneously. To
141 estimate the level of intraspecific fighting on the islands, the same researcher (CMD) counted the
142 number of corporeal bite scars of each individual in each year (following e.g. Vitt et al. 1974;
143 Vitt & Cooper 1985; Olsson 1994; Lappin & Husak 2005; Lappin et al. 2006; Donihue et al.
144 2016).

145
146 **Collection and extraction of lizard glandular secretions.** In May 2018, as part of the annual
147 population census, we randomly selected 10 adult male lizards from the experimental and source
148 populations for this study. The source population survey in 2018 was conducted by the same
149 researchers in the same manner as the initial capture of the seed populations in 2014 in an
150 attempt to eliminate any systematic detection bias. As epidermal glands develop at the onset of
151 sexual maturity, and their activity is greatest during the reproductive period, we exclusively
152 sampled adult males during the mating season (that is, spring to early summer; Arnold and
153 Ovenden 2002; Carretero 2007). Immediately after the lizards were captured, we collected
154 epidermal gland secretions by gently squeezing around the femoral pores (Fig. 1). We extracted
155 secretions from both hind limbs, resulting in 2 to 6 mg of secretions per individual for chemical
156 analysis. The extraction procedure is harmless, and the lizards are able to rapidly replenish the
157 harvested secretions following their release back to the wild (Baeckens et al. 2017b).
158 Immediately following collection, we transferred the secretions to glass vials with glass inserts
159 sealed with Teflon-lined lids. Blank controls were also created to exclude any contaminants from
160 the handling procedure or the environment and to examine potential impurities in the solvent or
161 analytical procedure. All vials were thereafter stored at -20°C before chemical analysis.

162 The identification of each chemical compound and estimation of its relative abundance
163 (as percentage) was determined using gas chromatography–mass spectrometry (GC–MS),
164 following the methodology of previous studies (e.g. Martín and López 2006, 2007, 2014, 2015;
165 García-Roa et al. 2018). Details on the chemical analyses can be found in the supporting
166 information. After the chemical content of the samples was determined, we estimated the

167 complexity of the chemical composition of each individual secretion sample by calculating the
168 chemical ‘richness’ and ‘diversity,’ following Baeckens et al. (2018a,b). The total number of
169 different lipophilic compounds found in each lizard secretion was considered the chemical
170 richness. Chemical diversity was estimated by the Shannon-Wiener diversity index (Shannon
171 1948).

172
173 **Statistical analyses.** Prior to any statistical analyses, proportion data was arcsin transformed
174 (Sokal and Rohlf 1995; Baeckens et al. 2017c, 2018a,b). Alternative transformations, such as the
175 compositional analysis for proportions (Aebischer et al. 1993), provided similar results. To test
176 for differences in the chemical profile of lizards from different populations, we performed a
177 single factor permutational multivariate analysis of variance (PERMANOVA; McArdle and
178 Anderson 2001). To do so, we first calculated Euclidean distances between every pair of
179 individual samples to produce a resemblance matrix that formed the basis of the PERMANOVA
180 (set at 9999 permutations). To assess interpopulation differences in more detail, we investigated
181 the chemical profiles using a canonical analysis of principal coordinates (CAP; Anderson and
182 Willis 2003) and a principal component analysis (PCA). While CAP investigates and
183 discriminates multivariate data among *a priori* groups, a PCA is useful in providing an
184 unconstrained ordination of multivariate data (but see Martin & Drijfhout 2009). We performed
185 two separate CAP analyses using a leave-one-out cross-validation: one using ‘population’ as the
186 grouping factor with six groups corresponding to the different populations, and another using
187 ‘treatment’ – the source population or experimental populations – as the grouping factor.
188 Combining constrained and unconstrained multivariate statistical approaches in this way yields
189 the most comprehensive insight into the patterns of variation in chemical profiles between these
190 populations. In addition to the multivariate analyses, we performed univariate analyses of
191 variance (ANOVAs) to test for interpopulation differences in PCA scores and chemical diversity.
192 Count data (i.e. chemical richness) was analysed using a generalized linear model (Poisson
193 distribution; Warton et al. 2016). Lastly, and by the use of three separate ANOVAs, we
194 specifically investigated interpopulation differences in the proportions of three compounds that
195 have previously been demonstrated to be important for intraspecific communication in lacertid
196 lizards: octadecanoic acid (Martín et al. 2007b), oleic acid (Martín and López 2010a; López and
197 Martín 2012; Heathcote et al. 2014), and α -tocopherol (Martín and López 2010b; Kopena et al.

2011; García-Roa et al. 2017). We used Tukey's HSD multi-comparison tests with Bonferroni corrections for all post-hoc comparisons. The data were analysed in R Studio (R Studio 2016; R Core Team 2017) and using the PRIMER V6.1.13 (Clarke and Gorley 2006) and PERMANOVA +V1.0.3 packages (Anderson et al. 2008).

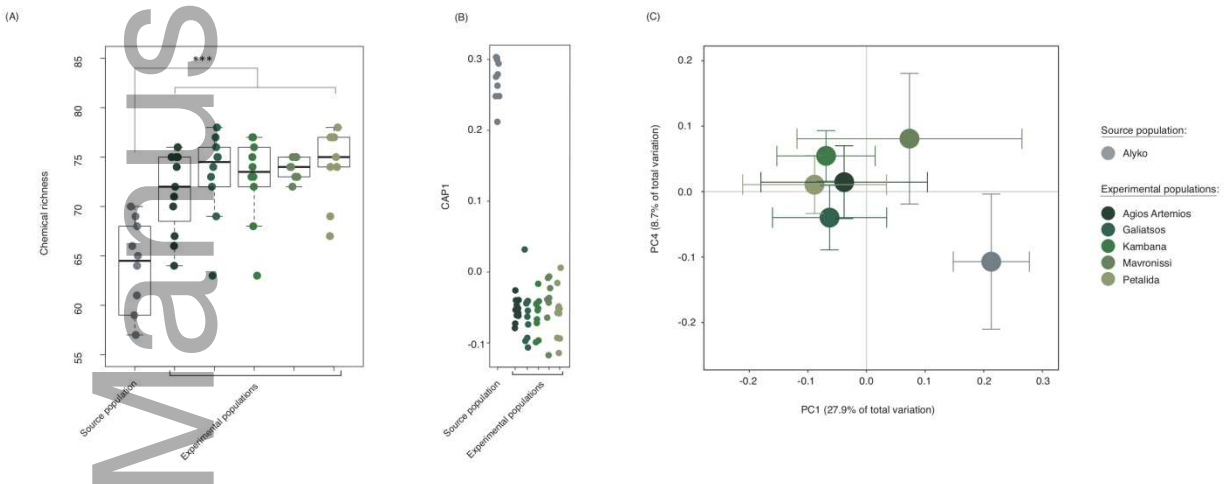
Results

In the four years following introduction, the populations on the islets have increased from 20 lizards each in 2014 to an average of 105 ± 32 lizards per islet in 2018. Accordingly, intraspecific fighting has also increased: in 2018 the lizards on the experimental islets had nearly twice as many conspecific bite scars (Fig. 1) as did the source population in the same year ($\bar{x}_{\text{BiteScars}} \pm \text{SE}$: Experiment: 15.3 ± 0.28 ; Source: 8.0 ± 0.56 ; $t_{564} = 11.595$, $P < 0.0001$). While the density of the source population was not measured in 2018, bite scar rates correlate with density across different islands in the Cyclades (Donihue et al. 2016).

Our analysis revealed a total of 81 different lipophilic compounds in the secretions (Table S1), including steroids (\bar{x} percent of the total ion current \pm SE; $71.19 \pm 1.25\%$), waxy esters ($15.46 \pm 0.91\%$), tocopherol ($3.31 \pm 0.40\%$), aldehydes ($2.32 \pm 0.09\%$), terpenoids ($2.28 \pm 0.56\%$), fatty acids ($2.62 \pm 0.30\%$), alcohols ($1.43 \pm 0.10\%$), amides ($1.30 \pm 0.19\%$), ketones ($0.37 \pm 0.02\%$), and furanones ($0.19 \pm 0.01\%$). Among these, we identified three compounds that have previously been recognized as important for chemical communication in other lacertid lizard species: octadecanoic acid (Martín et al. 2007b), 9-octadecenoic acid (oleic acid; Martín and López 2010a; López and Martín 2012; Heathcote et al. 2014), and α -tocopherol (Martín and López 2010b; Kopena et al. 2011; García-Roa et al. 2017).

The composition and proportions of chemical compounds in the secretions differed significantly among populations (PERMANOVA, pseudo $F_{5,54} = 3.614$, $P = 0.001$), with the primary differences manifesting between the source population and the five experimental populations. Although chemical diversity did not differ significantly among populations ($F_{5,54} = 3.34$, $P = 0.072$), we did find a statistically significant difference in chemical richness ($Z_{5,54} = 3.272$, $P < 0.001$): secretions from the experimental islets all had a significantly higher chemical richness than the source population, while the chemical richness of the secretions did not differ among the five experimental islets (Fig. 2; Table S2). Furthermore, a canonical analysis of

228 principal coordinates on the proportions of chemical compounds correctly classified 95% of the
 229 chemical profiles as belonging to either the experimental or source populations ($\delta_1^2 = 0.94$, $P =$
 230 0.001 ; Fig 2b). While the predominant pattern was a difference between the experimental and
 231 source populations, each experimental population also had some island-specific chemical
 232 characteristics, enabling assignment of 71.67% of the chemical profiles to the correct
 233 experimental population (factor ‘population’; $\delta_1^2 = 0.82$, $P = 0.001$; Fig 2a).



236

237 **Fig. 2.** Interspecific variation in the chemical composition of the glandular
 238 secretion in *P. erhardii* lizards. (A) The black lines in the boxplots depict the median
 239 chemical richness per population, with boxes and whiskers indicating the quartiles. A
 240 post-hoc test revealed a significant difference between lizards from the source
 241 population and lizards from the experimental populations (represented by the
 242 asterisks). (B) CAP analysis of the ‘treatment’ factor showing 95% correct
 243 discrimination of chemical profiles between the source and experimental populations.
 244 (C) Biplot of the unconstrained PCA analysis showing the centroids of the six
 245 populations in the space of the first and fourth principal component (PC). The error
 246 bars denote the 95% confidence intervals of the distribution of points around the
 247 centroids. The first and fourth PCs are plotted as ANOVAs demonstrated that these

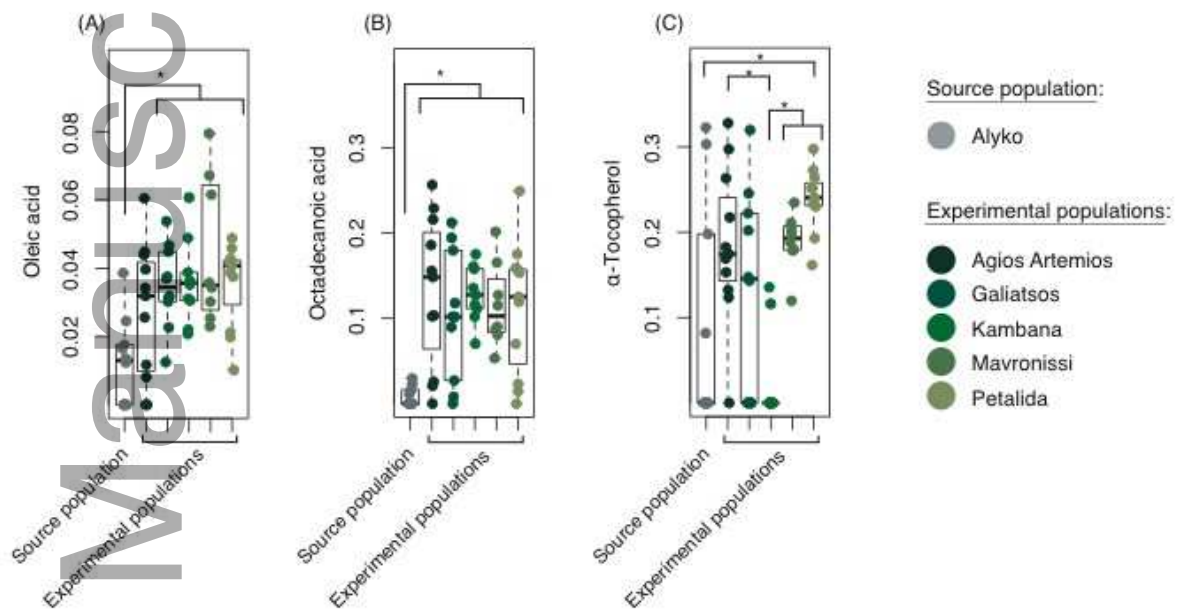
248 two PCs differed significantly among populations, particularly between the source
249 and the five experimental populations.

250

251 A principal component analysis (PCA) revealed similar patterns of variation in chemical
252 design of the secretion between the source and experimental populations (Fig. 2c). The four axes
253 of the PCA explained a total of 61.2% of the variation in the composition and proportions of
254 chemical compounds in the secretions (axis 1: 27.93%; axis 2: 13.52%; axis 3: 11.07%; axis 4:
255 8.68%), and we found significant interpopulation differences in PC1 ($F_{5,54} = 6.456$, $P = 0.0138$)
256 and PC4 ($F_{5,54} = 9.617$, $P = 0.003$). Specifically, post-hoc analyses showed that these observed
257 among-population differences in PC1 and PC4 are only statistically significant between the
258 source population and the five experimental islands, but not among the experimental islands
259 (Table S3): the source population differed in PC1 from Agios Artemios, Galiatsos, Kambana,
260 and Petalida, and in PC4 from Kambana and Mavronissi (Table S3). The results of these post-
261 hoc analyses, in combination with the PC loadings of the different compounds for PC1 and PC4,
262 thus reveal that the secretions of lizards from the experimental populations carried higher
263 proportions of steroids (e.g., cholest-4-en-3-one, cholest-5-en-3-one, and cholestane-3,6-dione)
264 and fatty acids (e.g., octadecanoic acid, hexadecanoic acid) in comparison to secretions of lizards
265 from the source population. Moreover, lizards from the experimental islets had lower proportions
266 of waxy esters (e.g., eicosyl 9-octadecenoate, eicosyl hexadecanoate, and tetradecyl 9-
267 octadecenoate) in their glandular secretions than conspecifics from the source population (see
268 Table S4 on PC loadings).

269 Beyond the overarching multivariate differences in chemical design of the secretions
 270 between lizards from the source population and the experimental populations, we also found
 271 significant interpopulation variation in the proportions of three compounds known to be
 272 important for lizard signalling: octadecanoic acid ($F_{5,54} = 6.707$, $P = 0.012$), oleic acid ($F_{5,54} =$
 273 14.580 , $P < 0.001$) and α -tocopherol ($F_{5,54} = 5.260$, $P = 0.026$) (Fig. 3).

274



275

276 **Fig. 3.** Intra- and interpopulation variation in the proportion of three important compounds for
 277 intraspecific communication in lacertid lizards: (a) oleic acid, (b) octadecanoic acid, (c) α -
 278 tocopherol. The black lines in the boxplots depict the median proportion of the compound per
 279 population, with boxes and whiskers indicating the quartiles. Significant differences among
 280 populations ($P < 0.05$) are indicated by asterisks. Note that all proportions have been arcsin
 281 transformed.

282

283 Discussion

284 We found a significant difference in chemical signal design between *P. erhardii* lizards
 285 living on experimental islets and those living on Naxos, the source of the populations that seeded
 286 the experimental islets four years prior. The chemical composition of the secretions of lizards on

287 the experimental islets was richer than that of the source population (Table S2) and contained
288 higher proportions of three compounds known to play a key role in territoriality and mate choice
289 in lacertid lizards (reviewed in Martín & Pilar 2014, 2015; Mayler et al. 2015). Moreover, the
290 divergence in chemical composition was largely consistent among the five experimental islets,
291 suggesting a deterministic mechanism underlying this trait change that was consistent across the
292 experimental populations.

293 One explanation for this pattern is the shift in ecological context experienced by the
294 lizards on the introduction islets. High population densities have likely led to strong intraspecific
295 competition for access to mates, and the lack of predation will have relieved the risk of chemical
296 eavesdropping. This combination of changes may have allowed the lizards to invest in a
297 different, more complex chemical signal design. This explanation is supported by our findings of
298 increased intraspecific fighting among the experimental populations: males had nearly twice as
299 many corporeal conspecific bite scars on the islets as on Naxos. Moreover, saurophagous
300 predators were never observed on the experimental islets, in contrast to Naxos, which is replete
301 with a diverse predator community (Brock et al. 2014; Li et al. 2014). Recent studies involving
302 chemical signal analyses and correlative behavioural experiments on closely related lizards lend
303 credence to this predation/competition explanation along several lines of evidence.

304 First, the glandular secretions of lizards on the experimental islands carried more
305 molecules of higher molecular weight with lower vapour pressures than those of lizards from the
306 source population (Weldon et al. 2008). Such chemical blends tend to increase the signal
307 persistence of scent-marks (Alberts 1992; Apps et al. 2015). As observed in other terrestrial
308 vertebrates, signal design features that allow scent-marks to remain detectable for a long period
309 of time are beneficial for intraspecific territory demarking (Apps et al. 2015) but may increase
310 the chance of predatory eavesdropping (Alberts 1992; Hughes et al. 2010, 2012).

311 Second, chemical richness of the secretions was consistently higher in lizards from the
312 experimental islets than those from the source population. Work on vocal and visual signals has
313 revealed how intraspecific competition can promote signals relevant in mate choice or rival
314 assessment and drive the evolution of novel signal elements (e.g., Endler et al. 2005; Cardoso et
315 al. 2012; Chen et al. 2012). In line with these studies, one would expect more elaborate and
316 innovative, and thus complex, signals on the experimental islets where intraspecific fighting is

317 fierce. Indeed, we observed that islet lizards do produce secretions containing more lipophilic
318 compounds than lizards from the source populations. This competition-driven increase in
319 chemical richness might, in turn, be amplified by the direct effect of the lack of predatory
320 eavesdroppers on the experimental islets. Complex signals increase an animal's conspicuousness
321 to unintended receivers, therefore animals inhabiting predator-rich environments may benefit
322 from producing simple signals, which decrease the chance of detection by predators, rather than
323 investing in elaborate signals to increase attractiveness towards mates (Endler 1993; Guilford &
324 Dawkins 1993; Zuk & Kolluru 1998). In contrast, free from the danger of predatory
325 eavesdroppers and signal exploitation, animals may not have to compromise between mate
326 attractiveness and avoidance of detection and are unhindered to invest in highly elaborate and
327 complex signals (Endler 1993; Guilford & Dawkins 1993; Zuk & Kolluru 1998). While this
328 theory may explain the observed difference in chemical richness between lizards from the source
329 island and experimental islets, more behavioural research is needed to determine whether lizard
330 gland secretions of high chemical richness are more conspicuous for predators than those of low
331 chemical richness.

332 Finally, males from the experimental islets consistently had significantly higher
333 proportions of octadecanoic and oleic acids in their secretions than those from the source
334 population (Table S5). In lacertid lizards, oleic acid functions as a chemical badge to demark
335 territories and attract females (Martín and López 2015); female lizards have been shown to
336 discriminate between male secretions with different proportions of oleic acid (Martín and López
337 2010a; López and Martín 2012; Heathcote et al. 2014). Previous studies have demonstrated that
338 the proportion of oleic acid in glandular secretions connotes overall male quality in *Iberolacerta*
339 *cyreni* and *P. muralis*, two species that are closely related to *P. erhardii* (Mendes et al. 2016).
340 Moreover, female *I. cyreni* lizards are more attracted to, and spend more time in territories
341 marked with, high levels of oleic acids (López and Martín 2012). Octadecanoic acid is also
342 known to act as a chemical ornament, signalling individual health in another lacertid lizard,
343 *Psammodromus algirus* (Martín et al. 2007b). The patterns of inter-population variation in α -
344 tocopherol were somewhat less consistent. Broadly, the proportion of α -tocopherol varied
345 significantly between the source and experimental populations, but we also found variation
346 among the experimental populations (Table S5, Fig 3). In a range of lizard species, α -tocopherol
347 is used as an honest sexual signal, with high proportions of the chemical increasing the

348 attractiveness of a male's scent to female conspecifics (Kopena et al. 2011; García-Roa et al.
349 2017).

350 Despite these lines of evidence, we acknowledge that alternative drivers may exist for the
351 observed differences in chemical signal design. After each islet population was seeded, the
352 populations began independent evolutionary trajectories and may have been subjected to founder
353 effects and subsequent genetic drift. While it is highly unlikely that all five populations shifted
354 by chance towards similar chemical signal designs incorporating chemicals that have
355 demonstrated behavioural relevance in congeners, the experimental design does not enable us to
356 definitively rule out genetic drift. In addition, because small islets with predators do not exist in
357 this ecosystem, we could not experimentally test a predator-induced mechanism using a
358 predator/islet treatment. Finally, while it is possible that our sampling of the initial seed
359 population was not random and was systematically biased towards, for example, bold males,
360 because the capture of lizards, including those from the source population in 2018, was
361 consistent in every year and conducted by the same researchers, any detection bias should also be
362 consistent, enabling comparison.

363 Further behavioral research is needed first to gauge whether the glandular secretions of
364 lizards on the experimental islets are more chemically conspicuous to predatory snakes than the
365 secretions of lizards from the source population, and second, to test whether females respond
366 differently towards glandular secretions from males from the source population in comparison to
367 males from the experimental islets.

368 In addition, while climate (Martín et al. 2015; Baeckens et al. 2018a) and diet (Kopena et
369 al. 2011; Baeckens et al. 2017c; García-Roa et al. 2017) can affect lizard chemical signal design,
370 our preliminary data suggest these factors are unlikely drivers of the observed divergence
371 between the source and islet populations. As the source population was peninsular and at sea
372 level, and due to the close physical proximity of the source and experimental populations
373 (maximum linear distance of 28 km), all of the populations experience comparable temperature,
374 precipitation, and wind (Belasen et al. 2017; Table S6). Furthermore, preliminary data show no
375 differences in insect availability or diet composition between the populations in May, during the
376 mating season when these glandular secretion samples were collected (Table S7 and Fig. S1).
377 While additional experiments will be needed to conclusively determine what role, if any,

378 environmental conditions play in chemical signal design for *P. erhardii*, the documented
379 differences in predation and competition seem to best explain this pattern

380 As compared to the literature on insect pheromones (Wilson and Bossert 1963; Wilson
381 1965; Nakagawa et al. 2005; Symonds and Elgar 2008), the study of chemical communication in
382 vertebrates, especially reptiles, has numerous important gaps (Mason and Parker 2010,
383 Buesching 2019). For example, the heritability of lizard chemical signals has yet to be
384 investigated. Therefore, we do not yet know whether heritable, genetic changes drove this
385 context-dependent divergence in chemical signal design. Alternatively, there is growing evidence
386 for the evolutionary importance of phenotypic plasticity (Forsman 2015; Levis and Pfennig
387 2016), which could also be a mechanism for the observed divergence in chemical signal design.
388 Regardless of the ultimate basis for these trait changes, the chemical signal design of the
389 experimental lizard populations is fundamentally different from the source population still living
390 on Naxos, demonstrating a rapid, convergent shift in signal design in the experimental ecological
391 conditions.

392 Although chemical communication is pervasive in the natural world, spanning the three
393 domains of life (Wyatt 2014), we still have much to learn about the eco-evolutionary feedbacks
394 that drive chemical signal design. In particular, the interplay of different components of natural
395 selection can create highly localized selective pressures for chemical signals, potentially leading
396 to considerably more intraspecific diversity and tailoring of these signals than previously
397 imagined. Likely reflecting humans' own sensory biases and the technical complexity of
398 chemical analyses, chemical signals have not received the same empirical and experimental
399 investigation as signals of the visual and acoustic communication modalities (Symonds and Elgar
400 2008), particularly with respect to intraspecific, context-dependent variation. The availability and
401 increasing economy of chemical analytical techniques paired with field and laboratory
402 behavioural experiments are revealing the diversity in form and function of chemical signals and
403 the importance of chemical communication in vertebrates. Here, we provide initial evidence
404 suggesting that a release from predation leads to rapid population expansion, resulting in
405 elevated intraspecific agonistic interactions, and a shift in chemical signals important for
406 mediating sociality but which are attractive to predators and thus suppressed in their presence.
407 Our results suggest that chemical signal design of animals may shift rapidly and predictably in
408 response to new ecological contexts.

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