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On the flick of the tongue: male island and mainland lizards' responses to self and conspecific chemical stimuli

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Abstract

Self and conspecific recognition allows many animals to effectively navigate complex social environments. However, these discriminatory abilities come with substantial sensory and neurological costs and therefore should be more prevalent in populations where recognizing self-other and individual cues is essential. Populations on islands may experience reduced benefits from self and conspecific recognition due to the distinct ecological and social conditions of insular life (e.g. high population densities, decreased territoriality, minimal hybridization risk, challenging signalling environment). To test this hypothesis, we compared the discriminatory abilities for self and conspecific chemical recognition of mainland and island Italian wall lizards (*Podarcis siculus*), a species much dependent on chemoreception. We sampled lizards from three locations on the Italian mainland and three Adriatic islands and assessed their tongue flick behavior when confronted with water (control), their own odour, or that of conspecifics. Our results indicated that both mainland and island lizards could discriminate between their own scents and those of other individuals within their population, as well as between two distinct individuals, as evidenced by significant increases in tongue-flick rates. This indicates self-other and conspecific recognition on the basis of chemical cues, in both mainland and island populations. However, we do find some evidence of chemosensory deprivation in the island populations, as increases in tongue flick rates were lower in island lizards compared to mainland lizards. In addition, island lizards tongue flicked at much lower rates than mainland lizards, suggesting a reduced use of the chemosensory channel in insular conditions. Nevertheless, if insular lizards have a chemosensory deficiency, it does not seem to jeopardize self and conspecific chemical recognition.

Introduction

The ability to differentiate self from other, or among conspecifics, is an essential communicative skill and crucial for navigating through agonistic or amiable social interactions (Gokcekus et al., 2021; Mateo, 2004; Tibbetts & Dale, 2007; Tsutsui, 2004). As such, self and conspecific recognition can provide significant fitness benefits (Beletsky & Orians, 1989; Bressan & Zucchi, 2009; Gilby et al., 2013; Lage et al., 2022; Parker, 1997; Silk et al., 2003; Tibbetts & Dale, 2007; Tsutsui, 2004). In a wide variety of animal species, conspecific recognition reduces the costs of conflicts, or territory maintenance and defence (e.g. Husak & Fox, 2003; Jaeger, 1981; López & Martín, 2001, 2002; Paz-y-Miño et al., 2004; Robinson et al., 2015; Whiting, 1999), lowers the risk of hybridization, facilitates the maintenance of pair bonds and enhances parental care (e.g. Aubin et al., 2000; Gabirot et al., 2010; Robertson, 1996; Svensson et al., 2007). In addition, self and conspecific recognition may enhance social learning skills (Herold & Akhtar, 2008; Heyes, 2016), as social cognition theoretically depends on one's ability to become the object of their own attention (or self-awareness) and to choose whom to learn from (Gallup Jr, 1982, 1985; Heyes, 2016; Laland, 2004). Indeed, chimpanzees (*Pan troglodytes*) that demonstrated self-recognition in a mirror test outperformed those that failed the mirror test in several social cognition tasks (Krachun et al., 2019). Similarly, White's skinks (*Liopholis whitii*) that were 'instructed' by a familiar partner performed better in a reversal task, than those 'instructed' by an unfamiliar individual (Munch et al., 2018).

Self and conspecific recognition can be mediated by various sensory channels (e.g. acoustic, Cynx, 1993; visual, Gallup Jr, 1970; chemical, Horowitz, 2017; tactile, Kaitz et al., 1993), and depend on the appropriate neuroanatomical structures and cognitive abilities needed to detect and process signals (Bekoff & Sherman, 2004; Brecht & Nieder, 2020; Miller et al., 2020; Tibbetts & Dale, 2007; Wiley, 2012; Yorzinski, 2017). Developing and maintaining sensory and brain tissue, as well as neural networks, is energetically costly (Aiello & Wheeler, 1995; Isler & van Schaik, 2009; Miller et al., 2020), so their use and level of sophistication are likely adapted to meet socio-ecological demands (Baeckens et al., 2018; Cooper, 1995; Miller et al., 2020; Yohe & Brand, 2018). In species or populations where the social and ecological context does not require precise individual recognition, the development and complexity of recognition systems may be the reduced or different (Tumulty & Bee, 2020; Tumulty & Sheehan, 2020; Ward et al., 2009).

Species and populations living on islands presumably face ecological and social conditions where the benefits of accurate individual recognition are reduced, and this happens for several reasons. First, insular animals typically occur in much higher densities than their mainland conspecifics (Adler & Levins, 1994; Buckley & Jetz, 2007; Novosolov et al., 2016). Large assemblages, either because of the sheer number of individuals around or the instability of associations between individuals, may increase the costs of precise individual recognition (Rohwer, 1982; Sheehan & Bergman, 2015; but see Höjesjö et al., 1998). Second, crowded conditions on islands may also reduce territoriality, as the costs of defending a territory against potential intruders and contenders are expected to increase in comparison to the mainland (Stamps & Buechner, 1985). Hence, insular animals may gain fewer benefits from recognizing familiar individuals or neighboring territory owners compared to their mainland counterparts. Third, animals from smaller species-poor islands may face negligible risk of hybridization, as they often coexist with fewer congeneric species (Abbott, 1975; Grant, 1966). Therefore, insular animals may rely less on conspecific recognition to guide their reproductive decisions, aiming to avoid mating with heterospecifics. Finally, the particular environmental conditions of some islands, such as higher temperatures and stronger winds (Baeckens et al., 2018; Groot & Zizzari, 2019), may reduce the efficiency of chemical signal transmission by accelerating the degradation of scent marks. This makes communication more challenging. On resource-limited islands, investing in effective individual recognition may be too costly for island populations. Unfortunately, to our knowledge, none of these assumptions have hitherto been thoroughly tested.

In this study, we compared island and mainland Italian wall lizards' ability to distinguish their own scents and that of conspecifics. While this is not a direct test of self and individual recognition (which involves complicated cognitive processes, Mateo, 2004; Yorzinski, 2017), the ability to discriminate sensory input cues can be seen as the necessary first step and prerequisite to recognize individuality (Johnston & Bullock, 2001; Thom & Hurst, 2004; Yorzinski, 2017). In lizards, chemosensory discrimination is typically assessed using tongue-flick assays. Tongue flick rates in response to environmental stimuli are known to depend on the functionality of the vomeronasal organ (Cooper & Alberts, 1991; Graves & Halpern, 1990), making tongue-flick assays a rapid, non-invasive, and relatively reliable method for assessing chemosensory discrimination in lizards (Cooper, 1998). Lizards sample air-born or substrate-bound molecules by rapidly protruding and retracting their tongue (i.e. tongue flick) (Cooper, 1994; Schwenk, 1995). These molecules are delivered to a sophisticated vomeronasal system, including the specialized chemosensory Jacobson's organ (Baeckens et al., 2017; Halpern & Martınez-Marcos, 2003; Schwenk, 1995; Simon, 1983) and are used to identify and locate prey (e.g. Cooper, 1995), predators (e.g. Cooper Jr, 1990; Lloyd et al., 2009) and heterospecifics (e.g. Barbosa et al., 2006). Lizards can also extract a rich amount of information (e.g. age, body size, sex, dominance status, heath state, kinship) about conspecifics based on chemicals from their gland secretions or faeces, enough to differentiate between kin or unrelated, familiar or unfamiliar, rival, mate, competitor, or other (e.g. Bull et al., 2000; Carazo et al., 2007, 2008; Fenner & Bull, 2010; Lattanzio et al., 2014; Léna et al., 1998; Martín & López, 2000, 2006; Mason & Parker, 2010; Nisa Ramiro et al., 2019). A series of papers has also established that some reptiles recognize their own chemical cues from those of conspecifics (e.g. Aguilar et al., 2009; Alberts, 1992; Chiszar et al., 1991; Graves & Halpern, 1991; Martín et al., 2020; Szabo & Ringler, 2023). Presenting different chemical stimuli can reveal variations in tongue-flick responses, allowing for inferences about chemical detection and discrimination (Cooper, 1994, 1998). Based on the reasons outlined above, we hypothesized that mainland lizards would have better chemical discrimination abilities compared to island lizards, manifested as an increased ability to discriminate between odours from different conspecifics or between self-produced scents and those of others.

Materials and methods

Study system and animal housing

The Italian wall lizard (*Podarcis siculus*) is a diurnal lacertid that occurs in a variety of semi-open habitats in the Mediterranean basin. The species has established new populations worldwide well outside its native range (Italian peninsula and Sicily), possibly aided by its considerable morphological, physiological and behavioral plasticity and synanthropic nature (Capula & Aloise, 2011; Damas-Moreira et al., 2018; Kapsalas et al., 2016; Vervust et al., 2007). From mainland Italy, *P. siculus* has colonized many islands, where populations have since undergone substantial phenotypic diversification (Avramo et al., 2021; Gorman et al., 1975; Podnar et al., 2005; Radovanović, 1956; Raia et al., 2010).

In April and May 2024, we caught 153 adult male lizards (mean snout-vent-length, SVL: 67.93 mm, range = [56.12, 78.88] mm) from populations on mainland Italy (Rodi Garganico, $N = 25$; Termoli, $N = 28$; Vieste, $N = 26$; Fig. 1) and

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small islands in the Adriatic Sea (Pod Mrčaru, $N = 25$; Pod Kopište, $N = 25$; Sušac, $N = 24$; Fig. 1). We focused on males to avoid catching gravid females, which could lead to egg deposition in captivity and jeopardize the survival of their progeny. Lizards were transported to the lab and individually housed in large plastic terraria (28 × 56 × 39 cm), each containing a sandy substrate and enrichment material (plastic vegetation and rocks). A bowl with fresh water was accessible at all times. A 45-Watt bulb suspended above each terrarium provided light and heat between 7 am and 7 pm so that lizards could maintain their body temperatures within the preferred range. To avoid excess stress from unnecessary handling, all experiments were performed in the lizards' home terraria. Lizards had at least 24 h between capture and the start of the experimental trials to become accustomed to their home terraria. Just prior to the onset of the experiments, all lizards were allowed at least an hour to thermoregulate to ensure proper assessment of their chemoreceptive abilities (Van Damme et al., 1990).

Experimental procedure

In order to evaluate the ability of male lizards to discriminate their own odour and that of conspecifics, we compared their tongue flick rates (Cooper, 1998) in response to three different chemical stimuli: self odour, conspecific (i.e. other male lizard from the same population) odour and blank control. Preceding the first experimental trial, odours were extracted by rubbing cotton swabs damped with distilled water on the cloacal area and femoral pores of the donor lizards (López & Martín, 2002). For the blank control treatment, we used a clean cotton swab that was dipped in distilled water and did not contain any chemical cues. Each cotton swab was attached to a thin (⌀ 0.5 cm) and long (ca. 70 cm) wooden stick that allowed the researcher to remotely present the different cotton swabs to the lizards in the terraria. Fifteen minutes before the beginning of each trial, enrichment material that could disrupt visual contact with the lizards was gently removed from their home terraria.

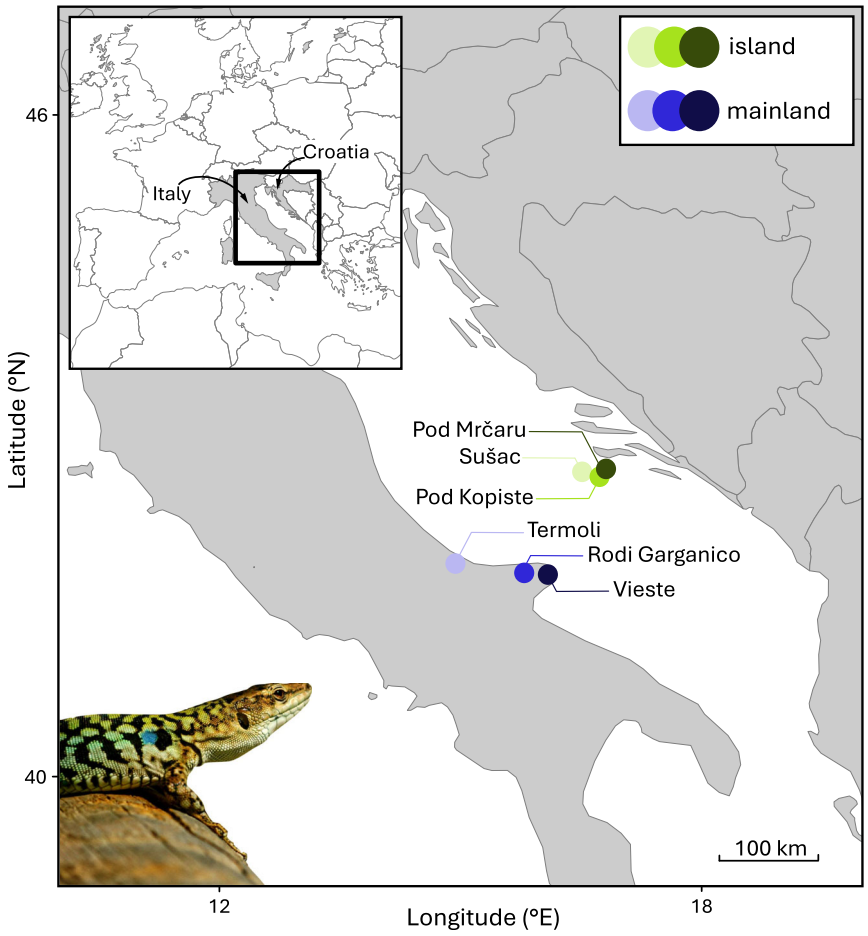

Figure 1 Map of the study area: Island populations are represented with green shades and mainland populations with blue shades. In the top left inset, a broader geographic map of Europe provides context, with a frame indicating the location of the zoomed-in study area. An image of the Italian wall lizard, the study species, is displayed in the bottom left corner.

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We followed a habituation-dishabituation protocol during which each lizard was first presented with the same cotton swab permeated with the same stimuli for three consecutive trials followed by a fourth 'dishabituation' trial in which lizards were presented with a new cotton swab and a treatment stimulus (Mangiacotti et al., 2020). We exposed individuals to three different habituation-dishabituation treatments: self odour versus conspecific odour, a conspecific's odour versus another conspecific's odour, and blank control versus another blank control. We size-matched focal lizards with conspecific donors from the same population (mean SVL difference = 15 mm, SE = 0.05 mm, range = [0, 99]), as much as possible. We also tried to use each conspecific donor as little as possible to avoid any confounding effects of specific donors on tongue flicking.

Each individual was tested in all treatments on the same day, in randomized order, by the same experimenter (IG), who was blind to the treatments. Each lizard underwent a total of 12 trials, with a 1-min interval between consecutive trials. At the start of each trial, the researcher slowly approached the lizard's terrarium, stopping approximately half a meter away. After 1 min, the researcher used the wooden stick to position the attached cotton tip ca. 1 cm in front of the focal lizard's snout. Immediately after and for the next 60 s, the researcher visually counted the number of tongue flicks (i.e. the number of rapid protrusions and retractions of the tongue) directed to the cotton swab (Cooper, 1998; Mangiacotti et al., 2020; Van Damme & Quick, 2001). At the end of each trial, the researcher briefly stepped back without leaving the room before proceeding with the next trial using the same procedure. Upon the completion of the study, all lizards were returned in good health to their original capture locations.

Statistical analysis

All analyses were performed in R (version 4.4.1; R Core Team, 2024).

In a first analysis, we examined how lizards responded to the three types of chemical stimuli (control, self odour and conspecific odour), using only the first three habituation trials in each treatment. We used a mixed effect Poisson generalized linear model (GLMM) (*glmer* function; *lme4* package; Bates et al., 2015), after verifying that overdispersion was not an issue (dispersion = 1.13, $P = 0.55$; *DHARMa* package; Hartig, 2024). This model was used to investigate whether and how the number of tongue flicks changed across habituation trials (1–3) and whether it differed among treatments (control, self, and conspecific) and between locations (island and mainland). The interaction term (treatment * location) was included to test whether the effect of the chemical stimuli on tongue flicks differed between lizards from the mainland and the islands. As we performed all trials on the same day, we also accounted for the order of each trial (between 1 and 12) in our model. Population and individual ID nested within populations were included as random effects in the model to account for repeated measures for each individual and population effects.

We performed a similar analysis to examine whether lizards distinguished (as reflected by elevated tongue flick rates) between their own odour and that of conspecifics and whether island and mainland lizards differed in their ability to do so. We used another Poisson GLMM with the number of tongue flicks as the response variable, which exhibited only mild overdispersion (dispersion = 1.77, $P = 0.02$; *DHARMa* package; Hartig, 2024). This time we included treatment (control vs. control, self vs. conspecific, conspecific vs. another conspecific), location (mainland vs. island) and trial number (factor with 4 levels) as well as their three-way interaction as the fixed predictors. To reduce the complexity and meet the convergence criteria of the model, we excluded the order of trials from the predictors, as we expected the negative effect to be equal among treatments that were performed in a randomized order. Individual ID, nested within populations, was again included as a random effect in the model.

We obtained overall effects for each predictor in both models via the models' summary and type III ANOVA (*Anova* function; *car* package; Fox & Weisberg, 2019). We performed post-hoc pairwise comparisons (*emmeans* package; Lenth, 2024) to investigate more detailed differences in tongue flicking for each combination of treatment and location, and each combination of treatment, location, and trial number.

Results

Tongue flick rates decreased with the number of habituation trials ($\beta = -0.51$, SE = 0.02, $P < 0.005$), indicating that lizards indeed became less interested when confronted with the same odour repeatedly. Tongue flicks also differed among treatments ($\chi^2 = 36.02$, d.f. = 2, $P < 0.005$), between locations ($\chi^2 = 7.96$, d.f. = 1, $P < 0.005$) and according to the interaction between the two (treatment * location: $\chi^2 = 11.98$, d.f. = 2, $P < 0.005$). Mainland lizards had overall higher tongue flick rates than insular lizards (Fig. 2). The effect of treatment depended on location. Pairwise comparisons of the first (out of three) habituation trials of each treatment showed that mainland lizards exhibited equally elevated tongue flick rates in response to self and conspecific odours; both were significantly higher than that observed in the blank control (Fig. 2). In island lizards, conspecific odour—but not own odour—elicited higher tongue flick rates than distilled water, although the difference in the number of tongue flicks was minimal (Fig. 2). The number of tongue flicks also significantly decreased with trial order ($\beta = -0.19$, SE = 0.005, $P < 0.005$), probably due to habituation to the experimental procedure or increased stress from repeating testing.

When we included all trials in the second analysis, tongue flicks depended on trial number ($\chi^2 = 254.09$, d.f. = 3, $P < 0.005$), location ($\chi^2 = 3.83$, d.f. = 1, $P = 0.05$) but not on treatment ($\chi^2 = 4.74$, d.f. = 2, $P = 0.09$). The interaction terms were all statistically significant (treatment * trial number: $\chi^2 = 78.38$, d.f. = 6, $P < 0.005$; treatment * location: $\chi^2 = 14.23$, d.f. = 2, $P < 0.005$; treatment * trial number * location: $\chi^2 = 20.80$, d.f. = 6, $P < 0.005$) except for the one between location and trial number ($\chi^2 = 6.31$, d.f. = 3, $P = 0.09$). Pairwise comparisons of tongue flick rates in the third habituation trial and the dishabituation trial revealed that lizards increased their tongue flick rate in the dishabituation trials of the self vs conspecific and the conspecific versus new

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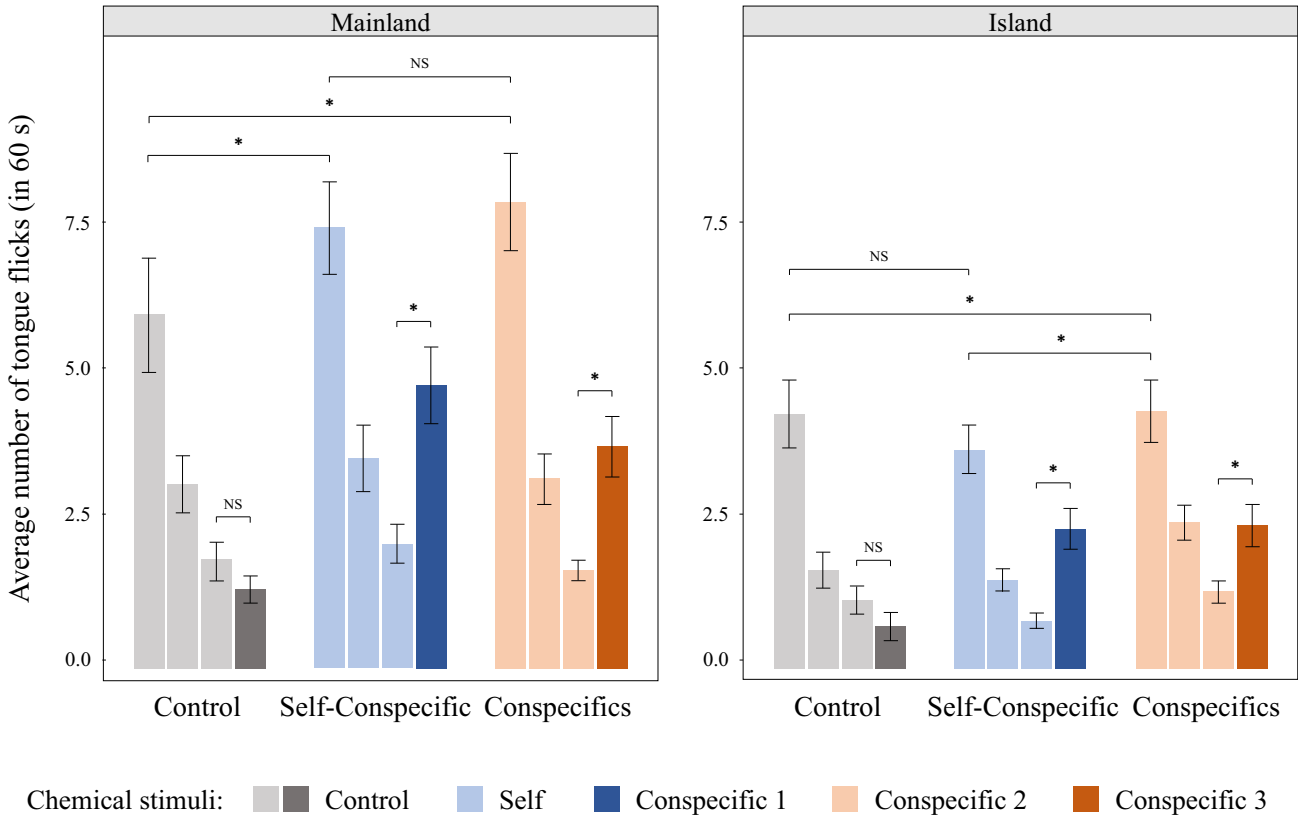

Figure 2 Average number of tongue flicks (per minute) in mainland (left panel) and island (right panel) lizards across the four trials: the first three habituation trials (light shade) and the fourth dishabituation trial (dark shade). Results are shown for the three treatments: (1) control versus control (grey colour), (2) self versus conspecific odour (blue) and (3) one conspecific versus another conspecific odour (orange). Error bars represent the standard error (SE) of each mean and asterisks (*) denote statistically significant differences ($P < 0.05$) of biologically important (i.e. among chemical stimuli within locations, or between the last habituation and the dishabituation trial) pairwise comparisons, while 'NS' indicates no significant difference.

conspecific trials but not in the control versus another control trials. This pattern was observed in both mainland and island lizards (Fig. 2). However, the relative change (%) in tongue flicking between the third habituation and the fourth dishabituation trial was generally greater in the mainland (control vs control, mean = 38%, SE = 6; self vs conspecific, mean = 144%, SE = 21; conspecific vs new conspecific, mean = 104%, SE = 19) than on the islands (control vs control, mean = 40%, SE = 7; self vs conspecific, mean = 112%, SE = 16; conspecific vs new conspecific, mean = 87%, SE = 14).

Discussion

Our experiments show that Italian wall lizards are able to distinguish (as reflected in elevated tongue flick rates) between their own and a conspecific's odour, as well as between the odours of two different conspecifics. This observation supports previous findings in other lizard species, showing that lizards were capable of distinguishing between themselves and conspecifics, and among conspecifics based on their odour (e.g. Aguilar et al., 2009; Bull et al., 2000; Carazo et al., 2007, 2008; Font & Desfilis, 2002; Graves & Halpern, 1991; López & Martín, 2001, 2002; Nisa Ramiro et al., 2019; Szabo & Ringler, 2023).

Contrary to our expectations, both insular and mainland lizards were capable of distinguishing between the odours of different conspecifics. We expected that insular lizards would derive fewer benefits from conspecific recognition compared to their mainland conspecifics based on several assumptions. Population densities of lizards tend to be much higher than on the mainland (Buckley & Jetz, 2007; Novosolov et al., 2016). Although we do not have density estimates for all our study sites, *Podarcis siculus* follows this pattern. For instance, Vervust et al., 2009 report densities of 1045 and 3082 individuals per ha for Pod Kopište and Pod Mrčaru (populations included in our study), while estimates for the mainland remain much lower (Maura et al., 2011: 5–25 ind/ha; Raia et al., 2010: 341–388 ind/ha). Higher densities would increase the costs of producing, processing, and retaining individual signals, as insular lizards are expected to encounter a higher number of other individuals than their mainland counterparts. Whether this

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number precludes the production or recognition of distinctive individual signatures is unclear, however. Higher densities and therefore increased encounter rates may not hinder conspecific recognition altogether and instead promote reliance on more general and less precise forms of it (e.g. Ward et al., 2009; but see Höjesjö et al., 1998). Insular lizards are generally believed to be less territorial than their conspecifics on the mainland because the surplus of non-territorial floating males on islands would render the defence of a territory less economical (Stamps & Buechner, 1985). This may alleviate the need for individual recognition. Indeed, territorial male *Psammodromus algirus* lizards distinguish between different unfamiliar older territorial males, while the younger non-territorial ones do not show any individual discrimination (Martín, López, et al., 2024). However, comparative studies on the territoriality of insular and mainland lizards are currently lacking, leaving open the possibility that lizards may still hold and defend territories on islands. Regardless of territoriality, crowded conditions often lead to intense intraspecific aggression and competition even on islands (Donihue et al., 2016; Itescu et al., 2016; Pafilis et al., 2009; Stone et al., 2003; Vervust et al., 2009). In this context, conspecific recognition may still provide benefits to insular lizards by helping them avoid aggressive, dangerous or more dominant conspecifics, thereby reducing the costs associated with conflicts. In addition, *P. siculus* probably coexists or coexisted in the recent past with other lacertids, such as the Dalmatian wall lizard (*Podarcis melisellensis*) and the sharp-snouted rock lizard (*Dalmatolacerta oxycephala*), at least in some of the islands (Nevo et al., 1972; pers. obs.). Hence, conspecific recognition mechanisms may have been maintained in insular populations, as they help or helped in the recent past to avoid hybridization. However, further studies on both male and female *P. siculus* mating preferences and their ability to recognize conspecifics are required to confirm this hypothesis.

Both mainland and island lizards were also capable of differentiating between their own odour and that of a conspecific. However, whether such capability reflects lizards' true self-other recognition ability is difficult to conclude (Gallup & Anderson, 2018). Lizards may not necessarily assign their own identity to their own chemical signal. Instead, they might treat their own scent as that of a conspecific, or simply as a familiar scent. In that case, the self-other comparison here would simply echo another conspecific versus new conspecific comparison, or a familiar versus unfamiliar one. However, in both island and mainland lizards, the relative increase in tongue flicking between the habituated self versus a new conspecific odour (mainland: 144%, island: 112%) was higher than the one between a habituated conspecific versus a new conspecific odour (mainland: 112%, island: 87%). The different contrast between the two sets of odours may indicate that lizards compare different types of odours in each case, indicative of the existence of both self and conspecific recognition. Nevertheless, further chemical discrimination tests with multiple controls that are coupled with detailed behavioral data are needed to clarify whether lizards are capable of true self recognition. Whether the females of the species exhibit similar patterns in their discriminatory abilities remains also unknown.

Although both male island and mainland lizards can distinguish between their own scents and that of conspecifics, mainland lizards did show a stronger increase in their tongue flick rates during both self-other and between conspecifics tests. However, it is unclear whether greater changes in tongue flick rates reflect stronger interest, or superior detection and discrimination abilities. Nevertheless, a stronger response from mainland lizards in comparison to their insular conspecifics, suggests that there may be some selective pressures against discriminatory ability on islands, albeit very weak ones. Reliance on multiple underlying mechanisms (and hence phenotypic traits or genes), low heritability, weak selection gradients or short divergence times may limit the evolution (Futuyma, 2010; Gomulkiewicz & Houle, 2009; Teplitsky et al., 2014) of self and conspecific recognition on islands. In addition, mainland and insular lizards may not differ in their ability to distinguish between distinct scents, but rather in their chemoreceptive efficiency, the required chemical sampling, or their perceptual mechanisms and underlying cognitive processes or forms of recognition (e.g. binary, class-level, or 'true' individual recognition) (Gokcekus et al., 2021; Mateo, 2004; Tibbetts & Dale, 2007; Yorzinski, 2017). As such reduced tongue-flick rates may not indicate a lower reliance on chemical cues or reduced interest but instead reflect a more efficient sampling strategy, where lizards extract the same amount of information with fewer tongue flicks (Baeckens, 2019). In any case, further investigation is required to test these alternative hypotheses.

When exposed to any chemical stimuli—whether control or ecologically relevant—insular lizards in our experiments generally exhibited lower tongue-flick rates compared to their mainland conspecifics. Lizards on islands often live in very different environments than their mainland conspecifics (Blanco et al., 2014; Buckley & Jetz, 2007; Losos & Ricklefs, 2009; Novosolov et al., 2016; Terborgh, 2023), and as a consequence, they differ from their mainland conspecifics in some aspects of their ecology (e.g. Andrews, 1976; Castilla et al., 2008; Eloy de Amorim et al., 2017; Novosolov et al., 2013; Sagonas et al., 2014). Insular environments may also select for reduced chemosensory sensation because of the dearth of chemical challenges. For example, low predation rate or predator species richness may alleviate the need for accurate chemoreception of predators by insular lizards (Durand et al., 2012; Mencía et al., 2017; Van Moorleghem et al., 2020). Indeed, mainland Dalmatian wall lizards showed higher tongue-flick rates and distress behavior when confronted with scents of both native and introduced predators, while insular lizards did not respond to any of the predator cues (Van Moorleghem et al., 2020). Similarly, simplified insular prey communities, changes in prey mobility or incorporation of plant material in the diet of insular lizards may affect their foraging strategies, which may not require extensive use of chemical senses to track, trail or actively search for food (Cooper, 1995, 2000; Herrel et al., 2008; Taverne et al., 2019; Van Damme, 1999). The reduced tongue-flick rates observed in insular lizards may reflect an overall chemosensory deficiency on islands. Whether insular lizards compensate for their chemoreception deficiency by relying on other types of cues, such

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as visual or acoustic, presents another interesting new avenue for future studies.

Alternatively, the higher tongue-flick rates observed in mainland lizards compared to their insular counterparts may be attributed to inherent behavioral differences between these populations. Tongue-flicking is context-dependent and can be influenced by various factors, including exploratory activity, risk-taking tendencies, anti-predatory responses and reactions to novel stimuli (Gove & Burghardt, 1983; Graves & Halpern, 1990). Insular environments impose distinct ecological pressures that shape these behaviors in diverse ways (reviewed in Gavriilidi et al., 2022), potentially affecting baseline tongue-flicking rates. Consequently, rather than indicating a reduced chemosensory capacity, the lower tongue-flick rates in insular lizards may partly reflect their altered behavioral profiles. In the absence of detailed behavioral observations, further investigation is needed to disentangle the underlying causes of reduced tongue-flicking on islands.

Another factor that may disfavour the use of chemical signals is the distinct climatic conditions of islands. The often unpredictable combination of hot, windy and dry weather in island environments, such as those in the Mediterranean basin, may pose challenging conditions for chemical signaling in lizards. These factors can accelerate evaporation rates, reducing the longevity and effectiveness of scent marks (Alma et al., 2022; Baeckens et al., 2018; Martín & López, 2013; Martín, Navarro-Castilla, et al., 2024). As a result, the production, transmission, and reception of chemical signals may be less advantageous on islands compared to the mainland. Rather than investing in heavier molecular-weight compounds in scent marks that could better withstand the challenging abiotic conditions of island life, a potential adaptive strategy for insular lizards might be to reduce investment in chemical communication altogether. The observed lower tongue-flick rates in our insular lizard populations may reflect this shift. In addition, xeric insular abiotic conditions may also impose water constraints for lizards, which may explain why insular lizards did not differ in their tongue flicks directed to their self odour in comparison to the control. Instead of reduced inspection of the self odour, this pattern may be the result of an overall reduction in tongue flicking in combination with an increased attraction of insular lizards to water, resulting from their willingness to readily inspect and exploit any water source they can find (Brock et al., 2014; Mačát et al., 2015). However, more empirical research is needed to confirm whether the abiotic conditions of islands indeed constrain lizards' chemical communication.

While our study provides valuable insights into the effects of insularity on chemical discrimination in lizards, several limitations should be acknowledged. First, we did not collect data on the femoral glands of mainland and insular lizards, leaving open questions about potential differences in scent mark composition and the specific chemical compounds mediating discrimination. Future studies incorporating chemical profiling of both proteinic and lipophilic components of femoral gland secretions (Mangiacotti et al., 2023) would help clarify these aspects. Second, we employed an experimental approach to assess chemosensory abilities, which may not fully capture how lizards use chemical cues in natural settings. Further research in more ecologically relevant conditions could help refine our understanding of these processes. Third, additional behavioral comparisons are needed to better understand the mechanisms driving the observed reduction in tongue-flick rates on islands. Investigating factors such as exploratory tendencies, boldness, and stress responses across different ecological contexts would provide a more comprehensive picture. Finally, our study focused exclusively on male responses, and interactions between sexes were not examined. Including both sexes in future research would be important for understanding the role of chemical communication in mating, social interactions and potential evolutionary adaptations in insular environments.

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Conflict of interest

The authors have no conflicts of interest to declare.

Author contributions

RVD and IG conceived the ideas and designed the methodology; IG and LVL collected the data; IG analyzed the data; IG led the writing of the manuscript with substantial input from RVD and SB. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

The data that support the findings of this study are openly available in Figshare (doi: 10.6084/m9.figshare.28625297).

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