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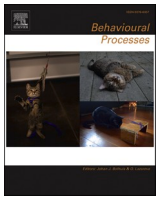

Conspecific presence affects foraging decisions of insular and mainland Aegean wall lizards (*Podarcis erhardii*)

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ABSTRACT

Conspecifics often constitute a valuable source of information. For instance, animals are often attracted to a foraging site by the presence of conspecifics, a phenomenon known as 'local enhancement'. Theory predicts that animals should engage in local enhancement only when associated benefits (efficient resource detection) outweigh the costs (increased interference competition), a trade off that depends on environmental context. Insular and mainland habitats differ in key ecological factors, such as predation pressure, competition, and food availability, which likely affect how animals use social cues while foraging. Here, we compared the local enhancement behaviour of Aegean wall lizards from three small islets, two larger islands, and two mainland sites in Greece. In the wild, lizards were offered food near a transparent container that either held a conspecific (social trials) or was empty (control). We then compared whether and how fast individuals would (1) emerge near, (2) approach, and (3) start eating the food, between social and control situations, and among habitats (mainland, island, or islet). We also looked at whether the presence of conspecifics – confined, or free-roaming when multiple lizards were attracted – provoked interference competition. Conspecific cues influenced foraging decisions in a complex manner. The presence of confined conspecifics had only minor effects, but other free roaming conspecifics accelerated or inhibited foraging activities, depending on their type (emerging, approaching, eating). Insular lizards also engaged in more aggressive interactions than mainland ones. Our results indicate that the costs and benefits of local enhancement may vary geographically, but they are inconclusive due to methodological limitations. Further research is needed to identify the environmental conditions favouring the evolution of local enhancement and social cognition.

1. Introduction

Conspecifics can be a valuable source of environmental information. Whether intentionally (signals) or not (inadvertent social information) (Wagner and Danchin, 2010), conspecifics can transmit information on the availability and profitability of resources in the environment (Kiester, 1979; Stamps, 1987; Valone and Templeton, 2002). For example, the presence, behaviour, or performance of a conspecific may act as a social cue used by animals to locate or assess the quality of food resources (Danchin et al., 2004; Dall et al., 2005; Pérez-Cembranos and Pérez-Mellado, 2015). In many cases, animals are attracted to a particular foraging site or a food item by the current or past presence of conspecifics (or their products) – an example of 'local enhancement' (Thorpe, 1963 after Hoppitt Laland, 2013; but see Zentall and Galef, 1988; Heyes et al., 2000; Galef, 2013 for a debate on the use of the terms). This phenomenon has been reported in many social species (e.g. cliff swallows, Brown, 1988; stingless bees, Slaa et al., 2003; bumblebees, Avarguès-Weber and Chittka, 2014; seabirds, Thiebault et al., 2014, Bairos-Novak et al., 2015), but even solitary foragers occasionally rely on the presence of conspecifics to locate and assess profitable food patches. For example, juvenile crab spiders *(Mecaphesa asperata)* are attracted to flowers on which there are already a number of conspecifics (Hanna and Eason, 2013); and timber rattlesnakes (*Crotalus horridus*) prefer ambush sites with chemical cues from conspecifics over

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non-scented ones (Clark, 2007).

Attraction to conspecifics can benefit animals in multiple ways (Pöysä 1992; Galef and Giraldeau, 2001). In a foraging context, the tendency to be drawn to other individuals can increase the chances of locating clumped food, facilitate the discovery of novel food sources or new food items, and enhance feeding efficiency and safety (Pöysä 1992; Cadieu et al., 1995; Beauchamp et al., 1997; Galef and Giraldeau, 2001; Beauchamp, 2003; Downes and Hoefer, 2004). Hence, the benefits of local enhancement behaviour are expected to be maximized in environments with poor, ephemeral, or unpredictable food conditions (Deygout et al., 2010; Boyd et al., 2016; Rouviere and Ruxton, 2022). On the other hand, approaching food items that are already being exploited by conspecifics might increase the risk of intraspecific aggression (Baude et al., 2011), and/or vulnerability to predation (e.g. Botham et al., 2005; Carere et al., 2009). With increasing density, conspecifics would act as competitors rather than informers (Ruxton et al., 1995; Fletcher, 2007; Baude et al., 2011; but see Pérez-Cembranos and Pérez-Mellado, 2015), and larger aggregations may be more conspicuous to predators (Vine, 1973; Jackson et al., 2005; Ioannou and Krause, 2008), or result in increased conspecific aggression that may distract individuals from anti-predator behaviour ("distracted prey" hypothesis; Chan et al., 2010; Hammer et al., 2023). However, conspecific attraction may serve as an anti-predator strategy, as larger numbers provide protection through dilution and increased vigilance (Hamilton, 1971; Lehtonen and Jaatinen, 2016). In any case, this indicates that the trade-off between the costs and benefits of local enhancement may be density and predation dependent.

Animals on islands live in ecological conditions that differ from those on the mainland. They tend to occur in higher densities, enjoy reduced predation risk and interspecific competition (Adler and Levins, 1994; Buckley and Jetz, 2007; Novosolov et al., 2016; Baeckens and Van Damme, 2020 and references within), but often must cope with intense intraspecies competition (Itescu et al., 2017) and less or more variable dietary resources (Blanco et al., 2014; but see Sale and Arnould, 2013). All of these environmental conditions may affect the way animals gather, process, and use ecological information (Metcalfe et al., 1987; Dall et al., 2005; Kendal et al., 2005; Fletcher, 2007; Parejo and Avilés, 2016), for example when foraging. In addition, the visual, acoustic, and/or chemical transmissibility of the habitat itself may also determine the costs and benefits of using different sources of information (Parejo and Avilés, 2016). For instance, the behavioural choices of ungulate prey species on the African savanna depends on actual lion density, but also on lunar luminosity levels, which affect visibility of and by predators (Palmer et al., 2017).

Ecological factors, such as population density, predation, and food availability, may thus flip the balance between personal and social information use (Fletcher, 2007; Doligez et al., 2004; Baude et al., 2011). In insular environments, where food may be scarce or unpredictable, and predation risk is low in comparison to the mainland, relying on conspecifics to discover food sources may be a profitable strategy. Indeed, Pérez-Cembranos and Pérez-Mellado (2015) found evidence of local enhancement in the insular lizard *Podarcis lilfordi*, where individuals were attracted to food items with feeding conspecifics. However, increased intraspecific densities on islands may cause more aggressive interactions when animals aggregate around valuable food items. With increasing densities, the costs of intraspecific aggression will soon outweigh the benefits of earlier detection and skill learning. For example, *Ameiva corax* lizards on the Caribbean Little Scrub Island often feed in the company of conspecifics, but aggression increases when the food item is too small for the number of claimants (Eifler and Eifler, 2014). Although many studies have reported local enhancement either in island (e.g. Pérez-Cembranos and Pérez-Mellado, 2015; Eifler and Eifler, 2014) or mainland (e.g. Whiting and Greeff, 1997, 1999) populations, none so far, to our knowledge, has compared island and mainland populations of the same species. We think that such a comparison would contribute to our understanding of the conditions favouring the evolution of local enhancement, a concept that has hitherto been studied mostly in a theoretical framework (e.g. Deygout et al., 2010; Arbilly Laland, 2014; Boyd et al., 2016; Rouviere and Ruxton, 2022).

In this study, we compared the role of local enhancement in the foraging behaviour of the Aegean wall lizard (*Podarcis erhardii*) from populations inhabiting small islets (< 1 km^2), larger islands, and mainland habitats. Local enhancement has been observed – both under experimental conditions and in the field – only in a handful of lizard species thus far (Whiting and Greeff, 1997, 1999; Eifler and Eifler, 2014; Drakeley et al., 2015; Pérez-Cembranos and Pérez-Mellado, 2015). In the field, we offered lizards food and noted whether and how fast individuals would approach the food item and start eating. We compared the lizards' foraging decisions across populations and between social situations (i.e. with and without conspecifics present). In addition, we looked at the occurrence and level of interference competition. We hypothesized that insular lizards, typically living under low predation, high density, and high food variability, will exhibit stronger local enhancement behaviour, but engage more in aggressive interactions than their mainland conspecifics due to the more intense intraspecific competition.

2. Methods

2.1. Study system

The Aegean wall lizard (*P. erhardii*) is a small (snout-vent-length, SVL of adults up to 75 mm), ground-dwelling, diurnal lizard species, native to the Balkans and many Aegean islands, where it occupies a variety of habitats (Valakos et al., 2008; Brock et al., 2015). Its diet consists primarily of arthropods (Adamopoulou et al., 1999), but individuals have been observed feeding opportunistically on fruits, other plant matter, dangerous prey (e.g. scorpions and Mediterranean banded centipedes), and even on conspecifics (Brock et al., 2014; Madden and Brock, 2018; Patharkar et al., 2022; pers.obs.). Although knowledge on the social behaviour of *P. erhardii* is limited, it is not a group-living species, and interactions between individuals tend to be aggressive (Donihue et al., 2016; Brock et al., 2022).

Between May and August in 2023 and 2024, we performed field observations at seven study sites: three on small islets (Aspronissi, Fidoussa, and Parthenos; <1 km^2), two on larger islands (Naxos; 448 km^2, Anafi; 40 km^2) in the Cyclades (Aegean Sea), and two in mountain regions (Mt. Parnitha, Attica and Mt. Ochi, Evia) in mainland Greece (Fig. 1a).

The climate of the area is Mediterranean, with warm, dry summers and cool, rainy winters. The islands, due to their proximity to the sea, experience more temperate conditions (Valakos et al., 2008), but with higher seasonal variation in precipitation and productivity than the mainland (De Meester et al., 2021). The vegetation at the sampling areas on the mainland consists of dense shrubland with scattered trees and open rocky areas (De Meester et al., 2021; pers. obs.). Study sites on the Cycladic islands include rocky areas, drystone walls, and coastal sandy habitats that are dominated by Mediterranean phrygana and maquis vegetation (Brock et al., 2015; Donihue et al., 2016; pers. obs.).

Although detailed demographic data are lacking, lizard densities on the Aegean islands and especially the islets are typically high compared to the mainland (Brock et al., 2015; Itescu et al., 2019; Table S2 supplementary material). In addition, mainland habitats have richer predator communities than the islands, and especially the smaller islets (Pafilis et al., 2009; Brock et al., 2015; Foufopoulos et al., 2023, Table S2 supplementary material; but note that predator species richness does not necessarily reflect predation intensity, efficiency, or risk; Jaksic and Busack, 1984; Itescu et al., 2017). Food availability probably fluctuates more strongly and stochastically on islands, and insular lizards are more likely to face food resource shortages, especially during the hot and dry summer months (Janzen, 1973; Di Castri and Vitali-Di Castri, 1981;

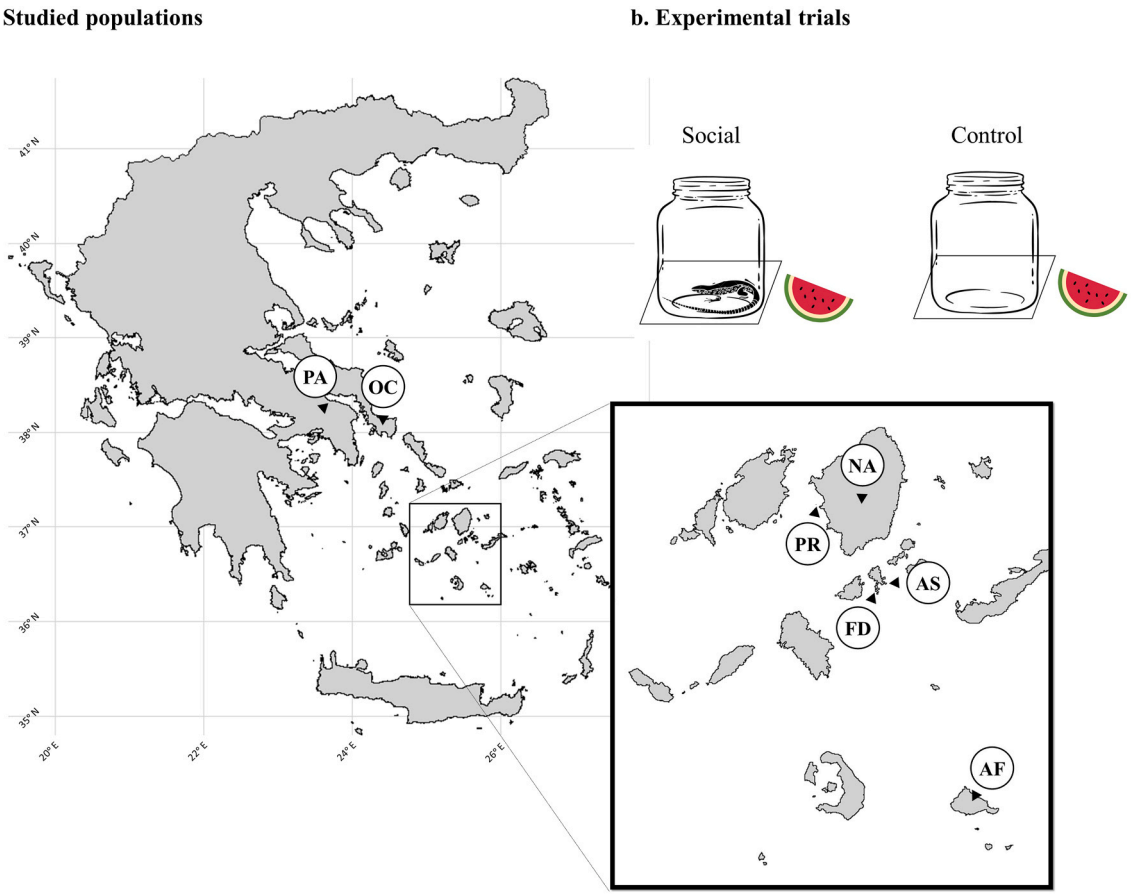

Fig. 1. a. Map of the study sites in mainland Greece and the Cycladic archipelago: Mt. Parnitha (PA), Mt. Ochi (OC), Anafi (AF), Naxos (NA), Aspronissi (AS), Fidoussa (FD), Parthenos (PR); b. Illustration of the experimental set-up.

Adamopoulou and Legakis, 2002; De Meester et al., 2021).

2.2. Experimental procedure

We performed field trials during which we offered lizards a food item (a piece of watermelon, approximately 2 × 2 x 15 cm) in one of two conditions. In 'social' trials, we placed a transparent jar (9 cm diameter x 14 cm height) containing a conspecific next to the fruit. In 'control' trials the jar was left empty (protocol adjusted from Pérez-Cembranos and Pérez-Mellado, 2015) (Fig. 1b). A wet piece of paper was placed under the jars, irrespective of treatment, to slow down heat transfer and avoid overheating the lizards during the social trials. For practical reasons and to avoid overstressing a single individual, we frequently replaced the individual in the jar with other individuals caught *in situ*. To standardize the procedure among locations, the conspecific in the jar was always an adult male (SVL= 64.97 mm [range 53.48, 78.93], N = 131), except for a few trials (N = 13) where inadvertently an adult female was used (mean SVL= 64.97 mm [57.87, 69.36], N = 5). At the end of all trials, the confined lizards were released at the spot where they were captured, after making sure that they were sufficiently hydrated.

Trials were conducted between 8:00 am and 19:00 pm, when the lizards were most active. We walked separately through the study site until we spotted a lizard, upon which we placed the food and the jar as close to the lizard as possible, or near to the refuge into which it had resorted. We then withdrew to a distance that minimized disturbance, but at the same time allowed the observation of the lizards using binoculars (mean=5.6 m, [min 4 m, max 11 m]). Emergence latency (Lem) was defined as the time elapsed between the placement of the food and the moment a lizard was spotted within ~2 m of the set-up. This could be the focal lizard, or any other lizard. If the focal lizard stayed in sight during the placement of the set-up, Lem was recorded as 1 s. If no lizard appeared within 10 min, this was noted and we proceeded to a subsequent trial in a new location.

We defined latency to approach (Lapp) as the time it took an emerged lizard to approach the food to within 2 SVLs. If no emerged lizards approached the food within 10 min after emerging, we noted that and we moved on to a new location. Latency to eat (Leat) was logged for those lizards that approached the set-up, as the time they spent within 2 SVLs of the food until they started eating from it. For all lizards that emerged close to the set-up, we also noted whether they inspected the jar, and the latency to do so for the first time (Lins).

We observed lizards eating from the watermelon for 10 min, during which we noted the duration of their feeding activity as well as how often it was interrupted. Feeding duration was calculated from the moment lizards initiated eating until they retreated at a ~2 SVLs distance away from the fruit and did not come back within the time window of the observation period. In cases where lizards did not retreat, the duration of feeding activity was the same as the observation period (10 min). We also counted the number of interruptions, i.e. when lizards suspended their feeding activity, diverting their attention away from the fruit to inspect their surroundings, or when they engaged in aggressive interactions with approaching conspecifics. We also recorded the number of aggressive interactions of each individual with the conspecific in the jar, or with other free-roaming lizards.

In cases where multiple lizards emerged within the same trial, we counted their number and recorded their latencies to emerge, approach, eat, and inspect the jar. In addition, for each trial we recorded the total number of aggressive interactions among all individuals that appeared. Whenever possible, we also recorded the additional information (feeding interruptions and duration), but we mostly focused on the first

individual eating, as it was not always feasible to track multiple lizards at the same time. All latencies were recorded in seconds. Where possible, we noted the sex and age class (juvenile, subadult, adult) and tail status (recently autotomized or not) of the focal lizards, but due to low sample sizes per category, we decided not to include these variables in the analyses.

In total we performed 1187 trials ($N_{mainland}$ =295, N_{island} =570, N_{islets} =322) which resulted in 1607 observation entries (sample sizes per population are mentioned in Table S1 of supplementary material).

2.3. Statistical analysis

All analyses were performed in R (version 4.4.2; R Core Team, 2024). Our preliminary analysis did not show any significant effects of year, so we pooled the data from 2023 and 2024 in order to increase our sample size and statistical power.

To investigate whether treatment (control vs social), habitat (mainland – island – islet) or their interaction, affected the likelihood for a lizard to emerge (0: did not emerge or 1: emerged) within the first 10 min of observation time (N = 1577), we ran a binomial generalized mixed effect model (GLMM) (*lme4* package; Bates et al., 2015). Observer identity (3 different observers) was included in the model as a fixed factor, and population was included as mixed effect, to account for observer and population effects respectively. For the subset of lizards that emerged during the trials (N = 1262), we used binomial GLMMs to test whether treatment, habitat, or their interaction, as well as the number of other conspecifics already feeding (range=[0,4]) played a role in their decision to approach the food or not, and to inspect the jar or not. Observer identity was included as a fixed covariate and population as a random effect. Similarly, for the subset of lizards that approached the food item within 10 min (N = 862), we used a binomial GLMM with the same model structure as before, and their decision to eat or not as the response variable.

We performed a similar analysis for the number of lizards that emerged, approached, ate the fruit, or inspected the jar in each trial (emerge: N_{trials} = 1189; approach and inspected the jar: N_{trials} = 881; eat: N_{trials} = 613) using a series of Poisson GLMMs. Treatment (social vs control), habitat (mainland – island – islet), their interaction, as well as the presence of at least one other lizard eating during the trial (yes vs no) were the main fixed predictors. Population was included as a random effect, and observer as a fixed covariate. Overall predictor effects were obtain with type III ANOVA (*car* package; Fox and Weisberg, 2019) and predictor-level differences were further investigated with post-hoc pairwise comparisons (*emmeans* package; Lenth, 2024).

All latency (or time-to-event) variables (Lem, Lapp, Leat, and Lins) were analysed using mixed effect Cox Proportional hazard models (*coxme* package; Therneau, 2024). For statistical purposes, the maximum duration of each observation period plus one second was assigned as latency for the lizards that did not emerge, approach, or eat the fruit, or inspect the jar, which were treated as censored times. Binary variables (emerge or not, approach or not, eat or not, inspect or not) were included to identify the censored latency times. Tied emerge, approach, eat, or inspect event times were handled using the Efron approximation method (Hertz-Picciotto and Rockhill, 1997). Habitat, treatment, their interaction, and observer identity were the fixed predictors, while population was included as a random effect. In the cases of Lapp, Leat, and Lins, we additionally tested the effect of the number of other free roaming conspecifics feeding by including it in the fixed factors. We tested the significance of each parameter using likelihood ratio tests.

Lastly, we investigated whether the number of feeding interruptions and aggressive interactions differed among habitats and between treatments, and whether it depended on the presence of free roaming conspecifics. We used a mixed effect Poisson GLM with treatment, habitat, and their interaction, as well as the number of other feeding conspecifics and observer identity as fixed factors. When modelling the number of interruptions, we accounted for how long each individual fed, by including feeding duration as an offset term (log-transformed to match the scale of the linear predictor; Atkinson et al., 2008). For each trial, we calculated the total number of aggressive interactions by tallying the aggression events among free roaming individuals, or between free roaming individuals and the conspecific held in the jar. We used a mixed effect Poisson GLM with the number of aggressive interactions as the response variable, and habitat, treatment, their interaction, and the number of conspecifics around (i.e. that approached the fruit during the trial, range=[0,5]) as fixed predictors. Observer identity was included as a fixed covariate and population was entered in all models as a random factor. The overall significance for each factor was obtained with type III ANOVA (*car* package; Fox and Weisberg, 2019) and pairwise comparisons were performed using the *emmeans* package.

3. Results

The likelihood of a lizard emerging within 10 min after installing the experimental set-up did not differ between treatments ($\chi^2 = 0.03$, df=1, P = 0.87), among habitats ($\chi^2 = 1.89$, df = 2, P = 0.39), or observers ($\chi^2 = 4.94$, df = 2, P = 0.09) (Fig. 2**a**). The interaction between treatment and habitat was also not significant ($\chi^2 = 3.81$, df = 2, P = 0.15). Lizards inspected the jar more often when it held a conspecific ($\chi^2 = 4.17$, df = 1, P = 0.04) (Fig. 2**b**), but none of the other factors examined affected lizards' decision to inspect the jar or not (habitat: $\chi^2 = 2.43$, df = 2, P = 0.30; treatment*habitat: $\chi^2 = 2.59$, df = 2, P = 0.27; number of other free roaming lizards eating: estimate =0.006, SE = 0.12, P = 0.96; observer: $\chi^2 = 1.61$, df = 2, P = 0.45). The tendency of lizards to approach the food within 10 mins after emerging was also independent from treatment alone ($\chi^2 = 0.06$, df = 1, P = 0.81), or in the interaction term ($\chi^2 = 0.75$, df = 2, P = 0.69) and from the observer ($\chi^2 = 3.03$, df = 2, P = 0.22), but differed across habitats ($\chi^2 = 9.01$, df = 2, P = 0.01) (Fig. 2**c**). Mainland lizards approached the food item less often than their island (estimate =−1.12, SE = 0.33, P < 0.005), or islet (estimate =−1.08, SE = 0.32, P < 0.005) conspecifics, while there was no difference among insular lizards (estimate =0.04, SE = 0.30, P = 0.99). The tendency of lizards to approach the fruit increased with the number of other free roaming lizards feeding on it (estimate =0.28, SE = 0.14, P = 0.05). Once lizards approached the food item, their tendency to eat or not was not affected by treatment ($\chi^2 = 0.33$, df = 1, P = 0.56), the interaction term ($\chi^2 = 3.39$, df = 2, P = 0.18) or the observer ($\chi^2 = 4.43$, df = 2, P = 0.11). However, lizards' decision to eat varied among habitats ($\chi^2 = 5.92$, df = 2, P = 0.05) (Fig. 2d). Pairwise comparisons revealed that mainland lizards had somewhat lower tendencies to eat than their island conspecifics (estimate =−1.35, SE = 0.59, P = 0.06), but the difference between mainland and islet (estimate =−0.99, SE = 0.55, P = 0.16), or island and islet (estimate =0.35, SE = 0.53, P = 0.78) lizards was not statistically significant. Lizards were also less likely to join the feast with an increasing number of other conspecifics already feeding on the fruit (estimate =−0.43, SE = 0.16, P = 0.008).

The total number of lizards that emerged within 10 mins per trial was independent from all the factors considered (treatment: $\chi^2 = 0.19$, df = 1, P = 0.67; habitat: $\chi^2 = 3.35$, df = 2, P = 0.19; treatment*habitat: $\chi^2 = 2.34$, df = 2, P = 0.31; observer: $\chi^2 = 2.40$, df = 2, P = 0.30) (Fig. 2a). Per trial, more lizards inspected the jar in social treatments ($\chi^2 = 3.94$, df = 1, P = 0.05; Fig. 2b) and with an increasing number of other conspecifics eating (estimate =1.25, SE = 0.11, P < 0.005). Neither habitat, alone ($\chi^2 = 2.28$, df = 2, P = 0.32) or in interaction with treatment ($\chi^2 = 1.65$, df = 2, P = 0.44), nor observer ($\chi^2 = 2.48$, df = 2, P = 0.29) affected the total number of lizards that inspected the jar per trial. The total number of lizards that approached the food within 10 mins was also independent of treatment, alone ($\chi^2 = 0.14$, df = 1, P = 0.71) or in interaction with habitat ($\chi^2 = 0.76$, df = 2, P = 0.68) and of observer ($\chi^2 = 0.005$, df = 2, P = 1.00). However, it differed across habitats ($\chi^2 = 8.92$, df = 2, P = 0.01), as less mainland lizards

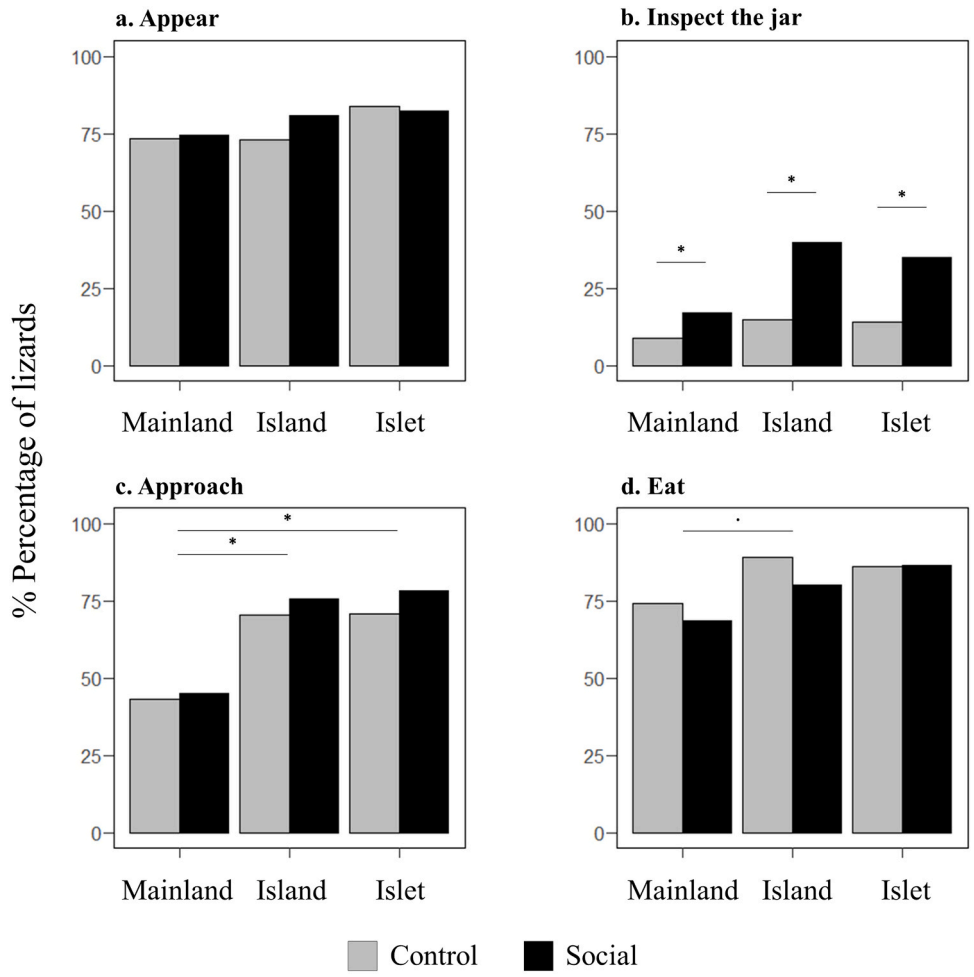

Fig. 2. Percentage of mainland, island and islet lizards that (a) appeared close to the fruit item, (b) inspected the jar, (c) approached the fruit item, and (d) ate from the fruit and in the two treatments, control (gray colour) and social (black colour). Statistically significant ($P < 0.05$) (*) or near significant ($P < 0.06$) (·) differences are indicated with horizontal lines.

approach the fruit than island (estimate =−0.54, SE = 0.14, $P < 0.005$) and islet (estimate =−0.55, SE = 0.14, $P < 0.005$) ones (Fig. 2**c**). A larger number of lizards approached the fruit when there was another individual already feeding on it (estimate:0.36, SE = 0.10, $P < 0.005$). The total number of lizards that decided to eat per trial was independent from all factors considered (treatment: $\chi^2 = 0.25$, df = 1, P = 0.62; habitat: $\chi^2 = 1.79$, df = 2, P = 0.41; treatment*habitat; $\chi^2 = 0.29$, df = 2, P = 0.87; observer: $\chi^2 = 0.86$, df = 2, P = 0.65; other free roaming lizards eating: $\chi^2 = 0.02$, df = 1, P = 0.88) (Fig. 2d).

Latency to emerge was independent of treatment ($\chi^2 = 5.94$, df = 3, P = 0.12), habitat ($\chi^2 = 2.54$, df = 4, P = 0.64), or their interaction ($\chi^2 = 2.42$, df = 2, P = 0.30) (Fig. 3a), but we detected observer effects ($\chi^2 = 12.47$, df = 2, $P < 0.005$). Treatment affected lizards' latency to inspect the jar ($\chi^2 = 97.79$, df = 3, $P < 0.005$), as lizards inspected jars that held a conspecific sooner than the empty ones (hazard ratio =2.49, CI=[1.17, 5.34], P = 0.02) (Fig. 3b). Lizards also waited longer to inspect the jar with an increasing number of free roaming conspecifics already feeding on the fruit nearby the jar (hazard ratio =0.70, CI=[0.56, 0.88], $P < 0.005$). Neither habitat alone ($\chi^2 = 4.89$, df = 4, P = 0.30) or in interaction with treatment ($\chi^2 = 1.02$, df = 2, P = 0.60), nor the observer ($\chi^2 = 1.42$, df = 2, P = 0.49) had significant effects on lizards' latency to inspect the jar. Latency to approach did not differ between treatments (alone: $\chi^2 = 5.55$, df = 3, P = 0.14; in interaction term: $\chi^2 = 0.47$, df = 2, P = 0.79) or among observers ($\chi^2 = 2.12$, df = 4, P = 0.71) but there was a marginal effect of habitat ($\chi^2 = 9.00$, df = 4, P = 0.06). Mainland lizards hesitated more to approach the fruit, than their island (estimate =0.82, SE = 0.21, $P < 0.005$) and islet conspecifics (estimate =0.74, SE = 0.20, $P < 0.005$) (Fig. 3c). Lizards' latency to approach reduced with an increasing number of other free roaming conspecifics eating (hazard ratio =1.16, CI=[1.03, 1.32], P = 0.02). Latency to eat was independent from habitat alone ($\chi^2 = 1.99$, df = 4, P = 0.74) or in interaction with treatment ($\chi^2 = 1.81$, df = 2, P = 0.41) (Fig. 3d), and from the number of free roaming conspecifics already eating ($\chi^2 = 1.21$, df = 1, P = 0.27), while the effect of observer was marginal ($\chi^2 = 5.38$, df = 2, P = 0.07). Treatment significantly improved the fit of the model ($\chi^2 = 11.84$, df = 3, P = 0.008), but the pairwise comparison did not reveal any significant differences between social and control levels (hazard ratio =0.96, CI=[0.60, 1.52], P = 0.85). Nonetheless, on average, lizards took twice as long time to start eating in the social treatments (mean =30.88 s, SE = 4.04) in comparison to the controls (mean =15.88 s, SE = 2.42).

Lizards interrupted more their feeding in the presence of the confined conspecific (average number of interruptions =8.6, SE = 0.3) than in control (average number of interruptions =6.6, SE = 0.3; estimate =0.37, SE = 0.05, $P < 0.005$). The number of feeding interruptions differed among observers ($\chi^2 = 8.29$, df = 2, P = 0.02), while it was independent from the number of feeding free roaming conspecifics ($\chi^2 = 0.03$, df = 1, P = 0.87) or the interaction between treatment and habitat ($\chi^2 = 1.24$, df = 2, P = 0.54). Habitat had an overall effect on the number of feeding interruptions ($\chi^2 = 5.93$, df = 2, P = 0.05), but pairwise comparisons were not significant when corrected for multiple testing (mainland-island: estimate =−0.31,

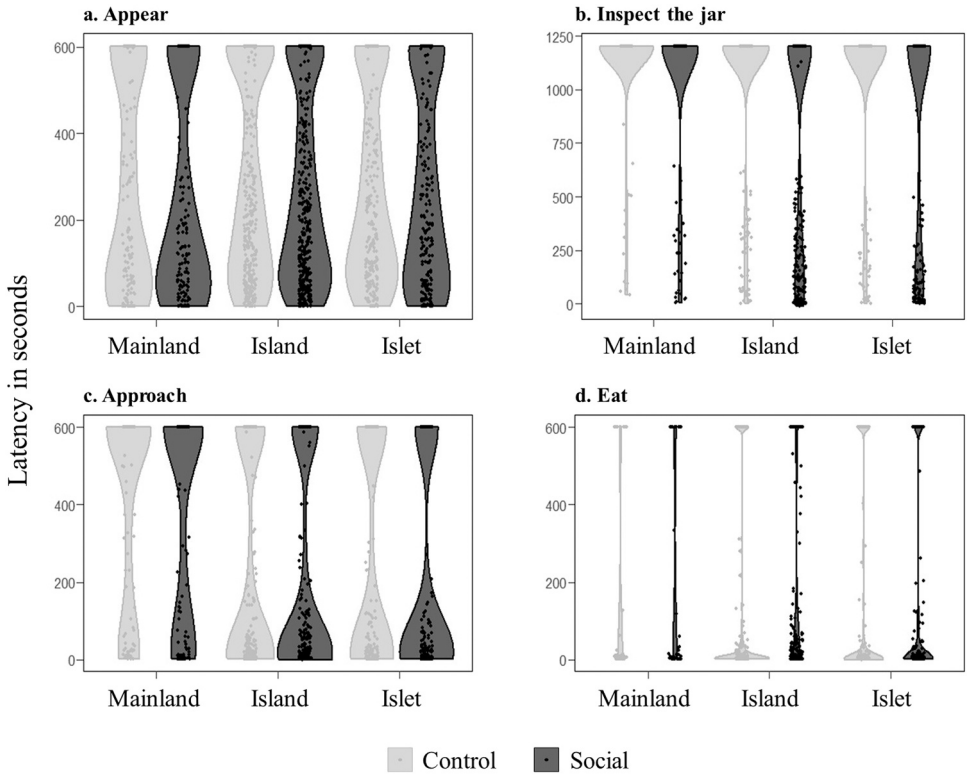

Fig. 3. Violin plots of latencies (measured in seconds) of mainland, island, and islet lizards to (a) appear close to the fruit, (b) inspect the jar, (c) approach the fruit, and (d) eat from the fruit and in the two treatments, control (gray colour) and social (black colour). Dots represent the raw data points.

SE = 0.16, P = 0.13; mainland-islet: estimate =−0.03, SE = 0.15, P = 0.98; island-islet: estimate =0.28, SE = 0.14, P = 0.12).

The number of aggressive interactions was affected by treatment (χ^2 = 6.80, df = 1, P < 0.005), habitat (χ^2 = 12.05, df = 2, P < 0.005), and their interaction (χ^2 = 6.66, df = 2, P = 0.04) (Fig. 4a), and they intensified with the number of conspecifics around (estimate =0.97, SE = 0.04, P < 0.005) (Fig. 4b). Detailed pairwise comparisons revealed that in control trials, mainland lizards engaged in significantly less aggressive interactions than their island (estimate =−2.26, SE = 0.70, P < 0.005), and islet (estimate =−2.33, SE = 0.68, P < 0.005)

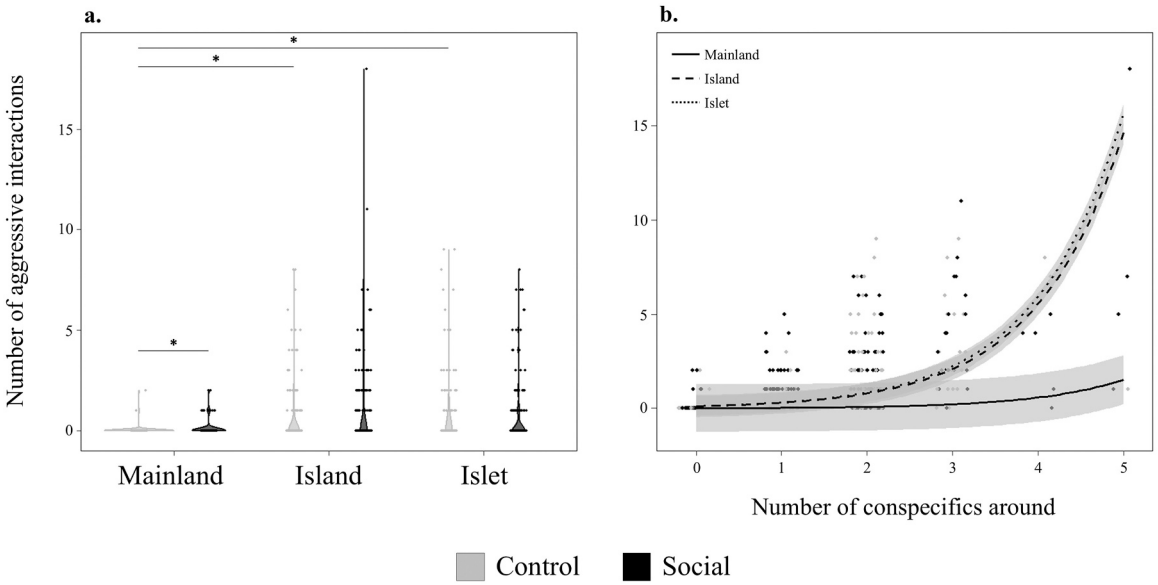

Fig. 4. a) Violin plots representing the distribution of the number of aggressive interactions per habitat (mainland, island, islet) and treatment (control in gray and social in black colour). Each raw data point is represented by a dot and lines indicate statistically significant (*) comparisons (P < 0.05). b) Relationship between the number of conspecifics around the fruit and the number of aggressive interactions for the three habitats (mainland, island, and islet) based on output of the generalized linear mixed-effects model. Lines represent predicted values, with solid, dashed, and dotted lines corresponding to mainland, island, and islet habitats, respectively. Shaded areas indicate 95 % confidence intervals around the predictions. Raw data points are depicted by dots and grouped by treatment (control: gray; social: black).

conspecifics, while the differences were not significant in social trials. This was probably due to the fact that in control trials there were on average more individuals around on islands (mean =0.71, SE = 0.05) and islets (mean =0.91, SE = 0.07) in comparison to the mainland (mean =0.35, SE = 0.04). Mainland lizards engaged also in significantly less aggressive interactions during the control trials in comparison to the social trials (estimate =−1.64, SE = 0.63, P = 0.009), as on average they directed their attacks towards the jar more when it held a conspecific (average jar attacks =0.27, SE = 0.08) than when it was empty (average jar attacks =0.00, SE = 0.00). We also detected observer effects ($\chi^2 = 12.63$, df = 2, P < 0.005).

4. Discussion

Our results confirm that social cues influence foraging decisions of the Aegean wall lizards, but also reveal unexpected complexity in the nature of the animals' response. The presence of conspecifics accelerated or inhibited foraging activities, depending on the conspecifics' situation (free or confined) and the type of activity (emerging, approaching, eating). Aegean wall lizards also exhibit considerable geographic variation in their foraging behaviour.

The presence of confined lizards in the social treatment elicited more aggression and attracted conspecifics to the jar, showing that focal lizards were at least able to see their restrained conspecifics. Otherwise, the experimental treatment had no effect on the focal lizards' tendencies and latencies to approach or eat the fruit nearby. This suggests that the conspecifics in the jar did not present a strong social stimulus. The confined lizards had little room to move, and were not eating, which may have rendered them poor indicators of feeding opportunities. Indeed, the limited movements of the confined conspecifics may not suffice to catch the attention of lizards from a long distance; lizard species exhibit a strong attention bias towards rapidly moving objects (Phillips and Alberts, 1992; Whiting and Greeff, 1997, 1999). At a closer range, the behaviour, rather than the mere presence of conspecifics, is considered important in guiding decisions in lizards (Whiting and Greeff, 1997, 1999). The fact that the confined lizards in our setup were not eating may therefore have contributed to the fact that we found so little treatment effects.

In sharp contrast, the presence and the number of free-roaming lizards eating induced lizards to approach the food resource more often and faster. This suggests that cues originating from eating peers encouraged them to approach the fruit, which would be in line with the social enhancement hypothesis. However, the presence of conspecifics eating slowed, rather than accelerated, the next stage in the foraging process: lizards were less likely to start eating, and waited longer to do so, in the presence of other free-roaming lizards. Social enhancement, profitable as it may be (e.g. by improving prey detectability; Thiebault et al., 2014), bears also significant costs, especially when foraging conspecifics are not happy to share a meal (e.g. Thomson et al., 1987, Beauchamp, 1998, Prior and Weatherhead, 1991, Sandlin, 2000). That these costs are real in Aegean wall lizards, follows from the substantial rise in aggressive interactions with increasing numbers of co-occurring individuals. The costs and risks associated with group foraging may become more imminent as the lizards approach the feeding area, prompting approaching lizards to become more vigilant (Lung and Childress, 2007). The concurrent increase in the number of feeding interruptions suggests that lizards indeed respond to the predicament of eating together with conspecifics. These intricate results suggest that foraging activities may require animals to take a series of decisions (whether and when to emerge, approach, eat), each of which can be influenced by social cues in different ways (a 'decision hierarchy', Stephens, 2008). For instance, aggregations of feeding individuals may alert and attract a conspecific from a certain distance, but once they arrived individuals might decide not to join the feast, on the basis of more accurate information on e.g. the level of competition, predation risk, or the profitability of the food source (Prior and Weatherhead, 1991; Drakeley et al., 2015).

In contrast to our expectations, we did not detect major differences in how mainland and insular lizards' change their foraging behaviour in response to the presence of conspecifics. Cost-benefit models suggest that the profitability of local enhancement may depend on environmental factors, including the availability and spatiotemporal distribution of (food) resources, the degree of interference competition, and the likelihood of eavesdropping predators (Pöysä 1992; Spieler and Linsenmair, 1999; Arbilly and Laland, 2014; Boyd et al., 2016; Rouviere and Ruxton, 2022), as well as internal stimuli, such as hunger level (Galef, 2013). Geographic variation in local enhancement would then arise from an interplay between ecological conditions and internal state (Croy and Hughes, 1991; Stephens, 2008; Luttbeg and Sih, 2010; Drakeley et al., 2015). Our results seem to contradict these predictions. However, this conclusion is based on the lack of a habitat*treatment interaction on most of the behavioural variables considered. It might be that the social treatment fell short to adequately mimic the condition in which conspecifics attract lizards. Unfortunately, we were unable to test for differential effects of free-roaming conspecifics on insular and mainland lizards, due to the fact that on the mainland trials with multiple lizards feeding at the same time were rare. In principle, the fact that communal feeding proved rare on the mainland could be due to a reduction in social enhancement. However, it could also be a consequence of lower population densities, which may or may not be caused by increased territoriality. Although there are no data on the territorial behaviour of island versus mainland Aegean wall lizards, island populations are often thought to exhibit relaxed territoriality (Stamps and Buechner, 1985) which would permit more overlapping of the space used by neighbouring individuals. In accordance, mainland lizards in our tests behaved clearly aggressive to the experimentally confined conspecific, which they may have seen as an intruder in their territory. The role of territoriality in the evolution of local enhancement deserves further attention.

In our study, we observed considerable geographic variation in mainland and insular lizards' overall foraging behaviour. Mainland lizards hesitated more to approach the fruit than their insular conspecifics. Hungrier insular inhabitants are expected to take more risks, be less neophobic, and readily exploit every feeding opportunity, novel or familiar, especially under relaxed predation (Castilla et al., 2008; De Meester et al., 2018). Indeed, insular lizards are known to consume atypical food items and especially fruits (Pérez-Mellado and Corti, 1993; Van Damme, 1999; Brock et al., 2014; Valido and Olesen, 2019), a behaviour that – if not under-reported – seems to be rather uncommon on the mainland. This could explain the overall higher feeding propensity (irrespective of social cues) of the insular lizards, in relation to their mainland conspecifics, in our study. In addition, the xeric insular abiotic conditions probably impose water constraints on insular lizards. Watermelon perhaps attracted insular lizards more due to the high water contain and, as such, would have been perceived as a more profitable source by insular than mainland lizards.

In conclusion, Aegean wall lizards incorporate social information in their foraging decisions, but whether populations exhibit geographic variation in local enhancement behaviour remains inconclusive. Exactly which aspects of the environment have forged the local enhancement behaviour is unclear, but food availability, the intensity of intraspecific competition, and predation risk seem likely candidates. Intrinsic differences between mainland and insular lizards (e.g. territoriality and hunger motivation) may play a role in their foraging decisions. Future studies should measure, compare, and/or manipulate these factors to better understand their influence on social information use, in isolation and in concert.

CRediT authorship contribution statement

Ioanna Gavriilidi: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition,

Formal analysis, Conceptualization. **Cristina Aanei:** Writing – review & editing, Visualization, Methodology, Investigation. **Clara Vinyeta-Cortada:** Writing – review & editing, Methodology, Investigation. **Panayiotis Pafilis:** Writing – review & editing, Supervision. **Raoul Van Damme:** Writing – review & editing, Supervision, Methodology, Conceptualization.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2025.105234.

Data availability

The data that support the findings of this study are openly available in Figshare (https://doi.org/10.6084/m9.figshare.29436515)
Local enhancement research data (Figshare)

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