

# Local enhancement and social foraging in a non-social insular lizard

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**Abstract** Even in solitary foragers, conspecifics can provide reliable information about food location. The insular lizard *Podarcis lilfordi* is a solitary species with high population densities that sometimes aggregate around rich food patches. Its diet includes novel and unpredictable resources, such as carcasses or plants, whose exploitation quickly became widespread among the population. We tested the use of social information by lizards through some field experiments in which they had to choose one of the two pieces of fruit. Probably due to local enhancement, lizards preferred to feed on the piece of fruit where conspecifics or lizard-shaped models were already present. Conspecifics' behaviour, but also their mere presence, seems to be a valuable source of information to decide where to feed. Lizards also showed a strong attraction to conspecifics, even in the absence of food. Maybe the presence of a group is interpreted as an indirect cue for the presence of food. The group size was not important to females, but males had a significantly higher attraction towards groups with three conspecifics. We discuss some characteristics of *P. lilfordi* at Aire Island that can explain the development of the observed social foraging, as well as their possible consequences.

**Keywords** Social information · Foraging behaviour · Conspecific attraction · Islands · *Podarcis lilfordi*

## Introduction

Solitary foragers usually have to sample the environment by themselves, obtaining personal information. Nevertheless, conspecifics can provide social information (Valone and Templeton 2002), either signals or inadvertent social information (ISI, Danchin et al. 2004). Signals are evolved behavioural traits elicited with the intention of communicating, whereas ISI is inadvertently produced by individuals engaged in some activity (Maynard-Smith and Harper 2003, p. 3). Some authors divide ISI into social cues and public information; the former would give discrete information about the presence or the absence of some resource or feature, while public information (Valone 1989) provides graded and continuous information about the quality of a given resource (Dall et al. 2005; Wagner and Danchin 2010). Thus, every individual undertaking an activity is inadvertently sending information that can be received by other conspecifics. If local population density is high, social information can be shared by several individuals (Fletcher 2006).

A conspecific is an excellent integrator of all the environmental variables (Kiestler 1979). Not only its behaviour can be a source of social information about the patch or resources, but also its mere presence guarantees a minimal quality of that area or resource (Stamps 1987; Valone and Templeton 2002; Danchin et al. 2004). Even more, the presence of a conspecific in a patch where there is usually food is an informative cue even in the absence of food (Giraldeau et al. 2002; Coolen et al. 2005). Attraction to feeding conspecifics has been reported in different social species (Beauchamp et al. 1997; Galef and Giraldeau 2001; Leadbeater and Chittka 2005; Sontag et al. 2006; Aragón 2009). In reptiles, Rand et al. (1975) and Kiestler (1975) described how *Anolis agassizi* and *Diploglossus*

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*millepunctatus*, both from Malpelo Island (Colombia), were attracted to food and rapidly aggregated around it, identifying this behaviour as social facilitation. Nevertheless, they were not sure how much of the attraction was due to the food itself and how much to the presence or activity of lizards. Greenberg (1976) reported observations in laboratory conditions of social feeding and social facilitation in the lizards *Sceloporus cyanogenus* and *Anolis carolinensis*. Whiting and Greef (1997) showed that *Platysaurus broadleyi* is attracted to conspecifics eating figs, even in areas of high fig availability. More recently, Eifler and Eifler (2014) studied some aspects of the social foraging behaviour in the insular lizard *Ameiva corax* and their recruitment to noteworthy items in the environment.

Relying on conspecifics as cues can be advantageous when direct assessment of territory, mate or food quality is difficult or time-consuming (Stamps 1987). Moreover, it reduces the variance in reward rate of food and, hence, chances of not encountering any food at all (Ruxton et al. 1995; Galef and Giraldeau 2001). In addition, conspecific attraction may lead to local enhancement (Leadbeater and Chittka 2007), that is, the “apparent imitation resulting from directing the animal’s attention to a particular object or to a particular part of the environment” (Thorpe 1963, p. 134). According to Hoppitt and Laland (2013), local enhancement takes place when, after or during a demonstrator’s presence or interaction with objects at a particular location, an observer is more likely to visit or interact with objects at that location. In species that usually forage individually, local enhancement may work at a coarse level (Pöysä 1992). In those cases, one or several feeding individuals attract more individuals to the feeding patch by the visual conspicuousness of group members.

In this study, we address the use of social information by the Balearic lizard, *Podarcis lilfordi*, in free-living individuals from Aire Island. *P. lilfordi* is a non-social species, but its high population density (Pérez-Mellado et al. 2008) and the frequent visual contact among several individuals would allow the use of social information by lizards while foraging. Aire Island, as many Mediterranean coastal islets, is characterised by a poor and unpredictable food supply (Pérez-Mellado and Corti 1993), promoting the omnivory of lizards and the use of a large variety of food resources (Pérez-Mellado 1989; Pérez-Mellado and Corti 1993). Moreover, lizards are able to exploit any novel and unpredictable resource, such as new plant species recently arrived to the island (Pérez-Mellado et al. 2000a, 2007), marine subsidies, carcasses from dead animals or even conspecifics (Pérez-Mellado and Corti 1993). Some of these resources are too big to be consumed only by one individual, and it is common that several lizards exploit the same piece of food at the same time (pers. obs.).

In this scenario, we could expect that the foraging activity of lizards could provide relevant cues to conspecifics to orient towards the exploitation of novel food resources. Through some field experiments, we want to explore the use of social information and conspecific attraction in *P. lilfordi* when choosing between two foraging patches. We examined (i) whether free-living lizards are more attracted towards a patch of food where some conspecifics are eating than to an equivalent patch without conspecifics; (ii) whether the number of conspecifics eating in a patch is an important factor to make the decision of what patch to feed at; (iii) whether visual cues of immobile conspecifics are attractive enough for lizards or if lizards’ movement, activity and/or chemical cues is important; and (iv) whether lizards show attraction towards a group of conspecifics through visual signals even if there is no food.

## Materials and methods

### Site and species

The study was conducted at Aire Island, off the coast of Menorca (Balearic Islands, Spain), during July and August 2007, 2011 and 2013, on sunny days from 07:00 to 11:00 UTC.

*Podarcis lilfordi* (Squamata, Lacertidae) is a medium-sized lizard that inhabits the coastal islets of Menorca, Mallorca and Cabrera archipelago (Pérez-Mellado 1998). This lizard reaches high densities in Aire Island (Pérez-Mellado et al. 2008). Balearic lizards are solitary foragers, mainly insectivorous, but they also consume vegetal matter, carrion, conspecifics or leftovers carried by tourists (Pérez-Mellado and Corti 1993; Pérez-Cembranos et al. in press.). They frequently interact aggressively, but there is no evidence that lizards are strongly territorial (Pérez-Mellado 1998; Pérez-Mellado et al. 2013).

### Experimental design

#### *Food and conspecific stimuli*

As food stimuli, in each trial, we used two identical pieces of watermelon (*Citrullus lanatus*) of around 50 g and same shape and size (Fig. 1a). We replaced the two pieces by two new pieces every 3–4 trials or when pieces were clearly bitten by lizards.

As lizard stimuli, we employed living lizards and copper models of lizards, trying to dissociate between the stimulus of a moving lizard and the stimulus of a lizard without movement. In the case of living lizards and in order to keep them together, we put lizards in a transparent glass jar, 21 × 15 × 15 cm, with a hermetic seal. In this way, we tried to prevent any odour from lizards acting as an

additional stimulus. We used another identical empty jar as a control (Fig. 1c).

We employed black lizard-shaped copper models moulded from a preserved specimen of an adult male of the Balearic lizard of 65 mm SVL (Herpetological collection of Animal Biology Department, University of Salamanca) to test lizards' shape as a stimulus without movement. We placed four copper models touching one of the pieces of fruit, simulating conspecifics eating the fruit (Fig. 1b).

#### Experimental enclosure

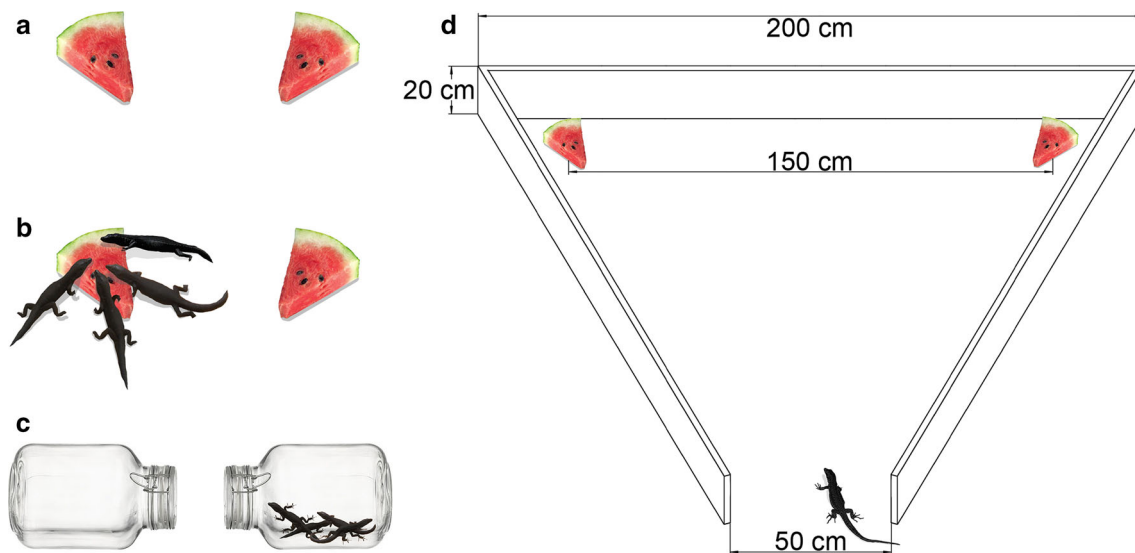
We made a triangular enclosure with three wooden boards 2 m long and 20 cm high each. Two vertices were jointed with a hinge and the third was open. In each trial, we placed the enclosure in an open area arranging an entrance of 50 cm width. Lizards were only able to access the inner part of the enclosure from the entrance. We placed the two stimuli 1.5 m apart and near to closed vertexes. Arriving at the entrance of the enclosure, lizards were equidistant from both stimuli (Fig. 1d). We arranged the set of enclosure trials in this way because during the trials without enclosure, we observed some individuals that approached to the nearest piece of fruit from their initial location. We eliminated those trials without enclosure in which a lizard clearly approached closer to one of the pieces of fruit.

#### Behavioural observations

In each trial, we placed paired stimuli, with or without enclosure, in an open area where lizards were active. Two

observers withdrew a minimum of 4 m and stood motionless. In trials where the two stimuli were unequal, that is, the jar with four living lizards versus the jar without lizards, or fruit with copper models versus the fruit without copper models, we exchanged the position of jar with lizards and copper models in each trial. To avoid pseudo-replications, we carried out the trials in four different areas of the island, 100–500 m apart from one another. Also, within each area, we moved the two stimuli 3–10 m away in each trial. The very high lizard density on Aire Island (around 4,000 individuals  $\text{ha}^{-1}$ , Pérez-Mellado et al. 2008) and the size of *P. lilfordi* home ranges during July on Aire Island (95.62–127.58  $\text{m}^2$ , Pérez-Mellado et al. 2013) make it less probable to resample the same individual. Even so, when it was possible, we captured by noosing the lizards that arrived at the stimulus and marked them with a dorsal painted spot. We did not repeat any trial with a marked lizard.

For each trial, we recorded the sequential arrival of the first lizard and next individuals to the stimuli, identifying their sex and age. In trials with food and without copper models, the first lizard acted as demonstrator for the second one, which acted as observer. In the same way, the first and the second lizard acted as demonstrators for the next lizards. In trials with copper models or with glass jars, the demonstrators were the copper models and the lizards inside the jar, while the first lizard that approached the experiment was the observer. We determined that a lizard had chosen one of the stimuli when it began to eat the fruit or when it approached closer than 2 cm to the glass jar. In trials with watermelon pieces as stimuli and without copper



**Fig. 1** Experimental design. **a–c** The three kinds of paired stimuli used in the experiments: **a** two pieces of watermelon; **b** two pieces of watermelon and four copper models touching one of them; **c** four living lizards into one of the two glass jars. **d** Scheme of the

experiments made with the triangular enclosure. We placed the two stimuli in the two closed vertexes of the enclosure. Lizards gained access to the experimental set through the open vertex, where it was equidistant from the two stimuli

models, we waited until five individuals had chosen any of the stimuli. We also considered the observation finished if one of the lizards chose the stimulus without conspecifics.

We conducted the following sets of trials:

- (a) 67 trials without the enclosure and with two pieces of fruit as stimuli (Fig. 1a). We tested whether lizards from a large area were attracted towards the piece of fruit with foraging conspecifics, using both visual and chemical cues. We also tested the role of the number of conspecifics in the decision of the arriving lizard.
- (b) 118 trials with the enclosure and with two pieces of fruit as stimuli (Fig. 1a, d). We tested whether lizards were attracted towards the piece of fruit with conspecifics, using both visual and chemical cues. These trials were done in a more controlled way than the trials without the enclosure. We also tested the importance of the number of foraging conspecifics in the decision of the arriving lizard.
- (c) 80 trials with the enclosure, two pieces of fruit and four copper models of lizards in one of the pieces of fruit (Fig. 1b, d). In these trials, we tried to remove some possible inadvertent cues sent by conspecifics, such as movement or chemical cues, and to test whether the mere presence of lizard copper models close to a piece of food was enough to attract lizards.
- (d) 31 trials with the enclosure, with two glass jars as stimuli, one jar containing four lizards and one jar empty (Fig. 1c, d). We tested whether the presence and activity of a group of conspecifics was attractive for lizards, even in the absence of food. Due to the low participation of females, we were unable to obtain a higher sample size in this condition.

### Statistical analyses

Statistical analyses were carried out with R version 3.1.0 (R Core Team 2014). We used two-tailed binomial tests to check whether the proportion of lizards choosing one stimulus was significantly different than expected by chance. If the two stimuli in each set of trials were equally attractive or if lizards chose one of them just by chance, the expected frequency of choosing each stimulus was 0.5. In the trials with two pieces of fruit, we used the decision of the first individual as a control for the equivalence of the two pieces of fruit.

In addition, we examined the choice of the stimulus made by the observer lizard with a generalised linear model (GLM) with binomial errors (Crawley 2013). The response variable was the “choice of the observer”. The explanatory variables were the following: the “side of the demonstrator”, the sex of the demonstrator lizard, the sex of the

observer lizard and the interactions among all these variables. “Side of the demonstrator” includes, in the case of trials with two pieces of fruits, the piece where the first lizard arrived and, in trials with copper models, the piece where models were placed, as well as in the trials with jars, the jar with the four enclosed lizards. The “choice of the observer” and “side of the demonstrator” variables had two levels: “left” and “right”, in reference to the side, viewed from our position, of the chosen stimulus. We initially defined the saturated model for each set of trials, with all the explanatory variables and their interactions. We obtained the minimal adequate model following a stepwise deletion of the non-significant ( $P > 0.05$ ) factors and interactions and using the Akaike’s information criterion (AIC, Burnham and Anderson 2004). For each model, we verified that there was no overdispersion (Crawley 2013).

To test whether the number of demonstrator lizards at the stimulus had an influence on the decision made by the next lizard approaching, we compared the relative frequencies of visits to the stimulus with lizards when number of demonstrators ranged from one to four. We pooled data for trials with and without the enclosure with pieces of fruit after ascertaining that there were no significant differences due to the kind of treatment in the response of the third and next individuals (Fisher tests). In this way, we obtained a higher sample size of trials with four lizards eating at the same piece. We compared those relative frequencies with a  $G$  test with Williams’ correction.

We tested whether four copper models produced a similar effect as four living lizards, and whether four lizards at a piece of fruit elicited a similar response in the observer lizard as four lizards enclosed in a jar without any food stimulus. We compared the relative frequencies of lizards that chose the stimulus with lizards or models in the different situations with  $G$  tests with Williams’ correction. Significance tests were two-tailed with  $\alpha = 0.05$ .

## Results

### Two pieces of fruit without enclosure

We performed 67 trials. In 36 of them, the first individual to access the fruit was an adult male and in 31 trials it was an adult female. As lizards arriving in the second place, we observed 42 adult males and 25 adult females.

The first lizards of each trial showed no preference for either the right- or left-hand side piece of fruit (binomial test,  $P = 0.6254$ , probability of success = 0.5373,  $N = 67$ ). The next observers approached to the piece of fruit where the demonstrator was eating significantly more frequently than to the unoccupied piece ( $P < 0.001$ ,

probability of success = 0.8210). Both male and female demonstrators were followed by an observer in proportions significantly different from 0.5 (males  $P < 0.001$ , probability of success = 0.917; females:  $P = 0.0295$ , probability of success = 0.71). Nevertheless, the relative frequency of observers that followed a male demonstrator was significantly higher than the relative frequency that followed a female demonstrator ( $G$  test,  $G = 4.7727$ ,  $df = 1$ ,  $P = 0.029$ ). After simplifying the saturated GLM model, we found that the choice of the observer was significantly driven by the side of the demonstrator, but not by the sex of the demonstrator or the observer (Table 1).

### Two pieces of fruit within the enclosure

We observed 118 lizards arriving to pieces of fruit as the first individuals; 62 were adult males, 54 were adult females and 2 were subadult lizards. We performed the statistical analyses only with adult lizards. As the second individuals arriving to pieces of fruit we observed 74 adult males and 42 adult females.

Again here, the proportion of first individuals that chose the right-hand side piece of fruit was not different from 0.5 (binomial test,  $P = 0.1634$ , probability of success = 0.5690). All four combinations of the sex of the first and the second individuals showed significant differences from 0.5 in the proportion of observers that ate the piece of fruit where the demonstrator was eating (see results in Table 2). Moreover, the choice of the observer was only significantly driven by the side where the observer was eating (Table 3).

### Copper models within the enclosure

We performed 80 trials, 40 of them with adult males, 35 with adult females and 5 with subadult individuals. We only examined the results of trials with adult individuals.

Overall, lizards significantly preferred to approach and eat from the fruit with the four lizard-shaped copper models (binomial test,  $P = 0.0011$ , probability of success = 0.693). However, while males showed a preference

**Table 1** Minimal adequate model from the GLM analysis for the choice of the observer in trials without the enclosure and two pieces of fruit

	Estimate	SE	$z$ value	$P$
Intercept	1.2993	0.6513	1.995	0.0461
SexDem	1.0033	0.9870	1.016	0.3094
SideDem	-1.9054	0.8257	-2.308	0.0210
SexDem/sideDem	-2.9621	1.5195	-1.949	0.0512

Residual deviance: 57.232 on 63 degrees of freedom

*SexDem* sex of the demonstrator, *SideDem* side of the demonstrator

**Table 2** Results from two-tailed binomial tests for enclosure trials with two pieces of fruit

SexDem.	SexObs.	$N$	Proportion	$P$
Male	Male	37	0.7838	0.0008
Male	Female	25	0.76	0.0146
Female	Male	37	0.6757	0.0470
Female	Female	17	0.8235	0.0064

*SexDem.* and *SexObs.* sex of the demonstrator and observer,  $N$  total number of trials, *Proportion* proportions of observers that chose the piece of fruit where the demonstrator was eating,  $P$   $P$  values obtained from two-tailed binomial tests

**Table 3** Minimal adequate model from the GLM analysis for the choice of the observer in enclosure trials with two pieces of fruit

	Estimate	SE	$z$ value	$P$
Intercept	1.4053	0.3095	4.541	5.61e-06
SideDem	-2.1591	0.4332	-4.984	6.24e-07

Residual deviance: 128.18 on 114 degrees of freedom

*SideDem* side of the demonstrator

**Table 4** Minimal adequate model from the GLM analysis for the choice of the observer in enclosure trials with two pieces of fruit and copper models

	Estimate	SE	$z$ value	$P$
Intercept	-0.8602	0.3597	-2.392	0.0168
SideDem	1.6334	0.5012	3.259	0.0011

Residual deviance: 92.431 on 73 degrees of freedom

*SideDem* side of the copper models

for the fruit with copper models ( $P = 0.0064$ , probability of success = 0.725), females' decision did not differ from 0.5 ( $P = 0.0895$ , probability of success = 0.6571). Nevertheless, male and female relative frequencies were not significantly different ( $G$  test,  $G = 0.394$ ,  $df = 1$ ,  $P = 0.5302$ ). We confirmed that lizards preferred a piece of fruit only because of the presence of copper models, irrespective of the sex (Table 4).

### Two glass jars within the enclosure

We performed 31 trials, with 18 adult males, 5 adult females and 8 subadults. Lizards significantly approached more frequently the jar with enclosed lizards (binomial test,  $P < 0.001$ , probability of success = 0.8064). Males chose the jar with lizards more frequently than expected ( $P = 0.0013$ , probability of success = 0.8889), but females' and subadults' differences were not significant (females:  $P = 1$ , probability of success = 0.6; subadults:  $P = 0.2891$ , probability of success = 0.75), probably due



to our small sample size. The choice of the observer significantly differed depending on the side where the jar with lizards was. We did not find differences between the response of males, females and subadults (Table 5).

### Number of conspecifics

We conducted 183 trials with two pieces of fruit where a second lizard arrived to the trial after a conspecific. 81 lizards approached the pieces of fruit when the first and the second lizard were eating the same piece of fruit; 50 lizards approached the pieces of fruit when the three previous lizards were eating the same piece, and 36 lizards also approached the piece of fruit with four lizards eating together.

Individuals of both sexes chose significantly more times the piece of fruit with one lizard, two or three lizards (Fig. 2). With four lizards at one of the pieces of fruit, males significantly chose that piece, but not females (males:  $P < 0.001$ , probability of success = 0.8696; females:  $P = 1$ , probability of success = 0.5385; see Fig. 2). These relative frequencies of males and females as individuals arriving in the fifth position were significantly different ( $G$  test,  $G = 4.4349$ ,  $P = 0.0352$ ). The frequencies of females that chose the occupied piece were similar to one to four demonstrators ( $G$  test,  $G = 3.3285$ ,  $df = 3$ ,  $P = 0.3437$ ). We observed differences in the frequencies of males that chose the occupied piece depending on the number of demonstrators ( $G = 9.372$ ,  $df = 3$ ,  $P = 0.0247$ ). Specifically, there were significant differences between the frequencies shown with one and three demonstrators ( $G = 8.5331$ ,  $df = 1$ ,  $P = 0.0035$ , Fig. 2).

In trials with four copper models, the response of the lizards was similar to that shown in trials with four living lizards at the same piece of fruit ( $G$  test,  $G = 0.3787$ ,  $df = 1$ ,  $P = 0.5383$ ). Also the number of lizards that chose the glass jar with four conspecifics was similar to the number of lizards that chose the piece of fruit with four conspecifics ( $G$  test,  $G = 0.2969$ ,  $df = 1$ ,  $P = 0.5858$ ).

## Discussion

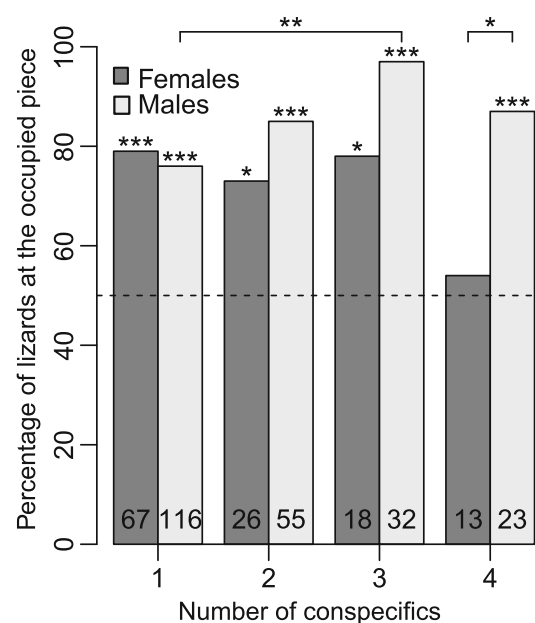
Local enhancement may be a consequence of conspecific attraction (Leadbeater and Chittka 2007). Although local

**Table 5** Minimal adequate model from the GLM analysis for the choice of the observer in trials with two glass jars

	Estimate	SE	$z$ value	$P$
Intercept	1.3863	0.6455	2.148	0.0317
SideDem	-2.8526	0.9094	-3.137	0.0017

Residual deviance: 30.455 on 29 degrees of freedom

SideDem side where the glass jars with four living lizards were placed



**Fig. 2** Proportion of lizards that chose the piece of fruit with demonstrators expressed according to the number of demonstrators ( $I$  to 4). The asterisks directly above the bars indicate a significant difference from an even distribution, set at 50%. The asterisks above segments indicate significant differences between the analysed groups ( $*P < 0.05$ ;  $**P < 0.01$ ;  $***P < 0.001$ ). Numbers within bars are sample sizes

enhancement does not necessarily result in social transmission, it could cause groups of animals to acquire similar behavioural repertoires (Hoppitt and Laland 2013). Lizards can use social information to learn how to enhance their foraging opportunities (Doody et al. 2013; Kis et al. 2014; Noble et al. 2014).

In our experiments, when lizards had the opportunity to choose between two identical pieces of fruit, they significantly ate from the piece where there was a conspecific. The alternative piece of fruit may be a better option, because the newcomer would not share it with any other competitor until the arrival of the next lizard. That is, conspecifics would act as competitors (Baude et al. 2011), and observers would be expected to avoid the patch where another conspecific is foraging. Some studies support the idea that conditions are optimal at intermediate densities of competitors. With a low density of conspecifics, they would act as informers, but with a higher density, conspecifics would act as competitors (Fletcher 2006; Baude et al. 2011 and references therein). Our findings do not match these predictions. In Aire Island, with one of the highest known lizard densities (Pérez-Mellado et al. 2008), conspecifics apparently would act mainly as informers. Hence, a foraging conspecific sends out inadvertent social information about the profitability and perhaps the quality of food (Valone and Templeton 2002; Danchin et al. 2004).

Even more, lizards were attracted to a group of conspecifics even if there was no food, as we observed in the trials with glass jars. [Hanna and Eason \(2013\)](#) showed that juvenile crab spiders, *Mecaphesa asperata*, are attracted to flowers where there is a small number of conspecifics, suggesting that conspecifics are a powerful and accurate cue of productive foraging sites even for solitary foragers.

Our results with artificial copper models show that *P. lilfordi* also choose to feed from the piece of fruit occupied by models. That is, it seems that *P. lilfordi* recognises these models as conspecifics. When the demonstrator is a live conspecific, the observer can use its presence, movement or chemical cues. However, copper models just give visual and static information. Movement and activity of conspecifics can attract lizards from long distances ([Rand et al. 1975](#); [Whiting and Greef 1999](#)), while the behaviour of conspecifics is more likely to be useful at shorter distances ([Whiting and Greef 1997, 1999](#)). The decisions made by the observer lizards with real and artificial models confirm that the mere presence of a conspecific is enough to show a minimal quality of the piece chosen in contrast to the alternative ([Stamps 1987](#); [Valone and Templeton 2002](#); [Danchin et al. 2004](#)).

Some studies show a different use of social information depending on the sex of demonstrator and/or observer ([Aragón et al. 2006](#); [Aragón 2009](#); [Carazo et al. 2014](#)). We observed that males and females of *P. lilfordi* gave and used social information with a similar reliability. Nevertheless, when a piece of fruit was exploited by more than four lizards, females seemed not to use conspecific information and approached the occupied and the empty patch in a similar proportion, but in this case, sample size was too low to give much confidence. Male lizards are differentially attracted to the occupied patch depending on the number of foraging conspecifics. Several studies suggest that conspecific attraction is positively related to the number of conspecifics on a patch (e.g. [Beauchamp et al. 1997](#); [Stamps et al. 2005](#); [Rieucan and Giraldeau 2009, 2011](#)). Newcomers may use the number of conspecifics as a cue to assess patch quality or may decide to join a group to benefit from foraging in larger groups. As higher groups of individuals are usually associated with richer foraging patches, the attraction to those higher groups would reduce the time and energy spent on searching for productive foraging patches ([Beauchamp et al. 1997](#)). Males of *P. lilfordi* showed more attraction towards the piece of fruit with three than with one foraging conspecifics. We do not know how the response with a larger group of conspecifics is, although it would be desirable to test whether the response is asymptotic or whether it declines ([Stamps et al. 2005](#)). Our experimental setting precluded that situation because it was difficult to get enough trials with five or more lizards eating the same piece of fruit to statistically test this hypothesis. Thus, we decided to stop the trial after

the choice of the fifth lizard. A higher number of conspecifics exploiting a patch also imply a higher number of competitors for an exhaustible resource. For example, hungry young crab spiders, *M. asperata*, are attracted to flowers with a relatively low number of conspecifics, but avoid flowers with four or more individuals ([Hanna and Eason 2013](#)). Thus, the weaker competitors would be more affected by the increase in the number of foraging conspecifics and would show a lower level of conspecific attraction ([Caraco et al. 1989](#)). That could be the reason why, in *P. lilfordi*, females do not show any difference on conspecific attraction with different number of conspecifics. However, we cannot discard other reasons related to the differences between male and female social roles ([Carazo et al. 2014](#)). Nevertheless, we would need to increase the sample size with four foraging conspecifics to obtain meaningful results about the similarities and differences between sexes.

*Podarcis lilfordi* have several characteristics in common with other lizards that also show social foraging ([Kiestler 1975](#); [Rand et al. 1975](#); [Whiting and Greef 1997, 1999](#); [Eifler and Eifler 2014](#)). The majority of them inhabit islands with poor and unpredictable resources and a low predation pressure, allowing lizards to be generalist foragers ([Kiestler 1975](#); [Rand et al. 1975](#); [Pérez-Mellado and Corti 1993](#); [Eifler and Eifler 2014](#)). Social foraging as the result of attraction to feeding conspecifics is mostly observed on divisible and temporally abundant food, such as eggs, fruits or carcasses ([Kiestler 1975](#); [Rand et al. 1975](#); [Whiting and Greef 1997, 1999](#); [Eifler and Eifler 2014](#); pers. obs). In Aire Island, lizards also forage on some plants with similar results ([Pérez-Mellado et al. 2000a, b, 2007](#); [Pérez-Cembranos and Pérez-Mellado in press](#)).

In summary, our experiments reveal that *P. lilfordi* shows a strong attraction towards foraging conspecifics, at least up to three or four in number, but also towards a foraging patch with immobile lizards or even towards a group of conspecifics without food. Thus, the Balearic lizard is able to use conspecifics as a source of information to locate food and to decide where to feed, even if they can choose an alternative empty patch. The most parsimonious explanation to this behaviour is that there is a conspecific attraction and local enhancement.

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**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical standard** The experiments reported in this paper complied with the current laws of the country where they were performed (Spain). Lizards were studied thanks to special permits from the Servei de Protecció d'Espècies, Conselleria de Medi Ambient, Balearic Government, Spain (CEP 03/2011 and CEP 34/2013).

## References

- Aragón P (2009) Sex-dependent use of information on conspecific feeding activities in an amphibian urodelian. *Funct Ecol* 23:380–388. doi:[10.1111/j.1365-2435.2008.01519.x](https://doi.org/10.1111/j.1365-2435.2008.01519.x)
- Aragón P, Massot M, Gasparini J, Clobert J (2006) Socially acquired information from chemical cues in the common lizard, *Lacerta vivipara*. *Anim Behav* 72:965–974. doi:[10.1016/j.anbehav.2005.11.023](https://doi.org/10.1016/j.anbehav.2005.11.023)
- Baude M, Danchin E, Mugabo M, Dajoz I (2011) Conspecifics as informers and competitors: an experimental study in foraging bumble-bees. *Proc R Soc Lond B* 278:2806–2813. doi:[10.1098/rspb.2010.2659](https://doi.org/10.1098/rspb.2010.2659)
- Beauchamp G, Bélisle M, Giraldeau LA (1997) Influence of conspecific attraction on the spatial distribution of learning foragers in a patchy habitat. *J Anim Ecol* 66:671–682
- Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociol Methods Res* 33:261–304. doi:[10.1177/0049124104268644](https://doi.org/10.1177/0049124104268644)
- Caraco T, Barkan C, Beacham JL, Brisbin L, Lima S, Mohan A, Newman JA, Webb W, Withiam ML (1989) Dominance and social foraging: a laboratory study. *Anim Behav* 38:41–58. doi:[10.1016/S0003-3472\(89\)80064-8](https://doi.org/10.1016/S0003-3472(89)80064-8)
- Carazo P, Noble DWA, Chandrasoma D, Whiting MJ (2014) Sex and boldness explain individual differences in spatial learning in a lizard. *Proc R Soc B* 281:20133275. doi:[10.1098/rspb.2013.3275](https://doi.org/10.1098/rspb.2013.3275)
- Coolen I, Ward AJW, Hart PJB, Laland KN (2005) Foraging nine-spined sticklebacks prefer to rely on public information over simpler social cues. *Behav Ecol* 16:865–870. doi:[10.1093/beheco/ari064](https://doi.org/10.1093/beheco/ari064)
- Crawley MJ (2013) *The R book*, 2nd edn. Wiley, Chichester
- Dall SRX, Giraldeau LA, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. *Trends Ecol Evol* 20:187–193. doi:[10.1016/j.tree.2005.01.010](https://doi.org/10.1016/j.tree.2005.01.010)
- Danchin E, Giraldeau LA, Valone TV, Wagner RH (2004) Public information: from nosy neighbors to cultural evolution. *Science* 305:487–491. doi:[10.1126/science.1098254](https://doi.org/10.1126/science.1098254)
- Doody JS, Burghardt GM, Dinets V (2013) Breaking the social–non-social dichotomy: a role for reptiles in vertebrate social behavior research? *Ethology* 119:95–103. doi:[10.1111/eth.12047](https://doi.org/10.1111/eth.12047)
- Eifler DA, Eifler MA (2014) Social foraging in the lizard *Ameiva corax*. *Behav Ecol* 25:1347–1352. doi:[10.1093/beheco/aru129](https://doi.org/10.1093/beheco/aru129)
- Fletcher RJ (2006) Emergent properties of conspecific attraction in fragmented landscapes. *Am Nat* 168:207–219. doi:[10.1086/505764](https://doi.org/10.1086/505764)
- Galef BG, Giraldeau LA (2001) Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Anim Behav* 61:3–15. doi:[10.1006/anbe.2000.1557](https://doi.org/10.1006/anbe.2000.1557)
- Giraldeau LA, Valone TJ, Templeton JJ (2002) Potential disadvantages of using socially acquired information. *Philos Trans R Soc Lond B Biol Sci* 357:1559–1566. doi:[10.1098/rstb.2002.1065](https://doi.org/10.1098/rstb.2002.1065)
- Greenberg N (1976) Observations of social feeding in lizards. *Herpetologica* 32:348–352
- Hanna CJ, Eason PK (2013) Juvenile crab spiders (*Mecaphesa asperata*) use indirect cues to choose foraging sites. *Ethol Ecol Evol* 25:161–173. doi:[10.1080/03949370.2012.742464](https://doi.org/10.1080/03949370.2012.742464)
- Hoppitt W, Laland KN (2013) *Social learning: an introduction to mechanisms, methods and models*. Princeton University Press, Princeton
- Kiester AR (1975) Notes on the natural history of *Diploglossus millepunctatus* (Sauria: Anguillidae). In: Graham JB (ed) *The biological investigation of Malpelo Island, Colombia*. Smithsonian contributions to zoology, vol 176. Smithsonian Institution Press, Washington DC, pp 39–43
- Kiester AR (1979) Conspecifics as cues: a mechanism for habitat selection in the Panamanian grass anole (*Anolis aeneus*). *Behav Ecol Sociobiol* 5:323–330. doi:[10.1007/BF00292522](https://doi.org/10.1007/BF00292522)
- Kis A, Huber L, Wilkinson A (2014) Social learning by imitation in a reptile (*Pogona vitticeps*). *Anim Cogn*. doi:[10.1007/s10071-014-0803-7](https://doi.org/10.1007/s10071-014-0803-7)
- Leadbeater E, Chittka L (2005) A new mode of information transfer in foraging bumblebees? *Curr Biol* 15:R447–R448. doi:[10.1016/j.cub.2005.06.011](https://doi.org/10.1016/j.cub.2005.06.011)
- Leadbeater E, Chittka L (2007) The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*). *Behav Ecol Sociobiol* 61:1789–1796. doi:[10.1007/s00265-007-0412-4](https://doi.org/10.1007/s00265-007-0412-4)
- Maynard-Smith J, Harper D (2003) *Animal signals*. Oxford University Press, Oxford
- Noble DWA, Byrne RW, Whiting MJ (2014) Age-dependent social learning in a lizard. *Biol Lett* 10:20140430. doi:[10.1098/rsbl.2014.0430](https://doi.org/10.1098/rsbl.2014.0430)
- Pérez-Cembranos A, Pérez-Mellado V (in press) The effect of plant consumption in the overall diet of an omnivorous lizard. Salamandra
- Pérez-Mellado V (1989) Estudio ecológico de la lagartija balear *Podarcis lilfordi* (Günther 1874) en Menorca. *Revista de Menorca* 80:455–511
- Pérez-Mellado V (1998) *Podarcis lilfordi* (Günther 1874). In: Salvador A (coord.) *Reptiles*. In: Ramos MA et al (eds) *Fauna Ibérica*, vol 10. Museo Nacional de Ciencias Naturales, CSIC, Madrid, pp 272–282
- Pérez-Mellado V, Corti MM (1993) Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). *Bonn Zool Beitr* 44:193–220
- Pérez-Mellado V, Cortázar G, López-Vicente M, Perera A, Sillero N (2000a) Interactions between the Balearic lizard *Podarcis lilfordi* and the plant *Dracunculus muscivorus*. *Amphib Reptil* 21:223–226. doi:[10.1163/156853800507390](https://doi.org/10.1163/156853800507390)
- Pérez-Mellado V, Ortega F, Martín-García S, Perera A, Cortázar G (2000b) Pollen load and transport by the insular lizard, *Podarcis lilfordi* (Squamata, Lacertidae) in coastal islets of Menorca (Balearic Islands, Spain). *Isr J Zool* 46:193–200. doi:[10.1560/QMY9-PXWF-AG43-RP6F](https://doi.org/10.1560/QMY9-PXWF-AG43-RP6F)
- Pérez-Mellado V, Riera N, Hernández-Estévez JA, Piccolo V, Potter C (2007) A complex case of interaction between lizards and plants. The dead horse arum (*Dracunculus muscivorus*) and the Balearic lizard (*Podarcis lilfordi*). In: Biaggini M, Corti C, Lo Cascio P (eds) *Mainland and insular lacertid lizards: a Mediterranean perspective*. Firenze University Press, Firenze, pp 133–160
- Pérez-Mellado V, Hernández-Estévez JA, García-Díez T, Terrassa B, Ramón MM, Castro J, Picornell A, Martín-Vallejo J, Brown R (2008) Population density in *Podarcis lilfordi* (Squamata, Lacertidae), a lizard species endemic to small islets in the Balearic Islands (Spain). *Amphib Reptil* 29:49–60. doi:[10.1163/156853808783431587](https://doi.org/10.1163/156853808783431587)
- Pérez-Mellado V, García-Díez T, Hernández-Estévez JA, Herrero-Ayuso C, Riera N, Catalán I (2013) El uso del espacio en la lagartija balear *Podarcis lilfordi*. Factores causales en la Isla del Aire. *Revista de Menorca* 92:189–218



- Pöysä H (1992) Group foraging in patchy environments: the importance of coarse-level local enhancement. *Ornis Scand* 23:159–166
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org/>
- Rand AS, Gorman GC, Rand WM (1975) Natural history, behaviour, and ecology of *Anolis agassizi*. In: Graham JB (ed) The biological investigation of Malpelo Island, Colombia. Smithsonian contributions to zoology, vol 176. Smithsonian Institution Press, Washington DC, pp 27–38
- Rieucou G, Giraldeau LA (2009) Persuasive companions can be wrong: the use of misleading social information in nutmeg manikins. *Behav Ecol* 20:1217–1222. doi:10.1093/beheco/arp121
- Rieucou G, Giraldeau LA (2011) Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. *Philos Trans R Soc B* 366:949–957. doi:10.1098/rstb.2010.0325
- Ruxton GD, Hall SJ, Gurney WSC (1995) Attraction toward feeding conspecifics when food patches are exhaustible. *Am Nat* 145:653–660
- Sontag C, Wilson DS, Wilcox RS (2006) Social foraging in *Bufo americanus* tadpoles. *Anim Behav* 72:1451–1456. doi:10.1016/j.anbehav.2006.05.006
- Stamps JA (1987) Conspecifics as cues to territory quality: a preference of juvenile lizards (*Anolis aeneus*) for previously used territories. *Am Nat* 129:629–642
- Stamps J, McElreath R, Eason P (2005) Alternative models of conspecific attraction in flies and crabs. *Behav Ecol* 16:974–980. doi:10.1093/beheco/ari083
- Thorpe WH (1963) Learning and instinct in animals, 2nd edn. Methuen, London
- Valone TJ (1989) Group foraging, public information, and patch estimation. *Oikos* 56:357–363. doi:10.2307/3565621
- Valone TJ, Templeton JT (2002) Public information for the assessment of quality: a widespread social phenomenon. *Philos Trans R Soc Lond B* 357:1549–1557. doi:10.1098/rstb.2002.1065
- Wagner RH, Danchin E (2010) A taxonomy of biological information. *Oikos* 119:203–209. doi:10.1111/j.1600-0706.2009.17315.x
- Whiting MJ, Greef JM (1997) Facultative frugivory in the Cape flat Lizard, *Platysaurus capensis* (Sauria: Cordylidae). *Copeia* 1997:811–818. doi:10.2307/1447298
- Whiting MJ, Greef JM (1999) Use of heterospecific cues by the lizard *Platysaurus broadleyi* for food location. *Behav Ecol Sociobiol* 45:420–423. doi:10.1007/s002650050579