



# Foraging decisions of rock lizards may be dependent both on current rival assessment and dear enemy recognition

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## ABSTRACT

Foraging strategies aim to maximize the amount of food obtained while minimizing searching costs. To reduce these costs, animals use different strategies based on the use of personal or social information to exploit food patches. At the same time, the social attraction for food resources could increase competition intensity for them. Prior experiences of animals regarding social risk and the foreknowledge of the competitors might drive the foraging strategies. In this paper, we examined experimentally whether rock lizards used behavioural strategies to reduce the risks of foraging in presence of potential competitors. We measured the foraging behaviour of a lizard resident to a territory (i.e. terrarium), in the presence of both familiar and unfamiliar conspecifics (potential competitors). We considered whether foraging choices between two food sources of different value (i.e. quantity) are influenced by familiarity with the intruder and the evaluation of its competitive ability based on body size differences between lizards. We found differences in the number of attacks performed to the best food source, with more attacks when the intruder was unfamiliar. The results suggest evidence of both dear enemy recognition and current rival assessment modulate the foraging choices depending on the identity and the social relationship with the intruder.

## 1. Introduction

Foraging behaviour is affected by factors such as predation risk, social interactions, learning experience, or physiological condition of animals (Perry and Pianka, 1997). The Foraging Theory predicts that an animal should select the patch with the highest prey abundance when choosing between two patches containing the same prey type (MacArthur and Pianka, 1966). However, foraging strategies are constrained by maximizing the amount of food obtained while at the same time minimizing searching costs (Charnov, 1976). To deal with this trade-off, animals may opt for obtaining 'Personal Information', searching for food on their own; or for using 'Social Information', looking at other foraging conspecifics (Kendal et al., 2004).

Social sources of information and their availability have great relevance and may cause direct and indirect density-dependent effects in animal populations (Gil et al., 2018; Krebs, 1974) due to conspecific attraction (Beauchamp and Ruxton, 2014; Fletcher, 2006; Stamps, 1988). An example of how social information drives some kinds of conspecific attraction (Dal, 2005; Thorpe, 1963) is 'local enhancement'. This occurs when interactions with an object, such as food, are more

frequent due to the past or present interactions of other conspecific with the object (Hoppitt and Laland, 2008). Local enhancement has been described in several birds (Cadieu et al., 1995; Bairos-Novak et al., 2015; but see Gerhardt and Taliaferro, 2003), amphibians (Chapman et al., 2015), and reptiles (Pérez-Cembranos and Pérez-Mellado, 2015). Particularly in lizards, the ability to use Social Information from conspecifics and heterospecifics during foraging has been recently demonstrated (Damas-Moreira et al., 2018).

Searching dynamics and information acquisition when foraging occurs in the presence of others have been explained using the cost-benefits balance of each individual's strategy (Kendal et al., 2004; Rieucan and Giraldeau, 2011). For example, the trade-offs and the evolutionary stability in social foraging strategies have been modelled under the 'Producer-Scrounger game' framework (Barnard and Sibly, 1981). However, the behavioural strategies of producers (active foragers) and scroungers (competitors using social vigilance) might not be always persistent (but see Harten et al., 2018). Those strategies might show some plasticity (Morand-Ferron et al., 2011a) according to social contexts like population density (Coolen, 2002; Dumke et al., 2016) or dominance (Liker and Barta, 2002). While at the same time the

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individual differences between animals remain consistent (Morand-Ferron et al., 2011b).

In this paper, we focus on the perspective of solitary foragers, which obtain personal information but, simultaneously, could be releasing it as public information available for conspecific intruders (Dall, 2005; Gir-aldeau et al., 2002). The presence of competitors influences the foraging behaviour have been tested just in a few species and taxa, for example, crabs *Carcinus maenas* (Chakravarti and Cotton, 2014) and humming-birds *Calothorax lucifer* (Márquez-Luna et al., 2017). Foraging behaviour may be conditioned by 'Social risk', which is defined as the risk posed by rivals. Social risk is also associated with the presence of competitors and less often with changes in food density (Beauchamp, 2019). Then, conspecifics may exert social vigilance over foragers (Beauchamp, 2015), which could have a differential social-foraging behaviour depending on perceived social risk. We explored foraging decisions of the forager when a conspecific intruder (a potential competitor) is present in relation to the foreknowledge of the intruder, being either familiar for the forager (dear enemy recognition) or unfamiliar (current rival assessment).

We used Carpetan rock lizard *Iberolacerta cyreni* as a model. Males of this lizard defend territories according to their quality in the abundance of dietary resources and females (Aragón et al., 2004; Martín and Salvador, 1995). We designed a laboratory experiment in which a resident forager was exposed to a food-choice test between two sources of food with the same type of prey but in different amounts and, in the presence of a conspecific intruder. This intruder was considered only as a 'potential' competitor because, in our experiment, it could not interact with the food but just exert social vigilance over the forager's behaviour (Beauchamp, 2015). Male rock lizards are often found in high densities in the wild, leading to the emergence of dominance hierarchies (Martín and Salvador, 1997, 1993). Furthermore, it is known that this lizard species uses strategies to reduce the costs of agonistic encounters such as memorizing information about the competitive ability of rivals (Aragón et al., 2000), recognizing them individually (Aragón et al., 2001a, b), and scent matching of the resource holders (López and Martín, 2011). Then, our study can be understood using the framework of territorialism and the 'Dear enemy recognition' theory, in which behavioural responses are different to familiar competitors than to strangers (Jaeger, 1981; Wilson, 2021) as it has been previously described in this lizard (Aragón et al., 2007).

According to previous findings in which *I. cyreni* was exposed to a similar food-choice test (Recio et al., 2021), we expected that the lizards would interact more often with the highest food source (searching, hunting...). We expected that an animal would interact with a food source in presence of a conspecific intruder in a different way when the intruder was familiar (i.e. higher frequency of interactions with the best food source) than when it was unfamiliar. We assumed that differences in body size between two lizards determine their potential dominance relationships (Aragón et al., 2007). Thus, we hypothesized that, if the frequency of social interactions differed between familiar and unfamiliar lizards, then the mechanism involved in familiar recognition and current rival assessment should be different; while the absence of differences would not allow us to conclude that recognition and assessment of the intruder through social interactions was taking place. Nevertheless, we expected that differences in foraging behaviour according to familiarity with the intruder might reflect dear enemy recognition instead of current rival assessment. Finally, we hypothesized that, if there was an effect of dominance in foraging behaviour, there would exist a relationship between the difference in body size with the intruder and the frequency of interactions with food (i.e. fewer interactions with food when the intruder was bigger).

## 2. Methods

### 2.1. Study animals

Subjects were 37 adult male *I. cyreni* lizards captured in June 2016 at Alto del Telégrafo (Guadarrama Mountains, Central Spain) over an area of around 18 ha. Distances between captures were at least 25 m which was quite larger than the mean overlap distance between home ranges (13,7 m<sup>2</sup>) (Aragón et al., 2001b) and enough to assume that the lizards were not familiar. Lizards were housed in captivity for two weeks before the experiments at "El Ventorrillo" field station (MNCN-CSIC), about 5 km away from capture sites. The animals were measured (snout-vent length, head length, head width, head high, to the nearest 0.01 mm) and weighted (to the nearest 0.01 g). We housed lizards for 15 days in individual terraria (n = 10) or in one of three communal terraria (n = 27, 9 individuals/group) (see below 'Experimental design' section). Every outdoor terrarium (71 × 46 × 37 cm, length x width x high) had coconut fibre as a substrate, a brick for shelter, and a cup with water. Crickets (*Achaeta domestica*) were provided *ad libitum* as food during the first 10 days of housing; while four days before the experiment, lizards fasted. To ensure that all animals had enough food, we checked every day if there were still uneaten crickets in the terraria.

### 2.2. Experimental design

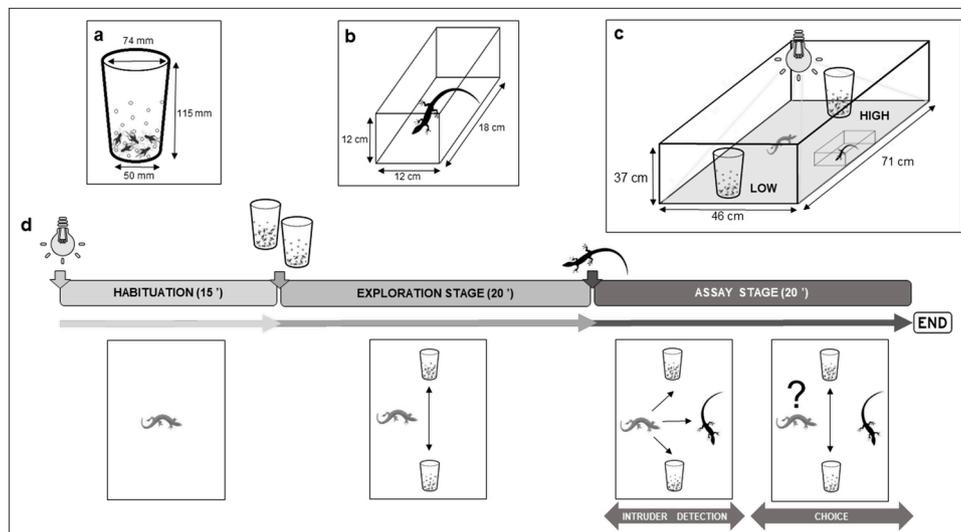
We compared the foraging behaviour of the focal lizard in presence of a conspecific competitor in two different situations: a) with a familiar intruder (that previously had been housed together in the same terrarium) or b) with an unfamiliar one (lizards housed in different terraria), using a counterbalanced design with repeated measures. The procedure to allow lizards to become familiar by housing together in a communal terrarium has been used before in this species with successful results (Aragón et al., 2001a). We selected randomly, from the communal terraria, the lizards that were tested as foragers against a familiar intruder. Lizards acting as intruders, whether familiar or unfamiliar, were selected randomly and each individual was used only in one test.

To allow acclimation, the day before starting the trial, focal lizards were housed in experimental individual terraria with a brick for shelter and a cup with water. The room was set with constant temperature (30 °C) and the only source of light was a bulb (Exo Terra Solar-Glo 125 W) located above the centre of each terrarium. Thirty minutes before starting the experiment, the shelter and the cup were removed and the bulb turned on. Trials were recorded with a digital camera (Panasonic HC-V160, Kodama, Japan).

In each test, the lizard was exposed simultaneously to two different stimuli from the same prey type (crickets) of the same size but with different abundance: 'High' (10 crickets) and 'Low' (5 crickets). Crickets were placed inside plastic transparent cups covered with transparent plastic paper on the rim and perforated in the walls to allow also chemical detection of prey (Fig. 1a). The position of the feeders in each test was randomized. Trials were performed between 12:00 h and 15:00 h (GMT) when lizards were fully active. Each animal was tested on two different days leaving one day between assays.

The trials started when we placed food-containers on each side of the experimental arena (Fig. 1c, d). Each trial consisted of two consecutive stages of 20 min. In the first one, the lizard was allowed to explore the arena, to detect and to assess the value of the two sources of food on its own, without the presence of a conspecific. We did not measure the lizard behaviour at this stage. The second stage was the actual behavioural assay. During which, a conspecific lizard, acting as an intruder and a potential competitor, was placed inside a cage of metallic mesh (wire width < 1 mm, mesh size = 5 mm), and this cage placed in the centre of the arena (Fig. 1b, c), near the terrarium wall.

We measured the number of tongue flicks (TFs) directed to each food-container, the number of visits, and the time spent near to each food-container (in every case approaching the head at least 2 cm next to



**Fig. 1.** a Diagram of the containers with prey-stimulus. b Measures of the cage in which was introduced the intruder. c Diagram of the experimental arena. d Timeline of the experimental procedure.

the container) as behavioural proxies of interest in prey. We also considered the number of attacks directed to food as a clear indication of foraging decisions at any time (Cooper, 1994; Cooper and Burghardt, 1990). Besides, to consider the interactions with the intruder as indicative of rival assessment, we measured the time spent near to the conspecific as well as the number of visits (at least 2 cm next to the cage) and TFs directed to it. To ensure that the lizard was aware of the presence of food and a conspecific intruder, we considered at least valid if the focal animal had visited the two containers in the first stage and had detected the conspecific by approaching near to the cage in the second stage ( $n = 10$ ).

### 2.3. Data analyses

Statistical analyses were performed in R statistical software (version 4.0.2.; R Core Team, 2020). We fitted General Linear Mixed Model ('lme4' package: Bates et al., 2015) with time near the food container as dependent variable; this variable was log-transformed. For the variables visits, TFs, and attacks we fitted Generalized Mixed Models with a Negative Binomial distribution. In the models, we included the intruder's foreknowledge (familiar vs. unfamiliar) and the feeder visited as fixed factors and also the interaction between them. To take into account dominance and fight capacities between lizards we used the differences in body size between forager and intruder which influences agonistic behaviour in this species (Aragón et al., 2000). We summarized all the body measures (log-transformed) using a Principal component analysis (PCA). The difference in the first component scores (87.9 % variance explained) between the forager lizard and the intruder was considered an indirect proxy of dominance and was included in the fixed part of the model as a covariate. As random factors, we included the individual tested, due to the repeated measures design, and also the feeder visited, to control for non-independence.

We also fitted General Linear Models to analyse the time near the intruder and Generalized Linear Models with a Negative Binomial distribution for visits and TFs. As an explanatory factor was added the familiarity with the intruder and, as a covariate, the difference in size between both lizards. The interaction between familiarity and size was also included. We tested the significance of general linear models using the F statistic as the omnibus test, and the likelihood ratio test (LRT) ('lmerTest' package: Zeileis and Hothorn, 2002) in generalized linear models and mixed. The significance of the effects was tested using a Chi-square Wald's test ('car' package: Fox and Weisberg, 2019). We used Tukey's tests for pairwise comparisons ('emmeans' package: Lenth,

2020). In every case, we tested that the models met the assumptions of normality, linearity, and homoscedasticity; and the significance of effects was confirmed using confidence intervals at 95 % level (Bates et al., 2015) (not reported).

## 3. Results

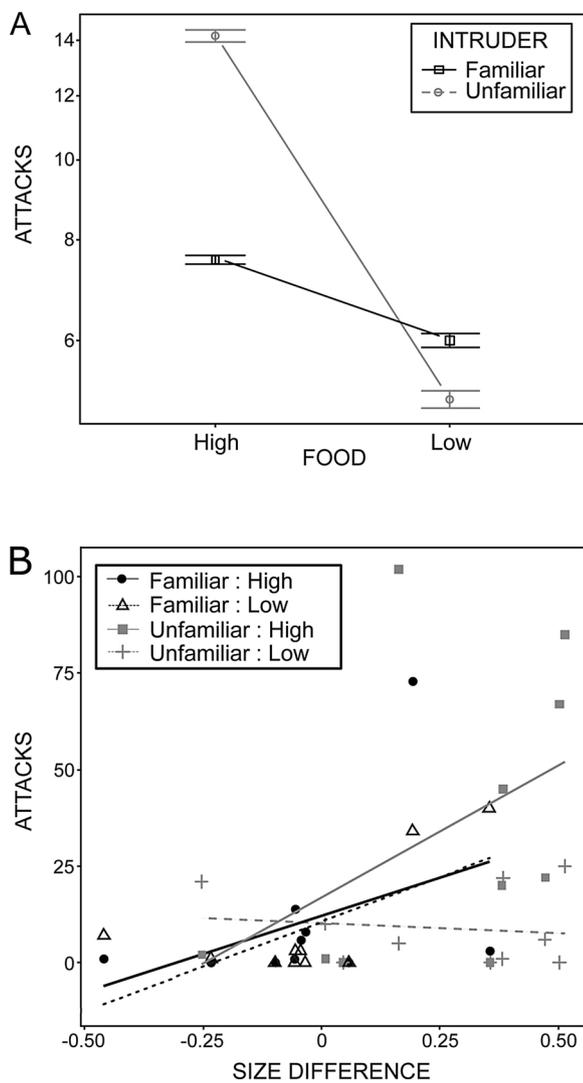
### 3.1. Interactions with the intruder

Regarding the behaviours of interactions with the intruder, none of the models passed the omnibus test for any of the variables measured. Neither in time spent near to the intruder ( $F = 1.52$ ;  $df = 316$ ;  $P = 0.25$ ), the number of visits (LRT:  $X^2 = 1.85$ ;  $df = 2,3$ ;  $P = 0.60$ ) nor the number of TFs directed to the cage (LRT:  $X^2 = 1.34$ ;  $df = 2,3$ ;  $P = 0.72$ ).

### 3.2. Interactions with food

Neither the prior knowledge of the intruder nor the differences in size and the feeders were related to the time spent near the food sources (LRT:  $X^2 = 111.97$ ;  $df = 4,8$ ;  $P = 0.74$ ), neither to the number of TFs (LRT:  $X^2 = 7.61$ ;  $df = 4,8$ ;  $P = 0.11$ ) or visits to the food-containers (LRT:  $X^2 = 0.84$ ;  $df = 4,8$ ;  $P = 0.93$ ). However, this relationship was significant for the number of attacks to food (LRT:  $X^2 = 23.08$ ;  $df = 4,8$ ;  $P = 0.0001$ ). In this case, all the effects included in the model were highly significant.

The number of attacks directed to the higher amount of food was more frequent than to the low food in both treatments ( $X^2 = 326.78$ ;  $P < 0.0001$ ) (Fig. 2). However, there were also significant differences depending on the familiarity with the intruder ( $X^2 = 2536.95$ ;  $P < 0.0001$ ), and in the interaction between feeder type and familiarity ( $X^2 = 4001.24$ ;  $P < 0.0001$ ) (Fig. 2a). Pairwise comparisons revealed that the attacks directed to the feeder with a higher amount of food were significantly much more frequent when the intruder was unfamiliar than when it was familiar (Tukey's tests  $P < 0.0001$  in all comparisons). Finally, the differences in size between intruder and forager contributed to explaining the frequency of attacks ( $X^2 = 51577.05$ ;  $P < 0.0001$ ). The number of attacks was lower when the forager was smaller than the intruder (Fig. 2b). However, the number of attacks when the intruder was familiar increased with the difference of size irrespectively of the food amount, while the trend was different when the intruder was unfamiliar. In this latter case, when the forager was bigger than the intruder, the frequency of attacks to the high food feeder was greater



**Fig. 2.** a. Measures (mean  $\pm$  SE) of attacks in response to feeders (High and Low) according to intruder was familiar or unfamiliar to the resident. b. Size difference between forager and intruder against frequency of attacks for each of the feeders and, according to the foreknowledge with the intruder (Familiar and Unfamiliar) supplementation treatments. Smooth lines were adjusted using generalized linear models for each level factor.

than to the low food one (Fig. 2b).

#### 4. Discussion

The experiment revealed that foreknowledge of the potential competitor might drive the foraging decisions. The presence of differences in the time spent near the intruder or in the number of TFs and visits to it would have thrown light on how recognition and current rival assessment took place. However, since none of the interactions were significant, we did not find evidence about the existence of a differential process involved in rival recognition or assessment. Then, we only could refer to the behavioural outputs regarding the foraging and the preference for food. We expected that familiarity with the intruder might be a key factor affecting the forager's decisions. We found differences in the frequency of attacks directed to prey, but not in the time spent near food-containers, neither in the number of visits and TFs. The number of TFs is conceived as a proxy of the exploration behaviour (Cooper, 1994; Halpern, 1992). Nevertheless, since our experimental design allowed the forager lizard to explore and interact with both food sources (i.e. to recognize food) before starting the counting of TFs, we used TFs as a

proxy of interest on the stimulus that elicited it. Similarly, we considered the number of visits and the time spent next to food as variables that could be capturing other aspects about the interest of lizards in food. However, the meaning of attacks unambiguously reflects the decision of foraging; consequently, the clear results of this variable are solid despite the lack of significance in the rest of them.

In both treatments, when the intruder was either familiar or unfamiliar to the forager, the number of attacks directed to the high source of food was more frequent. This result fits with previous experiments made in this species in which there was a preference for the higher amount of food in absence of competitors (Recio et al., 2021).

The result of the lower number of attacks to food when the forager lizard had prior knowledge of the intruder suggests that the choice of foraging is determined by previous experiences with this particular individual intruder. When the intruder was familiar, the resident lizard did forage less frequently. On the contrary, when the intruder was unfamiliar, the lizard performed more attacks. Besides, the preference for the higher amount of food, as compared with the lower, when the intruder was unknown was more extreme than the preference showed when the intruder was familiar. The lack of knowledge about the intruder implies an uncertainty degree that only could be decreased by rival assessment. Then, this behaviour might indicate an active defence of the high-quality food source when the unique source of information about the competitor is its competitive ability. A comparable effect of food-guarding related to the resource value and the balance of costs and benefits between foraging and agonistic behaviours has been reported in the zebrafish *Danio aequipinnatus* (Chapman and Kramer, 1996) and in the hummingbirds *Selasphorus platycercus* and *S. rufus* (Camfield, 2006).

However, according to the results, not only familiarity with the rival but the difference in size between both lizards was relevant. While in the familiar treatment the number of attacks increased by the forager's size, when the rival was unfamiliar this increment of attacks just occurred directed to the higher amount of food, but not to the other food source. This suggests an evaluation of the fighting ability of the rival based on size differences and a foraging decision in which the values of the resources have been taken on account. Similar effects in which the foraging choices between food sources of different value are dependent on the size of the heterospecific competitor have been reported in the hummingbird *Amazilia tzacatl* (Dearborn, 1998). This differential preference for the high-value food source when the intruder was smaller than the forager provide more evidence of current rival assessment during the experiment. At the same time, the contrast with the behaviour when the rival was familiar also suggested that rival recognition was also taking place.

To memorize the result of previous agonistic contests (Hsu and Wolf, 1999), and modulate behaviour according to it, is an adaptive way to avoid waste of energy. This memory effect attributed to previous agonistic encounters was previously found in this lizard (Aragón et al., 2000) and other lizards such as *Podarcis hispanica* (López and Martín, 2001) or *Anolis carolinensis* (Qualls and Jaeger, 1991). A similar effect regards a higher social tolerance associated with differences in body size between lizards was explained by the 'Dear enemy recognition' hypothesis in this species (Aragón et al., 2007) and also in *P. hispanica* (Carazo et al., 2008). In this species, it has been described the existence of rival assessment based on chemical detection of some compounds in femoral secretions produced by males that may signal body size or competitive ability (López and Martín, 2011; Martín and López, 2007). The results of the experiment revealed that, when foraging, both rival assessment and rival recognition play a role dependent on the specific context. While rival assessment took place during the experiment, the dear enemy recognition was possible just by sharing the same space before the experiment. Similar effects due to familiarity with the intruder but dependent on the body sizes have been reported in the European catfish, *Silurus glanis*, (Slavík et al., 2016), and in the Damselfish, *Stegastes fuscus* (Silveira et al., 2020). In lizards, comparable effects of recognition of the intruder in relationship with dominance

traits have been reported in the tropidurid lizard *Eurolophosaurus nanuzae* but in terms of aggression and indirect energetic costs (Quintana and Galdino, 2017). New experiments including the effects caused by actual dominance hierarchies should be done to explore this issue further. This will allow us to understand the role of dominance in the foraging decisions when the conspecific competitor is dominant or subordinate over the forager animal.

## 5. Conclusions

Based on our results, we conclude that foreknowledge of an intruder could modulate foraging behaviour in *I. cyreni*. Specifically, the foraging decisions were based on the foreknowledge of the intruder and its recognition as a competitor and, at the same time, the assessment of the competitive ability of the rival when it was unknown. Our study provides new insights into the importance of the specific social relationships between animals when studying behaviour under a social context.

## Author statement

**Gonzalo Rodríguez-Ruiz:** Conceptualization, Methodology, Experimental design, Data collection, Formal analyses, Writing the original draft and Reviewing and Editing.

**Pablo Recio:** Data curation, Formal analyses, and Reviewing and Editing.

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**José Martín:** Conceptualization, Experimental design, Data collection, Reviewing and Editing.

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