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# Social Information Use for Spatial Decision in the Common Lizard (*Zootoca vivipara*)

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## Abstract

Individuals' movements are conditioned by the acquisition of information from personal interactions with the environment or social sources. Despite the importance of social information in movement decision-making, little is known about how individuals proceed when social information comes from multiple sources. Here, we specifically tackled this by experimentally testing (i) how social information from multiple sources is used to make relocation decisions, and (ii) whether a contrast in this information enables individuals to orient themselves in space. Using the common lizard (*Zootoca vivipara*) as a model species, we conducted repeated experiments in which a focal neonate received information from two other neonates coming from peripheral environments, before being given the opportunity to relocate to either peripheral environment. We focused on information on resource availability and intra-specific competition by considering the informants' body mass at birth (BM) and subsequent food intake.

Our analyses revealed that the amount of resources in the informants' environment affected relocation decisions, depending on the focal individual's BM: the probability of relocation increased when the informants' food intake and the focal individual's BM decreased or when both increased. It suggests that focal individuals adjusted their relocation response to social information in function of their needs and/or physical abilities. On the other hand, we found no effect of BM differences between informants or spatial variability in resource availability on spatial orientation. This study highlights that multiple sources of social information can be used for movement decisions, probably because these sources of information reflect the quality of the surrounding environment (competition or resource availability).

**Keywords:** Common lizard, Information transfer, Information use, Movement decision, Social information, Spatial orientation.

## Highlights

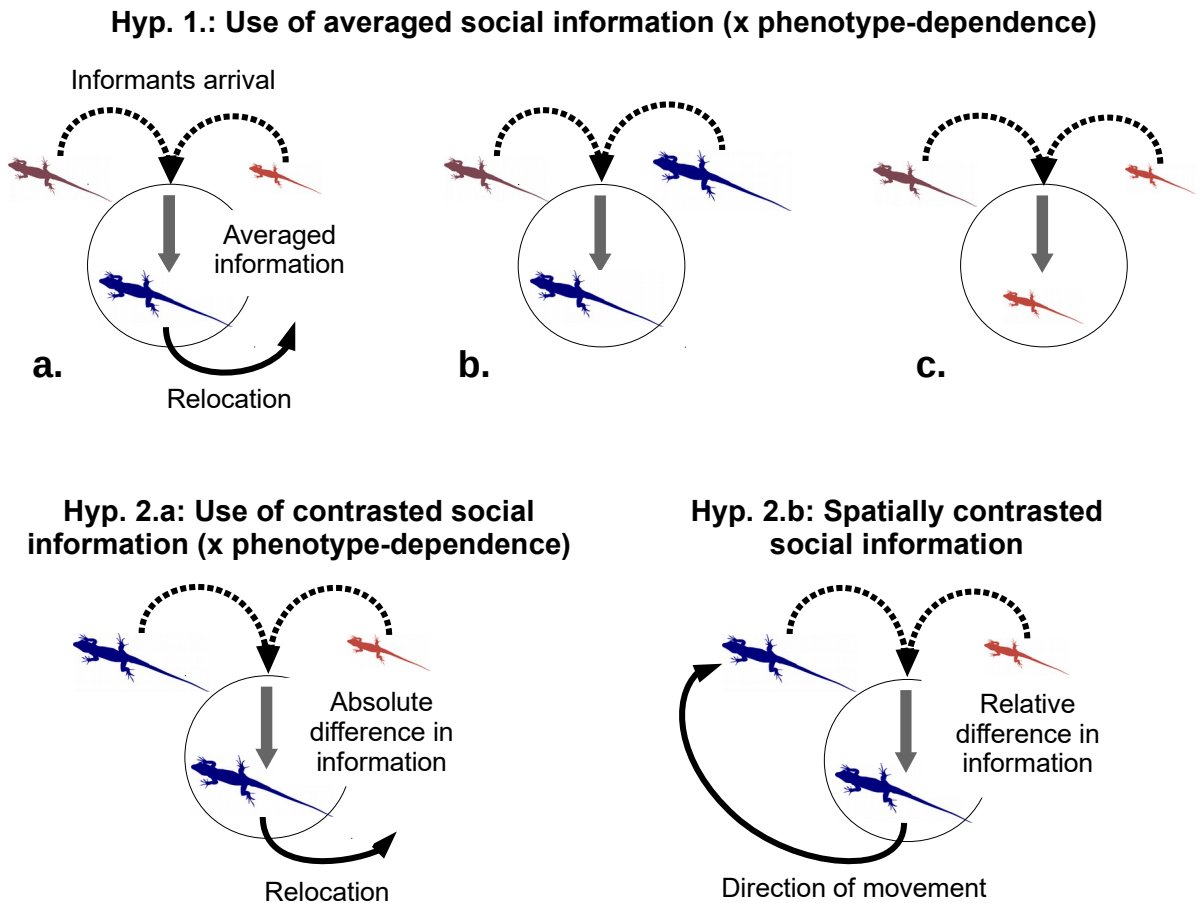
- Common lizard neonates can use multiple social information for relocation decision
- Social information is processed based on the information receiver's condition
- Relocation increased/decreased with informants' food intake and receiver's body mass

## Introduction

Information acquisition is central for an individual to assess the biotic and abiotic quality of its environment, and therefore to take appropriate decisions to feed, survive and reproduce (Dall et al. 2005, Schmidt et al. 2010). Information can be obtained via personal interactions with the environment (i.e., personal information, Dall et al. 2005) or social interactions with conspecifics and/or heterospecifics (i.e., social information, Dall et al. 2005, Schmidt et al. 2010), through the perception of detectable traits from these individuals (e.g., behaviour, performance, body condition, odours; Moreira et al. 2008, Clobert et al. 2009). These social interactions are for example known to inform individuals about breeding habitat quality (e.g., Doligez et al. 2002, 2004), conspecific density (e.g., Endriss et al. 2018), resource availability (e.g., Webster and Hart 2006, Weimerskirch et al. 2010), and predator presence (e.g., Weary and Cramer 1995, Goodale and Kotagama 2008). Although social information can be intentionally transmitted by informant individuals through signals such as calls or territorial marking (Johnson 1973, Macedonia et al. 1993), it can also be inadvertently conveyed by cues (Danchin et al. 2004, Schmidt et al. 2010). It is for example the case for breeding habitat quality in the collared flycatcher, an information demonstrated to be conveyed by the reproductive success (i.e. the number and quality of fledglings), of conspecifics (Doligez et al. 2002, 2004). Social information has long been recognised to be key in organisms' decisions to move through their environment and is known to influence the optimisation of spatial decision-making for microhabitat use (e.g., Moreira et al. 2008, Winandy et al. 2021), habitat selection (Doligez et al. 2002, 2004)

and dispersal (Cote and Clobert 2007, Jacob et al. 2015). Social information is expected to be particularly relevant in spatially heterogeneous environments, where individuals may face a mosaic of cues or signals carried by either local inhabitants or immigrants, respectively informing on the specificities of close (Wey et al. 2015) and distant habitats (Cote and Clobert 2007, Jacob et al. 2015). Yet, little is known about the way an individual detects, processes, and prioritises social cues to inform decision-making when multiple sources of social information (i.e., multiple conspecifics reflecting different surrounding areas) are simultaneously accessible. More specifically, in the context of movement ecology, two questions remain to be addressed. First, how are multiple information sources processed by individuals to decide to relocate or not? Second, if the individual relocates, how are multiple sources of information used to orientate and choose a specific destination of relocation?

We believe two non-mutually exclusive hypotheses are to be considered to answer the first question. On the one hand, one may expect that the *averaged* information on surrounding areas should prevail (Hyp. 1: Social information synthesis, Figure 1). An individual would decide whether to relocate or not by processing all available information (i.e., each cue/signal provided by all the different sources) to get global information about its environment (Stamps 2001, Clobert et al. 2004, Bowler and Benton 2005), whatever the quality and origin of the cue or signal. Note that the use of information on surrounding areas could be either based on the provided social information only (Figure 1, panel a. vs b.) or depend on the phenotype of the informed individual, which would adjust relocation decision to its own condition (Figure 1, panel a. vs c.). Many examples in the liter-



**Figure 1: Experimental aims.** Graphical representation of the different hypotheses investigated in our experimental design. Individuals with different phenotypes are represented by different colors and sizes. Hyp. 1 - Social information synthesis: relocation depends on averaged information gathered from conspecifics (e.g. relocation only occurs when averaged information about small/orange, brown conspecifics is provided, panel a. vs b.), possibly in interaction with the focal individuals' phenotype (e.g. only big/blue individuals relocate for such information, panel a. vs c.). Hyp. 2 - Contrasted social information: a) relocation would depend on the variability between information sources (i.e. absolute difference, e.g. individuals relocate when there is a high difference between information sources), b) direction of relocation would depend on the relative difference between information sources (e.g. movement toward the origin of the big/blue informant).

ature illustrate such phenotype-dependent use of social information for spatial decisions. For example, social cues can be processed differently according to personality (Smit and van Oers 2019, Morinay et al. 2020a), age (Morinay et al. 2018, 2020b), reproductive success (Parejo et al. 2007), and body condition (Cote and Clobert 2007, Baines et al. 2019).

On the other hand, one may also expect individuals to use the *absolute difference* between available information sources (Hyp. 2.a: Contrasted social information use, Figure 1). In this hypothesis, individuals would assess environmental variability and/or information reliability (i.e., the probability of correctly identifying the surrounding environment based on the available information) by comparing the concordance or discordance of social cues between sources. Such concordance/discordance may indeed result from the diversity of the source environments (i.e., inter-environment variability) and/or from the diversity of phenotypes existing in a same environment (i.e., intra-environment diversity, potentially blurring inter-environment variability signals). The importance of conflicting information (i.e., discordance) for movement decisions has already been observed when conflicts exist between personal and social information (e.g., Cronin 2013, Winandy et al. 2021). In such contexts, prioritisation of personal information seems to happen in most cases (Kendal 2009), although it may be weighted differently when personal information is particularly uncertain (e.g., van Bergen et al. 2004, Smolla et al. 2016) or when social information is more reliable and associated to safe rewards (e.g., Wray et al. 2012, Dunlap et al. 2016). Again, such information use may interact with the focal individual's phenotype, depending on abilities to take risks and endure potential associated

costs (e.g., individuals' boldness and activity profile; Marchetti and Drent 2000, Kurvers et al. 2010, Rosa et al. 2012).

The answer to the second question (i.e., how does an individual orientate when facing multiple sources of information?) lies in the spatial integration of information gathered from multiple sources. One likely hypothesis is that the *relative difference* between the information sources (distinguished through their spatial origin) allows the individual to locate the most appropriate environment (Hyp. 2.b: Spatially contrasted social information use, Figure 1). In other words, the differences in informants' traits could inform the individual on the direction of areas with a higher fitness expectancy, if the surrounding areas are associated with social cues whose values vary as a function of local fitness expectancy (Schmidt et al. 2010).

To answer these questions, we used the common lizard (*Zootoca vivipara*, Jacquin 1787) as a model species. The common lizard is known to use social information in different contexts. Notably, individuals can acquire information about the reproductive strategy and aggressiveness of females (for habitat selection: Vercken et al. 2012; for local avoidance of competitors: Vercken and Clobert 2008), as well as immigrant-based information about the dispersal status of conspecifics and about the density of surrounding populations (Aragón et al. 2006a, Cote et al. 2008, Cote and Clobert 2007). Further, the use of personal and social information is of particular importance for neonates as it shapes natal dispersal decisions (Clobert et al. 2012, Cote and Clobert 2012). Here, contrary to previous studies focusing on a single source of information, we aimed to test for the use of multiple simultaneous information sources for relocation and orientation decisions, before natal dispersal occurs.

Specifically, we conducted a replicated, reduced-scale arena experiment (see Figure 2 for detailed design) to test how focal neonates (one per replicate) used social information from two different informants (a unique pair per replicate) to make decisions about 1. relocation (Hyp. 1, Figure 1) and 2. relocation direction (Hyp. 2, Figure 1). Relocation refers here to the movement of the focal individual from its original terrarium to a peripheral one, corresponding to a local, short-scale movement similar to that which the individual could perform in its home range. In our experiment, informants differed in several ways. First, they entered the experimental arena from two different locations. Second, they originated from areas (unique to each one from their birth) that varied in environmental quality, here represented by different access to food (present or not). Finally, informants also differ in their body mass at birth (BM). Body mass is a cue often used as a proxy of competitive abilities (Le Galliard et al. 2004, Meylan and Clobert 2004) and quality of habitat of origin (Massot et al. 1992, Le Galliard et al. 2005a: physical condition varying with conspecific density). Consequently, we hypothesised that informants could transmit social information through their BM and subsequent food intake, both informing on the presence of resources in their area of origin and/or on their abilities to endure starvation or to acquire food (i.e., how competitive they are). We therefore expected the focal individual to relocate in the direction from which the fed informant and/or the less competitive informant came. We also expected this information to be used differently depending on the focal individual's own competitive abilities.

## Materials & Methods

### Species and study sites

*Zootoca vivipara* (Jacquin 1787) is a small size ground-living species of the Lacertidae family. This species is widespread in Northern Europe and Asia and lives in heathlands, bogs, and wet meadows. The home range of an individual is about a 15m radius with some variation with age and sex (Massot and Clobert 2000, Lecomte et al. 1994, Massot 1992). Individuals move inside this range to forage, thermoregulate and reproduce. This species is non-territorial, with important overlapping among individuals' home ranges (Massot et al. 1992, Lecomte et al. 1994). Social encounters are frequent, particularly during the mating period, where males present important antagonistic interactions between them (Heulin 1988) and with females (Le Galliard et al. 2005b, 2008). Individuals used in this study were sampled from seven study sites, located in the Massif Central mountain range, France (Figure S1). Sites ranged from 1000m to 1500m in altitude and covered the diversity of possible habitats in this region (Rutschmann et al. 2016). In the Massif Central, mating takes place just after individuals emerge from hibernation, between March and April. Parturition usually occurs between late June and late July (between July 2nd and 24th in our study), depending on local temperature conditions (Rutschmann et al. 2016). Females lay on average five eggs (range 1-12, Massot and Clobert 1995). In our sites, neonates emerge from the egg within a few hours after parturition. Dispersal of neonates occurs mostly a few days after birth (Massot 1992, around 6 days old on average: Léna et al. 1998). Such natal dispersal has been defined as a perennial relocation of at least 30m from

the neonate birthplace (Clobert et al. 1994, Massot and Clobert 1995, 2000, Massot et al. 2002, Cote and Clobert 2007), a threshold for which there is no return of dispersers to their initial home range (Clobert et al. 1994, Massot and Clobert 1995, 2000). During the early stages of life, neonates of this species acquire social information about resources: notably, their natal dispersal responses depend on the density of conspecifics or the body condition of familiar adult females (Clobert et al. 2012, Cote and Clobert 2012).

### Capture and rearing condition

Twenty pregnant females were captured at each site between June 12th and 24th, in 2019. These females were brought to a field laboratory. Females were maintained in individual plastic terrariums (18.5 x 12 x 11 cm), containing a shelter made from two slots of a cardboard egg box and a 2 cm substrate of sterilised soil (Massot and Clobert 2000). Terrariums were placed under an incandescent bulb of 25W providing light and heat for 6 hours a day to allow basking (from 9 a.m. to 12 p.m. and from 2 p.m. to 5 p.m.). Terrariums were sprayed with water three times a day. Females were fed with one mealworm or three crickets, every second day.

Right after parturition (0 to 6h), neonates from a same clutch were isolated from their mother in an empty terrarium (day 0). Neonates' snout-to-vent length (SVL) and body mass (BM) were measured the day after their birth (day 1), before any feeding treatment. Only BM ( $157.7 \pm 18.2$  mg SD) was used subsequently, as SVL ( $20 \pm 1$  mm SD) was not variable enough at this age to detect a potential effect (respective coefficient of variation of 11.5 and 5%). Of note, neonates' BM and SVL were highly correlated (Pearson correlation test:  $p < 0.001$ ,  $r = 0.54$ ). Sex was as-

essed by counting ventral scales, following the method provided in Lecomte et al. (1992, >95% efficiency). The same day, neonates were isolated to individual terrariums (25 x 15 x 15 cm, hereafter called 'home terrarium'), containing a shelter made from two slots of a cardboard egg box and layered with two sheets of absorbent paper. Neonates were left for another day (day 2) in their respective terrarium before experiments started on day 3, so they could consider this terrarium as their living area (Aragón et al. 2006a). All neonates and mothers were fed (respectively with one mealworm or three small crickets) and released at the mother's capture site on day 4.

### Experimental design

The experiment aimed at testing whether informants' BM and food intake, in interaction with the focal individual's BM, influenced the focal individual's spatial relocation decisions, from an area it was accustomed to (comparable to a local area in its home range). Each of the 56 replicates of the experiment required three neonates (one focal individual confronted to two informants), for a total of 168 neonates used along all replicates. Each neonate was tested once and there was no reuse of individuals among replicates. Note that multiple-individuals encounters are likely to occur in natural conditions, as this species is living at high density in the sampled habitats (e.g., Massot et al. 1992) with individuals sharing spatial resources for basking or sheltering (personal observations). As such, our experimental design reflects potential encounters likely to happen in natural populations.

One day before the encounter between the focal individual and the informants, one of the two informants had access to food: three



small crickets, from 3 to 5 mm, were introduced in the fed informant's terrarium. The number of consumed crickets (0 to 3) was recorded just before the experiment (referred to as the fed informant's food intake further on). Different cues could be used to quantify such food intake. They can be related to individuals' odour (Havlíček et al. 2019, see Martin and Lopez 2015 for examples on lizards), to the individual's behaviour (Cote et al. 2010, Horváth et al. 2016), locomotor performance (Ford and Shuttlesworth 1986, Martin 1996) or to the gain of weight following food intake. Of note, there was no correlation between the fed informant's food intake and the informants' BM (Pearson correlation test:  $p=0.19$ ). The focal individual was never fed before the experiment to increase the probability of responses to social information about food availability (Wurtz et al. 2021).

For each replicate ( $n=56$ ), neonates were selected among clutches of mothers from the same capture site. When possible, informants had the same laying date ( $n=49$ ). Most experimental replicates ( $n=37$ ) took place 3 days after the birth of focal individuals but some replicates happened 2- ( $n=10$ ) or 4-days ( $n=9$ ) after birth, when there were too few births on the same day. Similarly, 2- ( $n=10$ ) and 4-days old ( $n=13$ ) informants were used when necessary. The ages of the focal individual and informants were the same in most of the experimental replicates ( $n=39$ ). In all cases, the neonates were young enough to not have made dispersal decisions yet (Massot et al. 1992, Léna et al. 1998). The fed informant was also old enough to be fed (Massot and Aragon 2013, meal at two days old), such an early meal having dramatic effects on growth and survival in this species. Of note, the age of the fed informant the day before the experiment was not correlated with its food

intake (Kruskal-Wallis test,  $p=0.85$ ).

Focal individuals were always selected from a different brood than the informants, but informants from the same brood were used in the same experimental replicate ( $n=19$ ) when there were too few births. Simultaneous encounters of related individuals are likely to occur in natural conditions as siblings share the same natal area before dispersing.

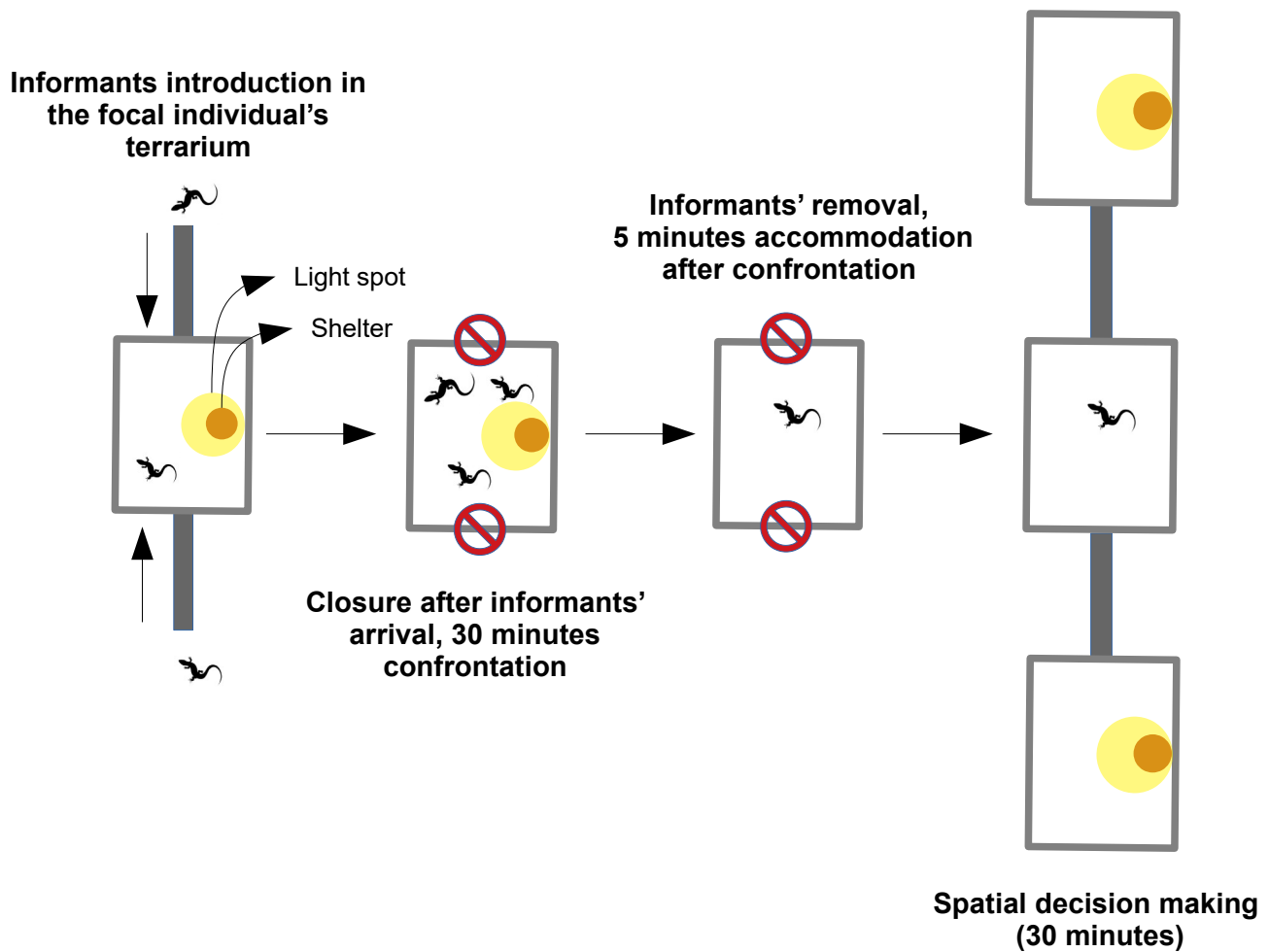
Because the number of daily births was limited, we chose to include individuals of both sexes in our experiment using a fully balanced design (see Supplementary Materials for further details). Of note, there was no difference between sexes in the neonates' BM (Wilcoxon test:  $p=0.2$ ) or in the fed informant's food intake (Wilcoxon test:  $p=0.19$ ).

Replicates took place from July 5th to 27th between 7 a.m. and 8 p.m. We summed up the timing of experiments in a categorical variable, accounting for the lighting periods in the field laboratory, with four classes: early morning (7 am to 9 am,  $n=13$ ), morning (10 am to 12 am,  $n=23$ ), afternoon (1 pm to 4 pm,  $n=13$ ) and evening (5 pm to 8 pm,  $n=7$ ).

All metrics other than the variables of interest (BM and fed informant's food intake), resulting from presented experimental constraints, have *a priori* no effects on focal neonate relocation decisions (Supplementary Materials for further details) and do not correlate (see previous statistics presented in this section) or relate with variables of interest.

## Experimental assay

The home terrarium (see "Capture and rearing condition" section for details) of the focal individual was placed on an isolated table. Corridors (PVC tubes of 25 cm length and 16 mm internal diameter) were introduced at each side of this terrarium. Informants were placed in corridors' extremities



**Figure 2: Experimental design.** This scheme details the experimental design, which consists of four main steps presented successively. Corridors are represented as filled grey rectangles, and terrariums as empty rectangles. The crossed-out signs represent access closure.

(Figure 2) and their arrival in the focal terrarium was synchronised by slightly brushing their tails. We alternated the introduction position (left or right) of the fed informant and of males and females between each replicate so that the position was not biased towards a treatment or an informant's sex. Once the informants entered the focal terrarium, corridors were removed and entrances were plugged. The dimension of the focal terrarium was sufficient to accommodate the three neonates together while allowing them to avoid each other. The three neonates interacted together for thirty minutes (Figure 2). The three neonates interacted together for thirty minutes (Figure 2). The three neonates interacted together for thirty minutes (Figure 2). During this time, we observed frequent interactions between the three neonates (across all experiments, during the last twenty minutes of confrontation:  $191 \pm 160$  s of time spent in close proximity,  $3.6 \pm 3.8$  interactions with direct contact; see Supplementary Materials for details). After that period, informants were put back by hand (with gloves to avoid any unwanted odour deposits) in their respective terrariums. In the home terrarium, absorbent paper, shelter, and heat/light source were removed to promote departure (Aragón et al. 2006a). The focal individual was left for five minutes in these conditions to acclimatise (Figure 2). Then the corridors used previously were attached again at each extremity of the focal terrariums (without any modification since the informants' passage) and connected to two identical and clean terrariums. The focal individual was left for thirty minutes in this system (Figure 2), before stopping the experiment. All used side terrariums were washed with water between replicates. Corridors were used only once. Experiments were entirely filmed with three webcams (Creative Live Camera Sync HD 720p) placed above

each terrarium (with the corridors visible) to follow the focal individual's movements.

## Ethical note

The 'Office Nationale des Forêts', the 'Parc National des Cévennes', and the regions Auvergne, Rhône Alpes, and Languedoc Roussillon delivered permits to capture and handle lizards (permits 81-17 2013-05; 2013274-0002, 2013/DREAL/259). An ethical committee (DAP number 5897-2018070615164391-v3) validated the capture and rearing conditions to ensure the welfare of the animals involved. We provided the individuals with an environment that accounts for their welfare (see above sections for detailed protocols). Adult females were regularly fed, while neonates were fed at least once before release (relying on their yolk reserves right after birth). Neonates spent no more than four days in the facility to minimize stress due to prolonged captivity and biological effects upon release into the natural environment. During the rearing period, individuals were provided with light and heat, following natural conditions. Each day, we regularly sprayed terrariums with water to meet the humidity requirements of this species. Individuals were always able to seek shelter, either under the provided structure or substrate, as they naturally behave. To avoid any agonistic interaction, we housed individuals separately. To avoid any stress caused by human activity or the proximity of other individuals, we made terrariums opaque. Of note, successive handling and promotion of departure may cause stress to focal neonates. However, these artificial manipulations were necessary to obtain a sufficient number of replicates for statistical analyses in the short frame available to run the experiment. Although the experimental setting

does not perfectly replicate the natural environment, the differential relocation responses observed as a function of informants' traits (see Results section) support an effect of our treatment. As we exposed all individuals to the same procedure over all replicates, we believe it is possible to conclude about the use of social information in terms of spatial response in this experimental context, and that it remains conclusive on how individuals of this species might process social information. It is important to note that response latency or the proportion of relocation may vary in a natural context compared to our experiment, due to the potential stress sensitivity of focal individuals. Yet, a later complementary study on field data indeed confirmed the main experimental results obtained here. The study found that averaged social information is used similarly in natural conditions, even in more complex cases where more than two information sources are considered concurrently (Brevet 2022).

## Data analyses

We analysed relocation of focal individuals (leaving or not its initial terrarium for another peripheral one, in which direction) through video analysis of the three webcams filming each experimental replicate. To prevent any observer bias, we used blinded methods when the behavioural data were recorded (with no observer in the experimental room during the video recording) and when the videos were analysed (no knowledge of the feeding treatments or neonates' traits associated with the replicates during their analysis).

We first analysed the relocation probability of focal individuals after their confrontation with the two informants (Hyp. 1, 2.a, Figure 1). To do so, we used a logistic regression with a binary response variable (relocating or

not) and considered the reference group to be the individuals staying in their terrariums. Variables used as explanatory variables to test our hypotheses are described in Table 1. We tested for the population of origin as a potential random effect prior implementing the model (Zuur et al. 2009). Note here that a daily effect was partially nested in the population variable as the different capture sites are associated with different hatching periods (Rutschmann et al. 2016) and as only one or two capture sites were used each day of experiments. Yet, this random effect appeared non-significant (analysis of deviance test between null models with and without random effects, using standard logistic regressions;  $p = 0.47$ ) and was dropped in our subsequent models (Zuur et al. 2009). The variance inflation factor (VIF) of our model was sufficiently low (maximal VIF of 1.15) not to apply any correction to our statistical tests (O'brien 2007). Model quality was assessed with a Nagelkerke pseudo-R-squared method (Nagelkerke 1991). Effects of variables were tested through an analysis of deviance (likelihood-ratio tests, "car" R package, Fox and Weisberg 2018).

A second analysis was conducted to test which of the informants' traits influenced the direction of relocation (Hyp. 2.b, Figure 1) when focal individuals left their terrarium ( $n=22$ ). We used a logistic regression with a binary response variable (leave toward left or right), the reference group being the individuals going to the right side. In this second model, we used the fed informant's spatial origin (coming from left or right) and difference in informants' BM (left-coming minus right-coming informants) as explanatory variables. The model was diagnosed as presented before. Again, VIF (maximum equal to 1.15) was sufficiently low for interpreting our results.

All statistical analyses were performed with R software (R Development Core Team, 2008, version 3.6.3). Graphs were produced using the package “ggplot2” (Wickham 2016).

## Results

Over the 56 experimental replicates, 22 focal individuals left their terrariums, with no return to their home terrarium during the experiment.

Both informants’ traits and focal individuals’ traits were found to significantly influence relocation probability. All tests’ statistics are described in Table 1. The relocation probability of focal individuals tended to decrease ( $p=0.065$ ) when the fed informant’s food intake decreased (Figure S2-A, representative of the overall food availability as only one informant had access to food). We further found that the food intake of the fed informant interacted with the phenotype of the focal individual to impact the focal individual’s probability of relocation ( $p=0.012$ , Figure 3). Relocation probability was high for a focal individual with a low body mass at birth (BM) confronted to an informant with poor food intake or for a focal individual with a high BM confronted to an informant with high food intake. Finally, the relocation probability of focal individuals tended to increase ( $p=0.08$ ) when the focal individual’s BM and the averaged informants’ BM both increased or both decreased (Figure S2-B). We obtained a Nagelkerke R-squared of 0.35 for this model, which reflects a rather good fit to the data.

Concerning the relocation direction of the 22 focal individuals which left their terrariums, we found that nine individuals went to the right and thirteen to the left. No significant

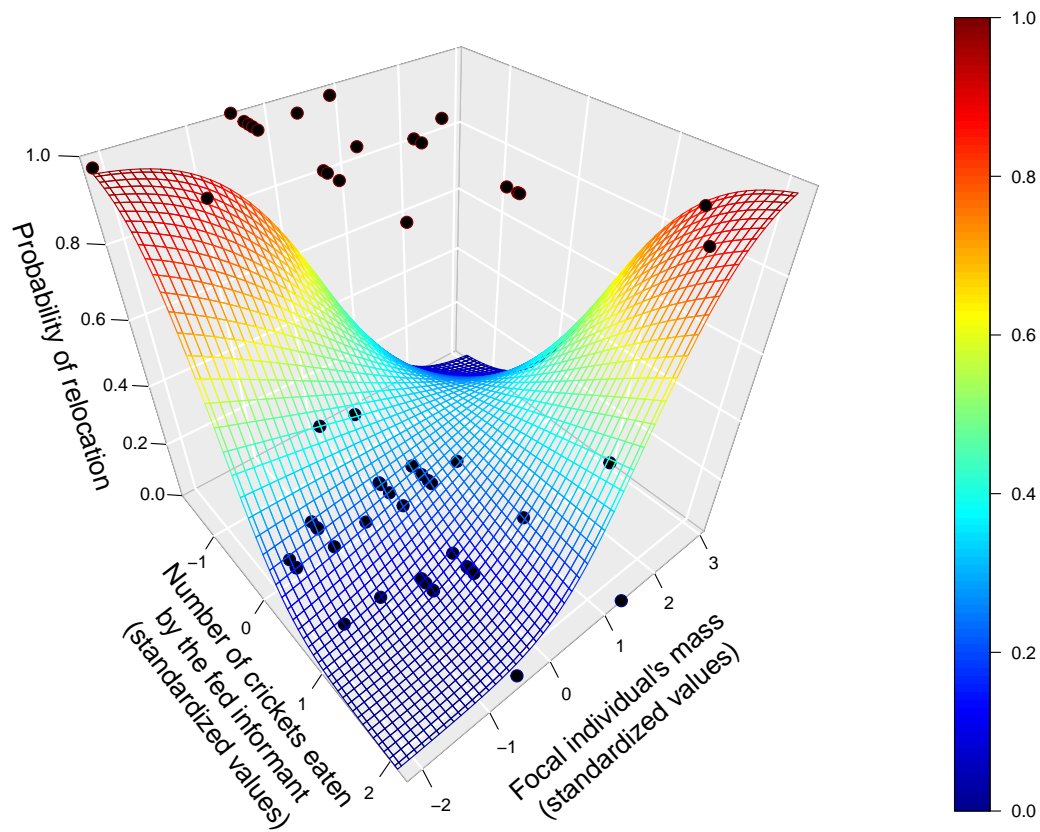
effect was found among the tested variables, including the feeding treatment (Table 2, Figure S3). We obtained a Nagelkerke R-squared of 0.05 for this model, which indicates a poor fit to the data.

## Discussion

We experimentally investigated how social information is used for movement decision-making when simultaneous sources of information (i.e., informant individuals) are available. We found the relocation probability of focal individuals to depend on the interaction between the social information present in their environment and their own phenotypes (in support of Hyp. 1: Figure 1). Relocation probability increased either when both the fed informant’s food intake and the focal individual’s body mass at birth (BM) increased or when they both decreased. We found no significant influence of contrasts in BM between informants on the relocation probability of focal individuals (contrary to the expectations from Hyp. 2.a: Figure 1). Finally, when focal individuals left their terrarium, we found no effect of the position of the informant which had access to food on the direction of relocation, as for differences in BM between informants (contrary to the expectations from Hyp. 2.b: Figure 1).

### Use of social information from multiple sources

Our results suggest that focal individuals are able to use the information from multiple sources to make movement decisions (here, relocate or not from their initial location). Indeed, we observed that the averaged informants’ BM and the fed informant’s food in-



**Figure 3: Joint effects of the fed informant’s food intake and the focal individual’s state on relocation probability of focal individuals.** The graph was produced by plotting the predicted probabilities as a function of the variable of interests’ and the intercept’s coefficients. Black dots display observations from all experimental replicates: a dot on the 0 probability surface corresponds to a focal individual who did not relocate, a dot on the 1 probability surface corresponds to a relocation. These dots were slightly jittered horizontally to gain in readability.

	Parameter	Coefficient	SE	$\chi^2$	df	P-value
	Intercept	-0.69	0.34			
<b>Informants' and focal individual's traits</b>	Focal individual's BM	-0.09	0.38	0.7	1	0.402
	Informants' BM	-0.55	0.36	1.42	1	0.234
	Fed informant's food intake	-0.89	0.41	3.39	1	0.065 <sup>•</sup>
<b>Informants' x focal individual's traits (interaction terms)</b>	Informants' x Focal individual's BM	0.71	0.42	3.07	1	0.08 <sup>•</sup>
	Fed informant's food intake x Focal individual's BM	0.99	0.43	6.34	1	0.012*
<b>Contrasted informants' traits (x focal individual's traits)</b>	Contrast in informants' BM	0.12	0.34	0.07	1	0.794
	Contrast in informants' BM x Focal individual's BM	-0.54	0.48	1.36	1	0.244

**Table 1: Logistic regression on focal individuals' relocation probability (analysis of deviance).** Results of the logistic regression on focal individuals' relocation probability are displayed here. The informants' BM parameter refers to the informants' average BM values, and the contrast in informants' BM refers to the absolute difference between informants' BMs. For each variable we displayed the average coefficient and its standard error. Likelihood ratio tests (analysis of deviance) were performed to test for the significance of each variable effect : we displayed here the associated statistics and p-values. Asterisks indicate the degree of significance. <sup>•</sup> : 0.05<p<0.1, \* : 0.01<p<0.05, \*\* : 0.001<p<0.01, \*\*\* : p<0.001

Parameter	Coefficient	SE	$\chi^2$	df	P-value
Intercept	0.76	0.64			
Fed informant origin	-0.82	0.95	0.78	1	0.38
BM differences between informants	0.2	0.49	0.17	1	0.68

**Table 2: Logistic regression on direction-taking (analysis of deviance).** Results of the logistic regression on focal individuals' direction-taking are displayed here. For each variable, we displayed the average coefficient and its standard error. Likelihood ratio tests (analysis of deviance) were performed to test for the significance of each variable effect: we displayed here the associated statistics and p-values. Asterisks indicate the degree of significance.  $\cdot$  :  $0.05 < p < 0.1$ , \* :  $0.01 < p < 0.05$ , \*\* :  $0.001 < p < 0.01$ , \*\*\* :  $p < 0.001$

take significantly correlated with the relocation of focal individuals, while the differences in informants' traits were not used by focal individuals in our experiments. The use of information from multiple sources may benefit the focal individual by giving it a broad overview of the surrounding context, allowing it to take an informed decision to leave or not its initial location. The absence of effects related to traits variability was unexpected, as variability is needed to orientate toward the most beneficial environment. Further, if we consider low contrast between traits as an indication of information reliability (i.e., homogeneous information in the surroundings), the absence of effect is also surprising. Indeed, if individuals could not identify the spatial origin of information sources (which seems to be the case here), we could have expected individuals to decrease their propensity to relocate using social information when the outcomes of using such information are less certain (Heinen and Stephens 2006, Riotte-Lambert et al. 2020). Yet, such a decrease in relocation propensity with information heterogeneity might only appear in interaction with the information content itself. Thus, more risk-prone decisions (uncertainty to arrive in the right environment) could be made

only when the information is associated with particularly advantageous potential outcomes (e.g., Wurtz et al. 2021). Such hypotheses remain to be tested in our model species, perhaps with experimental designs integrating higher information diversity between sources (e.g., more information sources: see Brevet 2022 for such an application in natural conditions).

We also found focal individuals to use social information according to their own physical condition. Our results indeed highlight a conditional use of social information about food availability, that depended on the BM of the focal individual. Such phenotype-dependence of spatial decision-making was already observed in the studied species (Cote and Clobert 2007, Cote and Clobert 2010), but also in other species (Lindstedt and Hamilton 2013, Baines et al. 2019). As in these other studies, this result reflects that decision-making depends on the individual's needs and abilities. More specifically, the energetic costs required for relocation movements or competition in the relocation environment are probably better supported when having a better physical condition.

In any case, it might be interesting to en-



large the studied variables to other key informant's traits in future experiments, by including social metrics such as personality traits or other traits related to dominance status in common lizards (as ventral coloration, Vercken and Clobert 2008, Vercken et al. 2012). It would allow us to compare the importance of different kinds of social information and verify whether information prioritisation may occur. For example, a possible expectation is that information associated with immediate context (e.g. mass) may be considered more reliable than long-term information (e.g. coloration; Seppänen et al. 2007, Spencer et al 2012). Since long-term context information can often prove to be unreliable because of changing environmental conditions over time, focusing on information about short-term context might prevent maladaptive decisions (Dubois et al. 2012).

### **On the meaning of studied traits**

The fed informants' food intake (number of eaten crickets) could be considered as an indicator of resource availability in the immediate surrounding environments (informants representing conspecifics encountered in the local environment of the focal individual). As resources in early life have a significant impact on an individual's growth and survival (Mugabo et al. 2010, Massot and Aragón 2013), this cue could be used to initiate a departure from the current environment. On the other hand, the morphology of a neonate lizard immediately after birth directly reflects the amount of energetic reserve available from yolk reserves in the egg and influences its performance in the early stage of life (Sinervo 1990, Olsson et al. 2002). As movements entail energetic costs (for displacement itself or potential interactions with competitors and predators, Bonte et al. 2012), larger

reserves provide an advantage for successfully relocating toward another area. Good physical condition is also associated with an increase in neonates' survival rate (Le Galliard et al. 2010, 2013) and higher physical performances (Le Galliard et al. 2004, Meylan and Clobert 2004), reflecting higher competitive abilities (Garland et al. 1990). As such, experimental individuals with high BM probably possessed sufficient competitive abilities to decide to relocate. Such a relationship between neonates' physical condition and movements has already been observed during common lizard natal dispersal (Meylan et al. 2002), but also in the case of the local avoidance of potential competitors (Meylan et al. 2017).

Thus, when the fed informant's food intake and the focal individual's physical condition were both low, the increase in relocation probability could be understood as an avoidance of a local environment with insufficient resources, especially given the needs of the focal individual, which was in poor condition and therefore with low energetic reserves. On the other hand, when the fed informant's food intake and the focal individual's physical condition were both high, focal individuals appeared to avoid unnecessary competition for resources with an individual that had successfully captured prey (potentially leading to higher future performances for such individuals: Mugabo et al. 2010, Massot and Aragón 2013), while having a good enough physical condition to relocate. Yet, this second relationship is to be considered more cautiously, as it appears to be supported by fewer observations than the first one (see Figure 3).

Informants' BM also reflects broader quality of the environment, as neonates' reserves often correlate with the maternal habitat's quality (e.g., Shine and Downes 1999; Swain and Jones 2000, Itonaga et al. 2012 in

viviparous lizards: poor offspring's physical condition when restricting mother's access to food and/or basking opportunities) or with intraspecific competition (low physical conditions in dense environments in our species: Massot 1992, Galliard et al. 2005a). Remarkably, when the focal individual's and informants' BM both increased or decreased, the relocation probability tended to increase (Figure S2-B). Thus, focal individuals would avoid surrounding areas cued with low access to resources (low maternal habitat quality, high intra-specific competition) when being themselves in poor condition (low energetic reserves, low competitive abilities). On the other hand, they would avoid individuals with high reserves (i.e., more competitive individuals) even though they have sufficient reserves to relocate. Such trade-offs between the benefits of social information and the costs of intra-specific competition were already observed in other species (Lindstedt and Hamilton 2013, Szymkowiak et al. 2016, Baines et al. 2019), but without any particular emphasis on processing multiple sources of information.

## Direction of relocation

Previous findings have shown an existing ability to orientate in space for the common lizard (Strijbosch et al. 1983), in accordance with the spatial cognition abilities of reptiles (Wilkinson and Huber 2012). In particular, there is accumulating evidence on various species of lizards highlighting important spatial memory abilities (Ladage et al. 2012), including for orientation (e.g., Zuri and Bull 2000, Day et al. 2003). Lizards have also long-term memory of encountered conspecifics (Korzan et al. 2007). For these reasons, we could have hypothesised that the lizards were capable of orienting themselves,

on the basis of the cues obtained from social interactions, toward the direction from which came the informant with the better condition. Yet, we found no effect of the relative differences between informants (including the difference in food access) on movement orientation when relocation occurred. Given the small sample size for direction analyses (22 replicates) and the poor fit of our model to data, we have to be very cautious about the validity of such effects. These results might simply reflect that the cues or signals at stake here do not allow any orientation. Another potential explanation is the impossibility for the focal neonate to distinguish information about each informant separately in the present condition. In particular, individuals might not have had access to sufficient cues for visual orientation, the design being symmetrical and the arrival lasting a few seconds only. In the present experimental design, orientation would have been more likely based on scent deposit, as they are known to influence the selection of an environment according to the conspecifics' quality (Léna and de Fraipont 1998, 2000, Aragón et al. 2006b, but also Moreira et al. 2008, Scott et al. 2013). It is likely that the time spent by informants in the corridors or the corridors substrate was not adapted to establish an exploitable trail, or chemical compounds at stake here were too volatile to form such a trail. Further experiments, focusing for example on pheromones carried by informants, would be necessary to make any conclusion on the actual use of these odours for orientation. Alternatively, such an absence of orientation could also suggest that focal individuals considered social cues or signals from present information sources as information about very nearby conditions, for which no orientation would be necessary.

## Conclusion

Our experiment showed that social information from multiple sources was conveyed by conspecifics interacting with the focal individual, and that the use of such information depended on the physical condition of the focal individual. Contrasts between information sources, on the other hand, had no significant effects on either relocation or orientation decisions in our experiments. The importance of these information transfers for the relocation decision could be understood as an assessment of the quality of the surrounding environment, consisting mainly of probable cues about the availability of resources (abundance and competition for access). Spatial decisions based on this assessment seemed to depend on the focal individual's energetic needs and ability to sustain relocation costs.

## Author contributions

MB, AR, JCl, JCo, MR, and SJ designed the experiment. MB, AR and JCl performed the field work. MB performed all experiments and analyses. MB, AR, JCl, JCo, MR, and SJ wrote the manuscript.

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## Data availability

Analyses reported in this article can be reproduced using the data provided in the supplementary materials.

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## Competing interests

The authors have no competing interests to declare.

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## Supplementary Materials

### Sex distribution in the experimental design

Because of the dependence on the number of daily births, we chose to include individuals of both sexes in our experiment. In order to check whether there was any effect of the informants' and focal individual's sex on the relocation choices, we allocated the individuals in such a way as to represent the different possible combinations between the sexes. Thus, each focal female (n=29) or male (n=27) was confronted with either two informant males, two informant females, or one informant of each sex. These combinations were balanced between replicates within an experimental day. In the replicates with one informant male and one informant female, the fed informant was the male in nearly half of the replicates (n=14) and the female in the other half (n=16).

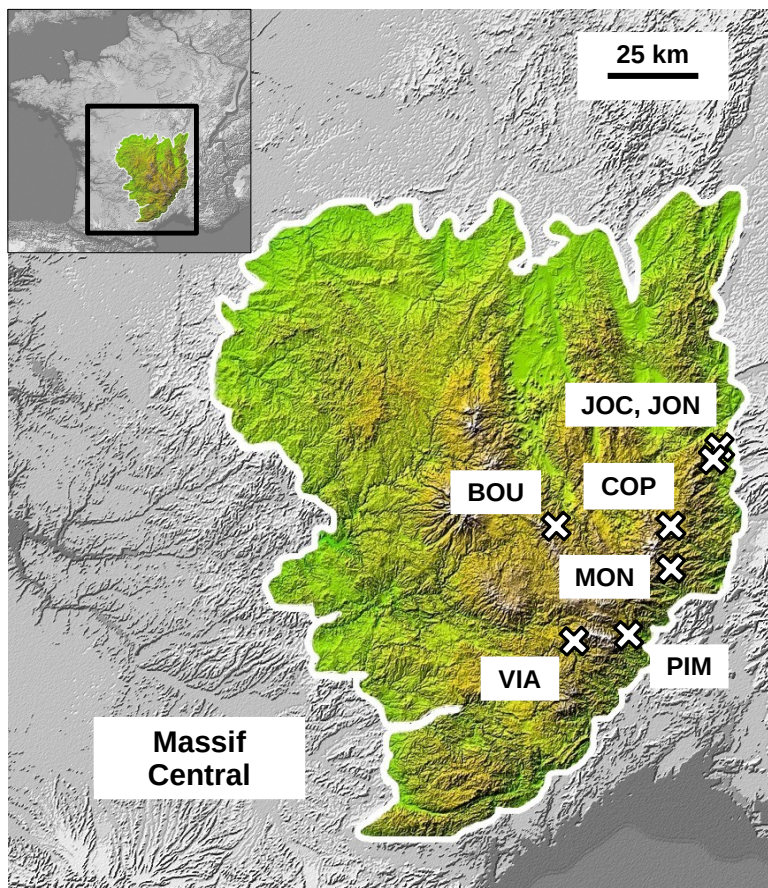
### Effects of experimental constraint products on relocation decisions

Informants' sex and focal individuals' sex had *a priori* no impact on the focal individual's relocation (Fisher's tests: respectively p=0.46 and p=0.42). Similarly, spatial position of informants' sex had no impact on the focal individual's relocation direction (Fisher's test: p=0.52). Other by-products of experimental constraints (difference in age between informants, age difference between focal individuals and informants, informants' kinship, and timing of experiments) had *a priori* no significant effect on relocation probability (Fisher's tests: respectively p=0.41, p=0.38, p=0.61, and p=0.26). The difference in age between informants also had no *a priori* significant effect on relocation direction (Fisher's test: p=0.74).

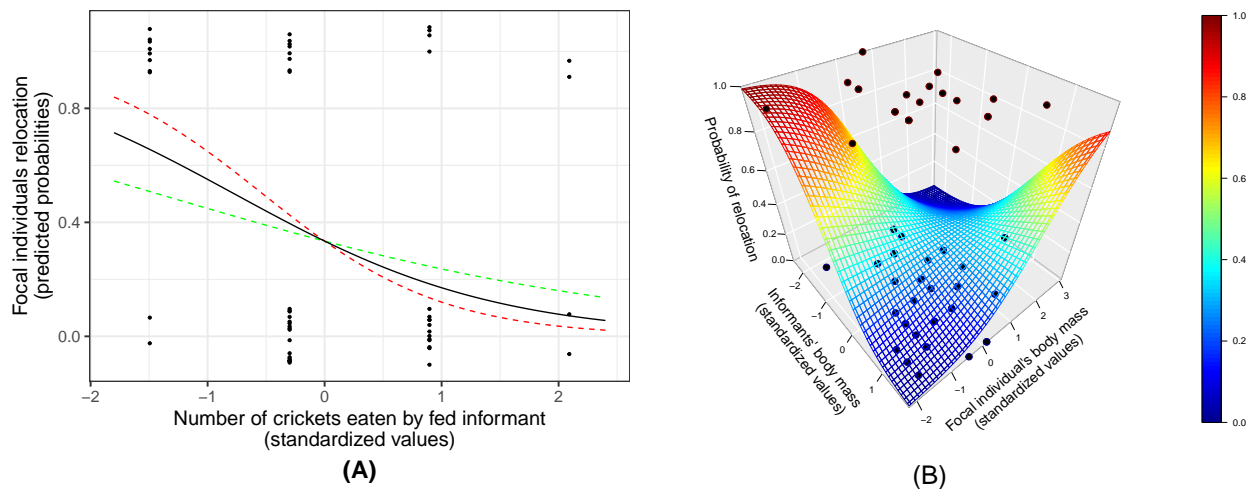
### Interactions between neonates during experiments

We measured the level of interactions between the three neonates during the confrontation part of the experiments (Figure 2), using the experimental recordings (see the Materials & Methods section for details). Due to the poor quality of our recordings, we could not distinguish between the behaviour of informants and focal individuals. As a result, we analysed the joint behaviour of the three juveniles together for the last twenty minutes of their confrontation, with the first ten minutes considered to be an accommodation period (Cote et al. 2008). We used the BORIS software (Friard and Gamba 2016) to quantify the following interaction: non-aggressive close proximity (time spent motionless by at least two individuals in close proximity, i.e. at a distance less than the size of an individual) and competitive direct interactions (number of contacts between two individuals that resulted in the flight of at least one individual).

## Supplementary figures



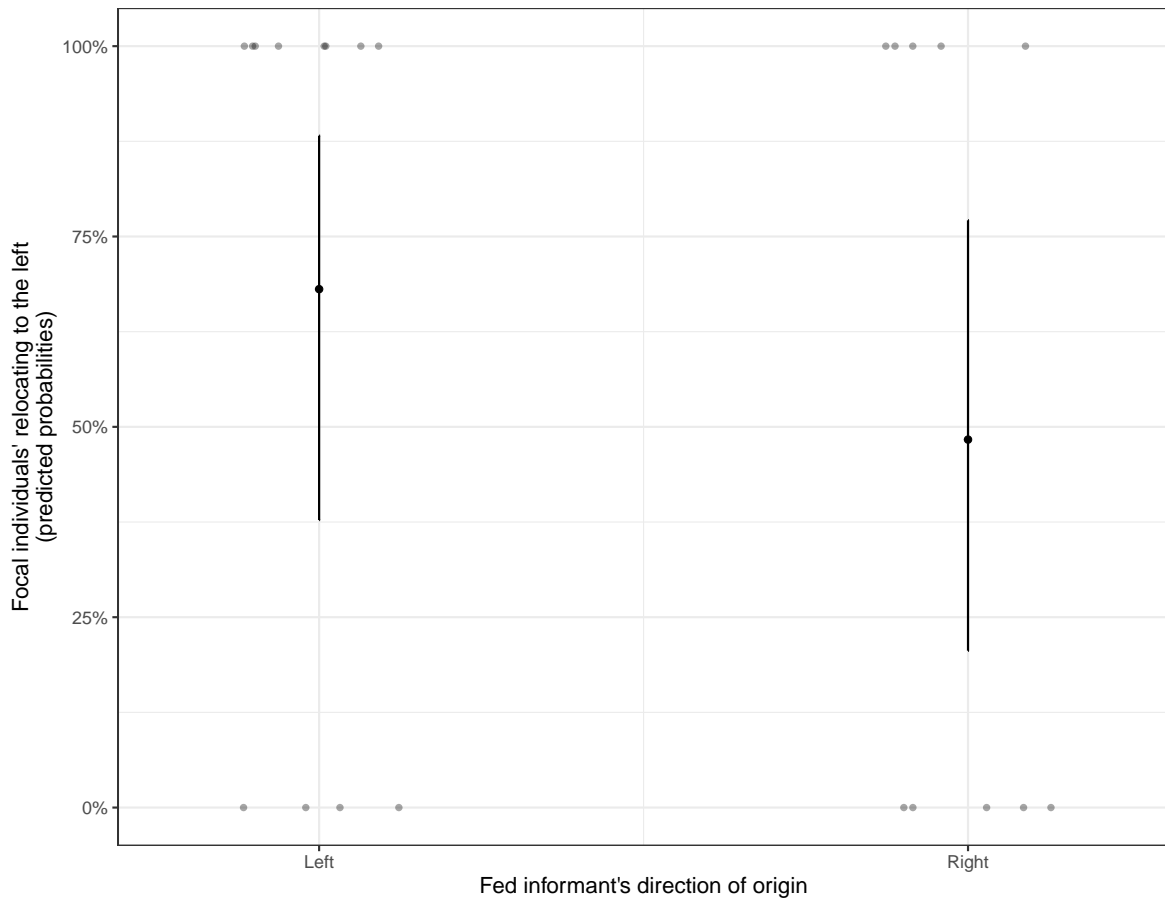
**Figure S1: Sampled site locations in Massif Central, France.** All sampled sites are located on the above map, here are the different localities corresponding to these sites: PIM (Pic du Mont-Lozère), VIA (Vialas), COP (Col du Pendu), MON (Montselgues), JOC, JON (Gerbier des Joncs), BOU (Baraque du Bouvier). The Massif Central is delimited on the map by the white line and appears in colour. This map was reproduced from Rutschmann et al. (2016), the map background was adapted from an original map under the CC BY-SA 3.0 licence, available at the following link: <https://commons.wikimedia.org/wiki/user:Technob105>.



**Figure S2: Informants' traits effects on focal individuals' relocation probability.** We looked at the distribution of focal individuals' relocation predicted probability as a function of informants' marginally significant traits ( $0.05 < p < 0.1$ ). Plots were obtained from the logistic regression results (Table 1) by plotting the predicted probabilities as a function of the variable of interest's and the intercept's coefficients (all other coefficients were fixed to 0, i.e. their average or their baseline level as they are standardised). Effects degree of significance is displayed in table 1. Black dots display observations from all experimental replicates: a dot around the 0 probability line/surface corresponds to a focal individual who did not leave his terrarium, a dot around the 1 probability line/surface corresponds to a focal individual who left his terrarium. These dots were slightly jittered horizontally to gain in readability.

**A- Predicted probabilities of focal individuals' relocation as a function of the fed informant's food intake.** Dots were also jittered vertically to gain in readability. The black line was plotted using the fed informants' food intake coefficient obtained from the logistic regression. Red and green dashed lines were plotted using the same coefficient plus (green) or minus (red) the coefficient's standard error.

**B- Predicted probabilities of focal individuals' relocation as a function of the informants' and focal individual's BM.**



**Figure S3: Feeding treatment absence of effect on orientation.** We looked at the distribution of focal individuals' relocation direction predicted probability as a function of fed informant original direction (through a logistic regression). Effect degree of significance is displayed in Table 2. The graph was obtained by plotting the predicted probabilities as a function of the variable of interest's and the intercept's coefficients (all other coefficients were fixed to 0, i.e. their average, or were fixed to their mean level for categorical variables), the R package "ggeffects" was used to produce the plot. Black bars represent 95% confidence intervals for predicted probabilities. Grey dots represent observations from all experimental replicates: a dot on the 0% line corresponds to a focal individual who left his terrarium to the right, a dot on the 100% line corresponds to a focal individual who left his terrarium to the left. These dots were horizontally jittered to gain in readability.