

Social information use for spatial decision in

Zootoca vivipara

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Abstract

1

2 Movements of individuals are conditioned by information acquisition coming from either
3 personal or social sources. Yet, little is known about the processes used by individuals
4 to make movement decisions when facing multiple sources of social information simul-
5 taneously. This study aimed to test experimentally how social information from multiple
6 sources is used to make movement decisions, and whether a contrast in this information
7 allows individuals to orientate in space. We used common lizards (*Zootoca vivipara*)
8 in a replicated experimental setting: one focal individual received information from two
9 other individuals coming from peripheral environments, before being given the opportu-
10 nity to relocate in one or another of the peripheral environments.

11 Our analyses revealed that the behavior of informants, their mother's morphology, as well
12 as the quality of informants' environment, affected movement decisions: the probability
13 to relocate from the focal area increased when informants displayed traits associated with
14 low resources (no food intake, poor maternal condition) or high competition (high activ-
15 ity). The physical condition of individuals also mediated the use of social information
16 about food intake, with a match between resource availability in informants and personal
17 condition. Conversely, spatial orientation was not affected by the contrast of phenotype
18 between informants nor by spatial variability in resource availability.

19 This study highlights that multiple social information sources can be used for movement
20 decisions, likely because these information sources reflect the quality of the surrounding
21 environment (e.g., competition level or resources availability). It also emphasizes that
22 social information use for movement is conditioned by individual phenotype.

23 **Keywords:** Social information, Movement decisions, Spatial orientation, Common lizard,
24 Information transfer, Information use

25 **Introduction**

26 Information acquisition is central for an individual to assess the quality of its environment
27 and to take appropriate decisions to feed, survive and reproduce (Dall et al. 2005, Schmidt et
28 al. 2010). Information can either be obtained via personal interactions with the environment
29 (i.e., personal information, Dall et al. 2005) or via social interactions (i.e., social information,
30 Dall et al. 2005, Schmidt et al. 2010). Social information is acquired through the observa-
31 tion of conspecific's or heterospecific's detectable traits (e.g., behavior, performance, body
32 condition, odors; Moreira et al. 2008, Clobert et al. 2009) and can inform individuals about
33 both abiotic and biotic characteristics of the local and distant environments such as breeding
34 habitat quality (Doligez et al. 2002 and 2004) or conspecific density and resource availability
35 (Endriss et al. 2018). Social information can be intentionally transmitted by informant indi-
36 viduals through signals such as calls or territorial marking (Johnson 1973, Macedonia et al.
37 1993) but may also be inadvertently conveyed by cues (Schmidt et al, 2010), as it is the case
38 for breeding habitat quality, informed by reproduction performances in some bird species
39 (Doligez et al. 2002, 2004).

40 Social information has long been recognized to be key in organisms' decisions to move
41 through their environment and is notably known to influence the optimization of spatial deci-
42 sion making for microhabitat use (e.g., Moreira et al. 2008), habitat selection (Doligez et al.
43 2002, 2004) or dispersal (Cote and Clobert 2007, Jacob et al. 2015). In spatially heteroge-
44 neous environments, social information is expected to be especially useful for any movement
45 decision. Indeed, in such environments, the social information is made of a mosaic of cues
46 or signals carried by either local inhabitants or immigrants, respectively informing on the
47 specificities of close and distant habitats (Cote and Clobert 2007, Jacob et al. 2015). With
48 increasing heterogeneity, environmental predictability is expected to decrease and socially ac-
49 quired information can increase an individual knowledge of the general environment, hence
50 reducing the probability of erroneous decisions due to environmental uncertainty (Dall et al.

51 2005, Riotte-Lambert et al. 2020). In other words, informed individuals are more likely to
52 make the right movement decisions (i.e., the one that maximizes their fitness) if they acquire
53 knowledge about the suitability of surrounding habitats throughout social information, com-
54 pared to when relying on their local prospects only, especially if their movement abilities are
55 restricted.

56 Yet, little is known about the use of social information for movements decision when multi-
57 ple sources of social information are simultaneously accessible to an individual (i.e., multiple
58 conspecifics reflecting different surrounding habitats). More specifically, two important ques-
59 tions have to be addressed. First, when multiple sources of information are available, how
60 information sources are used to decide whether the individual should relocate or not? One
61 may expect that the averaged information on surrounding habitats should prevail (Hyp. 1.a:
62 Social information synthesis, figure 1): an individual would optimize its movement by syn-
63 thesizing all sources of information available (i.e., each social cue or signal among sources),
64 whatever the quality and origin of the cue or signal, to get a global idea of the amount of
65 resource and level of intraspecific competition in the vicinity (Stamps 2001, Clobert et al.
66 2004, Bowler and Benton 2005). The use of information on surrounding habitats could also
67 depend on the phenotype of the informed individual, which would adjust movement decision
68 to its condition and relocate only when necessary (Hyp. 1.b: Phenotypic-dependent social
69 information synthesis, figure 1). Many examples in the literature illustrate such phenotype-
70 dependent use of social information, with dependence on personality (Smit and van Oers
71 2019, Morinay et al. 2020), age and success (Parejo et al. 2007), or body condition (Cote
72 and Clobert 2007). One may also expect individuals to use the contrast between available
73 information sources (Hyp 1.c: Contrasted social information use, figure 1): by comparing
74 the concordance or discordance of social cues or signals between sources, individuals might
75 be able to assess information reliability or environmental variability in the vicinity. The im-
76 portance of conflictual information for movement decisions has already been observed for

77 conflicts between personal and social information (e.g., Cronin 2013, Winandy et al. 2020),
78 with prioritization of personal information in case of conflicts (Kendal 2009).
79 The second question lies in the spatial integration of information gathered from multiple
80 sources coming from different locations: how does an individual use multiple sources of in-
81 formation to orientate, and therefore to choose a specific destination of relocation between
82 alternative habitats? One likely hypothesis (Hyp. 2: Spatially contrasted social information
83 use, figure 1) is that differences in information between multiple sources originating from
84 different habitats allow spatial orientation for the information receivers. Such differences in
85 information could indeed inform the individual on the direction of habitats with a higher fit-
86 ness expectancy, since the surrounding habitats are possibly associated with different social
87 information quality as a function of their fitness expectancy (Schmidt et al. 2010).
88 To investigate these questions, we used the common lizard (*Zootoca vivipara*, Jacquin 1787)
89 as a model species. This lizard is known to use social information in different contexts, and
90 notably to acquire information about the dispersal status of conspecifics (Aragon 2006 b.),
91 the reproductive strategy and aggressiveness of other females from their ventral coloration
92 (Vercken et al. 2012), or the population density in the surrounding habitats through immi-
93 grants (Cote and Clobert 2007, Cote et al. 2008 a.). In this species, the use of personal and
94 social information is also known to occur immediately after birth and to shape natal dispersal
95 decisions (Clobert et al. 2012, Cote and Clobert 2012).
96 Here, we tested how common lizards use social information from two contrasted habitats,
97 varying in food availability (present or not), to take decisions of relocation from their local
98 area. We also tested whether such information could influence movements' orientation when
99 relocation occurred. To do so, we placed juvenile lizards (neonates from 2 to 4 days, born
100 in our facilities from caught gravid females) in a three-chamber system (figure S1), where
101 an information receiver (referred to as the focal individual further on) was confronted with
102 two individuals coming from independent chambers and carrying contrasting information (re-

103 ferred to as informants further on). One informant came from an experimental environment
104 where food was provided, while the other came from an experimental environment where
105 food was absent. We generated all possible combinations of informants' sexes introduced to
106 the focal individual and measured multiple phenotypic traits that might convey information
107 about informants and their habitats. We hypothesized that informants could transmit social
108 information through their phenotype (e.g., behaviors, feeding, age, sex, or morphology) but
109 also through their mothers' condition (i.e., maternal effects, Bernardo 1996). These pheno-
110 typic traits are known to be related with short term sexual and resource competition contexts
111 (Massot 1992, Léna et al. 1998, Galliard et al. 2005 a. for sex and morphology; Lecomte
112 1994, Cote et al. 2008 a. for behaviors), or with the long-term environmental context through
113 maternal condition effects (Sorci and Clobert 1997, Uller and Olsson 2005, Mugabo et al.
114 2011). Note here that these phenotypic traits do not only inform about the competition in the
115 standardized experimental setup, but possibly also about the competition level present in the
116 habitat of origin of the individuals.

117 We expected relocation of the focal individual to vary with its phenotypic traits (Phenotype-
118 dependence of movement) as already shown for body condition (Cote and Clobert 2007), sex
119 (Galliard et al. 2005 a., Aragon et al. 2006 b.), age (Massot 1992, Léna et al. 1998), behaviors
120 (Cote et al. 2010) or maternal body condition (kin competition, Léna et al. 1998, Meylan et al.
121 2002). Using this set-up, we tested whether the focal individuals could use social information
122 from conspecifics to decide to relocate (or not) from their initial area. More specifically, we
123 expected focal individuals to increase their movements when information about high qual-
124 ity surrounding habitats is on average provided (Hyp. 1.a, figure 1): low competition for
125 resources (i.e., poorly active informants with poor physical conditions); long-term quality
126 of the habitat (i.e., informants' mothers with good physical conditions); low sexual compe-
127 tition (i.e., low male informants' number) or sufficient resources availability (i.e., well-fed
128 informants). The use of social information to adjust movement decisions might furthermore

129 depend on the phenotype of focal individuals (Hyp. 1.b, figure 1), we specifically focused
130 here on the phenotype dependence of social information use about food availability. For in-
131 stance, we expected an increased probability of movements when focal individuals are in
132 low condition and provided with information about a high amount of resources, long-term
133 high habitat quality, or low competition in the vicinity. In contrast to average social informa-
134 tion, the contrast of traits between informants might reflect the heterogeneity of information
135 on surrounding environments (Hyp. 1.c, figure 1). Individuals might choose to decrease
136 their movements when heterogeneity of information about surrounding environments, and
137 thus possibly information uncertainty, increases (Riotte-Lambert et al. 2020, e.g. Heinen
138 and Stephens, 2006). Finally, we expected focal individuals to adjust movement direction
139 depending on social information differences between sources (Hyp. 2, figure 1), possibly
140 moving towards the chamber of the informant having access to food, with a better physical
141 condition, displaying low competitive behaviors, or being of the opposite gender.

142

143 **Materials & Methods**

144 **Species and study sites**

145 *Zootoca vivipara* (Jacquin 1787) is a small size ground-living species in the Lacertidae fam-
146 ily. This widespread species spans Northern Europe and Asia and lives in heathlands, bogs,
147 and wet grasslands. Individuals used in this study have been sampled in seven populations
148 in the Massif Central mountain range (France). These sites range from 1000m to 1500m and
149 cover the diversity of possible habitats in this region (Rutschmann et al. 2016). In the Massif
150 Central, mating takes place just after individuals emerge from hibernation, between March
151 and April. Parturition usually occurs between late June and late July, depending on temper-
152 ature conditions (Rutschmann et al. 2016). In our sites the current mode of reproduction is
153 ovoviviparity and juveniles emerge from the egg within a few hours after parturition. Some
154 of the juveniles disperse from their natal site a few days after birth (Massot 1992).

155 **Capture and rearing condition**

156 The capture and rearing conditions have been validated by an ethical committee (DAP number
157 5897-2018070615164391-v3). Twenty pregnant females were captured at each site between
158 June 12th and 24th, in 2019. These females were brought to a field laboratory, where we
159 measured snout to vent length. Females were maintained in individual plastic terrariums
160 (18.5 x 12 x 11 cm), containing a shelter made from two slots of a cardboard egg-box and a
161 2 cm substrate of sterilized soil (Massot and Clobert 2000). Terrariums were placed under an
162 incandescent bulb of 25W providing light and heat for 6 hours a day to allow basking (from 9
163 a.m. to 12 p.m. and from 2 p.m. to 5 p.m.). Terrariums were sprayed with water three times
164 a day. Females were fed with three mealworms, every second day.
165 After parturition (between July 2nd and 24th), neonates from a same clutch were isolated
166 from their mother in a terrarium (day 0). Females that just gave birth were immediately

167 weighed. Neonates' snout to vent length (SVL) and body mass (BM) were measured the
168 day after their birth (day 1), before any feeding treatment. Sex was assessed following the
169 Lecomte et al. 1992 method. The same day, neonates were isolated to individual terrariums
170 (25 x 15 x 15 cm), containing a shelter made from two slots of a cardboard egg-box and
171 layered with two sheets of absorbent paper. Juveniles were left for another day (day 2) in
172 their respective terrarium before experiments started on day 3, so they could consider this
173 terrarium as their living area (Aragon et al. 2006 b.). All juveniles and mothers were fed and
174 released at the mother's capture site on day 4.

175 **Experimental design**

176 The experiment aimed at testing if the spatial decisions of a focal individual were influenced
177 by informants' phenotypes and food intake. Each of the 56 replicates of the experiment re-
178 quired three juveniles (two informants and one focal individual). Each juvenile was tested in
179 a single replicate. For each replicate, juveniles were selected among clutches of mothers from
180 the same capture site. When possible, informants had the same laying date. Most experimen-
181 tal replicates (n=37) took place 3 days after the birth of focal individuals but some replicates
182 happened 2- (n=10) or 4-days (n=9) after birth when there were too few births on the same
183 day. Similarly, 2 (n=10) and 4 days old (n=13) informants were used when necessary. Sev-
184 enteen replicates were associated with a difference of age between the focal individual and at
185 least one of the informants. When possible, the three individuals were selected from different
186 broods, but informants from the same brood were used in the same experimental replicate
187 when there were too few births (n=19).

188 One day before the confrontation between individuals, one of the two informants had access
189 to food: three small crickets, from 3 to 5 mm, were introduced in the terrarium. The number
190 of consumed crickets (0 to 3) was counted just before the experiment (referred to as the fed
191 informant's food intake further on). The focal individual was never fed before the experiment.

192 Our experiment further manipulated the combination of informants' sexes orthogonally to the
193 information about food access. Each focal female (n=29) or male (n=27) was confronted with
194 two informant males, two informant females, or one informant male and one informant fe-
195 male. These combinations were balanced between replicates within an experimental day. In
196 the replicates with one informant male and one informant female, the fed informant was the
197 male in nearly half of the replicates (n=14) and the female in the other replicates (n=16).
198 Furthermore, the three juveniles had variable phenotypes (SVL and BM, mothers' SVL and
199 BM) that we did not control for in the preparation of our experiments. However, we analyzed
200 their effects on movement decisions, since they displayed sufficient variability to be potential
201 social cues (informants SVL: 20 ± 1 mm, informants BM: 157.7 ± 18.2 mg, informants'
202 mothers SVL: 62.2 ± 4.1 mm, informants' mothers BM: 3616 ± 566.7 mg).
203 Replicates took place from July 5th to 27th between 7 a.m. and 8 p.m. We summed up the
204 timing of experiments in a categorical variable, accounting for the lighting periods in the field
205 laboratory, with four classes: early morning (7 a.m. to 9 a.m., n=13), morning (10 a.m. to 12
206 a.m, n=23), afternoon (1 p.m. to 4 p.m, n=13) and evening (5 p.m to 8 p.m, n=7).
207 By-products of experimental constraint (age difference between informants, informant kin-
208 ship and time windows) had no significant effect on relocation probability when individually
209 added in the selected model about relocation probability (respectively (z-value, p) = (-1.08,
210 0.28) / (-0.85, 0.39) / (from 0.26 to 1.22, from 0.22 to 0.80)). Difference in age between infor-
211 mants did not impact movement decision when added in the model about movement direction
212 ($\chi^2 = 1.39$, p = 0.24).

213 **Experimental assay**

214 The home terrarium of the focal individual was placed on an isolated table. Corridors (PVC
215 tubes of 25 cm length and 16 mm internal diameter) were introduced at each side of this terrar-
216 ium. Informants were placed in corridors' extremities and their arrival in the focal terrarium

217 was synchronized by slightly brushing their tails (figure S1). We alternated the introduction
218 position (left or right) of the fed informant and males and females between each replicate so
219 that the position was not biased towards a treatment or an informant's sex. Once the infor-
220 mants entered the focal terrarium, exits were plugged. The dimension of the focal terrarium
221 (25 x 15 x 15 cm) was sufficient to accommodate the three juveniles together while allowing
222 them to avoid each other. The three juveniles interacted together for thirty minutes (figure
223 S1). After that period, informants were put back in their respective terrariums. In the home
224 terrarium, absorbent paper, shelter, and heat/light source were removed to promote departure
225 (Aragon et al., 2006 b.). The focal individual was left five minutes in these conditions to
226 accommodate (figure S1). Then the corridors used previously were attached again at each ex-
227 tremity of the focal terrariums (without any modification since the informants' passage) and
228 connected to two identical and clean terrariums. The focal individual was left thirty minutes
229 in this system (figure S1). After this time, the experiment was stopped and we observed if
230 the focal individual had left his terrarium and in which direction. Terrariums in which focal
231 individuals arrived were washed with water between replicates. Corridors were used only
232 once. Experiments were entirely filmed with three webcams (Creative Live Camera Sync HD
233 720p) placed above each terrarium to analyze the three individuals' joint behaviors.

234 **Data analyses**

235 **Joint behaviors of focal and informant individuals**

236 Behaviors of focal and informant juveniles were measured to test their impact on relocation
237 decisions (Phenotype-dependence of movement and Hyp. 1.a, in figure S1). Due to technical
238 constraints (i.e., videos quality), we could not distinguish the behavior of informants and focal
239 individuals. As a consequence, we analyzed the joint behaviors of the three juveniles together
240 through the last twenty minutes of their confrontation, the first ten minutes being considered

241 as an accommodation time (Cote et al. 2007, 2008 a.). We used BORIS software (Friard and
242 Gamba, 2016) to quantify the following behavioral traits (the description and interpretation
243 of behaviors are detailed in table 1): activity, sheltering, escaping attempt, boldness behav-
244 ior, non-aggressive proximity, competitive interactions, and tongue-flicking. These behaviors
245 were considered apart from other focal individuals' traits or informants' traits because they
246 described the behaviors of both focal and informant individuals simultaneously and cannot
247 individually be ascribed.

248 We synthesized behavioral information using a principal component analysis (PCA) (figure
249 S3; all analyses were performed with the “FactoMineR” R package, Lê et al. 2008). Given
250 the explained variance distribution (figure S2-A, computed from eigenvalues, with the same
251 distribution) we retained the first axis, explaining 50.4% of the variance, for subsequent anal-
252 yses. This axis could be described as the global activity level, with non-negligible (loadings
253 > 0.4, variables close to this threshold were also displayed) positive contribution of activity,
254 competitive interactions, non-aggressive proximity and tongue-flicking behaviors, and a neg-
255 ative contribution of sheltering behavior (figure S2-B and table 2 for details). This axis will
256 be subsequently referred to as juveniles' joint activity level. The second PCA axis (which
257 mainly described the boldness behavior, figure S2-B) explained a non-negligible part of the
258 variance (18.5%). Yet, when including this variable in our models we found no significant
259 effects of this variable on focal individuals' relocation (z -value = -1.13, p = 0.26) and it did
260 not change the other variables' significance.

261 **Condition of informants and focal individuals**

262 In our models, we considered three groups of variables describing informants' and focal indi-
263 viduals' condition (Table 2): the condition of focal individuals (age, SVL, BM, mother's SVL
264 and BM; testing for phenotype-dependence of movement and Hyp. 1.b in figure 1), the con-
265 dition of informants (mean age, mean SVL and BM, mean mothers' SVL and BM; testing for

266 Hyp 1.a and Hyp 1.b in figure 1) and the absolute difference between informants' traits (SVL,
267 BM, mothers' SVL and BM; testing for Hyp 1.c in figure 1). Note that for the orientation
268 decision (see later), the latter group of variables was replaced by the raw difference between
269 informants' traits (SVL, BM, mothers' SVL and BM, left informant minus right informant
270 traits; testing for Hyp 2 in figure 1), to spatially polarize the contrast between informants.
271 To synthesize these variables we used a PCA and conserved the axes explaining most of the
272 variance in each group (all selected axes explained > 70% of the variance, figures S3-A, S4-
273 A, S5-A, and S6-A). All selected PCA axes and the respective part of explained variance are
274 described in table 2.

275 Briefly, the first two axes of the focal individual's condition PCA (figure S3-B) resume the
276 morphology (i.e., SVL and BM concomitant variations) of the focal individual's mother and
277 the focal individual's state (define as SVL, BM, and age concomitant variations). The first two
278 axes of the informants' condition PCA (figure S4-B) resume the morphology of informants'
279 mothers and informants' morphology. The first two axes of the contrasts in informants' con-
280 dition PCA (figure S5-B) resumed the contrast in the morphology of informants' mothers and
281 the contrast in informants' morphology. Finally, the first two axes of the PCA on differences
282 in informants' condition (figure S6-B) synthesized the difference in morphology of infor-
283 mants' mothers and difference in informants' morphology. In addition to these four PCAs
284 axes, we also considered in our models the focal individual's sex, informants' sex ratio, and
285 the fed informant's food intake. Of note, there was no correlation between the fed informant's
286 food intake and informants' morphology (Pearson correlation test, $p = 0.54$) or morphology
287 of informants' mothers (Pearson correlation test, $p = 0.48$), and between sex and physical
288 condition (Wilcoxon tests; focal individual's sex and state: $p = 0.47$, informants' sex-ratio
289 and morphology: $p = 0.42$).

290 **Statistical Analyses**

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

293 First, we analyzed the relocation probability of focal individuals after their confrontation with
294 the two informants (Hyp. 1.a.b.c, figure 1). To do so, we used a Firth logistic regression (Firth
295 1993, ‘brglm’ function with a logit link, in “brglm” R package, Kosmidis and Firth 2021), a
296 penalized likelihood regression method. This method was chosen to take into account data
297 separation (Heinze and Schemper 2002), i.e. a predictor variable perfectly predicting the out-
298 come variable (Albert and Anderson 1984), and quasi-separated data, that is likely present in
299 our dataset given our sample size. We first tested for the population of origin as a potential
300 random effect (Zuur et al. 2009). Note here that a daily effect was partially nested in the pop-
301 ulation variable as the different capture sites are associated with different hatching periods
302 (Rutschmann et al., 2016) and as only one or two capture sites were used each day of ex-
303 periments. The population random effect appeared non-significant (analysis of deviance test
304 between null models with and without random effects, using standard logistic regressions; $p =$
305 0.47) and was dropped in our subsequent models. Then, we performed a model selection (Ta-
306 ble S1) among the set of candidate variables, describing the informants and focal individual
307 joint behaviors (activity level PCA axis; to test for phenotype-dependence of movement and
308 Hyp. 1.a), the focal individual’s condition (morphology of focal individuals’ mothers and fo-
309 cal individuals’ state PCA axes, and focal individuals’ sex; to test for phenotype-dependence
310 of movement), informants’ condition (morphology of informants’ mothers and informants’
311 morphology PCA axes, informants’ sex-ratio and the fed informant’s food intake; to answer
312 Hyp. 1.a), contrasts in informants’ condition (contrast in morphology of informants’ mothers
313 and contrast in informants’ morphology PCA axes; to test for Hyp. 1.c) and the interactions
314 between the fed informant’s food intake and the focal individual condition variables (food
315 intake with every three focal individuals’ condition variables; to test for Hyp. 1.b). All used

316 quantitative variables were scaled. This model selection was performed using the function
317 ‘dredge’ (package MuMIn, Barton et al. 2009). Only one model appeared in $\Delta AICc < 2$
318 (threshold for the best models; Burnham and Anderson 2004), this model was used for all
319 subsequent analyses.

320 The resulting model showed a sufficiently low variance inflation factor (maximal VIF of 1.71)
321 for the interpretation of our statistical results (O’Brien 2007). We measured the quality of our
322 selected model by implementing a Nagelkerke pseudo-R-squared (Nagelkerke 1991). Effects
323 of retained variables were tested through Wald tests on the selected model variables (since
324 model comparison approach on Firth’s regression still an on-going research, Kosmidis and
325 Firth 2021). We also used partial Nagelkerke pseudo-R-squared on our model to rank vari-
326 ables by their level of explained variance and relative importance obtained from the model
327 selection (sum of Akaike weights) to estimate all the variables’ degree of importance (includ-
328 ing the ones that did not appear in our selected model).

329 A second analysis was conducted to test which of the informants’ traits influenced the direc-
330 tion of relocation (Hyp. 2, figure 1) when focal individuals left their terrarium (n=22). This
331 time, we used simple logistic regressions with a binary response variable (leave toward left or
332 right). In this model, we used the spatial distribution of male and female informants (female
333 coming from the right and male coming from the left, male coming from the right and female
334 coming from the left or the same sex left and right), fed informant spatial origin (coming from
335 left or right), difference in informants’ morphology (Table 2) and difference in morphology
336 of informants’ mothers (Table 2). The model was diagnosed as presented before, with an
337 analysis of deviance instead of Wald tests for testing the variables effects (likelihood-ratio
338 tests, “car” R package, Fox and Weisberg 2018). Again, we obtained a sufficiently low VIF
339 (maximum equal to 1.38) for the interpretation of our results.

340 **Results**

341 Over the 56 experimental replicates, 22 focal individuals left their terrariums. The regression
342 results revealed significant ($p < 0.05$), or marginally significant ($0.05 < p < 0.1$), effects of focal
343 individuals' state (age, morphology) and sex, informants' traits (maternal morphology, the
344 fed informant's food intake), focal individuals' and informants' joint activity level, and the
345 interaction term between the focal individual's state and the fed informant's food intake. All
346 tests' statistics are available in Table 3. Shortly, the relocation probability of focal individuals
347 decreased with their age and increased with their morphology (figure S7-A) and was lower for
348 males compared to females (figure S7-B). The relocation probability further decreased with
349 larger informants' maternal morphology (figure S8-B, table 3) and the fed informant's food
350 intake (figure S8-A, table 3). Relocation also depended on the joint activity level of focal and
351 informant individuals (figure S9): it increased with the increase of activity, with higher levels
352 of social interaction (non-aggressive proximity and competitive interactions), and with higher
353 levels of exploration behaviors but decreased with increased sheltering behaviors (Mat&Met,
354 figure S2-B and Table 2). We also found that the food intake of the fed informant interacted
355 with the phenotype of the focal individual to impact the focal individual's probability of re-
356 location (figure 2): relocation probability increased for an informant with poor food intake
357 confronted to a focal individual with a low score of individual's state (i.e. smaller morpho-
358 logical traits and older age) or for an informant with high food intake confronted to a focal
359 individual with a high score of individual's state (i.e. larger morphological traits and younger
360 age). Overall, the fitting quality of this model was good, with a Nagelkerke R-squared of
361 0.68.

362 We computed explained variance estimates for each variable included in the selected model
363 by using Nagelkerke's partial R-squared (Table 3). Food intake of fed informants and joint
364 behaviors had relatively high partial r-squared of 0.49 and 0.4; the sex of focal individuals
365 and morphology of informants' mothers had respective r-squared of 0.21 and 0.22; the state

366 of focal individuals (age and morphology) had an r-squared of 0.13. The r-squared of the
367 interaction between the fed informants' food intake and the focal individual's state (0.44)
368 was rather important relatively to the previously described values. The relative importance
369 of all tested variables (obtained from model selection, Table S1) showed that the importance
370 of the other non-selected variables was much lower (relative importance inferior to 0.27 for
371 non-selected variables and superior to 0.84 for selected variables).

372 We then analyzed the movement direction of the 22 focal individuals which left their terrari-
373 ums; nine individuals went to the right and thirteen to the left. No significant effect was found
374 among the tested variables, including the feeding treatment (Table 4, figure S10). Overall, we
375 obtained a Nagelkerke R-squared of 0.15, suggesting a poor quality for the model.

376 **Discussion**

377 We experimentally investigated how social information is used for movement decisions when
378 simultaneous sources of information (i.e., informant individuals), coming from different en-
379 vironments, are available for decision making.

380 We found the relocation probability of focal individuals to be phenotype-dependent (in sup-
381 port of the expected phenotype-dependence of movement): relocation was more likely to
382 occur for females, to decrease with individual's age, and to increase with their score of mor-
383 phology (SVL and BM). We also found that the relocation probability of focal individuals
384 increased when informants ate fewer available prey and originated from mothers with smaller
385 morphological traits (low BM and SVL), suggesting the use of averaged social information
386 for movement decisions (in support of Hyp. 1.a: figure 1). We further observed a phenotype-
387 dependence of the use of social information about food availability (in support of Hyp. 1.b:
388 figure 1). We found no significant influence of contrasts in traits between informants, poten-
389 tially representative of information variability or reliability, on the relocation probability of
390 focal individuals (contrary to the expectations from Hyp. 1.c: figure 1). Finally, when focal
391 individuals left their terrarium, the position of the informant having access to food did not
392 influence the direction of the movement, as for other differences in traits between informants
393 (contrary to the expectations from Hyp. 2: figure 1).

394 **Phenotype dependence of relocation**

395 In many species, movement from one location to another can be related to environmental fac-
396 tors or the individual's phenotype (respectively context- and phenotype-dependence, Bowler
397 and Benton, 2005). In the common lizard for example, dispersal is known to depend on the ju-
398 venile's phenotype such as its level of stress or its physical condition (Clobert et al., 2012). In
399 our experiments, we further observed that the focal individual's state variable correlated with

400 the relocation probability: it increased with larger morphology (BM and SVL) and decreased
401 with age. The morphology of a neonate lizard, just after birth, directly reflects the amount
402 of energetic reserve available from initial yolk reserves in the egg and therefore influences
403 its performance in the early stage of life (Sinervo 1990, Olsson et al. 2002). As movements
404 implied energetic cost (for displacement itself or potential interactions with competitors and
405 predators, Bonte et al. 2012), larger reserves should provide an advantage for successfully re-
406 locating toward another habitat if necessary. Such a relationship between juveniles' physical
407 condition and movements had already been observed in common lizards for natal dispersal
408 (Meylan et al. 2002). Similarly, in the absence of any food intake, neonates only rely on
409 the energetic reserves inherited from the eggs' yolk for early physiological performance. As
410 a consequence, younger individuals may be more inclined to allocate such reserves towards
411 relocation than older individuals, forced to conserve their energy for foraging. It could be
412 an advantage to rapidly use their natal reserves for displacement or exploration, especially
413 as early-stage appeared to be central for future survival (Mugabo et al. 2010, Massot and
414 Aragon, 2013). Another possible hypothesis to explain the increase of relocation probability
415 for younger juveniles is that individuals may try to escape competition with their mother and
416 sibling by relocating as soon as possible from their birth location (Galliard et al. 2003, Cote
417 et al. 2007, Cote and Clobert 2010). We also observed an effect of focal individuals' sex on
418 their relocation probability: the propensity for juveniles to relocate was higher for females
419 than for males. This is a surprising result as male-biased movements are often observed in
420 lizard species (e.g., Doughty et al. 1994, Schofield et al. 2012), including the common lizard
421 (Galliard et al. 2005 b.). Yet, this result echoes what has been found in earlier experiments
422 (Aragon et al. 2006 b.), where, when relocating after a confrontation with another neonate,
423 female juveniles relocated with lower latency than males. Thus, it is likely that the observed
424 female-biased movement would have disappeared if we had let the juveniles dispersed for a
425 longer period, to potentially give way to male-biased movements.

426 Finally, the positive effect of the joint level of activity of informants and focal individual on
427 the focal individual's relocation probability might result from independent or joint effects of
428 the focal individual behavior or of informants' competitiveness (that we will discuss later) that
429 we cannot distinguish in our experiment. When considering the focal individual's behavior,
430 a more active and explorative individual (high movement rate, low sheltering, high chemi-
431 cal exploration through tongue-flicking, high non-aggressive proximity with conspecifics) is
432 indeed more likely to leave its home environment (Cote et al. 2010).

433 **Use of social information from multiple sources**

434 In our experiment, interacting conspecifics might convey information about either the local
435 or the distant habitat. Although distinguishing between these two non-exclusive hypotheses
436 would require further experimental investigation that is beyond the scope of this paper, we
437 here elaborate on the patterns expected under each scenario and how they match (or not) with
438 our findings. If informants mainly carried information about the local habitat, we would ex-
439 pect focal individuals to stay in the current environments when confronting individuals bear-
440 ing cues or signals related to high-quality environments. On the contrary, a relocation of the
441 focal individual in presence of individuals carrying cues or signals related to high-quality en-
442 vironments would suggest that the phenotypic traits of informants convey information about
443 their habitat of origin.

444 We observed that relocation propensity increased when the morphology of informants' moth-
445 ers decreased, and when focal lizards were facing fed informants which did not eat much.
446 These observations are in favor of our second hypothesis as they are indicators of low re-
447 source availability in the close environment, and therefore related to an avoidance of a poor
448 local environment given the importance of resources for survival (Mugabo et al. 2010, 2011,
449 Massot and Aragon 2013). The physical condition of informants' mothers could also be
450 representative more broadly of habitat quality as it could vary with other important envi-

451 ronmental parameters as density (Massot et al. 1992) or abiotic parameters as temperature
452 (Chamaillé-Jammes et al. 2006). Avoidance of informants whose mothers were of poor phys-
453 ical condition could then reflect the avoidance of a local environment of low quality. Such an
454 avoidance had already been observed with dispersal increase in case of too high competition
455 (Léna et al. 1998, Cote et al. 2008 a.) or abiotic parameter that does not match energetic re-
456 quirement (Bestion et al. 2015). We also observed that relocation propensity increased with
457 juveniles' (informants and focal individual) activity. More knowledge about the individual
458 behaviors of informants would have helped to refine our interpretations but the presence of
459 active and aggressive conspecifics is likely to reflect high levels of direct competition in the
460 local environment (Sih et al. 2004, e.g. Garland et al. 1990). A measure of stress hormones
461 (as corticosterone, see Belliure et al. 2004) would be useful to precise the influence of infor-
462 mants' stress level on focal individuals' relocation.

463 Finally, we also observed that relocation probability increased when the fed informant food
464 intake and the focal individual's physical condition were both low or both high. Again, this
465 result suggests that relocation preferentially occurs when local resource availability does not
466 match the focal individual phenotype. In the first case, individuals seemed to avoid a local
467 environment with insufficient resources given their conditions (low energetic reserves), while
468 in the second case, they seemed to escape unnecessary competition for resources while hav-
469 ing a good enough physical condition to relocate toward a less competitive habitat. Such
470 results further suggest that the use of social information is mediated by the phenotype of the
471 focal individuals, a dependency that has been already observed in previous studies (Cote and
472 Clobert 2007, Cote and Clobert 2010, but also Parejo et al. 2007 in other species) but never
473 with information on direct resources availability at stake.

474 **On the meaning of informants' traits**

475 In our experiment, interacting conspecifics might convey information about either the local
476 or the distant habitat. Although distinguishing between these two non-exclusive hypotheses
477 would require further experimental investigation that is beyond the scope of this paper, we
478 here elaborate on the patterns expected under each scenario and how they match (or not) with
479 our findings. If informants mainly carried information about the local habitat, we would ex-
480 pect focal individuals to stay in the current environments when confronting individuals bear-
481 ing cues or signals related to high-quality environments. On the contrary, a relocation of the
482 focal individual in presence of individuals carrying cues or signals related to high-quality en-
483 vironments would suggest that the phenotypic traits of informants convey information about
484 their habitat of origin.

485 We observed that relocation propensity increased when the morphology of informants' moth-
486 ers decreased, and when focal lizards were facing fed informants which did not eat much.
487 These observations are in favor of our second hypothesis as they are indicators of low re-
488 source availability in the close environment, and therefore related to an avoidance of a poor
489 local environment given the importance of resources for survival (Mugabo et al. 2010, 2011,
490 Massot and Aragon 2013). The physical condition of informants' mothers could also be
491 representative more broadly of habitat quality as it could vary with other important envi-
492 ronmental parameters as density (Massot et al. 1992) or abiotic parameters as temperature
493 (Chamaillé-Jammes et al. 2006). Avoidance of informants whose mothers were of poor phys-
494 ical condition could then reflect the avoidance of a local environment of low quality. Such an
495 avoidance had already been observed with dispersal increase in case of too high competition
496 (Léna et al. 1998, Cote et al. 2008 a.) or abiotic parameter that does not match energetic
497 requirement (Bestion et al. 2015). Yet, we also observed that relocation propensity increased
498 with juveniles' (informants and focal individual) activity. More knowledge about the individ-
499 ual behaviors of informants would have helped to refine our interpretations but the presence

500 of active and aggressive conspecifics is likely to reflect high levels of direct competition in
501 the local environment (Sih et al. 2004, e.g. Garland et al. 1990). A measure of stress hor-
502 mones (as corticosterone, see Belliure et al. 2004) would be useful to precise the influence of
503 informants' stress level on focal individuals' relocation.

504 Finally, we also observed that relocation probability increased when the fed informant food
505 intake and the focal individual's physical condition were both low or both high. Again, this
506 result suggests that relocation preferentially occurs when local resource availability does not
507 match the focal individual phenotype. In the first case, individuals seemed to avoid a local
508 environment with insufficient resources given their conditions (low energetic reserves), while
509 in the second case, they seemed to escape unnecessary competition for resources while hav-
510 ing a good enough physical condition to relocate toward a less competitive habitat. Such
511 results further suggest that the use of social information is mediated by the phenotype of the
512 focal individuals, a phenotype dependence of social information use that has been observed
513 previously (Cote and Clobert 2007, Cote and Clobert 2010, but also Parejo et al. 2007 in
514 other species) but never with information on direct resources availability at stake.

515 **Direction of movement**

516 Previous findings have shown a limited but existing ability to orientate in space for the com-
517 mon lizard (Strijbosch et al, 1983). Here, we found no effect of the difference in food access
518 between informants or other observed contrasts between informants on movement orientation
519 when relocation occurred. Given the small sample size for direction analyses (22 replicates),
520 we have to be very cautious about the validity of such effects. These results might suggest that
521 focal individuals considered social cues or signals from present information sources as infor-
522 mation about local conditions, for which no orientation is needed. Alternatively, individuals
523 might not have had access to sufficient cues for visual orientation, the design being symmet-
524 rical and the arrival lasting few seconds only. Decisions on direction would then mainly rely

525 on informants' arrival with olfactory signals or cues left by informants in corridors (Aragon
526 et al. 2006 a. and c.). Further experiments, focusing for example on pheromones carried by
527 informants, would be necessary to make any conclusion on the actual use of these odors.

528 **Conclusion**

529 Our experiment showed that the averaged social information coming from multiple sources
530 was transmitted by interacting conspecifics, with mediation in the use of some information by
531 the phenotype of focal individuals. Yet, contrasts between information sources were not used
532 in our experiments for relocation decisions or orientation. The importance of these informa-
533 tion transfers for spatial use could be understood as surrounding habitat quality assessment,
534 with indication on resource availability and degree of intra-specific competition. We also
535 showed that, for the common lizard, information prioritization could occur, with a preference
536 over information related to the immediate environment.

537 **Author contribution**

538 MB, MR, JC, SJ and AR designed the experiment. MB, JC and AR performed the field work.
539 MB performed all experiments and analyses. MB, MR, JC, SJ and AR wrote the manuscript.

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550 **Data availability**

551 Analyses reported in this article can be reproduced using the data provided by Brevet et al.
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800 **Figure legends**

801 **Figure 1: Experimental aims.** These schemes present the different hypotheses that we in-
802 vestigated through our experimental design. We hypothesized that relocation would depend
803 on a synthesis of all social information on surrounding habitats. Such use of multiple sources
804 of social information might consist in using an averaged value of multiple information sources
805 (Hyp. 1.a), potentially mediated by focal individual's phenotype (Hyp. 1.b). Conversely, the
806 use of social information could consist in using the contrast between information sources as
807 an indicator of information variability/reliability (Hyp. 1.c). Finally, we hypothesized that the
808 existing contrast between information sources could allow the focal individual to orientate in
809 space in order to join the best of the surrounding habitats (Hyp. 2).

810

811 **Figure 2: Joint effects of the fed informant's food intake and the focal individual's state**
812 **on relocation probability of focal individuals.** We looked at the distribution of focal in-
813 dividuals' relocation predicted probability as a function of the fed informant's food intake
814 (number of eaten crickets, standardized values) and the focal individual's state (standardized
815 values). The graph was produced using the Firth's logistic regression results (see Table 3),
816 by plotting the predicted probabilities as a function of the variable of interests' and the inter-
817 cept's coefficients (all other coefficients were fixed to 0, i.e. their average or their baseline
818 level as they are standardized). Black dots display observations from all experimental repli-
819 cates: a dot on the 0% probability surface corresponds to a focal individual who did not leave
820 his terrarium, a dot on the 100% probability surface corresponds to a focal individual who
821 left his terrarium.

822 Tables

Table 1: Joint behaviors of the focal individuals and informants.

Behavior	Description	Unit	Mean value	Sd
Activity	Cumulative time spent moving by the three individuals (Aragon et al. 2006 a., Cote et al. 2008 a.)	Seconds	949	389
Sheltering	Cumulative time spent sheltering by the three individuals (Cote et al. 2008 a.)	Seconds	1381	795
Escaping attempt	Time spent by at least one individual trying to escape the terrarium by scratching or climbing the walls (Aragon et al. 2006 a.)	Seconds	64.8	78.6
Boldness	Time spent by at least by one individual basking above the shelter (Cote et al. 2008 b.)	Seconds	177	232
Non-aggressive proximity	Time spent motionless by at least two individuals in close proximity to each other, i.e. at a distance less than the approximate size of an individual (Aragon et al. 2006 b.)	Seconds	192	160
Competitive interaction	Number of contacts between two individuals leading to the flight of at least one individual (Aragon et al. 2006 b.)	Events count	3.61	3.86
Tongue-Flicking	Olfactory cues acquisition that could be interpreted as a chemical exploration (Cooper 1994, Aragon et al. 2006 b.)	Events count	2.88	3.43

Description of the joint behaviors of the three juveniles, measured during the last twenty minutes of their confrontation (see Mat&Met). We did not use cumulative times for escaping attempts and boldness behavior because these behaviors were performed extremely rarely by several individuals at the same time (4% and 2.7% respectively). Bibliographic references used to define these metrics are cited in the description column. Mean and standard deviation have been computed over all experimental replicates.

Table 2: Variables describing the condition of juveniles.

Set of variables	PCA axes (retained for analysis)	Described traits (high contribution variables)	Explained variance
Joint behaviors of juveniles	Activity level	Activity (0.49) / Competitive interaction (0.43) / Non-aggressive proximity (0.42) / Tongue-flicking (0.38) / Sheltering (-0.44)	50.4%
Focal individual's condition	Morphology of focal individual's mother	SVL of focal individual's mother (0.63) / BM of focal individual's mother (0.68)	41.2%
	Focal individual's state	Focal individual's SVL (0.57) / Focal individual's BM (0.53) / Focal individual's age (-0.52)	31.3%
Informants' condition	Morphology of informants' mothers	SVL of informants' mothers (0.68) / BM of informants' mothers (0.68)	39%
	Informants' morphology	Informants' SVL (0.49) / Informants' BM (0.43)	31.3%
Contrasts in informants' condition	Contrast in morphology of informants' mothers	Contrast in SVL of informants' mothers (0.62) / Contrast in BM of informants' mothers (0.62) / Informants' BM contrast (0.46)	48.6%
	Informants' morphology contrast	Informants' SVL contrasts (0.83) / Informants' BM contrasts (0.45)	29%
Differences in informants condition	Difference in morphology of informants' mothers	Difference in SVL of informants' mothers (0.63) / Difference in BM of informants' mothers (0.57)	48.5%
	Informants' morphology difference	Informants' SVL difference (0.59) / Informants' BM difference (0.60) / Informants' mothers' BM difference (0.44)	37%

This table displays most of the retained variables for statistical analyses (to which must be added the focal individual's sex, informants' sex ratio, and the fed informant's food intake), describing the condition of the focal individual and informants. These variables were obtained by using PCA analyses to synthesize each measured variable set. PCA axes are presented in their order of appearance. Traits with the most important contribution to PCA axes are described, with their loadings displayed in brackets. A positive loading was associated with a positive correlation with the PCA axis and a negative one with a negative correlation.

Table 3: Selected Firth’s logistic regression about focal individuals’ relocation probability.

	Parameter	Coefficient	SE	z-value	df	P-value	R²
	Intercept	-0.46	0.53	-0.86		0.39	
	Sex (male)	-1.86	0.92	-2.03	1	0.043*	0.21
Focal traits	Individual’s state (age/morphology)	0.85	0.49	1.75	1	0.081 •	0.13
Informants’ traits	Mothers’ morphology	-0.87	0.42	-2.08	1	0.038*	0.22
	Fed informant’s food intake	-2.26	0.77	-2.96	1	0.003**	0.49
Focal / informants interactions	Food intake x focal condition	1.91	0.66	2.87	1	0.004**	0.44
	Joint activity level	1.59	0.6	2.67	1	0.008**	0.40

Analysis of the selected model (the only one in $\Delta AICc < 2$) is displayed here. For each retained variables (see Mat&Met) we displayed the average coefficient and its standard error. The partial Nagelkerke pseudo-R-squared (R^2) of each variable in the selected model was also displayed. Wald-tests 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. • : $0.05 < p < 0.1$, * : $0.01 < p < 0.05$, ** : $0.001 < p < 0.01$, *** : $p < 0.001$

Table 4: Logistic regression on direction taking (analysis of deviance).

Parameter	χ^2	df	P-value
Fed informant origin	0.71	1	0.4
Sex contrast between informants	1.88	2	0.39
Morphologies contrast between informants	0.004	1	0.95
Morphologies contrast between informants' mothers	0.034	1	0.85

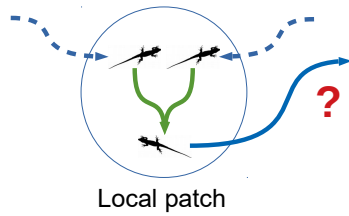
Results of the logistic regression on focal individuals' direction taking are displayed here. An analysis of deviance was performed to test for the significance of each variable effect (likelihood ratio tests). For each test, the chi-squared statistic and the associated p-values are displayed. Asterisks indicate the degree of significance.

• : $0.05 < p < 0.1$, * : $0.01 < p < 0.05$, ** : $0.001 < p < 0.01$, *** : $p < 0.001$

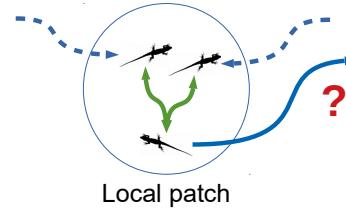
823 Figures

Figure 1: Experimental aims.

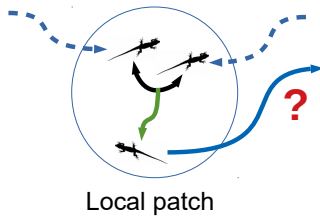
Hyp. 1.a: Social information synthesis (SIS)
Use of averaged social information for relocation



1.b: Phenotypic-dependent SIS
Use of averaged social information relatively to focal individual's traits for relocation



1.c: Contrasted social information (CSI)
Use of contrasted social information for relocation



2: Spatially CSI
Use of contrasted social information for orientation

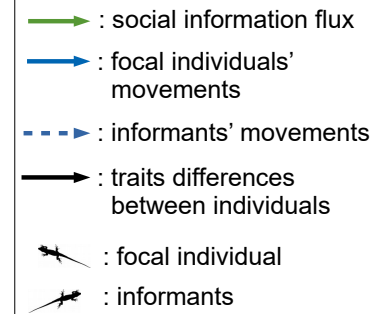
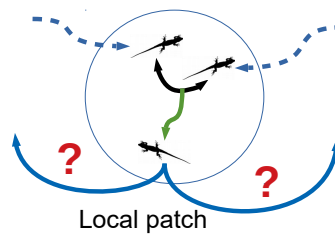


Figure 2: Joint effects of the fed informant's food intake and the focal individual's state on relocation probability of focal individuals.

