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1 **Dispersers are more likely to follow mucus trails in the land snail *Cornu aspersum***

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15 **Abstract**

16 Dispersal, movement leading to gene flow, is a fundamental but costly life history trait. The use of  
17 indirect social information may help mitigate these costs, yet we often know little about the  
18 proximate sources of such information, and how dispersers and residents may differ in their  
19 information use. Terrestrial molluscs, which have a high cost of movement and obligatorily leave  
20 information potentially exploitable by conspecifics during movement (through mucus trails), are a  
21 good model to investigate links between dispersal costs and information use. We studied whether  
22 dispersers and residents differed in their trail-following propensity in the snail *Cornu aspersum*.  
23 Dispersers followed mucus trails more frequently than expected by chance, contrary to non-  
24 dispersers. Trail following by dispersers may reduce dispersal costs by reducing energy expenditure  
25 and helping snails find existing habitat or resource patches. Finally, we point that ignoring the  
26 potential for collective dispersal provided by trail-following may hinder our understanding of the  
27 demographic and genetic consequences of dispersal.

28 **Keywords** costs of movement, dispersal syndromes, social information, Y-maze

29

## 30 **Introduction**

31 Dispersal, i.e. movement potentially leading to gene flow in space, is a key trait connecting ecological  
32 and evolutionary dynamics (Jacob et al. 2015a; Bonte and Doherty 2017). Costs and uncertainty  
33 associated with dispersal (Bonte et al. 2012) can be reduced by obtaining information about current  
34 and prospective habitats (Cote et al. 2007; Clobert et al. 2009; Chaine et al. 2013). Indirect social  
35 information, obtained from the presence, traits and/ or performance of conspecifics, can provide  
36 information about nearby habitats without the need for costly prospecting (Cote et al. 2007; Chaine  
37 et al. 2013; Jacob et al. 2015b).

38 Movement in terrestrial gastropods (snails and slugs) is among the costliest in animals, as mucus  
39 secretion leads to substantial energy and water losses even over short distances (Denny 1980; McKee  
40 et al. 2013). As mucus production is obligatory, many crawling gastropods have unsurprisingly  
41 evolved trail following behaviour to locate conspecifics or potential gastropod prey (Ng et al. 2013).  
42 Information on phenotype can additionally be gathered from mucus trail physical and chemical  
43 characteristics (Ng et al. 2013). Crawling on pre-existing trails may reduce the need for mucus  
44 production, leading to significant energy savings (Davies and Blackwell 2007). However, trail  
45 following has mostly been studied in aquatic gastropods and knowledge about its frequency and  
46 function in terrestrial snails is comparatively limited (Ng et al. 2013).

47 The brown garden snail *Cornu aspersum* (Müller) (Helicidae ; syn. *Helix aspersa*) is a well-studied  
48 generalist land snail, able to thrive and disperse even in strongly fragmented habitats (Doherty et al.  
49 2016a; Balbi et al. 2018). *Cornu aspersum* snails are sensitive to mucus accumulations (Dan and  
50 Bailey 1982) and adjust dispersal decisions to conspecific density (Doherty et al. 2016b). They appear  
51 to follow trails slightly more than expected by chance (Bailey 1989), but there is no evidence so far  
52 that they use trails during dispersal or that dispersers and residents react differently to social  
53 information. Using a Y-maze setup and ecologically relevant tests of dispersal propensity, we tested  
54 the hypotheses that *Cornu aspersum* snails are trail followers, and that dispersers would be more

55 likely to follow trails. Indeed, they would benefit more from potential energy savings and from  
56 information about conspecific presence than residents, which, given the costs of movement, are not  
57 expected to stray far from an already established group of conspecifics.

## 58 **Methods**

### 59 *Rearing conditions*

60 Snails (greater shell diameter > 25 mm) were obtained from two sources in April - May 2016. First,  
61 we selected 50 individuals (see below for details) among 120 snails used in a previous dispersal study  
62 (Dahirel et al. 2017), which were collected from natural populations in parks in Rennes, France  
63 ( $\approx 1^{\circ}38'W$ ,  $\approx 48^{\circ}7'N$ , hereafter the “natural population”). We also tested 47 new individuals randomly  
64 chosen from a set of 130 stock snails obtained from a snail farm in Corps-Nuds, close to Rennes  
65 ( $1^{\circ}36'37'' W$ ,  $47^{\circ}58'44''N$ , hereafter the “farm population”). Snails were kept under controlled  
66 conditions ( $20 \pm 1$  °C; 16L: 8D; *ad lib* cereal-based snail food, Hélinove, Le Boupère, France), in  
67 polyethylene boxes covered by a net ( $30 \times 45 \times 8$  cm) and lined by synthetic foam kept saturated  
68 with water. Snails were used in the experimental tests presented here between three to six weeks  
69 after collection. They were housed in groups of at most forty before use, and then in groups of eight  
70 to ten individually marked snails (with paint markers) for at least one week before dispersal tests.  
71 Boxes were cleaned and linings changed every week.

### 72 *Behavioural tests*

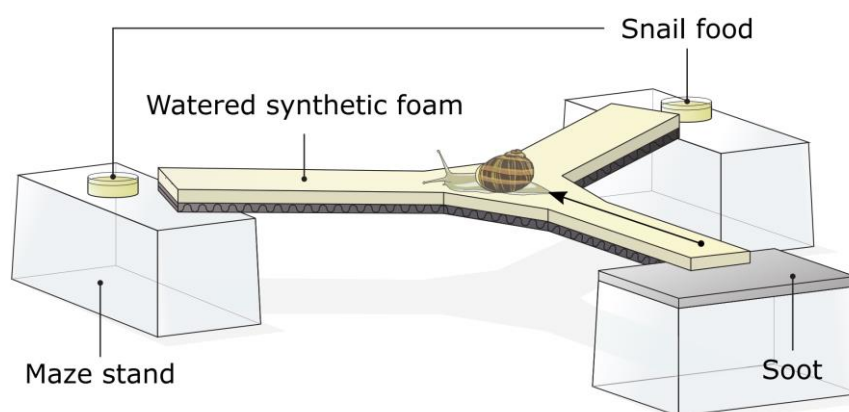
73 All snails were tested both for dispersal and trail following (see below for protocols). Snails from the  
74 natural population were tested for dispersal first, within the framework of a previous study (Dahirel  
75 et al. 2017), and then 25 dispersers and 25 residents (randomly selected among snails with greater  
76 shell diameter > 25 mm) were tested for trail following a week after dispersal testing. In the farm  
77 population, trail following was instead tested before dispersal for logistical reasons. Dispersal was  
78 then assessed a week later; 15 out of 47 tested “farm” snails were dispersers.

### 79 *Dispersal tests*

80 We assessed dispersal in an outdoor asphalted area on the Beaulieu university campus, Rennes  
81 (1°38'15"W, 48°6'59"N; see Dahirel et al. 2017 for details on protocols and their relevance to *Cornu*  
82 *aspersum* ecology). Briefly, rearing boxes (including food and water) were placed in the middle of the  
83 test area and left open for one night (19:00 to 09:00). Snails found more than 1 m outside of the box  
84 in the morning, i.e. beyond the typical *Cornu aspersum* home range (Dan 1978; M. Dahirel,  
85 unpublished data), were considered dispersers. This protocol qualitatively recovers phenotypic- and  
86 context-dependency in dispersal previously found in more natural settings (Dahirel et al. 2016a, b,  
87 2017). All dispersers were more than 1.5 m from their box, and all but one more than 3 m away; with  
88 one exception (found 10 cm from the box), all residents were found inside their box.

### 89 *Trail following experiment*

90 We studied trail following using Y-mazes (Ng et al. 2013) in a dark room, as snails are nocturnal (Fig.  
91 1). The experimenter (AV) wore latex gloves during setup and experiments to limit uncontrolled  
92 disturbance by human odours. Plastified cardboard mazes were lined with watered synthetic foam  
93 (as in rearing boxes), and 7g of snail food were placed at the extremities of both choice arms to  
94 stimulate movement. To limit escapes, Y-mazes were raised by 11 cm and the stand on which the  
95 starting arm of the maze rested was covered in soot, repulsive to snails (Shirtcliffe et al. 2012; Fig. 1).



96

97 **Figure 1.** Experimental setup (Y-maze) for the trail-following experiments (not to scale; arm width:  
98 3.5 cm; main arm length: 10 cm; choice arm length: 15 cm; angle between arms: 120°).

99 First, a “marker” snail randomly chosen among untested stock adult snails was placed in the main  
100 arm of the maze and left free to move for 10 minutes. Trails with U-turns or using both choice arms  
101 were excluded from further tests. Within 10 minutes after removing the marker, a “tracker” snail was  
102 placed at the start of the maze and left free to move for 10 minutes. All tracker snails made a choice;  
103 they were counted as trail followers if they chose the same arm as the marker snail. Maze linings and  
104 feeders were discarded and replaced with pristine ones between each test (i.e. between each  
105 marker-tracker combination). Preliminary tests with no marker snail were done to confirm that snails  
106 had no intrinsic left-right bias (Ng et al. 2013) (47.5 % chose the left side, binomial test against a 50%  
107 expectation,  $N = 40$ ,  $p = 0.87$ ). Following this, left-right symmetry during actual tests was enforced by  
108 alternately proposing left-side and right-side trails to successive tracker snails, randomly selected  
109 from simultaneously generated trails.

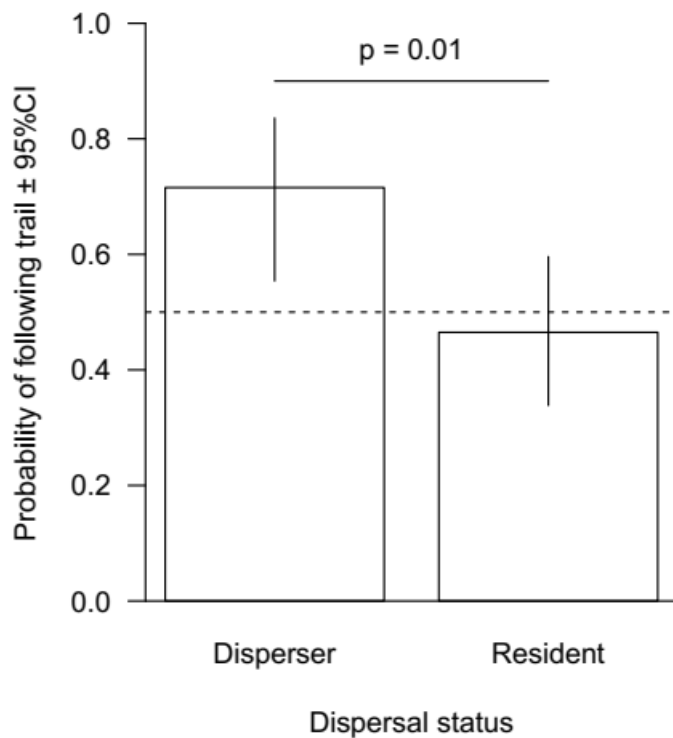
#### 110 *Statistical analyses*

111 We used a binomial generalized linear model to test for an effect of dispersal status, population of  
112 origin and their interaction on trail following probability. Analyses were done using R, version 3.5.1 (R  
113 Core Team 2018).

#### 114 **Results**

115 Dispersers were more likely to follow trails than residents (72.5% versus 47.4%,  $N = 40$  and  $57$ ,  $\chi^2_1 =$   
116  $6.40$ ,  $p = 0.01$ , Fig. 2). Contrary to dispersers, residents were not more likely to follow trails than the  
117 50% expected by chance (Fig. 2). There was no significant effects of population of origin or dispersal  
118 status  $\times$  population interaction ( $\chi^2_1 = 0.17$  and  $1.20$ ,  $p = 0.68$  and  $0.27$ , respectively).

119



120

121 **Figure 2.** Trail following rate as a function of dispersal status (model predictions and 95% confidence  
 122 intervals based on binomial GLM, the non-significant effect of origin population is averaged out ; N =  
 123 97).

124 **Discussion**

125 Dispersers, but not residents, were more likely to follow trails than expected by chance, indicating  
 126 that mucus trails are usable sources of indirect social information in *Cornu aspersum* snails. A non-  
 127 exclusive alternative is that trail-following is an energy saving measure (Davies and Blackwell 2007),  
 128 which would be more useful for dispersers. Intuitively and importantly, our results also indicate that  
 129 tests realized without knowledge of dispersal status may falsely conclude to the absence of trail  
 130 following behaviour under ecologically realistic dispersal rates (see Supplementary Material).

131 Mucus trails may even have higher value for dispersers compared to previously studied sources of  
 132 indirect social information, as they may not only give information about meta-population level



133 habitat quality or population density (Cote et al. 2007; Chaine et al. 2013; Jacob et al. 2015b), but  
134 also about the spatial location of other patches (or at least other snails), further reducing dispersal  
135 costs. This may be especially valuable in fragmented urban areas where *Cornu aspersum* is common,  
136 where artificial porous substrates may make movement more costly (McKee et al. 2013) and inter-  
137 patch distances are often larger than the (low) perceptual range of *C. aspersum* (Dahirel et al. 2016a).  
138 Following trails in the same direction as the trail layer, as in our experiment, would give dispersers  
139 information on patch location from residents homing back to their roosts (Bailey 1989). If they are  
140 also able to follow trails with negative polarity (which is likely; Ng et al. 2013), they might additionally  
141 be able to “walk back” trails left by immigrants to reach their departure point.

142 The well-documented effects of within-habitat mucus accumulations on life-history and behaviour  
143 are size- and species-specific (Dan and Bailey 1982), and recent evidence suggest this is also the case  
144 for trail following in at least one land snail group (Holland et al. 2018). An important next step will be  
145 to determine how social information and phenotype combine to shape dispersal, especially in the  
146 context of matching habitat choice (Jacob et al. 2015a) Furthermore, dispersers following trails  
147 (potentially laid by previous dispersers) may provide a mechanism for collective dispersal in snails,  
148 several individuals following an initial trail-blazer (Cote et al. 2017). As pointed out by Cote et al.  
149 (2017), such collective dispersal would have wide-ranging yet poorly studied consequences for  
150 population dynamics, evolution and genetic structure, and affect our ability to infer spatial dynamics  
151 from population genetics data. Land snails, by combining ease of behavioural study in controlled and  
152 naturalistic conditions, trail following ability and a long and ongoing history as population genetic  
153 models (Backeljau et al. 2001; Balbi et al. 2018), are one of the best taxa to investigate these  
154 questions.

155 **Acknowledgements** We warmly thank Baptiste Averly for his involvement in the preliminary  
156 experiments that led to this study.

157 **Ethical approval** All applicable international, national, and institutional guidelines for the care and  
158 use of animals were followed. No ethical board recommendation is needed to work on *Cornu*  
159 *aspersum*.

160 **Funding** MD was funded by a Fyssen Foundation postdoctoral grant.

161 **Conflicts of interest** The authors have no conflicts of interest to declare.

162 **Data accessibility** Data are available on Figshare (doi: 10.6084/m9.figshare.6840179)

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222 **Supplementary material for: Dispersers are more likely to follow mucus trails in the land snail**

223 ***Cornu aspersum***

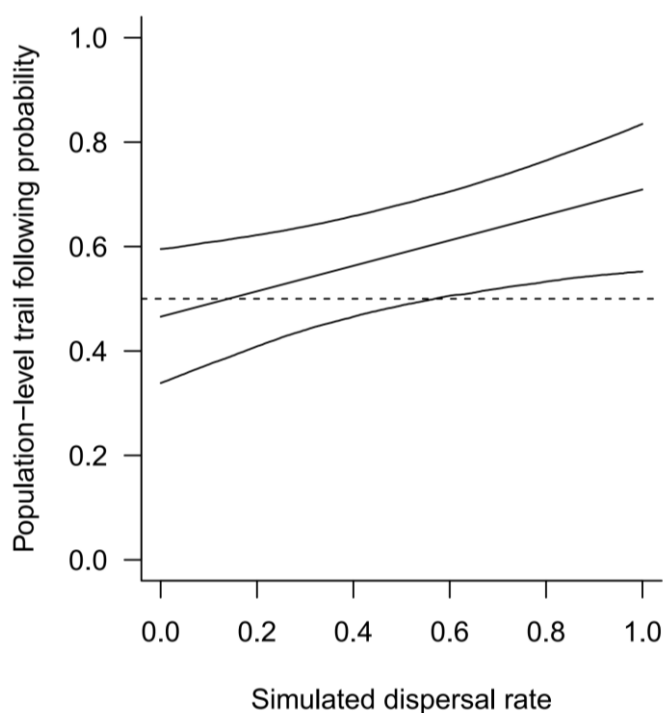
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225 **On the probability of detecting trail-following when one does not know the dispersal status of**  
226 **tested snails.**

227 In the main text, we showed that dispersers and residents differed in their trail following propensity,  
228 the latter not choosing the trail side more than expected by chance (binomial GLM; main text Fig. 2).  
229 We here use this binomial GLM predictions to estimate the relationship between population-level  
230 dispersal rate and the expected probability that a randomly chosen individual of unknown dispersal  
231 status would exhibit trail following.

232 We find that unless more than  $\approx 55\%$  of the tested individuals are dispersers, an investigator using Y-  
233 mazes and blind to dispersal status would conclude to no trail following in the studied population,  
234 even though a significant, non-random subset of the population does exhibit trail following  
235 (Supplementary Fig. 1).

236 This non-independence (behavioural syndrome) of dispersal status and trail following status thus  
237 needs to be accounted for, as dispersers are generally the minority in populations (e.g. (Dahirel et al.  
238 2016) for snails), and even when specifically selecting subgroups with high dispersal propensity, one  
239 may still find dispersal rates  $< 50\%$  in subpopulations (Dahirel et al. 2017).



240

241 **Supplementary Figure 1.** Relationship between population dispersal rate and predicted population  
242 level trail following probability. Predicted line and confidence bands are fitted assuming individual  
243 dispersers and residents follow trails according to the model presented in main text (main text Fig.  
244 2).

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