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

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

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Abstract

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

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

Introduction

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

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

The brown garden snail *Cornu aspersum* (Müller) (Helicidae ; syn. *Helix aspersa*) is a well-studied generalist land snail, able to thrive and disperse even in strongly fragmented habitats (Dahirel et al. 2016a; Balbi et al. 2018). *Cornu aspersum* snails are sensitive to mucus accumulations (Dan and Bailey 1982) and adjust dispersal decisions to conspecific density (Dahirel et al. 2016b). They appear to follow trails slightly more than expected by chance (Bailey 1989), but there is no evidence so far that they use trails during dispersal or that dispersers and residents react differently to social information. Using a Y-maze setup and ecologically relevant tests of dispersal propensity, we tested the hypotheses that *Cornu aspersum* snails are trail followers, and that dispersers would be more likely to follow trails. Indeed, they would benefit more from potential energy savings and from information about conspecific presence than residents, which, given the costs of movement, are not expected to stray far from an already established group of conspecifics.

Methods

Rearing conditions

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

Behavioural tests

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

Dispersal tests

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

Trail following experiment

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

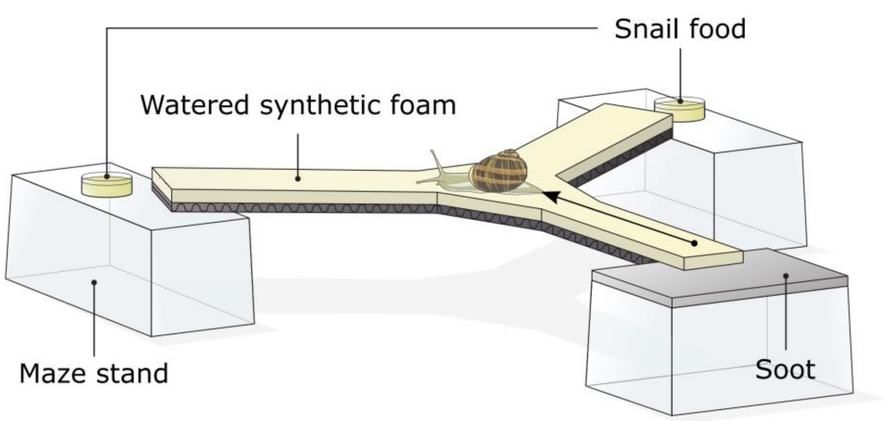

Figure 1. Experimental setup (Y-maze) for the trail-following experiments (not to scale; arm width: 3.5 cm; main arm length: 10 cm; choice arm length: 15 cm; angle between arms: 120°).

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

Statistical analyses

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

Results

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

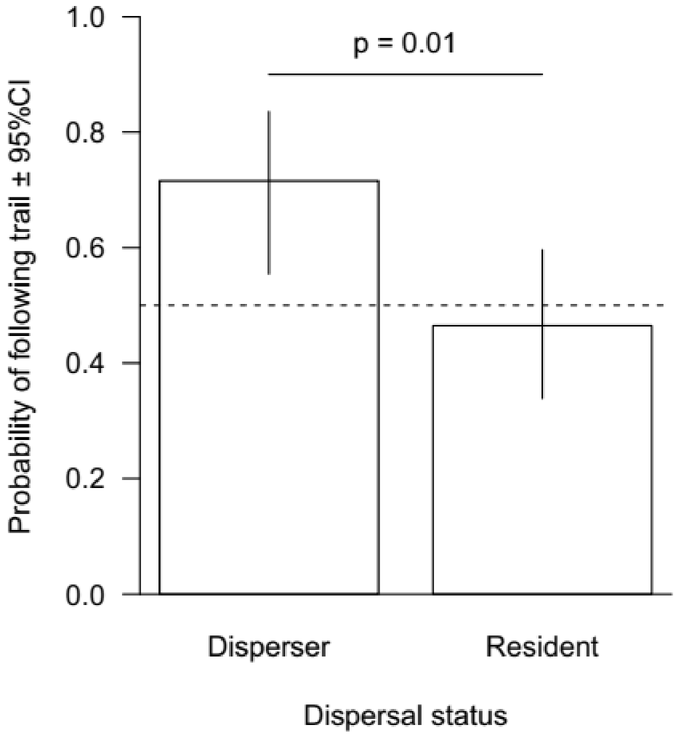

Figure 2. Trail following rate as a function of dispersal status (model predictions and 95% confidence intervals based on binomial GLM, the non-significant effect of origin population is averaged out ; N = 97).

Discussion

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

Mucus trails may even have higher value for dispersers compared to previously studied sources of indirect social information, as they may not only give information about meta-population level habitat quality or population density (Cote et al. 2007; Chaine et al. 2013; Jacob et al. 2015b), but also about the spatial location of other patches (or at least other snails), further reducing dispersal costs. This may be especially valuable in fragmented urban areas where *Cornu aspersum* is common, where artificial porous substrates may make movement more costly (McKee et al. 2013) and inter-patch distances are often larger than the (low) perceptual range of *C. aspersum* (Dahirel et al. 2016a). Following trails in the same direction as the trail layer, as in our experiment, would give dispersers information on patch location from residents homing back to their roosts (Bailey 1989). If they are also able to follow trails with negative polarity (which is likely; Ng et al. 2013), they might additionally be able to "walk back" trails left by immigrants to reach their departure point.

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

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

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

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

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

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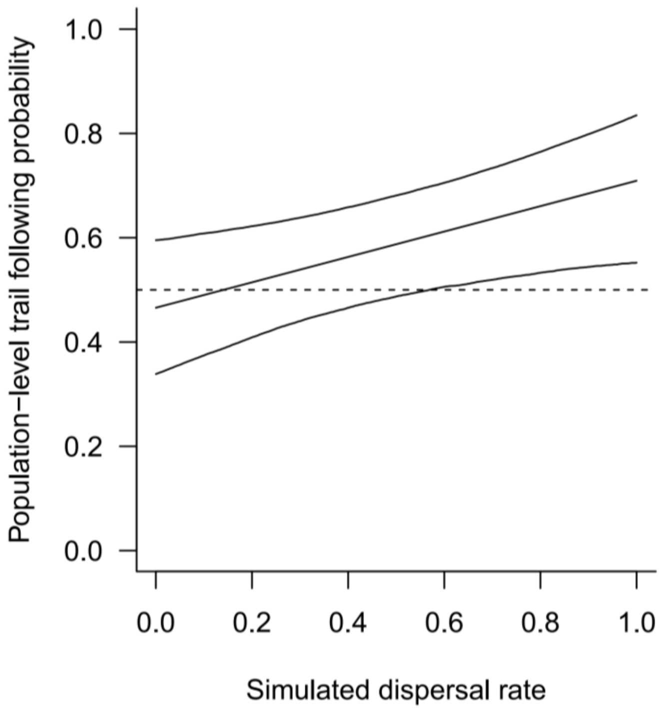
On the probability of detecting trail-following when one does not know the dispersal status of tested snails.

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

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

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



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

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