Increased population density depresses activity but does not influence dispersal in the snail *Pomatias elegans*

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Abstract

Dispersal is a key trait linking ecological and evolutionary dynamics, allowing organisms to optimize fitness expectations in spatially and temporally heterogeneous environments. Some organisms can both actively disperse or enter a reduced activity state in response to challenging conditions, and both responses may be under a trade-off. To understand how such organisms respond to changes in environmental conditions, we studied the dispersal and activity behaviour in the gonochoric land snail *Pomatias elegans*, a litter decomposer that can reach very high local densities, across a wide range of ecologically relevant densities. We found that crowding up to twice the maximal recorded density had no detectable effect on dispersal tendency in this species, contrary to previous results in many hermaphroditic snails. *Pomatias elegans* is nonetheless able to detect population density; we show they reduce activity rather than increase dispersal in response to crowding. We discuss these results based on the ability of many land snails to enter dormancy for extended periods of time in case of unfavourable conditions. We propose that dormancy ("dispersal in time") may be more advantageous in species with especially poor movement abilities, even by land mollusc standards, like *P. elegans*. Interestingly, dispersal and activity were correlated independently of density; this dispersal syndrome may reflect a dispersal-dormancy trade-off at the individual level. Additionally, we found snails with heavier shells relative to their size tended to be less mobile, which may reflect physical and metabolic constraints on movement and/or survival during inactivity. We finally discuss how the absence of density-dependent dispersal may explain why *P. elegans* is often found at very high local densities, and the possible consequences for ecosystem functioning and litter decomposition.

Keywords

Defence, dispersal syndromes, dormancy, ecosystem functioning, gastropod, sex-biased dispersal

Introduction

Dispersal, i.e. movement potentially leading to gene flow in space, is a key organismal trait influencing and linking ecological and evolutionary dynamics in sometimes complex ways (Ronce, 2007; Clobert *et al.*, 2012; Bonte & Dahirel, 2017). As the cost-benefit balance of dispersal is expected to vary depending on individual phenotype and experienced conditions, dispersal is often highly context- and phenotype-dependent (Bowler & Benton, 2005; Clobert *et al.*, 2012; Baines, Ferzoco & McCauley, 2019; Endriss *et al.*, 2019). This multicausality of dispersal likely explains why even well-studied environmental factors, like increased population density and competition, may lead to very different dispersal responses depending on populations and species (Bowler & Benton, 2005; Matthysen, 2005; Kim, Torres & Drummond, 2009; Fronhofer, Kropf & Altermatt, 2015; Baines *et al.*, 2019; Harman *et al.*, 2020). To understand the context-dependency of dispersal, it is thus necessary to study a broader range of life histories and contexts, including organisms that have alternative strategies to escape negative environmental conditions, such as dormancy, sometimes seen as a form of "dispersal in time" (Buoro & Carlson, 2014).

The land winkle *Pomatias elegans* (Müller 1774)(**Fig. 1**) is a common gastropod species in forests and hedgerows across Europe (Kerney & Cameron, 1999; Falkner *et al.*, 2001; Welter-Schultes, 2012). As a caenogastropod, it has separate sexes, contrary to the majority of land molluscs which are hermaphrodite (Barker, 2001). Its active dispersal capacities are poorly studied but expected to be very low, even by land mollusk standards (Kramarenko, 2014); average dispersal distances after 42 days are below 20 cm, according to one of the only (indirect) records available in the peer-reviewed literature (Pfenninger, 2002). Like many other land snails, it is able to survive up to several months under unfavourable conditions by entering dormancy (Falkner *et al.*, 2001). *P. elegans* is often distributed in a very aggregated way across landscapes, and when a population is present, local densities can be highly variable, going from fewer than one to several hundred individuals.m^{-2} (Pfenninger, 2002). When it is present, *P. elegans* plays a key role in ecosystem functioning, by decomposing litter and altering its chemical and physical characteristics (Coulis *et al.*, 2009; De Oliveira, Hättenschwiler & Tanya Handa, 2010).

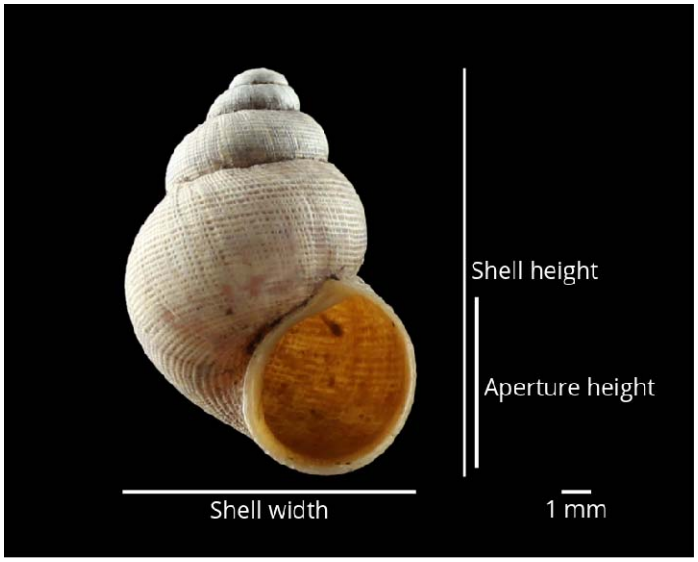

Figure 1. *Pomatias elegans* shell showing the measurements used in the present study (photograph: Armelle Ansart).

We here tested the hypothesis that active dispersal and activity were density-dependent in *P. elegans*. As in many other species, including other land molluscs (Baur, 1993; Bowler & Benton, 2005; Matthysen, 2005; Dahirel *et al.*, 2016), we expected dispersal to overall increase with population density and associated competition levels. We expected dispersers to be more active than residents, in agreement with general predictions about dispersal-dormancy syndromes and the pace-of-life hypothesis (Cote *et al.*, 2010; Réale *et al.*, 2010; Buoro & Carlson, 2014). If activity merely is a correlate of dispersal, or vice-versa, we would expect them to both change with density in the same way. If low activity is also/instead a correlate of dormancy, we may expect the opposite response to density: indeed, some previous snail studies showed depression of activity in response to density (Cameron & Carter, 1979). In accordance with the phenotypic compensation hypothesis, which predicts that risk-taking behaviour should be associated with morphological traits limiting vulnerability to predators (e.g. Ahlgren *et al.*, 2015), we also expected dispersers/active individuals to be better defended, by having heavier shells. Finally, we accounted for sex differences, given sex-biased dispersal is often observed in other taxa with separated sexes (Trochet *et al.*, 2016).

Material and methods

We collected *P. elegans* snails in spring 2017 in leaf litter and at the bottom of calcareous walls (Falkner *et al.*, 2001) in Arcais, France (approximate location: 46°17'60"N, 0°41'21"W). They were then kept under controlled conditions (20°C, L:D 16:8) in plastic boxes (25 × 25 × 9 cm, about 500 snails.m^{-2}) with a 1 cm layer of soil and a roughly 2-3 cm thick layer of leaf litter (predominantly oaks

80 *Quercus robur* and *Q. petraea* and beech *Fagus sylvatica*) collected in urban and suburban woodlots
81 and hedgerows on and close to the University of Rennes Beaulieu campus. We provided humidity by
82 watering soil and litter every 10 to 15 days.

83 *Dispersal experiment*

84 In June 2017, we created two-patch systems by adapting the system we developed for slugs in
85 Fronhofer et al. (2018), but with a shorter inter-patch gap and longer dispersal period to account for
86 the more limited dispersal capacities of *P. elegans*. We divided 32 × 12 cm^2 transparent plastic boxes
87 (height: 9 cm) in two 12 × 12 cm^2 patches ("release" and "arrival") and one central 10 × 12 cm
88 matrix, using plastified cardboard walls. A 2 × 12 cm^2 slot was left open in each wall to allow snails to
89 leave and enter patches. Both patches were filled with watered soil and litter as in maintenance
90 boxes (see above), with the matrix was kept dry and empty.

91 We then placed between 1 and 30 snails in each "departure" patch, and first closed the patches for
92 24 h to let the snails habituate. We then let them free to move for 4 days, and recorded which snails
93 stayed in their release patch (hereafter "residents") and which snails dispersed to the arrival patch.
94 We tested the following group sizes: 1, 2, 3, 4, 5, 10, 15, 20, and 30 snails per box, with respectively
95 30, 20, 10, 9, 6, 4, 3, 3, and 2 replicates (total: 371 snails in 87 replicates). We chose these replicate
96 numbers to have at least 30 individuals and 2 replicates per group size. The selected group sizes
97 correspond to initial densities ranging from 69.4 to 2083.3 snails.m^{-2} (taking only departure patch
98 surface area into account), and likely provide a good coverage of natural densities. Indeed, densities
99 of up to 1072 detected snails.m^{-2} have been found using 25 × 25 cm^2 quadrats in natural populations
100 (Pfenninger, 2002), and a separate study indicates this species has a field detectability in the 0.5 to
101 0.9 range when hand collected, especially because many individuals may have buried themselves in
102 the substrate at any one time (Albano *et al.*, 2015). Tests were spread haphazardly over the month
103 due to logistical constraints (start dates ranging from June 2 to June 26); no reproduction was
104 observed during this interval.

105 *Sexing*

106 We aimed to have balanced sex ratios across densities (in line with natural populations (Boycott,
107 1916)). However, reproductive organs are not externally visible in *Pomatias elegans*, and body size is
108 not an accurate enough correlate, meaning a classification in males and females can only be done by
109 dissection (Creek, 1951). We nonetheless used the fact that females are on average slightly bigger
110 and wider than males (Boycott, 1916; Jordaens, Platts & Backeljau, 2001) to putatively sex snails
111 before the experiment, and then assigned equal numbers of putative males and females to densities

112 and boxes. To predict sex, we first measured the shell height, shell width and aperture height (**Fig. 1**)
113 to the nearest 0.1 mm in a set of 26 individuals not used in dispersal experiments, and sexed them by
114 dissection after freezing at -20°C. We used these individuals to fit an initial Linear Discriminant
115 Analysis (LDA) predicting sex as a function of shell characteristics, and used this LDA to predict the
116 sex of our focal snails. Experimental individuals were then added to the LDA dataset once dissected
117 after each test session, in order to improve its predictive ability. Overall, 96 individuals out of 371
118 (25.88%) were misclassified prior to experiments (49 out of 185 males, based on reproductive
119 organs, were first classified as females, 47 females out of 186 first classified as males). There was no
120 evidence of sex bias in the final dataset, whether overall or relative to test density (**Supplementary**
121 **Material 1**).

122 *Post-dispersal phenotyping*

123 Within 24h after dispersal tests, we placed each snail on a small (8 cm diameter) clean patch of wet
124 substrate (synthetic upholstery foam) and recorded the latency to activity, snails being defined as
125 active if their operculum was open and both their foot and tentacles were visible out of the shell. All
126 snails that had not moved after 20 minutes remained inactive, operculum closed, for at least two
127 hours, indicating they were not simply slower individuals, but actually behaved differently from the
128 active ones. Indeed, a limited number was further monitored and remained fully inactive even after 7
129 hours. We therefore analysed activity as a binary variable (active within 20 minutes/ not active for at
130 least two hours). After sexing (see above), shells were dried at room temperature before being
131 weighed twice (to the nearest 0.1 mg; CP224S scale, Sartorius, Göttingen, Germany). Twenty-four out
132 of 371 shells were partly broken during dissection and could not be weighed.

133 *Statistical analyses*

134 All analyses were done in a Bayesian framework, using Stan (Carpenter *et al.*, 2017; Stan
135 Development Team, 2018) with R (R Core Team, 2019) and the *brms* package (Bürkner, 2017).
136 Scripting, analysis and plotting relied on the *tidybayes*, *bayesplot*, and *patchwork* packages, as well as
137 the *tidyverse* family of packages (Gabry *et al.*, 2019; Kay, 2019; Pedersen, 2019; Wickham *et al.*,
138 2019).

139 We used a multivariate generalized linear mixed model (GLMM) framework (Dingemanse &
140 Dochtermann, 2013), which allowed us not only to draw inferences on dispersal and activity, but also
141 on their correlations with each other and with (relative) shell mass, while handling missing shell mass
142 data by in-model imputation (McElreath, 2016). A full write up of the model is given in
143 **Supplementary Material 2**. Briefly, we analysed the probability of dispersing and the probability of

activity as individual-level binary variables (dispersed/did not disperse; active/not active) using Bernoulli GLMMs with a logit link. We tested whether dispersal or activity state depended on experienced population density, sex and body size (defined as shell height; **Fig. 1**). The models also included a random effect of storage box, as well as a random effect of individual identity. Importantly, the latter was set to be identical (same values) in both the dispersal and activity models. In effect, this means it corresponds to a latent individual "behaviour" variable that would influence both dispersal and activity. This allowed us to estimate the effect of dispersal on activity (and vice-versa), while accounting for the fact both are estimated with uncertainty and the causal path from one to the other is unknown. Note that using instead dispersal status as a covariate in the activity model leads to similar inferences (**Supplementary Material 3);** it however prevents us from doing the analyses described in the next few sentences. To be able to separate the effects of relative shell mass from those of body size, we used a third submodel. We fitted a linear mixed model in which ln(Shell mass) was a function of ln(Shell height), sex, and a random effect of individual identity. The use of repeated measures (see "Post-dispersal phenotyping") of shell mass allowed us here to separate individual variation from residual error, and facilitated the estimation of the former. Finally, individual-level random effects were included in a variance-covariance matrix, allowing us to evaluate the correlation between "relative" shell mass (after accounting for body size) and the latent behavioural variable. All continuous variables were centred and scaled to unit standard deviation (**Supplementary Material 4**), and the "sex" variable was converted to a centred dummy numerical variable (-0.5 = "Male"; +0.5 = "Female")(Schielzeth, 2010).

We set weakly informative priors by following McElreath (2016)'s suggestions for continuous and proportion variables. We used a Normal(μ = 0, σ = 1.5) prior for the dispersal and activity fixed effects intercepts, and a Normal(0, 1) prior for all the other fixed effects. We set a half-Normal(0, 1) prior for all standard deviations (random effects as well as residual variance of shell mass), and a LKJ(η = 2) prior for the random effects correlation matrix.

We ran four chains for 25000 iterations, with the first 5000 of each chain used for warmup. We checked mixing graphically and confirmed chain convergence using the improved $\widehat{R}$ statistic (Vehtari *et al.*, 2020). The chains were run longer than the default number of iterations (2000), to ensure effective sample size was satisfactory for all parameters (bulk- and tail-ESS sensu Vehtari *et al.*, 2020 > 1000). All posterior summaries are given as: mean [95% Higher Posterior Density Intervals].

Results

144 snails out of 371 (38.81%) dispersed across all test boxes. There was no detectable effect of box population density (**Fig. 2A**), sex or shell height on dispersal probability (**Table 1**).

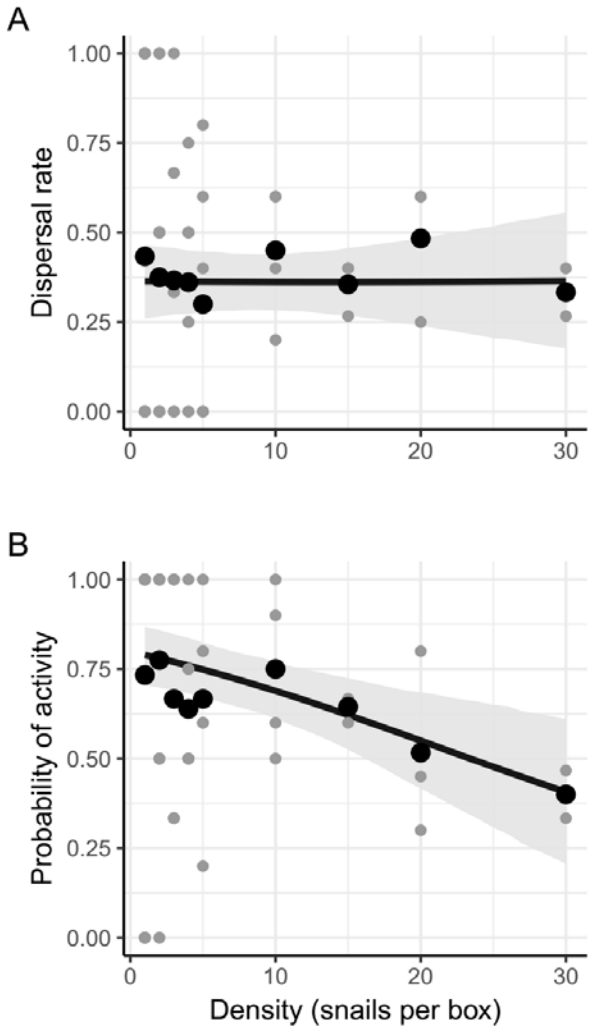

Figure 2. Effect of population density (in snails per box) on *Pomatias elegans* dispersal rate (A) and probability of activity (B). Grey points are observed proportions for each test box, black points averages for each density; black curves give posterior predicted means and grey bands 95% credible intervals.

Snails exposed to higher population densities were less likely to be active afterwards (**Table 1**, **Fig. 2B**). There were no clear effects of sex or size (**Table 1**). Analysis of the latent behavioural variable shows dispersers were also more likely to be active on average, and vice-versa (mean differences on the logit scale: 0.65 [0.12; 1.19] and 0.69 [0.12; 1.26], respectively; **Fig. 3 and Supplementary Material 3**). After accounting for shell length, sex and measurement error, individual shell mass was negatively correlated with the behavioural latent variable: dispersers/active snails tended to have lighter shells, relative to their size, than residents/inactive individuals (**Fig. 4, Table 1**).

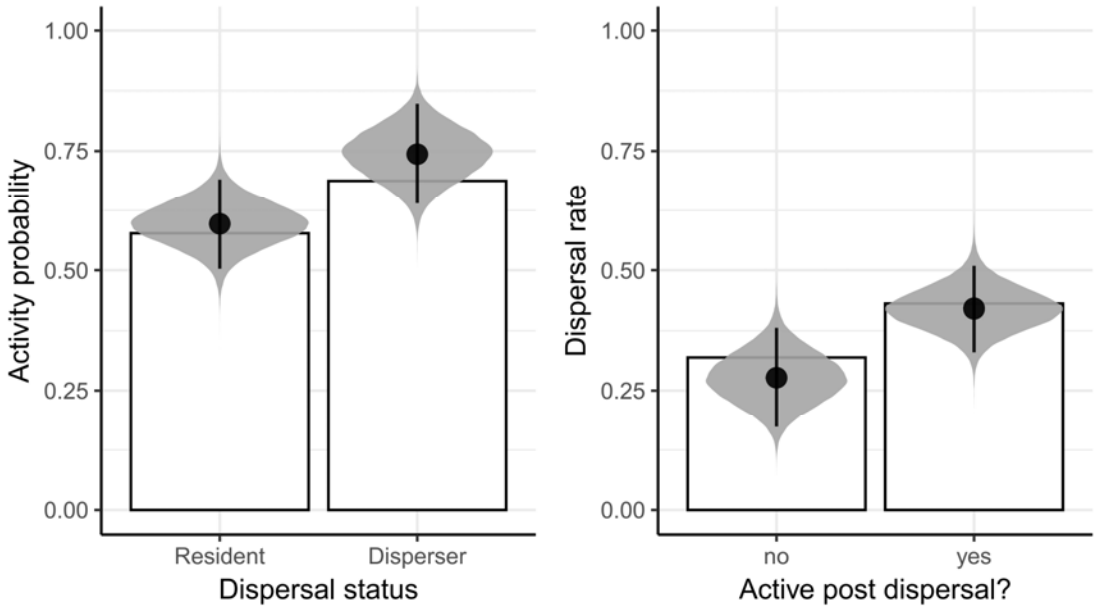

Figure 3. Relationship between dispersal status and activity post-dispersal. White bars correspond to observed frequencies, grey "eyes" to posterior predictions based on model intercepts and individual-level random effects, i.e. averaging out the effects of sex, size and population density (black dots: posterior means; segments: 95% credible intervals).

Discussion

We studied the relationship between *Pomatias elegans* dispersal and population density over most of the known range of natural densities (Pfenninger, 2002), yet found no evidence of density-dependent dispersal. There was however a negative relationship between density and activity, and dispersal, activity and (relative) shell mass co-vary in this species.

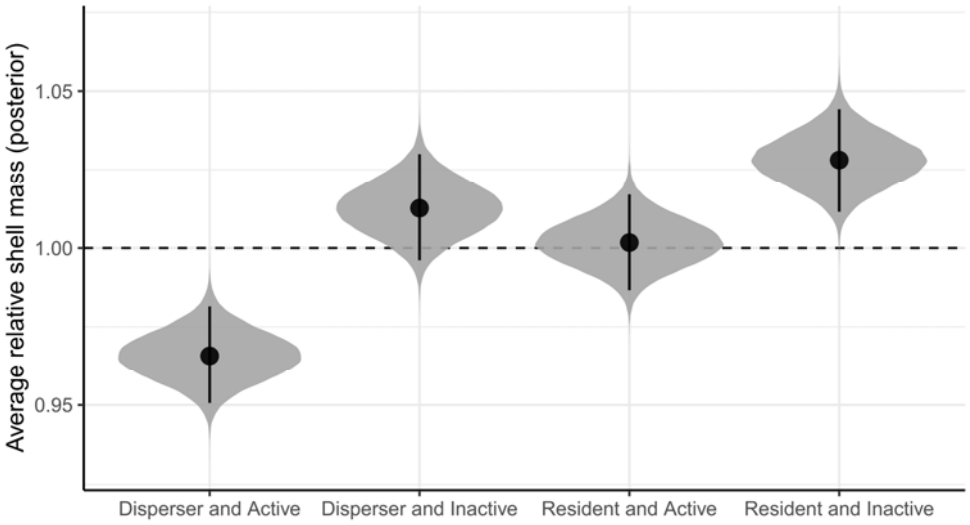

Figure 4. Relationship between dispersal status, activity post-dispersal, and mean predicted shell mass, that is relative to the shell mass predicted for an otherwise average snail of same shell height and sex (black dots: posterior means; segments: 95% credible intervals).

We additionally found no evidence of sex bias in dispersal probability or activity. While sex-biased dispersal is abundantly documented in non-molluscan groups (Bowler & Benton, 2005; Trochet *et al.*, 2016), there are numerous species with no bias. Broadly, sex-dependent dispersal is predicted to arise when there are sex-differences in spatio-temporal fitness variation due to e.g. sex differences in resource use and/or in local mate competition (Hovestadt, Mitesser & Poethke, 2014; Trochet *et al.*, 2016; Li & Kokko, 2019). Our results, in light of dispersal theory, imply that male and female *P. elegans* use resources similarly and that they do not present polygyny or any mating system leading to predictable sex differences in spatio-temporal fitness variation. While sex ratio is, overall, balanced in this species (Boycott, 1916), the other predictions remain to be tested by the collection of further natural history data. We should additionally note that our experimental setup (one measure of dispersal, after 4 days, and groups that were sex-balanced on average) may not have allowed us to detect finer sex differences in dispersal, i.e. in timing (Li & Kokko, 2019), or conditional strategies dependent on locally experienced sex-ratio (Hovestadt *et al.*, 2014).

The absence of density-dependent dispersal was more surprising, as other land mollusc species have been shown to alter their dispersal in response to population density (Oosterhoff, 1977; Hamilton & Wellington, 1981; Livshits, 1985; Baur, 1993; Dahirel *et al.*, 2016), and density-dependent dispersal is common in many other groups (Bowler & Benton, 2005; Matthysen, 2005; Mathieu *et al.*, 2010;

222 Bitume *et al.*, 2013; Fronhofer *et al.*, 2015; De Bona *et al.*, 2019, among many others). Additionally,
223 the costs of competition, which can trigger dispersal, are well-documented in land molluscs
224 (Oosterhoff, 1977; Hamilton & Wellington, 1981; Dan & Bailey, 1982). However, density-independent
225 dispersal also exists in this group, and despite population density likely being one of the most studied
226 drivers of dispersal, we do not have a systematic understanding of how species traits or
227 environmental effects drive differences in the dispersal-density reaction norm (Baines *et al.*, 2019). *P.*
228 *elegans*, contrary to most land molluscs has separate sexes, and differences in reproductive systems
229 may drive the evolution of different dispersal strategies (Eppley & Jesson, 2008). Indeed, all things
230 equal, hermaphrodites are *a priori* more likely than species with separate sexes to find a mate in
231 small populations (Tomlinson, 1966). This means the density threshold at which the costs of
232 competition outweigh the benefits of grouping (Kim *et al.*, 2009; Fronhofer *et al.*, 2015) and the costs
233 of dispersal (Bonte *et al.*, 2012) is likely lower for hermaphrodites. We hypothesize that context
234 being equal (including e.g. movement costs), this may make hermaphrodites more likely than
235 gonochoric species to exhibit positive density-dependent dispersal over a range of natural densities.
236 In any case, our study shows that further comparisons between hermaphroditic and gonochoric
237 species sharing ecological and life-history characteristics are crucially needed to clarify the role of
238 reproductive system in shaping context-dependent dispersal.

239 Alternatively (but not exclusively), the absence of density response in dispersal may reflect the fact
240 *Pomatias* snails possess other mechanisms to respond to unfavorable densities. Indeed, by contrast
241 with dispersal, activity propensity did decrease with increasing population density (**Fig. 2B**). Like
242 many other shelled land gastropods, *P. elegans* is able of reduced activity and dormancy when
243 context is unfavourable (up to several months in response to dry conditions; Falkner *et al.*, 2001).
244 Dormancy has mostly been studied with respect to abiotic factors in molluscs (Cook, 2001), but
245 activity reduction in response to increased competition has been observed in several species
246 (Oosterhoff, 1977; Cameron & Carter, 1979; Dan & Bailey, 1982). This is generally thought to result
247 from interference (mediated through mucus and/or faeces) by the most competitive individuals,
248 which remain active. However, when the experimental/observational setup also allowed for
249 dispersal, species that reduced activity in response to density (*Cepaea nemoralis, Cornu aspersum,*
250 *Xerocrassa seetzenii*) did however also exhibit density-dependent dispersal (Oosterhoff, 1977;
251 Shachak, Leeper & Degen, 2002; Dahirel *et al.*, 2016). Given the very limited dispersal capacities of *P.*
252 *elegans* (Pfenninger, 2002) even compared to other snails (Kramarenko, 2014), the least competitive
253 *Pomatias* snails may well be more successful reducing activity to wait out more favourable
254 conditions, in a form of "temporal dispersal", than by attempting to find better by moving away
255 (Buoro & Carlson, 2014). The fact there was no effect of body size on activity suggests the loss of

256 activity is not simply an inhibition of activity by competitive individuals, leading to competitive
257 exclusion. Indeed, in that case we would have expected larger individuals to stay active at high
258 densities while smaller less competitive snails are inhibited (Dan & Bailey, 1982). Note that we only
259 studied emigration, the first step of dispersal, and density-dependent responses may also happen
260 during transience (Shachak *et al.*, 2002; Poethke, Gros & Hovestadt, 2011; Dahirel *et al.*, 2016). In any
261 case, our results show that studying the effect of population density across life histories may help
262 shed light on its influence on dispersal in space and/or time.

263 All three phenotypic traits we studied were linked. First, dispersers were more likely to be active
264 post-dispersal test, and vice versa (**Fig. 3**, **Supplementary Material 3**), independently of density
265 context. These results line up with predictions on dispersal syndromes and the pace-of-life
266 hypothesis (Cote *et al.*, 2010; Réale *et al.*, 2010), which predicts a metabolically-underpinned link
267 between activity and risk taking behaviour (such as dispersal). They can also be interpreted as a
268 trade-off between dispersal in space and in time (Buoro & Carlson, 2014), in which individuals that do
269 not disperse are more likely to be dormant at any point in time, even after accounting for density
270 effects. Second, we found that more mobile snails (higher activity and/or dispersal) had on average
271 lighter shells (**Fig. 4**, **Table 1**), compared to inactive/resident snails. This result goes against our
272 predictions based on the phenotypic compensation hypothesis, which states that risk-taking
273 individuals should have better morphological defences against predators (Hulthén *et al.*, 2014;
274 Ahlgren *et al.*, 2015; Kuo, Irschick & Lailvaux, 2015). However, phenotypic compensation is not a hard
275 rule (De Winter *et al.*, 2016), and while thicker/heavier shells are harder to break (see e.g. Rosin *et*
276 *al.*, 2013), variation in shell characteristics depends on many abiotic and biotic parameters
277 (Goodfriend, 1986). Indeed, thicker shells may also better conserve humidity (Goodfriend, 1986),
278 which may be adaptive for snails more prone to be dormant for extended periods of time. Heavier
279 shells are likely to increase the costs of movement (Herreid & Full, 1986); given the already high costs
280 of movement in land molluscs (Denny, 1980), this may explain why mobile individuals have lighter
281 shells, despite the potentially increased predation risk. Experimental manipulations of the costs and
282 benefits of heavier shells (by e.g. testing snails under varying humidity conditions, and/or by adding
283 weights to shells), may help disentangle the underpinnings of this dispersal/shell mass syndrome.

284 Although *P. elegans* is overall much less abundant than other macroinvertebrate decomposers at the
285 landscape scale (David, 1999), it can locally reach very high densities (Pfenninger, 2002). Our study
286 shows that increased densities do not trigger increased movement from crowded to empty habitats
287 in this species. This helps explain the maintenance of this strong spatial heterogeneity and high local
288 densities, as dispersal cannot play its "equalizing" role as well. Given decomposition by *P. elegans* can
289 have marked effects on litter characteristics (Coulis *et al.*, 2009; De Oliveira *et al.*, 2010), and

facilitate decomposition by other co-occuring macroinvertebrates (De Oliveira *et al.*, 2010), this absence of a common context-dependency in dispersal may have broader implications for local heterogeneity in soil ecosystem functioning and soil communities.

Acknowledgments

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Data availability

Data and analysis script are archived on GitHub (https://github.com/mdahirel/pomatias-dispersal-2017) and Zenodo (doi: 10.5281/zenodo.3691977) (latest release at time of submission: v1.0)

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Tables

Table 1. Posterior means [and 95% credible intervals] for the parameters of the multivariate model of dispersal, activity and shell mass. See **Supplementary Material 2** for the full write-up of the model, and **Supplementary Material 4,** for original means and SDs of transformed variables (*N* = 371 snails, except for Shell mass, *N* = 347 snails, measured twice)

	Dispersal probability	Activity probability	Shell mass (ln-transformed then scaled)
Fixed effects			
Intercept	-0.57 [-0.94 ; -0.21]	0.66 [0.29 ; 1.06]	-0.01 [-0.09 ; 0.06]
Population density (scaled)	-0.01 [-0.37; 0.38]	-0.60 [-1.00 ; -0.21]	--
Sex (effect of being female)	-0.16 [-0.77 ; 0.47]	0.24 [-0.41 ; 0.86]	0.18 [-0.02 ; 0.37]
Body size (shell height, ln-transformed then scaled)	0.01 [-0.31 ; 0.33]	0.18 [-0.16 ; 0.51]	0.62 [0.52 ; 0.71]
Random effects			
Box-level SD	0.64 [0.01 ; 1.13]	0.68 [0.11; 1.22]	--
Individual-level SD	0.93 [0.43 ; 1.41]		0.74 [0.68 ; 0.79]
Correlation between box-level SDs	0.05 [-0.69; 0.74]		--
Correlation between individual-level SDs	-0.39 [-0.66; -0.14]		
Residual SD	--	--	0.03 [0.03 ; 0.03]

468 **Figure legends**

469 **Figure 1.** *Pomatias elegans* shell showing the measurements used in the present study (photograph:
470 Armelle Ansart).

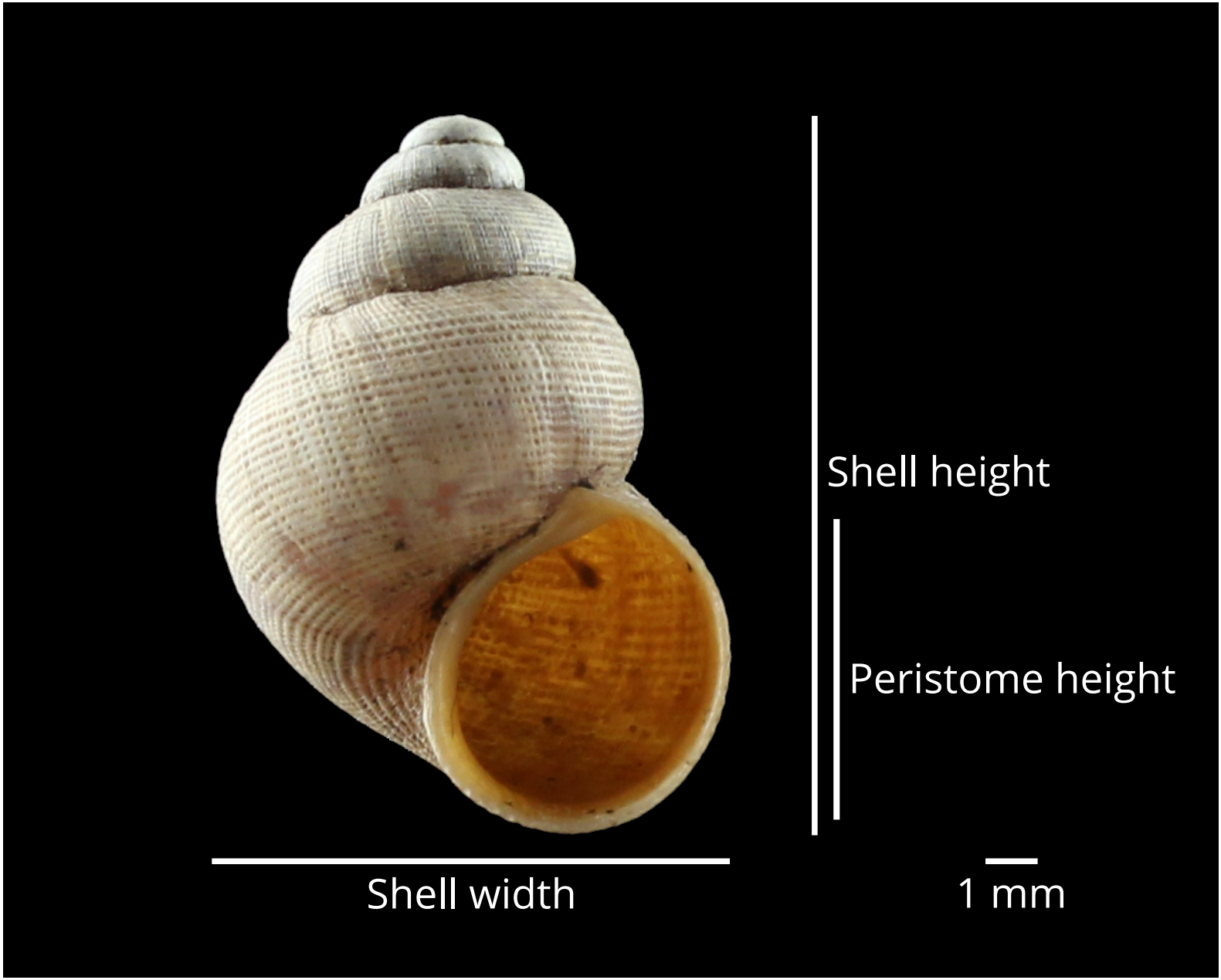
471 **Figure 2.** Effect of population density (in snails per box) on *Pomatias elegans* dispersal rate (A) and
472 probability of activity (B). Grey points are observed proportions for each test box, black points
473 averages for each density; black curves give posterior predicted means and grey bands 95% credible
474 intervals.

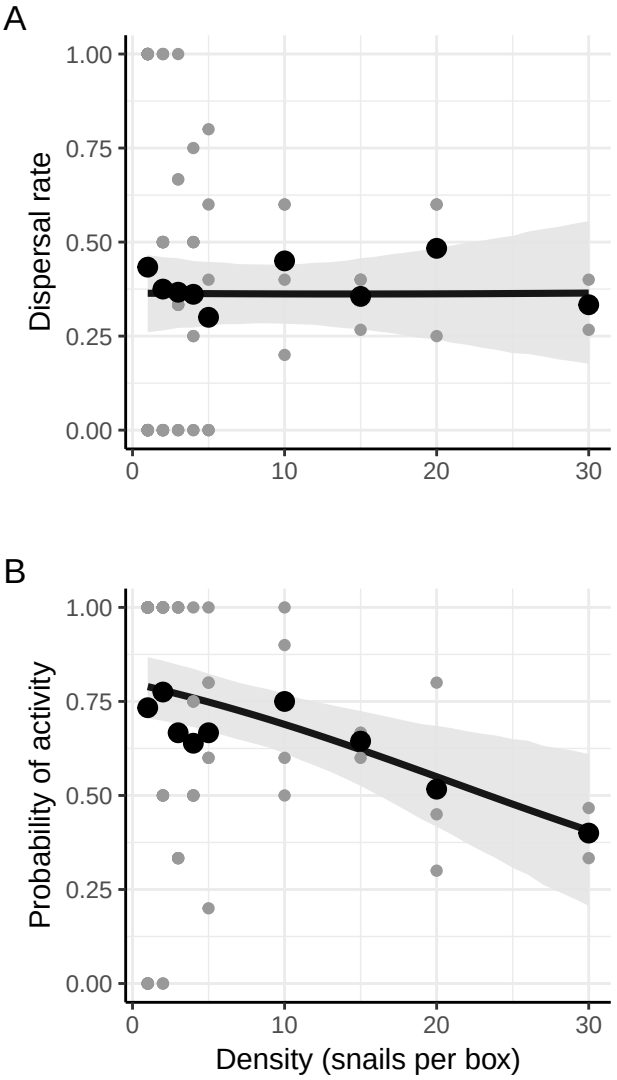
475 **Figure 3.** Relationship between dispersal status and activity post-dispersal. White bars correspond to
476 observed frequencies, grey "eyes" to posterior predictions based on model intercepts and individual-
477 level random effects, i.e. averaging out the effects of sex, size and population density (black dots:
478 posterior means; segments: 95% credible intervals).

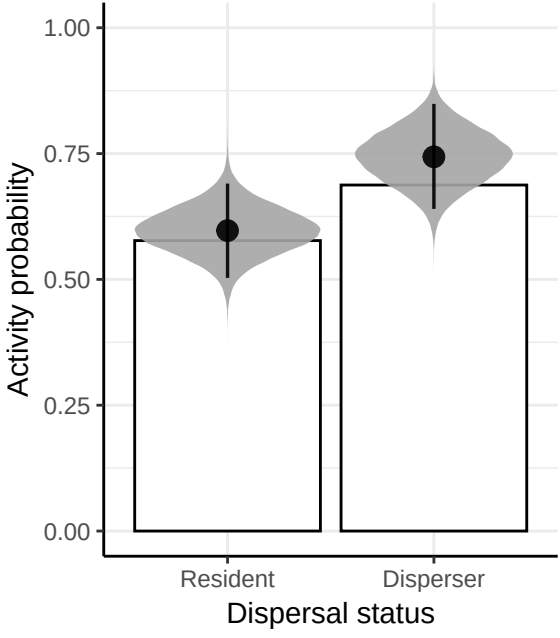
479 **Figure 4.** Relationship between dispersal status, activity post-dispersal, and mean predicted shell
480 mass, that is relative to the shell mass predicted for a snail of same shell height and sex (black dots:
481 posterior means; segments: 95% credible intervals).

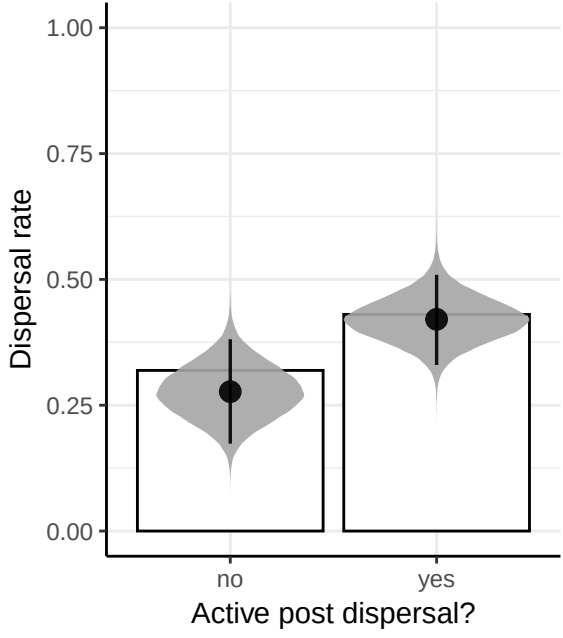
482

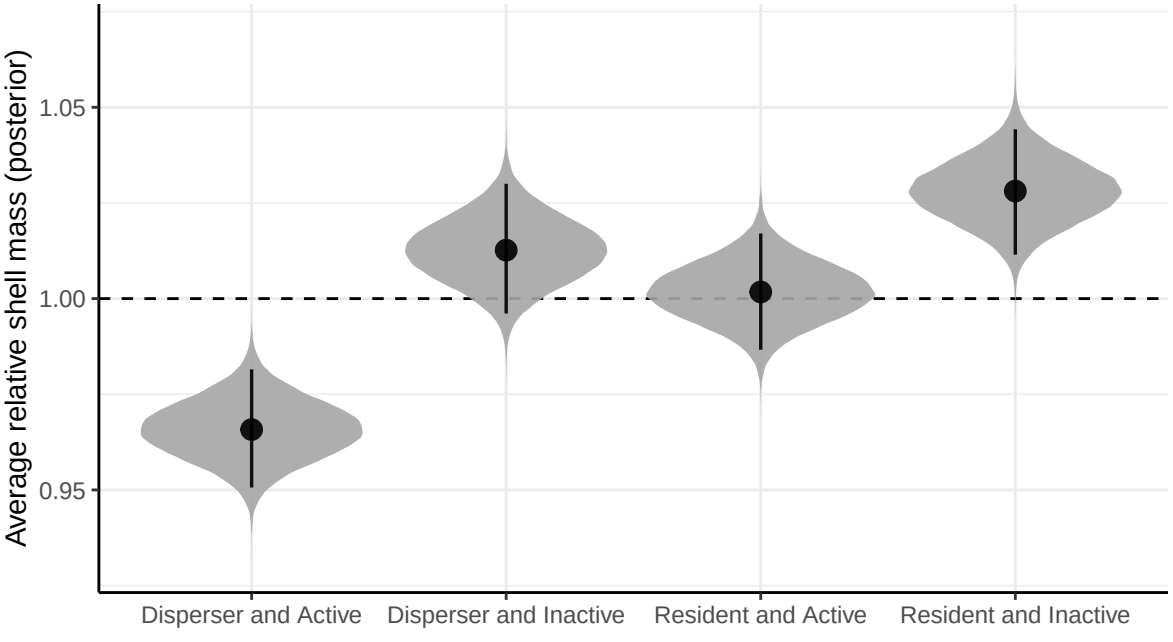
483


Shell height
Peristome height
Shell width
1 mm


A
Dispersal rate
1.00
0.75
0.50
0.25
0.00
0
10
20
30
B
Probability of activity
1.00
0.75
0.50
0.25
0.00
0
10
20
30
Density (snails per box)


1.00
0.75
0.50
0.25
0.00
Activity probability
Resident
Disperser
Dispersal status


1.00
0.75
0.50
0.25
0.00
Dispersal rate
no
yes
Active post dispersal?


Average relative shell mass (posterior)
1.05
1.00
0.95
Disperser and Active
Disperser and Inactive
Resident and Active
Resident and Inactive