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**Density-dependence across dispersal stages in a hermaphrodite land snail: insights from discrete choice models<sup>1</sup>**

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## Abstract

Dispersal movements, i.e. movements leading to gene flow, are key behaviours with important, but only partially understood, consequences for the dynamics and evolution of populations. In particular, density-dependent dispersal has been widely described, yet how it is determined by the interaction with individual traits, and whether density effects differ between the three steps of dispersal (departure, transience, and settlement), remains largely unknown. Using a semi-natural landscape, we studied dispersal choices of *Cornu aspersum* land snails, a species in which negative effects of crowding are well documented, and analysed them using dispersal discrete choice models, a new method allowing to analyze dispersal decisions by explicitly considering the characteristics of all available alternatives and their interaction with individual traits. Subadults were more dispersive than adults, confirming existing results. In addition, departure and settlement were both density-dependent: snails avoided crowded patches at both ends of the dispersal process, and subadults were more reluctant to settle into crowded patches than adults. Moreover, we found support for carryover effects of release density on subsequent settlement decisions: snails from crowded contexts were more sensitive to density in their subsequent immigration choices. The fact that settlement decisions were informed indicates that costs of prospecting are not as important as previously thought in snails, and/or that snails use alternative ways to collect information, such as indirect social information (e.g., trail following). The observed density-dependent dispersal dynamics may play an important role in the ability of *Cornu aspersum* to successfully colonise frequently human-disturbed habitats around the world.

**Keywords:** competition · conditional logit models · *Helix aspersa* · informed dispersal · terrestrial gastropods

## Introduction

Dispersal, i.e. movement leading to gene flow in space (Ronce 2007), is a key life-history trait with important consequences for the dynamics and evolution of populations, especially in changing environments (Clobert et al. 2012). It is generally defined as a three-stage process, with an emigration or departure phase, a transient stage, and an immigration, or settlement, phase (e.g., Clobert et al. 2009). Broadly speaking, dispersal is a response to spatial and temporal variation in expected fitness, which arises because of the relatedness structure of populations and/or spatio-temporal heterogeneity in environmental conditions (Starrfelt and Kokko 2012). As costs and benefits of dispersal vary between individuals and depend on environmental context (Bonte et al. 2012; Clobert et al. 2012), condition- and context-dependent dispersal rules are expected to evolve (Clobert et al. 2009). Such rules, which allow organisms to rapidly escape locally unfavourable environments, have been widely described (see Bowler and Benton 2005; Clobert et al. 2009; and Clobert et al. 2012 for reviews). However, our understanding of condition- and context-dependent dispersal is complicated by the fact that a given causal factor may have different effects at each stage of dispersal, and interact with others in synergistic or contradictory ways (Matthysen 2012; Marjamäki et al. 2013; Rémy et al. 2014).

Dispersal in response to unsuitable population density (too high or too low) has been observed empirically in a wide variety of taxa (Moksnes 2004; Matthysen 2005; Mathieu et al. 2010; Nowicki and Vrabec 2011; Kuefler et al. 2012; Bitume et al. 2013) and is thought to be one of the main mechanisms of context-dependent dispersal (Bowler and Benton 2005; Enfjäll and Leimar 2009; Matthysen 2012). On one hand, dispersal allows individuals to escape from crowded habitats with high levels of competition for resources and/or mates (e.g., Marjamäki et al. 2013). On the other hand, an aggregation of conspecifics can indicate higher-quality habitat or the presence of potential mates (Stamps 2001; Välimäki and Itämies 2003).

Furthermore, in some species, benefits from social aggregations, such as extra-pair mating opportunities or better protection from predators, can outweigh the costs of crowding (Serrano et al. 2005; Kim et al. 2009). While positive density-dependent dispersal, where dispersal increases with population density, is more frequently assumed or studied, negative density-dependent dispersal has been observed in several species (Matthysen 2005; Chaput-Bardy et al. 2010). The direction and strength of the density-dependence of dispersal is expected to have important consequences for (meta-)population dynamics or the speed of range expansions (Sæther et al. 1999; Amarasekare 2004; Travis et al. 2009; Altwegg et al. 2013; Bocedi et al. 2014). Yet, how the intensity and direction of density-dependence is determined by individual traits, environmental quality, or their interaction, and how it changes depending on the scale considered, remains largely unknown (but see Kim et al. 2009; Marjamäki et al. 2013). In addition, studies of density-dependent dispersal have generally focused on emigration only, neglecting the transience and immigration phases (Matthysen 2005; Bowler and Benton 2005); the picture is further complicated when one takes into account the fact that density may have different effects at different stages of dispersal (Křivan 2008; Matthysen 2012).

Terrestrial gastropods (land snails and slugs) are good models to study the relationship between dispersal and population density, as they occur naturally in a wide range of densities (Dan 1978; Baur 1993b), and high population densities have deleterious effects on snail activity and growth, even when resources are not limited (Dan and Bailey 1982). This interference effect is thought to be mediated by the accumulation of mucus or faeces in crowded shelters, and affects more strongly juveniles and subadults, compared to adults (Dan and Bailey 1982). On the other hand, aggregations of snails and/or slugs in a shelter may create a microclimate more favourable to their survival, and increase their probability to find a mate (Cook 2001). Additionally, snail and slug movement is extremely costly (Denny 1980),

which may put strong constraints on dispersal decisions (Stamps et al. 2005). In the literature, studies showing positive, negative or no effects of snail density on dispersal are found with similar frequencies, but wide differences in protocols used between and within studies make generalisation difficult (see Baur 1993a for a review).

In this context, we examined the density dependence of dispersal decisions of a common snail species, the brown garden snail *Cornu aspersum* (Müller), in a standardized semi-natural landscape, with populations within the range of naturally occurring population densities (Selander and Kaufman 1975; Dan 1978; Perrott et al. 2007; personal observations). We analysed individual snails' decisions by using dispersal discrete choice models (DDCMs), a newly developed method which allowed us to study simultaneously in one analysis the three stages of dispersal, from emigration to immigration, and their determinants (Vardakis et al. 2015). We investigated whether snails differing by size or by life-history stage differed in their emigration responses to population density, and whether population density also affected settlement decisions. Contrary to other approaches, based only on realised choices (Välimäki and Itämies 2003), dispersal discrete choice models allowed us to explicitly test this hypothesis by taking into account the characteristics of all available patches, as well as potential cascading effects of previous experience on immigration choices (*sensu* Clobert et al. 2009).

## **Material and Methods**

### **Study species**

The brown garden snail *Cornu aspersum* (Müller) (fam. Helicidae; syn. *Helix aspersa* Müller) is a relatively large (shell diameter at maturity: 25 to 40 mm), anthropophilous and generalist land snail (Welter-Schultes 2012). Native from the Mediterranean region, it has been introduced worldwide, both voluntarily, for food purposes, and accidentally (Guiller et al.

2012). *Cornu aspersum* presents a determinate growth pattern (e.g., Gomot and Enée 1980): individuals having ended their somatic growth (adults) can be distinguished from subadults by the presence of a reflected lip around their peristome. In this species, dispersal tendency has been shown to differ between life-history stages, with subadults being more dispersive than adults (Dahirel et al. 2014). *Cornu aspersum*, like at least several other snails and slugs, is suspected to be a protandric simultaneous hermaphrodite (*sensu* Baeza 2007), with subadult individuals being able to mate, but male-biased compared to adults (Bride and Gomot 1991; Dahirel et al. 2016).

#### Collection and maintenance of snails

Snails were collected one month before each of the three release experiments in a large suburban population near Rennes (French Brittany, 1°47'25" W, 48°09'11" N). Only individuals whose greater shell diameter was higher than 20 mm (i.e. subadult and adult life-history stages, Dahirel et al. 2014) were used. 630 snails were kept in controlled conditions (20°C, 80% R.H., 16:8 L: D photoperiod) before release. All snails were measured (greater shell diameter) to the nearest 0.1 mm using a vernier calliper, and individually marked on the shell using industrial grade felt tip paint markers (Henry and Jarne 2007). They were housed in polythene boxes (30 × 45 × 8 cm) covered with a plastic mesh, in groups of 10, 20, or 40 individuals (3 groups of each density per experimental session, Fig. 1). Mean shell diameter and proportion of subadults varied between groups, but were set up to not significantly differ between densities (overall mean shell size  $\pm$  SE = 27.7  $\pm$  0.1 mm, linear mixed model with a random effect of group and ANOVA,  $F_{2,22.3} = 0.68$ ,  $P = 0.51$ ; overall proportion of subadults = 51.3  $\pm$  2.0 %, binomial GLMM and Wald test,  $X^2 = 0.01$ ,  $P = 0.99$ ;  $n = 630$  individuals in 27 groups). To provide sufficient moisture for the snails, the bottom of each box was lined with synthetic foam kept saturated in water. Snails were fed *ad libitum* with composite snail

food (cereal powder supplemented with calcium; Ets Berton, France). Boxes were cleaned and the lining changed after two weeks.

### Experimental landscape setup

To study snail dispersal in semi-natural conditions, an experimental fragmented landscape was installed in a 45 × 11 m meadow, on the University of Rennes 1 Beaulieu campus (Brittany, France; 01°38'05" W, 48°06'51" N, Fig. 1). It was composed of nine central circular patches (diameter 1 m), where snails were released, plus six square boundary patches (side length 0.9 m) at the northern and southern extremities of the meadow, used to provide empty patch opportunities and catch snails leaving the landscape. Patch boundaries were constructed with concrete blocks laid down on the ground. The experimental area limits were also marked by concrete blocks, with anti-hail nets laid on ground to slow down snail evasion (mesh size: 12 mm). The central patches were clustered in three groups of three patches; two patches belonging to a same cluster were separated by 2.5 m (distance between patch boundaries) and neighbouring clusters being separated by about 16.7 m (distance between cluster centroids). As the average home range of *Cornu aspersum* snails in resource-rich, low-competition environments seems to be about 1 m<sup>2</sup> (Dan 1978; Bailey 1989), such inter-patch distances should limit the use of multiple patches by non-dispersing snails, while insuring the distance between two nearby patches could be travelled in one night by dispersing individuals (Dahirel et al. 2014). In addition, larger between-clusters distances were designed to detect rarer long-distance dispersal events: *C. aspersum* snails are able to disperse up to 10 m in a night and 50 m in a month (Dahirel et al. 2014). Slates and hollow bricks were placed in each patch to be used as shelters, in large enough quantities to shelter about 100 individuals per patch without physical contact between snails. Nettle (*Urtica dioica* L., 2 potted plants per patch) and ivy (*Hedera helix* L., 3 potted plants per patch) fully developed plants were added in the 9 central patches. Nettle is particularly palatable to *C. aspersum* (Iglesias and Castillejo 1999) and ivy



is one of its main host plants (Stratton 1964). Helicid snails, despite being generalists, can acquire strong and relatively long-lasting feeding preferences toward given food resources after conditioning (Teyke 1995). Therefore, to account for food conditioning during the pre-release phase, and to homogenise trophic conditions between sessions, we also added 100 g of composite snail food in each patch, refilled every week, in plastic plates under the shelters (preliminary observations showed that isolated adult snails with no other resource consumed on average  $0.38 \pm 0.05 \text{ g.day}^{-1}$  of this food;  $N = 5$  snails observed for 4 days; M. Dahirel, unpublished data); plates were always refilled before being fully emptied. The area outside designated habitat patches was mowed monthly, to maintain it in a poor quality matrix state (maximal height 5 cm), with more than 95% of the area occupied by Poaceae (mainly *Festuca rubra* L., *Lolium perenne* L. and *Dactylis glomerata* L.) or bare soil. Brown garden snails are able to consume Poaceae (Chevalier et al. 2001), but generally avoid them: they often represent a limited part of their diet in the wild, independent of their abundance (Iglesias and Castillejo 1999). A thermo-hygrometer probe (Log32 datalogger, Dostmann, Reicholzheim, Germany in a white instrument shelter) was installed at the south of the meadow to record ground-level temperature and relative humidity at hourly intervals.

#### Population setup and monitoring of snail dispersal

Snails were released in the experimental landscape described above on three occasions: 29-May-2013, 9-Jul-2013 and 9-Sep-2013. Each session lasted 21 days. Sessions were separated by at least two weeks, during which the matrix was mowed, remaining snails searched and removed when found, and the shelters cleaned thoroughly with water. At the beginning of each session, each of the nine boxes of snails (10, 20 or 40 snails per box  $\times$  3; see above) was randomly released in one of the 9 central patches, for a total of 210 snails per session. To limit dispersal due to translocation stress, snails were released in dry days, during the afternoon (i.e. the inactivity period), and were placed in the shelters with the synthetic foam lining,

presenting familiar food, faeces and mucus odours, on which they were maintained. One hour after release, no individuals were found outside the shelters. Snails were searched for at least twice a week, in the experimental landscape itself and in a 2 m wide buffer zone around it. Searches took place during the inactivity period, between 10 am and 5 pm. When a marked snail was found in the buffer zone, it was placed at the nearest point on the experimental landscape boundary.

We used the coordinates of snails during all recapture visits and a simplified version of Börger and Fryxell's (2012) nonlinear logistic mixed model (with random individual effects for the asymptotic value only, not scale and shape parameters, as the full version did not converge), to determine how the squared beeline distance from release, or net squared displacement, changed with time. We determined that, on average, snail displacement reached a plateau after 12.9 [12.3; 13.4] days (predicted mean [95% confidence interval]). Thus, only the locations of snails during the last (third) week of monitoring were used to determine dispersal choices. Some individuals were not recaptured during the last week of monitoring (171 of 630) and were therefore not used in dispersal choice analyses as their status was uncertain. These "discarded" snails did not differ significantly from other snails in terms of mean shell size ( $27.9 \pm 0.2$  against  $27.7 \pm 0.1$ , LMM with ANOVA,  $F_{1,627.2} = 0.24$ ,  $P = 0.62$ ) or proportion of subadults ( $48.0 \pm 3.8$  % against  $52.5 \pm 2.3$  %, binomial GLMM,  $X^2 = 1.95$ ,  $P = 0.16$ ), and the proportion of "discarded" snails in a patch did not depend on its population density at release ( $25.6 \pm 4.6$  %,  $30.0 \pm 3.4$  % and  $26.1 \pm 2.3$  % for 10, 20 and 40 snails at release respectively, binomial GLMM,  $X^2 = 0.35$ ,  $P = 0.83$ ).

#### Statistical analyses

To determine how snail dispersal choices depend on population density and which phenotypic trait best explained observed individual differences, we built several candidate models using

the Dispersal Discrete Choice Model (DDCM) framework recently developed by Vardakis et al. (2015). In short, discrete choice models (DCMs) are a type of multinomial logit regression models widely used in econometrics, and to a lesser extent, foraging ecology (e.g., May et al. 2010), to describe the choices made by individuals among a finite set of mutually exclusive alternatives (e.g., patches). Dispersal Discrete Choice Models are a type of DCM in which individual patch choices are modelled as a function of alternative patch characteristics (e.g., size, habitat type, population density...), individual traits (e.g., sex, age, body condition, previous experience...) and variables specific to the combination individual-alternative (e.g., the distance from the patch of origin). Through careful specification of variables, decision processes at the three stages of dispersal (departure, transience and settlement) can potentially be disentangled and investigated. Based on these variables, DDCMs assign a utility or “attractiveness” value to each patch, including the patch of origin, for each individual (the use of the terms “utility” or “attractiveness” do not imply in itself any underlying cognitive process or fitness outcome behind patch choices). The probability for an individual to choose a given patch is equal to this patch’s  $e^{attractiveness}$  divided by the sum of all patches’  $e^{attractiveness}$  for this individual.

In all models, the probability of choosing a given patch was assumed to be dependent on its distance from the release patch, excluding models with no distance effect on the basis of low biological plausibility, as many costs accumulate with distance travelled (Bonte et al. 2012; Hovestadt et al. 2012). Given the importance of weather conditions for snail activity and dispersal (Cook 2001; Dahirel et al. 2014), we also included distance  $\times$  session interactions to account for weather variations between our three sessions of observation (Fig.1). Starting with these minimal models, we added an effect of density at release site and an effect of individual characteristics (either life-history stage or shell size). These effects were entered as interactions with distance to the release patch: we hypothesized that snails differing in terms

of experienced density and/or phenotype would differ in their tendency to stay or settle close to their release site. We considered the probability for dispersers to settle in a new patch could also be dependent on its mean density during the session; these densities were estimated by analyzing the patch-specific recapture histories of all 630 snails using Cormack-Jolly-Seber mark-recapture models (Rcapture package; Baillargeon and Rivest 2007). Individuals able to get information on surrounding patches can be assumed to have access to similar information on their release patch; therefore, models including this alternative-specific effect of density but no effect of release density were excluded from the candidate set on the basis on low plausibility. The most complex models also included phenotype  $\times$  density interactive effects, as snails differing in terms of size, competitive ability or reproductive state could be expected to react differently to population density (Marjamäki et al. 2013; Rémy et al. 2014), and interactions between the two main density variables, to account for potential carryover effects of release patch density on subsequent settlement choices (Clobert et al. 2009). These hypotheses on dispersal choices determinants were incorporated into a set of 19 different models (Table 1). Continuous parameters (shell diameters, distances and densities) were standardized in all models, in order to increase estimability and interpretability (Schielzeth 2010).

Parameters were estimated with Bayesian procedures using Markov Chain Monte Carlo (MCMC) methods (McCarthy 2007). Analyses were done in WinBUGS version 1.4.3 (Lunn et al. 2000), and R versions 3.1.1 to 3.2.2 (R Core Team 2015), using the R2WinBUGS package (Sturtz et al. 2005) to link the two programs. We used the same independent normal prior distributions  $N(0, 0.0001)$  for all model parameters. For each model, two MCMC chains of 200 000 samples were generated, with a thinning rate of 0.1 and the first 100 000 samples discarded as burn-in when computing the final estimates. We checked for convergence using Gelman's  $\hat{R}$  (Brooks and Gelman 1998), and found no evidence of convergence failure.

Candidate models were compared using the Deviance Information Criterion (DIC; Spiegelhalter et al. 2002), and their performance assessed using two goodness-of-fit procedures derived from Vardakis et al. (2015). First, we calculated for each individual the probability assigned by the model to its actual choice, examined the distribution of these probabilities for all individuals, and compared it (i) to the average probability of 1/15 expected under a null model without any information on individual choices, and (ii) to the probabilities expected under the “null” models with no effects of patch density and individual characteristics (models 18 and 19, Table 1), using Kolmogorov-Smirnov tests. Second, for all starting patch  $\times$  session  $\times$  life-history stage combinations, we also compared the observed and predicted probabilities a snail chose one of the 15 possible patches (hereafter “patch-level fit”) using linear regressions; comparisons were done separately for dispersal and resident choices (Table 1).

## Results

Overall, 127 of the 459 observed snails were dispersers (empirical emigration rate =  $0.27 \pm 0.02$ ); their average dispersal distance was equal to  $4.95 \pm 0.35$  m. Only 6 snails settled more than 10 m from their release site, and only one dispersed more than 20 m (35.5 m). In all models, the predicted probabilities for the observed choices were better than those expected if snail choices were completely random (based on Kolmogorov-Smirnov tests,  $P < 0.001$ ), and both these probabilities ( $P < 0.01$ ) and the  $r^2$  for the patch-level fits were better than those obtained for the null models with only distance and distance  $\times$  session effects (Table 1, Online Resource 1). However, based on DIC values, models with shell size as an individual-specific effect were always outperformed by their equivalents using life-history stage (adult/subadult; see for instance model 1 vs. model 8 in Online Resource 1), and models excluding either stage, density prior to release or snail density of alternative patches tended to perform poorly (Online Resource 1). Based on DIC values, the best model was the most complex one,

including effects of density both on departure and settlement decisions, as well as effects of life-history stage (adult/subadult) and density  $\times$  stage interactions (Tables 1, 2; Fig. 2; Online Resource 1).

Based on this best model, dispersal choices were strongly distance-dependent, and the decrease in settlement probability with distance was session-dependent: the decrease in patch attractiveness value with distance was predicted to be much stronger in July compared to the two other months, indicating that snails dispersed less and/or less far in July (Table 2) (including non-dispersing snails, observed mean dispersal distances  $\pm$  S.E. were  $2.5 \pm 0.25$ ,  $0.24 \pm 0.11$  and  $1.95 \pm 0.39$  m in June, July and September respectively). The decrease in patch attractiveness value with distance was also dependent on both individual traits and patch context (Table 2): subadults emigrated on average more and dispersed farther from their release patch than adults, as did snails coming from high-density patches compared to individuals coming from low-density patches (Fig. 3, Online Resource 2).

Regarding settlement decisions of individuals that left their release patch, there were complex interactions between the mean snail density of alternatives, the density experienced before release and the life-history stage (Table 2, Fig. 4). Overall, low-density patches had higher predicted attractiveness values, meaning they were more likely to be chosen, than more crowded patches, distance to the release site being equal. Based on the best model, this density effect was stronger in subadults than adults, and was also dependent on the density experienced prior to release: the difference in attractiveness between low-density and high-density patches was stronger for snails coming from more crowded contexts (Fig. 4). However, models without stage $\times$ density or density<sub>release</sub> $\times$ density<sub>settle</sub> interactions still had good DIC values (models 2 to 4; Table 1), indicating these were not as well supported by data as other effects.

## Discussion

Using recently developed dispersal discrete choice models and a semi-natural standardised landscape, we were able to show that not only emigration, but also immigration decisions were density-dependent, with snails avoiding crowded patches at both ends of the dispersal process (Table 2, Figs. 3 and 4). In particular, DDCMs allowed us to directly and more realistically test hypotheses on immigration drivers by comparing, for all individuals, chosen patches with a realistic set of patches that could have been chosen, instead on focussing only on the former (e.g., Välimäki and Itämies 2003). Subadults tended to disperse more and farther than adults (Fig. 3; Table 2), and appeared to be more sensitive to population density in their settlement decisions (Fig. 4). There was also important seasonal variation in dispersal distances, probably linked to weather variation (Table 1, Table 2): average dispersal distances were at their lowest level in July, the driest and hottest of the three monitoring periods (Fig. 1). This is in line with previous results in *Cornu aspersum* (Dahirel et al. 2014) and in the invasive snail *Xeropicta derbentina* (Aubry et al. 2006). Indeed, many characteristic traits of land snails (such as ectothermy, abundant use of water for mucus production, or their permeable integument) make them particularly sensitive to weather variations (Cook 2001).

We found that snails emigrated more, and move farther from their release site, when they came from high-density patches compared to less crowded groups. Such positive density-dependent emigration has been found in a wide variety of species belonging to many phyla, in both field and controlled conditions (Moksnes 2004; Matthysen 2005; Mathieu et al. 2010; Nowicki and Vrabec 2011; Kuefler et al. 2012; Bitume et al. 2013). It is generally interpreted as a response to decreased fitness prospects caused by exploitative and/or interference competition (Bowler and Benton 2005). In our setup, resource depletion effects were controlled by regular refill of food trays; thus, interference competition seems to determine density-dependent emigration in *Cornu aspersum*. Interference effects on dispersal can be

direct, through aggression (in the crab *Carcinus maenas*, Moksnes 2004), or indirect, through e.g. chemical compounds. Aggressive interactions have been recorded in some slug species (Cook 2001), but never in *Cornu aspersum* (including our personal observations), while mucus accumulation is known to negatively affect performance in this species (Dan and Bailey 1982).

We found that, at all densities, subadult snails were more likely than adults to leave their release patch, in line with existing results (Tomiyama and Nakane 1993; Dahirel et al. 2014). Subadults differ mainly from adults in terms of body size and investment in female reproduction, the latter being an important determinant of patch-leaving propensity (Dahirel et al. 2016). This is confirmed here, as models using size as a phenotypic variable were consistently outperformed by models using stage (Online Resource 1), meaning body size was not the main trait explaining the dispersal differences between subadults and adults. Because of these phenotypic differences, we expected subadults and adults to react differently to an increase in population density, as the balance between costs and benefits of dispersal in response to density would differ between the two life-history stages. While emigration increased with population density for both adults and subadults (Fig. 3), settlement decisions of subadults appeared to be more sensitive to population density (Fig. 4). On one hand, costs of settling in high-density habitats should be lower in adults, as they are less sensitive to intraspecific competition (Dan and Bailey 1982). On the other hand, high population density patches also have more potential mates; in the related snail *Arianta arbustorum*, the frequency of multiple matings is higher in larger populations (Kupfernagel et al. 2010). In gonochoric species, the interaction of competition for resources, competition for mates, and attraction towards potential partners can lead to between-sex differences in the slope of the relationship between dispersal and density (e.g. in spiders: De Meester and Bonte 2010; in horses: Marjamäki et al. 2013). In protandric hermaphrodite species, such as *Cornu aspersum*, the



picture is expected to be more complex; how this peculiar reproductive system influences dispersal decisions of male-biased subadults and hermaphrodite adults needs to be studied extensively, but our results suggest that in the former, competition (which would lead snails to avoid high-density sites) has a stronger effect on dispersal than attraction towards mates (which would lead individuals towards high-density sites, Välimäki and Itämes 2003), compared with the latter.

Individuals are expected to make informed dispersal decisions, which help maximize their fitness prospects (Enfjäll and Leimar 2009; Clobert et al. 2009; Bocedi et al. 2012). However, information acquisition is generally incomplete, and dispersal decisions expected to be disproportionally based on local patch quality, especially when it is difficult or costly to acquire information on other patches (Doligez et al. 2002; Bowler and Benton 2005; Matthysen 2012). Therefore, we expected snails to make informed emigration decisions based on release density, but to make random settlement decisions relative to density (Křivan 2008). Contrary to the latter expectation, snails settlement decisions were density-dependent, which raises questions on how snails manage to obtain information on other patches. Terrestrial Gastropods are able, at short distances (< 20-50 cm), to detect aggregations of conspecifics (Chase et al. 1978) or small food sources (Dahirel et al. 2015) through olfaction, but their ability to perceive more distant odours has been understudied in natural conditions (Speiser 2001). Anecdotal evidence suggests that *Cornu aspersum* snails may in some cases be able to detect patches at distances comparable to their dispersal distances (about 5 m, but less than 20 m, Dunstan and Hodgson 2014), which might explain how snails are able to make informed settlement decisions relative to conspecific density, despite the potentially high costs of exploratory movements. It is possible, on the other hand, that energetic and water movement costs in land snails are not as limiting as commonly thought, as even sedentary individuals can travel over relatively large cumulative distances while searching for food (Rollo and

Wellington 1981). In *Cornu aspersum*, cumulative travel distances of 10 m and more in one night can occur (Dahirel et al. 2014; M. Dahirel, unpublished data), which would allow dispersing snails, in fragmented environments, to “sample” several colonies over the course of a few nights (Selander and Kaufman 1975; Dan 1978). Additionally, the use of indirect, social information may help reduce these costs (Chaine et al. 2013). In snails, the chemical composition, number or direction of mucus trails produced by immigrants or emigrants might give potential dispersers valuable information on not only the quality, but also the direction of nearby patches (Ng et al. 2013).

We also found support for a carryover effect of release patch density on further settlement decisions: snails dispersing away from crowded patches were more likely to settle in low-density patches (Fig. 4). Literature on breeding habitat selection shows evidence for cascading effects of several natal habitat features on subsequent habitat choices (Davis 2008). However, carryover effects of departure patch density, despite their potential ubiquity and consequences on population dynamics, are much less described (Cote and Clobert 2007; Clobert et al. 2009). High densities alter the growth and activity patterns of snails (Dan and Bailey 1982), and so may have persistent effects on their morphology and physiology, with expected consequences on both emigration decisions and immigration success (Benard and McCauley 2008; Clobert et al. 2009). Different decisions during settlement are to be expected if snails dispersing at high densities form a phenotypically different subset of the population than snails dispersing from less crowded patches (Cote and Clobert 2007), for instance if snails leaving crowded patches because of competition are competitively inferior, and therefore less able to insert themselves in other crowded patches. There are limited indications that this is indeed the case in our dataset (Online Resource 3). Independently of the underlying cause, the existence of potential carryover effects shows that our understanding of dispersal will not only benefit from research on how information is acquired, but also on how long acquired

information can affect subsequent behavioural decisions. More generally, it highlights the fact that all dispersal steps have to be studied together, and not separately, in order to obtain a clear understanding of dispersal.

When both emigration and settlement are informed by density, actively moving dispersers are predicted to “move on” if they encounter a low quality/ high density patch, instead of settling in the first patch encountered, until they find a suitable site in terms of population density and/or until cumulated costs of dispersal become too high (Poethke et al. 2011; Bitume et al. 2013). Extending this theoretical argument, we may expect, in a given environment, individuals more sensitive to population density to be more “picky” and settle farther on average. In line with this hypothesis, groups of snails (stage  $\times$  release density) whose patch attractiveness values were the most influenced by target patch density were also the least sensitive to the distance between the departure patch and the target patch, leading to a negative correlation between the two effects (Fig. 5).

Theoretical models also predict that dispersal strategies leading individuals to leave crowded patches tend to decrease extinction probability in spatiotemporally variable environments, by maintaining smaller populations above viability thresholds (Sæther et al. 1999; Amarasekare 2004; Hovestadt and Poethke 2006). In *Cornu aspersum*, our results show this rescue effect may be amplified, given snails appear to settle actively in low-density habitats instead of simply “spilling over” from crowded sites, as is generally assumed in dispersal models (see Travis et al. 2012 for a review; but see Sæther et al. 1999; or Bocedi et al. 2014), and because carryover effects accentuate the contrast in responses between snails coming from different contexts. The combination of hermaphroditism, which leads to lower viability thresholds as all reproductively active individuals are potential mates (Tomlinson 1966), with the observed density-dependent dispersal strategy may thus play a major role in the ability of *Cornu aspersum* to colonise and thrive in frequently human-disturbed habitats.

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445 All applicable institutional and/or national guidelines for the care and use of animals were  
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## 447 **Conflicts of interest**

448 The authors declare that they have no conflict of interest.

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## 670 Tables

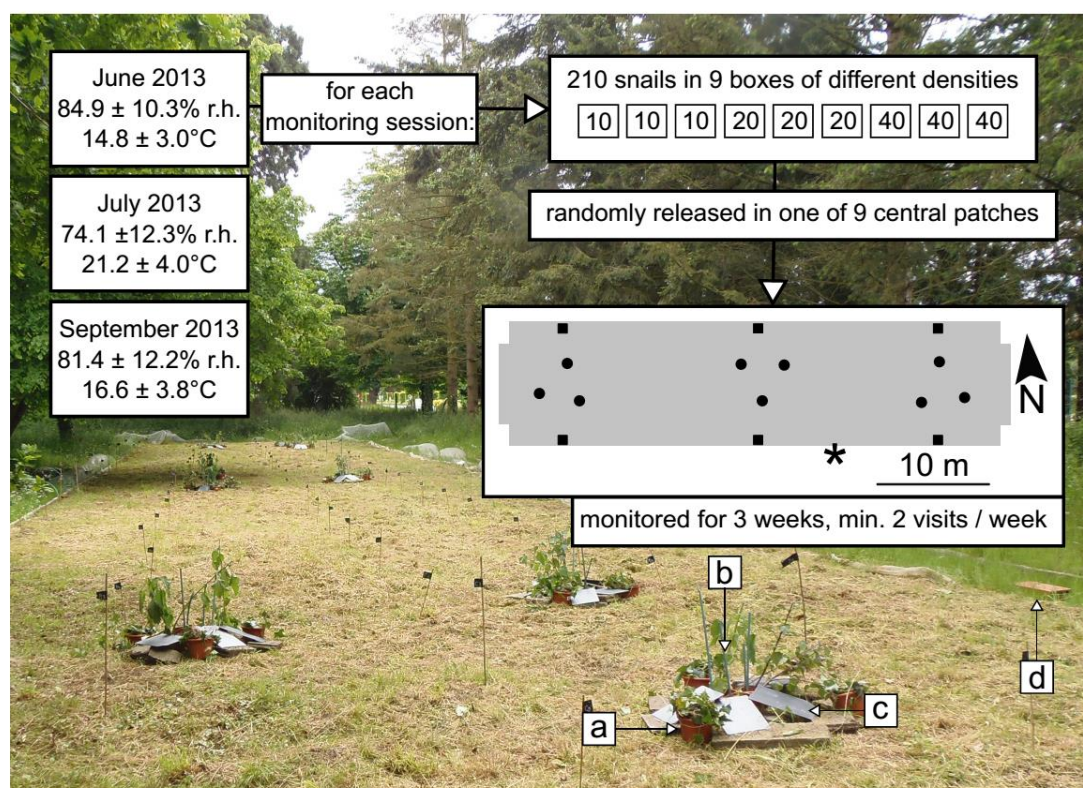
671 **Table 1** Partial model selection table, summarizing the performance of candidate Dispersal  
672 Discrete Choice Models in explaining brown garden snails dispersal choices. Models are  
673 ranked by increasing Deviance Information Criterion (DIC) values, the model with the lowest  
674 DIC being considered the best (only the four best and the two worst models are presented  
675 here; see Online Resource 1 for the full table). pD corresponds to the effective number of  
676 parameters. "density<sub>release</sub>" and "density<sub>settle</sub>" refer to the snail density experienced prior to  
677 departure, and to the alternative-specific mean snail density, respectively. "Observed  
678 probability" is the average probability assigned by the model to the observed choice;  $r^2$   
679 (dispersers) and  $r^2$  (residents) refer to linear regressions testing how well observed  
680 probabilities of choosing a specific patch are explained by model predictions (see Fig. 2).

	Model (A = predicted patch attractiveness value)	DIC (pD)	Observed probability	$r^2$ (dispersers)	$r^2$ (residents)
1	<b>A = distance + session*distance + stage<sub>subadult</sub>*distance + density<sub>release</sub>*distance + stage<sub>subadult</sub>*density<sub>release</sub>*distance + density<sub>settle</sub> + stage<sub>subadult</sub>*density<sub>settle</sub> + density<sub>release</sub>*density<sub>settle</sub></b>	<b>860 (8.8)</b>	<b>0.60</b>	<b>0.28</b>	<b>0.49</b>
2	A = distance + session*distance + stage <sub>subadult</sub> *distance + density <sub>release</sub> *distance + density <sub>settle</sub> + density <sub>release</sub> *density <sub>settle</sub>	862 (6.9)	0.59	0.26	0.49
3	A = distance + session*distance + stage <sub>subadult</sub> *distance + density <sub>release</sub> *distance + stage <sub>subadult</sub> *density <sub>release</sub> *distance + density <sub>settle</sub> + stage <sub>subadult</sub> *density <sub>settle</sub>	863 (7.9)	0.59	0.29	0.5
4	A = distance + session*distance + stage <sub>subadult</sub> *distance + density <sub>release</sub> *distance + density <sub>settle</sub>	864 (5.9)	0.59	0.27	0.51
...	...	...	...	...	...
18	A = distance + session*distance	900 (3.0)	0.57	0.21	0.40
19	A = distance	1038 (1.0)	0.48	0.13	0.04

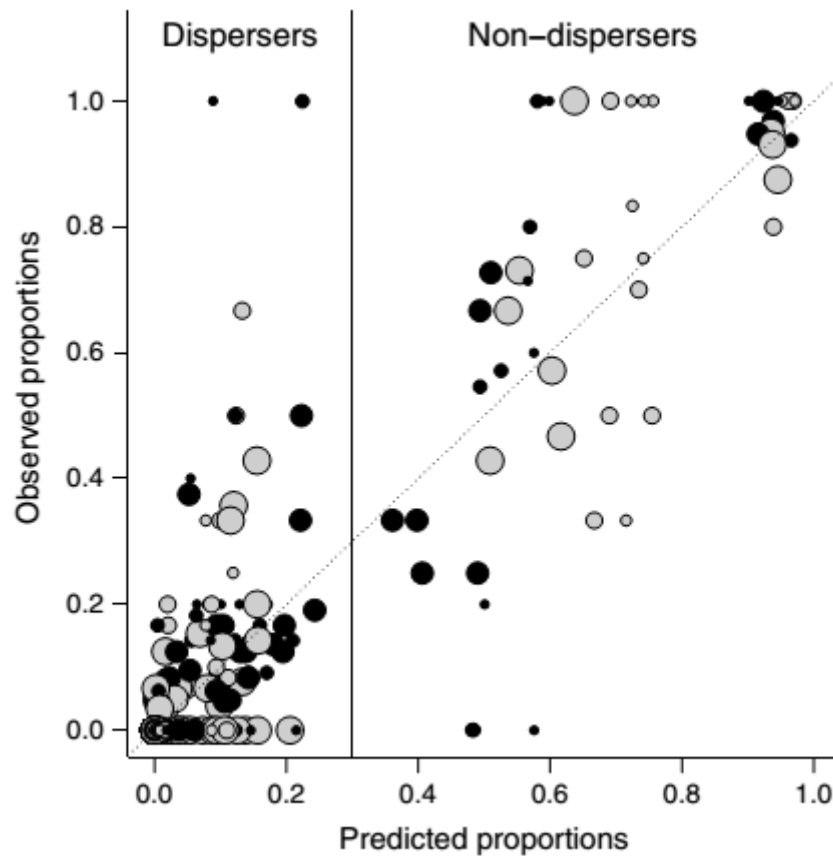


**Table 2** Posterior estimates of the effects of life stage, population densities and distance from the release site on the attractiveness of a given patch (from the best model in Table 1, mean  $\pm$  standard deviation and 95% credible intervals). Estimates are taken from 200 000-samples MCMC runs, with the first 100 000 samples discarded as burn-in and a thinning rate of 0.1.

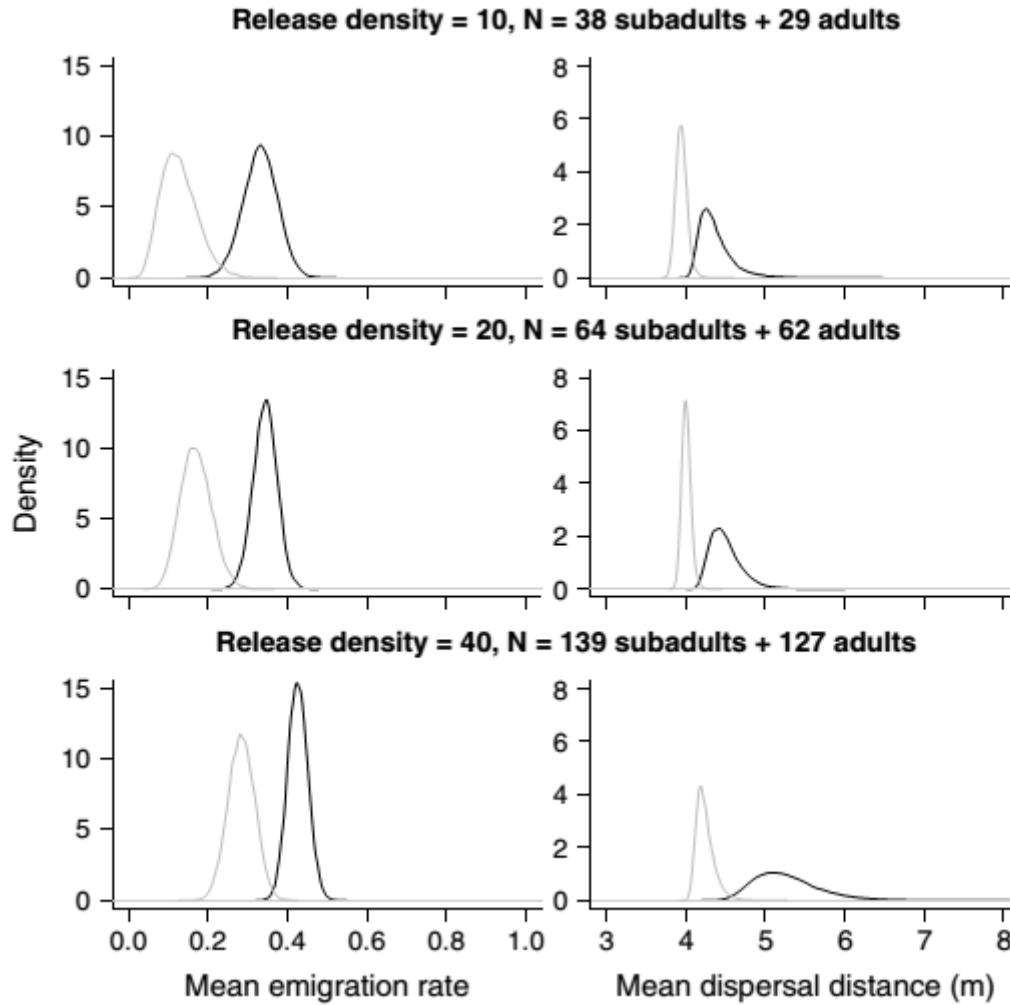
Parameter	Mean	S.D.	95% Credible Interval	
			2.50%	97.50%
distance	-4.78	0.57	-5.92	-3.73
session <sub>July</sub> *distance	-6.99	0.94	-8.94	-5.26
session <sub>September</sub> *distance	-0.57	0.43	-1.42	0.27
stage <sub>subadult</sub> *distance	2.39	0.59	1.26	3.58
density <sub>release</sub> *distance	1.28	0.57	0.22	2.44
stage <sub>subadult</sub> *density <sub>release</sub> *distance	-0.71	0.62	-1.94	0.47
density <sub>settle</sub>	-0.21	0.16	-0.55	0.09
stage <sub>subadult</sub> *density <sub>settle</sub>	-0.56	0.23	-1.02	-0.1
density <sub>release</sub> *density <sub>settle</sub>	-0.23	0.11	-0.45	-0.02



**Fig. 1** Summary of the experimental setup used to study brown garden snail (*Cornu aspersum*) dispersal. Left: values indicate the average ground-level relative humidity and temperature ( $\pm$  SD) for each release session. Center right: schematic representation of the experimental landscape, showing the disposition of the nine central patches where *Cornu aspersum* snails were released (circles) and the six boundary patches, initially empty (squares). The asterisk marks the location of the thermo-hygrometer probe. Photograph: picture of the experimental landscape, taken from the western side (29-May-2013). A set of 3 release patches can be seen in the foreground, the other two in the background. a: ivy plant (3 per patch); b: nettle plants (2 per patch); c: shelters, plastic plates with additional snail food are present under shelters; d: shelter from one of the six boundary patches.



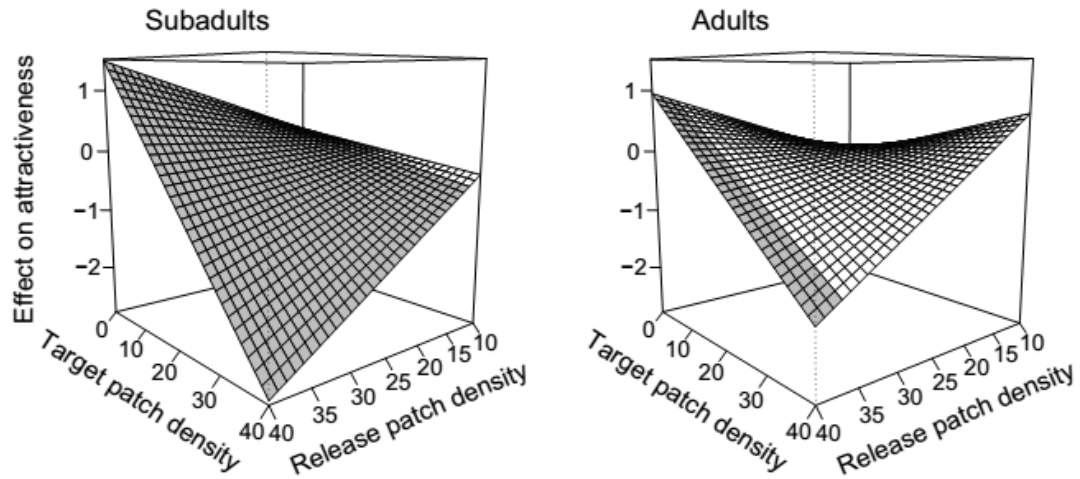
**Fig. 2** Comparison of the predicted and observed probabilities a snail chooses a patch, given its characteristics and site of origin. Each point represents one of the possible combinations of release patch, final patch, life stage and session ( $N = 810$  combinations; black: subadults; grey: adults; the size of symbols increases with release patch density; the dashed line corresponds to Observed = Predicted). Predictions are based on the best model Tables 1 and 2. The vertical line separates the points corresponding to dispersal choices (left,  $N = 756$ ) from those corresponding to sedentary choices (right,  $N = 54$ );  $r^2$  for both categories are presented in Table 1 and Online Resource 1.



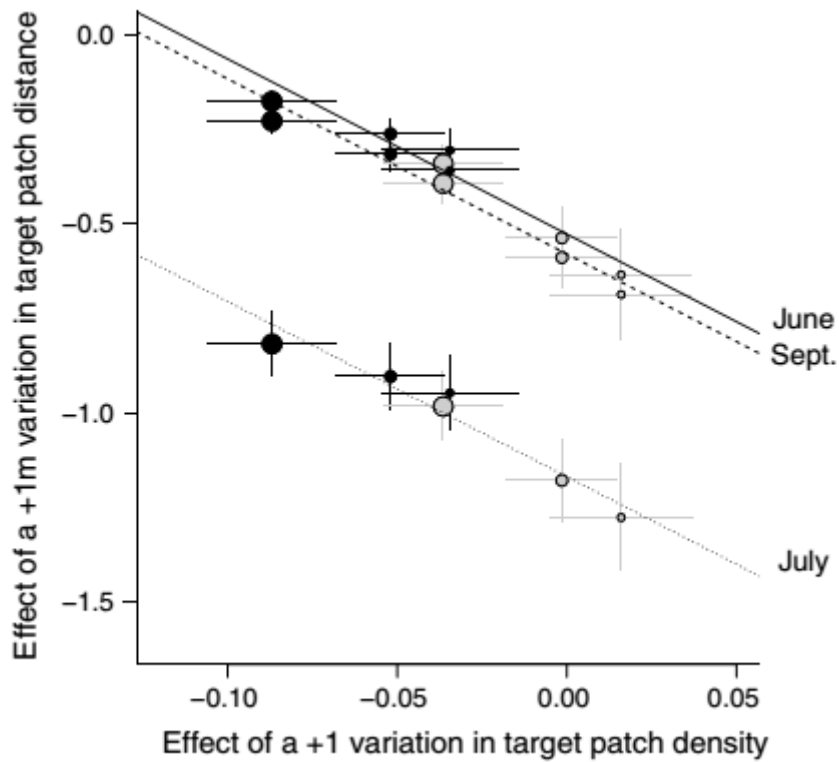
709

710 **Fig. 3** Posterior distributions of the mean emigration rate (left) and the mean dispersal  
 711 distance (excluding residents, right), as a function of life-history stage (grey = adults, black =  
 712 subadults) and release patch density. Values are based on the best model, data from the three  
 713 monitoring sessions and from all relevant patches are pooled. To allow for meaningful  
 714 comparisons of choices made in different contexts, predictions are made assuming that all  
 715 focal snails were released in the same patch (the westernmost site Fig. 1) and that the  
 716 population density of all other patches was equal to the mean density experienced in target  
 717 patches (11.13 snails/patch; for the effect of variation in target patch density, see Fig. 4);  
 718 empirical values and “naïve” predictions are presented in Online Resource 2.

719



**Fig. 4** Predicted effect of population density on target patch attractiveness, distance to the release patch being held equal, based on the best model (left: subadults, right: adults). The range of release densities for which *Cornu aspersum* snails are sensitive to target patch density (i.e. for which the effect of target patch density is different from 0, based on 95% credible intervals) is coloured in grey.



**Fig. 5** Comparison of the effects ( $\pm$  SD) of distance from release patch and mean population density on the predicted attractiveness values of target patches (based on the best model Tables 1 and 2; black: subadults; grey: adults; the size of symbols increases with release patch density;  $R^2 = 0.99$ ,  $N = 18$ ,  $P = 2.18 \times 10^{-13}$ )



**Online Resource 1: Full model selection table**

Table. Performance of the 19 candidate Dispersal Discrete Choice Models in predicting brown garden snails dispersal choices. Models are ranked by increasing Deviance Information Criterion (DIC) values, the model with the lowest DIC being considered the best. pD corresponds to the effective number of parameters. "density<sub>release</sub>" and "density<sub>settle</sub>" refer to the snail density experienced prior to departure, and to the alternative-specific mean snail density, respectively. "Mean probability of observed" is the average probability assigned by the model to the observed choice; "Patch-level fit" refers to linear regressions of predicted versus observed probabilities of choices (see Fig. 2); underlined coefficients denote slopes significantly different from 1, i.e the slope expected when Observed = Predicted.

	Model (A = predicted patch attractiveness value)	DIC	pD	Mean probability of observed	Patch-level fit (Intercept, Slope, $r^2$ )	
					Dispersers	Non-dispersing individuals
1	A = distance + session*distance + stage <sub>subadult</sub> *distance + density <sub>release</sub> *distance + stage <sub>subadult</sub> *density <sub>release</sub> *distance + density <sub>settle</sub> + stage <sub>subadult</sub> *density <sub>settle</sub> + density <sub>release</sub> *density <sub>settle</sub>	860	8.77	0.60	-0.00, 1.02, 0.28	-0.09, 1.14, 0.49
2	A = distance + session*distance + stage <sub>subadult</sub> *distance + density <sub>release</sub> *distance + density <sub>settle</sub> + density <sub>release</sub> *density <sub>settle</sub>	862	6.87	0.59	-0.00, 0.97, 0.26	-0.07, 1.13, 0.49
3	A = distance + session*distance + stage <sub>subadult</sub> *distance + density <sub>release</sub> *distance + stage <sub>subadult</sub> *density <sub>release</sub> *distance + density <sub>settle</sub> + stage <sub>subadult</sub> *density <sub>settle</sub>	863	7.87	0.59	-0.00, 1.03, 0.29	-0.09, 1.15, 0.50
4	A = distance + session*distance + stage <sub>subadult</sub> *distance + density <sub>release</sub> *distance + density <sub>settle</sub>	864	5.87	0.59	-0.00, 0.99, 0.27	-0.07, 1.13, 0.51
5	A = distance + session*distance + shell size*distance + density <sub>release</sub> *distance + density <sub>settle</sub> + density <sub>release</sub> *density <sub>settle</sub>	870	6.86	0.59	-0.00, 0.95, 0.25	-0.07, 1.15, 0.48



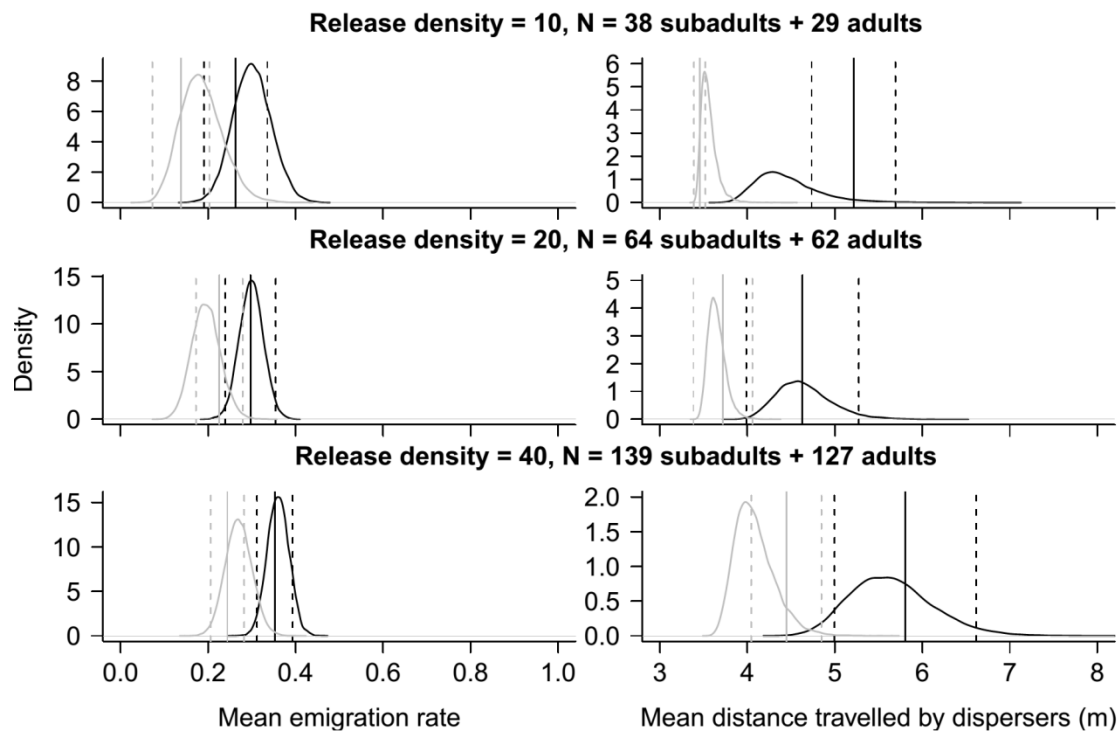
Table. (continued)

	Model (A = predicted patch attractiveness value)	DIC	pD	Mean probability of observed	Patch-level fit (Intercept, Slope, $r^2$ )	
					Dispersers	Non-dispersing individuals
6	A = distance + session*distance + shell size*distance + density <sub>release</sub> *distance + density <sub>settle</sub>	872	5.92	0.59	-0.00, 0.96, 0.26	-0.08, 1.14, 0.49
7	A = distance + session*distance + density <sub>release</sub> *distance + density <sub>settle</sub> + density <sub>release</sub> *density <sub>settle</sub>	874	5.95	0.59	-0.00, 0.91, 0.25	-0.01, 1.06, 0.42
8	A = distance + session*distance + shell size*distance + density <sub>release</sub> *distance + shell size*density <sub>release</sub> *distance + density <sub>settle</sub> + shell size*density <sub>settle</sub> + density <sub>release</sub> *density <sub>settle</sub>	874	8.78	0.59	-0.00, 0.95, 0.25	-0.07, 1.14, 0.47
9	A = distance + session*distance + shell size*distance + density <sub>release</sub> *distance + shell size*density <sub>release</sub> *distance + density <sub>settle</sub> + shell size*density <sub>settle</sub>	876	7.78	0.59	-0.00, 0.97, 0.26	-0.08, 1.14, 0.49
10	A = distance + session*distance + density <sub>release</sub> *distance + density <sub>settle</sub>	876	4.96	0.58	-0.00, 0.93, 0.25	-0.01, 1.06, 0.43
11	A = distance + session*distance + stage <sub>subadult</sub> *distance + density <sub>release</sub> *distance	881	4.92	0.58	0.00, <u>0.83</u> , 0.22	0.02, 1.03, 0.49
12	A = distance + session*distance + stage <sub>subadult</sub> *distance + density <sub>release</sub> *distance + stage <sub>subadult</sub> *density <sub>release</sub> *distance	883	5.89	0.58	0.00, <u>0.83</u> , 0.22	0.03, 1.02, 0.49
13	A = distance + session*distance + stage <sub>subadult</sub> *distance	886	3.93	0.57	0.00, <u>0.78</u> , 0.22	0.10, 0.96, 0.47
14	A = distance + session*distance + shell size*distance + density <sub>release</sub> *distance	890	4.86	0.58	0.00, <u>0.82</u> , 0.22	0.02, 1.04, 0.48

Table. (end)

	Model (A = predicted patch attractiveness value)	DIC	pD	Mean probability of observed	Patch-level fit (Intercept, Slope, $r^2$ )	
					Dispersers	Non-dispersing individuals
15	A = distance + session*distance + shell size*distance + density <sub>release</sub> *distance + shell size*density <sub>release</sub> *distance	892	5.85	0.58	0.00, <u>0.82</u> , 0.22	0.02, 1.04, 0.47
16	A = distance + session*distance + shell size*distance	894	3.95	0.57	0.00, <u>0.76</u> , 0.21	0.09, 0.98, 0.46
17	A = distance + session*distance + density <sub>release</sub> *distance	895	3.94	0.57	0.00, <u>0.78</u> , 0.21	0.08, 0.96, 0.42
18	A = distance + session*distance	900	2.97	0.57	0.00, <u>0.72</u> , 0.21	0.16, 0.89, 0.40
19	A = distance	1038	1.01	0.48	0.00, <u>0.63</u> , 0.13	-1.08, 2.83, 0.04

**Online Resource 2: Observed vs predicted emigration rates and distances travelled by dispersers in the snail *Cornu aspersum***



**Supplementary Figure.** “Naïve” posterior distributions of the mean emigration rate (left) and the mean dispersal distance (excluding residents, right), as a function of life-history stage (grey = adults, black = subadults) and release patch density, along with associated observed mean values (solid vertical lines)  $\pm 1$  SE (dashed vertical lines). Predictions are based on the best model, data from the three monitoring sessions and from all relevant patches are pooled. By contrast with Fig. 3 in the main text, predictions here are not corrected to account for differences in spatial context and neighbour patches’ densities (hence the term “naïve”). This means these predictions cannot meaningfully be compared with each other to infer differences in responses between treatments; however, this also means they can directly be compared to observed values to assess model quality.

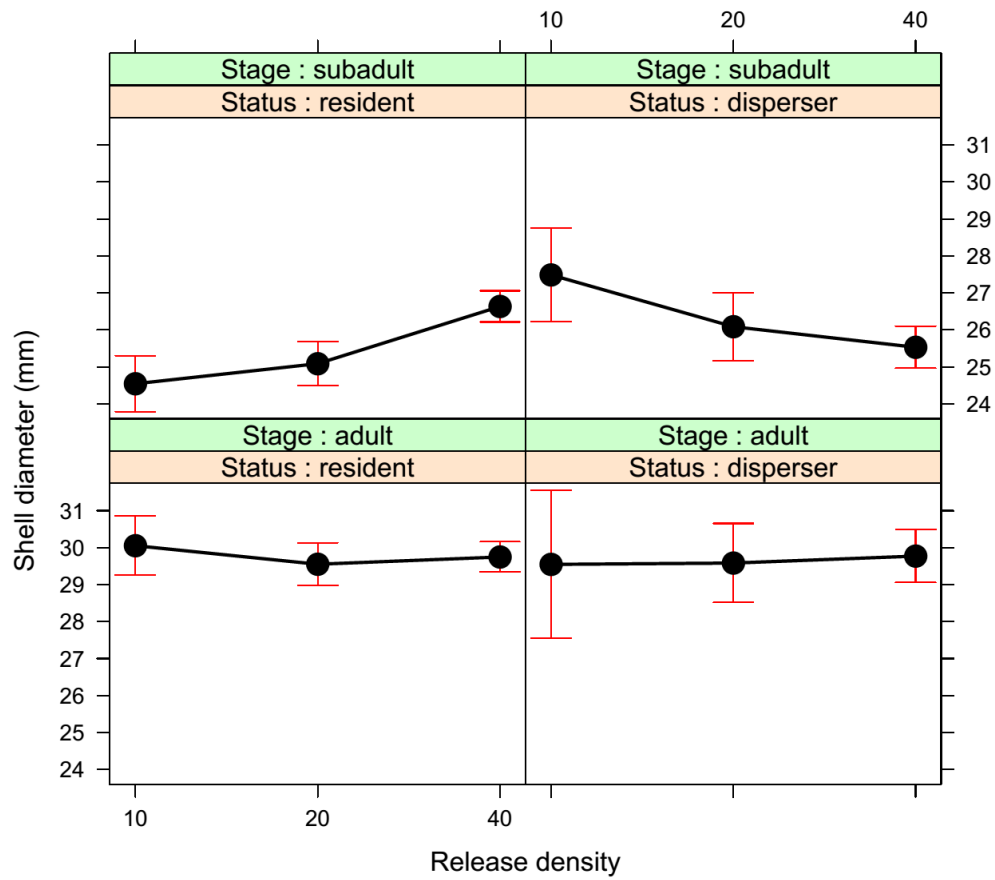
**Online Resource 3: On comparing the body size distribution of dispersers and residents across densities in the snail *Cornu aspersum*.**

In the main Discussion, we wrote that “different decisions during settlement are to be expected if snails dispersing at high densities form a phenotypically different subset of the population than snails dispersing from less crowded patches (Cote and Clobert 2007), for instance if snails leaving crowded patches because of competition are competitively inferior, and therefore less able to insert themselves in other crowded patches”.

Here, to test the hypothesis that snails dispersing at high densities form a different subset of populations than snails dispersing at low densities, we compared observed shell size distributions using a 2-factor ANOVAs (Dispersal status x Release density) separately in adults and subadults.

In subadults, there were significant effects of release density ( $F_{2,235} = 4.432$ ,  $P = 0.013$ ) and the interaction density  $\times$  dispersal status ( $F_{2,235} = 11.11$ ,  $P = 2.5 \times 10^{-5}$ ) on shell size. Using least square means to compare treatments, and limiting ourselves to meaningful comparisons (i.e. comparing different dispersal statuses at the same density, or the reverse), we found that in subadults, dispersers appear to be larger than residents at the lowest density (size difference =  $2.94 \pm 0.84$  mm,  $t = 3.50$ , FDR-adjusted  $P = 0.0017$ ), while they seem to be smaller than residents at high density (size difference =  $-1.1 \text{ mm} \pm 0.41$  mm,  $t = -2.72$ , FDR-adjusted  $P = 0.016$ )(Supplementary Figure next page). In adults on the other hand, there was no significant effect of release density ( $F_{2,212} = 0.64$ ,  $P = 0.53$ ), dispersal status ( $F_{2,212} = 0.0063$ ,  $P = 0.94$ ), or their interaction ( $F_{2,212} = 0.15$ ,  $P = 0.86$ )(Supplementary Figure).

However, these results should be interpreted with caution: indeed, to properly test the hypothesis that dispersers and residents differ phenotypically, one should not only contrast the dispersers and residents at the population level, but patch by patch, using mixed models with a patch-level random effect of dispersal status. This is however impossible here, as for a large number of session  $\times$  patch  $\times$  life stage combinations (22 out of 54), only data for residents or dispersers are available, not for both. Given the impossibility to properly test this hypothesis with our data, we decided not to present this analysis in the main text.



**Supplementary Figure.** Mean shell size of observed *Cornu aspersum* snails ( $\pm$  95% confidence intervals, overall  $N = 459$ ) as function of life stage, dispersal status and release snail density.