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## **Simple settlement decisions explain common dispersal patterns in territorial species**

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### **Summary**

1. Dispersal is one of the least-understood aspects of animal behaviour. For example, little is known of the mechanisms that determine how individuals express different dispersal behaviours in different circumstances. Uncovering these mechanisms is important for our understanding of spatial population dynamics.

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2. Using agent-based simulations, we examine how simple decision rules generate individual-level dispersal plasticity, and how this can influence population-scale dispersal dynamics. We model a territorial, monogamous population inhabiting a completely homogeneous environment. Dispersal variability therefore emerges solely as a result of between-individual interactions (competition, settlement, reproduction), which are governed by simple decision-making algorithms.
  3. We show that complex dispersal dynamics, including sex biases and strong density dependence, emerge naturally from simple rule-based behaviours. Dispersal is particularly sensitive to the inclusion of mate availability as a criterion for settlement: if neither sex evaluates mate availability, dispersal distances tend to decline at low densities, leading to a strong Allee effect from reduced pairing success. If one sex evaluates mate availability (females), Allee effects are largely avoided, but female-biased dispersal generates increasingly male-biased adult sex ratios at low densities. Sex biases are eliminated if both sexes evaluate mate availability, but population growth rates tend to be reduced due to survival costs and reduced pairing success.
  4. Our models suggest that simple decision mechanisms can explain several dynamic patterns that are commonly observed among territorial species. Importantly, these patterns emerge in the absence of environmental heterogeneity or between-individual variation in dispersal phenotypes, two conditions that are often invoked to explain dispersal heterogeneity in nature. This has implications for studies seeking to examine the causes of dispersal variability in wild populations, suggesting that observed patterns could be largely driven by the social and demographic conditions experienced by sampled individuals.

5. Further insights could be gained by examining how selection operates on decision rules in different life-history and environmental circumstances, and how this might interact with selection on other demographic traits. Uncovering the decision-rules used during settlement should be a priority for those wishing to understand and predict dispersal patterns in nature.

**Keywords:**

Animal dispersal, settlement criteria, spatial population dynamics, Allee effects, movement ecology, dispersal kernel, density dependence, mate finding

**Introduction**

Dispersal is critically important for many ecological and evolutionary processes, but remains a weak link in our understanding of population biology (Gillespie et al. 2012; Travis et al. 2012; Kubisch et al. 2014). For example, the proximate causes of variation in dispersal behaviour remain poorly understood (Nathan et al. 2008; Hawkes 2009; Stevens et al. 2010). Empirical evidence suggests that phenotypic variation (Tarwater & Bessinger 2012; Stevens et al. 2012) and maternal effects (Duckworth 2009; Larios & Venable 2015) can play key roles in determining consistent differences in dispersal propensity between individuals. Another source of dispersal variation is within-individual behavioural plasticity (Nathan et al. 2008; Morales et al. 2010), whereby individuals express different dispersal behaviours when exposed to different circumstances (Bowler & Benton 2005; Clobert et al. 2009). Understanding the mechanisms that underpin this plasticity is an essential precursor for accurate modelling of spatial population dynamics (Travis et al. 2012; Bocedi et al. 2014; Buoro & Carlson 2014).

Dispersal is generally defined as a movement in space that results in gene flow (Ronce 2007). In species that disperse actively, the degree of individual plasticity in dispersal will depend in part on decision-making mechanisms that govern movement and settlement. Despite considerable interest in modelling the mechanics of dispersal behaviour (e.g. Palmer et al. 2011; Travis et al. 2012; Bocedi et al. 2014; Ponchon et al. 2015), few studies have examined how the basic decision-making mechanisms that underpin dispersive movements influence emergent patterns (Gilroy & Lockwood 2012; Ponchon et al. 2015). Decision algorithms are difficult to elucidate from empirical data (Mabry & Stamps 2008; Schick et al. 2008), but simulations offer a promising means of examining how decision frameworks influence dispersal outcomes (Gilroy & Lockwood 2012). These frameworks take into account a range of variables that determine whether dispersal will result in gene flow, including the availability of space, resources and mates. Previous studies suggest that simple decision-theoretic algorithms can give rise to complex dispersal patterns in random walk models (Gilroy & Lockwood 2012). However, it is unclear whether such models can explain the patterns of dispersal we typically observe in nature.

In this paper, we model the population dynamics of a territorial monogamous species inhabiting a homogeneous landscape. Evidence suggests that such species typically show fat-tailed dispersal kernels (Bowler & Benton 2005; Van Houtan et al. 2007), increased dispersal at high population densities (Matthysen 2005; Lowe & McPeck 2014), and female-biased dispersal if males are the territory establishing sex (e.g. in birds, Greenwood et al. 1980; mammals, Lawson-Handley & Perrin 2007; butterflies, Stevens et al. 2012). Also, adult sex ratios are often skewed towards males, particularly at low population densities (e.g. in butterflies, Kuussaari et al. 1998; beetles, Herzig 1995; birds, Dale et al. 2001; Donald 2007). These well-documented patterns are often explained in terms of between-individual variation in dispersal phenotypes

(Johnson & Gaines 1990; Bowler & Benton 2005), or context-dependent dispersal associated with environmental variation (e.g. Schtickzelle et al. 2006; Bowler & Benton 2009). Here, we examine whether these patterns emerge in simulated populations where all same-sex individuals possess identical dispersal traits, within environments that are completely homogenous in space and time. As such, our models explore the dispersal patterns that emerge solely from intraspecific interactions, as governed by simple decision mechanisms. We show that these simple mechanisms can explain several commonly observed dispersal patterns in nature, suggesting that these mechanisms deserve greater consideration in studies of the causes and consequences of dispersal heterogeneity.

## **Methods and materials**

### *Model environment and demographic parameters*

We simulate population dynamics in a gridded cellular environment where all cells are identical, and each cell supports a single territory (625 in total). The environment is toroidal, such that individuals moving beyond the outermost cell in any direction will emerge at the opposite side of the environment (following Haefner et al. 1991). Time is modelled in discrete days and years, with 100 days in each year and 1,000 years in a simulation run. At the start of each run, the environment is populated with 1,000 unpaired individuals (i.e. just below carrying capacity) with equal sex ratio, placed at random starting locations. On each subsequent day, individuals make decisions concerning the suitability of their occupied cell, processing information via simple decision trees (see below & Fig. 1). At the end of each year, all living females that are successfully settled and paired to a living male produce a random number of offspring drawn from a bounded uniform distribution ( $\sim U(2,6)$ ), with offspring sexes allocated

by Bernoulli trials with probability 0.5. All offspring start the following year in their natal cell.

For simplicity, we set the maximum longevity of all individuals to be one year. Because dispersal is invariably costly (Bonte et al. 2012; Kubisch et al. 2014), we also set a reduced daily survival rate for dispersers relative to settled individuals. For each individual, daily survival is modelled with fixed probability  $S$ , where  $S$  is lower for individuals that are yet to settle ( $S=0.980$ ) than for those that have settled ( $S=0.998$ ).

To examine how dispersal varies with respect to population density, we also introduce crashes in population size at 50 year intervals during each model run. We do this by reducing  $S$  for all individuals on the first day of the year to a random value drawn from a uniform distribution ( $\sim U(0.05,0.5)$ ). Examining patterns of population growth following these crashes allows us to evaluate Allee effects. All other model parameters remain unchanged throughout each run.

### *Dispersal decision rules*

In all of our models, individuals move around the environment via a random walk with fixed speed. The random walk is an effective null model for animal dispersal measured at fine spatial scales (Hawkes 2009; Morales et al. 2010). At each time step, individuals either remain in their current cell ('settle') or move to a randomly selected adjacent cell. The decision to move or settle depends on the outcome of information processing via a decision tree (Fig. 1). Perceptual range is limited to the cell in which the individual is located, and movement speed limited to one cell-width per time step.

Each decision tree involves a hierarchy of criteria that are considered sequentially (Fig. 1). We compare three scenarios that differ in whether individuals assess the availability of mates prior to settlement (Fig. 1). In scenario 1 (Fig. 1A), settlement decisions are based solely on the availability of a competitor-free cell, with neither sex considering mate availability. In this case, the first criterion concerns whether settlement criteria have been met previously; if so, the individual will remain settled. The second criterion concerns whether the cell is already occupied by one or more competitors (i.e. other males for male individuals, other females for females). If their current cell is available (i.e. no competitors present), they will settle there.

In scenario 2 (Fig. 1B), females also consider whether or not their cell contains an available mate, alongside the criteria considered in Scenario 1. Thus, for females the first criterion is modified to include assessment of whether their existing mate remains alive and present in the cell in the current time step (Fig. 1B). The second criterion is also modified for females: settlement will only occur if there is an unpaired male present in the cell. The decision tree for males in this scenario is identical to that of Scenario 1 (Fig 1).

In the third scenario, both sexes consider mate availability as part of the decision tree framework (Fig. S1). Therefore, both males and females will only settle when there is no prior occupier of the same sex, and the cell contains an unpaired potential mate.

In all three scenarios, we assume that territory holders cannot be displaced by other individuals: once an individual has settled, that cell becomes unavailable for settlement by other same-sex individuals until the death of the cell holder (which will occur at or before the end of the year). Similarly, once an individual of either sex is paired, it will remain paired until the end of the year unless one member of the pair dies. Note that these behaviors themselves are

emergent properties of the decision tree framework, as the absence of a prior occupier is a basic criterion in all scenarios (Figs. 1 & S1).

The order in which individuals move is randomized each day. If two or more individuals of the same sex simultaneously move into the same unoccupied cell during the same day, the last individual to move in the subsequent day will have the opportunity to settle, if its other settlement criteria are fulfilled (Fig. 1). As dispersal evolution is strongly influenced by the costs of inbreeding, we included a mechanism of kin avoidance whereby individuals are unable to pair and reproduce with full siblings. In the scenarios with mate-dependent settlement (i.e. scenarios 2 and 3), therefore, only non-siblings are considered as potential mates in the settlement algorithm. Relaxing the assumption of kin avoidance brought little change to the results (see Figs. S2 & S3).

#### *Monitored parameters*

We calculated linear dispersal distances for each individual in each year, as a straight-line distance from the natal cell to the occupied cell at reproduction. We therefore define dispersal exclusively as movements that result in reproductive success (Ronce 2007). We record the following parameters at the end of each year of each run: 1) mean dispersal distance of each sex; 2) skewness and kurtosis of the distribution of dispersal events for each sex; 3) survival rate of each sex; 4) pairing success, measured as the proportion of surviving females that successfully settled with a living male at the end of the year; 5) adult sex ratio, calculated as the proportion of males in the population at the end of the year, prior to reproduction; 6) population density, calculated as the mean number of individuals (males + females) per cell at the start of the year; 7) annual population growth rate, calculated as the total annual number of births minus deaths, as



a proportion of the population size at the start of the year. All simulations were carried out in R Statistics version 3.0. 2 ([www.r-statistics.org](http://www.r-statistics.org)), using scripts provided in Appendix S1.

## Results

In all models, mean dispersal distances tended to increase as populations approached carrying capacity (Fig. 2). The population-wide distribution of dispersal distances also tended to become more fat-tailed at higher densities, showing greater positive skew (Fig. 2) and kurtosis (Fig. S4) for both sexes. This positive relationship between density and dispersal distance emerged universally because the availability of free cells (i.e. not containing a same-sex competitor) formed a core component of decision trees in all modelled scenarios (Fig. 1). Free cells become increasingly difficult to encounter at high densities, elevating mean dispersal distances for both sexes.

At lower population densities, dispersal distances were sensitive to whether mate availability was considered as a settlement criterion (Fig. 2). In scenario 2, where females evaluate mate availability, dispersal tended to become increasingly female-biased at low densities (Fig. 2C), as mean dispersal distances for males declined, along with skewness (Fig. 2D). In scenario 3, where both sexes evaluate mate presence, no sex bias in dispersal distance was observed (Fig. 2E & F). Whenever mate availability was considered within the decision tree, annual mean dispersal distances became increasingly stochastic at low densities (Fig. 2D, E & F), reflecting the effects of random variation in the spatial arrangement of individuals following periodic population crashes, and how this influences subsequent between-individual interactions.

Emergent population dynamics varied markedly between the three scenarios (Figs. 3 & 4), despite all three having identical survival and productivity parameters, and differing only in

settlement criteria (Fig. 1). In scenario 1, where both sexes settle solely according to competitor absence, annual population growth rates tended to fall below replacement levels at population densities below  $\sim 0.8$  individuals cell<sup>-1</sup>, indicating a strong Allee effect (Fig. 3A). This outcome emerged due to diminishing pairing success at lower densities (Fig. 4A), as individuals were more likely to settle and remain in free cells that did not contain a potential mate. Consequently, populations in this scenario showed high rates of extinction following induced population crashes (Fig. 3B).

This mate-finding Allee effect was largely relaxed when mate presence was included as a criterion for settlement (scenarios 2 & 3, Fig. 3C-F). Mate-dependent settlement allowed pairing success to remain relatively high at low population densities (Fig. 4B & C), such that annual population growth rates were typically positive even at densities of below  $\sim 0.25$  individuals cell<sup>-1</sup> (Fig. 3C & E). Rates of extinction following periodic population crashes were therefore far lower in scenario 2 (43.7% of populations extinct after 1,000 years) and scenario 3 (48.0% extinct after 1,000 years) than in scenario 1 (100% extinct after 1,000 years; Fig. 3).

Adult sex ratios became strongly male-biased at lower densities in scenario 2 (Fig. 4E). This emerged as a result of females dispersing longer distances on average than males, bringing associated costs to female survival as a result of performing longer movements (Fig. 4B). Despite this, population growth rates were highest on average at all densities in this scenario (Fig. 3C), as pairing success for surviving females was highest (Fig. 4B). Male biased adult sex ratios were largely eliminated when we relaxed the assumption that dispersal carries costs to survival (Fig. S5). In scenario 3, where both sexes evaluated mate presence as a settlement criterion, mean dispersal distances always remained relatively high at low densities (Fig. 2E & F), and therefore both sexes incurred similar survival costs, maintaining equal sex ratios (Fig.

4F). This came at a cost of reduced mean pairing success at lower densities relative to scenario 2 (Fig. 4C), explaining why population recovery tended to be somewhat slower following crashes in scenario 3 (Fig. 3F). In models where we relaxed the assumption that dispersal was costly, differences between scenarios 2 and 3 were largely eliminated (Fig. S6).

## Discussion

Our models show that the decision rules underpinning settlement can explain a high degree of between-individual variation in animal dispersal distances, as well as population dynamics. We show that several ubiquitous patterns observed among monogamous territorial species emerge in random walk models when simple settlement decision-rules are imposed. This occurs even in the absence of environmental heterogeneity or between-individual variation in dispersal phenotypes, indicating that neither of these conditions is necessarily prerequisite for significant within-population variability in dispersal (Bowler & Benton 2009; Stevens et al. 2010).

Female-biased dispersal distances and male-biased adult sex ratios are commonly seen amongst territorial monogamous species (Donald 2007; Kuussaari et al. 1998; Herzig 1995). Our simulations show that these biases emerge naturally when females, but not males, evaluate mate availability during settlement (scenario 2). Our model of this scenario produced higher rates of pairing success and population growth than an equivalent scenario where both sexes evaluate mate availability, particularly at lower densities. Mate assessment by females, but not males, is likely to be the most common pattern in nature among territorial species, given that males typically establish territories prior to acquiring a mate (Berec & Boukal 2004). We suggest that the widespread observation of male-biased adult sex ratios in wild species, particularly at low

densities (Donald 2007), could therefore be a simple outcome of dispersing females assessing mate availability prior to settlement. The emergence of male-biased adult sex ratios in our models depended on an assumption that dispersal is costly, and that costs increase with the time spent moving, such that survival rates are lower for long-distance dispersers than individuals that settle quickly. Evidence suggests that such costs are indeed commonplace in wild populations (Bonte et al. 2012).

Our models examine spatial population dynamics within a continuous, homogeneous environment. In nature, the environments occupied by wild species are rarely homogeneous, and populations typically utilize habitat resources that are patchy in space. Indeed, dispersal is often studied at the scale of inter-patch movements, rather than the finer-scale movements represented by our models (Wiens 2001; Urban 2005). It is possible that the mechanisms governing larger-scale movements, for example emigration between patches, may differ from those that govern fine-scale settlement choices. Nevertheless, the patterns revealed by our models could still be relevant for dispersal at larger scales. For example, the probability of inter-patch movement might increase if individuals are unable to fulfil their settlement criteria within the patch they occupy (Schtickzelle & Baguette 2003). Our models suggest that this is particularly likely to occur due to mate scarcity at low densities, and competition for space (or mates) at high densities.

Our finding that complex dispersal variation emerges from simple rule-based interactions has important implications for the study of dispersal in nature. Our models show that density-dependent dispersal can arise even when all individuals possess identical traits, and when the environment is completely homogeneous. Moreover, we show that several emergent dispersal patterns are highly sensitive to the hierarchy of rules used by individuals to make settlement

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decisions. Failure to consider this source of variation may lead to erroneous inferences when analysing real-world dispersal data. For example, a naïve analysis could falsely interpret interaction-driven dispersal variability as an outcome of habitat selection, or of between-individual differences in dispersal propensity. There is ample evidence that individuals do indeed differ in dispersal propensity, and that these differences can be linked to other traits (i.e. dispersal syndromes, Stevens et al. 2012). Nevertheless, our results suggest that care must be taken to separate the outcomes of between-individual differences from those driven by context-dependent dispersal decisions. The consistency of between-individual differences in dispersal, for example, could offer a robust line of evidence in favour of propensity variation, as such consistency does not emerge from our simple rule-based models. Direct comparison of observed patterns against predictions from mechanistic rule-based ‘null’ models could offer a fruitful avenue for testing hypotheses in real-world systems (Travis et al. 2012; Bocedi et al. 2014).

Evolutionary models of dispersal often assume that selection acts directly on the distance moved by individuals, or the probability of emigrating from a natal patch (e.g. Travis & Dytham 1999; Poethke & Hovestadt 2002; Poethke et al. 2011; Rodruiges & Johnston 2014). However, for active dispersers, dispersal is perhaps better viewed as an emergent consequence of underlying decision-making algorithms. These algorithms themselves are likely to be shaped by selection, in ways that we do not yet understand. Settlement is arguably the most poorly-understood element of the dispersal process, but it is critically important in determining how dispersal patterns vary in relation to environmental conditions and population density. By focussing on how selection might influence the components and structure of dispersal decision rules, future studies can generate greater insight into the mechanics of dispersal behaviour. In particular, useful insights likely stem from examining how selection might operate

simultaneously on settlement rules and other reproductive traits (e.g. sex ratio, number of offspring) and life history parameters (e.g. territoriality, age structure).

Our approach reveals how the simplest decision-making algorithms can generate complex dispersal patterns that closely mirror those observed in nature, without invoking effects of trait-variation or environmental heterogeneity (Nathan et al. 2008; Hawkes 2009). We anticipate that further advances will be made by examining the dispersal decision-making process in greater detail, from both empirical and theoretical perspectives. In particular, it may be useful to explore whether fine-scale decision mechanisms, and their population-scale dispersal consequences, can be adequately modelled using more compact analytical approaches (e.g. reaction-diffusion models, Lévy flights; Petrovskii *et al.* 2011) rather than computationally inefficient agent-based models. Doing so could help to integrate the fundamental dynamics of between-individual interactions into more tractable models that can be used to predict large-scale spatial dynamics in real-world settings (Kareiva & Odell 1987).

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### **Data Accessibility**

R scripts to generate all simulation data are provided in Appendix S1.

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The following Supporting Information is available for this article:

Appendix S1 –R script to run model

Figure S1 – Decision tree for scenario 3

Figure S2 – Dispersal distances for models without kin avoidance

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Figure S3 – Population time series for models without kin avoidance

Figure S4 – Kurtosis of dispersal distributions

Figure S5 – Pairing success and sex ratios in models without dispersal costs

Figure S6 – Population time series for models without dispersal costs

**Figure 1 Decision trees showing the settlement criteria used in basic models of dispersal in a homogeneous environment.** In scenario 1 (A), settlement for both sexes depends solely on the absence of a competitor (i.e. member of the same sex) in the current cell. In scenario 2 (B), females also consider whether the cell contains an available mate, whilst the male decision tree is the same as scenario 1. In a third scenario (not shown), both sexes consider mate presence prior to settlement (see Fig. S1).

**Figure 2. Variation in mean annual dispersal distances in relation to population density.** Points are colour-scaled according to the skewness of dispersal distributions. When settlement is based only on the availability of a competitor-free cell (scenario 1, top row), dispersal distances increase with population density for both females (A) and males (B). In scenario 2 (middle row), where females consider mate availability prior to settlement, but males do not, female dispersal distances tend to remain high at lower densities (C) whilst male dispersal distances decline (D). When both sexes consider mate availability (scenario 3, bottom row), the relationship between dispersal distance and population density is similar for both females (E) and males (F).

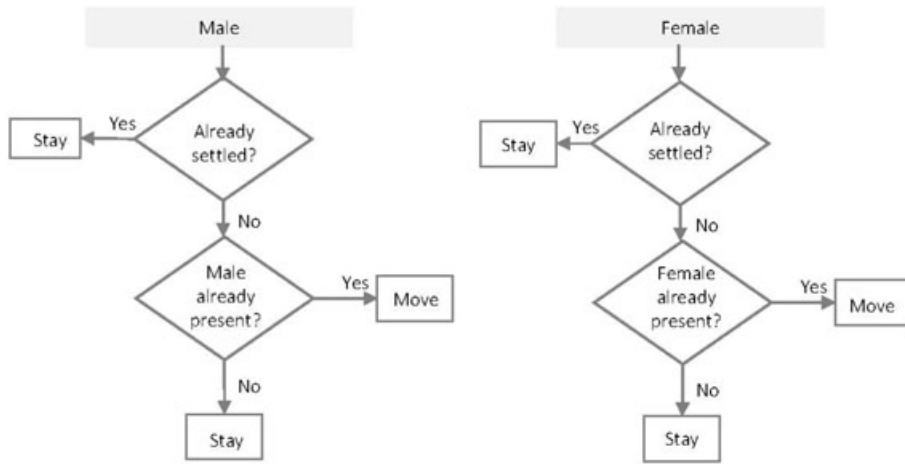
**Figure 3. Population growth rates (left hand panels) and population time-series (right hand panels, first 300 years shown) for models with differing settlement criteria.** When criteria for both sexes depend only on the availability of competitor-free cells (scenario 1), population growth rates tend to fall below replacement levels at lower population densities (A, lines show

best fit of third-order polynomials), resulting in high rates of extinction following induced population crashes (B). When females evaluate mate availability prior to settlement (scenario 2), population growth rates tend to remain positive at lower population densities (C), reducing extinction frequency (D). When both sexes evaluate mate presence (scenario 3), population growth rates tend to be slightly lower at all densities (E), with slightly more frequent extinctions (F). Population densities reflect the mean number of individuals per cell across the landscape at the start of each year. Results are shown for 250 simulation runs for each scenario.

**Figure 4. Variation in pairing success and adult sex ratios in relation to population density.**

In scenario 1 (settlement based solely on competitor absence), female pairing success (the proportion paired at end of year) tends to decline at low densities (A), whilst adult sex ratios become highly stochastic with a mean around parity (C, horizontal line shows 0.5 ratio). In scenario 2, where females consider mate availability but males do not, female pairing success remains relatively high even at low densities (B), although sex ratios become increasingly male-biased (C). When both sexes consider mate availability (scenario 3), female pairing success (C) tends to be lower than in scenario 2 (B), particularly at low densities, despite adult sex ratios remaining close to parity (D).

A. Scenario 1



B. Scenario 2

