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# Idea paper: Incorporating sexual differences in dispersal decision making into metapopulation theory

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**Abstract**

Dispersal is crucial for both individual fitness and spatiotemporal population dynamics. In sexual organisms, females and males have different reproductive strategies and therefore have different reproductive demands (i.e., reproductive resources and mating partners, respectively), which leads to differences in dispersal decision making between sexes. Although many studies have described sexual differences in dispersal behavior, little is known about the consequences for spatiotemporal population dynamics because metapopulation theory has considered only either nonrandom dispersal in asexual systems or random dispersal in sexual systems. To fill the knowledge gap, we propose a modeling framework that incorporates nonrandom and sex-specific dispersal into metapopulation theory. It allows us to ask how female-biased (e.g., in mammals) or male-biased (e.g., in birds) dispersal can influence persistence of sexual organisms.

**KEYWORDS**

mathematical and computational modeling, metapopulation, population, reproductive fitness, sexual difference

## 1 | RESEARCH QUESTION

Females and males have different reproductive demands (i.e., reproductive resources and mating partners, respectively), which causes sexual differences in dispersal decision making (Li & Kokko, 2019; Trochet, Courtois, Stevens, & Baguette, 2016). Here, we theoretically address under what conditions sex-specific dispersal decision making can increase (or decrease) persistence of a metapopulation.

## 2 | VALUE

The present metapopulation framework can better describe spatiotemporal population dynamics of sexual organisms, thereby contributing to the further development of metapopulation theory (see RELEVANT

HYPOTHESIS for details). Biologically, it is relevant to the question of how female-biased (e.g., in mammals) and male-biased (e.g., in birds) dispersal (Dobson, 1982; Greenwood, 1980) will differentially influence the spatial distributions of sexual organisms. Such theoretical insights would be useful for conservation and management.

## 3 | RELEVANT HYPOTHESIS

Existing metapopulation theory had considered only either nonrandom dispersal in asexual systems or random dispersal in sexual systems. Nonrandom is usually referred to as density-dependent (Sæther, Engen, & Lande, 1999) or fitness-dependent (Amarasekare, 2007; Armsworth & Roughgarden, 2005; Lin, Hsieh, & Miki, 2013). Density-dependent dispersal is defined such
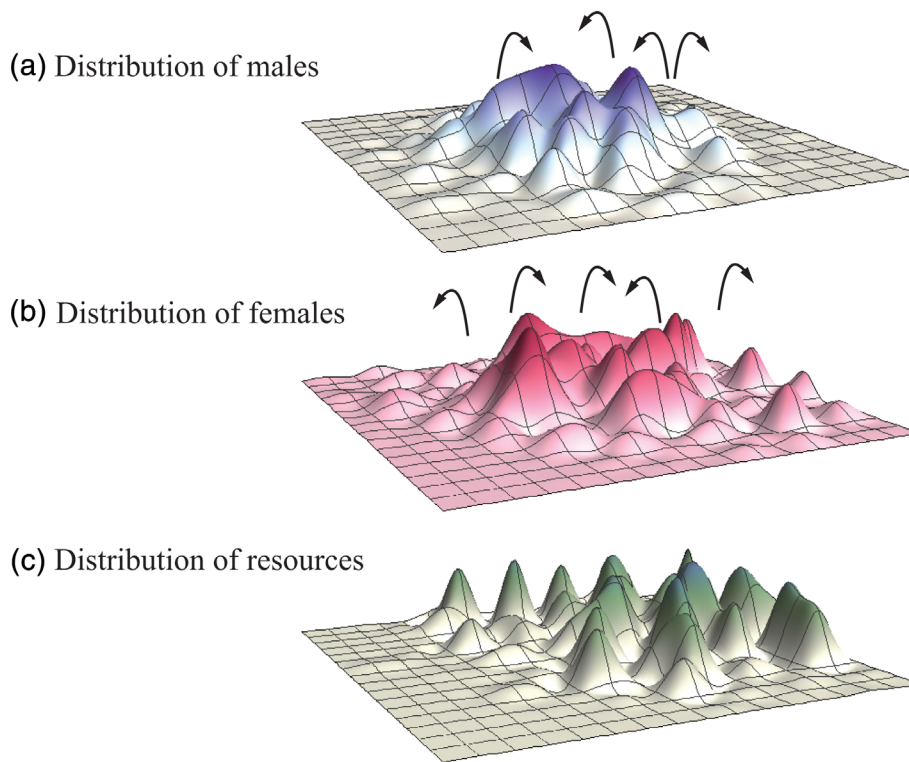
(a) Distribution of males

(b) Distribution of females

(c) Distribution of resources

**FIGURE 1** The conceptual illustration of the present metapopulation model. (a) Males disperse into patches where unmated females are more abundant. (b) Females disperse into patches where unoccupied reproductive resources are more abundant. (c) Reproductive resources of females are distributed heterogeneously in space [Color figure can be viewed at wileyonlinelibrary.com]

that how frequently organisms emigrate from a focal patch depends on the conspecific abundance. Meanwhile, fitness-dependent dispersal is defined such that organisms can assess habitat quality and move to a patch of better quality (higher fitness). For example, Armsworth and Roughgarden (2005) predicted that fitness-dependent dispersal will decrease extinction risk. However, such metapopulation models are asexual and cannot consider the complex (meta)population consequences of sexual structure (see below).

Another line of research has implemented sex-specific dispersal (Ranta, Kaitala, & Lindström, 1999), which highlights that sex plays an important role in local population dynamics. For example, Allee effect and skewed sex ratio will decrease population growth (Rankin & Kokko, 2007). Sexual differences (niche separation) can mitigate intraspecific (intersexual) competition and increase population growth, but too many males (e.g., due to decreased male-specific mortality) may intensify intersexual competition and decrease population growth (Rankin & Kokko, 2007). Further, population stability can dramatically change with the mating system (Boukal, Berec, & Křivan, 2008). Indeed, Ranta et al. (1999) predicted that metapopulation dynamics of polygamous species are more likely to fluctuate (go extinct locally) than those of monogamous species. However, such metapopulation models have assumed random dispersal for each sex and cannot consider nonrandom dispersal caused by reproductive demands.

Overall, it is still unclear and not straightforward how sex-specific nonrandom dispersal will influence persistence of a metapopulation. The nonrandom dispersal may increase persistence (see above). However, if the sexual difference is too large (e.g., females are more sensitive to reproductive demands than males and vice versa), it may cause a time lag (or a spatial mismatch) between female and male dispersal, which could skew local sex ratio and decrease persistence of a metapopulation. Furthermore, such effects may vary with the mating system (Ranta et al., 1999).

## 4 | NEW RESEARCH IDEA

We highlight the fact that females and males have distinct reproductive strategies and sex-specific standards for dispersal decision making. Greenwood (1980) addressed two hypotheses, resource defense hypothesis and mate defense hypothesis, to explain sexual differences in dispersal decision making. These hypotheses stress the importance of reproductive resources (e.g., breeding territory and food) for female dispersal and mating partners (females) for male dispersal, respectively (Figure 1). Both hypotheses have been supported by empirical evidence (Carval, Perrin, Duyck, & Tixier, 2015; Dobson, 1982). Our new idea is to incorporate those mechanisms into metapopulation theory.

## 5 | HOW TO SOLVE THE QUESTION THROUGH THE NEW IDEA

The Levins (1969) model is a classical metapopulation framework. However, it does not explicitly consider local population dynamics, sexual structure and nonrandom dispersal, though some assumptions can be relaxed (Hastings & Wolin, 1989). More recent models have numerically simulated an expanding sexual population in the context of biological invasion (Shaw, Kokko, & Neubert, 2018). However, such models have assumed that the sex-specific dispersal kernel depends on the absolute distance traveled; that is, dispersal is somewhat random without attractive forces of reproductive demands.

We propose that fitness-dependent and sex-specific dispersal can be integrated into metapopulation dynamic as follows:

$$\frac{dF_x}{dt} = rfP[F_x, M_x]Q[F_x]F_x - (m_{FF}F_x + m_{MF}M_x)F_x$$

$$- E_{F,x}[F_x]F_x + I_{F,x}[F_x] \tag{1a}$$

$$\frac{dM_x}{dt} = (1-r)fP[F_x, M_x]Q[F_x]F_x - (m_{FM}F_x$$
$$+ m_{MM}M_x)M_x - E_{M,x}[F_x, M_x]M_x + I_{M,x}[F_x, M_x] \tag{1b}$$

where $F_x$ and $M_x$ represent the number of females and males, respectively, in patch $x$ ($x = 1$ to $n$). For each sex, the first term describes the birth process, which includes the sex ratio at birth $r$, the per-female fecundity $f$, the fertilization probability $P[F_x, M_x]$, and the proportion of receptive females obtaining sufficient reproductive resources $Q[F_x]$. The fertilization probability $P[F_x, M_x]$ depends on female and male abundances and mating systems (e.g., monogamy and polygyny). We formulate $P[F_x, M_x] = \min(1, hM_x/F_x)$, where $h$ is the number of females one male can mate with (i.e., harem size; e.g., $h = 1$ for monogamy and $h > 1$ for polygyny; Bessa-Gomes, Legendre, & Clobert, 2004). Likewise, we formulate the proportion of receptive females $Q[F_x] = \min(1, b_x/F_x)$ where $b_x$ is the capacity of receptive females that is determined by the amount of reproductive resources at patch $x$. Note that the fertilization probability $P[F_x, M_x]$ can be lower than one (some females cannot mate with males) if males are scarce and/or the harem size $h$ is low, whereas the proportion of receptive females $Q[F_x]$ can be lower than one (some females cannot have sufficient reproductive resources) if the resource availability $b_x$ is low. Therefore, the functions $P[F_x, M_x]$ and $Q[F_x]$ determine sex-specific dispersal decision making (see below), following mate

defense hypothesis and resource defense hypothesis, respectively (Greenwood, 1980). The second term describes the death process, wherein $m_{ij}$ determines the density-dependent mortality rates due to intraspecific competition from sex $i$ to $j$. The third and last terms describe the emigration and immigration processes, respectively.

We modify a fitness-dependent dispersal kernel of previous asexual models in a sex-specific manner. Amarasekare (2007) formulated fitness-dependent emigration as $E_x = d\sum e^{sX}/(1 + e^{sX})$, where $d$ is the maximum emigration rate, $X$ is the difference in fitness (per-capita population growth rates) between patches and $s$ is a scaling parameter determining the sensitivity to fitness difference between patches. Because it is difficult to formulate the per-capita population growth of sex-structured systems, we consider that the availability of reproductive resources determines their reproductive success and dispersal decision. We then assume that females (or males) tend to emigrate from the local patch when the remains of reproductive resources (or females) decrease compared to other patches. As such, the sex-specific emigration rates are formulated as follows (see Amarasekare, 2007 for details):

$$E_{F,x}[F_x] = d_F \sum_{k \neq x}^{n} \frac{\exp[s_F(b_k - Q[F_k]F_k) - s_F(b_x - Q[F_x]F_x)]}{1 + \exp[s_F(b_k - Q[F_k]F_k) - s_F(b_x - Q[F_x]F_x)]} \tag{2a}$$

$$E_{M,x}[F_x, M_x] = d_M \sum_{k \neq x}^{n} \frac{\exp[s_M(F_k - P[F_k, M_k]F_k) - s_M(F_x - P[F_x, M_x]F_x)]}{1 + \exp[s_M(F_k - P[F_k, M_k]F_k) - s_M(F_x - P[F_x, M_x]F_x)]} \tag{2b}$$

The sex-specific immigration rates are derived as follows:

$$I_{F,x}[F_x] = d_F \sum_{k \neq x}^{n} \frac{\exp[s_F(b_x - Q[F_x]F_x) - s_F(b_k - Q[F_k]F_k)]}{1 + \exp[s_F(b_x - Q[F_x]F_x) - s_F(b_k - Q[F_k]F_k)]} F_k \tag{3a}$$

$$I_{M,x}[F_x, M_x] = d_M \sum_{k \neq x}^{n} \frac{\exp[s_M(F_x - P[F_x, M_x]F_x) - s_M(F_k - P[F_k, M_k]F_k)]}{1 + \exp[s_M(F_x - P[F_x, M_x]F_x) - s_M(F_k - P[F_k, M_k]F_k)]} M_k \tag{3b}$$

Future options for model modification are wide ranging. We assumed that individuals can access all the patches (global dispersal), but this assumption can be modified for the local dispersal scenario by adjusting the upper bound of summation $n$ to the number of adjacent patches. Various spatial configurations can also be considered (e.g., stepping stone and lattice models). The present dispersal kernels assume that dispersal occur in a much faster timescale than population dynamics

(Equations (2a), (2b), (3a) and (3b)). To relax the assumption, each sex may be separated into different phases (e.g., departure, transience, assessment, and settlement; Clobert, Le Galliard, Cote, Meylan, & Massot, 2009). Analytically, it is important to assess how regional abundance and its temporal variability will change with sex-specific dispersal parameters (the maximum emigration rate $d_i$ and the sensitivity to reproductive demands $s_i$ in Equations (2a), (2b), (3a) and (3b)). By manipulating them, one can examine how female-biased (e.g., in mammals) and male-biased (e.g., in birds) dispersal will differentially influence persistence of sexual organisms.

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## REFERENCES

Amarasekare, P. (2007). Spatial dynamics of communities with intraguild predation: The role of dispersal strategies. *The American Naturalist*, *170*, 819–831.

Armsworth, P. R., & Roughgarden, J. E. (2005). The impact of directed versus random movement on population dynamics and biodiversity patterns. *The American Naturalist*, *165*, 449–465.

Bessa-Gomes, C., Legendre, S., & Clobert, J. (2004). Allee effects, mating systems and the extinction risk in populations with two sexes. *Ecology Letters*, *7*, 802–812.

Boukal, D. S., Berec, L., Křivan, V. (2008) Does sex-selective predation stabilize or destabilize predation-prey dynamics? *PLoS One*, *3*, e2687.

Carval, D., Perrin, B., Duyck, P. F., & Tixier, P. (2015). Local and neighbor patch conditions alter sex-specific movement in banana weevils. *Ecology and Evolution*, *5*, 5735–5743.

Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S., & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, *12*, 197–209.

Dobson, F. S. (1982). Competition for mate and predominant juvenile male dispersal in mammals. *Animal Behaviour*, *30*, 1183–1192.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, *28*, 1140–1162.

Hastings, A., & Wolin, C. (1989). Within-patch dynamics in a metapopulation. *Ecology*, *70*, 1261–1266.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *American Entomologist*, *15*, 237–240.

Li, X.-Y., & Kokko, H. (2019). Sex-biased dispersal: A review of the theory. *Biological Reviews*, *94*, 721–736.

Lin, W. T., Hsieh, C. H., Miki, T. (2013) Difference inadaptive dispersal ability can promote species coexistence in fluctuating environments. *PLoS One*, *8*, e55218.

Rankin, D. J., & Kokko, H. (2007). Do males matter? The role of males in population dynamics. *Oikos*, *116*, 335–348.

Ranta, E., Kaitala, V., Lindström, J. (1999) Sex in space: Population dynamic consequences. Proceedings of the Royal Society of London. *Series B: Biological Sciences*, *266*, 1155-1160.

Sæther, B. E., Engen, S., & Lande, R. (1999). Finite metapopulation models with density-dependent migration and stochastic dynamics. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*, 113–118.

Shaw, A. K., Kokko, H., & Neubert, M. G. (2018). Sex difference and Allee effect shapes the dynamics of sex-structured invasions. *Journal of Animal Ecology*, *87*, 36–46.

Trochet, A., Courtois, E. A., Stevens, V. M., & Baguette, M. (2016). Evolution of sex-biased dispersal. *The Quarterly Review of Biology*, *91*, 297–320.