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Gender-Specific Emigration Decisions Sensitive to Local Male and Female Density

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Abstract: Increasing interest is directed on understanding how individuals utilize information to come to dispersal decisions. We assume individuals base emigration decisions on male and female density in their natal patches. We derive gender-specific functions for emigration probability of species with discrete generations and polygynous mating under the premise that dispersal strategies equalize fitness expectations of emigrants and philopatric individuals: migration decisions should then always depend on a critical threshold density of the own gender. Whether density of the opposite sex affects emigration depends on details of resource competition: (1) Without competition, females should never emigrate, while males should emigrate in response to local sex ratio. (2) Under extreme competition among females or offspring, females and males should respond to the local density of their own gender only. (3) If both sexes compete over resources, emigration responds to the density of both sexes, but the dependence differs quantitatively between females and males. (4) Male-biased dispersal is the general expectation for polygynous species, but the model allows specifying conditions under which more females than males might nonetheless emigrate. The model provides guidelines for implementing density-dependent dispersal in simulations and specifies principal patterns that should emerge in empirical data.

Keywords: conditional dispersal, sex-biased dispersal, decision rule, ideal free distribution.

Introduction

Dispersal is an ecological key factor with considerable influence on population dynamics, metapopulation persistence, or the formation of communities (e.g., Clobert et al. 2001; Bullock et al. 2002; Leibold et al. 2004; Lobel et al. 2009). Equally, dispersal decisions have a substantial influence on individual and inclusive fitness. Consequently, dispersal traits and behavior are life-history attributes underlying strong selective pressure. This is emphasized by, for example, the observation that dispersal traits evolve rapidly in response to changing landscape structure (e.g., Hill et al. 1999; Léotard et al. 2009).

Many theoretical models (especially older ones) of the evolution of dispersal (e.g., Comins et al. 1980; Hastings 1983; McPeek and Holt 1992; Gandon and Michalakis 1999) as well as of metapopulation dynamics (Levins 1970) assume “uninformed” (random) emigration. Yet there are good reasons for believing that “informed dispersal,” that is, dispersal decisions that take the actual status of a variable environment into account, would be superior to just random dispersal (Clobert et al. 2009; Enfjall and Leimar 2009; Hovestadt et al. 2010; also see Nathan et al. 2008; McNamara and Dall 2010). Factors that may affect local fitness expectations and, consequently, dispersal decisions include local population density or patch capacity (Travis et al. 1999; Poethke and Hovestadt 2002), habitat quality (e.g., Baguette et al. 2011), predation or parasitism (Poethke et al. 2010), and aspects of social status or of the individual’s own physiological condition (Bowler and Benton 2005). The impact of each of these factors on dispersal decisions should ultimately depend on their fitness relevance and thus a species’ life history. Evidence is accumulating that informed dispersal is widespread (e.g., Bowler and Benton 2005; Clobert et al. 2009).

An obvious question in the context of such informed dispersal is how exactly to utilize information about the environment (or even an individual’s own internal state) in decision making. What we, and for that matter natural selection too, need to figure out is (i) what information is of fitness relevance in principle and (ii) what are the appropriate response functions linking information about some environmental attribute to the behavioral response, for example, emigration.

Individuals rarely have full and accurate information about their environment (Dall et al. 2005; Klaassen et al. 2006). In the context of dispersal, it is likely that an individual may collect information about the state of the
patch of residence (natal or already dispersed to in a previous dispersal episode) but cannot collect comparable information about the status of other, distant patches. This seems to be the case, for example, in ladybeetles, where emigration from a patch is proportional to population density while immigration appears to be random (Krivan 2008). Consequently, an emigration decision should depend on the situation only in the residence patch. Only when travel between patches becomes cheap (in terms of energy and time invested, or risks taken) might an individual make exploratory excursions before deciding where to settle (Doligez et al. 2004; Ward 2005; Bach et al. 2007; Part et al. 2011; Cox and Kesler 2012). There is also evidence that individuals sometimes gather information about the status of other patches from immigrating individuals (e.g., Cote and Clobert 2007; Baguette et al. 2011).

A further complication is that individuals of a population are not identical and their fitness expectations may be affected differently by the state of the environs. Most noticeably, the two sexes differ, sometimes dramatically so, in their dispersal behavior (e.g., Greenwood 1980; Pusey 1987; Dobson 2013). Examples of both female- and male-biased dispersal have been reported. The former is prominent among birds (Greenwood 1980; Clarke et al. 1997; but corresponding evidence has recently been questioned: Mabry et al. 2013) or damselflies (Beirinckx et al. 2006), and the latter is typical among mammals (e.g., Handley and Perrin 2007) or reptiles (e.g., Keogh et al. 2007; Lee et al. 2007). The existence of gender-specific dispersal has often been linked to attributes of the mating, or social system (Perrin and Mazalov 2000; Handley and Perrin 2007), for example, the typically monogamous mating in birds (Greenwood 1983) and the typically polygamous mating system in mammals, the need to avoid inbreeding (Gandon 1999; Perrin and Mazalov 1999; Perrin and Mazalov 2000), and the timing of mating (Hirota 2005). Some have pointed out that fitness expectations may be more variable in space and time for one sex (typically males) than the other and that this would promote higher dispersal for that sex (Perrin and Mazalov 2000; Gros et al. 2009). However, even though these models consider gender-specific emigration, they assume noninformed (random) emigration decisions that are not based on information about the actual (and variable) status of the environment. Empirical evidence suggests, however, that factors mentioned above play a role in dispersal decisions of the two sexes (e.g., Richardson et al. 2010). Further, if the life histories of the two sexes are not similar and their fitness expectations are affected differently by environmental conditions (see Perrin and Mazalov 2000), information about the environmental state might affect their dispersal decisions in different ways.

Local resource competition should be a dominant driver of dispersal evolution (Perrin and Mazalov 2000), and utilization of information about population density (or other indicators of resource competition) in emigration decisions should thus be beneficial. As the strength and type of resource competition may vary greatly between species, however, we will analyze two extreme cases that span the spectrum of competitive situations, from no resource competition to extremely intense resource competition. Scenarios for intermediate competition will be analyzed in the appendix, available online. We will further separate between cases where only females or their offspring compete over critical resources, or where adults of both sexes are involved in such competition. Following the fundamental arguments outlined above, we will derive how in species with polygynous mating the emigration response should quantitatively be linked to information about local female or male density in either sex, under the assumption that individuals are capable of collecting such information about their natal patch but not about any other patch.

**Material and Methods**

**General Model Structure and Assumptions**

For the case of a continuous population growth, Metz and Gyllenberg (2001) derived the appropriate response to information about local population density in populations where all individuals follow the same emigration strategy independent of their gender. Based on similar reasoning, Poethke and Hovestadt (2002) provided a response function for the case of nonoverlapping generations and a brief and discrete dispersal phase. A recent approach by Geritz et al. (2009) integrates the impact of resource density (habitat quality) and population density on dispersal based on a more mechanistic approach. The reasoning followed by Metz and Gyllenberg (2001) and Poethke and Hovestadt (2002) resembles the argument underlying the concept of the “ideal free distribution” (IFD) of Fretwell and Lucas (1970; Krivan et al. 2008) and is based on the principle that dispersal is fundamentally driven by spatiotemporal stochasticity in fitness-relevant habitat attributes (see Gros et al. 2009; Meier et al. 2011; Nelson and Greeff 2011). Accordingly, behavioral decisions (rules) should ultimately evolve in such a way that fitness expectation for individuals exposed to the same conditions and sharing similar information should become similar whatever they decide to do. Both approaches assume that individuals have information only about local population density but not about conditions in other patches—an IFD thus cannot emerge globally (see Cressman and Krivan 2006). However, Poethke et al. (2007) verified that fitness expectations for
dispersing or philopatric individuals following this strategy and originating from the same natal patch would indeed become identical and that any patches producing emigrants will have similar (apart from stochastic variation) population densities after the dispersal phase.

We apply the same reasoning in deriving the principal structure of the appropriate response functions separately for each sex. We consider a metapopulation with a large (infinite) number of patches, each with independent population dynamics. Populations follow a certain growth dynamics, but population sizes (and sex ratios) may fluctuate due to demographic and environmental stochasticity—this separates our set of assumptions from other theoretical approaches where population size or habitat quality is deterministic and fixed (e.g., Perrin and Mazalov 2000; Leturque and Rousset 2003; Wild and Taylor 2004). Throughout we assume that females will always find a mating partner in a patch, that is, that populations never become so small that finding a mating partner would become difficult for a female. Patches are linked by dispersal before mating; for simplicity, we assume global dispersal. Emigrating individuals carry a certain mortality risk \( \mu \) independent of the patch of origin or the target patch; that is, they arrive in another patch only with probability \( 1 - \mu \) (in principle, \( \mu \) could also reflect other dispersal-related fitness costs; see Bonte et al. 2012). We will evaluate implications and limitations of these assumptions in “Discussion.”

We consider only polygynous mating; that is, females mate only in the patch of residence (after possible dispersal), while males can mate repeatedly. We do not consider effects of inbreeding depression in our model but return to this topic in “Discussion.” We further assume nonoverlapping generations and that dispersal occurs in a (brief) discrete phase where, based on information collected earlier, all individuals have to decide at (about) the same moment whether to emigrate or not; this may be the case in insects where the adult season and life span is short or in species where migration occurs only at a specific time in the year. If emigration decisions were taken by just one individual at a time, the approach should follow that of Metz and Gyllenberg (2001). There is no social- or physiologically based population structure; that is, individuals of the same gender are identical and no individual can dominate others; dominance could promote dispersal of the subdominant sex, as seems to be the case with female great tits (Michler et al. 2011) or with subdominant individuals within a sex as is possibly the case in male Glanville fritillary butterflies (Nitepold et al. 2011). Thus, in all scenarios considered, individuals of the same sex compete on identical terms (“lottery competition”).

Competition over resources may be a key driver of dispersal (e.g., Janosi and Scheuring 1997; Travis et al. 1999; Perrin and Mazalov 2000; Geritz et al. 2009). Consequently, we will contrast the effect of two types of population growth spanning the possible spectrum of resource-based population regulation in the main text. The first is geometric growth with no local resource competition. The second is severe resource competition with an inverse relation between the number of females (or adults) in a population and the number of surviving offspring per female. These two scenarios correspond to those considered by Perrin and Mazalov (2000). These two model versions are certainly unrealistic, but they simplify analysis, make the flow of arguments more transparent, and cover the extremes of the possible spectrum in competition intensity. However, the two scenarios are just limiting cases of the more general Beverton-Holt logistic competition model that we develop in the appendix.

**Geometric Growth—No Resource Competition**

In the case of geometric population growth, the increase in female population size \( F \) (see table 1 for list of symbols and sub- and superscripts used) from generation \( t \) to the next \((t + 1)\) is defined by

\[
F_{t+1} = R_0 \times F_t.
\]  

(1)

In this scenario, resource competition does not occur and population size obviously has no effect on the fitness expectation of a female: a mated female can expect \( R_0 \) daughters (and obviously the same number of sons), whatever the population density in the patch. Thus, the expected fitness for a philopatric female is

\[
f_{R_0}^p = R_0,
\]  

(2a)

while that of a dispersing female (as long as all patches are identical; see “Discussion”) is

\[
f_{R_0}^D = R_0(1 - \mu),
\]  

(2b)

with \( \mu \) the dispersal mortality (or other fitness-reducing dispersal costs). Throughout the text we use the superscript to indicate the fitness expectations specific to the dispersal decision \((P = \text{philopatric}, D = \text{dispersing})\), the first subscript to indicated the gender of individual under question \((F = \text{female}, M = \text{male})\), and the second subscript to indicate the type of resource competition model (here \( G \) for “geometric growth”).

Obviously, the fitness expectation for dispersing females is always smaller than that of philopatric females except when the costs of dispersal are null. As individuals do not compete, kin does not compete either, and avoidance of kin competition, which generally can be a strong driver of dispersal evolution (Hamilton and May 1977; Taylor 1988; Poethke et al. 2007), should not be a factor promoting emigration. Consequently, according to this sce-
nario, emigration can never be a worthwhile option for a female (fig. 1a)—clearly a trivial conclusion (but see “Discussion”). We feel that outlining this simple scenario here is useful, however, as a reference case for what will follow.

For a male, any mating with a female will contribute $R_0$ offspring to its fitness. For a nondispersing male, the expected mating success is defined by the postdispersal sex ratio in its natal patch; remember that we assume mating after dispersal. As females will not disperse, the latter is exclusively determined by the predispersal number of females ($F$) and males ($M$), which are both known to the male, the male emigration probability ($p_{M,G}$), and the number of male immigrants ($I_M$). Term $I_M$ cannot be predicted accurately; it is just a long-term average expectation and thus a constant in the equation.

$$f_{M,G}^p = R_0 \times \frac{F}{M(1 - p_{M,G}) + I_M}. \quad (3a)$$

Without exploration an emigrating male cannot, however, foresee in which specific condition it will end up. The expected benefit of emigrants is thus a constant independent of the patch of origin and depends on the expected (average) postdispersal sex ratio in prospective target patches, $R_0$, and dispersal mortality:

$$f_{M,G}^p = R_0 \left( \frac{F}{M} \right) (1 - \mu). \quad (3b)$$

To equalize fitness expectations of emigrants and philopatric individuals, the appropriate response function must consequently regulate local postdispersal population size to a specific and, in all patches (with emigration), identical size independent of the predispersal population density—otherwise local fitness equalization between philopatric and dispersing individuals would not be possible (see Metz and Gyllenberg 2001; Poethke and Hovestadt 2002).

Postdispersal mate competition obviously decreases with the number of emigrating males. According to the principles outlined above, males should thus emigrate in just such proportions (i.e., with probability $p_{M,G}$) that fitness expectations of emigrating and philopatric males become identical:

$$R_0 \times \frac{F}{M(1 - p_{M,G}) + I_M} = R_0 \left( \frac{F}{M} \right) (1 - \mu). \quad (4)$$

Solving for $p_{M,G}$ and excluding negative emigration probabilities yields

$$p_{M,G} = \max \left[ 0, 1 - \frac{T_{M,G}}{M} \right], \quad (5)$$

with the critical threshold density for male emigration

$$T_{M,G} = \frac{F}{\langle F/M \rangle (1 - \mu) - I_M}.$$

We want once more to stress that according to our model assumptions, a male cannot foresee (it has no information about) the population density in the patch it would possibly migrate to, the specific mortality risk it takes when emigrating, or the specific number of males immigrating ($I_M$) into its natal patch. We assume that it is able to gather only patch-specific information about the magnitude of $F$ and $M$ in its natal patch, while $I_M$ and $\langle F/M \rangle (1 - \mu)$ are

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### Table 1: List of symbols and indices used throughout text

<table>
<thead>
<tr>
<th>Symbols</th>
<th>Definition</th>
</tr>
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<tbody>
<tr>
<td>$K$</td>
<td>Patch carrying capacity</td>
</tr>
<tr>
<td>$F, M$</td>
<td>Female and male population size, respectively</td>
</tr>
<tr>
<td>$R_0$</td>
<td>Net reproductive rate counting only daughters</td>
</tr>
<tr>
<td>$f$</td>
<td>Fitness expectation (no. female offspring)</td>
</tr>
<tr>
<td>$\mu$</td>
<td>Dispersal (mortality) cost</td>
</tr>
<tr>
<td>$p$</td>
<td>Emigration probability</td>
</tr>
<tr>
<td>$\langle \rangle$</td>
<td>Expected (mean) value of attribute in other habitat patches; relevant for fitness expectation of successful emigrant</td>
</tr>
<tr>
<td>$I_F, I_M$</td>
<td>Expected number of female and male immigrants, respectively</td>
</tr>
<tr>
<td>$T$</td>
<td>Emigration density threshold</td>
</tr>
<tr>
<td>$a$</td>
<td>Competition term of Beverton-Holt model (see eq. [A1])</td>
</tr>
<tr>
<td>Subscript $F, M$</td>
<td>Indicating solutions from female and male perspectives, respectively</td>
</tr>
<tr>
<td>Superscript $P, D$</td>
<td>Indicating perspective of philopatric and dispersing individuals, respectively</td>
</tr>
</tbody>
</table>
constants reflecting long-term averages. “Guesses” or “estimators” of these constants could be coded into the genome or possibly be transferred by other modes of “inheritance,” for example, culturally; natural selection will single out the bearers of the most accurate estimators. It is also important to recognize that the terms $I_M$ and $(F/M)$ will themselves depend on the resident dispersal strategy in the metapopulation; that is, a recursive relationship exists between the magnitude of these terms and the dispersal threshold $T_{MLG}$ (cf. Leturque and Rousset 2003; Poethke et al. 2003). This is especially true because dispersal affects the between-population variance in $F/M$ and the expected number of immigrants $I_M$. This is the reason we cannot provide direct solutions for the evolving threshold value. For our principal message, this is also not necessary, but we return to this issue in “Discussion.”

Equation (5) is structurally equivalent to the asymptotic threshold equation already derived in Poethke and Hovestadt (2002) and analogue to the simple threshold solution derived for the case of continuous population growth with overlapping generations (Metz and Gyllenberg 2001). However, other than in the original model, the threshold for male dispersal ($T_{MLG}$) is not just a constant but a linear function of local female number. Thus, no emigration will occur as long as male density and the local sex ratio are favorable enough. Indeed, it is obvious that emigration probability of males should be sensitive to local mate competition, that is, the local sex ratio $F/M$ (Leturque and Rousset 2004; Hirota 2007; Nelson and Greeff 2011). Less obviously, males should also relate their emigration decision to the absolute number of resident males and the ratio of the expected number of male immigrants $I_M$ to the number of resident males $M$ (fig. 1b). This is, however, not difficult to understand as the postdispersal sex ratio (and thus the postdispersal competition among males for mating opportunities) is proportionally more strongly affected by immigration of males when the number of males in the natal patch is small, for example, because the habitat patch is small. Inversely, large populations promote philopatry, as male immigration would have a comparable smaller effect on the resident males’ reproductive chances; an inverse relationship between patch size and the thresh-

**Figure 1:** Schematic illustration of the expected relationship between local female and male population size and emigration probability (disp. prob.). Top row shows the females’ response, the bottom row the corresponding males’ response. a, d, Geometric growth scenario. b, e, Intense resource competition among females or offspring only. c, f, Intense resource competition among adults. In generating these schematic figures we have assumed a dispersal survival $(1 - \mu) = 0.9$, a patch capacity $K = 100$, and female and male ($I_F$, $I_M$) immigration of 5 individuals each.
Severe Resource Competition among Females or Offspring

In an inclusive-fitness model for the evolution of dispersal, Taylor (1988; also Bulmer 1994) proposed a rather simple approach to model severe intraspecific competition. Modeling population growth in discrete time steps, he assumed that, independent of current population size, populations were expected to always produce $N = K$ (surviving) offspring; the latter may vary due to stochastic effects, however. This assumption, which is relaxed in the logistic model of the appendix, is clearly unrealistic if taken to its extreme. However, it may approximately be valid for populations that are characterized by high fertility (as many insects) and that fluctuate not too widely in population size. Given the assumption the fitness expectation of a female in a patch with carrying capacity $K$ (only relating to females) would be $K/F$. However, taking emigration and immigration into account the fitness expectation of a philopatric female is given by

$$f_{p,c} = \frac{K}{F(1-p_{e,c}) + l_p}, \quad (6a)$$

with $l_p$ the expected number of female immigrants and $p_{e,c}$ the emigration probability of females. The fitness expectation of a dispersing female will depend on the dispersal mortality ($\mu$) and on the mean fitness expectation in prospective target patches $K/F$. Thus, a dispersing female can expect fitness

$$f_{e,c}^D = \frac{K}{F} \left\{ \frac{1}{F(1-p_{e,c}) + l_p} \right\} = K \left\{ \frac{1}{F} \right\} (1-\mu). \quad (6b)$$

Note that, with the introduction of resource competition, avoidance of kin competition becomes relevant (Hamilton and May 1977; Taylor 1988; Gandon 1999; Poethke et al. 2007); for the sake of simplicity, we will ignore this here (justified if populations are large and dispersal occurs frequently enough) but return to the issue in “Discussion.” Obviously, females should disperse only if the expected fitness of a dispersing female (eq. [6b]) surpasses that of a philopatric one (eq. [6a]). If so, they should again emigrate in such proportion that the expected fitness of dispersing and philopatric females becomes identical. Assuming constant $K$ across patches (not a fundamentally necessary assumption) the critical condition is

$$\frac{K}{F(1-p_{e,c}) + l_p} = K \left\{ \frac{1}{F} \right\} (1-\mu). \quad (7)$$

Solving equation (7) for $p_{e,c}$ gives

$$p_{e,c} = \max \left\{ 0, 1 - \frac{T_{e,c}}{F} \right\}, \quad (8)$$

$$\text{with } T_{e,c} = \frac{1}{(1/F)(1-\mu)} - l_p.$$

A female’s decision to emigrate should thus only depend on information about female density in the natal patch; $T_{e,c}$ itself contains only constants that reflect average fitness expectations of dispersing females and of local immigration. Thus, $T_{e,c}$ should evolve as an accurate summary “estimator” of these constants. Accordingly, females should emigrate with larger probability as female abundance $F$ becomes larger (fig. 1c). The magnitude of the evolving $T_{e,c}$ depends on (i) the dispersal costs $\mu$, (ii) the expected number of immigrating females $l_p$, and (iii) the inverse of the harmonic mean $(1/F)$ of female abundance across the landscape. Note that the harmonic mean is especially sensitive to the smallest values of $F$ occurring and thus tends to be small if populations fluctuate widely around $K$. The emigration threshold is consequently reduced (emigration is favored) where population density is variable introducing considerable spatiotemporal variation in fitness expectations—a conclusion in agreement with previous findings (Poethke et al. 2003).

To estimate males’ fitness expectation, we need to multiply the expected fitness per mating with the expected number of matings. For philopatric males, this is

$$f_{m,c}^p = \frac{K}{F} \times \frac{\tilde{F}}{M(1-p_{e,c}) + l_p} = \frac{K}{M(1-p_{e,c}) + l_p}, \quad (9a)$$

with $\tilde{F} = F(1-p_{e,c}) + l_p$ the postemigration female density. For dispersing males, the fitness expectation is
to with for females and for males

\[ f_{\text{M,C}} = \left( \frac{K}{F} \times \frac{F}{M} \right) (1 - \mu) \]

\[ = K \left( \frac{1}{M} \right) (1 - \mu). \quad (9b) \]

By equating and solving for \( p_{\text{M,C}} \) we get a solution exactly corresponding with that for females

\[ p_{\text{M,C}} = \max \left[ 0, 1 - \frac{T_{\text{M,C}}}{M} \right] \]

\[ \text{with } T_{\text{M,C}} = \frac{1}{(1/M) (1 - \mu) - I_M}. \quad (10) \]

Thus, males should respond in their dispersal decision to the males’ population size but not to female number (fig. 1d). This conclusion is surprising only in the first moment. With the specific density regulation assumed here, a population is always expected to produce \( K \) offspring, whatever the number of females in the patch. As each offspring has a mother and a father, the two sexes simply compete independently over “motherhood” and “fatherhood.” As already noted by Perrin and Mazalov (2000), a sex bias in dispersal is as such not expected in this specific scenario.

Severe Resource Competition among Adults

In deriving equations (6) and (9), we implicitly assumed that the competition for resources occurs only among females or only among their offspring. This may be the case if, for example, females specifically need to build fat reserves for offspring reproduction or care. Alternatively, in many insects, resource competition mostly emerges in the larval phases, for example, when feeding on a specific host plant. In this case, only the number of egg-laying females defines the intensity of (future) competition. Nonetheless, in other species competition for resources may involve all adults, that is, the number of surviving offspring a female expects to produce depends on adult female and male density combined. To account for this, we can modify and again equate the set of fitness defining expressions (6) and (9) to

\[ f_{\text{F,CA}} = \frac{K}{F(1 - p_{\text{F,CA}}) + I_F + M} \]

\[ = K \left( \frac{1}{F + M} \right) (1 - \mu) \]

\[ = f_{\text{F,CA}}^0, \quad (11) \]

with \( \tilde{M} = M(1 - p_{\text{M,CA}}) + I_M \) for females and for males to

\[ f_{\text{M,CA}}^p = \frac{K}{\tilde{F} + M(1 - p_{\text{M,CA}}) + I_M} \]

\[ \times \frac{\tilde{F}}{M(1 - p_{\text{M,CA}}) + I_M} \]

\[ = K \left( \frac{1}{F + M} \times \frac{F}{M} \right) (1 - \mu) \quad (12) \]

with \( \tilde{F} = F(1 - p_{\text{F,CA}}) + I_F \).

Note that in this scenario from a female’s perspective, males are—like other females—resource competitors; the presence of any male thus reduces expected number of offspring to the same degree as the presence of other females (a more gradual weighting of male vs. female resource competition could easily be included). For a male, however, other males compete in two ways—first, as before, for access to females. But second, the presence of other males also “devalues” any mating a male achieves because other males’ resource competition reduces the number of surviving offspring produced by any female the focal male mates with. Equation (12) thus includes a quadratic term in \( M \).

Equations (11) and (12) can be solved for \( p_{\text{F,CA}} \) and \( p_{\text{M,CA}} \), that is,

\[ p_{\text{F,CA}} = \max \left[ 0, 1 - \frac{T_{\text{F,CA}}}{F} \right] \]

\[ \text{with } T_{\text{F,CA}} = \frac{1}{E_{\text{F,CA}}(1 - \mu) - I_F - \tilde{M}}, \]

\[ E_{\text{F,CA}} = \left( \frac{1}{F + M} \right). \quad (13) \]

The corresponding solution for males is

\[ p_{\text{M,CA}} = \max \left[ 0, 1 - \frac{T_{\text{M,CA}}}{M} \right] \]

\[ \text{with } T_{\text{M,CA}} = \frac{1}{2} \left[ \sqrt{\frac{4 \times \tilde{F}}{E_{\text{M,CA}}(1 - \mu) + \tilde{F}^2} - \tilde{F}^2} - \tilde{M} \right], \]

\[ E_{\text{M,CA}} = \left( \frac{1}{F + M} \times \frac{F}{M} \right). \quad (14) \]

Other than in the previous scenario emigration should—for both sexes—become a function of the density of the opposite sex (fig. 1e, 1f). However, this dependency vanishes at the moment where the density of the other sex becomes larger than that sex’s own emigration threshold. This is because the function specifying the emigration
probability $p$ has—as soon as density surpasses the critical threshold—the property of always reducing postmigration density to this threshold (see Poethke and Hovestadt 2002). The product $F(1 - p_{\text{E,CA}})$ is thus always either $F$ (if $F \leq T_{\text{E,CA}}$, and $p_{\text{E,CA}} = 0$) or $T_{\text{E,CA}}$ (if $F > T_{\text{E,CA}}$). Correspondingly, the same applies to males, that is, $M(1 - p_{\text{M,CA}})$ takes either the value $M$ or $T_{\text{M,CA}}$. Consequently, if both sexes’ densities are above their corresponding threshold density the two equations collapse into

$$T_{\text{E,CA}} = \frac{1}{(E_{\text{E,CA}} + E_{\text{M,CA}})(1 - \mu)} \times \frac{E_{\text{M,CA}}}{E_{\text{E,CA}}} - l_{M},$$

$$T_{\text{M,CA}} = \frac{1}{(E_{\text{E,CA}} + E_{\text{M,CA}})(1 - \mu)} - l_{M}. \quad (15)$$

For both sexes the dependency of the emigration threshold on the density of the opposite gender thus disappears as soon as the other sex itself emigrates (or is expected to do so). The inherently larger variance due to the added dependency in the sex ratio $F/M$ will make $E_{\text{M,CA}}$ typically larger than $E_{\text{E,CA}}$ (especially in small populations) and consequently $T_{\text{E,CA}}$ will typically be larger than $T_{\text{M,CA}}$. This again indicates a general tendency toward male-biased emigration; note that more male emigration would in turn tend to increase the value of $l_{M}$ (expected male immigrants) compared to $l_{E}$.

In the appendix we present further derivations for populations that follow a more gradual logistic growth. The set of fitness-defining equations becomes slightly more complex but remains structurally identical to those derived in the main text; the solutions presented here emerge as limiting cases where resource competition either approaches zero (geometric growth) or becomes extremely intense (offspring number fixed at $K$).

**Discussion**

To our knowledge, this is the first derivation making predictions concerning the gender-specific utilization of information about local conditions in emigration decisions. This is an issue not touched by the many different analytical approaches dealing with sex-specific dispersal (e.g., Perrin and Mazalov 2000; Leturque and Rousset 2003, 2004; Wild and Taylor 2004; Wild et al. 2006) as such models typically assume constant habitat conditions. In the context of understanding gender-specific “informed dispersal,” our approach copes with two issues: (i) identifying the attributes that are of fitness relevance from the perspective of a specific category of individuals, thus identifying which kind of information about the environment should affect emigration decisions, and (ii) how to exactly utilize and respond to such information. According to our model, dispersal decision should result in balancing fitness expectations of philopatric individuals and emigrants in any specific patch (but not necessarily globally)—an approach of very general applicability (see, e.g., Krivan et al. 2008). Accordingly, and if general model assumptions are met, an individual’s emigration probability should always be determined by a response function of the type $p = 1 - G/H$, with $G$ the local density of its own gender (i.e., either $F$ or $M$), and a certain threshold density $T$. This affirms previous findings (Poethke and Hovestadt 2002; Hovestadt et al. 2010): there should be no emigration from a patch as long as the number of individuals of the own sex is below the critical threshold $T$. This analysis, however, specifies that local population sizes (or densities) of the two sexes should affect dispersal decisions of the two sexes in different ways (see table 2 for summary), depending on the intensity of local resource competition (LRC) and whether LRC is among only females (or their offspring) or among all adults. For example we would predict—for a system where resource competition occurs between offspring but density regulation is intermediate—that females should emigrate in response to female density only while males should consider male and female density (see appendix). This seems to be true in the case of short-distance dispersal of the spider *Erigone atra*, where female emigration is affected by female density only while males respond to the density of both sexes (De Meester and Bonte 2010).

In our argument we ignore the potential roles of kin competition and inbreeding depression on the evolution of dispersal. Both are factors known to promote dispersal (e.g., Hamilton and May 1977; Gandon 1999; Costello et al. 2008). More importantly, it has been shown that the existence of inbreeding depression would generally favor the evolution of sex-biased dispersal (Gandon 1999; Perrin and Mazalov 1999). However, these models are mute regarding predicting which of the two sexes should become the more dispersive one, and they do not provide (quantitative) predictions concerning the response to variable population density of either sex as they consider only deterministic scenarios without population variability.

Neither kin competition nor the risk of inbreeding principally undermine the argument presented here. Kin competition basically has the effect of devaluing the fitness expectation of philopatric individuals and thus promoting earlier emigration (reducing the critical threshold density), but this does not affect the principal logic of the argument applied, that is, that there should be a critical threshold density below which emigration is not a sensible option. Further, an important role of kin competition (and inbreeding avoidance) in dispersal evolution would typically be limited to small, stable, and poorly connected populations (Gandon 1999), that is, conditions that principally select for low dispersal. It is questionable whether inbreeding avoidance would indeed be a sufficient force to induce
a (significant) sex bias in dispersal under more realistic scenarios (Guillaumet and Perrin 2006). If habitat conditions are variable and population dynamics underlie noticeable stochastic effects, a typical situation in many insect species (e.g., Dempster et al. 1995; Thomas et al. 2002, 2011; Hochkirch and Damerau 2009), evolution of dispersal will be dominated by such environmental attributes (Poethke et al. 2007). The general trend toward male bias predicted by our approach is traceable to the fact that between-patch variability in fitness expectations should typically be larger for males than for females. Clearly, however, the different lines of reasoning are not exclusive and habitat variability, kin competition, and inbreeding will simultaneously affect the evolution of dispersal (e.g., Gandon and Michalakis 2001; Poethke et al. 2007).

In our model, we made the assumption of global dispersal. This is quite typical for this kind of model, but clearly the assumption must be unrealistic in many cases. In a previous article (Poethke et al. 2011), we evaluated the effect of nearest-neighbor dispersal on emigration without accounting for gender-specific dispersal. Neighborhood dispersal has the unavoidable effect of introducing spatial correlation of postdispersal density due to the flow of migrants between neighboring patches. Neighbor- ing patches will thus be more similar in postdispersal pop- ulation density, and this makes dispersal generally a less attractive opportunity as the chance of increasing fitness by dispersing away from a high-density patch is reduced (target patches are likely to be high-density patches too). At the same time, we could show that this very effect selects for an increase in dispersal distance. In the framework of our equation system, short-distance dispersal would have the consequence that the right term of the fitness equality equations (fitness expectations of migrants) becomes more similar to that of philopatric individuals, thus selecting for higher threshold values (and lower dispersal) compared to a version with global dispersal.

The primary purpose of this article was not to generate statements on sex bias in dispersal (see Handley and Perrin 2007 for a review) but rather on how females and males should quantitatively respond to information about their environment when taking dispersal decisions. Nonetheless, acknowledging the different perspectives of females and males naturally leads to predictions concerning sex-biased dispersal that generally reiterate previous findings. The difference in perspectives becomes most evident in the case of geometric growth: without resource competition there is no reason for females to disperse at all, as fitness expectations are identical everywhere (but see further discussion below); consequently, strongly male-biased dispersal is expected. Quantitatively, the magnitude of the male bias should depend on the relative strength of mate versus resource competition and becomes smaller as local resource competition becomes more intense (see explanations in appendix). Note in this context that LRC among females has an (indirect) effect on the males’ fitness expectation too, as it devalues the value of any mating production, this leads to the prediction of on-average symmetric emigration because from the males’ perspective, the added benefit of a mating opportunity provided by an extra female is completely canceled out by this female’s...
effect on future offspring survival. Following a different argument, this has already been shown for uninformed dispersal by Perrin and Mazalov (2000).

It is not trivial to find empirical evidence supporting or contradicting our model. First, the effect of population density may readily be confounded by the effect of habitat quality in empirical (field) studies. More importantly, to recognize the relationship between emigration and population density predicted here, empirical studies would need to measure emigration over a wide spectrum of different densities and distinguish between the density of males and females; to our knowledge, this has rarely been done. However, there is some suggestive evidence. An experimental study in at least qualitative agreement with our predictions is that on the emigration of voles carried out by Aars and Ims (2000). Females, which typically compete over resources, emigrated only under high-density regimes. In the experimental setup, males from the founding (lab) generation always emigrated in very high proportion regardless of founding density, but in the following (field) generations, they emigrated preferentially from low-density patches where the sex ratio was male biased.

It is important to recognize that under informed emigration, local conditions may at times be such that a generally expected male bias in emigration may be reversed. For example, in Spanish deer populations with high F/M ratios, female-biased emigration has been reported, while male-biased dispersal is the general rule in this species (Perez-Gonzalez and Carranza 2009). This observation is in good agreement with our predictions as high female densities should favor male philopatry on the one hand and promote female emigration on the other, especially if females compete over resources.

The model presented here is strictly limited to just one possible mating system, polygyny. The fundamental asymmetry between males and females emerging in all scenarios (except in the scenario with constant offspring production and competition between offspring only) obviously does not exist in the case of monogamy due to the inherent symmetry in the two parents' role that also often included shared upbringing of their offspring; symmetric dispersal is expected in this case (e.g., Perrin and Mazalov 2000). Emergence of sex-biased dispersal may then be affected by other aspects, for example, the value of maintaining a familiar territory—believed to promote male philopatry in birds, for instance (Gienapp and Merila 2011) or bats (Nagy et al. 2007)—or the rules underlying social interaction, group formation, or (kin) cooperation (overview in, e.g., Handley and Perrin 2007). For passerine birds it has also been proposed that females compete more strongly over suitable territories (i.e., those holding a male) than males do, promoting female-biased dispersal (Avril et al. 2011). On the other hand, harem systems may lead to an even larger discrepancy in spatiotemporal variability in fitness expectations between males and females, thus intensifying the tendency toward male-biased dispersal (Gros et al. 2009).

We also do not consider the potential role of other kinds of interactions between individuals not directly related to (resource) competition. For example, emigration of female butterflies seems to be promoted by male harassment in several species (Odendaal et al. 1989; Baguette et al. 1998), presumably because interactions with males are costly for females already mated. Such an effect could, however, readily be accounted for in our model.

The conclusion drawn from our model should be taken with care, especially with respect to the geometric growth scenario. The model ignores some biological aspects that presumably also influence the evolution of emigration. First, equation (2b) implies that \( R_s \) is homogeneous in space, that is, that all habitat patches are of the same quality. If this were not the case, a female obviously should emigrate as soon as \( R_s > \left( R_{a}^w \right) \times (1 - \mu) \), where \( R_{a}^w \) is the (expected) average in growth conditions. This applies similarly, however, to any female in the population independent of the decisions of others, so that females should completely desert a low-quality patch. Males should similarly desert such patches as the same argument applies for them too (i.e., they have to follow the females). A comparable situation may emerge, for example, in ephemeral (successional) habitats where habitat quality deteriorates over time and individuals have to decide to desert such habitat patches at some moment (see Ronce and Olivieri 1997; Ronce et al. 2005).

More importantly, the situation of (nearly) competition-free geometric growth typically is associated with low growth and/or short population persistence, that is, situations characterized by frequent population extinction and foundation as they occur, for example, in small populations strongly affected by environmental stochasticity. In such circumstance females must follow a bet-hedging strategy (Friedenberg 2003; Ronce 2007; Delattre et al. 2010) to avoid the risk of line extinction. If this frequently involves colonization of empty sites, it includes the possibly substantial risk of not finding mating partners (especially for dispersing males) but also the chance of colonizing pristine habitat (especially for females). In such conditions predispersal mating and female-biased dispersal may actually be favored (Hiroti 2007), while males move to find females in their natal patch. More generally, males might in turn disperse, prior to females’ enclosure (Guillon and Bottein 2011). In many insect species, males do indeed hatch before females (protandry), and females are fertilized right after enclosure in their natal patch (Wiklund and Fagerström 1977). Whether dispersal in such groups is generally biased in favor of one sex is to our knowledge...
not well documented, but some evidence in favor of female bias exists (Baguette et al. 1998; Chaput-Bardy et al. 2010).

The mathematical models derived in this article seemingly provide direct analytical solutions for predicting (optimal) emigration behavior in the two sexes. However, important metapopulation attributes are themselves emergent properties depending on the resident dispersal strategy (e.g., Poethke et al. 2003; Ronce and Olivieri 2004); that is, dispersal directly feeds back on critical terms of the fitness equations such as the immigration terms and the fitness expectation of emigrants. Numerical solutions can possibly be found, however, by either applying an iterative method (a momentum method based on estimates of the distribution of individual numbers across habitat patches) or by simulating the evolution of migration probabilities using individual-based models, where the critical dispersal parameters are allowed to evolve (e.g., Travis et al. 1999; Poethke and Hovestadt 2002; Bach et al. 2006; Kun and Scheuring 2006; Kubisch et al. 2011; Payne et al. 2011). Indeed, a recent simulation study that implicitly implemented an information-dependent emigration model supports some predictions concerning male dispersal provided by our model (Nelson and Greeff 2011). A simulation approach has the added benefit that it accounts, by default (see Bach et al. 2006; Poethke et al. 2007), for the influence of kin competition and that it can readily deal with various stochastic effects. Further, such models can easily be expanded to also account for the effect of inbreeding depression (e.g., Gros et al. 2008). Finally, such simulations would allow insights into whether and how quickly evolutionary trajectories would reach stable evolutionary equilibria. This will clearly depend on the number of parameters needed to specify strategies; in our models, always only one parameter is needed to define the females’ strategy but up to three to define the males’ strategy. With our derivations provided here, we provide guidelines for appropriately implementing gender-specific and informed dispersal strategies by defining functions linking information to decision taking that are theoretically derived. In a previous study, we demonstrated the superiority of the general threshold function over alternative such functions (Hovestadt et al. 2010).

In our derivations, we assume that individuals are able to accurately measure local population size, that is, the density of males and females (fitness expectation in site of residence), but not the densities in prospective target sites (fitness expectation for disperser). Information on the latter will typically not be attainable by individuals, but corresponding information on long-term (equilibrium) average conditions may be acquired as “lineage knowledge” inherited in the genome or culture. Obviously, drastic and rapid modifications of landscape attributes resulting, for example, in changes in dispersal mortality, could lead to a severe mismatch between the genetically encoded expectations and reality, and consequently to “maladapted” dispersal decisions. More generally, if global conditions underwent continuous and rapid change, the ever-changing parameters would make it difficult for natural selection to settle into well-adapted decision rules. This is a very fundamental concern not specific to the model we present here. Instead, it is an argument against the idea that information-dependent emigration could evolve at all: knowledge (about the natal patch’s status) turns into useful information only if it can be compared to some reference (here the average fitness expectation of emigrants). If the latter cannot be known, information-dependent emigration cannot evolve.

It has also been hypothesized that information about neighboring sites may sometimes be available from immigrants (Cote and Clobert 2007; Baguette et al. 2011). Further, if movement across the landscape is easy and information acquisition is fast, individuals may perform explorative excursions and also decide on settlement based on information about prospective target patches. In such conditions, predictions concerning emigration should hold “inversely” with respect to settlement, for example, females might prefer low-density sites and males sites with high $F/M$ ratios. This seems indeed to be the case in some systems. For example, male badgers prefer to immigrate into groups with a favorable sex ratio but also into groups that are generally larger (Macdonald et al. 2008). Comparable observations exist with respect to the movement of male red deer that prefer settlement into areas with large $F/M$ ratios and generally larger groups (Jarnemo 2011); in both cases, however, it is not clear whether individuals preferentially emigrate from sites showing the opposite attributes. In male ursine colobus monkeys, sex ratio seems to be important for both emigration and settlement decisions (Teichroeb et al. 2011).

In summary, by applying the general principle of “fitness homogenization” underlying the IFD approach, we recover the simple and general threshold relation between emigration probability $p$ and local individual number (density) already derived in a previous model (Poethke and Hovestadt 2002) and already shown to displace in direct evolutionary contest other response functions proposed in the modeling literature (Hovestadt et al. 2010). However, we more specifically and separately identify the environmental factors (here density of the two sexes as well as patch size, i.e., carrying capacity) that may influence emigration decisions in the two sexes and generate for the two sexes separate predictions concerning the functional relationship between environment status and dispersal response. Our model further identifies conditions under which, despite the general expectation of male-biased dispersal in polygynous systems, female-biased dispersal might be observed.
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