



The evolutionary stability of partial migration under different forms of competition

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Abstract

Partial migration is a unique form of phenotypic diversity wherein migrant and non-migrant individuals coexist together in a population. Recent research has shown that the partial migration can be an evolutionarily stable strategy (ESS) and convergent stable strategy (CSS) if migrants and non-migrants experience density-dependent competition among individuals of the same type during reproduction. However, not all partially migratory species experience this particular form of competition during reproduction. In this paper, we investigate how various degrees of competition between migrants and non-migrants influence whether or not partial migration is an ESS and CSS. We find that the degree of competition influences the evolutionary outcome of partial migration and provides sharp thresholds relating these degrees of competition to the carrying capacities of both phenotypes.

Keywords Partial migration · Evolutionarily · Stable strategies · Adaptive dynamics · Density-dependent competition

Introduction

In its most fundamental form, natural selection is predicted to lead to a single, optimal life-history type. Yet, very rarely is a single optimal life-history type observed in nature. More

often, multiple life-history types are observed coexisting together. This coexistence of life-history types is explained as the outcome of density-dependent competition. A classic example is “fighter” (hooknose) and “sneaker” (jack) coho salmon (Gross 1996). If the density of hooknose coho is high, they experience high competition and their fitness goes down relative to jack coho. If the density of jack coho is high, they experience high competition and their fitness goes down relative to hooknose coho. This process leads to a system in which both types are maintained at densities that cause their fitness to be equal, and they are referred to as evolutionarily stable and convergent-stable strategies (ESS and CSS; Diekmann 2004).

The notion of ESS and CSS has been widely used to explain coexistence of a variety of life-history types. Beyond the classic hooknose and jack coho salmon example, there are also caller and satellite male frogs (Arak 1988) and blue-, orange-, and red-colored side-blotched lizards (Sinervo and Zamudio 2001). One relatively lesser known form of life-history diversity is the coexistence of migratory and non-migratory individuals, also referred to as “partial migration.” Lack (1944). In partial migration, the partial refers to the population and not the individual. Although partial migration is not as well studied as other coexisting life-history types, it is widespread among well-known migratory species (Table 1). Recent research has shown that

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Table 1 Partially migratory species and their hypothesized forms of competition during reproduction

| Species | Male competition | Female competition | Source |
|---|-------------------------------|-------------------------------|--------------------------------|
| Birds | | | |
| Cory's shearwater <i>Calonectris diomedea</i> | Prior residence | Between phenotype | Perez et al. (2013) |
| House finch <i>Carpodacus mexicanus</i> | Between phenotype | Between phenotype | Able and Belthoff (1998) |
| American dipper <i>Cinclus mexicanus</i> | Within phenotype | Within phenotype | Morrissey (2004) |
| White-ruffed manakins <i>Corapipo altera</i> | Prior residence | Between phenotype | Boyle (2008) |
| European robin <i>Erithacus rubecula</i> | Within phenotype | Within phenotype | Adriaensen and Dhondt (1990) |
| Dark-eyed junco <i>Junco hyemalis</i> | Prior residence | Between phenotype | Rabenold and Rabenold (1985) |
| Great bustards <i>Otis tarda</i> | Between phenotype | Between phenotype | Alonso et al. (2000) |
| Blue tits <i>Parus caeruleus</i> | Between phenotype | Between phenotype | Smith and Nilsson (1987) |
| Willow tits <i>Poecile montanus</i> | Within phenotype ^a | Within phenotype ^a | Silverin et al. (1989) |
| Goldcrest <i>Regulus regulus</i> | Prior residence | Between phenotype | Hildén (1982) |
| Blackcaps <i>Sylvia atricapilla</i> | Within phenotype | Within phenotype | Pulido et al. (1996) |
| European blackbird <i>Turdus merula</i> | Between phenotype | Between phenotype | Lundberg (1985) |
| Tropical kingbird <i>Tyrannus melancholicus</i> | Prior residence | Between phenotype | Jahn et al. (2010) |
| Lanyu scops owl <i>Otus elegans botelensis</i> | Prior residence | Between phenotype | Bai et al. (2012) |
| Reptiles | | | |
| Aldabra tortoise <i>Aldabrachelys gigantea</i> | Between phenotype | Prior resident | Swingland and Lessells (1979) |
| Giant tortoise <i>Chelonoidis nigra</i> | Between phenotype | Prior resident | Blake et al. (2013) |
| Amphibian | | | |
| Red-spotted newt <i>Notophthalmus viridescens</i> | Prior residence | Between phenotype | Grayson and McLeod (2009) |
| Mammals | | | |
| Ungulates | | | |
| Moose <i>Alces alces</i> | Between phenotype | Between phenotype | Ball et al. (2001) |
| Pronghorns <i>Antilocapra americana</i> | Between phenotype | Between phenotype | White et al. (2007) |
| Bison <i>Bison bison</i> | Between phenotype | Between phenotype | Bruggerman et al. (2008) |
| Roe deer <i>Capreolus capreolus</i> | Between phenotype | Between phenotype | Cagnacci et al. (2011) |
| Red deer <i>Cervus elaphus</i> | Between phenotype | Between phenotype | Hebblewhite and Merrill (2011) |
| Elk <i>Cervus canadensis</i> | Between phenotype | Between phenotype | Hebblewhite et al. (2008) |
| Sika deer <i>Cervus nippon</i> | Between phenotype | Between phenotype | Sakuragi et al. (2003) |
| Wildebeest <i>Conochaetes taurinus</i> | Between phenotype | Between phenotype | Fryxell et al. (1988) |
| Mule deer <i>Odocoileus hemionus</i> | Between phenotype | Between phenotype | Nicholson et al. (1997) |
| White-tailed deer <i>Odocoileus virginianus</i> | Between phenotype | Between phenotype | Sabine et al. (2002) |
| Tibetan antelope/chiru <i>Pantholops hodgsoni</i> | Between phenotype | Between phenotype | Schaller (1998) |
| Reindeer <i>Rangifer tarandus platyrhynchus</i> | Between phenotype | Between phenotype | Hansen et al. (2010) |
| Isard <i>Rupicapra pyrenaica</i> | Between phenotype | Between phenotype | Crampe et al. (2007) |
| Bats | | | |
| Daubenton's bat <i>Myotis daubentonii</i> | Prior residence | Between phenotype | Senior et al. (2005) |
| Insects | | | |
| Common green darners <i>Anax junius</i> | Within phenotype | Within phenotype | May (2013) |
| Southern monarch <i>Danaus erippus</i> | Within phenotype | Within phenotype | Slager and Malcolm (2015) |
| Fish | | | |
| Common bream <i>Abramis brama</i> | Prior residence | Prior residence | Skov et al. (2011) |
| Black bream <i>Acanthopagrus butcheri</i> | Between phenotype | Between phenotype | Gillanders et al. (2015) |
| Shortnose sturgeon <i>Acipenser brevirostrum</i> | Between phenotype | Between phenotype | Altenritter et al. (2017) |
| European eel <i>Anguilla anguilla</i> | Between phenotype | Between phenotype | Tsukamoto et al. (1998) |
| Snotnape cardinalfish <i>Apogon notatus</i> | Between phenotype | Between phenotype | Fukumori et al. (2008) |
| White bream <i>Blicca bjoerkna</i> | Between phenotype | Between phenotype | Skov et al. (2008) |
| Atlantic herring <i>Clupea harengus</i> | Between phenotype | Between phenotype | Ruzzante et al. (2006) |

Table 1 (continued)

| Species | Male competition | Female competition | Source |
|--|-------------------|-------------------------------|---------------------------------|
| Pike <i>Esox lucius</i> | Within phenotype | Within phenotype | Engstedt et al. (2010) |
| Cod <i>Gadus morhua</i> | Between phenotype | Between phenotype | Cote et al. (2004) |
| Three-spined stickleback <i>Gasterosteus aculeatus</i> | Prior residence | Within phenotype | Kitamura et al. (2006) |
| Humpback chub <i>Gila cypha</i> | Between phenotype | Between phenotype | Yackulic et al. (2014) |
| White perch <i>Morone americana</i> | Between phenotype | Between phenotype | Kerr et al. (2009) |
| Striped bass <i>Morone saxatilis</i> | Between phenotype | Between phenotype | Secor et al. (2001) |
| Cutthroat trout <i>Oncorhynchus clarki clarki</i> | Migrant advantage | Within phenotype | Trotter (1989) |
| Masu salmon <i>O. masu</i> | Migrant advantage | Within phenotype | Morita et al. (2014) |
| Rainbow trout/steelhead <i>O. mykiss</i> | Migrant advantage | Within phenotype | Shapovalov and Taft (1954) |
| Sockeye salmon <i>O. nerka</i> | Migrant advantage | Within phenotype | Quinn (2005) |
| Chinook salmon <i>O. tshawytscha</i> | Migrant advantage | Within phenotype ^b | Larsen et al. (2013) |
| Smelt <i>Osmerus eperlanus</i> | Between phenotype | Between phenotype | Jonsson and Jonsson (1993) |
| Plaice <i>Plurionectes platessa</i> | Between phenotype | Between phenotype | Dunn and Pawson (2002) |
| Zulega <i>Prochilodus argenteus</i> | Between phenotype | Between phenotype | Godinho and Kynard (2006) |
| Spotted sorubim <i>Pseudoplatystoma corruscans</i> | Between phenotype | Between phenotype | Godinho et al. (2007) |
| New Zealand smelt <i>Retropinna retropinna</i> | Within phenotype | Within phenotype | Northcote and Ward (1985) |
| Roach <i>Rutilus rutilus</i> | Between phenotype | Between phenotype | Skov et al. (2008) |
| Atlantic salmon <i>Salmo salar</i> | Migrant advantage | Within phenotype ^b | Hutchings and Myers (1985) |
| Brown trout <i>S. trutta</i> | Migrant advantage | Within phenotype | Jonsson (1985) |
| Arctic charr <i>Salvelinus alpinus</i> | Migrant advantage | Within phenotype | Jonsson and Jonsson (2001) |
| Bull trout <i>S. confluentus</i> | Migrant advantage | Within phenotype | Nelson et al. (2002) |
| Brook charr <i>S. fontinalis</i> | Migrant advantage | Within phenotype | Morinville and Rasmussen (2003) |
| White-spotted charr <i>S. leucomaenis</i> | Migrant advantage | Within phenotype | Morita et al. (2009) |
| Dolly varden <i>S. malma</i> | Migrant advantage | Within phenotype ^b | Maekawa and Nakano (2002) |
| Spiny dogfish <i>Squalus acanthius</i> | Between phenotype | Between phenotype | McFarlane and King (2003) |

^aAdults are all resident; only juveniles are partially migratory

^bFemales are all migrant; only males are partially migratory

populations of elk, monarchs, birds, and salmon are in fact partially migratory. In all of these examples, coexistence is based on an assumption of density-dependent competition, but the specific form of competition is rarely explicit.

Recent work in the partial migration literature has shown that when migrants compete only with migrants, and non-migrants compete only with non-migrants during reproduction, partial migration is an ESS and CSS (De Leenheer et al. 2017; Lundberg 2013). Lundberg (2013) first proved that this form of competition would lead to partial migration as a “weak ESS,” and De Leenheer et al. (2017) then demonstrated that it was a true ESS and CSS. In contrast, De Leenheer et al. (2017) demonstrated that when migrants and non-migrants compete with each other directly during reproduction, partial migration will never be an ESS. These results are informative for the partially migratory species that experience these forms of competition during reproduction, but not all partially migratory species do. In fact, many species, as well as sexes

within a species, experience different forms of competition during reproduction. In this study, we set out to examine whether other forms of competition cause partial migration to be an ESS and CSS, or not. We identify additional forms of competition and use adaptive dynamics to determine whether partial migration is an ESS and CSS.

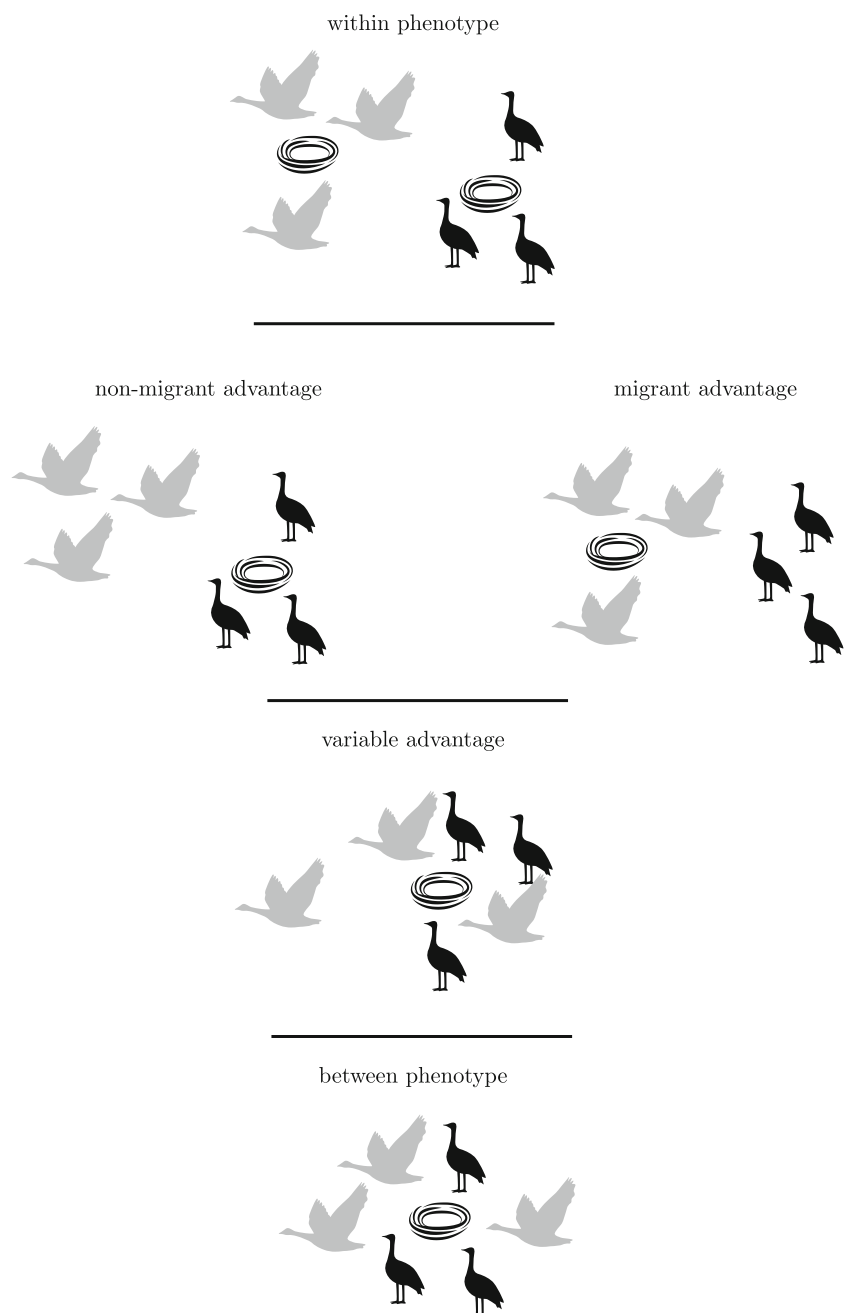
Methods

Forms of competition

We consider five forms of competition based on empirical data (Table 1 and Fig. 1) and population models (Kokko 2011; Lundberg 2013; Griswold et al. 2010; Taylor and Norris 2007). The forms are:

1. Within phenotype: migrants compete only with other migrants for a resource and non-migrants compete

Fig. 1 Five forms of density-dependent competition experienced by partial migrants during reproduction. The black standing geese represent non-migrants, the gray flying geese represent migrants, and the nest represents a limited resource related to reproduction. The resource could be nesting habitats, mates, or food resources. Within-phenotype competition occurs when migrants and non-migrants compete for different resources (such as different types of nesting habitat). Non-migrant-advantage competition occurs when non-migrants have a competitive advantage over migrants. This can occur through the prior-residence effect (Kokko et al. 2006) or through superior competitive ability. Migrant-advantage competition occurs when migrants are the superior competitors (Fleming 1996). Variable advantage represents the less extreme cases of migrant and non-migrant advantage. Between-phenotype competition occurs when migrants and non-migrants compete for the same resource



- only with non-migrants for a resource. Examples are if migrants and non-migrants nest in different habitats (Morrissey 2004; Quinn 2005) or if reproduction occurs at different times.
2. Non-migrant advantage: non-migrants have a complete competitive advantage due to a factor such as larger body size or arrival timing. The “prior-residence effect” is the most common form of non-migrant advantage and occurs when non-migrants are able to choose nesting

3. Migrant advantage: migrants have a complete competitive advantage due to a factor such as larger body size.
4. Variable advantage: migrants and non-migrants compete, but neither has the complete advantage.
5. Between phenotype: migrants and non-migrants compete for the same resource, at the same time, and with the same competitive ability.

Notice that these forms encompass species that share breeding habitat and those that do not (Chapman et al. 2011; Griswold et al. 2010).

The within- and between-phenotype forms of competition have been analyzed previously by De Leenheer et al. (2017) and Mohapatra et al. (2016), respectively. However, we include them in this paper because the direct comparison is informative, and the analysis presented here is more intricate because the systems are no longer monotone dynamical systems, which is a key property needed to establish the mathematical results.

We make hypotheses about the forms of competition experienced during reproduction for each of the species in Table 1. We hypothesize the form of competition based on descriptions of the mating system, whether a breeding resource (i.e., nesting habitat or female mate) was shared or not, arrival time, and size differences between migrants and non-migrants. For example, if non-migrants are present at the breeding site first and they occupy a nesting site prior to migrants, then we hypothesize non-migrant advantage. If non-migrants are on the breeding site first, but are smaller than migrants and have to compete for mates at the same time as migrants, we hypothesize migrant-advantage competition. If migrants and non-migrants are present at the breeding location at the same time, and there is no reported difference in size or breeding habitat use, we hypothesize between-phenotype competition.

The population model

We consider the following density-dependent model.

$$\begin{pmatrix} x_1(t + 1) \\ x_M(t + 1) \\ x_N(t + 1) \end{pmatrix} = \begin{pmatrix} 0 & f_M(z_M(t)) & f_N(z_N(t)) \\ \phi s_M & 0 & 0 \\ (1 - \phi) s_N & 0 & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_M(t) \\ x_N(t) \end{pmatrix}, \tag{1}$$

where $x_1(t)$, $x_M(t)$, and $x_N(t)$ are non-negative real numbers, respectively, representing the abundances of eggs, migrant adults, and non-migrant adults at time t . A fraction $\phi \in [0, 1]$ of eggs at time t will become migrant adults, provided they survive a season, which is captured by the survival probability $s_M \in (0, 1]$ in the model. Similarly, a fraction $1 - \phi$ of eggs will become non-migrant adults, after surviving a season, with survival probability $s_N \in (0, 1]$. It is assumed that both survival probabilities s_M and s_N

are constants that do not depend on any of the system’s abundances. The parameter ϕ represents an allocation strategy whereby each phenotype (migrant or non-migrant) produces offspring that can mature into an adult of the migrant phenotype.

The functions $f_M(z_M)$ and $f_N(z_N)$ are per capita fertilities of migrants and non-migrants, assumed to be smooth, non-negative, decreasing functions, with limits:

$$f_{M,\infty} = \lim_{z \rightarrow \infty} f_M(z) \text{ and } f_{N,\infty} = \lim_{z \rightarrow \infty} f_N(z)$$

Moreover, the functions $g_M(z) = f_M(z)z$ and $g_N(z) = f_N(z)z$ are assumed to be increasing. This condition expresses that, although the per capita fertilities decrease as the adult abundances increase, the total fertilities of migrants and residents are in fact increasing. Finally, we also assume that the functions f_M and f_N are strictly convex, i.e., that f''_M and f''_N are positive. This condition means that (negative) density dependence is attenuated: at larger densities, the negative effect on the fertilities is not as strong as at lower densities.

A specific density-dependent function that meets these criteria is the commonly used Beverton-Holt function, which is expressed as

$$f_i(z) = \frac{a_i}{1 + b_i z_i}. \tag{2}$$

a_i is the number of offspring produced in the absence of competition, and b_i captures the intensity of competition because it controls the rate of decline in $f_i(z_i)$ with increased z_i .

z_i (with i for migrant M or non-migrant N) represents the total number of competing individuals experienced by phenotype i during reproduction, and it is given by

$$z_M(t) = x_M(t) + p x_N(t) \tag{3}$$

and

$$z_N(t) = x_N(t) + q x_M(t) \tag{4}$$

with $0 \leq p, q \leq 1$. Here, p is a parameter representing the fraction of the non-migrant population competing with each migrant adult. Similarly, q represents the fraction of the migrant population that competes with each non-migrant adult.

The values of p and q vary depending on the form of competition being considered:

Within phenotype: $p, q = 0 : z_M = x_M$ and $z_N = x_N$ (5)

Non-migrant advantage: $p > 0, q = 0 : z_M = x_M + px_N$ and $z_N = x_N$ (6)

Migrant advantage: $p = 0, q > 0 : z_M = x_M$ and $z_N = qx_M + x_N$ (7)

Variable advantage: $0 < p, q < 1 : z_M = x_M + px_N$ and $z_N = x_N + qx_M$ (8)

Between phenotype: $p, q = 1 : z_M = x_M + x_N$ and $z_N = x_M + x_N$ (9)

Fitness and the basic reproduction number

Model (1) can be re-written more compactly in vector form as

$$x(t + 1) = A_1(x(t), \phi)x(t), \tag{10}$$

where

$$x = \begin{pmatrix} x_1 \\ x_M \\ x_N \end{pmatrix}, \text{ and } A_1(x, \phi) = \begin{pmatrix} 0 & f_M(z_M) & f_N(z_N) \\ \phi s_M & 0 & 0 \\ (1 - \phi)s_N & 0 & 0 \end{pmatrix}.$$

By splitting $A_1(x, \phi)$ as:

$$A_1(x, \phi) = F + T, \text{ where } F = \begin{pmatrix} 0 & f_M(z_M) & f_N(z_N) \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix},$$

$$\text{and } T = \begin{pmatrix} 0 & 0 & 0 \\ \phi s_M & 0 & 0 \\ (1 - \phi)s_N & 0 & 0 \end{pmatrix},$$

we can associate the basic reproduction number to the non-negative matrix $A_1(x, \phi)$ in the usual way (Caswell 2000; Li and Schneider 2002):

$$R_0(x, \phi) := \rho(F(I - T)^{-1}) = \phi s_M f_M(z_M) + (1 - \phi)s_N f_N(z_N), \tag{11}$$

for every $(x, \phi) \in \mathbb{R}_+^3 \times [0, 1]$. Here, $\rho(F(I - T)^{-1})$ denotes the spectral radius of $F(I - T)^{-1}$.

For notational convenience, we also define

$$R_0(\infty, \phi) = \phi s_M f_{M,\infty} + (1 - \phi)s_N f_{N,\infty},$$

for every $\phi \in [0, 1]$.

Global stability of the population model

The populations described by the system (1) with a fixed allocation strategy ϕ will settle at a globally stable fixed point, provided that the basic reproduction number near the extinction fixed point is larger than 1. This can be established using the same method of proof as given in De Leenheer et al. (2017), and relies critically on the monotonicity property of the model:

Theorem 1 Assume that the functions $f_M(z)$ and $f_N(z)$ satisfy all the conditions mentioned above in this section, and that the basic reproduction numbers satisfy:

$$R_0(\infty, \phi) < 1 < R_0(0, \phi), \text{ for all } \phi \in [0, 1]. \tag{12}$$

Then, the following holds:

1. For all $\phi \in (0, 1)$, system (1) has a unique, positive fixed point $x^*(\phi)$ which is linearly stable, and which attracts all positive solutions of Eq. (1).
2. If $\phi = 0$, then system (1) has a unique, nonzero fixed point $(\tilde{x}_1, 0, \tilde{x}_N)$, where $\tilde{x}_N > 0$ is the unique positive solution to the equation $s_N f_N(z) = 1$, and $\tilde{x}_1 = \tilde{x}_N/s_N$. This fixed point is linearly stable and attracts all positive solutions of system (1).
3. If $\phi = 1$, then system (1) has a unique, nonzero fixed point $(\hat{x}_1, \hat{x}_M, 0)$, where $\hat{x}_M > 0$ is the unique positive solution to the equation $s_M f_M(z) = 1$, and $\hat{x}_1 = \hat{x}_M/s_M$. This fixed point is linearly stable and attracts all positive solutions of system (1).

The function $\phi \rightarrow x^*(\phi)$ is smooth, and $\lim_{\phi \rightarrow 0} x^*(\phi) = (\tilde{x}_1, 0, \tilde{x}_N)$ and $\lim_{\phi \rightarrow 1} x^*(\phi) = (\hat{x}_1, \hat{x}_M, 0)$.

Remark 1 Notice that condition (12) is equivalent to:

$$s_M f_M(0) > 1, s_N f_N(0) > 1, \text{ and } s_M f_{M,\infty} < 1, s_N f_{N,\infty} < 1.$$

because $R_0(0, \phi)$ ($R_0(\infty, \phi)$) is a convex combination of the numbers $s_M f_M(0)$ and $s_N f_N(0)$ ($s_M f_{M,\infty}$ and $s_N f_{N,\infty}$).

Also note that $f_{M,\infty} = f_{R,\infty} = 0$ in case f_M and f_R are Beverton-Holt functions, and hence the condition that $R_0(\infty, \phi) < 1$ is automatically satisfied for all $0 \leq \phi \leq 1$, because $R_0(\infty, \phi) = 0$.

Remark 2 The parameters \hat{x}_M and \tilde{x}_N from (1) and (2) are the carrying capacities of migrant- and non-migrant-only populations (i.e., $\phi = 1$ or 0). The carrying capacities represent the maximum number of migrants or non-migrants that can be supported for a given combination of habitat, fecundity, survival, and competition parameters (such as the a_i and b_i in case the fertilities are modeled

by Beverton-Holt functions). These carrying capacities are largely theoretical because in nature populations are partially migratory and contain both migrants and non-migrants. However, these carrying capacities turn out to be an important conceptual tool for understanding the evolution of partial migration, as will be shown later in the paper.

Adaptive dynamics and ESS

We consider a resident population that uses strategy value ϕ , and assume invasion by a mutant population using strategy value $\phi' \neq \phi$. The resulting dynamical population model takes the following form:

$$X(t + 1) = A(X(t))X(t), \tag{13}$$

where

$$X(t) = \begin{pmatrix} \text{resident egg abundance } (x_1(t)) \\ \text{resident migrant adult abundance } (x_M(t)) \\ \text{resident non-migrant adult abundance } (x_N(t)) \\ \text{mutant egg abundance } (y_1(t)) \\ \text{mutant migrant adult abundance } (y_M(t)) \\ \text{mutant non-migrant adult abundance } (y_N(t)) \end{pmatrix},$$

$$A(X(t)) = \begin{pmatrix} A_1(x(t) + y(t), \phi) & 0 \\ 0 & A_1(x(t) + y(t), \phi') \end{pmatrix}$$

with

$$x = \begin{pmatrix} x_1 \\ x_M \\ x_N \end{pmatrix}, \quad y = \begin{pmatrix} y_1 \\ y_M \\ y_N \end{pmatrix},$$

$$\text{and } A_1(x, \phi) = \begin{pmatrix} 0 & f_M(z_M) & f_N(z_N) \\ \phi s_M & 0 & 0 \\ (1 - \phi) s_N & 0 & 0 \end{pmatrix}$$

Here, $z_M = x_M + px_N$ and $z_N = x_N + qx_M$ for given parameters values for p and q . We assume that all assumptions of Theorem 1 continue to hold here for system (13). Hence, for each ϕ in $[0, 1]$, system (13) has a fixed

point $X^*(\phi) = \begin{pmatrix} x^*(\phi) \\ 0 \end{pmatrix}$, where $x^*(\phi) = \begin{pmatrix} x_1^*(\phi) \\ x_M^*(\phi) \\ x_N^*(\phi) \end{pmatrix}$ is

the unique nonzero fixed point of system (1) featured in Theorem 1.

Definition 1 We say that ϕ^* in $[0, 1]$ is an evolutionarily stable strategy (ESS) if $X^*(\phi^*)$ is a locally asymptotically stable fixed point of system (13) for all $\phi' \neq \phi^*$ in some neighborhood of ϕ^* .

This notion captures that if the resident population has adopted an ESS, then it cannot be invaded by mutants that use nearby strategies.

Definition 2 We say that ϕ^* in $[0, 1]$ is a convergence stable strategy (CSS) if there is a neighborhood N of (ϕ^*, ϕ^*) such that $X^*(\phi)$ is not an asymptotically stable fixed point of system (13) for all pairs (ϕ, ϕ') in N that satisfy that either $\phi < \phi' < \phi^*$ or $\phi^* < \phi' < \phi$, but an asymptotically stable fixed point of system (13) for all pairs (ϕ, ϕ') with ϕ in N that satisfy that either $\phi' < \phi < \phi^*$ or $\phi^* < \phi < \phi'$.

The intuitive idea behind this definition is as follows: Suppose that the resident ϕ has adopted a strategy that is nearby, but distinct from a CSS ϕ^* . Suppose also that a mutant ϕ' is introduced whose strategy is farther away from the CSS value. This mutant will then fail to invade the environment occupied by the resident. But over time, a mutant may arise whose strategy value is closer to the CSS value. Such a mutant will be able to successfully invade the resident’s environment. Iterating this process yields a sequence of successfully invading mutants whose strategies converge monotonically towards the CSS.

Linear invasion analysis

To investigate whether the mutant can successfully invade the resident population, we fix a (resident, mutant) strategy pair (ϕ, ϕ') in $[0, 1] \times [0, 1]$, and linearize system (13) near the fixed point $X^*(\phi)$. By Theorem 1, the upper diagonal block of the linearization near $X^*(\phi)$ is a stable matrix, and thus we focus on the 3×3 matrix in the lower-diagonal block, which takes the form:

$$A_1(x^*(\phi), \phi') = \begin{pmatrix} 0 & f_M(z_M^*(\phi)) & f_N(z_N^*(\phi)) \\ \phi' s_M & 0 & 0 \\ (1 - \phi') s_N & 0 & 0 \end{pmatrix},$$

where $z_M^*(\phi) = x_M^*(\phi) + px_N^*(\phi)$ and $z_N^*(\phi) = x_N^*(\phi) + qx_M^*(\phi)$.

The mutant can successfully invade if the dominant eigenvalue of this matrix is larger than 1, and it cannot invade if it has dominant eigenvalue less than 1. Since this dominant eigenvalue and $R_0(x^*(\phi), \phi')$ are always on the same side of 1 as shown in Li and Schneider (2002), the success or failure of invasion by the mutant can be determined by checking the sign of:

$$W(\phi, \phi') := R_0(x^*(\phi), \phi') - 1 = \phi' s_M f_M(z_M^*(\phi)) + (1 - \phi') s_N f_N(z_N^*(\phi)) - 1, \tag{14}$$

where we have used formula (11). In the context of adaptive dynamics, the function $W(\phi, \phi')$ is often referred to as the fitness of the mutant adopting strategy ϕ' in an environment occupied by a resident population adopting strategy ϕ . If $W(\phi, \phi') > 0$, then the mutant can successfully invade; if $W(\phi, \phi') < 0$, then the mutant fails to invade.

Remark 3 Observe that if there is a resident strategy ϕ^* such that $W(\phi^*, \phi') < 0$ for all $\phi' \neq \phi^*$ in some neighborhood of ϕ^* , then ϕ^* is an ESS by definition. If $W(\phi^*, \phi') = 0$ for all ϕ' in some neighborhood of ϕ^* , then a linear analysis is not sufficient to conclude whether ϕ^* is an ESS or not. In this case, a nonlinear stability analysis needs to be performed.

We next simplify the function $W(\phi, \phi')$ by using the fact that $x^*(\phi)$ is the unique nonzero fixed point of system (1), or equivalently of system (10). The Perron-Frobenius Theorem implies in particular that the dominant eigenvalue of $A_1(x^*(\phi), \phi)$ is equal to one, and hence by Li and Schneider (2002) that:

$$R_0(x^*(\phi), \phi) = \phi s_M f_M(z_M^*(\phi)) + (1 - \phi) s_N f_N(z_N^*(\phi)) \equiv 1, \text{ for all } 0 \leq \phi \leq 1.$$

Therefore,

$$W(\phi, \phi') = (\phi' - \phi)(s_M f_M(z_M^*(\phi)) - s_N f_N(z_N^*(\phi))). \tag{15}$$

This simplification reveals that $W(\phi, \phi')$ is the product of $(\phi' - \phi)$ and a function that depends only on ϕ . We further investigate the latter function and focus on which value(s) of ϕ in $(0, 1)$, this function is zero. Indeed, values of ϕ in $(0, 1)$, where this function is not zero, cannot be an ESS, because the function W will change sign whenever the diagonal $\{\phi = \phi'\}$ in the unit square is crossed along the vertical line through ϕ . This is due to the first factor $(\phi' - \phi)$ in the expression for W . In other words, values of ϕ in $(0, 1)$, where the second factor in W , $s_M f_M(z_M^*(\phi)) - s_N f_N(z_N^*(\phi))$, is zero, are the only candidate ESS values that may correspond to partial migration.

We have that the second factor in W is zero if and only if $s_M f_M(z_M^*(\phi)) = s_N f_N(z_N^*(\phi))$. Since $x^*(\phi)$ is a positive fixed point of (1) when $0 < \phi < 1$ by Theorem 1, there holds that

$$x_1^*(\phi) = x_1^*(\phi) (\phi s_M f_M(z_M^*(\phi)) + (1 - \phi) s_N f_N(z_N^*(\phi))),$$

and therefore $s_M f_M(z_M^*(\phi)) = s_N f_N(z_N^*(\phi))$ if and only if

$$s_M f_M(z_M^*(\phi)) = 1 = s_N f_N(z_N^*(\phi)), \tag{16}$$

or equivalently, by invoking the definitions for $z_M^*(\phi) = x_M^*(\phi) + p x_N^*(\phi)$ and $z_N^*(\phi) = x_N^*(\phi) + q x_M^*(\phi)$, if

$$x_M^*(\phi) + p x_N^*(\phi) = \hat{x}_M \tag{17}$$

$$x_N^*(\phi) + q x_M^*(\phi) = \tilde{x}_N \tag{18}$$

Recall that \hat{x}_M and \tilde{x}_N are the respective unique solutions of the equations $s_M f_M(z) = 1$ and $s_N f_N(z) = 1$. We would like to solve system (17) and (18) for $x_M^*(\phi)$ and $x_N^*(\phi)$ in terms of p, q and \hat{x}_M and \tilde{x}_N . We can distinguish two cases:

Case 1 $p = q = 1$. In this case, and under the generic assumption that $\hat{x}_M \neq \tilde{x}_N$, systems (17) and (18) have no

solutions. In other words, in this case, there are no candidate ESS values in the interval $(0, 1)$.

Case 2 $pq \neq 1$. In this case, we can solve systems (17) and (18), and it has the unique solution:

$$x_M^*(\phi) = \frac{\hat{x}_M - p\tilde{x}_N}{1 - pq} \tag{19}$$

$$x_N^*(\phi) = \frac{\tilde{x}_N - q\hat{x}_M}{1 - pq} \tag{20}$$

Since $(x_M^*(\phi), x_N^*(\phi))$ is a positive fixed point of system (1) (by Theorem 1), it follows that the following inequalities must hold:

$$\hat{x}_M > p\tilde{x}_N \tag{21}$$

$$\tilde{x}_N > q\hat{x}_M \tag{22}$$

Recall that p and q are independent of the carrying capacities \hat{x}_M and \tilde{x}_N , and therefore these two inequalities (21) and (22) impose nontrivial necessary conditions on the model parameters for the existence of a candidate ESS in $(0, 1)$. When either of these two conditions fail, there is no candidate ESS in $(0, 1)$. We show next that if both (21) and (22) hold, then there is indeed a unique candidate ESS value in $(0, 1)$. To see this, note that since $(x_M^*(\phi), x_N^*(\phi))$ is a positive fixed point of system (1), and by dividing (19) by (20), there must hold that

$$\frac{x_M^*(\phi)}{x_N^*(\phi)} = \frac{\hat{x}_M - p\tilde{x}_N}{\tilde{x}_N - q\hat{x}_M} = \frac{s_M}{s_N} \frac{\phi}{1 - \phi}$$

The equation on the right can now be solved for ϕ , and this yields the following unique solution ϕ^* in $(0, 1)$:

$$\phi^* = \frac{\frac{\hat{x}_M - p\tilde{x}_N}{\tilde{x}_N - q\hat{x}_M}}{\frac{\hat{x}_M - p\tilde{x}_N}{\tilde{x}_N - q\hat{x}_M} + \frac{s_M}{s_N}} \tag{23}$$

Note that ϕ^* clearly belongs to $(0, 1)$, whenever (21) and (22) hold.

Summarizing **Case 2**, if either Eqs. 21 or 22 fails, there is no candidate ESS in $(0, 1)$; if both Eqs. 21 and 22 hold, then there is a unique candidate ESS in $(0, 1)$, and it is given by the expression for ϕ^* in Eq. 23.

Results

Having identified candidate ESS values, we now turn to the question whether these values are in fact, genuine ESSs. As mentioned before in Remark 3, this will require a nonlinear instability analysis, which is performed in detail in the Appendix. Our focus here will be to summarize these results based on the particular form of competition experienced by both phenotypes. The most common form of competition that we hypothesize in Table 1 is between-phenotype competition. We hypothesize it when specific information

about differences between migrants and non-migrants during reproduction is unavailable, in essence making between-phenotype competition our null hypothesis. Its commonness in Table 1 demonstrates how little is known about competition and phenotypic differences between migrants and non-migrants.

The specific results for each of the five forms of competition are as follows:

1. Within phenotype: $p = 0$ and $q = 0$.

In this case, Eqs. 21 and 22 always hold, and the candidate ESS ϕ^* in Eq. 23 simplifies to:

$$\phi^* = \frac{\frac{\hat{x}_M}{\tilde{x}_N}}{\frac{\hat{x}_M}{\tilde{x}_N} + \frac{s_M}{s_N}} \tag{24}$$

The nonlinear stability analysis in the Appendix reveals that ϕ^* is indeed an ESS, a result which was already derived in De Leenheer et al. (2017). The signs of $W(\phi, \phi')$ —determined in the next subsection—are summarized in Fig. 2 and indicate that ϕ^* is also a CSS.

2. Non-migrant advantage: $p > 0$ and $q = 0$.

In this case, Eq. 22 always holds, but Eq. 21 may or may not hold.

If Eq. 21 does not hold, then there is a unique ESS at $\phi = 0$ which is also a CSS, see Fig. 2. The population does not exhibit partial migration, and evolution will drive it to one consisting purely of non-migrant individuals.

If on the other hand, Eq. 21 does hold, then the candidate ESS ϕ^* in Eq. 23 simplifies to:

$$\phi^* = \frac{\frac{\hat{x}_M - p\tilde{x}_N}{\tilde{x}_N}}{\frac{\hat{x}_M - p\tilde{x}_N}{\tilde{x}_N} + \frac{s_M}{s_N}} \tag{25}$$

and turns out to be an ESS and CSS, as demonstrated in the Appendix, and illustrated in Fig. 2.

We note that inequality (21) provides a precise condition under which partial migration evolves when there is non-migrant advantage. Indeed, the migrant can and will only survive under evolutionary pressure, when its carrying capacity \hat{x}_M is sufficiently large. Exactly how large it ought to be is made clear by Eq. 21; namely, it should exceed the product of the carrying capacity \tilde{x}_N of non-migrants, and p which is a measure for the intensity of the competition by non-migrants as experienced by migrants at their carrying capacity.

3. Migrant advantage: $p = 0$ and $q > 0$.

The analysis of this scenario is analogous to that of non-migrant advantage, but reverses the role of migrants and non-migrants. Here, Eq. 21 always holds, but Eq. 22 may or may not hold.

If Eq. 22 does not hold, then there is a unique ESS/CSS at $\phi = 1$. Partial migration cannot evolve.

Instead, the population evolves towards one that consists entirely of migrant individuals.

If Eq. 22 does hold, then there is a unique ESS/CSS ϕ^* , given by

$$\phi^* = \frac{\frac{\hat{x}_M}{\tilde{x}_N - q\hat{x}_M}}{\frac{\hat{x}_M}{\tilde{x}_N - q\hat{x}_M} + \frac{s_M}{s_N}} \tag{26}$$

4. Variable advantage: $0 < p, q < 1$.

First note that Eqs. 21 and 22 cannot fail simultaneously, because this would imply that $pq \geq 1$. Thus, we are left to consider three cases: (i) (21) fails, but Eq. 22 holds. (ii) (21) holds, but Eq. 22 fails. (iii) Both Eqs. 21 and 22 hold.

Cases (i) and (ii) lead to similar conclusions: Partial migration cannot evolve in either case. In case (i), $\phi = 0$ is the unique ESS/CSS, and in case (ii), $\phi = 1$ is. Case (iii) is the only case where partial migration occurs at the ESS/CSS value ϕ^* given in Eq. 23.

5. Between phenotype: $p, q = 1$.

We have seen in the previous section that there are no candidate ESS values in $(0, 1)$ in this case. Under the generic assumption that $\hat{x}_M \neq \tilde{x}_N$, we have shown in De Leenheer et al. (2017) that $\phi = 0$ is the unique ESS/CSS when $\hat{x}_M < \tilde{x}_N$, but $\phi = 1$ is when this inequality is reversed. In other words, whichever phenotype has the larger carrying capacity will determine the fate of the population under evolution.

Sign of the W function and PIPs

In the previous subsection, we summarized the ESS/CSS values depending on the form of competition. Here, we explain how to determine the sign of the fitness function $W(\phi, \phi')$, for all ϕ and ϕ' in $[0, 1]$, which leads to a pictorial representation known as the pairwise invadability plot, or PIP for short. We shall only explain how the sign of W is determined for one of the cases, namely the variable advantage case; the approach is entirely similar for the other cases.

Suppose that $0 < p, q < 1$ (variable advantage), and assume that Eqs. 21 and 22 hold, i.e. that $p\tilde{x}_N < \hat{x}_M$ and $q\hat{x}_M < \tilde{x}_N$. Then, $W(\phi, \phi') = 0$ if and only if

$$\phi = \phi' \text{ or } \phi = \phi^* = \frac{\frac{\hat{x}_M - p\tilde{x}_N}{\tilde{x}_N - q\hat{x}_M}}{\frac{\hat{x}_M - p\tilde{x}_N}{\tilde{x}_N - q\hat{x}_M} + \frac{s_M}{s_N}}$$

$W(\phi, \phi')$ is a continuous function, which is zero if and only if either the pair (ϕ, ϕ') belongs to the diagonal where $\phi = \phi'$ or to the vertical line $\phi = \phi^*$. These two lines divide the square $[0, 1] \times [0, 1]$ in four open regions, where the sign of the function W is either positive or negative. The sign of $W(\phi, \phi')$ for pairs (ϕ, ϕ') in the SE region is the

same as the sign of $W(1, 0) = s_N f_N(q\hat{x}_M) - 1$, which is positive due to the facts that f_N is a decreasing function and $q\hat{x}_M < \tilde{x}_N$. Similarly, $W(0, 1) = s_M f_M(p\tilde{x}_N) - 1$ is positive as well because f_M is a decreasing function and $p\tilde{x}_N < \hat{x}_M$. Therefore, $W(\phi, \phi') > 0$ in the NW region. The sign of $W(\phi, \phi')$ for pairs (ϕ, ϕ') in the NE region is the same as the sign of $W(1, 1) = 1 - s_N f_N(q\hat{x}_M)$, which is negative. Thus, $W(\phi, \phi')$ is negative for all pairs (ϕ, ϕ') in the NE region. A similar argument shows that $W(\phi, \phi')$ is negative for all pairs (ϕ, ϕ') in the SW region.

In the variable advantage case when at least one of the inequalities (21) and (22) fail, the analysis is also similar, and simplified by the fact that there is no value for ϕ in $(0, 1)$ for which the second factor in the function $W(\phi, \phi')$ is zero.

Discussion

We can summarize our results for *all* competition forms and succinctly state that partial migration will occur if and only if

$$\hat{x}_M > p\tilde{x}_N \text{ and } \tilde{x}_N > q\hat{x}_M.$$

Fig. 2 Results of the adaptive dynamics analyses for each form of competition. The pairwise invasibility plots (PIPs) were drawn based on the general mathematical results, not specific parameters. The horizontal axes represent the resident migration propensity (ϕ), and the vertical axes represent the mutant migration propensity (ϕ'). The + sign and gray color indicate regions where the mutant has higher fitness in an environment set by the resident (i.e., the invasion fitness is positive), and the - sign and white color indicate regions where the mutant has lower fitness in the environment set by the resident (i.e., the invasion fitness is negative). The ESS and CSS migration propensities, ϕ^* , are indicated by black triangles

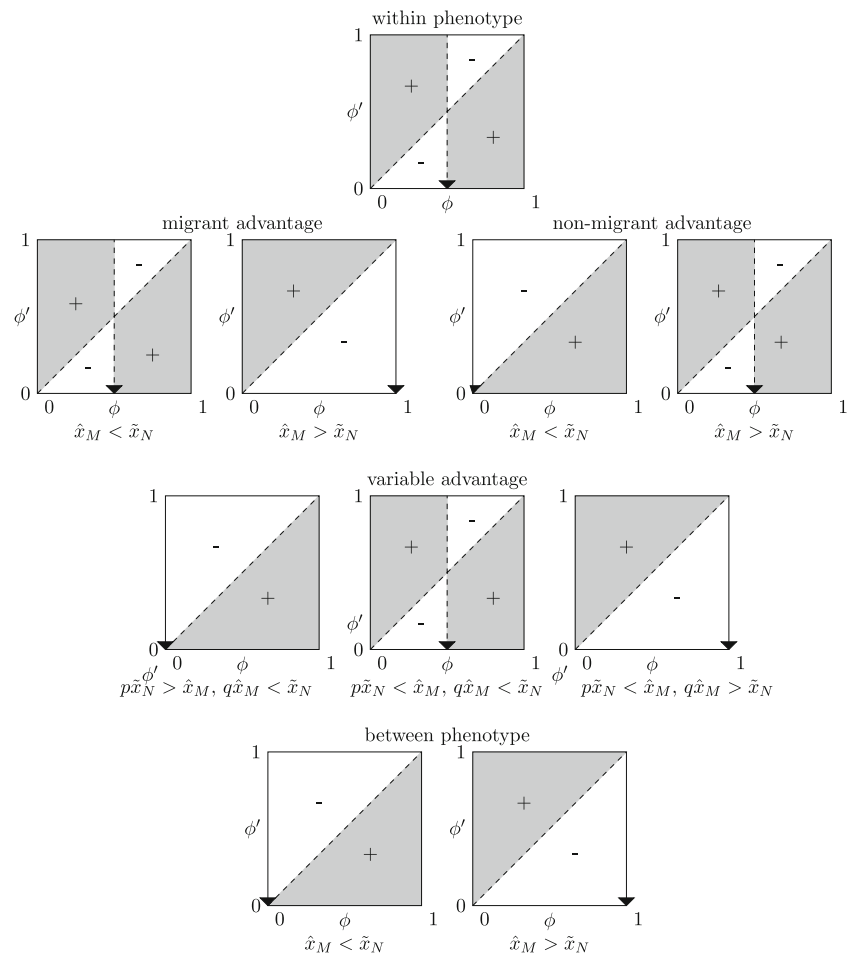
These conditions indicate that the carrying capacities of each phenotype should exceed the products of the carrying capacity of the other phenotype, multiplied by the intensity of competition the latter imposes on the former. Under these conditions, the allocation strategy:

$$\phi^* = \frac{\frac{\hat{x}_M - p\tilde{x}_N}{\tilde{x}_N - q\hat{x}_M}}{\frac{\hat{x}_M - p\tilde{x}_N}{\tilde{x}_N - q\hat{x}_M} + \frac{s_M}{s_N}}$$

corresponding to partial migration is an ESS and CSS for the following competition forms: within-phenotype competition, non-migrant advantage when $\hat{x}_M > p\tilde{x}_N$, migrant-advantage when $\tilde{x}_N > q\hat{x}_M$, and variable advantage when $p\tilde{x}_N < \hat{x}_M$ and $q\hat{x}_M < \tilde{x}_N$ (Fig. 2).

Partial migration is not an ESS and CSS for the following competition forms: between-phenotype competition, non-migrant advantage when $p\tilde{x}_N > \hat{x}_M$, migrant-advantage when $q\hat{x}_M > \tilde{x}_N$, and variable advantage when either $\hat{x}_M < p\tilde{x}_N < \text{or } q\hat{x}_M > \tilde{x}_N$ (Fig. 2).

The evolution of partial migration presented here is analogous to classic models of resource partitioning and species coexistence (Schoener 1974). When there is some fraction of a population that does not directly compete with



another population for a resource ($p = 0$, or $q = 0$), either by increased competitive ability or different habitat use, then both populations will be maintained, provided that the fraction that experiences competition has sufficiently high carrying capacity. This is the case when either the migrant or the non-migrant has a competitive advantage (Fig. 2). When populations do compete directly, only the stronger competitor will remain through a process called competitive exclusion (Hardin 1960). This is analogous to our between-phenotype cases, both analyzed here, and in De Leenheer et al. (2017), in that either exclusively non-migrant or exclusively migrant populations evolve under evolutionary pressure.

The most extreme form of resource partitioning we analyzed is the within-phenotype form of competition, in which migrants and non-migrants never compete. Within-phenotype always results in partial migration as an ESS and CSS, both in our analysis here and in De Leenheer et al. (2017). This is notable because if our results hold for competition that takes place in other life stages, within-phenotype competition is the most broadly applicable mechanism for partial migration. By definition, migrants and non-migrants in partially migratory populations spend some portion of their lives in separate environments. This could be marine and freshwater, as is the case for partially migratory salmon (Dodson et al. 2013), it could be aquatic and terrestrial, as is the case for partially migratory amphibians (Grayson et al. 2011), or it could be high and low latitudes, as is the case for partially migratory sea birds (Perez et al. 2013). If there is density-dependent competition during this life stage (which is often the case), and our results apply to that life stage, then the evolution of partial migration can be explained by within-phenotype competition alone.

It seems reasonable to ask why partial migration is not more common. The first answer is that it is likely more common than has been realized. We found references for 68 partially migratory species that come from very diverse taxa and diverse environments. Additionally, most of these references were only published in the last 20 years, so it seems likely that partial migration is more common than is currently known. The second answer is that there are likely some environments where migrants or non-migrants cannot sustain themselves, for example harsh winter conditions make non-migrant survival impossible. In these cases, either \hat{x}_M or \tilde{x}_N would be zero, violating a key assumption underlying our work, namely the right inequality in Eq. 12 which implies the positivity of both these carrying capacities. Lastly, we have shown that partial migration requires resource partitioning and in places that have numerous species, such as the Amazon, all possible niches may be filled by other species. There may be no

additional resources, or niche space, for life-history variants like partial migration to evolve.

Our results differ from previous studies in that partial migration is not simply a continuum between complete migration and non-migration under any form of competition (Taylor and Norris 2007; Griswold et al. 2010; Chapman et al. 2011; Fagan et al. 2012). Instead, our results point to a threshold system, which provides some insight into how populations may respond to future conditions. For example, populations experiencing migrant-advantage competition could be exclusively migrant or partially migratory, but never evolve to be exclusively non-migratory. The opposite is true for prior-residence competition. Populations experiencing within-phenotype competition will never be exclusively migrant or exclusively non-migrant. The opposite is true for populations experiencing between-phenotype competition, wherein the population will never be partially migratory. Another study found that in a population experiencing prior-residence competition, migration could be an ESS if non-migration produced a sink population (Kokko and Lundberg 2001). Assessing the circumstance of a sink population (i.e., $\tilde{x}_N = 0$) did not meet our modeling assumption that both types can persist in isolation, so we cannot directly compare to this result. However, it indicates that there may be some additional cases where complete migration could evolve.

The goal of this paper was to show that density dependence in the reproduction stage alone can be sufficient to explain partial migration—or the lack thereof. Density dependence effects could also occur during the maturation of juveniles to adults, and the methods applied here could be used to investigate that scenario by replacing the constant survival probabilities s_M and s_N in model (1) by functions that depend on the abundances of the various phenotypes in appropriate combinations reflecting the nature of the competition between migrants and non-migrants. Similarly, one could also apply these techniques to deal with non-semelparous populations. These can be modeled by adding nonzero survival probabilities on the second and third diagonal entries of the matrix in model (1). One of the mathematical implications of such a modification is that the global stability of the population model as established in Theorem 1 can no longer be proved based on monotonicity properties. Nevertheless, one could settle for local—rather than global—stability properties of the positive fixed points, and then apply the adaptive dynamics framework which, after all, is of local nature as well.

Although here we have focused exclusively on density dependence, other mechanisms could also underlie partial migration. For instance, temporal and/or spatial heterogeneity has been ignored here, but are often important features for partially migrating species that choose to respond or not,

precisely to environments that vary in time and/or space. The phenomenon of partial migration is therefore related to the problem of the evolution of dispersal. In temporally constant, but spatially varying environments for example, it is known that evolution favors slower dispersers (Hastings 1983; Dockery et al. 1998), suggesting that non-migrants would be favored in the context of partial migration. On the other hand, temporal variability in the environment creates habitats that are not always inhabitable, and this drives species to disperse to milder regions during those times. This shows that temporal variations can force species to become more mobile, and they could be another important mechanism to explain partial migration. Finally, the type of density dependence considered here (essentially, forms that behave like Beverton-Holt dynamics) could possibly also impact the evolution of dispersal. For instance, our results are not applicable to populations that are governed by Ricker dynamics where the growth function $g(z) = f(z)z$ is unimodal, rather than monotonically increasing. It is well-known that Ricker dynamics may give rise to chaotic dynamics, and this in turn can favor more mobile species under evolutionary pressure (Holt and McPeck 1996).

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Appendix

We rewrite the uncoupled system (1) as

$$x(t + 1) = A_1(x(t), \phi)x(t), \tag{27}$$

where

$$A_1(x, \phi) = \begin{pmatrix} 0 & f_M(x_M + px_N) & f_N(x_N + qx_M) \\ \phi s_M & 0 & 0 \\ (1 - \phi) s_N & 0 & 0 \end{pmatrix}$$

and $x = \begin{pmatrix} x_1 \\ x_M \\ x_N \end{pmatrix}$

When $\phi \neq 0$ and $\phi \neq 1$, this model has an important invariance property:

$$\frac{x_N(t)}{x_M(t)} = \frac{(1 - \phi) s_N}{\phi s_M} =: c_1(\phi) = c_1, \text{ for all } t = 1, 2, \dots \tag{28}$$

This means that the ratio of x_N and x_M is equal to the positive constant c_1 from time $t = 1$ onwards. In other words, all orbits reach the line $x_N/x_M = c_1$ in one time step and remain there forever after. Thus, the system reduces to a planar system, whose asymptotic behavior can be determined:

$$\begin{pmatrix} x_1(t + 1) \\ x_M(t + 1) \end{pmatrix} = \begin{pmatrix} 0 & f_M(d_{1p}x_M) + c_1 f_N(d_{1q}x_M) \\ \phi s_M & 0 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_M(t) \end{pmatrix}, \tag{29}$$

where $d_{1p} = c_1 p + 1$ and $d_{1q} = c_1 + q$. Note that since the functions g_M and g_N are increasing, where $g_M(z) = f_M(z)z$ and $g_N(z) = f_N(z)z$, the system (29) is monotone, and it has a positive fixed point $x^*(\phi) = (x_1^*, x_M^*)$.

The coupled model is:

$$\begin{pmatrix} x_1(t + 1) \\ x_M(t + 1) \\ y_1(t + 1) \\ y_M(t + 1) \end{pmatrix} = \begin{pmatrix} A_1(x(t) + y(t), \phi) & 0 \\ 0 & A_1(x(t) + y(t), \phi') \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_M(t) \\ y_1(t) \\ y_M(t) \end{pmatrix} \tag{30}$$

or more explicitly,

$$x_1(t + 1) = (f_M(d_{1p}x_M + d_{2p}y_M) + c_1 f_N(d_{1q}x_M + d_{2q}y_M)) x_M \tag{31}$$

$$x_M(t + 1) = \phi s_M x_1 \tag{32}$$

$$y_1(t + 1) = (f_M(d_{1p}x_M + d_{2p}y_M) + c_2 f_N(d_{1q}x_M + d_{2q}y_M)) y_M \tag{33}$$

$$y_M(t + 1) = \phi' s_N y_1 \tag{34}$$

where

$$c_2 = \frac{(1 - \phi') s_N}{\phi' s_M}$$

$$d_{2p} = 1 + pc_2$$

$$d_{2q} = c_2 + q$$

The system (30) has a fixed point at $X^*(\phi) = (x_1^*, x_M^*, 0, 0)$. From the PIP it is clear that ϕ^* is the only candidate for ESS. To prove that it is in fact an ESS, we perform a nonlinear stability analysis.

The nonlinear stability analysis when $q\hat{x}_M < \tilde{x}_N$ and $p\tilde{x}_N < \hat{x}_M$ hold

By means of the linear coordinate change

$$\tilde{X} = X - X^*(\phi^*),$$

we first translate the fixed point $X^*(\phi^*)$ of the K -monotone system (30) to the origin of \mathbb{R}^4 , and dropping tildes, we rewrite the transformed system, which is also K -monotone, as

$$X(t + 1) = F(X(t)). \tag{35}$$

We claim that as long as $\phi^* \neq \phi' \in (0, 1)$, the origin is an asymptotically stable fixed point for Eq. 35 with respect to perturbations $\Delta X = (\Delta x, \Delta y)$ near $X = 0$ for which Δx is arbitrary, but for which $\Delta y \geq 0$. We shall first show that there are two vectors $u_1 \leq_K 0$ and $0 \leq_K u_2$, such that the set $N = \{X \mid u_1 \leq_K X \leq_K u_2\}$ is a compact neighborhood of $X = 0$, and such that

$$u_1 \leq_K F(u_1) \leq_K 0 \leq_K F(u_2) \leq_K u_2. \tag{36}$$

To establish this claim, we first recall that Jacobian matrix $L(\phi^*, \phi')$ of $F(X)$ at $X = 0$ has eigenvalues L_{11} (which belongs to $(0, 1)$) and L_{22} (which equals 1 since $W(\phi^*, \phi') = 1$). By the Perron-Frobenius Theorem for K -monotone matrices (Vandergraft 1968), there exists an eigenvector $0 \leq_K V$ corresponding to the dominant eigenvalue 1. In fact, this eigenvector can be calculated explicitly, yielding:

$$V = \begin{pmatrix} -\frac{(d_{2p}f'_M + c_1d_{2q}f'_N)\phi'}{\phi(d_{1p}f'_M + c_1d_{1q}f'_N)} \\ -\frac{(d_{2p}f'_M + c_1d_{2q}f'_N)\phi's_M}{(d_{1p}f'_M + c_1d_{1q}f'_N)} \\ 1 \\ \phi's_M \end{pmatrix}$$

where we have dropped the arguments $d_{1p}x_M^*$ and $d_{1q}x_M^*$ of the derivatives f'_M and f'_N respectively, to economize on our notation. Note that V belongs to the interior of K for all $\phi' \in (0, 1)$. We now show that for all sufficiently small $\epsilon > 0$, there holds that $u_1 \leq_K F(u_1)$, when $u_1 = -\epsilon V$.

By using a Taylor expansion for F near $X = 0$,

$$F(u_1) = L(\phi^*, \phi')u_1 + h(u_1) + O(\|u_1\|^3) = u_1 + h(u_1) + O(\|u_1\|^3). \tag{37}$$

Here, $h = (h_1, h_2, h_3, h_4)^T$ with each $h_i(u_1) = u_1^T H_i u_1$ and H_i being the Hessian with respect to F_i . We have $h_2 = h_4 = 0$. We focus on finding the sign of $h_1(u_1)$ and $h_3(u_1)$.

We start by calculating $h_1(u_1) = u_1^T H_1 u_1$ where H_1 is the Hessian corresponding to F_1 . The reduced Hessian after dropping the zeros:

$$H_1^{red} = \begin{pmatrix} (H_1)_{22} & (H_1)_{24} \\ (H_1)_{24} & (H_1)_{44} \end{pmatrix}$$

where

$$\begin{aligned} (H_1)_{22} &= 2(d_{1p}f'_M + c_1d_{1q}f'_N) + x_M^*(d_{1p}^2f''_M + c_1d_{1q}^2f''_N) \\ (H_1)_{24} &= d_{2p}f'_M + c_1d_{2q}f'_N + x_M^*(d_{1p}d_{2p}f''_M + c_1d_{1q}d_{2q}f''_N) \\ (H_1)_{44} &= x_M^*(d_{2p}^2f''_M + d_{2q}^2c_1f''_N) \end{aligned}$$

We dropped the arguments $d_{1q}x_M^*$ and $c_1x_M^*$ of the derivatives f'_M, f''_M and f'_N, f''_N respectively, to economize on our notation throughout. A tedious calculation shows that $h_1(u_1) = u_1^T H_1 u_1 = ((u_1)_2, (u_1)_4) H_1^{red} \begin{pmatrix} (u_1)_2 \\ (u_1)_4 \end{pmatrix}$ can be simplified to:

$$h_1(u_1) = \frac{x_M^*(\phi's_M)^2}{(d_{1p}f'_M + c_1d_{1q}f'_N)^2} \left[(d_{1p}c_1d_{2q} - d_{2p}c_1d_{1q})^2 f'' + (f'_N)^2 + c_1(d_{1q}d_{2p} - d_{2q}d_{1p})^2 f''_N (f'_M)^2 \right]$$

Recall that $f''_M > 0, f''_N > 0$, and that $\phi^*, \phi' \in (0, 1)$ with $\phi' \neq \phi^*$. Moreover, $d_{1p}c_1d_{2q} - d_{2p}c_1d_{1q} \neq 0$ and $d_{1q}d_{2p} - d_{2q}d_{1p} \neq 0$. These facts imply that $h_1(u_1) > 0$, as claimed.

Similarly, $h_3(u_1) = u_1^T H_2 u_1$, where the reduced Hessian takes the form

$$H_3^{red} = \begin{pmatrix} (H_3)_{22} & (H_3)_{24} \\ (H_3)_{24} & (H_3)_{44} \end{pmatrix}$$

where

$$\begin{aligned} (H_3)_{22} &= 0 \\ (H_3)_{24} &= d_{1p}f'_M + c_1d_{2q}f'_N \\ (H_3)_{44} &= 2(d_{2p}f'_M + c_2d_{2q}f'_N) \end{aligned}$$

Another tedious calculation shows that $h_3(u_1)$ can be simplified to:

$$\begin{aligned} h_3(u_1) &= u_1^T H_3 u_1 = ((u_1)_2, (u_1)_4) H_3^{red} \begin{pmatrix} (u_1)_2 \\ (u_1)_4 \end{pmatrix} \\ &= 2 \frac{(\phi's_M)^2}{d_{1p}f'_M + c_1d_{1q}f'_N} \\ &\quad (c_1 - c_2)^2 (1 - pq) f'_M f'_N \end{aligned}$$

Using the facts that $f'_M, f'_N < 0, pq < 1$ and $c_1 - c_2 \neq 0$, we have $h_2(u_1) < 0$, as claimed.

The existence of a vector $0 \leq_K u_2$ such that $F(u_2) \leq_K u_2$ can be established as follows. We reconsider system (35) with $\phi = \phi^*$, and fixed, but arbitrary $\phi' \in (0, 1)$. Then, the

set $\{X = \begin{pmatrix} x_1 \\ x_M \\ y_1 \\ y_M \end{pmatrix} \mid y_1 = y_M = 0\}$ is invariant, and the

restriction of the monotone dynamics to this invariant set is such that all solutions with positive initial x -component converge monotonically to $x^*(\phi^*)$. Thus, there exists a positive vector b such that $0 \leq T(b) \leq b$ in R^2 , where $T(x)$ is the map on the right-hand side of equation (29) with $\phi = \phi^*$. Consequently, by setting

$$u_2 = \begin{pmatrix} b - x^*(\phi^*) \\ 0 \end{pmatrix},$$

it follows that $u_2 \geq_K 0$, and it can be verified that

$$F(u_2) = \begin{pmatrix} T(b) - x^*(\phi^*) \\ 0 \end{pmatrix} \leq_K \begin{pmatrix} b - x^*(\phi^*) \\ 0 \end{pmatrix} = u_2$$

Combining the existence of the vectors u_1 and u_2 with the properties listed above, and the fact that system (35) is K -monotone, establishes (36). Notice in particular that the vectors u_1 and u_2 are such that N is indeed a compact neighborhood of $X = 0$.

Now, since system (35) is K -monotone, Eq. 36 implies that the orbit starting at u_1 is increasing with respect to the partial order \leq_K , and bounded above (by the zero fixed point). Thus, it must converge to some fixed point X_1 in N . Similarly, K -monotonicity and (36) imply that the orbit starting in u_2 is decreasing with respect to the partial order \leq_K , and bounded below by the zero fixed point, and must also converge to some fixed point X_2 in N . We now claim that we can always shrink N by choosing $\epsilon > 0$ sufficiently small in the definition of u_1 , so that $X_1 = X_2 = 0$. Suppose that $(\tilde{x}_1, \tilde{x}_M, \tilde{y}_1, \tilde{y}_M)$ is any fixed point of system (35) in N , with $\tilde{y}_M, \tilde{y}_1 \geq 0$. If $\tilde{y}_M = 0$ or $\tilde{y}_1 = 0$, we first shrink N by choosing $\epsilon > 0$ sufficiently small in the definition of the vector u_1 , so that N does not include the fixed point $(-x^*(\phi^*), 0)$ of system (35). Then \tilde{x}_1 and \tilde{x}_M must also be equal to 0 since $(0, 0, 0, 0)$ is the unique fixed point in N of system (35) restricted to the invariant set where $y_M = y_1 = 0$. Therefore, any fixed point $(\tilde{x}_1, \tilde{x}_M, \tilde{y}_1, \tilde{y}_M)$ in N is necessary such that $\tilde{y}_M, \tilde{y}_1 \neq 0$. Thus, $(\tilde{y}_M, \tilde{y}_1)$ must necessarily be a positive vector because $\phi' \in (0, 1)$. Moreover, as shown above, for any fixed point $\tilde{x} = (\tilde{x}_1, \tilde{x}_M, \tilde{y}_1, \tilde{y}_M)$ in N , we have made sure that $\tilde{x} + x^*(\phi^*)$ is positive as well. Therefore, if N would contain a fixed point \tilde{x} , other than $X = 0$, then both $\tilde{x} + x^*(\phi^*)$ and \tilde{x} would be positive. Then, the original system (30) would have a positive fixed point as well which is not true, as we prove the system (30) can have at most one positive fixed point when $\phi = \phi^*$ and $\phi' \neq \phi^*$ as follows.

Let $(\tilde{x}_1, \tilde{x}_M, \tilde{y}_1, \tilde{y}_M)$ be a positive fixed point of Eq. 30

If we set

$$z_1 = d_{1p}\tilde{x}_M + d_{2p}\tilde{y}_M \tag{38}$$

$$z_N = d_{1q}\tilde{x}_M + d_{2q}\tilde{y}_M \tag{39}$$

then there must hold in particular that:

$$\begin{pmatrix} s_M\phi^* & c_{1s_M}\phi^* \\ s_M\phi' & c_{2s_M}\phi' \end{pmatrix} \begin{pmatrix} f_M(z_1) \\ f_N(z_2) \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}, \tag{40}$$

Let $B = \begin{pmatrix} s_M\phi^* & c_{1s_M}\phi^* \\ s_M\phi' & c_{2s_M}\phi' \end{pmatrix}$, and notice that $\det(B) = s_M s_N (\phi^* - \phi') \neq 0$ since $\phi' \neq \phi^*$. Hence, the system (40) can have at most one solution (z_1, z_2) because both functions f_M and f_N are decreasing, and are therefore

1-to-1 functions. Equations 38 and 39 can be re-written as follows:

$$\begin{pmatrix} d_{1p} & d_{2p} \\ d_{1q} & d_{2q} \end{pmatrix} \begin{pmatrix} \tilde{x}_M \\ \tilde{y}_M \end{pmatrix} = \begin{pmatrix} z_1 \\ z_2 \end{pmatrix} \tag{41}$$

Similarly, Eq. 41 has at most one solution $(\tilde{x}_M, \tilde{y}_M)$. Consequently, we have shown that the coupled system (30) can have at most one positive fixed point, as claimed.

By choosing $\epsilon > 0$ even smaller in the definition of u_1 , we can now ensure that the corresponding shifted fixed point for system (35), does not belong to N . Therefore, N is an isolating neighborhood for the fixed point $X = 0$, in the sense that it contains no other fixed points. In conclusion, we have proved the claim that $X_1 = X_2 = 0$ by appropriately choosing N , and therefore by K -monotonicity, all solutions in the compact, invariant neighborhood N , converge to $X = 0$. Going back to the original coordinates, we have proved that the fixed point $X^*(\phi^*)$ of the coupled system (30) is locally asymptotically stable, which completes the proof of the theorem.

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