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Seasonal density-dependence can select for partial migrants in migratory species

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Abstract

Whether, and which, individuals migrate or not is rapidly changing in many populations. Exactly how and why environmental change alters migration propensity is not well understood. We constructed density-dependent structured population models to explore conditions for the coexistence of migrants and residents. Our theoretical models were motivated by empirical data identified via a systematic literature review. We find that the equilibrium density in the season with the strongest density dependence of a strategy predicts whether the strategy will become dominant within the population. This equilibrium density represents strategy fitness in a seasonal environment and can be used to examine selection on migratory behavior. Whether partial migration can be maintained within a population depends on where in the annual cycle density dependence operates. Diversified bet-hedging, where parents produce a mix of migrants and residents, also maintains partial migration. Our study disentangles density-dependent and density-independent rates in a population with seasonal structure, potentially providing routes to explain the rapid change in migration strategies observed in many populations.

KEYWORDS
carrying capacity, density-dependence, migratory propensity, population structured model, rapid evolution, seasonal environment

INTRODUCTION

Changes in migration behavior have been widely reported in the face of rapid global change (Culbertson et al., 2022; Fiedler, 2003; Newton, 2010; Visser et al., 2009), with the migratory propensity of many populations rapidly shifting between being fully migratory, partially migratory, and fully resident. For example, house finch (*Haemorhous mexicanus*) populations that were originally resident became migratory over 30 years after being introduced to eastern North America (Able & Belthoff, 1998). In contrast, populations of other migratory species have become less migratory, including Eurasian blackbird (*Turdus merula*), white stork (*Ciconia ciconia*), elk (*Cervus elaphus*) and bull charr (*Salvelinus confluentus*) (Bolger et al., 2008; Flack et al., 2016; Fornasari et al., 2018; Nelson et al., 2002; Xu et al., 2021). Understanding how and why rapid changes in migratory propensity occur will allow us to better predict the consequences of environmental change on migratory behavior. Despite this, few studies have theoretically explored the drivers of change in migratory propensity.

Partial migration may be an evolutionary transient stage between fully migratory and fully resident (Berthold, 1996, 2001), which makes it an excellent system to study the evolution of migration strategy (Chapman et al., 2011; Gilroy et al., 2016; Lack, 1943; Reid et al., 2018). Theoretical studies prior to ours have largely focused on whether migrants and residents can coexist by identifying the evolutionary stable state of the population and suggest that density dependence plays an important role (Griswold et al., 2010; Kaitala et al., 1993; Kokko, 2011; Kokko & Lundberg, 2001; Lundberg, 1988, 2013; Ohms et al., 2019; Taylor & Norris, 2007). Empirical studies have also reported that density dependence in different seasons can affect partial migration, but that the life-history impacts of density dependence on migrants and residents do not appear to explain observed changes in migration propensity (Chapman et al., 2011). Migrants and residents have separate niches outside of the breeding season, although few studies have explored the interaction between density dependence in these different niches across seasons and how it might drive changes in migration propensity (but see, Taylor & Norris, 2007). The reason that such studies are important is that when different strategies coexist in a density-dependent nonseasonal environment, the strategy that can survive at the highest density is expected to become dominant (Kvalnes et al., 2022; Smallegange & Johansson, 2014; Svensson & Sinervo, 2000). In other words, in density-dependent nonseasonal environments, fitness is represented by the carrying capacity of a strategy (Charlesworth, 1994; Coulson et al., 2022; Kentie et al., 2020; Lande et al., 2009, 2017; Travis et al., 2023). Although density-dependent effects in nonmigratory species within constant environments are well understood, the implications of different density-dependent regimes across seasons for contrasting strategies have not been researched. Because population size fluctuates between seasons, the concept of carrying capacity does not easily translate to seasonal environments. Could the seasonal density-dependent regimes across different strategies help reconcile the currently contradictory empirical and theoretical results?

Migration is a strategy that frequently evolves in seasonal environments (Cox, 1968; Fretwell, 1972; Lack, 1968; Winger et al., 2019), so migratory species utilize both spatial and temporal variation in resources to maximize fitness. In partially migratory populations, migrants usually access resources that are not available to residents by escaping unfavorable environments, whereas residents usually have priority in occupying the best breeding territories (Alerstam et al., 2003; Fryxell & Sinclair, 1988). Migrants should compete with residents in the breeding season, while they compete only with individuals of their own type in the nonbreeding season, with such niche differences potentially promoting coexistence (Chesson, 2000). Different strategies may be limited in contrasting ways by density dependence in both the nonbreeding and breeding seasons, and this might feed through to impact their relative fitness. How does the interaction of competition between annual cycle stages across different environments impact the coexistence of migratory strategies?

The annual cycle stages of migrants are spatially separated but sequentially linked by their seasonal population dynamics (Catry et al., 2013; Liu et al., 2022; Norris & Marra, 2007), which means that carrying capacity may not always be an accurate predictor of fitness in populations that exhibit partial migration. Although the environments in which migration evolves may exhibit negative density dependence, migrants and residents potentially have different carrying capacities in the nonbreeding grounds if that is where density dependence operates, yet they will not be directly competing during this part of their annual cycle (Griswold et al., 2011; Ratikainen et al., 2008). When environmental changes operate differently on different parts of the annual cycle, the contrasting density-dependent regimes might lead to different trade-offs in life-history components across migrants and residents and result in negative frequency-dependent selection. The interaction between life-history trade-offs and population density might affect the maintenance of polymorphic strategies, then alter the population migratory propensity. Therefore, what determines strategy competitiveness in seasonal density-dependent environments, and how different density-dependent regimes might change their competitive relationship with one another, is central to understanding the evolution and coexistence of two migratory strategies within a population.

In this study, we investigate how different density-dependent regimes influence the evolutionary dynamics of population migratory propensity by developing a theoretical model. To better link the results of a theoretical model with empirical studies, our model is a population-structured model, which is motivated by empirical evidence from a literature review. In our model of a partially migratory population, migrants and residents share breeding grounds and overwinter apart. Based on such seasonal population structure, we constructed two monomorphic models, one with only migrants and the other with only residents, to calculate the strategy-specific equilibrium density for each season in the absence of between-strategy competition. We also developed a polymorphic model with two strategies competing in the same population to calculate the proportion of each strategy at equilibrium. We can thus explore when two strategies coexist and when they cannot by modeling different scenarios. We then examine how density-dependent reproduction, density-dependent winter survival, and density-independent impacts influence the population density in the breeding and nonbreeding seasons for both the monomorphic and polymorphic models, and affect the proportion of migrants in the polymorphic model. By analyzing these models, we identified three novel findings:

1. In seasonal environments, strategy fitness is predicted by the equilibrium strategy-specific density in the season with the strongest density dependence across the annual cycle. Density in this season then determines the dominant strategy in the polymorphic population.
2. Partial migration occurs in three situations when migrants and residents only produce their own type of offspring: no direct between-strategy competition occurs; two strategies compete directly with identical density-dependent and density-independent vital rates; and two strategies compete with trade-offs between density-dependent and density-independent processes. Partial migration also occurs when migrants and residents both produce offspring of both strategies.
3. The season with the strongest density dependence determines whether one strategy dominates or two strategies coexist within a population. When density dependence in the breeding season is the strongest, and where between-strategy competition operates, the dominant strategy outcompetes the other strategy and drives it extinct, and the population is either fully migratory or fully resident, determined by their respective strategy-specific density in the breeding season. When density dependence in the nonbreeding season is strongest and where within-strategy competition operates, the two strategies coexist in the population; the population is partially migratory, and the density in the nonbreeding season for each strategy determines their relative proportions.

REVIEW OF EMPIRICAL LITERATURE

We conducted a systematic search of empirical literature to gain insight into how density-dependent and density-independent processes affect population migratory propensity, and we used the information gained from the empirical studies to motivate the structure and analysis of our theoretical models.

First, we searched for studies published before 1 August 2023 using the keywords "(animal OR bird* OR avian OR mammal* OR fish OR insect* OR bat* OR whale*) AND (migration OR migratory OR migrating OR migrant* OR resident*) AND (partial* OR chang* OR shift*) AND (propensity OR tendency OR proportion) NOT (simulat* OR experiment*) NOT ('vertical migration' AND 'diel migration')" in the Web of Science, refining the results to relevant research areas, including: Biodiversity Conservation, Behavioral Sciences, Demography, Ecology, Environmental Sciences, Reproductive Biology and Zoology. Second, we conducted supplementary literature searches to identify publications cited in papers discovered via the keyword searches, which helped identify literature reviews and meta-analyses focusing on partial migration (Appendix S1: Section S1).

A total of 3737 studies were identified from the keyword searches. We filtered the studies according to the following criteria:

1. The study focused on partially migratory populations that contain migratory individuals and resident individuals. Differential strategies such as different migration distances in one population are not considered.
2. The study estimated at least one of the following parameters or relationships: the proportion of migrants (or residents), the proportion of migrants (or residents) as a function of time or an environmental driver, changes in potential drivers across years, demographic rates of migrants and residents, and the probability of passing the migration strategies from parents to offspring.

Of the studies identified, a substantial proportion documented partial migration, but most did not meet our second criterion. As a result, a total of 24 studies (19 different populations) were selected from both the keyword searches and supplementary literature searches, with taxa covered in these studies including birds, ungulates, and fish (Table 1, Appendix S1: Table S1). We summarized the potential mechanisms that are related to changes in population migratory propensity.

EMPIRICAL EVIDENCE: INSPIRATION FOR THEORETICAL MODELS

In the empirical studies we identified, the maintenance of, and changes in partial migration were studied by (1) investigating the relationship between population-level migration propensity and population density or

TABLE 1 Empirical evidence of potential density-dependent and density-independent processes in partial migrant populations.

Populations	Proportion of migrants	Vital rates	Population density and density-dependence	Density-dependence in the breeding season	Density-dependence in the nonbreeding season	Heritability/ plasticity	References
Blue tit (*Parus caeruleus*)	Increased	...	Increased in the breeding season, positively related to R_m	Uncertain	Residents: No temporal changes; positively related to R_m	...	Nilsson, Lindström, et al. (2006)
European shag (*Phalacrocorax aristotelis*)	Higher in extreme winters	Reproductive rate (mild winters): M < N Survival rate (extreme winters): M > N	...	...	...	...	Acker, Burthe, et al. (2021), Grist et al. (2017)
Great bustard (*Otis tarda*)	Decreased	Survival rate: M < N	Increased in the breeding season	Increased strength	Probably not density-dependent	...	Palacín et al. (2017)
Greater flamingo (*Phoenicopterus roseus*)	No temporal changes	Survival rate for juveniles: M < N Survival rate for adults: M > N	Density in the breeding season was not related to proportion of migrants for the first-year birds	...	Migrants: No temporal changes; negatively related to R_m	...	Sanz-Aguilar et al. (2012)
American dipper (*Cinclus mexicanus*)	35%	Reproductive rate: M < N Survival rate: M > N	...	...	...	Heritability: 0.38, 0.5 Individual switching rate: 0	Gillis et al. (2008), Green et al. (2015), Morrissey (2004)
Blackcap (*Sylvia atricapilla*)	Decreased	...	...	...	...	Heritability: 0.37–0.46	Berthold and Pulido (1997), Pulido and Berthold (2010)
European robin (*Erithacus rubecula*)	...	...	...	...	...	Heritability: 0.52	Biebach (1983)
European robin (*Erithacus rubecula*)	...	Reproductive rate: M ≈ N Survival rate: M < N	...	...	...	...	Adriaensen and Dhondt (1990)
Lanyu scops owl (*Otus elegans botelensis*)	53%–65%	Reproductive rate: M < N Survival rate: M > N	...	...	...	...	Bai et al. (2012)
Caribou (*Rangifer tarandus*)	Decreased	Survival rate: M > N	Decreased	...	Migrants: Increased strength	Individual switching rate: Increased	Williams et al. (2021)
Elk (*Cervus elaphus*) in BNP, Canada, 1972–2005[a]	Decreased	...	Density in the nonbreeding season was negatively related to R_m	Residents: Decreased strength, negatively related to R_m	Positively related to R_m	...	Hebblewhite et al. (2006)
Elk in BNP, Canada, 2002–2005[a]	Decreased	Demographic fitness: M ≈ N	Decreased	The strength for migrants was lower than residents	...	Individual switching rate: 0.02	Hebblewhite and Merrill (2007, 2011)
Elk in BNP Canada, 2002–2012[a]	Fluctuated	...	Decreased	...	Positively related to R_m	Individual switching rate: 0.15	Eggeman et al. (2016)
White-tailed deer (*Odocoileus virginianus*)[a]	Increased	...	Density in the nonbreeding season was negatively related to R_m	...	Increased strength, positively related to R_m	...	Fieberg et al. (2008)
Svalbard reindeer (*Rangifer tarandus platyrhynchus*)	Decreased	Reproductive rate: M > N	R_m was density-dependent	...	Migrants: Increased strength, positively related to R_m	...	Hansen et al. (2010)
Moose (*Alces alces*) in Poland[a]	Decreased	...	...	Migrants: Decreased strength, positively related to R_m	...	Individual switching rate: 0.22	Borowik et al. (2020)

TABLE 1 (Continued)

Populations	Proportion of migrants	Vital rates	Population density and density-dependence	Density-dependence in the breeding season	Density-dependence in the nonbreeding season	Heritability/plasticity	References
Moose in Norway[a]	29%	Reproductive rate: M > N Survival rate: M ≈ N	...	...	...	Individual switching rate: 0.06	Rolandsen et al. (2017)
Chinook salmon (*Oncorhynchus tshawytscha*)	...	...	Density in the breeding season was positively related to R_m	...	...	...	Sykes et al. (2009)
Arctic charr (*Salvelinus alpinus*)	Decreased	...	Density in the breeding season was positively related to R_m	Negatively related to R_m	...	...	Näslund et al. (1993)

Abbreviation: BNP, Banff National Park.

[a](1) Populations without asterisk are sharing-breeding ground partial migrants, and populations with asterisk are sharing nonbreeding ground partial migrants. (2) In the column of vital rates, "M > N" means the vital rate in migrants is larger than residents, and so on for "M < N" and "M ≈ N". Detailed information of density-dependent and density-independent processes of empirical studies can be found in Appendix S1: Table S1.

environmental factors, (2) comparing reproductive and survival rates between migrants and residents, and (3) exploring heritability and individual plasticity of migratory strategies (Table 1).

Of the 16 studies that estimated the proportion of migrants in the population, 10 of them documented rapid directional changes in migratory propensity over a few decades, and 8 of the 10 populations exhibited changes in density-dependent regimes in the breeding season and (or) the nonbreeding season. Density-dependence in different seasons usually had different impacts on reproductive and winter survival rates, so in our modeling exercise, we first separately explored the influence of density in each season on the population migration propensity and then examined the interactions across seasons.

In 12 studies that investigated the relationship between life-history components of the two strategies and the proportion of each strategy in the population, 11 studies focused on one or two vital rates, including annual and (or) lifetime reproductive success, pregnancy rate, twinning rate, winter and (or) annual survival rate, while one study estimated demographic fitness through multiple vital rates. Since limiting environments often affect reproductive rates in the breeding season and survival rates in the nonbreeding season, we considered density-dependent effects on these two vital rates in our models and examined the relationship between strategy-specific densities, the density of the polymorphic population, and the proportion of each strategy.

Six studies documented that an individual's rate of switching migratory strategy was between 0 and 0.22, and three studies reported that the heritability of migratory strategies was between 0.37 and 0.52, suggesting that environments can influence the migratory strategies of individuals. So, we incorporated a diversified bet-hedging process for the two strategies in our models.

THEORETICAL MODEL

Our modeling objective is to identify circumstances when fully migratory, fully resident, and partially migratory strategies evolve within a population. We do this by building a demographic model where we can modify when in the annual cycle density-dependent competition operates as well as the values of density-independent demographic rates. We identify a number of biological routes to both competitive exclusion of one strategy by another and coexistence, where partial migration is the evolutionarily stable strategy.

Motivated by our literature review, our model describes a simplified form of partial migration. It consists of residents and migrants that share a breeding ground but overwinter apart. We consider the breeding season (I) and the nonbreeding season (II) each year in our model. Individuals are categorized into six stages: resident juveniles (stage 1) that do not breed, resident young adults (stage 2) that breed, resident old adults (Stage 3) that have lower survival but breed, migratory juveniles (stage 4) that do not breed, migratory young adults (stage 5) that breed, and migratory old adults (stage 6) that have lower survival but breed. These age groups were chosen to capture a realistic life history of a bird species that shows senescence. The periodic stage structure is depicted as a life-cycle graph (Appendix S1: Figure S1). We assume that individuals follow the same strategy throughout life, and males are not limiting, such that our model is female dominant. Juveniles grow to the young adult stage after one nonbreeding season, and reproducing adults of each strategy produce both migrant and resident offspring at a ratio we specify.

We built a structured population model, with seasonal projection matrices capturing density-dependent and density-independent processes across the whole annual cycle for both migrants and residents. The matrices consist of functions describing how population size influences reproduction in the breeding season and survival in the nonbreeding season, with parameter estimates selected from the empirical studies we identified in our literature review. Since density-dependent reproductive and winter survival rates have been found for many migratory populations (Table 1), while density-dependent survival rates in the breeding season are less common (Fryxell & Holt, 2013), our model includes density-independent survival rates in the breeding season. Mortality during migration is usually density-independent, such that it was merged into the density-independent survival rates in the breeding and nonbreeding seasons to simplify the model structure. We do not explicitly incorporate genetic inheritance, but migratory and resident strategies are perfectly heritable in our model, and the model is deterministic in that rates are not stochastic. Matrices and vectors are shown as emboldened letters.

$\boldsymbol{B}_{\mathbf{I}}$ and $\boldsymbol{B}_{\mathbf{II}}$ are the projection matrices for the two seasons, and they can be specified to be density-dependent matrices. The population vectors for the start of the two seasons are: $\boldsymbol{N}_{\mathbf{I}}(t)$ and $\boldsymbol{N}_{\mathbf{II}}(t)$. The model is:

$$\boldsymbol{A}(\boldsymbol{N}(t)) = \boldsymbol{B}_{\mathbf{II}}(\boldsymbol{N}_{\mathbf{II}}(t))\boldsymbol{B}_{\mathbf{I}}(\boldsymbol{N}_{\mathbf{I}}(t)) \tag{1}$$

The matrix $\boldsymbol{A}(\boldsymbol{N}(t))$ projects the population through the whole year. $\boldsymbol{N}_{\boldsymbol{x}}(t)$ is projected from season x to season $x+1$ by matrix $\boldsymbol{B}_{\boldsymbol{x}}$, and year t is updated after each nonbreeding season (II). So, the population vectors for the two seasons are

$$\boldsymbol{N}_{\mathbf{II}}(t) = \boldsymbol{B}_{\mathbf{I}}(N_{\mathrm{I}})\boldsymbol{N}_{\mathbf{I}}(t) \tag{2}$$

$$\boldsymbol{N}_{\mathbf{I}}(t+1) = \boldsymbol{B}_{\mathbf{II}}(N_{\mathrm{II}})\boldsymbol{N}_{\mathbf{II}}(t) \tag{3}$$

And the population state vector is of the form:

$$\boldsymbol{N}_{\boldsymbol{x}}(t) = \begin{pmatrix} \eta_{x,1} \\ \eta_{x,2} \\ \eta_{x,3} \\ \eta_{x,4} \\ \eta_{x,5} \\ \eta_{x,6} \end{pmatrix}(t) \tag{4}$$

where $\eta_{x,i}$ indicates the number of individuals for stage i at season x, i ranges between 1 and 6, and $N_x(t) = \sum \eta_{x,i}(t)$.

The components of the population projection matrix

$\boldsymbol{B}_{\mathbf{I}}$ is a 6 × 6 demographic projection matrix that includes reproduction, survival, and transition rates in the breeding season. The reproductive rates are stage-specific and can be density dependent, such that

$$\boldsymbol{B}_{\mathbf{I}} = \begin{pmatrix} S_{\mathrm{I},1} & pS_{\mathrm{I},1}F_2(N_{\mathrm{I}},t) & pS_{\mathrm{I},1}F_3(N_{\mathrm{I}},t) & S_{\mathrm{I},1} & (1-q)S_{\mathrm{I},1}F_5(N_{\mathrm{I}},t) & (1-q)S_{\mathrm{I},1}F_6(N_{\mathrm{I}},t) \\ 0 & S_{\mathrm{I},2} & 0 & 0 & 0 & 0 \\ 0 & 0 & S_{\mathrm{I},3} & 0 & 0 & 0 \\ S_{\mathrm{I},4} & (1-p)S_{\mathrm{I},4}F_2(N_{\mathrm{I}},t) & (1-p)S_{\mathrm{I},4}F_3(N_{\mathrm{I}},t) & S_{\mathrm{I},4} & qS_{\mathrm{I},4}F_5(N_{\mathrm{I}},t) & qS_{\mathrm{I},4}F_6(N_{\mathrm{I}},t) \\ 0 & 0 & 0 & 0 & S_{\mathrm{I},5} & 0 \\ 0 & 0 & 0 & 0 & 0 & S_{\mathrm{I},6} \end{pmatrix}, \tag{5}$$

where $S_{\mathrm{I},i}$ is the survival rate of an individual in stage i in the breeding season, $F_i(N_{\mathrm{I}},t)$ is the reproduction function for an individual in stage i, p is the probability of residents producing residents, and q is the probability of migrants producing migrants (Appendix S1: Table S2). Survival in the breeding season is always density-independent.

The reproduction functions are described with the function:

$$F_i(N_{\mathrm{I}},t) = e^{(a_i + b_i N_{\mathrm{I}}(t))} \tag{6}$$

a_i is the intercept for stage i, which is the density-independent rate in the reproduction function, b_i is the slope for population size for stage i, which captures density-dependence in reproduction, N_{I} is the total population size at the start of breeding season at time t, $N_{\mathrm{I}}(t) = \sum \eta_{\mathrm{I},i}(t)$. To remove density-dependence from the function, we set $b_i = 0$.

$\boldsymbol{B}_{\mathbf{II}}$ is a 6 × 6 demographic projection matrix of winter survival rates and transition rates in the nonbreeding season, all juveniles grow to the young adult stage in the nonbreeding season, and the winter survival rates are stage-specific and can be density dependent, such that

$$\boldsymbol{B}_{\mathbf{II}} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ S_{\mathrm{II},1}(N_{\mathrm{II}},t) & (1-\mu_2)S_{\mathrm{II},2}(N_{\mathrm{II}},t) & 0 & 0 & 0 & 0 \\ 0 & \mu_2 S_{\mathrm{II},2}(N_{\mathrm{II}},t) & S_{\mathrm{II},3}(N_{\mathrm{II}},t) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_{\mathrm{II},4}(N_{\mathrm{II}},t) & (1-\mu_5)S_{\mathrm{II},5}(N_{\mathrm{II}},t) & 0 \\ 0 & 0 & 0 & 0 & \mu_5 S_{\mathrm{II},5}(N_{\mathrm{II}},t) & S_{\mathrm{II},6}(N_{\mathrm{II}},t) \end{pmatrix} \quad (7)$$

where μ_i is the probability that an individual in stage i grows to the next stage, $S_{\mathrm{II},i}(N_{\mathrm{II}},t)$ is the winter survival function for an individual in stage i in the nonbreeding season (Appendix S1: Table S2).

The winter survival functions $S_{\mathrm{II},i}(N_{\mathrm{II}},t)$ are described by:

$$S_{\mathrm{II},i}(N_{\mathrm{II}},t) = \frac{1}{1+e^{-(c_i + d_i N_{\mathrm{II}}(t))}} \quad (8)$$

c_i is the intercept for stage i, which is the density-independent winter survival rate, d_i is the slope for the population size of stage i, which captures density-dependence in winter survival. Migratory individuals and resident individuals overwinter apart in our model, so that when $i = 1, 2, 3$, $N_{\mathrm{II}}(t) = \sum_{i=1,2,3} \eta_{\mathrm{II},i}(t)$, while when $i = 4, 5, 6$, $N_{\mathrm{II}}(t) = \sum_{i=4,5,6} \eta_{\mathrm{II},i}(t)$. To remove density-dependence from a function, we set $d_i = 0$.

Polymorphic and monomorphic models

We call the above model the "polymorphic model", in which individuals of the two strategies compete in the breeding season. We use the polymorphic model to test whether migrants and residents coexist and how the migratory propensity of a population changes under different density-dependent regimes.

To calculate the strategy-specific equilibrium densities in the absence of between-strategy competition for two strategies under different density-dependent regimes, we set up two "monomorphic models": the "resident-only model" and the "migrant-only model." In the monomorphic models, only one strategy is in the population; parameters of the focal strategy are the same as in the polymorphic model for each density-dependence regime, whereas rows and columns for the other strategy are removed, and each strategy only produces the same type of offspring as the parents, where $p = q = 1$. The "resident-only model" and the "migrant-only model" are:

$$\boldsymbol{A}_{\boldsymbol{n}}(\boldsymbol{N}_{\boldsymbol{n}}(t)) = \boldsymbol{B}_{\mathbf{II},\boldsymbol{n}}(\boldsymbol{N}_{\mathbf{II},\boldsymbol{n}}(t))\boldsymbol{B}_{\mathbf{I},\boldsymbol{n}}(\boldsymbol{N}_{\mathbf{I},\boldsymbol{n}}(t)) \quad (9)$$

$$\boldsymbol{A}_{\boldsymbol{m}}(\boldsymbol{N}_{\boldsymbol{m}}(t)) = \boldsymbol{B}_{\mathbf{II},\boldsymbol{m}}(\boldsymbol{N}_{\mathbf{II},\boldsymbol{m}}(t))\boldsymbol{B}_{\mathbf{I},\boldsymbol{m}}(\boldsymbol{N}_{\mathbf{I},\boldsymbol{m}}(t)) \quad (10)$$

And the population state vectors for residents and migrants are in the form:

$$\boldsymbol{N}_{\boldsymbol{x},\boldsymbol{n}}(t) = \begin{pmatrix} \eta_{x,1} \\ \eta_{x,2} \\ \eta_{x,3} \end{pmatrix}(t) \quad (11)$$

$$\boldsymbol{N}_{\boldsymbol{x},\boldsymbol{m}}(t) = \begin{pmatrix} \eta_{x,4} \\ \eta_{x,5} \\ \eta_{x,6} \end{pmatrix}(t) \quad (12)$$

where the subscript n and m represent residents and migrants, respectively, $\boldsymbol{A}_{\boldsymbol{n}}(\boldsymbol{N}_{\boldsymbol{n}}(t))$ and $\boldsymbol{A}_{\boldsymbol{m}}(\boldsymbol{N}_{\boldsymbol{m}}(t))$ represent the projections of residents and migrants throughout the year. $\eta_{x,i}$ indicates the number of individuals for stage i at season x.

Model analysis

We start by setting $p = q = 1$ and all parameters equal between residents and migrants, establishing the polymorphic model as a baseline, where the two strategies coexist. We then analyzed the model in three steps. First, we explored the effect of density dependence in the breeding season, where both strategies had identical density-dependent reproductive rates but different density-independent winter survival rates; second, we explored the effect of density dependence when the strategies had different nonbreeding grounds, where the two strategies had identical density-independent reproductive rates and different density-dependent winter survival rates; third, we explored the interactions between different density-independent rates and the strength of density dependence in reproduction and winter survival functions for the two strategies across the two seasons. Lastly, we explored a diversified bet-hedging strategy by setting $p = q < 1$ (Figure 1, Table 2).

The monomorphic models and polymorphic model were set up synchronously for each step of the analysis to investigate the relationship between strategy-specific densities in the monomorphic populations, the density

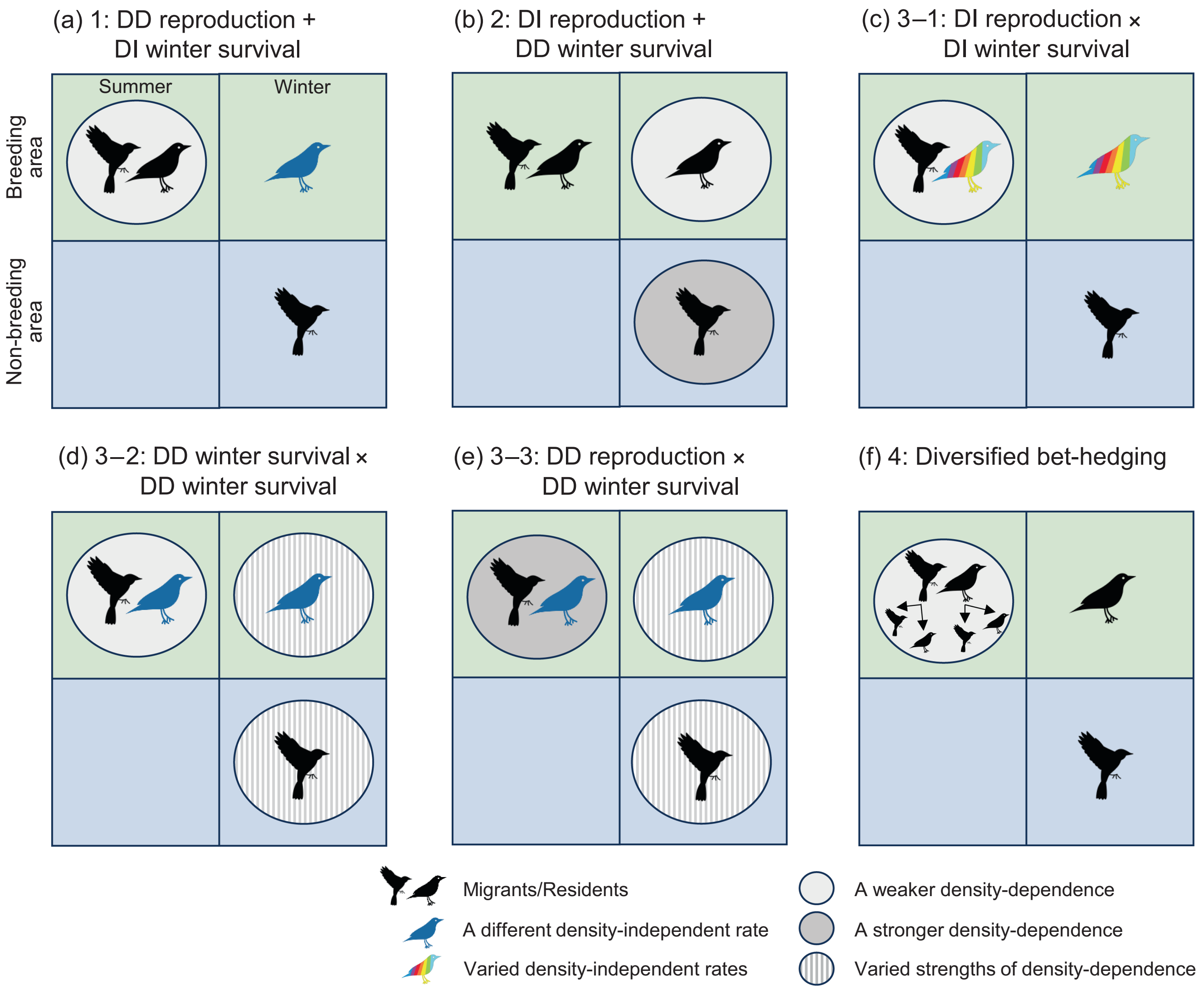

FIGURE 1 The four model scenarios that capture a range of different density-dependent regimes and a diversified bet-hedging strategy for a partially migratory population. (a) In scenario 1, migrants and residents have identical density-dependent reproductive rates but different density-independent winter survival rates, with $p = q = 1$. (b) In scenario 2, two strategies have identical density-independent reproductive rates and different density-dependent winter survival rates, with $p = q = 1$. Scenario 3 progressively introduces: (c) variation in density-independent rates for reproduction and winter survival of residents, with identical strength of density dependence on reproduction for both strategies (3–1); (d) variation in the strength of density dependence for winter survival for each strategy (3–2); (e) stronger density dependence on reproduction, combined with variation in the strength of density dependence for winter survival for each strategy (3–3). (f) In scenario 4, both migrants and residents can produce offspring of the two strategies, where $p = q < 1$. DD represents the strength of density dependence and DI represents density-independent rates. The silhouettes of resident and migrant are created by MD RIDUWAN MOLLA and Softscape respectively from Noun Project under CC BY-3.0 License (https://thenounproject.com/icon/bird-3237799/, https://thenounproject.com/icon/bird-4610156/), resident's silhouettes are colorized in panel (a), (c–e) and the legend.

TABLE 2 Key parameters in the theoretical model.

Parameters	Definitions
a_i	Density-independent rate in reproduction function for stage *i*
b_i	Strength of density-dependence in reproduction function for stage *i*
c_i	Density-independent rate in winter survival function for stage *i*
d_i	Strength of density-dependence in winter survival function for stage *i*
p	The probability of producing resident juveniles by resident adults
q	The probability of producing migratory juveniles by migratory adults
$k_{x,n}$	Strategy-specific density of residents at equilibrium at the start of season *x* in the resident-only model
$k_{x,m}$	Strategy-specific density of migrants at equilibrium at the start of the season *x* in the migrants-only model
Δk_x	Difference between the strategy-specific densities of migrants and residents at the start of season *x*
${k_{x,n}}^0$	Strategy-specific density of residents at equilibrium at the start of season *x* in the resident-only model, where density-dependence operates only in the breeding season
${k_{x,m}}^0$	Strategy-specific density of migrants at equilibrium at the start of season *x* in the migrant-only model, where density-dependence operates only in the breeding season
$K_{x,n}$	Density of residents at equilibrium at the start of season *x* in the polymorphic model
$K_{x,m}$	Density of migrants at equilibrium at the start of season *x* in the polymorphic model
R_m	The proportion of migrants at equilibrium in the polymorphic model

of each strategy in the polymorphic population, and the proportion of migrants within the polymorphic population. We calculated the population density of each strategy in each season once the model had reached a stationary state (equilibrium). Because the model was seasonal, the stationary dynamics were cyclical.

Scenario 1. Identical density-dependent reproductive rates in the breeding season but different density-independent survival rates in the nonbreeding season.

In the density-dependent reproduction scenario, we had identical density-independent rates in the reproduction functions (a_i) for residents and migrants and we set the strength of density-dependence in the reproduction function for both strategies as $b_i = -0.001$. We removed density-dependence from the winter survival functions for residents and migrants, such that $d_{i(i=1,2,3)} = 0$ and $d_{i(i=4,5,6)} = 0$, and set different density-independent rates in the winter survival functions (c_i) for the two strategies (Figure 1a).

Scenario 2. Identical density-independent reproductive rates in the breeding season but different density-dependent survival rates in the nonbreeding season.

In the density-dependent winter survival scenario, we removed density-dependence from the reproduction function by setting $b_i = 0$, and set the density-independent rates in the reproduction functions (a_i) for residents and migrants as being equal. We set the strength of density-dependence in the winter survival functions as $d_{i(i=1,2,3)} = -0.001$ and $d_{i(i=4,5,6)} = -0.002$ for residents and migrants respectively, and the density-independent rates in winter survival functions (c_i) for two strategies were kept equal (Figure 1b).

Scenario 3. Interactions between different density-independent rates and the strength of density-dependence in both reproduction and winter survival.

To explore the interactions between density-independent rates and the strength of density-dependence in the reproduction and winter survival functions for both strategies, we broke down three progressive parts in this model. First, in the scenario of varying density-independent rates of reproduction and winter survival (scenario 3–1), we built on the density-dependent reproduction scenario (scenario 1), kept the density-independent rates in the reproduction (a_5 and a_6) and winter survival functions (c_4, c_5 and c_6) for migrants fixed, and introduced 25 different combinations of density-independent rates in these functions for residents (a_2 and a_3 for reproduction, c_1, c_2 and c_3 for winter survival) (Figure 1c).

Second, in the scenario of varying density dependence in winter survival (scenario 3–2), we investigated the interaction between the strength of density dependence in the winter survival function for the two strategies and its effects. We selected a combination of density-independent rates in the reproduction (a_i) and winter survival functions (c_i) for residents and migrants from scenario 3–1 (Appendix S1: Table S3), which allows migrants to be the dominant strategy when density dependence operates only in the breeding season. We kept these density-independent rates fixed for both strategies and maintained the same density dependence in the reproduction function (b_i) as in scenario 3–1. We perturbed the strength of density dependence of the winter survival functions for the two strategies, where $d_{i(i=1,2,3)} \in [-0.001,0]$ and $d_{i(i=4,5,6)} \in [-0.001,0]$ with increments of 0.0002 (Figure 1d).

Third, in the scenario of varying density dependence across two seasons (scenario 3–3), we investigated the interaction between the strength of density dependence in both reproduction and winter survival functions for the two strategies and its effects. Based on scenario 3–2, we introduced stronger density dependence in the reproduction function (the value becoming more negative), where $b_i = -0.002$, while keeping density-independent rates in both demographic functions (a_i and c_i) and the strength of density dependence in the winter survival functions (d_i) for the two strategies the same as in scenario 3–2 (Figure 1e). We also investigated how the different density-dependent reproductive rates for the two strategies interact with a range of density-dependent winter survival rates. To do so, we kept the strength of density dependence in the reproduction function of migrants ($b_{i(i=5,6)}$) the same as in scenario 3–2, while setting the strength of density dependence in the reproduction function of residents to be stronger, equal to, or weaker than that of migrants, where $b_{i(i=2,3)} = \{-0.0015, -0.001, -0.0005\}$, and kept density-independent rates in both demographic functions as well as the strength of density dependence in the winter survival function the same as in scenario 3–2 (Appendix S1: Figure S2).

For scenarios 1–3, we first calculated the equilibrium strategy-specific densities for both migrants and residents in the absence of between-strategy competition, using the monomorphic models. We reported results at equilibrium population density, where the eigenvalue of the population projection matrix $\boldsymbol{A}$ is equal to one. The population density was the sum of the number of individuals in each stage class. We denoted the strategy-specific densities for two strategies at the start of the breeding season (I) and the nonbreeding season (II) as $k_{\mathrm{I},n}$, $k_{\mathrm{I},m}$ and $k_{\mathrm{II},n}$, $k_{\mathrm{II},m}$. We calculated the differences in strategy-specific equilibrium densities between two strategies in two seasons, denoting them as Δk_{I} and Δk_{II}, where $\Delta k_{\mathrm{I}} = k_{\mathrm{I},m} - k_{\mathrm{I},n}$ and $\Delta k_{\mathrm{II}} = k_{\mathrm{II},m} - k_{\mathrm{II},n}$.

Next, from the polymorphic model, we calculated the proportion of the population that consists of migrants (R_m) at the start of the nonbreeding season from $\boldsymbol{N}_{\mathbf{II}}$ and calculated the equilibrium densities for two strategies at the start of each season, which were denoted as $K_{\mathrm{I},n}$, $K_{\mathrm{I},m}$, $K_{\mathrm{II},n}$, and $K_{\mathrm{II},m}$. Model results were also reported at equilibrium. We examined the relationship between Δk, K, and R_m.

Scenario 4. A diversified bet-hedging strategy.

We also explored how bet-hedging affects the coexistence of two strategies. To do this, based on the parameters of the density-dependent reproduction scenario, where migrants drove residents extinct, we perturbed the value of p and q from 0.1 to 1 in increments of 0.1, with the constraint that $p = q$ (Figure 1f). At each p and q value, we calculated the R_m and the proportion of each stage class from the polymorphic model at equilibrium.

MODEL RESULTS

Scenario 1: identical density-dependent reproductive rates but different density-independent winter survival rates

In the baseline polymorphic model, when two strategies have identical density-dependent and density-independent rates in reproduction and winter survival functions in both seasons, unsurprisingly the two strategies coexist, and the R_m depends upon the starting conditions of the simulation. For example, when each stage class has an identical number of individuals in the initial population, migrants and residents coexist with 50% of each strategy in the population (Appendix S1: Figure S3).

In the density-dependent reproduction scenario, when migrants and residents experienced identical density dependence in the breeding season but had different density-independent winter survival rates in the nonbreeding season, the two strategies competed against one another directly. The strategy with the highest density-independent winter survival rate had the highest strategy-specific density at the start of the breeding season in the monomorphic model (Figure 2a) and dominated the polymorphic population, driving the other strategy extinct (Figure 2b). The population density in the polymorphic model was equal to the strategy-specific density of the dominant strategy in the monomorphic model, where $K_{\mathrm{I}} = k_{\mathrm{I},m}$, $K_{\mathrm{II}} = k_{\mathrm{II},m}$, $R_m = 1$.

Scenario 2: identical density-independent reproductive rates but different density-dependent winter survival rates

In the density-dependent winter survival scenario, when the two strategies had identical density-independent rates for both reproduction and winter survival but differed in the strength of density dependence in winter survival, the two strategies coexist (Figure 2c,d). This is because when density dependence only operates in the nonbreeding

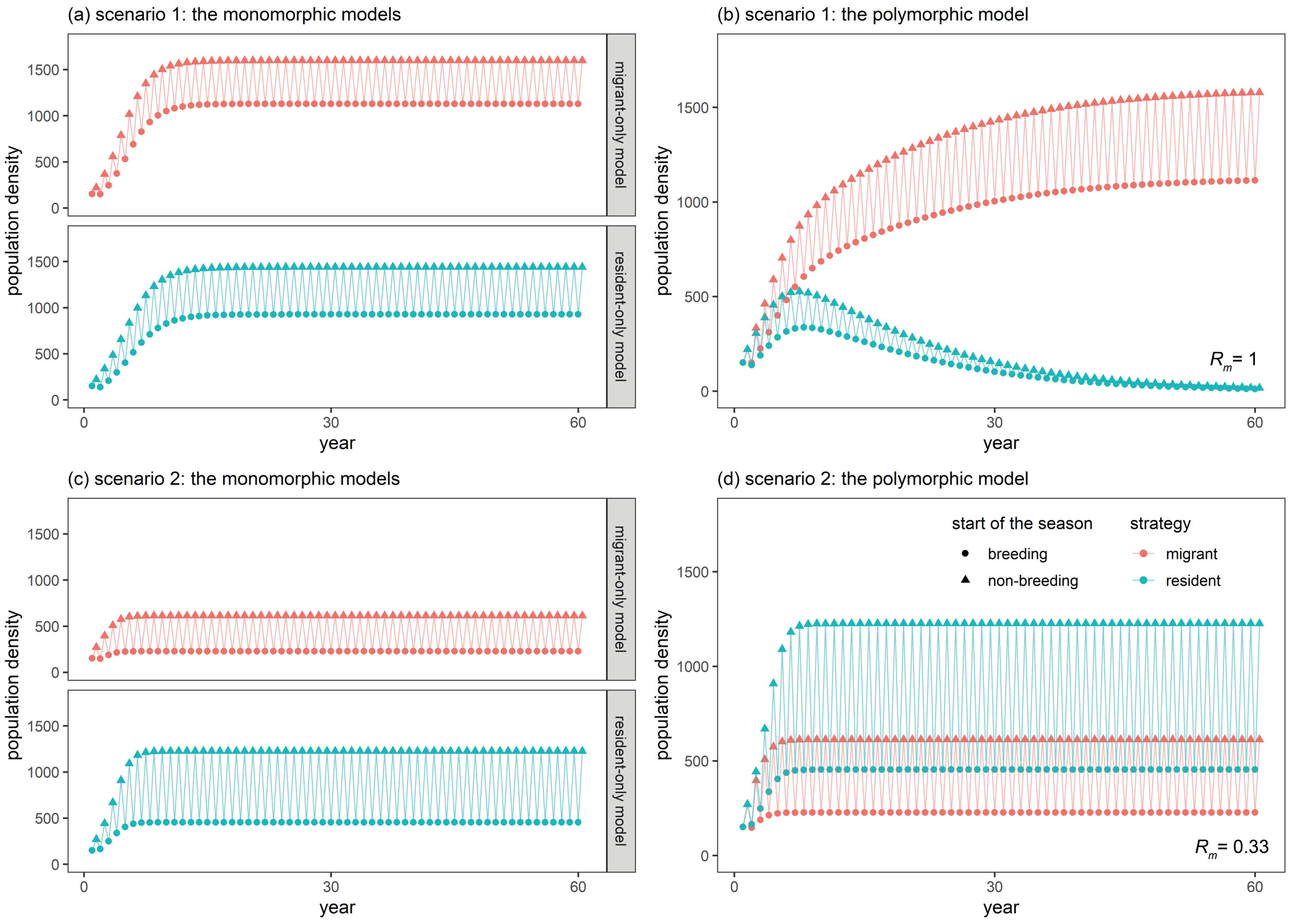

FIGURE 2 Seasonal population dynamics and the coexistence of two strategies when density dependence operates in only one season. In scenario 1, the population dynamics of two strategies in the monomorphic models (a) and in the polymorphic model (b); in scenario 2, the population dynamics of two strategies in the monomorphic models (c) and in the polymorphic model (d). Only 60 years of the simulation are shown in the figure. Color represents the type of migratory strategy, and shape represents the season.

season, the two strategies do not compete, as density dependence does not operate when they are in the same location. The population density in the polymorphic model was equal to the sum of strategy-specific densities of the two strategies, and the proportion of each strategy depends on the relative strength of density dependence in the nonbreeding season, with the strategy having the weakest density dependence being more common. Such that, $K_{\text{I}} = k_{\text{I},m} + k_{\text{I},n}$, $K_{\text{II}} = k_{\text{II},m} + k_{\text{II},n}$, $R_m = k_{\text{II},m}/(k_{\text{II},m} + k_{\text{II},n})$.

Scenario 3: interactions between density-independent rates and the strength of density dependence in both reproduction and winter survival

In the scenario of varying density-independent rates in both reproduction and winter survival, only one strategy persisted when the simulation reached equilibrium (Figure 3a). Here we refer to $k_{x,n}{}^0$ and $k_{x,m}{}^0$ for $k_{x,n}$ and $k_{x,m}$ when $d_i = 0$. The interactions of different density-independent rates of reproduction and winter survival functions for a strategy affected the strategy-specific density in the monomorphic models and population density in the polymorphic model. In the polymorphic model, the strategy with the highest strategy-specific density at the start of the breeding season was dominant, driving the other one extinct, such that when $k_{\text{I},m}{}^0 > k_{\text{I},n}{}^0$, then $K_{\text{I}} = k_{\text{I},m}{}^0$, $K_{\text{II}} = k_{\text{II},m}{}^0$, and $R_m = 1$; or when $k_{\text{I},m}{}^0 < k_{\text{I},n}{}^0$, then $K_{\text{I}} = k_{\text{I},n}{}^0$, $K_{\text{II}} = k_{\text{II},n}{}^0$, and $R_m = 0$. When densities at the start of the breeding season were identical between the two strategies, they coexist, where $k_{\text{I},m}{}^0 = k_{\text{I},n}{}^0$, $k_{\text{II},m}{}^0 = k_{\text{II},n}{}^0$, then $R_m = 0.5$ (Figure 3d).

In the scenario of varying density dependence in winter survival, where migrants had the highest strategy-specific density at the start of the breeding season, we increased the strength of density dependence in the winter survival rates (the value of d_i being more

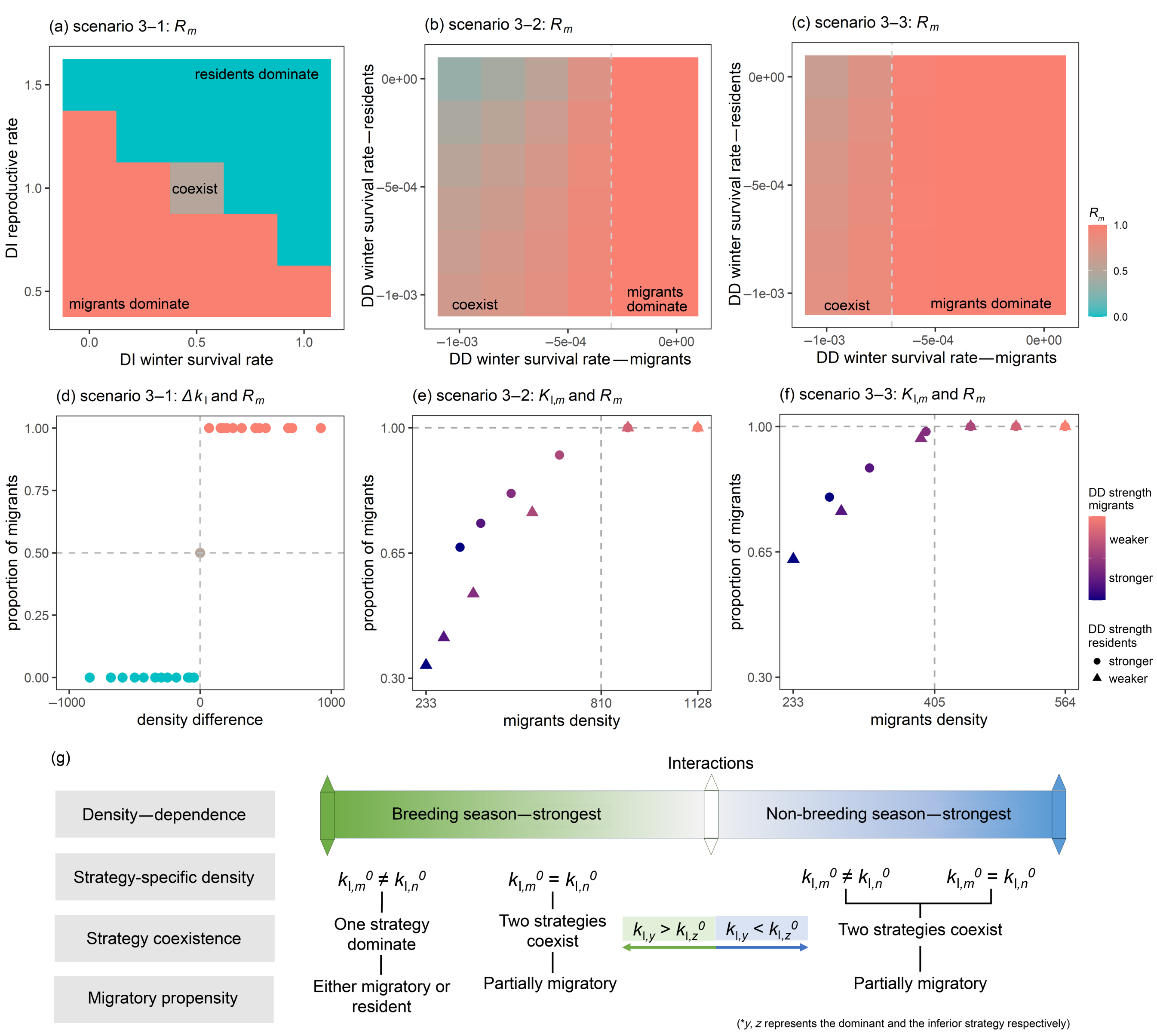

FIGURE 3 The proportion of migrants (R_m), population density at equilibrium in the polymorphic model (K), and strategy-specific density at equilibrium in the monomorphic model (k) under the interaction of density-dependent strength and density-independent rates in scenario 3. (a–c) The R_m in scenario 3–1, 3–2, and 3–3; (d) the relationship between the difference in strategy-specific densities (Δk_I) and R_m in scenario 3–1; (e–f) the relationship between migrant density in the polymorphic model ($K_{I,m}$) and R_m in scenario 3–2 and 3–3; (g) The summarized diagram of selection on population migratory propensity under different density-dependent and density-independent regimes. In (a–d), color represents the value of R_m. In (e) and (f), color represents the strength of density-dependence in the winter survival function for migrants ($d_{i(i=4,5,6)}$), shape represents the strength of density-dependence in the winter survival function for residents ($d_{i(i=1,2,3)}$), the horizontal dashed line shows where $R_m = 1$. In (b), (c), (e) and (f), the vertical dashed line shows where the population switches from fully migrants to partial migrants. DD represents the strength of density-dependence and DI represents density-independent rates.

negative) for the two strategies in both the monomorphic and polymorphic models. The original fully migratory population can be replaced by a partially migratory population, and whether the population migratory propensity would change depends on a threshold (Figure 3b).

The threshold value was the strategy-specific density of the inferior strategy (resident behavior) at the start of the breeding season, when density dependence operates only in the breeding season ($k_{I,n}{}^0$). As the strength of density dependence in winter survival for migrants increased (the value of $d_{i(i=4,5,6)}$ was more negative), the strategy-specific densities in the monomorphic model and population densities in the polymorphic model of migrants in the two seasons both decreased (Appendix S1: Table S3). As long as $k_{I,m} > k_{I,n}{}^0$, the between-strategy competition in the breeding season was stronger than the within-strategy competition in the nonbreeding season for migrants; migratory behavior was the dominant strategy in the population, the density of migrants in the polymorphic model was equal to its strategy-specific density, where $K_{\mathrm{I},m} = k_{\mathrm{I},m}$, and the increased strength of density dependence of winter survival for migrants had no effect on R_m. The population was fully migratory ($R_m = 1$). However, when $k_{\mathrm{I},m} < k_{\mathrm{I},n}{}^0$, the within-strategy competition in the nonbreeding season for migrants was stronger than the between-strategy competition in the breeding season. As a result, the density of migrants in the polymorphic model was lower than their strategy-specific density, where $K_{\mathrm{I},m} < k_{\mathrm{I},m}$; an increased strength of density dependence in winter survival for migrants led to decreases in R_m, while an increased strength of density dependence in winter survival for residents led to increases in R_m. The population was partially migratory ($0 < R_m < 1$) (Figure 3e). The border between the two regions indicates whether density dependence is strongest in the breeding season or the nonbreeding season across the annual cycle.

Under stronger density-dependent reproduction for both migrants and residents (Figure 3c,f), or varying density-dependence of reproduction for the two strategies (Appendix S1: Figure S2), the threshold value was affected. However, it still represented the strategy-specific density of the inferior strategy at the start of the breeding season, when density-dependence operates only in the breeding season ($k_{\mathrm{I},n}{}^0$ or $k_{\mathrm{I},m}{}^0$). The relative relationship between the strategy-specific densities of the two strategies still held true, determining whether the population is fully migratory (or fully resident) or partially migratory (Figure 3g). Therefore, the strategy-specific density in the season with the strongest density-dependence is the key to affecting population migratory propensity.

Scenario 4: a diversified bet-hedging strategy

Diversified bet-hedging leads to the coexistence of the two strategies and the persistence of partial migration. Since the density-dependent regime in this scenario favored migrants, R_m was greater than 0.5 in all simulations. As p and q decreased, each strategy produced more offspring of the other strategy, leading to a decrease in R_m (Figure 4).

DISCUSSION

Rapid evolution of phenotypic traits is an increasingly observed phenomenon in the face of recent global change. We built structured population models to explore factors associated with the evolution of polymorphic migratory strategies. By analyzing our models, we defined strategy fitness in seasonal environments, which is the key to determining whether the population exhibits fully migratory, partially migratory, or fully resident behavior under a range of density-dependent regimes. We found that partial migration occurs in three situations when parents only produce the same strategy of offspring: strategies do not compete; the strategies have identical density-dependent and -independent responses to the environment; and when trade-offs exist between the strength of density dependence and density independence across seasons. Partial migration also occurs when a diversified bet-hedging strategy exists.

We defined fitness for a population with seasonal structure as the density in the season with the strongest density dependence and showed that this is a key parameter in determining coexistence, or not, of migratory strategies. Since environmental changes can simultaneously affect multiple demographic factors in populations (Table 1), evolution is expected to minimize the demographic rate that is most strongly influenced by density (Travis et al., 2023). Considering only one or a few demographic rates might lead to either positive or negative relationships with population migratory propensity (Kaitala et al., 1993; Taylor & Norris, 2007). Previous models have pointed out the importance of mean population size at equilibrium in the selection of migratory propensity; however, these models have not incorporated the seasonal dynamics of migratory populations (Griswold et al., 2011; Ohms et al., 2019). Populations with a seasonal migratory lifestyle exhibit regular intra-annual structure (Hostetler et al., 2015; Reid et al., 2018), and density in one annual cycle stage can have impacts on the following stages via sequential density dependence (Catry et al., 2013; Harrison et al., 2011; Ratikainen et al., 2008). Therefore, our results indicated that densities in the season with the strongest density dependence determine the proportion of migrants in the population, rather than densities in the other season.

In our models, density dependence in the breeding and nonbreeding seasons has different effects on within- and between-strategy competition in a partially migratory population. When between-strategy competition is strongest, selection is expected to favor either a fully migratory or a fully resident strategy in the population. In contrast, when within-strategy competition is strongest, selection tends to favor partial migration. The results of our first two scenarios, where density-dependent competition occurs in only one season, are consistent with previous models (Kaitala et al., 1993; Ohms et al., 2019; Taylor & Norris, 2007). The results from our third scenario

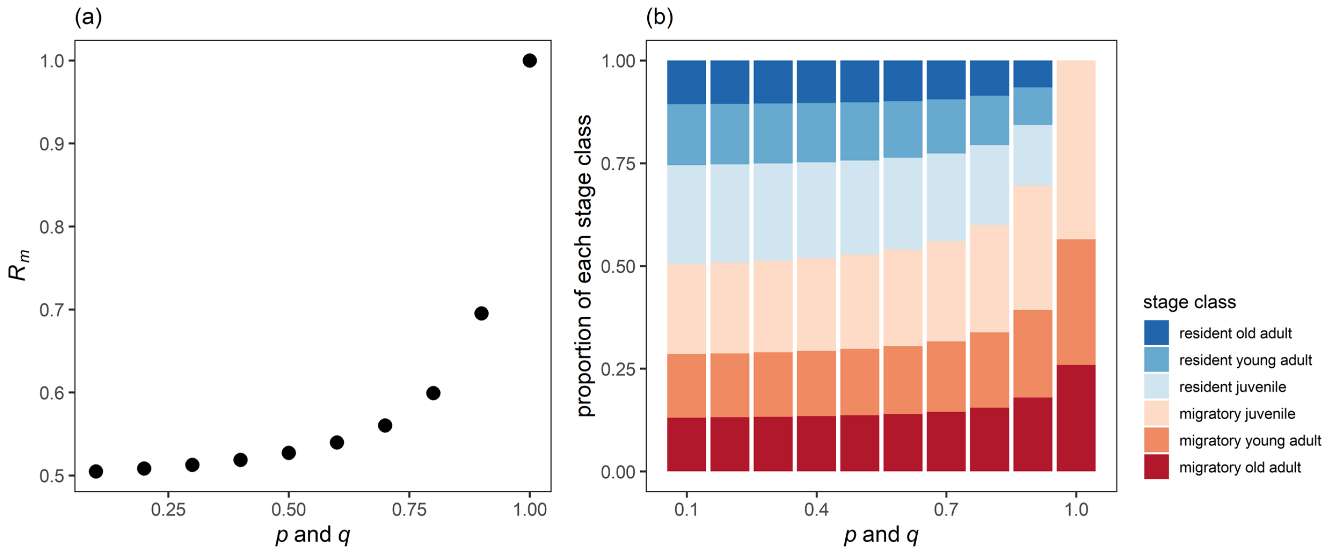

FIGURE 4 Diversified bet-hedging effect on the proportion of migrants (R_m) and the proportion of each strategy in the polymorphic model. (a) The effects of changing p and q on R_m. (b) The effects of changing p and q on the proportion of each stage class; color represents the stage class.

further provide insights into the interactions of density dependence across different seasons, a process that has received limited attention in previous studies (but see Griswold et al., 2010). Identical density-dependent and density-independent vital rates are rare in empirical studies (Table 1), since migrants and residents usually have different life-history components throughout their lifetimes (Buchan et al., 2020; Soriano-Redondo et al., 2020), in different seasons and environmental conditions (Acker, Daunt, et al., 2021; Grist et al., 2017) or at different ages (Sanz-Aguilar et al., 2012). However, balanced population growth rates between the two strategies have been found in an elk population, allowing partial migration to persist (Hebblewhite & Merrill, 2011), which is also consistent with previous theoretical predictions (Kokko, 2011; Lundberg, 1987). Although it is difficult to tell whether empirical studies in our literature review that do not show density-dependent effects in the breeding season fit the condition of no direct competition, or they simply did not explore such a mechanism, the relationships between changes in density dependence in the nonbreeding season and the proportion of migrants in these studies are consistent with our model predictions. Specifically, increases in density dependence in the nonbreeding season for a strategy decrease the proportion of the focal strategy in the population, as seen in blue tit (Nilsson, Lindström, et al., 2006), greater flamingo (Sanz-Aguilar et al., 2012), caribou (Williams et al., 2021) and Svalbard reindeer populations (Hansen et al., 2010).

The interaction of density-dependence across seasons balances the within- and between-strategy competition in the population; therefore, selecting for partial migration. This finding is consistent with the modern coexistence theory of species, but in our case applies to strategies. The theory focuses on the stabilizing mechanism that derives from niche differences and the equalizing mechanism that reduces fitness differences (Chesson, 2000). Since migrants and residents breed together but overwinter in different habitats, the niche differentiation of migrants and residents is a stabilizing mechanism, resulting in direct between-strategy competition operating only in one season. The interaction between the density-independent rates and the strength of density-dependence within a season is an equalizing mechanism, which reduces the difference in strategy-specific densities at equilibrium, allowing two strategies to coexist. Our findings not only support the importance of density-dependence in maintaining partial migration (Griswold et al., 2011; Holt & Fryxell, 2011; Kaitala et al., 1993; Kokko, 2011; Kokko & Lundberg, 2001; Taylor & Norris, 2007), but also demonstrate that the interaction of density-dependence between seasons is important to consider in studying migratory propensity. Additionally, density in the season with the strongest density-dependence can be the currency when examining the relationship between changes in density-dependence and changes in migratory strategy (Figure 3g).

Although we did not explicitly include environmental changes in our models, changes in density-dependent regimes can be influenced by environmental factors such as food resources, predation, habitat conditions, or parasitism (Bonenfant et al., 2009; Fryxell & Holt, 2013; Griswold et al., 2010; Sutherland & Dolman, 1994; Travis et al., 2023). Our model predictions offer a path to understanding the effects of environmental changes on migratory strategies. In our reviewed empirical studies, more than half reported that population density during a season is directly correlated with the proportion of migrants in the population (Table 1; Appendix S1: Table S2). Examples include blue tit (*Parus caeruleus*) (Nilsson, Lindström, et al., 2006), elk (*C.elaphus*) (Hebblewhite & Merrill, 2007, 2011), white-tailed deer (*Odocoileus virginianus*) (Fieberg et al., 2008), Svalbard reindeer (*Rangifer tarandus platyrhynchus*) (Hansen et al., 2010), chinook salmon (*Oncorhynchus tshawytscha*) (Sykes et al., 2009) and Arctic charr (*Salvelinus alpinus*) populations (Näslund et al., 1993).

Moreover, existing studies have investigated the interactions of potential density-dependent processes between seasons in elk, blue tit, and great bustard (*Otis tarda*) populations (Table 1). The results for blue tit and great bustard are largely in line with our model predictions, where increased density dependence in the breeding season enlarged the advantages of residents with higher demographic rates (Palacín et al., 2017), and increased density dependence in the nonbreeding season for residents reduced its proportion (Nilsson, Lindström, et al., 2006). Although elk display partial migration with shared nonbreeding grounds, where the seasons of within- and between-strategy competition are reversed compared with our model settings, the results are still comparable with our models. In particular, in the nonbreeding grounds, abundant food resources reduced the between-strategy competition and promoted the coexistence of two strategies; in the breeding ground, habitat enhancement for residents decreased within-strategy competition, such that the proportion of migrants decreased (Hebblewhite et al., 2006). Although densities of the two strategies were not investigated for the population between 1976 and 2005 (Hebblewhite et al., 2006), migrants and residents had balanced demographic fitness between 2002 and 2005 (Hebblewhite & Merrill, 2007, 2011). As we have shown, most of the studies focus on one or two demographic rates and density dependence in part of the annual cycle to explore changes in migration propensity (Table 1). This is insufficient to fully understand the evolutionary dynamic of migratory behavior in populations with seasonal structure. It is necessary to investigate the dynamic across the entire annual cycle (Gaillard, 2013; Reid et al., 2018) and identify where the density-dependent process operates most strongly.

Apart from seasonal density dependence, our results show that the coexistence of migrants and residents always occurs when each strategy can produce offspring of either strategy. This is consistent with previous findings that negative frequency dependence and diversified bet-hedging can promote the maintenance of partial migration (Biebach, 1983; Davies et al., 2012; Fitzpatrick et al., 2007; Lundberg, 1987). Although our model did not consider the mechanism at the genotype level, we used the probability of producing each type of offspring to mimic the process of diversified bet-hedging for strategies. When individuals can produce two types of offspring, regardless of the value of the probability, the difference in equilibrium densities between the two strategies reduces, resulting in the coexistence of the two strategies. Migration can be heritable (Berthold, 1996, 1999; Lack, 1943; Liedvogel et al., 2011; Nice, 1937; Pulido et al., 1996), and empirical studies show that the heritability of migratory strategy is often less than one (Table 1), suggesting that environments can affect the strategy of offspring. Apart from that, individuals can switch migratory strategies within their lifetime, as we found in caribou (Williams et al., 2021), elk (Eggeman et al., 2016; Hebblewhite & Merrill, 2007, 2011) and moose populations (Borowik et al., 2020; Rolandsen et al., 2017). Although individual plasticity can have impacts on the persistence of partial migration (Payo-Payo et al., 2022), it is beyond our main objective of exploring seasonal interactions of density dependence, so we did not consider this in our models. The selection of partial migration can be influenced by multiple mechanisms (Chapman et al., 2011; Lundberg, 1988; Reid et al., 2018); thus, future work should try to explore how different mechanisms intertwine in the maintenance of the complicated polymorphic migration behavior.

Our model only considers one common form of partial migration, which is that migrants and residents breed together but overwinter apart. Other forms, such as sharing nonbreeding ground partial migration and skip-breeding partial migration, are different from our model settings in density-dependent demographic rates or in seasons where the within- and between-strategy competition occurs (Griswold et al., 2010; Shaw & Levin, 2011). Nevertheless, seasonal interactions of density dependence might still play an important role. Our model can be extended to parameterize more realistic scenarios to allow a deeper understanding of the evolution of migration strategy.

In conclusion, our study reveals the strategy fitness in a seasonal environment and how density dependence in different seasons interacts with density independence to affect the population migratory strategy. Our work provides insights into how and why migration is rapidly changing in the face of environmental changes and also applies the framework for studying eco-evolutionary dynamics in a simplified seasonal structure (Coulson et al., 2017, 2022), providing a way to further explore the rapid evolution of seasonal strategies in nature.

AUTHOR CONTRIBUTIONS

Jin Liu and Tim Coulson conceived the idea. Jin Liu conducted the literature review, built the model, performed the analyses, and led the writing with substantial contributions from Tim Coulson. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Liu et al., 2025) are available in Dryad at https://doi.org/10.5061/dryad.sf7m0cgc9.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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