# The emergence and persistence of partial migration

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**Abstract**

Partial migration, where some individuals in a population migrate while others remain resident, is a widespread and complex behavioural phenomenon arising from the interplay of genetic, developmental, social, and environmental processes. These mechanisms often interact, as migratory strategies can be shaped by genetic variation, individual experience, social learning, and fluctuating environmental pressures. With rapid advances in our ability to study the genetic, social, developmental, and ecological determinants of migration, it is timely to revisit long-standing questions of how individual-level processes generate partial migration (emergence) and how migratory and resident strategies persist within populations over generations (persistence). Here, we provide evidence across different taxa to examine how interacting mechanisms shape both the emergence and persistence of partial migration. We focus on two linked questions: (1) why individuals within a population adopt different movement strategies, and (2) how the coexistence of migratory and resident individuals persists across generations. We further emphasize the importance of spatial and temporal scale in linking individual-level mechanisms to population-level patterns, as mismatches in scale can alter inference about underlying processes. This integrative perspective highlights how multiple mechanisms jointly structure variation in migratory behaviour and provides a framework for generating testable hypotheses and developing biologically realistic eco-evolutionary models. Beyond partial migration, this perspective may also help clarify how similar interacting processes shape other forms of animal movement across species and ecosystems.

**Keywords:** partial migration, eco-evolutionary dynamics, migration drivers, developmental plasticity, genetic variation, social learning, environmental variability, movement ecology, scaling frameworks, migration strategies

# 1. Introduction

Populations of many species include some individuals that migrate and others that do not, a behavior known as partial migration (Box 1). This phenomenon has increasingly been observed across diverse taxonomic groups and is expected to become more common, including among species that are currently considered fully migratory (Berg et al. 2019; Boyle 2008; Chapman et al. 2011; Menz et al. 2019). Understanding why partial migration emerges and how it persists over generations has intrigued researchers, as it is fundamentally a life history strategy that may reveal how animals balance trade-offs in survival, reproduction, and environmental conditions (Jahn et al. 2010; Lundberg 1988; Shaw and Levin, 2011).

Early studies focused primarily on explaining how partial migration could persist evolutionarily, leading to the development of several influential theoretical frameworks (Box 2; Kaitala et al. 1993; Lundberg 1988). For example, researchers speculated that residency and migration could coexist when different migratory strategies provided similar long-term fitness via the evolutionarily stable strategy framework (Lundberg 1988). Residents may gain reproductive advantages by establishing territories earlier despite higher overwinter mortality, whereas migrants increase survival by avoiding harsh winter conditions but may sacrifice access to high-quality breeding opportunities. This balance of costs and benefits allows the coexistence of alternative strategies within the same population and their persistence across generations.

Although these early frameworks successfully explained how alternative strategies could persist to form partial migration, they treated migration largely as a population-level outcome rather than a consequence of individual decision-making. However, with advances in animal-tracking technologies in the late 2000s, researchers revealed that partial migration emerges at the population level from variation in individual behaviors and decisions (Chapman et al. 2011). In recent years, research has increasingly shown that genetic, developmental, social, and environmental processes all contribute to the emergence and persistence of partial migration (Aikens et al. 2024; Delmore et al. 2020; Pulido 2011; Eggeman et al. 2016). Moreover, the individual migratory decisions that underlie partial migration emerge from interactions among multiple mechanisms rather than any single process alone (Acker et al. 2023; Buchan et al. 2020; Joly et al. 2025; Ranck et al. 2023; Soriano-Redondo et al. 2023). As a result, a diverse set of hypotheses arises to reveal multiple pathways to explain the emergence and persistence of partial migration (Box 3). For instance, the arrival time hypothesis explains why certain individuals remain resident year-round to secure early access to breeding territories. Although residency incurs substantial overwintering costs, particularly in seasonal environments, it may be favored if early access to breeding opportunities increases reproductive success. This pattern has been repeatedly documented in natural systems, providing empirical support for earlier theoretical predictions that divergent migratory strategies arise through interactions among environmental conditions, individual state, and life-history trajectories (Boyle 2008; Kokko 1999).

Given this complexity and the rapid advances in tracking and genomic technologies to explain the emergence and persistence of partial migration, we revisit historical trends in partial migration research and conceptually synthesize the mechanisms underlying its emergence and persistence. Here, we first provide a historical perspective and overview of how partial migration emerges and persists in nature (Figure 1). We then distinguish between the processes that underlie the emergence of partial migration (early-life learning and phenotypic plasticity) and those that contribute to its persistence over time (genetic polymorphism and cumulative cultural evolution). In the discussion, we outline key considerations for matching data types to appropriate research questions in partial migration studies and highlight the importance of validating spatial and temporal mismatches in the data, as these can mislead partial migration studies and prevent a comprehensive understanding of the underlying mechanisms of partial migration emergence and persistence.

## 2. Emergence of partial migration

Before we can understand why partial migration persists over evolutionary time and across species, we must first identify the underlying individual-level mechanisms that drive the emergence of migratory patterns in animals. To understand the emergence of partial migration, we focus on the earliest transitional phase in which populations were previously characterized by uniform migratory behavior, consisting entirely of either full migrants or full residents. Here, we consider that partial migration initially emerges from a combination of two mechanisms: (1) early-life learning, and (2) phenotypic plasticity (Figure 2). Individuals' migratory behaviors may depend on the information they obtain and how they use it (i.e., early-life learning; Abrahms et al. 2021; Byholm et al. 2022; Mueller et al. 2013). Researchers have also found that the migratory behavior in some animals exhibits phenotypic plasticity: the ability of a genotype to produce different phenotypes in various environments, depending on factors such as resource availability, individual state (e.g., body size or sex), or interactions among individuals (Eggeman et al. 2016; Sanz‐Aguilar et al. 2012).

### 2.1. Early-life learning

For long-lived species that perform multiple migrations over their lifetime, early life experiences can shape decisions about whether, where, and when to migrate later in life (Aikens et al. 2022; Sergio et al. 2014). According to the exploration-refinement hypothesis, long-lived birds are expected to explore and prioritize information gain during early life when they are not constrained by pressures to arrive early on the breeding grounds during the later reproductive phase of life (Campioni et al. 2020; Guilford et al. 2011). As a result, young individuals are expected to exhibit varied and wide-ranging behaviors that enable them to explore different environments; however, as adults, this flexibility becomes increasingly constrained, and routes are expected to be refined to increase reproductive success (Aikens et al. 2024; Campioni et al. 2020). Although this hypothesis originated to explain the development of migration routes and

tactics in birds, it may also apply more generally to other long-lived migratory species that are constrained by dependent young and extensive parental care. Thus, it is often assumed that early life is a sensitive developmental period when key information about whether, where, and when to migrate is acquired through individual experience or social learning (Aikens et al. 2022; Bontekoe et al. 2025). Importantly, this also means that early life is a period when young animals could innovate novel migrations or refine existing routes by developing distinct stopovers or seasonal destinations (Dufour et al. 2022; Tombre et al. 2019).

Evidence of ontogenetic shifts in migration (e.g., changes in migration over a lifetime) is growing, especially in avian species (e.g., Abrahms et al. 2021; Aikens et al. 2024; Campioni et al. 2020; Chan et al. 2024; Sergio et al. 2014; Witczak et al. 2024). For example, white storks explored new routes during their first fall and spring migrations, which allowed them to innovate faster and more direct migrations later in life (Aikens et al. 2024). Key information about the benefits and risks associated with migratory decision-making (e.g., suitable resource availability) can be acquired through individual or social learning (Bontekoe et al. 2025; Byholm et al. 2022; Loonstra et al. 2023; Sergio et al. 2014). Reintroduced whooping cranes, for instance, relied on social information to appropriately time migration during early life, but shifted to using personal information later in life (Abrahms et al. 2021).

Ontogenetic shifts in migration patterns have also been observed in ungulates, where migratory plasticity is relatively common (Berg et al, 2019). In some cases, the ontogenetic shifts observed are consistent with the exploration-refinement hypothesis. For example, as fawns, female mule deer follow their mothers during their first migrations, but as yearlings, a fraction of individuals explored and used completely new routes that persisted into adulthood when reproductive constraints set in (Jacopak et al. 2025). However, in other species, rather than canalization, migration becomes more variable with age (see plasticity section below). For example, a study of moose in Sweden found that while young moose (less than five years old) always migrated, older moose (five to fifteen years old) appeared to shift towards a conditional strategy mediated by snow conditions. Older individuals tended to migrate when snow depth was low, but were less likely to migrate at deep snow depths (Singh et al. 2012).

With growing evidence of early-life learning acting as a mechanism to shape migratory strategies in long-lived animals, further studies are needed to test explicitly whether this mechanism also contributes to the emergence of partial migration. Some indirect evidence suggests that age-related changes in migratory behavior may play a role in partial migration emergence (Chan et al. 2024). For example, juvenile European robins were likely to migrate, whereas older individuals increasingly adopted year-round residency (Adriaensen and Dhondt. 1990). This pattern is consistent with the exploration-refinement hypothesis that young individuals initially explore different migratory strategies before refining their behavior with experience as residents. Conversely, greater flamingos were more likely to remain resident during early life, whereas older individuals showed a greater tendency to migrate, supporting the

"early benefits to residents" hypothesis (Cayuela et al. 2025). Under this hypothesis, residency during early life may confer higher breeding opportunities than migration, whereas older individuals may increasingly migrate to avoid the costs associated with breeding as residents, such as intraspecific competition. However, because few studies have tracked individuals across their entire lifetime, it remains unclear whether early-life learning is a key mechanism driving the emergence of partial migration. Long-term individual-based datasets will thus be essential for further testing whether the ontogenic canalization is a key underlying mechanism that generates partial migration.

### 2.2. Phenotypic Plasticity

Animals alter migratory behavior in response to rapid environmental change through phenotypic plasticity (Chan, 2001; Chapman et al. 2011; Hegemann et al. 2019; Xu et al. 2021). In partially migratory systems, migratory decisions are often shaped by interactions between environmental conditions and individual physiological state, such as sex, breeding status, and physical condition (Berg et al. 2019; Cagnacci et al. 2011; Hegemann et al. 2019; Lavender et al. 2024; Mysterud et al. 2011). For many migratory fish, birds, and mammals, migratory plasticity reflects risk–reward tradeoffs that differ among individuals and populations (Riotte-Lambert et al. 2020). These tradeoffs suggest that phenotypic plasticity emerges from context-dependent behavioral decisions that balance survival costs and benefits in response to current environmental conditions. For example, the migratory behavior of male Sierra Nevada bighorn sheep is sensitive to both environmental conditions and physiological state, particularly body fat reserves (Denryter et al. 2024). Individuals with lower body fat are more likely to migrate to lower elevations to avoid severe winter conditions at higher elevations, despite facing increased predation risk at lower elevations (Denryter et al. 2024).

How phenotypic plasticity manifests across an animal's lifespan remains an active area of research. Current hypotheses suggest that the expression of migratory plasticity can shift across life stages as individuals accumulate experience and undergo changes in physiological condition or social status (Witczak et al. 2024). For instance, male red kites migrated during their first year of life but switched to residency upon reaching sexual maturity, likely to secure breeding territories (Witczak et al. 2024). Similar migration strategies were observed in female red kites; however, body size also influenced this adopted strategy. Larger mature females were more likely to remain residents, whereas smaller mature females were more likely to migrate, presumably because they were less able to compete with larger conspecifics for breeding opportunities and resources (Witczak et al. 2024). Ultimately, the relative influence of factors (both exogenous and endogenous) on migratory plasticity likely changes throughout an individual's lifetime, particularly as social hierarchy, reproductive status, and energetic demands shift with age (Gauthreaux 1982; Kokko 1999).

## 3. Persistence of partial migration

The persistence of partial migration within populations is explored through evolutionary theories describing how migrants and residents can coexist within a same population over time, despite differences in behavior, energetic costs, and fitness consequences (Lundberg 1988). Once variation in migratory behavior emerges within a population (see Section 2), several possible non-mutually exclusive processes may contribute to the long-term persistence of partial migration across generations.

Theoretical work commonly incorporates density dependence and population growth feedback as important implicit components shaping the long-term stability of partial migration (Shaw and Levin. 2011; Kokko 2011). This led to the development of evolutionary hypotheses to provide explanations for how partial migration persists once divergent migratory strategies are established within a population (see Box 2; Lundberg 1988). These theoretical frameworks explicitly incorporate genetically and culturally heritable variation in migratory behavior, drawing on earlier experimental research showing that, in some species, migration is genetically and culturally heritable (Berthold 1995; Chernetsov et al. 2004; Pulido 2011; Delmore et al. 2020; Whiten 2021; Byholm et al. 2022). In birds, individuals may exhibit consistent movement patterns over their lifetime regardless of environmental conditions, because they are genetically and/or culturally predisposed to migrate or remain resident (i.e., genetic polymorphism, cultural transmission; Berthold and Pulido 1994; Palacin et al. 2011; Justen et al. 2024). Accordingly, many hypotheses assume that an individual's migratory decision is primarily or entirely determined by heritable factors, allowing researchers to explore how migratory behaviors change in frequency across generations under natural selection and other evolutionary processes. While the emergence of partial migration likely originates through phenotypic plasticity and early-life learning (see Section 2), repeated expression of these initially plastic responses over evolutionary time may subsequently become genetically assimilated or recapitulated through cultural inheritance (Figure 3). Genetic or cultural inheritance of differences in migratory tendency among individuals reinforce and stabilize the long-term coexistence of migratory and resident behaviors once partial migration has already emerged within populations.

### 3.1. Genetic polymorphism

In many species, migratory behavior is thought to be at least partially influenced by genetic inheritance (Akesson and Hedenstrom 2007; Berthold 1991; Berthold and Querner 1981). The relative importance of genetic inheritance, alongside other factors such as learning and flexibility, may depend on species ecology and developmental history (Figure 3; Baker et al. 2025; Jesmer et al. 2025), but it is clear that some aspects of migration are inflexible and innate in certain obligate migratory species. However, the role of genetic inheritance within partially migratory populations is less well understood. Some populations of partial migrants, such as Eurasian Blackcaps (*Sylvia atricapilla*) and the European Shag (*Gulosus aristotelis*), have been the subject of quantitative genetic studies, confirming that individual migratory status is influenced by heritable genetic variance (Acker et al. 2023; Berthold and Terrill 1988). In the

shag, heritability of migratory status was found to be only 9%. By contrast, much more variation in the migratory phenotype was explained by "permanent individual variance," a metric that potentially reflects effects of early-life learning (see subsection 2.1) or non-additive genetic effects. Evaluating heritability in captive settings, as has been done in blackcaps, may artificially reduce effects of early-life environmental variation (i.e., through early-life learning) on individual migratory behaviors, thereby inflating apparent genetic heritability. Indeed, much of the variation in migration in partially migratory European Shags reflects contributions from genetic variance, environmental effects, and consistent among-individual differences, emphasizing the importance of studying populations in natural conditions and considering multiple potential mechanisms of partial migration (Acker et al. 2023).

For several decades, evidence that migration behavior can be heritable (e.g. Berthold and Querner 1981) has motivated attempts to identify specific genes that might play a role in migratory inheritance (reviewed in Gu et al. 2024), including in partial migrants. Genetic variants that correlate with variation in migratory phenotype can be identified as candidate genes that may influence the phenotype. This approach is feasible in diverse wild species because it requires only the collection of DNA sequence data and information about the phenotypes, rather than requiring controlled breeding or long-term experimental studies. However, these studies rarely identify genes with strong effects on migratory phenotype, highlighting a growing consensus that the genetic basis of migratory phenotypes may be highly complex, rather than being controlled by a few genes of large effect (Caballero-Lopez and Bensch 2024; Weissensteiner et al. 2025). For example, in the partially migratory European Blackbird (*Turdus merula*), migratory status was associated with variation in loci that overlap with the gene *PER2,* which is known to play a role in circadian rhythm (Weissensteiner et al. 2025). However, no variants of *PER2* were fixed between migrants and nonmigrants, indicating that this gene alone does not control migratory phenotype. The focus of migration genomic studies is beginning to move from investigation of variation in genes to investigation of more complex networks of gene regulation and gene expression, which may provide greater insight into the genetic influences on partial migration (Caballero-Lopez and Bensch 2024; Cavedon et al. 2019; Stapley et al. 2010).

### 3.2 Cumulative cultural evolution

Building on the genetic inheritance that influences the long-term coexistence of migratory and resident behaviors, migration can also be culturally inherited through social learning among individuals (Whiten 2021; Fugate et al. 2025). Animals can learn how to and where to migrate through various forms of social transmission during their lifetime, such as following parents (i.e., maternal care; Byholm et al. 2022; Miller et al. 2022), unrelated older and more experienced individuals (i.e., leaders; Mueller et al. 2013; Bontekoe et al. 2025), and members of the same generation (i.e., cohorts; Jesmer et al. 2018; Franks et al. 2020). As this culturally transmitted knowledge is passed to subsequent generations, individuals combine information gained through their own experiences with knowledge acquired through social

learning from previous generations, resulting in cumulative cultural evolution (Tennie et al. 2009).

Despite the increasing evidence for the role of culture in migratory populations, it remains unclear whether the persistence of partial migration can be explained by cumulative cultural evolution. Because migration is not optimal under all conditions, the fitness benefits of migration vary with the environmental conditions individuals experience (Figure 3; see Section 2.2; Phenotypic plasticity). Under these circumstances, seasonal migrants that experience harsh conditions may adopt a resident strategy in the following season and socially transmit this information to other migrations; conversely, residents may become migrants when environmental conditions favor migration and similarly transmit that information. However, determining whether cumulative cultural evolution contributes to the persistence of partial migration will require longitudinal data that track individuals throughout their lifetimes and across multiple generations. Combining such multigenerational tracking with phylogenetic data may reveal whether migratory and resident behaviors coexist over evolutionary timescales.

# 4. Discussion

## 4.1. Integrating mechanisms across spatial and temporal scales

Partial migration emerges and persists from processes that are structured across individual decision-making, population-level feedbacks, and spatially and temporally variable environments (Figures 2 and 3). Because these processes are inherently scale-dependent (Levin 1992; Spake et al. 2021; Brian and Catford 2023), mismatches between the spatial and temporal scales of data and the intrinsic dynamics of migratory systems can strongly affect ecological interpretation and predictive performance (Figure 4; Wiens 1989). Robust inference therefore requires aligning sampling design and analytical models with the characteristic spatio-temporal scales at which migratory processes operate. To achieve this goal, more extensive data collection is ideal, such as tracking individuals throughout their entire lifetime. However, only a few studies have tracked migratory patterns across an individual's entire lifetime, highlighting the challenges of collecting lifetime tracking data (Aikens et al. 2022). Alternatively, identifying the optimal fine-scale information that can be sampled at key life stages or time points believed to play a critical role in the emergence and persistence of partial migration may provide a more feasible approach (Figure 4). Furthermore, identifying data sources spanning from ground-based data (e.g., phylogeny and functional traits) to airborne data (e.g., environmental layers and tracking data), as well as methods to integrate them, may reveal better ways to infer how partial migration emerges and persists.

Given these scale-dependent constraints and their theoretical and modeling implications, we suggest that, going forward, the mechanisms driving partial migration should be examined from an integrative perspective in which the effect of each mechanism, as well as genetic and cultural components influencing the persistence of partial migration, varies across time and space

(Figure 4). For example, from a temporal lens, evidence indicates that heritable changes in migration within populations involve genetic changes over long evolutionary timescales (Gómez-Bahamón et al. 2020; Jahn et al. 2013). Conversely, genetic polymorphism might not explain variation in migratory behavior across individual lifespans. On shorter timescales, many populations may exhibit a strong propensity for migratory behaviors to evolve rapidly, often shifting from migration to partial migration or from residency to partial migration (Berthold 1999). This apparent rapidity with which migration can evolve may be a consequence of the joint influence of genetics and phenotypic plasticity in most populations (Able and Belthoff 1998; Gómez-Bahamón et al. 2020). A recently developed database integrating animal behavior into trait-based ecology (MoveTraits; Beumer et al., 2025) may be a useful tool for identifying signals of phenotypic plasticity in partially migratory populations. For future directions, developing data infrastructures and analytical frameworks that combine phylogeny, traits, and behaviors could help understand how partial migration is shaped across different temporal scales.

From a spatial lens, at macroecological scales, variation in migratory behavior is associated with long-term environmental gradients and historical changes in species' geographic distributions, which influence how migration strategies vary across populations (Winger et al. 2012; Zink and Gardner 2017). For example, some studies support that migration is an ancestral behavior present in most lineages (Zink 2011) and that migration patterns can shift – from full migratory to partial migratory to sedentary states – when environmental changes alter the benefits of seasonal movement, allowing species to track their realized niches and maximize their survival on their potential geographic distribution and over macroevolutionary time (Gómez-Bahamón et al. 2020, Winger et al. 2019). At local scales, the interaction between ecological mechanisms (e.g., competitive interactions) and biological differences between individuals (e.g., sex and age) is more relevant than macroecological factors or evolutionary mechanisms in dictating whether animals decide to migrate or not. For future directions, combining observational studies that span different scales may provide mechanistic understandings of the drivers of partial migration. For example, tracking individuals on the large spatial scales such as entire seasonal migratory pathways may signal the effects of learning on migratory behaviors. Conversely, capturing behaviors within breeding areas may reveal dynamics in competition among conspecifics that shape their decisions of whether to migrate.

### 4.2. Directed acyclic graph in partial migration studies

Graphical models (Jordan 2004) and directed acyclic graphs (DAGs) explicitly represent hypothesized causal pathways, allowing researchers to identify confounding variables and clarify assumptions before experimental design and subsequent analyses (Franks et al. 2025; Laubach et al. 2021; Siegel and Dee 2025). Formalizing relationships among variables in this way helps distinguish between informative and merely correlated predictors, enabling evaluation of whether observed patterns of partial migration are consistent with proposed causal mechanisms (Borger and Ramesh 2025).

Building on this approach, we present examples of four underexplored hypotheses in partial migration studies: social fence, sexual conflict, terminal investment, and trophic polymorphism (Figure 5). We use DAGs to illustrate the mechanisms and variables that may underlie partial migratory behavior (Figure 5). For instance, under the sexual conflict hypothesis, differences in the costs and benefits of migration between sexes can generate within-population variation in migratory strategies (Fudicker et al. 2013; Pearse et al. 2019). Males may gain greater fitness benefits from residency, such as increased access to mating opportunities, whereas females may benefit from migration through enhanced reproductive success, leading to sex-specific migration probabilities. In such cases, persistent differences in migratory behavior may reflect underlying genetic polymorphisms that reinforce these divergent strategies over time. Accordingly, capturing these dynamics requires data that span sex-structured populations across multiple habitat patches, with sampling that resolves both within-individual state variation and among-individual differences in migration outcomes, particularly where genetic variance and consistent individual effects are expected (see Figure 4 (1) Partial migration emergence green-colored boxes).

Importantly, constructing DAGs for each hypothesis clarifies the minimal data requirements needed to test proposed causal mechanisms. For example, in the terminal investment hypothesis (Box 4), a DAG linking early-life learning, age, reproductive investment, and migration probability implies that core processes operate at the level of individuals embedded within populations (Figure 4). This requires fine-scale individual data, ideally with repeated measures across life stages, to resolve within-individual state dynamics and distinguish them from between-individual differences in habitat use. To account for contextual effects and avoid attributing local environmental variation to individual state processes, intermediate spatial replication across populations or habitat patches is also required. At the temporal scale, short-term (seasonal migration decisions) and medium-term (ontogenetic progression across life stages) sampling are sufficient to capture both immediate behavioural responses and life-history driven shifts in migratory strategy. However, it is often difficult to collect such data in partial migration studies due to the expense of acquiring tagging equipment and the additional time required for fieldwork. Alternatively, DAGs can help researchers locate open-source data that meets the minimum requirements for their studies, eliminating the need to collect their own data and reducing the burden of rigorous fieldwork.

## Conclusion

Partial migration is a widespread and complex behavioral phenomenon shaped by the interplay of genetic, developmental, and environmental factors. Here, we review the diverse mechanisms that shape partial migration and explain how it emerges and persists over generations. We propose that partial migration may originate from the interaction between an individual's environmental sensitivity (phenotypic plasticity) and its developmental constraints (early-life learning). These plastic behavioral responses, when repeatedly expressed across

generations within a partially migratory population through cultural inheritance, may become genetically assimilated, contributing to the long-term persistence of partial migration in nature. To better understand the emergence and maintenance of partial migration, it is critical to recognize the importance of spatial and temporal context and to explicitly consider causal pathways during experimental design and subsequent analyses to identify potential confounding factors underlying its origin and persistence. Clarifying the sources of variation in movement strategies across migratory species provides researchers with a structured framework for generating testable hypotheses and developing biologically relevant eco-evolutionary models. More broadly, we encourage researchers to explore the interactions among the proposed mechanisms beyond partial migration, including in other movement types such as seasonal migration, nomadism, and dispersal.

# Figures

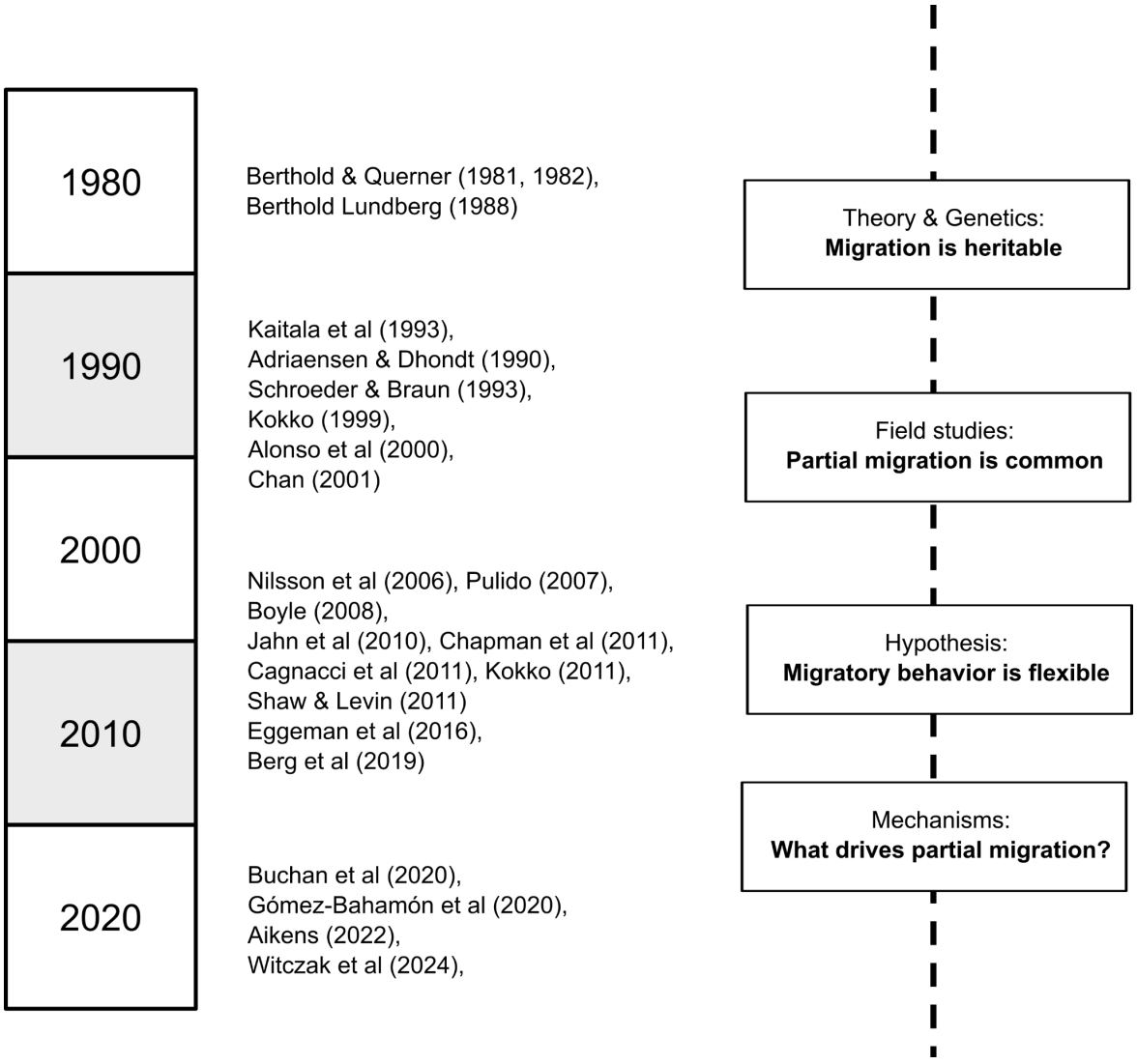


**Figure 1. History of advances in partial migration research over the last five decades (1980s - 2020s).** Listed papers are key reviews and research articles (above 100 citations) focusing on the evolution and ecology of partial migration. The right boxes represent key themes of partial migration research by evolutionary biologists and ecologists.

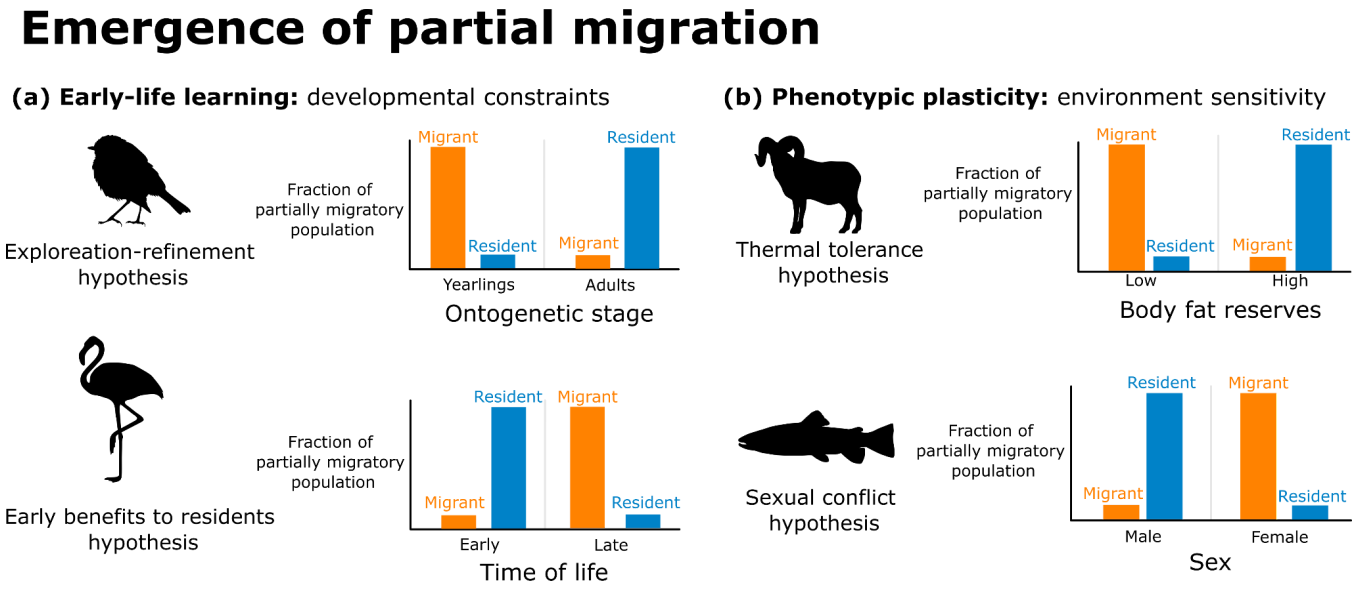


**Figure 2. Conceptual pathways leading to the emergence of partial migration through (a) early-life learning and (b) phenotypic plasticity.** (a) Under early-life learning, migratory strategies become progressively constrained during development through learning or early-life experiences. The first example illustrates the exploration–refinement hypothesis, in which individuals initially express migratory behaviours that become canalized with maturation, ultimately resulting in residency. The second example illustrates the early benefits to residents hypothesis, whereby early developmental advantages increase the probability of residency, although individuals may retain a propensity to migrate later in life. (b) Under phenotypic plasticity, migratory decisions vary in response to individual state, environmental conditions, or their interaction. The third example illustrates the thermal tolerance hypothesis, in which the proportion of migrants and residents shifts continuously along a gradient of body fat reserves under increasingly severe winter conditions. The fourth example illustrates the sexual conflict hypothesis, in which sex-specific differences in migration propensity arise from differences in the reproductive costs and benefits of migration between males and females. Conceptual orange bars denote migrants, whereas blue bars denote residents (not based on real data).

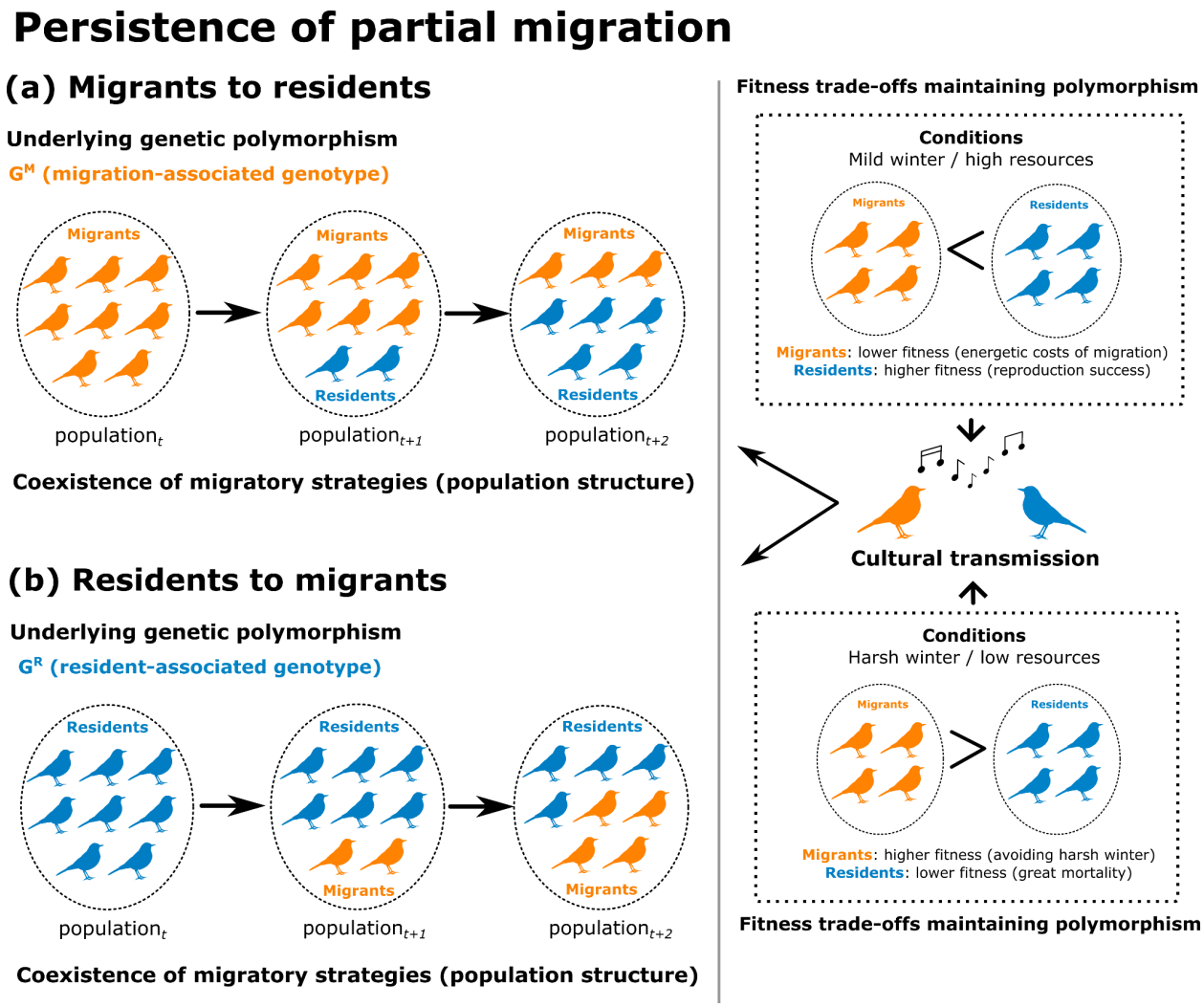


**Figure 3. Conceptual pathways leading to the persistence of partial migration through genetic polymorphism and cultural transmission.** Partial migration persists in a population where migrants and residents coexist over time. At the population level, individuals express alternative movement strategies, with some consistently migrating while others remain resident. This variation in movement strategies is underpinned by heritable genetic variation in migratory tendency, where distinct genotypes associated with (a) migration and (b) residence bias individuals toward migratory or resident strategies, respectively. Environmental heterogeneity as an example generates spatially and temporally variable fitness advantages for each strategy, leading to balancing selection. Cultural transmission of movement information among conspecifics can further stabilize these alternative movement strategies by allowing individuals to acquire migratory or resident behaviors, reinforcing genetically influenced movement tendencies and buffering populations against environmental variability. Migrants and residents each experience context-dependent fitness benefits, preventing the fixation of either strategy. The resulting feedback between selection and inheritance maintains genetic polymorphism and persist the long-term coexistence of migrants and residents within the same population.

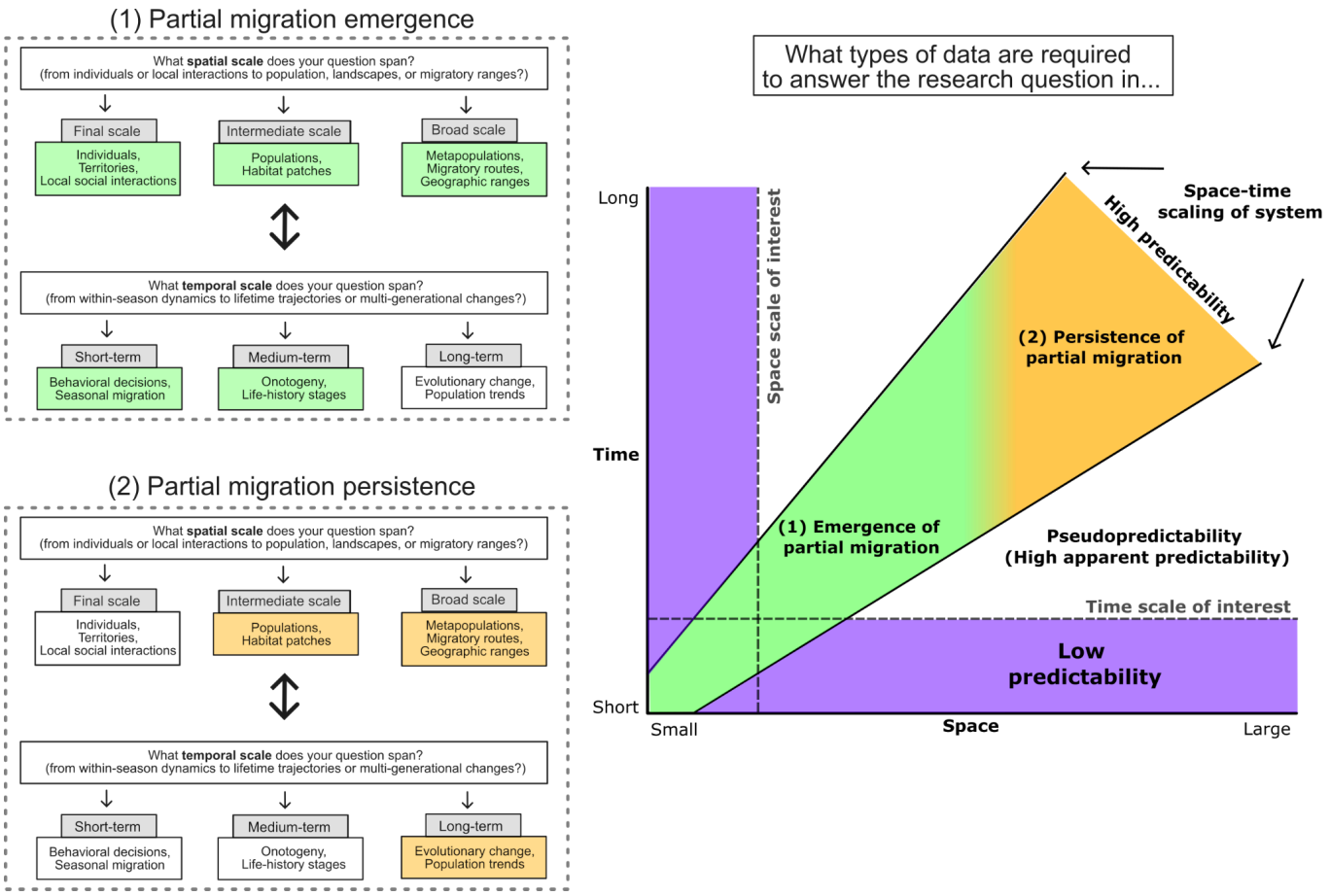


**Figure 4. Partial migration emerges across different spatial and temporal scales (see Section 4.1). A conceptual figure adapted from Wiens (1989), illustrating how spatio-temporal scaling of ecological data influences inference in partial migration studies.** In general, the spatial extent of a system increases with the temporal scale over which it is studied, requiring alignment between these dimensions to achieve robust inference. Mismatches in scaling can lead to systematic biases in predictability. Studies conducted over long temporal scales but restricted spatial extents (purple region) may exhibit low predictability due to incomplete representation of system variability, a challenge commonly associated with investigations of genetic polymorphism operating over evolutionary timescales. Conversely, studies conducted over short temporal scales and/or broad spatial extents (white regions) may yield pseudopredictability (i.e., high apparent predictability that does not reflect underlying system dynamics) and potentially bias inference toward mechanisms such as early-life learning and phenotypic plasticity when longer-term processes are not captured. The highest predictive power (green to orange region) emerges when spatial and temporal scales are appropriately matched to the dynamics of the system, facilitating more reliable inference. Depending on whether the research objective is to understand (1) the emergence (green) or (2) the persistence (orange) of partial migration, the appropriate spatial and temporal scales of data collection may differ. For example, understanding the role of early-life learning and phenotypic plasticity in partial migration may require broad spatial coverage within an individual's lifetime, spanning a relatively short temporal scale. In contrast, studying the persistence of partial migration may require multigenerational datasets spanning intermediate to broad spatial scales to capture evolutionary changes in migratory behavior. Despite longstanding recognition of scaling issues in

ecology, studies of partial migration continue to risk biased inference when conducted over limited temporal windows relative to the natural dynamics of the system.

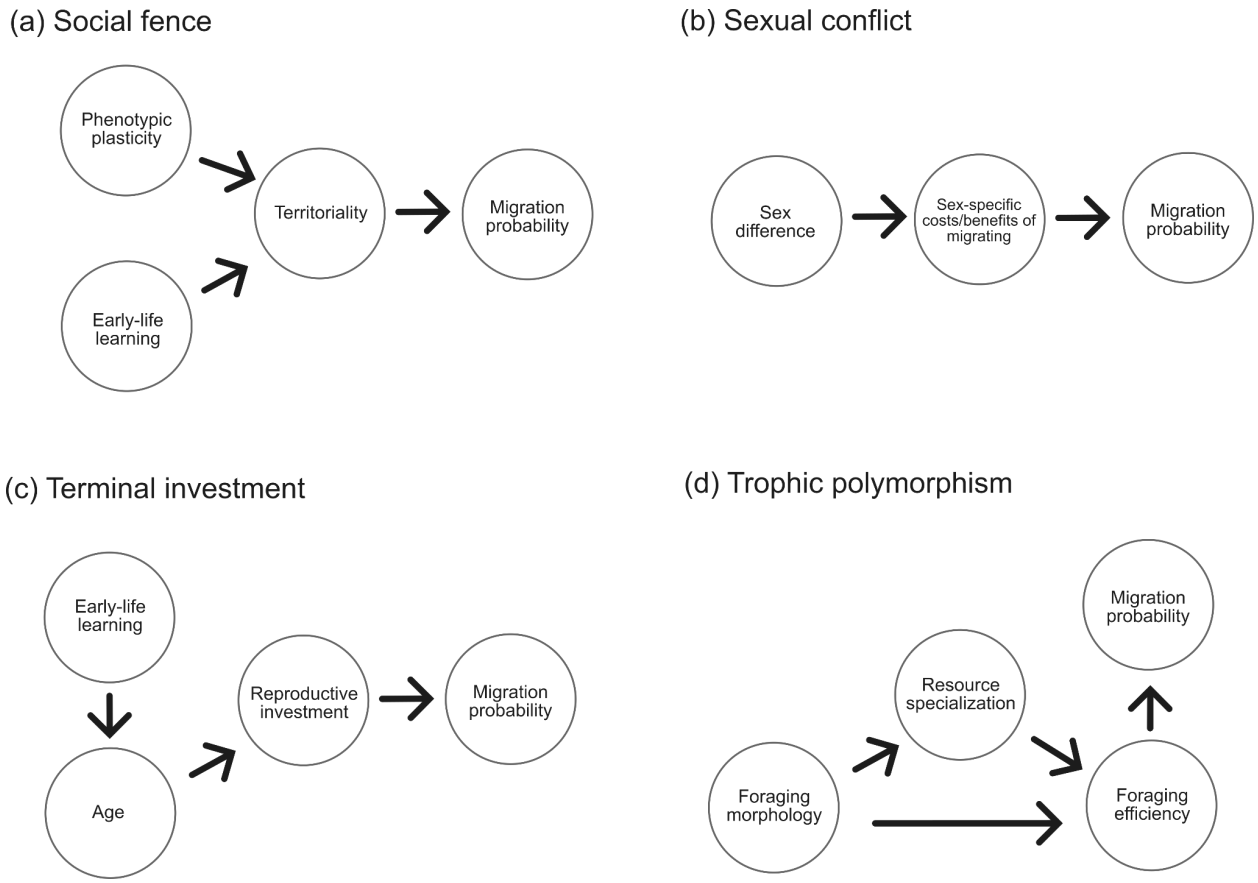


**Figure 5. Examples of the directed acyclic graphs (DAGs) on the four least studied partial migration hypotheses: (a) Social fence, (b) Sexual conflict, (c) Terminal investment, and (d) Trophic polymorphism hypotheses.** The effects of early-life learning and phenotypic plasticity on migration probabilities vary, depending on the hypotheses of interest. For example, the sexual conflict hypothesis may drive sex differences within a population, and different sex-specific costs and benefits of migrating drive migration probabilities (e.g., males may benefit from residency to secure mating opportunities, while females benefit from migration to increase reproductive success). Early-life learning may influence individuals' migration strategies depending on their ages to test the terminal investment hypothesis. The prime-aged individuals may remain as residents to increase their breeding opportunities, while older individuals invest in migration to increase their survival. The illustration of the DAGs is adopted from Borger and Ramesh (2025).

**Box 1.** Multiple definitions of partial migration.

Partial migration is commonly defined as "some individuals migrate and others stay" (Chapman et al. 2011; Fortuna et al. 2024; Lundberg 1988; Morrison et al. 2024). While this core idea is widely shared among biologists, the nuances of how partial migration is conceptualized vary across disciplines. These variations often reflect differences in the level of organization (population vs. species) and ecological context. In this synthesis, we define partial migration as the behavioral phenomenon in which some individuals in a single breeding population migrate in a given year, while other individuals from the same population remain resident (Chapman et al. 2011).

**1. Population-level partial migration**
Evolutionary theorists and ecologists often define partial migration as a fraction of individuals migrating within a single, commingled population while others remain resident (Lundberg 1988; Kokko 2011; Shaw & Levin, 2011).

**2. Geospatial partial migration**
Ornithologists frequently use partial migration to describe species that contain separate migratory and resident populations in different parts of their range (Pulido 2007). This pattern, termed geospatial partial migration, is typical of species whose breeding ranges span temperate/tropical transition zones. Individuals breeding in the temperate zone migrate after breeding, while those breeding in the tropics remain resident. Under this definition, mechanisms such as the arrival-time hypothesis operate between populations rather than within a single, mixed population. Differences in arrival time may reflect long-term genetic polymorphism and phenotypic plasticity.

**3. Population-level plasticity in mammals**
In mammalogy, partial migration is sometimes viewed as population-level plasticity in migratory behavior. For example, herds of ungulate species (e.g., reindeer) may switch between migratory and resident behaviors across years: the entire population may migrate in one year but remain resident the next (Pereira et al. 2024; Xu et al. 2021).

**Box 2.** Definitions of evolutionary hypotheses in terms of understanding the causes of partial migration. The details of the theories are summarized in Lundberg (1988).

**Evolutionary stable strategy**:
Partial migration persists because neither migrating nor staying provides a consistent advantage over the other.

**Bet-hedging**:
Both migrating and staying are risky, but becoming one or the other helps the population cope with unpredictable environments.

**State-dependent selection**:
An individual's decision to migrate depends on its own traits (e.g., age, body condition, sex).

**Frequency-dependent selection**:
The success of migrating versus staying depends on how many individuals use each strategy.

**Box 3.** Definitions of hypotheses related to the causes of partial migration. The details of the hypotheses are summarized in Berg et al. (2019), Boyle (2008), and Chapman et al. (2011).

**Arrival Time:**
Intrasexual competition for high-quality breeding areas keeps individuals residents, even when little food is available.

**Competitive release; Dominance:**
Migrants avoid intraspecific competition for limited resources.

**Fasting endurance:**
Migrants avoid a greater risk of starvation during periods of food scarcity.

**Foraging maturation:**
Migrants gain advantages by securing high-quality resources

**Predation vulnerability:**
Migrants avoid the high risk of dying by escaping predation.

**Sexual conflict:**
Males and females experience different costs and benefits of migrating.

**Social fence:**
Residents with secure territory force other incoming individuals to migrate.

**Terminal investment:**
Residents invest heavily in reproduction instead of migrating.

**Thermal tolerance; Body size:**
Individuals with great thermal tolerance remain as residents, while those with lower thermal tolerance migrate.

**Trophic polymorphism**:
Differences in foraging morphology drive individuals' migratory strategies.

**Box 4.** Linking causal structure to data resolution using a DAG for the terminal investment hypothesis.

The DAG (early-life learning → age → reproductive investment → migration probability) illustrates how individual state and life-history processes generate variation in partial migration, where residents invest heavily in reproduction instead of migrating. Mapping each node and pathway onto spatial (fine: individuals/territories; intermediate: populations/habitat patches; broad: metapopulations/migratory systems) and temporal (short-term: seasonal decisions; medium-term: ontogeny/life-history stages; long-term: evolutionary change) scales highlights the minimum data resolution required for inference. Green check marks indicate the spatial and temporal scales required to resolve causal relationships in the terminal investment framework, highlighting the need for fine-scale individual data, intermediate spatial replication, and short- to medium-term temporal sampling.

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