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. Because these mechanisms interact across scales, genetic variation, individual experience, social learning, and fluctuating environmental pressures can shape migratory strategies. 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 and how migratory and resident strategies persist within populations over generations. Here, we review evidence across mammals and birds to examine how interacting mechanisms through different types of phenotypic plasticity (irreversible versus reversible) 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 also 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, phenotypic plasticity, genetic variation, social learning, environmental variability, movement ecology, scaling frameworks, migration strategies

1. Introduction

Populations of many species include individuals that migrate and others that do not, a behavior known as partial migration (Box 1). 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 (Berg et al. 2019; Boyle 2008; Chapman et al. 2011; Jahn et al. 2010; Lundberg 1988; Menz et al. 2019; Shaw and Levin, 2011).

Early studies on partial migration focused primarily on explaining how it could persist over evolutionary time, leading to the development of several influential theoretical frameworks (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 alternative strategies to coexist within the same population and persist across generations.

With advances in animal-tracking technologies in the late 2000s (Nathan et al. 2022), partial migration 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 (Acker et al. 2023; Aikens et al. 2024; Boyle 2008; Buchan et al. 2020; Delmore et al. 2020; Joly et al. 2025; Kokko 1999; Pulido 2011; Eggeman et al. 2016). As a result, a diverse set of hypotheses has emerged to explain the emergence and persistence of partial migration (Chapman et al. 2021; Box 2).

Given this complexity and the rapid advances in tracking and genomic technologies, 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 mechanisms that drive the emergence of partial migration and those that contribute to its persistence over time. Lastly, 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 and persistence of partial migration

To understand the emergence and persistence of partial migration, we focus on the earliest transitional phase in which populations were either fully migrant or fully resident. Here, we consider that partial migration emerges and persists through fluctuating selection from a combination of different types of 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). We distinguish phenotypic plasticity into two types: irreversible plasticity and reversible plasticity, which describe how long the plastic effect lasts in individuals (Figure 2). Irreversible plasticity describes how individuals' responses to environmental and social cues become less flexible as they age and develop. For example, individuals' migratory behaviors may change frequently during developmental stages but become less flexible as they reach adulthood (Abrahms et al. 2021; Byholm et al. 2022; Mueller et al. 2013). Conversely, reversible plasticity indicates that individuals' migratory tactics (migration versus residence) become much more flexible depending on environmental and social conditions.

2.1. Irreversible plasticity: early-life learning

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, these ontogenetic shifts align 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 (Jakopak et al. 2025).

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). However, it remains unclear whether age-related changes matter in the emergence and persistence of partial migration. For example, Adriaensen and Dhondt (1990) observed no changes in the migratory behavior of an individual European robin during the course of its life, although Harper (1985) found changes in migratory behavior during the lives of robins. Importantly, this evidence in songbirds was based on endogenous control, and there is no very concrete evidence of whether individuals can change migratory strategy during their lifetime. A recent study of greater flamingos found that individuals 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 ontogenetic canalization is a key underlying mechanism that generates partial migration.

2.2. Reversible plasticity: environmental and social cues

2.2.1. Environmental cues

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 often reflect 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; Mysterud et al. 2011). For many migratory 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). In other species, migration becomes more variable with age. 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). 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).

2.2.2. Social cues: cumulative cultural evolution

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 growing evidence for the role of culture in migratory populations, it remains unclear whether cumulative cultural evolution can explain the emergence and persistence of partial migration. Because migration is not optimal under all conditions, the fitness benefits of migration vary with the environmental conditions individuals experience (See subsection 2.2.1; environmental cues). 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 migrants; 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.

3. The role of genetic polymorphism in partial migration

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 irreversible and reversible plasticity, may depend on species ecology and developmental history (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 (see section 2.1). However, the role of genetic inheritance within partially migratory populations is less well understood. Some partial migratory populations, 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). However, in the European 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 phenotypic plasticity (see Section 2) or non-additive genetic effects. Evaluating heritability in captive settings, as has been done in blackcaps, may artificially reduce the effects of environmental variation during its lifetime 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. Given that these studies rarely identify genes with strong effects on migratory phenotype, this highlights a growing consensus that the genetic basis of migratory phenotypes may be complex rather than 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). For future studies, the collection of DNA sequence data and information about the phenotypes in diverse wild species may be feasible, although it is important to acknowledge the difficulty of identifying and collecting such datasets, as large sample sizes are often needed for a polygenic trait, as well as controlling for population structures.

4. Does a combination of genetic inheritance and cultural transmission drive partial migration?

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 (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 partial migration likely originates through phenotypic plasticity (see Section 2), repeated expression of these initially plastic responses over evolutionary time may subsequently become genetically assimilated or recapitulated through cultural inheritance. However, the effects of genetic assimilation on partial migration in social animals have never really been tested. Conversely, the genetic basis has been demonstrated in songbirds; juveniles generally migrate alone, with no known cultural transmission (Justen and Delmore, 2022). Therefore, exciting future research can tackle questions of whether genetic or cultural inheritance of differences in migratory tendency among individuals reinforces and stabilizes the long-term coexistence of migratory and resident behaviors once partial migration has already emerged within populations.

5. 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 3; 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 3). Furthermore, identifying data sources spanning from ground-based data (e.g., phylogeny and functional traits) to airborne data (e.g., environmental layers and animal-borne bio-logging 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 3). 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 infrastructure 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 large-scale 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 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.

6. Implications for the conservation of migratory animals

As many migratory species are threatened, understanding the causes and consequences of partial migration is essential for outlining conservation strategies to reduce the rapid decline of migratory populations across spatial, temporal and phylogenetic scales (Johnston et al. 2025; Marra et al. 2026). We suggest that combining multiple ecological datasets under a unified probabilistic framework may enable close monitoring of how migratory birds respond to environmental change (O'Hara et al. 2025). For instance, a recent study (Liu et al. 2026) using an unprecedented population-level migration-timing dataset showed that the timing of migration in birds is seasonally dependent: advancing pre-breeding migration benefited abundance, whereas advancing post-breeding migration was detrimental. These findings highlight the potential role of phenotypic plasticity in bird migration as a main driving factor in the declines in bird populations (Liu et al. 2026). Thus, integrating standardized data across technologies, from traditional animal-banding to light-level geolocators and GPS tracking systems, can open new opportunities to closely observe how migratory animals respond to environmental changes and eventually help better understand intraspecific variation in migratory timing and routes, breeding and wintering sites, and the selection of stopover sites across the animal Tree of Life for multiple species (Kays and Wikelski 2023; Lapatas et al. 2015). Combining historical animal-banding programs (e.g., EURING, du Feu et al. 2016) and GPS tracking systems (e.g., reverse-GPS system ATLAS, Beardsworth et al. 2022) may also unveil unknown patterns of breeding and nonbreeding site selection, reveal factors that cause changes in migratory routes, and the species' responses to factors of global change. Therefore, understanding what drives partial migration

using data integration may help identify limiting factors that influence population declines in migratory species.

In addition, our systematic literature review revealed that social fences and density dependence were rarely quantified (Appendix S1), suggesting that quantifying the social landscape and conspecific density may limit our ability to evaluate multiple hypotheses simultaneously. Because migration can involve the splitting and merging of multiple populations and groups across spatial scales - from landscapes to bioregions (Cohen et al. 2018) - accurately capturing the social environment and density of conspecifics across the full annual cycle of migration remains a major challenge to overcome (Bontekoe et al. 2025). Addressing this challenge will require leveraging environmental sensors, such as radar (Van Doren and Horton 2018; Giuntini et al. 2025), acoustic recorders (Rhinehart et al. 2020) and high-resolution imagery from drones (Koger et al. 2023a) or low-orbit satellites (Liu and Wu, 2026), that can estimate animal presence and abundance, in combination with advances in machine learning to automate processes, classify, and interpret the large volumes of sensor data (Tuia et al. 2022; Reynolds et al. 2025). The deployment of these sensors at scale will further enable the quantification of social and density information at the correct spatial and temporal resolutions (Koger et al. 2023a, b). For example, using drones combined with computer vision and deep learning has successfully tracked individuals simultaneously in group-living species, allowing researchers to reconstruct spatial distribution and social structure of social animals (Koger et al. 2023a; White et al. 2025). Similarly, deep learning approaches applied to aerial imagery have been used not just to count animals but to identify individuals and infer social context, offering a path toward quantifying social fences and density dependence at fine scales (Aliane 2025).

7. 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 forms of phenotypic plasticity 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 and social sensitivity (reversible plasticity) and its developmental constraints (irreversible plasticity). When these plastic behavioral responses are repeatedly expressed across generations within a partially migratory population through reversible and irreversible plasticity, they 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

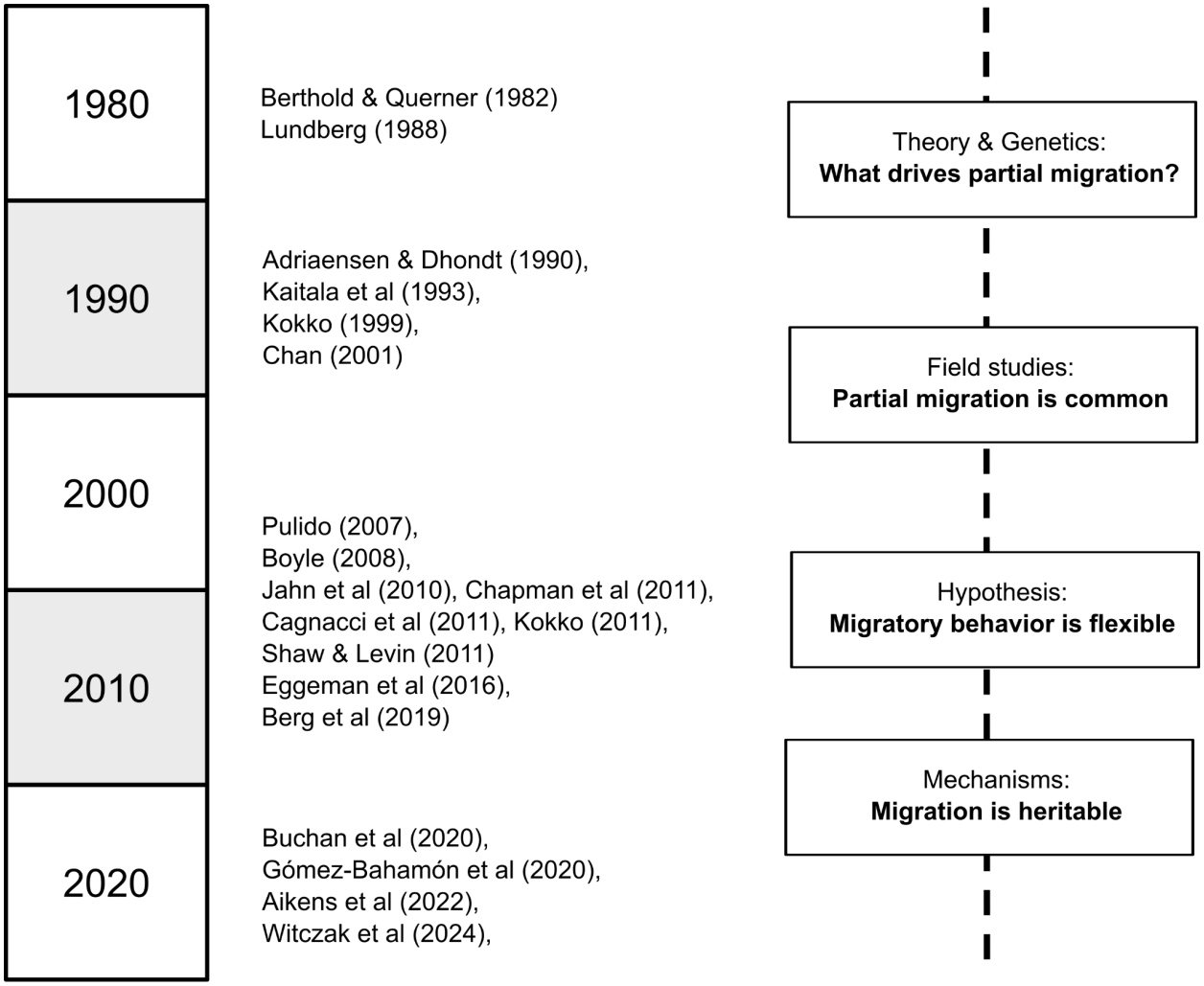


Figure 1. History of advances in partial migration research over the last five decades (1980s - 2020s). Listed papers are key reviews and research articles focusing on the evolution and ecology of partial migration. The right boxes represent key themes of partial migration research by evolutionary biologists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

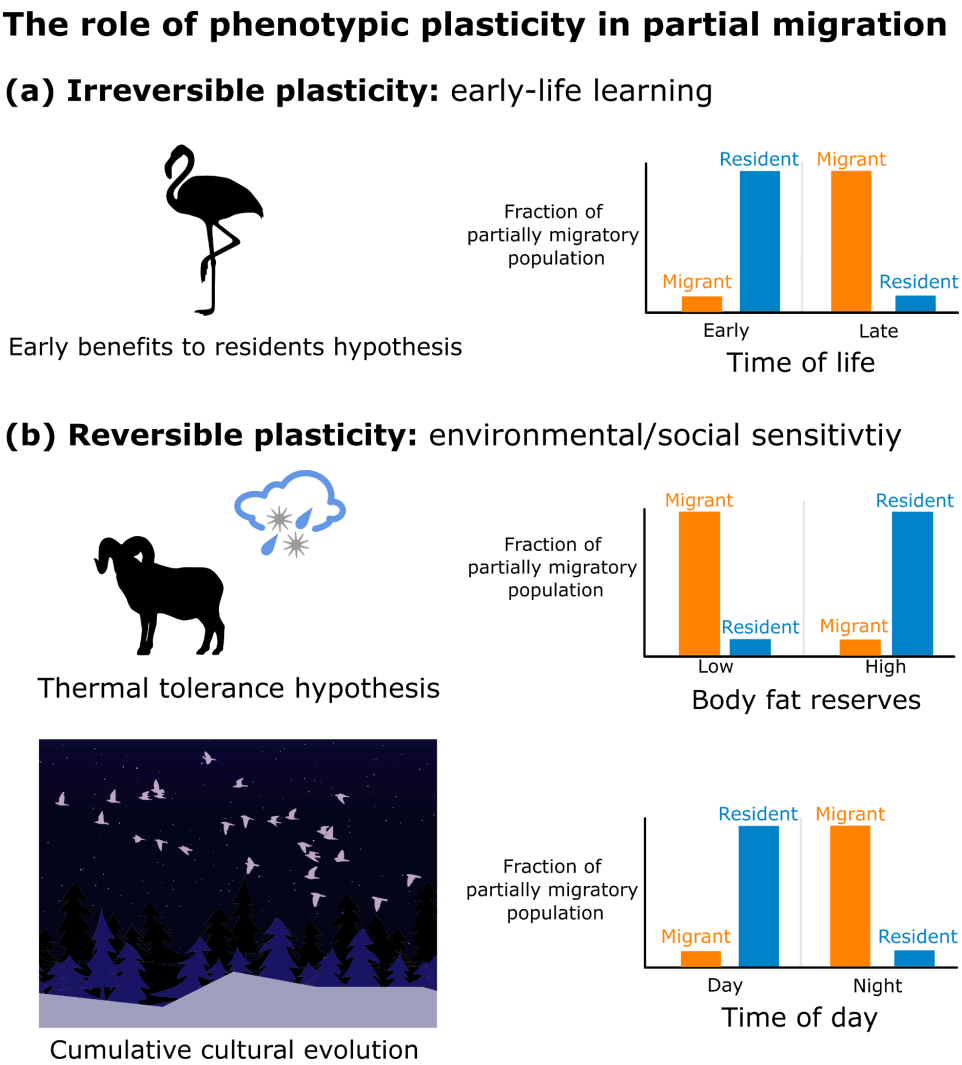
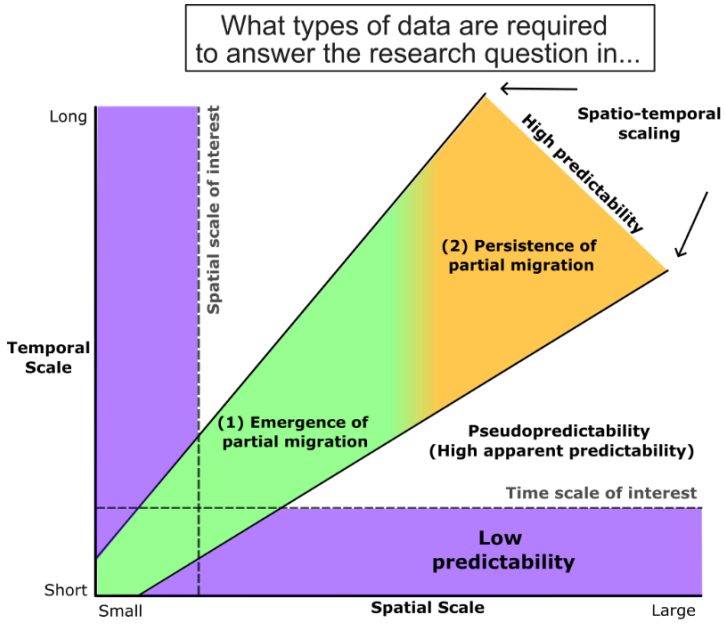


Figure 2. Conceptual pathways leading to the emergence and persistence of partial migration through (a) irreversible plasticity and (b) reversible plasticity. (a) Under irreversible plasticity, migratory strategies become progressively constrained during development through learning or early-life experiences. The first 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 reversible plasticity, migratory decisions vary in response to individual state, environmental conditions, or their interaction. The second 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 third example illustrates cumulative cultural evolution, in which silvereyes showing no migratory restlessness during spring and autumn migration began to exhibit nocturnal restlessness when placed with conspecifics that display migration, suggesting that migratory activity can be socially induced (Chan, 2005). Conceptual orange bars denote migrants, whereas blue bars denote residents (not based on real data).



(1) Partial migration emergence

What **spatial scale** does your question span?
(from individuals or local interactions to population, landscapes, or migratory ranges?)

- Final scale: Individuals, Territories, Local social interactions
- Intermediate scale: Populations, Habitat patches
- Broad scale: Metapopulations, Migratory routes, Geographic ranges

What **temporal scale** does your question span?
(from within-season dynamics to lifetime trajectories or multi-generational changes?)

- Short-term: Behavioral decisions, Seasonal migration
- Medium-term: Onotogeny, Life-history stages
- Long-term: Evolutionary change, Population trends

(2) Partial migration persistence

What **spatial scale** does your question span?
(from individuals or local interactions to population, landscapes, or migratory ranges?)

- Final scale: Individuals, Territories, Local social interactions
- Intermediate scale: Populations, Habitat patches
- Broad scale: Metapopulations, Migratory routes, Geographic ranges

What **temporal scale** does your question span?
(from within-season dynamics to lifetime trajectories or multi-generational changes?)

- Short-term: Behavioral decisions, Seasonal migration
- Medium-term: Onotogeny, Life-history stages
- Long-term: Evolutionary change, Population trends

Figure 3. Partial migration emerges across different spatial and temporal scales (see Section 3.3). 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. Dashed lines indicate the spatial and temporal scales of interest for each study. Studies conducted over long spatial scales and short temporal scales (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. 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 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.

Box 1. Multiple definitions of partial migration.

Partial migration is commonly defined as "some individuals migrate, and others stay" (Lundberg 1988; Chapman et al. 2011; Fortuna 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 review, 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, also known as "non-breeding partial migration" (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). Partial migration can fall into one of three categories: (1) non-breeding partial migration - species where residents and migrants share a breeding ground and winter apart, (2) breeding partial migration - species where residents and migrants share an overwintering ground and breed apart, (3) skipped breeding partial migration - non-migratory individuals forgo reproduction (Shaw & Levin, 2011). Also, note that different types of populations can emerge within the same species, such as fully resident, fully migratory, and mixed migrant/resident populations.

2. 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 (Xu et al. 2021).

Box 2. Definitions of hypotheses related to the causes of partial migration. The details of the hypotheses are summarized in Berg et al. (2019), Boyle (2008), Cauyela et al. (2025) and Chapman et al. (2011).

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

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

Early benefits to residents:
Young individuals may gain more breeding opportunities by staying resident, whereas older individuals may increasingly migrate to avoid costs of residency, such as intraspecific competition

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.

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