

Title: Proximate drivers of migration propensity: a meta-analysis across species

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Contributions: MB, ABAS, JMN designed the study; MB performed research and analyzed data;

MB wrote the manuscript with input from ABAS, JMN.

Running title: Proximate drivers of migration propensity

Keywords: partial migration, movement ecology, evolution, proximate cues

Type of article: Letter

Abstract word count: 150

Main text word count: 4952

Number of references: 83

Number of boxes: 1

Number figures: 1

Number of tables: 4

Data availability: All data and code are available on GitLab https://gitlab.com/WiDGeT_TrentU/ and Figshare <https://doi.org/10.6084/m9.figshare.25325911.v1>

24 **Abstract**

25 Animal migration is multifaceted in nature, but the relative strength of different cues that trigger
26 resulting patterns of migration is not well understood. Partially migratory populations offer an
27 opportunity to test hypotheses about migration more broadly by comparing trait differences of
28 migrants and residents. We quantitatively reviewed 45 studies that statistically modeled
29 migration propensity, extracting 132 effect sizes for internal and external proximate drivers
30 across taxa. Our meta-analysis revealed that internal and external drivers had medium (Cohen's d
31 > 0.3) and large (Cohen's $d > 0.5$) effect sizes on migration propensity respectively. Predator
32 abundance and predation risk had a large effect, as did individual behaviour (e.g., personality).
33 The abiotic environment and individual physiology had a medium effect on migration
34 propensity. Of the studies that examined genetic divergence between migrants and residents,
35 64% found some genetic divergence between groups. These results clarify broad proximate
36 drivers of migration and offer generalities across taxa.

37

38 Introduction

39 Every year, animals from all major branches of the animal kingdom undertake seasonal
40 migrations. These mass movements allow for species to persist in extreme climate and resource
41 gradients (e.g., Aikens et al. 2020; Winger & Pegan 2020) and contribute to nutrient transfer
42 between otherwise unconnected ecosystems (Bauer & Hoyer, 2014; Fudickar et al., 2021).
43 Migration is triggered by a combination of proximate cues, both internal and external, and the
44 resulting patterns of movement can vary across migrating individuals, populations, and species.
45 An individual's body condition, thermal tolerance, predation vulnerability, and life history status,
46 along with interactions between the environment and genetic variation, all play a role in the
47 expression of an individual's migratory phenotype (Fudickar et al., 2021).

48 Because of the multifaceted nature of migration, it can be difficult to tease apart the
49 underlying mechanisms influencing this behaviour across species. It is necessary to understand
50 these mechanisms, both to deepen our fundamental understanding of this behaviour in animals,
51 but also because migrations in many species, especially those spanning large landscapes and
52 steep environmental gradients, are considered vulnerable to environmental change (Shaw, 2016;
53 Tomotani et al., 2018). Climate warming, urbanization and rapid land-use change continue to
54 increase, leading to changes in both the biotic and abiotic landscape. Migration behaviour has
55 disappeared in many species (Norbu et al., 2017; Wilcove & Wikelski, 2008); and a broader
56 comprehension of the evolution of migration is needed to conserve species whose migrations are
57 at risk.

58 The evolution of migration behaviour is driven by ultimate mechanisms, such as the need
59 to increase access to resources, to escape unfavourable environmental conditions, or to reproduce
60 (Shaw, 2016). These ultimate drivers are non-mutually exclusive and overlap with proximate

drivers that have been hypothesized to drive the evolution of migration behaviour. Proximate drivers such as intra- and interspecific competition or conflict (Gauthreaux, 1982; Grayson & Wilbur, 2009), seasonal influences on foraging opportunities (Boyle et al., 2011; Ketterson & Nolan, 1976), predation vulnerability (Skov et al., 2011), and individual tolerance to thermal extremes (Ketterson & Nolan, 1976) have all received varying support as mechanisms in the evolution of migration behaviour (Box 1). Many proximate drivers are external to the animal and suggest that animals migrate in response to variation in their external environment. Less attention has been paid to internal factors, where differences in individual physiology, which is known to influence animal movement (Nathan et al., 2008), may drive an animal's propensity to migrate. Internal factors such as body size (Linossier et al., 2016; Rolandsen et al., 2017; Strait et al., 2021) and breeding status (Hegemann et al., 2015; Thériault et al., 2007), drive migration in some species. Internal factors are likely influenced by a combination of genetic variation and an animal's external environment. To develop a comprehensive understanding of the mechanisms underlying migration behavior in animals, both internal and external factors must be considered.

Recent studies have challenged the assumption that migration behaviours are static traits (Eggeman et al., 2016; Xu et al., 2021). Animal tracking technology has allowed researchers to monitor individuals and populations for longer periods of time and in more detail, shedding new light on migration behaviour. For example, many populations that were previously considered fully migratory in fact have individuals that remain resident year-round (Kessel et al., 2018; McGuire & Boyle, 2013). Similarly, longer-term monitoring of individual animals revealed that switching between migrant and resident strategies across years is more prevalent than previously thought (Hebblewhite & Merrill, 2011). This phenomenon, in which a portion of a population migrates, while the remaining portion are resident year-round is known as partial migration.

Partial migration has been demonstrated across taxa (Berg et al., 2019; Grayson et al., 2011; Hegemann et al., 2015; Satterfield et al., 2018) with several hypotheses suggested for the existence and maintenance of this behaviour, which is thought to be a precursor to full obligate migration (Box 1; Chapman, Bronmark, et al., 2011). Differences in physiology, behaviour, and genetics can elucidate underlying ecological factors that promote the expression of one migratory phenotype over another. As an extension, the genomes of migratory and non-migratory individuals can reveal genetic differences that underly phenotypic variance that correlates to migration propensity (Cavedon et al., 2022; Franchini et al., 2017; Kelson et al., 2020). Much of the work on partial migration systems focuses on birds and fishes, but more recently, research has focused on large mammals, as many ungulate populations show this behaviour (Berg et al., 2019; Eggeman et al., 2016; Mysterud et al., 2011). A review of the plasticity of ungulate migrations identified drivers of migration propensity including habitat loss, predation, density dependence, and extreme weather events (Xu et al., 2021).

Partially migratory species offer a unique opportunity to test hypotheses about migration more broadly, by examining trait differences of migrants and residents within the same population. Here, we conduct a meta-analysis of partial migrations, with the goal of understanding the mechanisms driving the evolution and maintenance of migration by quantifying the effect of both internal and external proximate drivers on migration propensity across species. Using partial migration systems as a model, we measured the differences of internal and external factors driving propensity to migrate. We used a meta-regression framework to draw conclusions about the overall empirical effect of drivers on migration propensity while accounting for species differences.

Methods

Literature search and selection criteria

We compiled a data set of relevant articles using the Web of Science search engine on 2 November 2021. Searches were conducted in English and did not include a restriction for the year of publication. We used the following search terms: *migrat** AND *partial**. Articles were filtered to include only empirical studies in the ecology and evolutionary biology categories.

The following criteria were applied:

1. The study had to focus on a migratory species of any animal taxa, except for humans. For the purpose of this study, we defined animal migration as seasonal movement between home ranges (Fryxell & Sinclair, 1988). Following the definition outlined by Dingle (2014), we considered populations or individuals as migratory if their movements were (a) persistent movements between geographic regions that were spatially and temporally predictable and characterized by distinct departure and arrival times; (b) mostly linear and undistracted by resources for extended periods; and (c) longer in duration than that characterized by average daily activity patterns.
2. The study had to have examined a partially migratory population in which some individuals were migratory and some were sedentary. Studies must have assessed both a migratory group and a non-migratory group and quantified the same trait in each group and reported either a difference in population means or the effect of the trait on the propensity to migrate.
3. Traits quantified by the study could include internal or external variables between migratory and non-migratory groups. We grouped traits post hoc into categories of environmental (e.g., temperature or precipitation differences experienced by each group),

genetic (e.g., functional, or neutral genetic differentiation), physiological (e.g., body size, condition indices), population density, predator dynamics (e.g., risk), behavioural (e.g., foraging tactics, personality), or sex.

4. Studies must have applied a frequentist statistical approach, and effect size (in the form of a beta coefficient from a logistic regression or F-statistic or t-statistic and associated p-value) had to be provided.
5. Studies carried out on any life-history stage of the animal and in either a laboratory or field setting were included.
6. Simulation studies and systematic reviews were excluded.

Data extraction and calculation of effect sizes

We extracted effect sizes for all factors that influenced migration propensity for all the studies that met selection criteria above (full list in Appendix I Table S1). Many studies investigated one or more factors that influenced migration propensity between migratory and sedentary groups in at least one species, and each factor was recorded as a unique observation. For each observation, we extracted the following explanatory variables: 1) trait, which included behaviour, sex, physiology, density, predator dynamics, environment, genetic variables; 2) taxonomic class; 3) study design (experimental or observational); (Table 1).

We calculated all standardized effect sizes and 95% confidence intervals using the effectsize R package (Ben-Shachar et al., 2020) in R (R Core Team, 2022). We used the standardized effect size, Cohen's d , which is used to describe the standardized mean difference of an effect (Cohen, 1988). Broadly, Cohen's d effect sizes can be interpreted as small ($d \approx 0.2$), medium ($d \approx 0.5$), and large ($d \approx 0.8$; Cohen, 1988). For studies reporting a beta coefficient (β) from a logistic

regression, we first converted β into an odds ratio (OR) and then converted OR to Cohen's d as follows:

$$OR = e^{\beta_1} \quad (1)$$

$$d = \frac{\log(OR) \times \sqrt{3}}{\pi} \quad (2)$$

For studies that reported a t-statistic we directly converted it into Cohen's d as follows:

$$d = 2 \times \frac{t}{\sqrt{df_{error}}} \quad (3)$$

For studies that reported an F-statistic we directly converted it into Cohen's d as follows:

$$d = 2 \times \sqrt{\frac{F}{df_{error}}} \quad (4)$$

Data analysis

To investigate potential publication bias in these compiled data, effect sizes were plotted against the natural log of sample size. Additionally, we plotted effect sizes against journal impact factor to assess bias associated with perceived impact of the research (Shafer & Wolf, 2013).

Model construction and selection

We used Cohen's d of each driver on the probability of migration as the response variable in a mixed-effects model, and the driver as the predictor variable. We examined the influence of drivers on effect size at two levels: one where the drivers were grouped into internal and external categories, and one where they were grouped as the subcategories of behaviour, physiology, sex, density, environment, and predator dynamics (Table 1). Candidate models were built using the `rma.mv` function in the `metafor` R package (Viechtbauer, 2010). In all models of effect size, study ID and within-study observation number (to account for multiple observations per study) were used as random effects to account for between- and within-study heterogeneity. Additional fixed effects included taxonomic class and study design type. Multiple competing models were

compared using AIC_C (Burnham & Anderson, 2002) to determine whether the additional fixed effects would improve the model fit. Where $\Delta\text{AIC}_C < 2$ we selected the model with the fewest fixed factors to avoid overfitting.

Our mixed model was a three-level meta-analytic model, in which levels 1, 2 and 3 represented the individuals, within-study variances, and between-study variances, respectively. Most articles in this meta-analysis provided multiple observations through either examining more than one trait or more than one species. Our three-level model allowed for the computation of an overall mean effect size while accounting for between-study and within-study heterogeneity. We used ANOVA to compare the fit of both a 3-level model and 2-level model to ensure the best fit for the data. We examined how much of the model heterogeneity was due to differences within and between studies by calculating a multilevel version of I^2 (Konstantopoulos, 2011). In conventional meta-analyses, I^2 represents the amount of variation not attributable to sampling error. In three-level models, this heterogeneity is split into within and between study variation. Thus, in our meta-analysis there were two values for I^2 quantifying the percentage of the total variation associated with either level 2 (within-study) or level 3 (between-study) variation.

Genetic summary

We were unable to convert the metrics used to assess the genetic differences between migratory and sedentary individuals such as F_{ST} or differential gene expression to Cohen's d , therefore, these studies were excluded from the meta-analytic models. Instead, we assessed the findings qualitatively by examining whether neutral or functional genetic divergence was detected between migratory and sedentary groups, or whether there were differences in the level of gene expression or methylation between groups. We also extracted information on whether each study

used whole nuclear genome, whole transcriptome, mitochondrial genome, reduced nuclear genome, or microsatellites for their analysis. These data were tabulated and compared across studies.

Results

The literature search produced 665 articles which were manually screened for relevance; we excluded and 511 articles immediately (e.g., human studies). The remaining 176 articles were read and deemed to meet all the requirements (45 studies) or excluded based on the selection criteria outline in the Methods section (131 studies, Table S1). A total of 132 effect sizes were extracted from the 45 studies (Figure S1). Of these, 75 observations measured internal factors and 57 measured external factors. The studies in the genetic category were not included in the comparative models ($n = 13$ observations, from 13 studies) and instead summarized separately. This left 119 observations from 32 studies for the models.

Of the 32 studies included in the meta-regression analysis, 12 were from class Actinopterygii, one from class Amphibia, 11 from class Aves, and 10 from class Mammalia. No studies involved species from class Insecta fit the criteria for inclusion in the study. Four of the studies were experimental and 30 were observational. Of the 13 genetic studies that were qualitatively assessed separately, seven were from class Actinopterygii, four from class Aves, and two from class Mammalia. No studies from class Amphibia or Insecta met the criteria for inclusion in the study. Of the genetic studies, six were experimental and seven were observational.

The mean Cohen's d for 57 observations of external factors influencing migration propensity was $0.67 (\pm SE = 0.25)$. The mean Cohen's d for 62 observations of internal factors was $0.55 (\pm SE = 0.21)$. At a finer level when these factors were divided into subcategories, the

mean Cohen's d was 1.47 (\pm SE = 0.96; n = 9 observations) for behaviour, 0.31 (\pm SE = 0.74; n = 6 observations) for density, 0.62 (\pm SE = 0.32; n = 40 observations) for environment, 0.40 (\pm SE = 0.19; n = 48 observations) for physiology, 1.20 (\pm SE = 0.48; n = 11 observations) for predator dynamics, and 0.41 (\pm SE = 0.75; n = 5 observations) for sex. Effect size was not correlated with natural log of sample size or journal impact factor (Figure S1).

All the competing models predicting the effect of internal and external factors on migration propensity were competitive with the top model (Δ AIC_C < 2), so we report the simplest model which used only the external and internal factors as a fixed effect. This parsimonious model predicted an overall Cohen's d of 0.70 (\pm SE = 0.13) for external and 0.50 (\pm SE = 0.11) for internal factors (Table 3, Figure 1a). For this model, I^2 = 0.95, conveying that 95% of variance was attributed to true heterogeneity as opposed to sampling variance. Of this variance, 13% was attributed to within-study clustering, and 82% was attributed to variance between studies (Table 3). Similarly, all the competing models predicting the effect of the subcategories on migration propensity had a AIC_C difference of <2 so we reported the simplest model including only the subcategories as a fixed effect. The model predicted a similarly large Cohen's d of 1.13 (\pm SE = 0.29) for behaviour, 0.30 (\pm SE = 0.30) for density, 0.63 (\pm SE = 0.12) for environment, 0.37 (\pm SE = 0.11) for physiology, 1.18 (\pm SE = 0.22) for predator dynamics, and 0.43 (\pm SE = 0.34) for sex (Table 3, Figure 1b). For this model, I^2 = 0.95. Of this variance, 95% was attributed to variance between studies (Table 3).

Of the 13 genetic studies, 11 studies examined genetic divergence between migratory and sedentary groups (Table 4). Four studies found no genetic divergence between migratory and sedentary groups while seven found some level of genetic divergence (four with neutral markers, and three with functional loci). Two studies detected significant differential gene expression

between migratory and sedentary groups, and one study found differential methylation between groups. Only two studies used a whole-genome approach while six used reduced genome or transcriptome. Five studies used microsatellites and whole mitochondrial genomes. We note that some studies used more than one method.

Discussion

The complex nature of migration behaviour can make it difficult to tease apart the underlying mechanisms contributing to its evolution. The effect of internal and external mechanisms is critical both for the eco-evolutionary dynamics of migration behaviour, and for conserving species whose migrations are considered vulnerable to environmental change. By quantitatively reviewing the literature on partially migratory systems, we were able to better characterize what drives migration and clarify the potential mechanisms of its evolution. Our models accounted for taxonomic differences across species, and, despite considerable heterogeneity between studies, our estimates of effect size provide empirical support for the hypotheses on what drives animal migration (Box 1).

Our meta-analysis confirms that migration is triggered by a combination of proximate cues, both internal and external. Our models revealed that internal and external factors had a medium and large effect on migration propensity, respectively (Table 3). That the external environment had a slightly larger effect on migration propensity compared to internal factors fits with current understanding of the evolution of migration. External cues such as temperature and photoperiod strongly influence an animal's migration (Abraham, Upham, Damian-Serrano, et al., 2022; Fudickar et al., 2021; Shaw, 2016) and thus are expected to have governed its evolution. However, migration is also driven by many internal proximate cues, such as individual body

condition and genotype (e.g., Debes et al., 2020; Mueller et al., 2011). The smaller effect size suggests that internal factors may elicit more fine-scale variation in propensity to migrate within a broader context of environment-mediated migration. For example, while the cyprinid fish roach (*Rutilus rutilus*) migrate following warmer summers, bolder individuals tend to migrate more than shy individuals (Chapman et al. 2011). Such nuances are likely present in many partially migratory populations and indicates a need to focus on both external and internal factors in combination to resolve the factors influencing this behaviour more comprehensively.

External drivers of migration propensity

Abiotic factors such as temperature and precipitation changes are important triggers for migration, particularly for species in temperate regions, and have been well documented in the literature (Cadahía et al., 2017; Finstad & Hein, 2012; Graham et al., 2016). This is consistent with our models showing a medium effect of environment on migration propensity; our models also showed a large effect of predation (Table 3), typically measured as predation risk or predator abundance. Studies show that prey species such as elk (*Cervus elaphus*) often migrate to reduce predation risk and are more likely to do so when predator abundance is higher (Eggeman et al., 2016; Hebblewhite & Merrill, 2007). This finding suggests predator-prey dynamics have a potentially large role in the evolution of migration. In addition, predator presence can affect migratory plasticity as found in common roach where individuals exposed to increased predation risk increased their likelihood of migrating (Hulthén et al., 2015).

Predation vulnerability is implicitly density dependent, as are other hypotheses to explain variation in migration propensity in partially migratory populations, such as competitive release and intrasexual competition (Box 1). Only a small number of studies explicitly assessed the effect of density on migration propensity, and most detected an effect. This supports the idea of

migration being a ‘conditional strategy’ (Lundberg 1988) where the fitness of the behaviour is determined by the intrinsic state of the individual or by the density-dependent extrinsic environment. Considering the paucity of studies and the pervasiveness of density effects (such as on forage availability and predation risk), further research on the influence of density on migration is warranted.

Internal drivers of migration propensity

The sub-categories reflecting internal factors tended to have smaller effect sizes than those measuring external factors, similar to the coarser analysis (Figure 1). Individual body size and internal condition can be important drivers of migration, particularly in species migrating to breeding grounds or towards refugia from extreme temperatures (Shaw, 2016). Body size is hypothesized to drive migration, but whether large or small bodied individuals are more likely to migrate is context-dependent. In ungulates, it is hypothesized that large individuals are more likely to migrate as they possess the size to accommodate for the metabolic costs of locomotion (Abraham, Upham, Damian-serrano, et al., 2022). In other taxonomic groups such as birds or fishes, it is hypothesized that smaller bodied individuals, at greater risk of starvation or not able to withstand thermal extremes, may be more likely to migrate. We found similar varying effects of body size on migration propensity, with larger individuals less likely to migrate for some systems (Brodersen et al., 2008; Hegemann et al., 2015; Strait et al., 2021), while, in other cases, body size did not affect migration probability (Fudickar et al., 2013; Hulthén et al., 2015; Rolandsen et al., 2017). The overall moderate effect of physiology in our models suggests that body size differences contribute to the evolution of migration behaviour, but the degree to which it plays a role is likely dependent on the system.

We found a strong effect of behaviour on migration propensity (Table 3, Figure 1b). The term behaviour, in the context of migration, can represent several phenomena, and indeed this presents a limitation in summarizing the literature whereby the variation across studies in measuring behaviours is wide. Behaviours could indicate a trade-off between forage and predation risk; for example, resident individual elk face greater predation risk by not migrating but make fine-scale foraging decisions that increase their access to high-quality forage (Hebblewhite & Merrill, 2009). Alternatively, consistent individual differences in personality can drive migration tendency; for example, bolder cyprinid fish are more likely to migrate (Chapman, Hulthén, et al., 2011). Despite the variety of factors in our sub-category of behaviour, our models still showed a strong effect. This outcome supports the idea of a migratory syndrome where the co-expression of multiple traits enables migration (Dingle, 2006; Sih et al., 2004). Dingle (2006) argues that migratory syndromes represent a convergence of traits to address the ultimate drivers of migration that are shared across taxa. Our results illustrate how many co-expressed proximate mechanisms contribute to the evolution of migration. More generally, correlated behaviours or co-expressed phenotypic traits likely contribute to the overall migratory phenotype across taxa. For example, a bolder individual may cover more area within a home range compared to a shyer individual (Spiegel et al., 2017). While home range size may not necessarily drive migration propensity, it may correlate to a trait that has more direct effect on migration behaviour. Teasing apart correlated behaviors from actual drivers of migration will be challenging, so focusing research with clearly articulated hypotheses grounded in theory will be key to moving this aspect of migration research forward.

While studies were few in number, some did report sex differences in migration propensity in birds (Bai et al., 2012) and amphibians (Grayson & Wilbur, 2009) but no effect of

sex on migration in ungulates (Cagnacci et al., 2011). Variation in migration propensity related to sex can occur where intraspecific competition for territories varies by sex, and migration serves as a strategy to escape costly sexual harassment or breeding (Chapman, Bronmark, et al., 2011). Therefore, sex might play a role in driving migration in some species while, in others, sex may not affect the decision of whether to migrate, but instead play a role in the timing or distance an individual migrates (Cagnacci et al., 2011).

A genetic basis for migration propensity

The expression of a migratory phenotype is likely driven by interactions between extrinsic environmental cues and underlying variation in genetics that can differ between populations or individuals. The molecular mechanisms underlying migration behaviour are still not well understood and are only more recently being explored in natural populations in part due to the availability of high-throughput sequencing technologies. The advantage to studying the genetic basis for migration in partially migratory populations is the existence of clear migrant and resident phenotypes that share a common environment before the departure of the migrants (Liedvogel et al., 2011). Using gene mapping and genome-wide associations, many of the studies reviewed here identified genes both neutral and functional, and areas of the genome associated with migration behaviour.

Two species particularly well studied in this regard are the salmonid *Oncorhynchus mykiss* (Baerwald et al., 2016; Kelson et al., 2020; McKinney et al., 2015; Strait et al., 2021) and the European blackcap *Sylvia atricapilla* (Perez-Tris et al., 2004) for which clear migrant and resident life histories exist in natural populations. Examples of key genes linked to differential migration behaviour include AHR2A (associated with circadian rhythm) and ZNF322 (involved in gene expression in response to environmental stimuli) for *O. mykiss* (Baerwald et al., 2016;

McKinney et al., 2015) and DRD4 (linked to exploratory behaviour and boldness) and ADCYAP1 (associated with responses to light) genes in blackcaps (Mueller et al., 2011; Sauve et al., 2021). Finding genes linked to differentiation in behavioural and physiological processes in these well-studied species is consistent with our results (Figure 1) and our models showed that behaviour and physiology likely affect migration evolution, as a genetic basis for these behavioural and physiological traits is necessary for natural selection or micro-evolution. Genes linked to differentiation in behavioural and physiological processes should be areas of focus when exploring the genetic architecture of migration in other species; for example, circadian rhythms play an important role in triggering migration events in many migratory species (Bossu et al., 2022; Dawson, 2008; Stuber et al., 2013), suggesting the potential to identify analogous genes in other species that express variation in migration timing.

Beyond characterizing the genomic architecture linked to migratory phenotypes, two studies identified differential gene expression in birds (Franchini et al., 2017) and fish (McKinney et al., 2015) which gives a more complete picture of the causal genes associated with the migratory phenotype. These authors found upregulation in the motilin receptor M1NR in migrants which is likely associated with increased fat uptake or glucose levels (Franchini et al. 2017), and upregulation in genes associated with growth and development of the brain in migrants (McKinney et al. 2015). Differential expression in these genes could affect variation in body size and behaviour between migrants and residents, two internal factors that our study has found have medium and large effects on migration propensity. This highlights the underlying genetic component associated with many of the internal factors considered to be driving migration behaviour. In addition, Baerwald et al. (2016) identified differentially methylated

regions between migrant and resident phenotypes of *O. mykiss* confirming that the expression of a migratory phenotype is dependent on interactions between genes and the environment.

Study limitations and future directions

This study provides a foundation for improving our empirical understanding of factors driving the evolution of migration. However, there are many variables that could influence migration propensity in partially migratory populations that we were not able to consider. The limited number of observations across a range of partial migration systems means that factors, such as species differences and variation in migration strategy (i.e., distances, timing), could not be controlled for. The appreciable heterogeneity among studies ($I^2 = 0.95$) suggest that the effect of internal and external factors on migration propensity are context-dependent, though this is not surprising given the broad range of migratory phenotypes.

We were also unable to empirically estimate the effect of genetics on migration propensity due to limitations in estimating effect size across studies. The role of genetics in driving migration behaviour across a variety of taxonomic groups remains an outstanding area of interest as most of the studies that assessed genetic differences examined fishes and birds. For example, the additive variation (Bonar 2023) and expression of genes associated with migration interact with environmental factors is a major question that still needs to be explored across a broader variety of taxa. Although we anticipate that future studies will uncover similar genetic patterns in other species, studies addressing these gaps in more taxa are needed to fully comprehend how both internal and external factors drive migration propensity.

Impacts of global environmental change

Migrations are threatened across many taxa and, in general, it is anticipated that they will become more imperiled with continued global change (Harris et al., 2009; Wilcove & Wikelski,

2008). The large effect of predation risk, behaviour, and abiotic environment on migration propensity demonstrated by our study (Table 3, Figure 1b) suggests that there could be detrimental consequences to migrating animals resulting from environmental changes that directly influence these factors. Anthropogenic factors such as harvesting and land-use change have led to a decrease in the number of apex predators across the globe (Fleming & Bateman, 2018; Sabal et al., 2021) and this could drastically change the landscape of predation risk. Reduced predation risk, based on its large effect size, could alter the selective pressures on migratory species, making migration behaviour less adaptive and potentially reducing the proportion of migratory animals or leading to a complete loss of migrations. Contrastingly, many areas have recovered once-extirpated predator populations, likewise rapidly recovering this potential selective pressure on migratory species (Sabal et al., 2021). Increased human density and urbanization can decrease migration propensity, with birds choosing to remain resident year-round in urban areas (Bonnet-Lebrun et al., 2020). Urbanization buffers against winter harshness and increases access to local recourses, making residency a viable tactic. More broadly, changing temperatures and precipitation can affect the distribution of migratory species both directly through thermoregulation costs, and indirectly through primary productivity changes. Temperature changes may make parts of migratory ranges uninhabitable, while making previously unsuitable areas more suitable than they were historically (Alves et al., 2019; Ambrosini et al., 2016; Tellería et al., 2016); this has cascading effects on demography. Finally, behaviours are likely to be affected by environmental change as migratory animals respond either plastically or through selection (Keith & Bull, 2017). The influence of environmental change on migration is expected to be context-dependent, but our models show that the response is likely to be strong in many areas. As migrations change and the number of migrants decline,

so too do the critical ecological contributions associated with migrating animals, such as the redistribution of resources and the consumption of forage (Subalusky et al., 2017; Wilcove & Wikelski, 2008).

Acknowledgements

We respectfully acknowledge that data analyses were conducted at Trent University, which is on the treaty and traditional territory of the Mississauga Anishinaabeg. This work was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant (ABAS and JMN) and NSERC Vanier PhD Fellowship (MB).

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Tables and Figures

Box 1. Proximate drivers of animal migration

Migration is triggered by a combination of ultimate causes and proximate cues. Proximate cues can be both internal and external, and it is likely the interaction among them results in the wide variation in migration behaviours exhibited across and within taxa. Hypotheses that have received support in the literature regarding the evolution of migrants and maintenance of partial migration systems are outlined below. (Based on Chapman, Bronmark, et al., (2011)).

Intrasexual conflict and competition

Competition for high quality breeding territory promotes residency in the sex more likely to incur a fitness benefit from remaining on the breeding grounds. Less competitive or more subordinate individuals migrate to avoid intrasexual competition especially when food is limited on the breeding ground (Fudickar et al., 2013; Lundblad & Conway, 2020).

Competitive release

Competition for limited food resources promotes migration to avoid intraspecific competition. Van Moorter et al. (2020) suggested this phenomenon as density-dependent and showed that when the seasonal distribution of quality habitat changes, partial migration occurs, and migration rates should increase as the quality of habitat increases (Moorter et al., 2021). In partially migratory populations it is hypothesized that the more dominant or competitive individuals will remain resident, while subordinate individuals will migrate (e.g., Grayson et al., 2011).

Thermal tolerance to extremes

Individuals migrate to escape the cost of enduring thermal extremes. Individuals experiencing more extreme ambient conditions (e.g., edge of geographic ranges) or individuals of either small or large body size, depending on the intolerance of extreme cold or hot respectively, are more likely to migrate (Boyle, 2008; Ketterson & Nolan, 1976).

Predation vulnerability

Individuals migrate to reduce their predation risk and trade off the potential for growth and development (Skov et al., 2011). Variation in predation vulnerability may explain why some individuals migrate and others remain resident, with more conspicuous or behaviourally vulnerable individuals more likely to migrate. For example, mothers and offspring may trade foraging opportunities in order to access safer habitats (e.g., White et al., 2014).

Limited foraging opportunity

A seasonal reduction in forage can trigger migration for those individuals unable to meet energetic demands (e.g., those in poorer body condition). Seasonal drivers of food limitation can include extreme temperatures, precipitation or aridity, and increased storm frequency. Support for this hypothesis shows that differences in body size mediate fasting ability and are associated with variation in migratory behaviour (e.g., Lundblad & Conway, 2020; Wilkinson & Jodice, 2023).

Table 1. Summary table and description of data extracted from full articles(n=45 articles; N=132 observations).

Variable	Level I	Level II	Description	N
Trait	Internal	Behaviour	Measures include: movement tactics, foraging tactics, personality, resource selection	9
		Physiology	Measures include: body size, gut microbiome composition, condition index, breeding status	48
		Sex	The sex of each migrant or resident	5
		Genetic	Measures include: genetic divergence, genetic diversity, differential gene expression, differential methylation	13
	External	Density	Population density of migrant and resident groups	6
		Environment	Measures include: temperature, precipitation, anthropogenic features, vegetation, topography	40
		Predator Dynamics	Measures include: predation risk, predator abundance, predator presence/absence	11
Taxonomic class	Actinopterygii		Ray-finned fishes	30
	Amphibia		Amphibians	3
	Aves		Birds	65
	Mammalia		Mammals	34
Study design	Experimental		Study involved experimental manipulation of traits on migrant and resident groups	15
	Observational		Study was observational	117

Table **Error! No text of specified style in document..** Competing candidate models predicting Cohen's d of migration propensity as a function internal (int) and external (ext) factors, and subcategories (sub cat). Additional fix factors included taxonomic class and study design, and all models had the random factor of unique study ID.

Models with external factors (Level I)		AIC_C	ΔAIC_C	weight
1	Cohen's $d \sim$ Level I (int/ext) + class + study design	290.07	0.00	0.32
2	Cohen's $d \sim$ Level I (int/ext) + class	290.39	0.32	0.27
3	Cohen's $d \sim$ Level I (int/ext)	290.68	0.61	0.24
4	Cohen's $d \sim$ Level I (int/ext) + study design	291.31	1.24	0.17
Models with subcategories (Level II)				
1	Cohen's $d \sim$ Level II (sub cat)	282.87	0.00	0.29
2	Cohen's $d \sim$ Level II (sub cat) + class + study design	283.00	0.13	0.21
3	Cohen's $d \sim$ Level II (sub cat) + class	283.00	0.14	0.21
4	Cohen's $d \sim$ Level II (sub cat) + study design	284.04	1.17	0.13

Table 3. Model statistics for best models predicting Cohen's d of migration propensity as a function of (a) internal and external factors, and (b) subcategories. All models account for multiple observations from studies with study ID as a random variable.

(a) Variable	Estimate	SE	t	Lower 95% CI	Upper 95% CI	p	I² (total)	I² (within-study)	I² (between-study)
External	0.6953	0.1339	5.1927	0.4301	0.9605	<.0001	95.1544	13.4648	81.6896
Internal	0.5042	0.1149	4.3861	0.2765	0.7318	<.0001			

(b) Variable	Estimate	SE	t	Lower 95% CI	Upper 95% CI	p	I² (total)	I² (within-study)	I² (between-study)
Behaviour	1.1337	0.2852	3.9750	0.5686	1.6987	0.0001	94.6991	0.0000	94.6991
Density	0.2995	0.2950	1.0153	-0.2849	0.8839	0.3121			
Environmental	0.6343	0.1158	5.4759	0.4048	0.8638	<.0001			
Physiology	0.3680	0.1068	3.4450	0.1563	0.5796	0.0008			
Predator dynamics	1.1794	0.2184	5.4004	0.7467	1.6121	<.0001			
Sex	0.4264	0.3404	1.2526	-0.2480	1.1008	0.2129			

Table 4. Qualitative summary of genetics articles. Inferences and fraction of the genome (or transcriptome in the case of differential gene expression) analyzed in migration studies – Wn = whole nuclear genome; Wt = whole transcriptome; Wm = whole mitochondrial genome; R = reduced nuclear genome; M = microsatellites; S = SNPs

Study	Taxonomic class	Study type	No divergence detected	Divergence at neutral loci	Divergence at functional loci	Differential gene expression	Differential methylation
Baerwald et al. 2016	Actinopterygii	Experimental					R
Karlsen et al. 2013	Actinopterygii	Experimental			Wn		
Kelson et al. 2020	Actinopterygii	Observational			R		
McKinney et al. 2015	Actinopterygii	Experimental				Wt	
Perry et al. 2005	Actinopterygii	Experimental		M			
Strait et al. 2021	Actinopterygii	Experimental		R			
Theriault et al. 2007	Actinopterygii	Observational	M				
Franchini et al. 2017	Aves	Observational	Wn			Wt	
Malpica & Ornelas 2014	Aves	Observational	Wm, M				
Miller et al. 2012	Aves	Observational		Wm, M			
Perez-Tris et al. 2004	Aves	Experimental	Wm				
Barnowe-Meyer et al. 2013	Mammalia	Observational		M			
Cavedon et al. 2019	Mammalia	Observational			R		

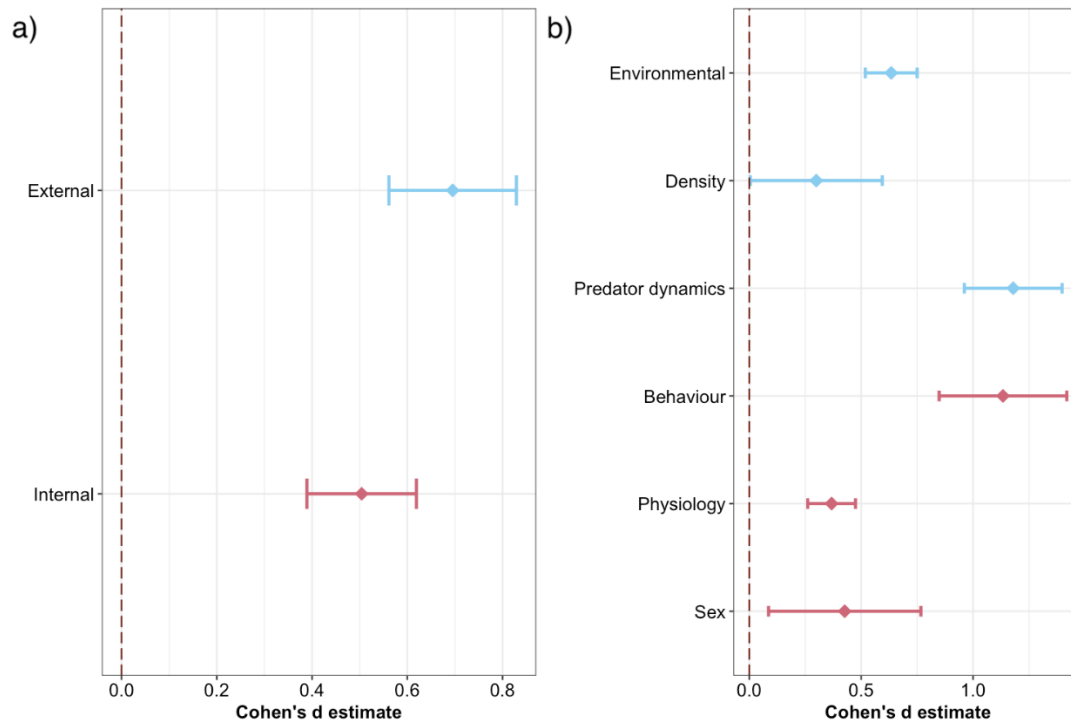


Figure 1. Forest plots of the Cohen's d derived from the best model predicting the effect of external factors (blue) and internal factors (red; a) and the effect of subcategories (b) on migration propensity.