

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

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April 19, 2024

## Abstract

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

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

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12 MB wrote the manuscript with input from ABAS, JMN.

13 Running title: Proximate drivers of migration propensity

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

15 Type of article: Letter

16 Abstract word count: 150

17 Main text word count: 4952

18 Number of references: 83

19 Number of boxes: 1

20 Number figures: 1

21 Number of tables: 4

22 Data availability: All data and code are available on GitLab [https://gitlab.com/WiDGeT\\_TrentU/](https://gitlab.com/WiDGeT_TrentU/)  
23 and Figshare <https://doi.org/10.6084/m9.figshare.25325911.v1>

**24 Abstract**

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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 & Hoye, 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

61 drivers that have been hypothesized to drive the evolution of migration behaviour. Proximate  
62 drivers such as intra- and interspecific competition or conflict (Gauthreaux, 1982; Grayson &  
63 Wilbur, 2009), seasonal influences on foraging opportunities (Boyle et al., 2011; Ketterson &  
64 Nolan, 1976), predation vulnerability (Skov et al., 2011), and individual tolerance to thermal  
65 extremes (Ketterson & Nolan, 1976) have all received varying support as mechanisms in the  
66 evolution of migration behaviour (Box 1). Many proximate drivers are external to the animal and  
67 suggest that animals migrate in response to variation in their external environment. Less attention  
68 has been paid to internal factors, where differences in individual physiology, which is known to  
69 influence animal movement (Nathan et al., 2008), may drive an animal's propensity to migrate.  
70 Internal factors such as body size (Linossier et al., 2016; Rolandsen et al., 2017; Strait et al.,  
71 2021) and breeding status (Hegemann et al., 2015; Thériault et al., 2007), drive migration in  
72 some species. Internal factors are likely influenced by a combination of genetic variation and an  
73 animal's external environment. To develop a comprehensive understanding of the mechanisms  
74 underlying migration behavior in animals, both internal and external factors must be considered.

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

84 Partial migration has been demonstrated across taxa (Berg et al., 2019; Grayson et al., 2011;  
85 Hegemann et al., 2015; Satterfield et al., 2018) with several hypotheses suggested for the  
86 existence and maintenance of this behaviour, which is thought to be a precursor to full obligate  
87 migration (Box 1; Chapman, Bronmark, et al., 2011). Differences in physiology, behaviour, and  
88 genetics can elucidate underlying ecological factors that promote the expression of one migratory  
89 phenotype over another. As an extension, the genomes of migratory and non-migratory  
90 individuals can reveal genetic differences that underly phenotypic variance that correlates to  
91 migration propensity (Cavedon et al., 2022; Franchini et al., 2017; Kelson et al., 2020). Much of  
92 the work on partial migration systems focuses on birds and fishes, but more recently, research  
93 has focused on large mammals, as many ungulate populations show this behaviour (Berg et al.,  
94 2019; Eggeman et al., 2016; Mysterud et al., 2011). A review of the plasticity of ungulate  
95 migrations identified drivers of migration propensity including habitat loss, predation, density  
96 dependence, and extreme weather events (Xu et al., 2021).

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

106

## 107 **Methods**

### 108 **Literature search and selection criteria**

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

113 The following criteria were applied:

- 114 1. The study had to focus on a migratory species of any animal taxa, except for humans. For  
115 the purpose of this study, we defined animal migration as seasonal movement between  
116 home ranges (Fryxell & Sinclair, 1988). Following the definition outlined by Dingle  
117 (2014), we considered populations or individuals as migratory if their movements were  
118 (a) persistent movements between geographic regions that were spatially and temporally  
119 predictable and characterized by distinct departure and arrival times; (b) mostly linear  
120 and undistracted by resources for extended periods; and (c) longer in duration than that  
121 characterized by average daily activity patterns.
- 122 2. The study had to have examined a partially migratory population in which some  
123 individuals were migratory and some were sedentary. Studies must have assessed both a  
124 migratory group and a non-migratory group and quantified the same trait in each group  
125 and reported either a difference in population means or the effect of the trait on the  
126 propensity to migrate.
- 127 3. Traits quantified by the study could include internal or external variables between  
128 migratory and non-migratory groups. We grouped traits post hoc into categories of  
129 environmental (e.g., temperature or precipitation differences experienced by each group),

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

133 4. Studies must have applied a frequentist statistical approach, and effect size (in the form  
134 of a beta coefficient from a logistic regression or F-statistic or t-statistic and associated p-  
135 value) had to be provided.

136 5. Studies carried out on any life-history stage of the animal and in either a laboratory or  
137 field setting were included.

138 6. Simulation studies and systematic reviews were excluded.

### 139 **Data extraction and calculation of effect sizes**

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

147 We calculated all standardized effect sizes and 95% confidence intervals using the effectsize R  
148 package (Ben-Shachar et al., 2020) in R (R Core Team, 2022). We used the standardized effect  
149 size, Cohen's  $d$ , which is used to describe the standardized mean difference of an effect (Cohen,  
150 1988). Broadly, Cohen's  $d$  effect sizes can be interpreted as small ( $d \approx 0.2$ ), medium ( $d \approx 0.5$ ),  
151 and large ( $d \approx 0.8$ ; Cohen, 1988). For studies reporting a beta coefficient ( $\beta$ ) from a logistic

152 regression, we first converted  $\beta$  into an odds ratio ( $OR$ ) and then converted  $OR$  to Cohen's  $d$  as  
 153 follows:

$$154 \quad OR = e^{\beta_1} \quad (1)$$

$$155 \quad d = \frac{\log(OR) \times \sqrt{3}}{\pi} \quad (2)$$

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

$$157 \quad d = 2 \times \frac{t}{\sqrt{df_{error}}} \quad (3)$$

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

$$159 \quad d = 2 \times \sqrt{\frac{F}{df_{error}}} \quad (4)$$

## 160 **Data analysis**

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

### 164 *Model construction and selection*

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

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

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

#### 190 *Genetic summary*

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

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

## 200 **Results**

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

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

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

220 mean Cohen's  $d$  was 1.47 ( $\pm$ SE = 0.96;  $n$  = 9 observations) for behaviour, 0.31 ( $\pm$ SE = 0.74;  $n$  =  
221 6 observations) for density, 0.62 ( $\pm$ SE = 0.32;  $n$  = 40 observations) for environment, 0.40 ( $\pm$ SE =  
222 0.19;  $n$  = 48 observations) for physiology, 1.20 ( $\pm$ SE = 0.48;  $n$  = 11 observations) for predator  
223 dynamics, and 0.41 ( $\pm$ SE = 0.75;  $n$  = 5 observations) for sex. Effect size was not correlated with  
224 natural log of sample size or journal impact factor (Figure S1).

225 All the competing models predicting the effect of internal and external factors on  
226 migration propensity were competitive with the top model ( $\Delta$ AIC<sub>C</sub> < 2), so we report the  
227 simplest model which used only the external and internal factors as a fixed effect. This  
228 parsimonious model predicted an overall Cohen's  $d$  of 0.70 ( $\pm$ SE = 0.13) for external and 0.50  
229 ( $\pm$ SE = 0.11) for internal factors (Table 3, Figure 1a). For this model,  $I^2$  = 0.95, conveying that  
230 95% of variance was attributed to true heterogeneity as opposed to sampling variance. Of this  
231 variance, 13% was attributed to within-study clustering, and 82% was attributed to variance  
232 between studies (Table 3). Similarly, all the competing models predicting the effect of the  
233 subcategories on migration propensity had a AIC<sub>C</sub> difference of <2 so we reported the simplest  
234 model including only the subcategories as a fixed effect. The model predicted a similarly large  
235 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)  
236 for environment, 0.37 ( $\pm$ SE = 0.11) for physiology, 1.18 ( $\pm$ SE = 0.22) for predator dynamics, and  
237 0.43 ( $\pm$ SE = 0.34) for sex (Table 3, Figure 1b). For this model,  $I^2$  = 0.95. Of this variance, 95%  
238 was attributed to variance between studies (Table 3).

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

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

247

## 248 **Discussion**

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

258         Our meta-analysis confirms that migration is triggered by a combination of proximate  
259 cues, both internal and external. Our models revealed that internal and external factors had a  
260 medium and large effect on migration propensity, respectively (Table 3). That the external  
261 environment had a slightly larger effect on migration propensity compared to internal factors fits  
262 with current understanding of the evolution of migration. External cues such as temperature and  
263 photoperiod strongly influence an animal's migration (Abraham, Upham, Damian-Serrano, et al.,  
264 2022; Fudickar et al., 2021; Shaw, 2016) and thus are expected to have governed its evolution.  
265 However, migration is also driven by many internal proximate cues, such as individual body

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

### 273 **External drivers of migration propensity**

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

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

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

#### 294 **Internal drivers of migration propensity**

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

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

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

334 sex on migration in ungulates (Cagnacci et al., 2011). Variation in migration propensity related  
335 to sex can occur where intraspecific competition for territories varies by sex, and migration  
336 serves as a strategy to escape costly sexual harassment or breeding (Chapman, Bronmark, et al.,  
337 2011). Therefore, sex might play a role in driving migration in some species while, in others, sex  
338 may not affect the decision of whether to migrate, but instead play a role in the timing or  
339 distance an individual migrates (Cagnacci et al., 2011).

#### 340 **A genetic basis for migration propensity**

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

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

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

368         Beyond characterizing the genomic architecture linked to migratory phenotypes, two  
369 studies identified differential gene expression in birds (Franchini et al., 2017) and fish  
370 (McKinney et al., 2015) which gives a more complete picture of the causal genes associated with  
371 the migratory phenotype. These authors found upregulation in the motilin receptor M1NR in  
372 migrants which is likely associated with increased fat uptake or glucose levels (Franchini et al.  
373 2017), and upregulation in genes associated with growth and development of the brain in  
374 migrants (McKinney et al. 2015). Differential expression in these genes could affect variation in  
375 body size and behaviour between migrants and residents, two internal factors that our study has  
376 found have medium and large effects on migration propensity. This highlights the underlying  
377 genetic component associated with many of the internal factors considered to be driving  
378 migration behaviour. In addition, Baerwald et al. (2016) identified differentially methylated

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

### 381 **Study limitations and future directions**

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

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

### 399 **Impacts of global environmental change**

400 Migrations are threatened across many taxa and, in general, it is anticipated that they will  
401 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,

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

428

#### 429 **Acknowledgements**

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

434

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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).

<b>Variable</b>	<b>Level I</b>	<b>Level II</b>	<b>Description</b>	<b>N</b>
<b>Trait</b>	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
<b>Taxonomic class</b>	Actinopterygii	Ray-finned fishes	30	
	Amphibia	Amphibians	3	
	Aves	Birds	65	
	Mammalia	Mammals	34	
<b>Study design</b>	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.

<b>Models with external factors (Level I)</b>		<b>AIC<sub>C</sub></b>	<b><math>\Delta</math>AIC<sub>C</sub></b>	<b>weight</b>
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
<b>Models with subcategories (Level II)</b>				
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.

<b>(a) Variable</b>	<b>Estimate</b>	<b>SE</b>	<b>t</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>p</b>	<b>I<sup>2</sup> (total)</b>	<b>I<sup>2</sup> (within- study)</b>	<b>I<sup>2</sup> (between- study)</b>
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>(b) Variable</b>	<b>Estimate</b>	<b>SE</b>	<b>t</b>	<b>Lower 95% CI</b>	<b>Upper 95% CI</b>	<b>p</b>	<b>I<sup>2</sup> (total)</b>	<b>I<sup>2</sup> (within- study)</b>	<b>I<sup>2</sup> (between- study)</b>
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

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

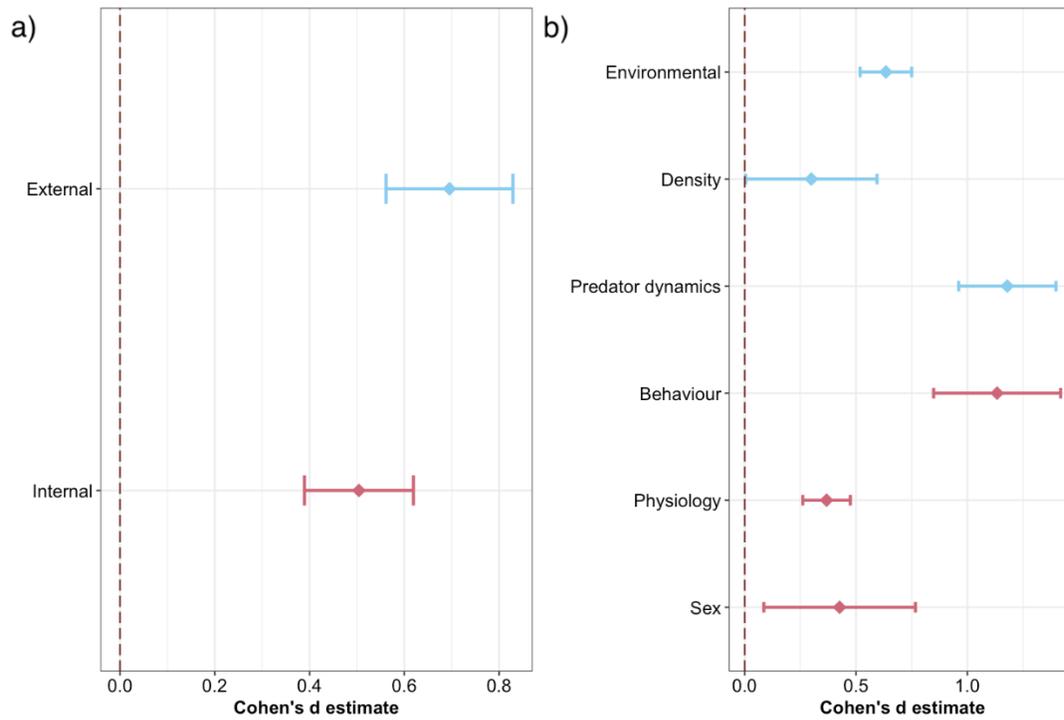


Figure 1. Forest plots of the Cohen's d derived from the best model predicting the effect of external factors (blue) and internal factors (red; a) and the effect of subcategories (b) on migration propensity.