The ecology and evolution of animal migration – an integrative approach to the drivers of phenotypic variation

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Abstract

The ecology and evolution of animal migration – an integrative approach to the drivers of phenotypic variation

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Animal migrations are ubiquitous and one of the most threatened ecological processes globally. Because of the multifaceted nature of migration – seasonal movements between home ranges – it can be difficult to tease apart the underlying mechanisms influencing this behaviour. It is necessary to understand these mechanisms, not only to deepen our fundamental understanding of migration in animals, but also because migrations in many species are vulnerable to environmental change. In Chapter 2, I first systematically identify the broad proximate drivers of migration and offer generalities across vertebrate taxa. I quantitatively reviewed 45 studies and extracted 132 observations of effect sizes for internal and external proximate drivers that influenced migration propensity. Through this meta-analysis, I found that internal and external drivers had a medium and large effect, respectively, on migration propensity. Predator abundance and predation risk had a large effect on migration propensity, as did individual behaviour. Of the studies that examined genetic divergence between migrant and resident populations, 64% found some genetic divergence between groups. In Chapter 3, I explore the genetic basis for migration and identified genes associated with migration direction from pooled genome-wide scans on a population of 233 migrating female mule deer (*Odocoileus hemionus*) where I identified genomic regions including FITM1, a gene linked to the formation of lipids, and DPPA3, a gene linked to epigenetic modifications of the maternal line. These results are consistent with the underlying genetic basis for a migratory trait which contributes to the additive genetic variance influencing migratory behaviours and can affect the adaptive potential of a species. Finally, in Chapter 4 I used a pedigree-free quantitative genetic approach to estimate heritability and sources of environmental variation in migration distance, timing, and movement rate of the same population of mule deer. I found low heritability for broad patterns of migration timing, and greater variation in heritability for behaviours during migration, with low heritability for distance and duration and high heritability for movement rate along the route. Insights into the genetic and environmental sources of variation for migration are critical both for the eco-evolutionary dynamics of migration behaviour, and for the conservation of species whose migrations may be vulnerable to environmental change. My thesis reveals that broad patterns of migration are driven largely by environmental effects while within these broad patterns, migration behaviour is driven to a measurable degree by genetic variation.

Keywords: migration, whole genome sequencing, reduced representation sequencing, heritability, *Odocoileus hemionus*

Preface

I have written my thesis in manuscript format. Chapter 2 will be submitted to *Animal Behaviour*, Chapter 3 was published in *Proceedings of the Royal Society B*, and Chapter 4 will be submitted to *Proceeding of the National Academy of Sciences*. Each data chapter is formatted in the style of its respective journal with a separate References section. I have used the collective "we" where applicable to reflect the collaborative nature of the work. During my PhD I have also contributed to the following papers:

Rheault, H., Anderson, C.R., **Bonar, M.**, Marrotte, R.R., Ross, T.R., Wittemyer, G., Northrup, J.M. 2021. Some memories never fade: Inferring multi-scale memory effects on habitat selection of a migratory ungulate using step-selection functions. *Frontiers in Ecology and Evolution* 9.

Northrup, J. M., Vander Wal, E., **Bonar, M.**, Fieberg, J., Laforge, M. P., Leclerc, M., Prokopenko, C. M., and Gerber, B. D. 2022. Conceptual and methodological advances in habitat-selection modeling: guidelines for ecology and evolution. *Ecological Applications* 32(1):e02470.

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What I am most grateful about the connections and relationships I have built over the course of this graduate program is that I have had many opportunities to learn about Indigenous history in Canada, Truth and Reconciliation, and Indigenous Knowledge. For the first time I have begun to reflect on my role in reconciliation both as a settler and an academic researcher. I would be remiss if I did not acknowledge the privilege I hold in getting to conduct this research and submit this dissertation for the degree of Doctor of Philosophy at Trent University. Trent University sits on the treaty and traditional territory of the Michi Saagiig Anishinaabeg. The land on which the data for this dissertation were collected is the ancestral homelands of the Ute peoples. I acknowledge that cultural relationships to the land and to the animals that I have the privilege of studying have been broken because of colonialism. I offer my gratitude to the First Peoples for their care and stewardship of the land, without which I could not hope to visit and generate knowledge about the land on which my study takes place. I believe that it is now my responsibility to sit with the discomfort of getting to benefit from the privilege that colonialism brings me and continue to educate myself on the barriers and issues facing Indigenous peoples in Canada and around the world.

This dissertation and many opportunities I had would not be possible without the support and guidance of my advisors Dr. Joseph Northrup and Dr. Aaron Shafer. Thank you for sharing your guidance and for continuously pushing me to improve the quality of my research and writing. I would like to thank my dissertation committee members, Dr. Erin Koen and Dr. James Schaefer, for providing valuable feedback and guidance throughout this project.

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Chapter 1. General Introduction

Migration, defined as seasonal movement between home ranges (Fryxell & Sinclair, 1988), is a fundamental component of the life histories of many wild animals. Migrations occur globally across all major branches of the animal kingdom and are critical for the persistence of species in variable environments, while providing important linkages between ecosystems through nutrient transfer and seed dispersal (Bauer & Hoye, 2014; Subalusky, Dutton, Rosi, & Post, 2017). Despite the ubiquity and widespread recognition of the importance of migration, it is one of the most threatened ecological processes (Harris, Thirgood, Hopcraft, Cromsigt, & Berger, 2009), and declines in migratory behaviour due to climate change and habitat loss have been observed, leading to the reduction in the variation in migration behaviours exhibited in nature (Berger, 2004; Bolger, Newmark, Morrison, & Doak, 2008; Festa-Bianchet, Ray, Boutin, Côté, & Gunn, 2011; Wilcove & Wikelski, 2008).

Migration behaviour is not uniform among species, populations, or even individuals. A wide range of migration behaviours occur in nature, ranging from short altitudinal migrations in birds and bats (Boyle, 2017; McGuire & Boyle, 2013), to the annual approximately 1000 km journey of wildebeest across East Africa (Fryxell, Greever, & Sinclair, 1988), to the 150 m migration of a spotted salamander from pond to wintering burrow (Blanchard, 1930). Intraspecific variation in migration behaviour is also common; for example, two genetically similar populations of wandering albatross that breed in the Indian Ocean exhibit drastically different migratory behaviours, with one population migrating and the other sedentary (Weimerskirch, Delord, Guitteaud, Phillips, & Pinet, 2015). In addition to these differences between species and populations, a growing number of studies are documenting variation in migration behaviour within populations, for example individuals from the same genetic subpopulation migrating in seemingly opposite directions (Northrup, Shafer, Anderson, & Coltman, 2014). Such variation in migration propensity, timing, and movement patterns can have critical implications for ecosystems connectivity (Bauer & Hoye, 2014) and might offer insights into the evolution and persistence of migration behavior.

While most research on migratory behaviour has focused on the environmental drivers (Finger et al., 2016; Macdonald, Patterson, Hague, & Ian, 2011), a significant amount of phenotypic variance can be explained by genetic variation (Cavedon et al., 2022; Franchini et al., 2017; Prince et al., 2017). Genes associated with migration direction and timing have been identified in birds (Bazzi, Cecere, et al., 2016; Bazzi, Galimberti, et al., 2016; Saino et al., 2015) and fishes (Hess, Zendt, Matala, & Narum, 2016), but large mammals remain less studied (e.g., Northrup, Shafer, Anderson, & Coltman, 2014). Heritability in timing, and prevalence of migration has been demonstrated in natural populations (Pulido, Berthold, Mohr, & Querner, 2001), and habitat selection during migration influences gene flow in migrating populations (Shafer et al., 2012). Recent advancements in sequencing technology can now be employed to screen for possible candidate migration loci – both genetic, and non-genetic influences on gene expression (i.e., epigenetic) – that might underlie divergent migratory behaviours. These advancements provide exciting opportunities for developing a more robust test of the factors driving variation in migration, which is a critical need for conserving this behaviour in the wild.

Study system

Two of the data chapters of my thesis use migrating mule deer (*Odocoileus hemionus*) as a model system to explore the genetic and environmental drivers of variation in migration behaviour. Mule deer have a wide geographic range, and their annual migrations are important for survival and reproduction. Migrations tend to match changes in resource availability, with mule deer attempting to optimize migratory timing relative to both plant productivity and weather on their summer range (e.g., Lendrum, Anderson, Monteith, Jenks, & Bowyer, 2013). Mule deer can migrate a wide range of distances (Sawyer, Merkle, Middleton, Dwinnell, & Monteith, 2018), while also showing variation in migration timing (Northrup, Shafer, Anderson, & Coltman, 2014). Mule deer are the subject of extensive management programs in North America due to their importance as a game species; their annual migrations are of interest to wildlife managers as recent anthropogenic development and climate change may threaten migratory routes (Lendrum et al., 2013; Northrup, Anderson, Gerber, & Wittemyer, 2021).

The Piceance Basin of northwestern Colorado, USA supports one of the largest populations of migratory mule deer, and one of the largest natural-gas reserves in North America. Natural gas development density varies across the summer ranges of mule deer in the Piceance Basin, with some areas being free from development and other areas having high levels of development (Northrup, Anderson, Gerber, & Wittemyer, 2021). Mule deer in Colorado have seen a protracted decline in abundance over the last 30 years with the ultimate causes remaining uncertain (Bergman, Doherty, White, & Holland, 2015). Variation in migration timing has already been linked to genetic differentiation and mitochondrial haplotypes in this population of mule deer (Northrup, Shafer, Anderson, & Coltman, 2014), suggesting a genetic basis for variation in migration strategies. The natural variation in migration behaviour within the population and among individuals makes this system excellent for exploring the ecology and evolution of migration.

Thesis objectives and data chapters

The overarching goal of my thesis is to develop a comprehensive understanding of migration by untangling the effects of genetic and environmental drivers of this fundamental process. The objectives of my thesis were to: i) measure the effect of both internal and external proximate drivers on migration propensity, ii) identify genes associated with migratory traits; and iii) partition the phenotypic variance of migration behaviours into additive genetic effects and environmental effects.

In **Chapter 2**, I quantitatively reviewed studies that measured the effects of internal and external proximate drivers on migration propensity across taxa. I used a meta-regression framework to draw conclusions about the overall empirical effect of certain drivers on migration propensity while accounting for species differences. This chapter clarifies the broad proximate drivers of migration and offers generalities across taxa. Further, I highlight the genetic basis for migration behaviour, and the need for more empirical studies addressing this topic. This lays the foundation for Chapters 3 and 4 which attempt to address this knowledge gap.

In **Chapter 3**, I identified genes associated with a migratory trait by undertaking pooled genome-wide scans on a natural population of migrating mule deer. Using DNA extracted from the blood samples of radio-tracked individuals, and whole genome sequencing, I assessed divergent genomic regions correlated with different migratory behaviour in an association analysis and identified candidate genes associated with migration direction.

In **Chapter 4**, I used a pedigree-free quantitative genetic approach to quantify the proportion of phenotypic variance explained by additive genetic effects in spring migration behaviours and body size in migrating mule deer. I generated restriction site-associated DNA sequencing libraries for each radio-tracked individual and used these libraries to generate a genomic relatedness matrix (GRM). I include the GRM as a measure of pairwise relatedness between individuals in the animal model approach, which partitioned the phenotypic variance of migration and body size traits into additive genetic variance, permanent environmental effects, and residual variance.

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Chapter 2. Proximate drivers of migration propensity: a meta-analysis across species

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A version of this chapter will be submitted to *Animal Behaviour*

Contributions: MB, ABAS, JMN designed the study; MB coordinated literature review and data collection; MB performed research and analyzed data; MB wrote the manuscript with input from ABAS, JMN.

Abstract

Animals that undertake seasonal migrations play a globally important ecological and economic role. Migration is assumed to be triggered by a combination of proximate internal and external cues, and the resulting patterns of movement can vary across individuals, populations, and species. Some individuals within a population migrate while others do not; these partially migratory populations offer a unique opportunity to test hypotheses about migration more broadly by comparing trait differences of migrants and residents. We quantitatively reviewed 45 studies and extracted 132 observations of effect sizes for internal and external proximate drivers that influenced migration propensity across taxa. Our meta-analysis revealed that internal and external drivers had medium and large effect sizes on migration propensity respectively. Predator abundance and risk had a large effect on migration propensity, as did individual behaviour. The abiotic environment and an individual's physiology had a medium effect on migration propensity. Of the studies that examined genetic divergence between migrant and resident populations, 64% found some genetic divergence between groups. These results clarify the broad proximate drivers of migration and offer generalities across taxa. Further, our study highlights the genetic basis for migration behaviour, and the need for more empirical studies addressing this topic. The large effect of predation risk and behaviour on migration propensity suggests that these are areas of focus for understanding and predicting subsequent consequences to migrations resulting from global environmental changes.

Introduction

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

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

The evolution of migration behaviour is driven by ultimate mechanisms such as the need to increase access to resources, to escape unfavourable environmental conditions, or to reproduce (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 (Gathreaux, 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 2.1). 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 (i.e., indirect genetic effects). 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 2.1; 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 are being recognized as partially migratory (Berg et al., 2019; Eggeman et al., 2016; Mysterud et al., 2011). A review of the plasticity of ungulate migrations (Xu et al., 2021) identified drivers of migration propensity including habitat loss, predation, density dependence, and extreme weather events.

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 certain 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 differences 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 S1.1). 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 2.1).

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 (*ß*) from a logistic regression, we first converted *ß* into an odds ratio (*OR*) and then converted *OR* to Cohen's *d* as follows:

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

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

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

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

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

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

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*.

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. 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 $\Delta AIC_C < 2$ 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

Studies that quantified genetic differences between migratory and sedentary groups were excluded from the meta-analytic models as we were unable to compute comparative effect sizes. 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 the fraction of the genome used in each study. These data were tabulated and compared across studies.

Results

The literature search produced 665 articles which were manually screened for relevance; we excluded and 511articles 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 S1.1). A total of 132 effect sizes were extracted from the 45 studies that met all requirements (Figure 2.1). 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 alone. 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 (±SE = 0.25). The mean Cohen's *d* for 62 observations of internal factors was 0.55 (±SE = 0.21). At a finer level when these factors were divided into subcategories, the mean Cohen's *d* was 1.47 (±SE = 0.96; n = 9 observations) for behaviour, 0.31 (±SE = 0.74; n = 6 observations) for density, 0.62 (±SE = 0.32; n = 40 observations) for environment, 0.40 (±SE = 0.19; n = 48 observations) for physiology, 1.20 (±SE = 0.48; n = 11 observations) for predator dynamics, and 0.41 (±SE = 0.75; n = 5 observations) for sex. Effect size was not correlated with natural log of sample size or journal impact factor (Figure S1.1).

All the competing models predicting the effect of internal and external factors on migration propensity were competitive with the top model ($\Delta AIC_C < 2$), 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 (±SE = 0.13) for external and 0.50 (±SE = 0.11) for internal factors (Table 2.3, Figure 2.2). 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 2.3). 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 (±SE = 0.29) for behaviour, 0.30 (±SE = 0.30) for density, 0.63 (±SE = 0.12) for environment, 0.37 (±SE = 0.11) for physiology, 1.18 (±SE = 0.22) for predator dynamics, and 0.43 (±SE = 0.34) for sex (Table 2.3, Figure 2.2). For this model, $I^2 = 0.95$. Of this variance, 0% was attributed to within-study clustering, and 95% was attributed to variance between studies (Table 2.3).

Of the 13 genetic studies, 11 studies examined genetic divergence between migratory and sedentary groups (Table 2.4). Four studies found no genetic divergence between migratory and sedentary groups while seven found some 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 five used reduced genome or transcriptome. Five of studies used microsatellites and whole mitochondrial genome. Only one study used single nucleotide polymorphism (SNP) data. 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 ultimately clarify the potential drivers 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 that drive animal migration (Box 2.1).

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 2.3). 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 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 or genotype (e.g., Debes et al., 2020; Mueller et al., 2011). The somewhat 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 research 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 (Table 2.3). Our models also showed a large effect of predation, typically measured as predation risk or predator abundance. This finding suggests predator-prey dynamics have a potentially large role in the evolution of migration. This is supported by the findings of individual studies included in our meta-analysis, showing 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). 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). These findings suggests that studies examining migration should aim to assess the role of predation risk in driving migration.

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 2.1). Only a small number of studies explicitly assessed the effect of density on migration propensity (n = 6), and most did quantify some 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

In our analysis, the sub-categories reflecting internal factors tended to have smaller effect sizes than those measuring external factors, similar to the coarser analysis (Figure 2.3). 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 (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. Indeed, ecology is replete with interactions (Bastille-Rousseau et al., 2016). Further research on the influence of individual physiology on migration will help resolve the contexts under which this factor is most influential.

We found a strong effect of behaviour on migration propensity (Table 2.3, Figure 2.3). 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 individuals 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 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. Therefore, studies examining migration should consider how correlated behaviours or co-expressed phenotypic traits contribute to the overall migratory phenotype. 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 (n = 5), 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 thanks 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-studies species is consistent with our results (Figure 2.3). Our models showed that behaviour and physiology likely affect migration evolution, as a genetic basis for these behavioural and physiological traits is a necessary for natural selection or micro-evolution. These findings suggest that these 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 mlnr 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 the body size and behavioural variation between migrants and residents, two internal factors that our study has found 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* providing evidence 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 in existence.

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, how the 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 2.3, Figure 2.3) 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 (Bonnet-Lebrun et al., 2020). Urbanization buffers against winter harshness and increases access to local recourses, making residency a viable tactic. 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 to changes 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).

Migration is a complex behaviour that is influenced by an array of diverse mechanisms. This meta-analysis provides empirical evidence for moderate effect of both internal and external proximate mechanisms that drive migration propensity. Our findings support, in many ways, our current understanding of the drivers of migration propensity such as the strong influence of predators and environmental variables and highlights the knowledge gap that still exists in our understanding of the genetic drivers of migration. Understanding the effects of both internal and external factors on migration behaviour is necessary to conserve animals whose migrations are at risk due to climate or anthropogenic change. Our study points to the need to quantify the degree to which genetics and the environment influence migration behaviour for a more comprehensive understanding of the evolution of migration behaviour.

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Tables and Figures

Box 2.2.1 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 to the migrating individual, and it is likely the interaction among them that 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) model 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 2.1 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 2.2 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* ~ Level I (int/ext) + class + study design	290.07	0.00	0.32
2	Cohen's *d* ~ Level I (int/ext) + class	290.39	0.32	0.27
3	Cohen's *d* ~ Level I (int/ext)	290.68	0.61	0.24
4	Cohen's *d* ~ Level I (int/ext) + study design	291.31	1.24	0.17
	Models with subcategories (Level II)			
1	Cohen's *d* ~ Level II (sub cat)	282.87	0.00	0.29
2	Cohen's *d* ~ Level II (sub cat) + class + study design	283.00	0.13	0.21
3	Cohen's *d* ~ Level II (sub cat) + class	283.00	0.14	0.21
4	Cohen's *d* ~ Level II (sub cat) + study design	284.04	1.17	0.13

Table 2.3 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**	**I^2 (total)**	**I^2 (within-study)**	**I^2 (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**	**I^2 (total)**	**I^2 (within-study)**	**I^2 (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 2.4 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			S		
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		

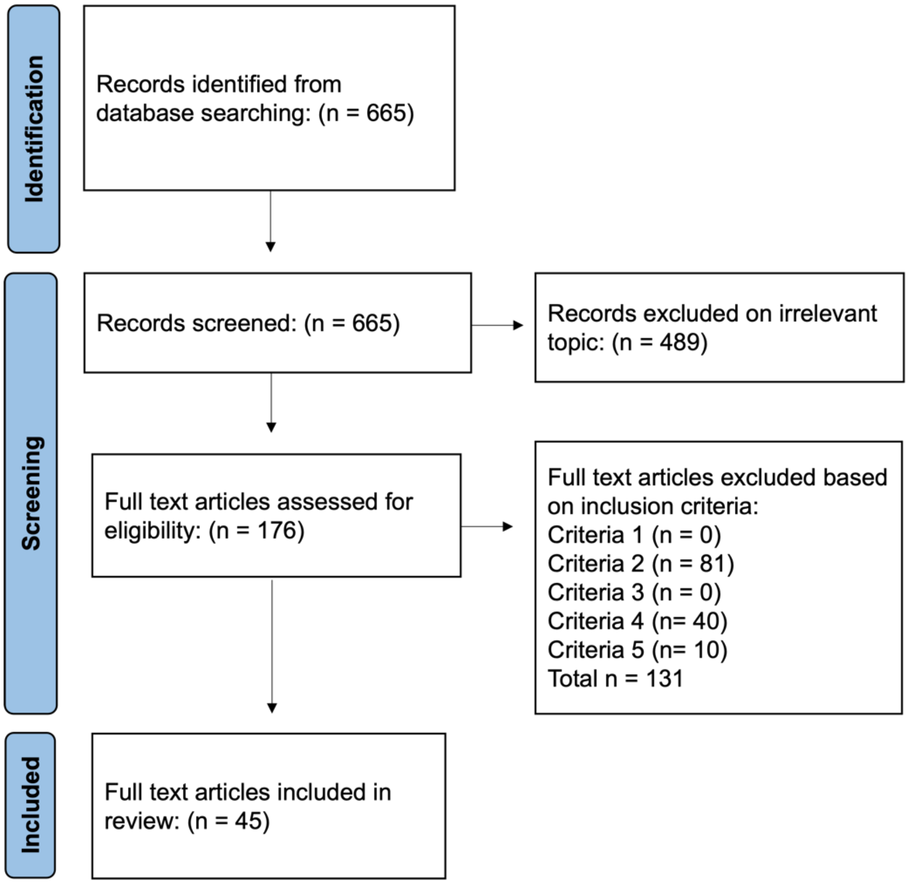

Figure 2.2 PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-analyses) flow chart depicting the criteria, steps, and number of articles (n) for inclusion in the meta-analysis of migration propensity.

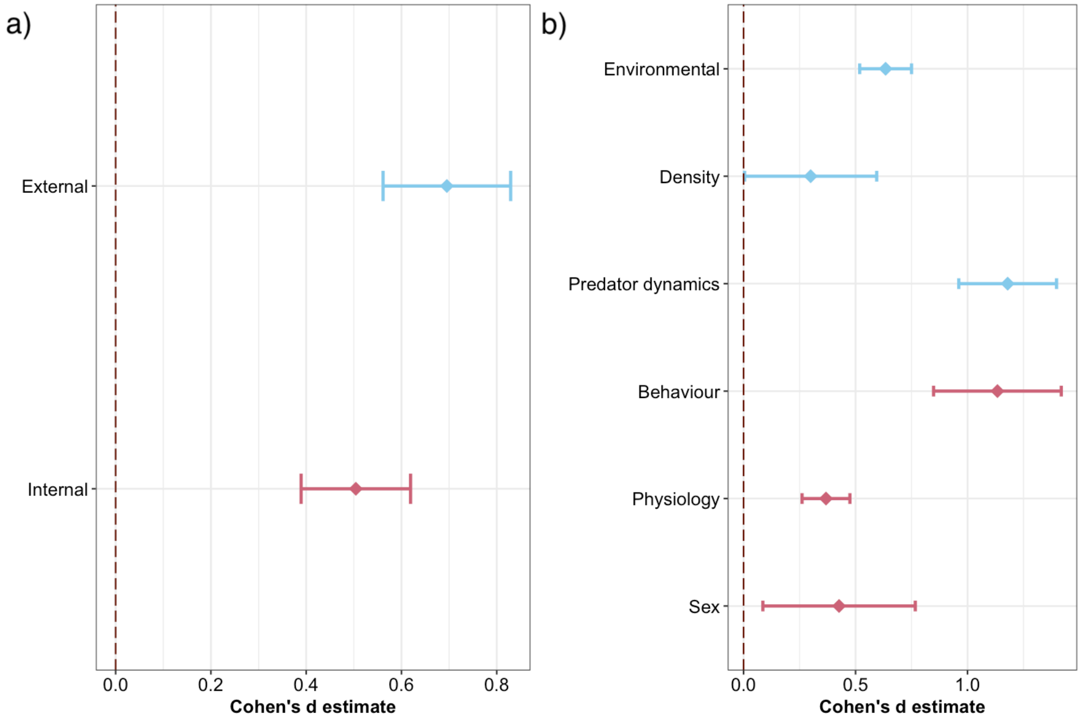

Figure 2.3 Forest plots of the Cohen’s *d* derived from the best model predicting the effect of external factors (blue) and internal factors (red; a) and the effect of subcategories (b) on migration propensity.

Chapter 3. Genomic correlates for migratory direction in a free-ranging cervid

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Contributions: MB, SJA, ABAS, JMN designed the study; JMN, CRA, GW coordinated data collection and sample curation; MB performed research and analyzed data; MB wrote the manuscript with input from SJA, ABAS, CRA, GW, JMN.

Abstract

Animal migrations are some of the most ubiquitous and one of the most threatened ecological processes globally. A wide range of migratory behaviours occur in nature, and this behaviour is not uniform among and within species, where even individuals in the same population can exhibit differences. While the environment largely drives migratory behaviour, it is necessary to understand the genetic mechanisms influencing migration to elucidate the potential of migratory species to cope with novel conditions and adapt to environmental change. In this study, we identified genes associated with a migratory trait by undertaking pooled genome-wide scans on a natural population of migrating mule deer. We identified genomic regions associated with variation in migratory direction, including FITM1, a gene linked to the formation of lipids, and DPPA3, a gene linked to epigenetic modifications of the maternal line. Such a genetic basis for a migratory trait contributes to the adaptive potential of the species and might affect the flexibility of individuals to change their behaviour in the face of changes in their environment.

Introduction

Migration, defined as the seasonal movement between home ranges [1], is critical for the persistence of species in variable environments. Animal migrations influence nutrient deposition across ecosystems and affect seed dispersal [2,3]. Migratory behaviour has been identified across all major branches of the animal kingdom and is a complex phenomenon that involves the interaction between environmental and genetic cues that can influence how individuals respond to selection [4]. Migration also is one of the most threatened ecological processes [5] and in some systems has declined due to climate change and habitat loss, leading to the reduction in the variation in migratory behaviours [6–8].

A wide range of migratory behaviours occurs in nature, ranging from short altitudinal migrations in birds and bats [9,10] to the annual approximately 1000 km journey of wildebeest across East Africa [11,12]. Migratory behaviour varies within species [13], between populations [14,15] and among individuals [16,17]. Variation in migration propensity, timing and movement patterns can have critical implications for ecosystems connectivity [2]. While variation in migratory behaviour is largely driven by the environment, which has been the focus of most research on migratory behaviour [18,19], a significant amount of phenotypic variance can be explained by genetic variation [20–22]. Genes associated with migration direction and timing have been identified in birds [23–25] and fishes [26], but large mammals remain less studied (e.g. [27]). Understanding the genetic mechanisms driving migration can help uncover the evolutionary origins and constraints of migration. This would help quantify the adaptive potential – the ability of a population to evolve adaptively in response to selection – of migratory species to environmental change. Furthermore, as migratory behaviour continues to disappear across the globe, we could see a reduction in genetic variance contributing to migratory behaviours, thereby reducing overall adaptive potential of migratory species [28].

Ungulates (hooved mammals) show substantial phenotypic variation in migratory behaviour. Broadly, migration propensity varies within partially migrating populations [29]. Variation exists in migration timing and migration distance, with some species of ungulates migrating thousands of kilometers [3] while others migrate less than 100 km [30,31]. Studies have primarily attributed migration in ungulates to variation in the abiotic and social environment [32–34]. Recently, Cavedon et al. [20] identified genetic markers associated with migration propensity in caribou (*Rangifer tarandus*), and Gervais et al. [35] found evidence that movement (i.e., speed) and space-use behaviours are heritable in roe deer (*Capreolus capreolus*), which suggests genetic underpinnings for migratory behaviour in ungulates.

This study aims to identify genes associated with a migratory trait by undertaking pooled genome-wide scans on a natural population of migrating mule deer (*Odocoileus hemionus*). Migration is important for survival and reproduction in this species. Mule deer have a wide geographical range and typically migrate from high altitude, productive summer ranges to low altitude winter ranges. Migrations typically match changes in resource availability, with mule deer attempting to optimize migratory timing relative to both plant productivity and weather on their summer range (e.g., [36]). Mule deer can migrate a wide range of distances [37], while also showing variation in migration timing [27]. Mule deer are the subject of extensive management programmes throughout North

America, due to their importance as a game species; their annual migrations are of interest to wildlife managers as recent anthropogenic development and climate change may threaten migratory routes [36,38]. Migratory plasticity may be one way for the population to buffer against the effects of rapid environmental change, however, Sawyer et al. [37] found that mule deer exhibited little to no plasticity in terms of whether or where to migrate, meaning they could be less resilient to change. Consequently, adaptation to a rapidly changing environment may require microevolutionary change, for which a genetic basis for migratory variation is required. Therefore, the existence of genetic correlations to variation in migratory traits in mule deer could provide insight into the effectiveness of management programs and aid managers in making decisions in the context of the evolutionary processes that maintain variation in natural populations.

We focused on four study areas of migrating mule deer in the Piceance Basin of northwestern Colorado, USA. These deer share the same winter range but migrate to two geographically distinct summer ranges (Figure 3.1, Appendix II Figure S2.1). The Piceance Basin supports one of the largest populations of migratory mule deer, and one of the largest natural-gas reserves in North America. Natural gas development density varies across mule deer summer ranges in the Piceance Basin, with some areas being free from development and other areas having high levels of development [38]. Mule deer in Colorado have seen a protracted decline over the last 30 years with the ultimate causes remaining uncertain [39]. Variation in migration timing has already been linked to genetic differentiation and mitochondrial haplotype in this population [27], suggesting a genetic basis for variation in migration strategies. The variation in migration to one of two distinct summer ranges presents an opportunity to assess the genomic basis for a migratory trait. An association analysis allows us to locate regions of the genome that likely contribute to phenotypic differences among individuals or populations by correlating marker variants (i.e., divergent regions of the genome) with variation in a trait of interest [40]. Using DNA extracted from the blood samples of radio-tracked individuals, and whole genome sequencing, we assess divergent genomic regions correlated with different migratory behavior and identified candidate genes associated with migration direction (e.g., [27]).

Materials and Methods

Data collection and migratory phenotypes

Adult (>1 year old) female mule deer were captured from 2008–2015 using helicopter net gunning on the four winter range study areas and fitted with store-on-board GPS radio collars (Advanced Telemetry Systems, Insanti, MN, USA) with three different relocation schedules (5 hours, 60 minutes, and 30 minutes) depending on the individual. Deer were spotted visually by the helicopter capture crew and captured using a net gun. Deer were then blindfolded, hobbled, and administered 0.5 mg/kg of Midazolam (and 0.25 mg/kg of Azaperone intramuscularly) to alleviate capture-related stress (dose of both drugs based on an average weight of 75 kg). Deer were transported to a central processing site typically within 2 km of the capture site, where they were weighed, measured for chest girth and hind foot length, and blood samples were collected for genetic analysis. We also obtained a body condition score by palpating the rump and measured the thickness of subcutaneous rump fat and the depth of the longissimus dorsi muscle using ultrasound [41–45]. We used the body condition score and ultrasound measurements to estimate the percent ingesta-free body fat of each deer [42,43]. Deer were released at the processing site immediately following blood sample collection and collar attachment. All procedures were approved by the Colorado State University (protocol ID: 10-2350A) and Colorado Parks and Wildlife (protocol ID: 15-2008) Animal Care and Use Committees.

The four winter range study areas located in the Piceance Basin are: 1) North Ridge, in the northeastern portion of the Basin; 2) Ryan Gulch in the southwestern portion of the Basin; 3) North Magnolia; and 4) South Magnolia in the central portion of the Basin (Figure 3.1). North Ridge and Ryan Gulch are both geographically separated from the other study areas by topography. It was initially thought that the deer in the Magnolia region were one contiguous group, however, GPS radio-collar data from the first year of the study indicated that individuals were split between the northern and southern half of the winter range, with most individuals from the two groups migrating to different summer ranges. We split our study area into North Magnolia and South Magnolia and assigned deer to an area based on where they spent the majority of the winter using the proportion of GPS radio-collar locations in each area [38]. Therefore, some overlap in space may occur between individuals in North and South Magnolia study areas. During spring migration, mule deer from the North Ridge and North Magnolia area move east-west towards the Flat Top Mountain Range, where they remain at high elevation for the summer. However, some mule deer whose GPS radio-collar data indicate that they spend the majority of the winter in North Magnolia and the mule deer from the South Magnolia and Ryan Gulch migrate north-south to high elevations along the Roan Plateau [36]. Elevation on the winter study areas ranged from 1,675 to 2,285 m and from 2,000 to 2,800 m on the summer study areas. Habitat characteristics (i.e., vegetation type) occurring along the migratory paths of mule deer was similar among study areas [46], however individuals that migrate east-west on average travel greater distances than individuals migrating north-south. To test for differences of body condition that may account for genetically linked differences between the groups, we compared body weight, chest girth, hind leg length, and ingesta-free body fat between north-south and east-west migratory individuals. We visually examined the GPS data for each individual to determine which summer range each mule deer migrated to on the year they were collared. Mule deer tend to show little plasticity in terms of their migratory behaviour, resulting in high fidelity to their migratory routes [37,38]. We then grouped individuals with the same migratory direction according to study area resulting in five groups as some individuals from North Magnolia migrate east-west while others migrate north-south (Figure 3.1). There is no apparent genetic subdivision among study areas [27].

DNA extraction and sequencing

We extracted DNA from each individual's blood sample using the DNeasy Blood and Tissue Kit (Qiagen, Inc., Valencia, CA, USA), following the manufacturer's protocol. We pooled the DNA of individuals from each of the five groups for sequencing using pooled sequencing (Pool-seq), [47]. Equal quantities of DNA (100 ng/sample) were combined into representative pools: North Ridge (east-west migrating, n=50); North Magnolia (east-west migrating, n=50), North Magnolia (north-south migrating, n =33); South Magnolia (north-south migrating, n=50); and Ryan Gulch (north-south migrating, n=50) to a final concentration of 20 ng/µl of combined DNA for each pool. Pool-seq produces accurate allele frequency estimates with pools of ~50 individuals, thereby making this a cost-effective approach to sequencing [47]. The Pool-seq approach is also valid for smaller sample sizes (<40 individuals) as analysis is carried out on genomic windows containing multiple SNPs instead of individual SNPs [47]. Each pool was sequenced across five lanes of an Illumina HiSeqX platform to a desired 50X coverage (total of 5 lanes) at The Centre for Applied Genomics in Toronto, Ontario (Table S2.1).

Genome alignment and SNP calling

Mule deer and white-tailed deer can hybridize [48], so we opted to use the long-read-based draft genome of white-tailed deer (*Odocoileus virginianus*) (Accession No. JAAVWD000000000) that was recently annotated [49]; we note that the currently available mule deer genome is simply a consensus sequence from reads mapped to earlier versions of the white-tailed reference [50]. We performed initial quality filtering for all reads using fastqc and trimmed reads for quality and adaptors using the default Trimmomatic v. 0.36 settings [51]. We aligned the pooled sequences to the unmasked white-tailed deer genome using BWA-mem v0.7.17 [52]. We used samtools v. 1.10 [53] to merge and sort all aligned reads into five files representative of each pool. We filtered for duplicates using Picard v. 2.20.6 [54], obtained uniquely mapped reads with samtools, and conducted local realignment using GATKv. 3.8 [55] before SNP calling. We called SNPs using samtools mpileup (parameters = -B -q20). We filtered out the masked regions and indels with 5 bp flanking regions and removed all scaffolds < = 50 kb.

Genome scan for population differentiation in migratory direction

We used an empirical F_{ST} approach [14,56] to identify potential SNPs relating to migratory phenotype between east-west migrating and north-south migrating pools. The trait of interest does not need to be under selection to locate divergent regions of the genome associated with phenotypic differences. We used a sliding window approach in calculating F_{ST} using the Popoolation2 software suite [57]. We used 2500bp sliding widows, and a minimum covered fraction of 0.8 and specified a minimum overall minor allele count of 3 for each pool. We had 5 pools that provided 10 pairwise comparisons, 6 opposite phenotype comparisons (east-west vs. north-south), and 4 same phenotype comparisons (1 east-west vs. east-west, 3 north-south vs. north-south). There is debate regarding the identification of outliers and the potential for false positives, specifically with regards to how the outlier cut-off level influences identification [59,59]. To address this, we defined an outlier window as the top 1% of F_{ST} values in at least 4/6 of the opposite phenotype comparisons and not within the top 1% of F_{ST} values in all 4 of the same phenotype comparisons. Outlier windows within the top 1% of F_{ST} values in same phenotype comparisons are likely differentiated due to drift. By removing any outlier windows within the top 1% of F_{ST} values in opposite phenotype comparisons that are also highly differentiated in the same phenotype comparison, we maximized the probability that windows are associated with differences in migration direction and not some unaccounted-for population variation. We also ran the same analysis using less conservative criteria and identified outlier windows from the top 1% of at least 3/6 of the opposite phenotype pairwise comparisons, and those results can be found in Appendix II. F_{ST} calculations account for sample size variation [60] and for pooled samples that are minimally affected by differences in sample size, even at small sample sizes [61,62]. We are using a window-based approach, requiring multiple SNPs within a region to be divergent, therefore our measurements of F_{ST} are unlikely to be a result of sampling [63].

We evaluated genetic differentiation between east-west-migrating and north-south-migrating pools by conducting a principal component analysis (PCA) using allele frequencies for the SNPs within outlier regions. We conducted one PCA using the major allele frequencies of all available biallelic SNPs across the whole genome and one using the major allele frequencies of the biallelic SNPs identified within the outlier regions identified through the F_{ST} approach. We expect that the PCA using the outlier SNPs putatively associated with the trait would show clear separation between the two migratory types, while the PCA using all SNPs would not. We also examined the PCA using the major allele frequencies of biallelic SNPs found within the top 1% of F_{ST} values of same migratory type comparisons as we would expect that these would not show separation between the two migratory types. For all pools, we examined the proximity to genic regions for all SNPs identified within outlier regions using SnpEff v4.3t [64]. For this, we generated VCF files using bcftools v. 1.9 [52] and bed files containing the coordinates of all outlier SNPs. All SNP locations were characterized as being in an intergenic/intragenic region, 25 kb up/downstream of a gene (i.e., regulatory), intron, or exon. We also assessed the putative proximity to the nearest gene for every identified SNP.

Gene ontology

To identify shared gene pathways among outlier SNPs, we used an analysis of gene ontology (GO) terms. We used the program Gowinda v. 1.12 [65] to determine GO term enrichment while accounting for gene length biases. We created a .gtf version of our annotation by removing duplicated genes, retaining only the longest version of each gene, which resulted in 15,395 unique genes in the annotation [49]. All outlier SNPs that

SnpEff identified as being on or within 25 kbp of genic regions were used to analyze gene ontology and compared to all outlier SNPs in every qualifying window. Finally, we plotted the GO results with WEGO (Web Gene Ontology Annotation Plot) to visualize annotations following the vocabularies and classifications provided by the GO Consortium [66].

Results

East-west and north-south migrating individuals did not significantly differ in body weight ($F_{1,231} = 0.371$, $p = 0.543$), hind leg length ($F_{1,230} = 2.439$, $p = 0.12$), chest girth ($F_{1,231} = 0.997$, $p = 0.319$), and ingesta-free body fat percentage ($F_{1,229} = 2.22$, $p = 0.138$; Figure S2.2).

Differentiated SNPs associated with migration

After filtering for coverage, INDELS, and minimum allele counts, 194,533 windows each 2500bp wide were evaluated for each of the migratory-study area groups. The genome-wide mean F_{ST} was 0.026, with 0.027 mean F_{ST} across each of the same migration direction comparisons and 0.026 mean F_{ST} across all opposite migratory group comparisons. Based on our pairwise comparisons, we identified 19 windows within the 99th percentile in at least 4/6 pairwise comparisons of opposite migratory types and not within the 99th percentile in the 4 same migratory type comparisons (Figure 3.2a). The average F_{ST} for these windows was 0.074 in the opposite migratory type comparisons and 0.027 in the same migratory type comparisons. Within these windows, 2,903 SNPs were identified as on or within 25kbp of genic regions (Figure 3.2b). The PCA using major allele frequencies from biallelic SNPs across the whole genome ($n = 21{,}944{,}208$), and the major allele frequencies from biallelic outlier SNPs ($n = 463$) revealed separation of the migratory groups along the PC2 axis (Figure 3.2c). Additionally, we confirmed that no such separation of migratory groups occurred for SNPs within the 99th percentile in the 4 same migratory type comparisons through a PCA of the major frequency of those biallelic SNPs (n = 8,128, Figure S2.3).

Eleven genes associated with migration

The results from GOWINDA showed that the non-intergenic outlier SNPs were found on or within 25kbp of 11 genes: ADGRB1, BSG, DPPA3, EMC9, FITM1, IKZF3, ITSN2, MAN2A2, PSME1, RNF216, and SETX. Two of note were FITM1, a gene linked to the lipid synthesis in humans, and DPPA3, a gene linked to epigenetic modifications of the maternal line. GO analysis yielded 214 GO terms which were classified into 31 functional groups belonging to three functional categories: cellular components (11 groups), molecular functions (10 groups), and biological processes (10 groups) (Figure 3.2d, Table S2.2). Some genes belonged to more than one functional group (e.g., protein binding and cell differentiation), which sometimes resulted in a sum exceeding 100% in a category (e.g., cellular components). Among the genes categorized as cellular components, 100% were classified as cell parts. Most of the genes with molecular functions were associated with protein binding (90.9%), and most of the genes categorized as having biological processes were involved in cellular processes (90.9%), biological regulation (81.8%), and metabolic processes (72.7%).

Discussion

Our results show genomic regions associated with migration direction in mule deer; such a genomic basis for a migratory trait can have implications for our understanding of the adaptive potential of migration and the flexibility of individuals to change their behaviour in the face of stochastic changes to their environment. Migratory behaviours continue to disappear globally, largely due to climate change and anthropogenic alteration of the environment [67]. The disappearance of migratory routes can affect prey abundance, impact terrestrial and aquatic nutrient cycling, and could reduce genetic variation across species [3]. When there is an underlying genetic basis for a migratory trait, this contributes to the additive genetic variance influencing migratory behaviours. A reduction in that variance can directly affect the adaptive potential of a species to cope with environmental change [35]. The amount of additive genetic variance associated with migratory traits might affect the response of a population to new selection regimes, and the rate at which adaptive evolution can occur [68]. Consistent directional selection on migration traits could lead to distinct changes in migration variation within populations over a relatively short period of evolutionary time. Uncovering a genomic basis for migration can provide managers with information on the levels of genetic variation for this adaptive behaviour, which could be used to prioritize populations for protection or identify individuals to translocate to boost diversity in a declining population [69,70].

Compared to studies using statistical thresholds of pooled genome-wide associations (e.g., [71]), our tiered window selection criteria seem to extract primarily functional outliers. Previous analysis of this mule deer population suggest that it is homogeneous [27] and a principal component analysis of individuals reveals no stratification that might lead to false positives [Appendix III Figure S3.2]. These outliers were localized to 15 out of 32 chromosomes which is expected with polygenic traits [72]. Of the 11 genes on which outlier SNPs were found, ADGRB1, BSG, PSME1, SETX, RNF216, ITSN2, and IKZF3 are associated with immunity, host-virus interaction, and cell differentiation. The ability of an animal to maintain its immune system or mount an immune response can depend on its nutritional health and energetic condition. Variations in immune function and condition have been linked to migration in bats [73] and stopover behaviour along a migration route in birds [74]. FITM1 is of note as it is related to the formation of lipid droplets and has been associated with fat storage in humans [75]. Body fat is an indicator of fitness in ungulates [76]. It can influence the annual survival of adult females [77], pregnancy and twinning rates [78] and the probability of a female rearing a fawn through summer [78,79]. The link between body condition and migration performance has been documented in several taxa, including migratory shorebirds [16], giant tortoises [80] and impalas [81]. Lipid metabolism rather than deposition may be the driving mechanism that supports FITM1 as a potential modulator of mule deer migration given that we found no significant differences between ingesta-free body fat percentage between the migratory groups (Figure S2.2) and genetic links to body fat and variation in migration timing were suggested for this mule deer population previously [27].

A final noteworthy gene was DPPA3 that is related to epigenetic modification of the maternal germ cell line. Epigenetics refers to changes in gene expression that occur without changes in the DNA sequence but through, for example, chemical modifications to the DNA (e.g., DNA methylation). Epigenetic variation can increase the phenotypic range encoded by a single genome and there is increasing evidence to show that such phenotypic plasticity can be inherited [82,83]. Heritable epigenetic mechanisms that lead to increasing phenotypic variation may increase the chance of offspring being able to cope with stochastic environments [83,84]. Our dataset consisted entirely of female deer, and while ungulate migration behaviour is thought to have a learned component (e.g., white-tailed deer fawns follow their mother's migration route [85]), previous work in this system has identified links between migratory timing and mitochondrial haplotype [27]. This, in conjunction with our results, could indicate that variation in migration behaviour is inherited at least partly epigenetically through the maternal line. Such inheritance could be beneficial for coping with future environmental change.

Investigations targeted at these outlier regions that we identified and individual genotypes appear warranted, and we suggest that screening for runs of homozygosity [86] and assaying differential methylation [82] may help elucidate how these genetic differences are being maintained within these populations. By validating these putative migration loci it is conceivable that a gene panel could be developed for characterizing the genetic profiles of migrating populations and be used in wildlife monitoring, such as to quantify genetic variation or population structure [69,87]. It has been established that differences in migratory behaviour exist between genetically distinct populations [14,88]. Typically, genome-wide association studies of migratory behaviour using natural populations have two very distinct groups that are often geographically separated [13]. We have shown that it is possible to detect genomic variation associated with migratory phenotypes in the absence of broad geographic separation. We were able to identify distinct differences in the genomes of individuals who overlap in space on their winter range while migrating to two different summer ranges, demonstrating that genomic differentiation between migratory strategies is detectable at a fine scale. It is likely that similar detectable patterns may exist in other taxa displaying population variation in migration behaviour. Many migratory ungulate species are considered at risk (e.g., caribou), raising concerns regarding population isolation and loss of genetic diversity. Screening for similar genetic associations in other imperiled ungulate populations may help shed light on local population dynamics, evolutionary potential, and could better inform management decisions as migration routes continue to be affected by environmental and anthropogenic change.

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Tables and Figures

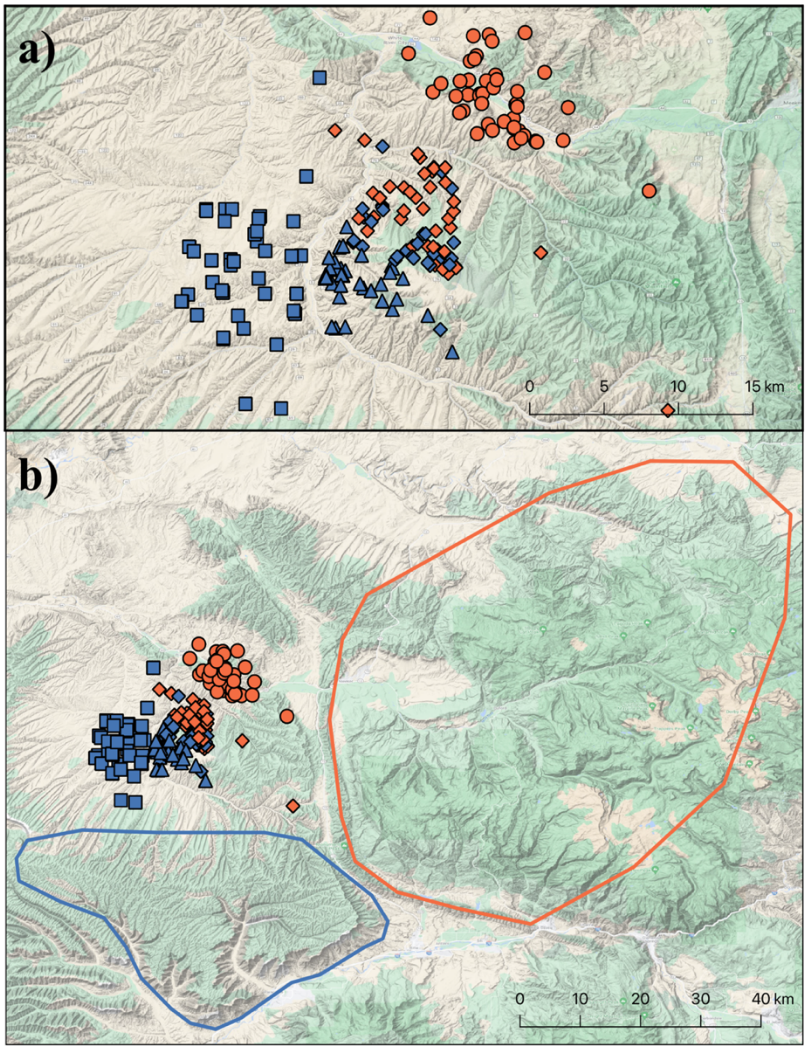

Figure 3.1 Winter range (a) and summer range areas (b) for Ryan Gulch (■), South Magnolia (▲), North Magnolia (◆), and North Ridge (•). Points are coded by colour representing migratory direction, with blue indicating north-south migration and orange indicating east-west migration. Points shown are the centroid of all GPS locations per individual while on the winter range. (b) Eastern and southern summer ranges are designated by the orange and blue outlines, respectively.

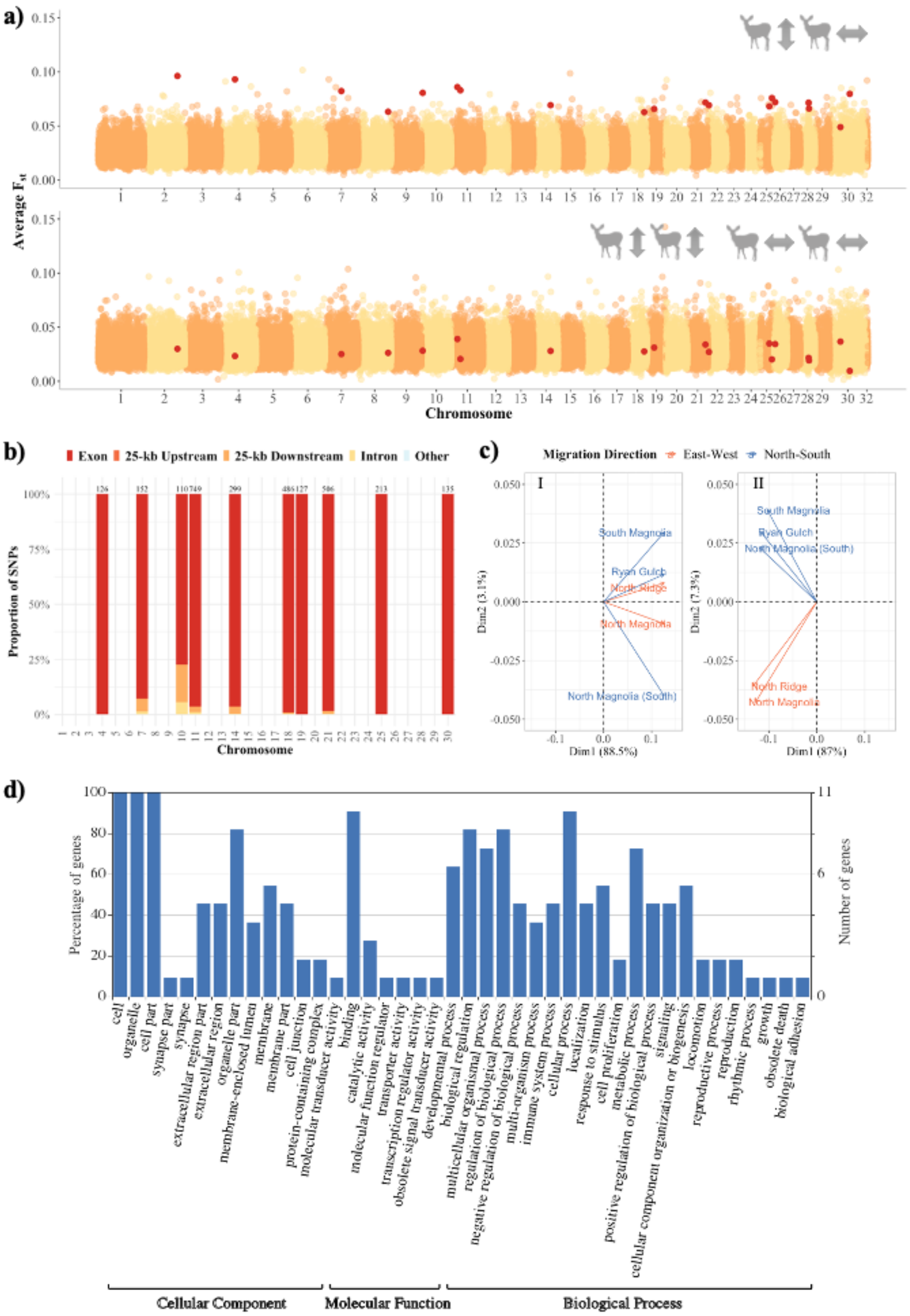
a)
Average F$_{st}$
0.15
0.10
0.05
0.00
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 32
Chromosome
b)
Exon
25-kb Upstream
25-kb Downstream
Intron
Other
126
152
110
749
299
486
127
506
213
135
100%
75%
50%
25%
0%
Proportion of SNPs
Chromosome
c)
Migration Direction
East-West
North-South
I
II
South Magnolia
Ryan Gulch
North Ridge
North Magnolia
North Magnolia (South)
Dim1 (88.5%)
Dim2 (3.1%)
Dim1 (87%)
Dim2 (7.3%)
d)
Percentage of genes
Number of genes
cell
organelle
cell part
synapse part
synapse
extracellular region part
extracellular region
organelle part
membrane-enclosed lumen
membrane
membrane part
cell junction
protein-containing complex
molecular transducer activity
binding
catalytic activity
molecular function regulator
transporter activity
transcription regulator activity
obsolete signal transducer activity
developmental process
biological regulation
multicellular organismal process
regulation of biological process
negative regulation of biological process
multi-organism process
immune system process
cellular process
localization
response to stimulus
cell proliferation
metabolic process
positive regulation of biological process
signaling
cellular component organization or biogenesis
locomotion
reproductive process
reproduction
rhythmic process
growth
obsolete cell death
biological adhesion
Cellular Component
Molecular Function
Biological Process

Figure 3.2 Genomic correlates of migratory direction (a) Manhattan plot for average F_{ST} values across the whole genome, for all opposite migration comparisons (top) and same migration comparisons (bottom). Each point represents a 2500kbp window. The highlighted points indicate outlier windows associated with migratory direction, determined to have high levels of differentiation in at least 4/6 of the opposite migration comparisons and low levels of differentiation in all same migration comparisons. (b) Distribution of 2903 outlier SNPs across chromosomes on or within 25kbp of genic regions. Bars indicate the proportion of SNPs on each chromosome distributed between exons, introns, 25kbp up- and downstream cites, and all other genic cites. Numbers above bars indicate the total number of outlier SNPs on each chromosome. (c) Principal component analysis plot of major allele frequencies across 21,944,208 biallelic SNPs on the whole genome (I) and 463 biallelic outlier SNPs differentiated based on migratory direction (II). Arrows represent the eigenvectors for the 5 study group-migration direction groups with east-west migrators shown in orange and north-south migrators shown in blue. (d) Gene ontology (GO) assignment plots based on white-tailed deer annotations. Functional groups (x-axis) were in three functional categories: cellular component, molecular function, and biological process. Number and percent of genes within a given functional category performing a specific function are indicated on the y-axis. Some genes belong to more than one functional group, which may result in a sum exceeding 100% in a category.

Chapter 4. The heritability of migration behaviours in a wide-ranging ungulate

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Contributions: MB, ABAS, JMN designed the study; JMN, CRA, GW coordinated data collection and sample curation; MB performed research and analyzed data; MB wrote the manuscript with input from ABAS, CRA, GW, JMN.

Abstract

Migration behaviour is declining globally in the face of rapid human-mediated environmental change. While many species exhibit individual plasticity in their migratory behaviour, not all species demonstrate sufficient variation to adapt to novel conditions. Selection on heritable behavioural components might, therefore, play a stronger role in the maintenance of migratory phenotypes for some species. Using GPS and genomic data from 143 individuals (256 animal-years) in a pedigree-free quantitative genetic approach, we estimated heritability, repeatability, and sources of environmental variation for migration traits in migrating mule deer (*Odocoileus hemionus*). We also quantified heritability in body size traits, known to be heritable in cervids, as a comparative assessment. We found these heritability estimates of body size traits comparable to those in the literature. We found low heritability for broad patterns of migration timing, distance, and duration, but high heritability for speed along the migratory route. This lack of heritability suggests that the broad patterns of migration, such as where to go and when, are driven by factors such as environmental gradients between wintering and summering areas and seasonal shifts in weather. Nevertheless, within these broad patterns, we uncovered variation among individuals which has a genetic component. Consequently, wild populations of migratory animals likely have the potential to respond (through microevolutionary changes in migration behaviours) to selection pressure generated by human activity or global environmental changes.

Significance Statement

Migration behaviour is critical for survival and reproduction in a wide variety of taxa, yet migrations have declined globally in the face of rapid human-mediated environmental change. Despite our understanding that migration behaviour has both genetic and environmental components, studies quantifying the sources of genetic variation contributing to migration polymorphism are lacking. Our study provides, to our knowledge, the first empirical evidence of heritability in migration behaviour in ungulates. These results have implications for the evolution and maintenance of migration behaviours in natural populations.

Introduction

The adaptive potential of a species is fundamental to evolutionary processes such as response to selection (1), while also holding practical relevance for conservation and management in evaluating long-term extinction risk (2, 3). The rate at which a wild population is expected to evolve in response to selection corresponds directly to the additive genetic variance (4–6). The proportion of phenotypic variance attributed to additive genetic effects determines the adaptive potential of a population or species. Quantifying the genetic variance underpinning phenotypic variation, specifically the relationships among individuals in a population and phenotypic traits, can be used to make inferences about the inheritance and evolutionary potential of those traits, without explicit knowledge of the genetic loci involved (7).

Heritability is the proportion of phenotypic variation explained by additive genetic effects. Models of heritability assume the infinitesimal model, under which trait variation is controlled by many alleles of small effect and environmental variation (8, 9). Both genetic and environmental effects must be considered when measuring heritability in natural populations. Laboratory populations, in contrast, are generally studied in a controlled environment. By partitioning phenotypic variation into additive genetic variance and other sources of variance such as permanent environmental effects, we can quantify the many processes contributing to the maintenance of genetic variance within a population, including life history trade-offs between different components of fitness (10), maternal genetic effects driving trait variation (11–13), and the contribution of individual repeatability (14). Decomposing trait variation into genetic and environmental components allows for the estimation of evolutionary potential in natural populations and can be extended to estimate the covariation with other fitness related traits to predict response to selection (15).

In natural populations, calculating additive genetic variance and trait heritability can be challenging. Such metrics rely on estimating the pairwise relatedness among individuals (7, 16), conventionally calculated from multigenerational pedigrees derived from field observations or from parentage assignments using multi-locus genotypes (7, 9, 17). Indeed, the long-term sampling effort required to construct a pedigree is a serious limitation (9) and in small sample sizes, molecular techniques can also bias the relatedness estimates (18). Such bias can affect derived estimates of heritability; models may return lower estimates of heritability compared to pedigree-based models (17).

To help overcome these limitations, genomic relatedness matrices (GRMs) can be generated from thousands of SNPs, typically arrays (19) or genome-wide sequencing data (20). These GRMs show high precision in estimating quantitative genetic parameters when compared to pedigree models or twin studies (1, 20, 21). GRMs are now more frequently used to estimate heritability in wild populations which broadens our understanding of important quantitative genetic traits: for example, heritability of morphological traits like body size and antlers in large ungulates (11, 22) and body size in passerine birds (23); physiological traits such as those linked to stress response (14, 24); and personality traits such as aggression and docility (12, 14). More recently, the heritability of movement and space use behaviours has been examined in large ungulates (14). Estimating heritability of behaviours linked to fitness can be of particular importance where variation in life-history phenology is driven by both a genetic and environmental component.

One such behaviour is migration. Such seasonal movements are critical for the reproduction and survival in a wide variety of taxa, yet populations have experienced global declines in migrations in the face of rapid human-mediated environmental change (25–28). While migratory behaviour is thought to be largely driven by environmental variation (29), behavioural variation is considered to have both a genetic component, where natural selection acts on a migratory phenotype, that is at least partially controlled by underlying genetic variation (30–32), and a socially transmitted component, in which socially learned behaviours are transmitted across generations (33). Migrating populations experiencing fluctuating environments can adapt to novel conditions through behavioural plasticity (34) and short-term evolution where selection acts on repeatable behavioural phenotypes that confer a fitness benefit (35). While many species exhibit individual plasticity in their migratory behaviour (34, 36), not all species demonstrate high levels of individual plasticity (37). Selection on heritable behavioural components might therefore play a stronger role in the maintenance of migratory phenotypes. By partitioning the effects of behavioural repeatability and plasticity of migratory traits and quantifying the extent to which repeatable behavioural variation is heritable, we can better predict how rapid environmental change affects the evolution of migration behaviour.

In this study we used a pedigree-free quantitative genetic approach to quantify the proportion of phenotypic variance explained by additive genetic effects in spring migration behaviours in migrating mule deer (*Odocoileus hemionus*). Mule deer typically migrate to match changes in resource availability and optimize migratory timing relative to both plant productivity and weather on their summer range (e.g., (38)). Mule deer exhibit variation in migration distances (37) and timing (39). Their migrations are of interest to wildlife managers as recent anthropogenic development and climate change may threaten migratory routes (38, 39) and alter behaviours along the route (40). While behavioural plasticity may be one way for at-risk populations to buffer against the effects of rapid environmental change, mule deer exhibit little to no migratory plasticity in terms of whether or where to migrate, meaning they could be less resilient to change (37). Consequently, adaptation to a rapidly changing environment might require micro-evolutionary change. Such adaptation depends on some degree of heritability in migratory variation. We estimated heritability and sources of environmental variation (e.g., permanent environmental effects) in migration distance, timing, and movement rate. To serve as a comparative assessment of our pedigree-free approach, we also included heritability estimates of weight, ingesta-free body-fat percentage, and body size measurements in our analyses.

Broadly, behaviour is often assumed to be highly plastic, suggesting that the magnitude of additive genetic variance should be low relative to the effect of environmental variation (41, 42). Accordingly, we expected the heritability of migration traits to be low compared to other traits such as morphological traits or life-history traits. A recent meta-analysis by Dochtermann et al. (43) reviews the current studies on the heritability of behaviour and reports the range of heritability of behavioural traits is 0.24–0.31. Although Dochtermann et al. (43) grouped migration and dispersal together in their models, they estimated moderate heritability of these traits ($h^2 = 0.46$; 95% CI:0.33–0.57). Given our current understanding of the genetic and environmental drivers of migration (29), we predict a large proportion of phenotypic variation in migration behaviour to be explained by permanent environmental effects, and additive genetic effects (i.e., heritability) to explain a smaller proportion of phenotypic variance. Another important metric to consider when evaluating heritability of migration is repeatability. Repeatability quantifies among-individual variation and is mathematically related to heritability in that the numerator of repeatability combines both additive genetic and permanent environment sources of variations, while only additive genetic variation is considered in the calculation of heritability (44). Thus, we predict low heritability for migration timing, as variation in migration timing across ungulates is known to be heavily influenced by plant phenology (30) and environmental effects. We predict low heritability for migration distance, duration, and movement rate however heritability for these traits will likely be greater than that of migration timing as movements along the route are more constrained by physiological processes which have a genetic component.

We predict high levels of repeatability for all migration traits given the large contribution of permanent environmental effects.

Materials and Methods

Study site

This study took place in the Piceance Basin of northwestern Colorado, USA (Figure 4.1a). The climate was characterized by cold winters (mean monthly temperature: −3.8°C, range: −37.2°C –22.8°C) and warm dry summers (mean monthly temperature: 17.5°C, range: −2.2°C –35.6°C) with monsoonal precipitation in the late summer (45). The area was topographically variable with the dominant vegetation consisting of big sagebrush (*Artemisia tridentata*) and shrub complexes composed of pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus ostesperma*). Other dominant shrubs included Utah serviceberry (*Amalenchier utahensis*), mountain mahogany (*Cercocarpus montanus*), bitterbrush (*Purshia tridentata*), and mountain snowberry (*Symphoricarpos oreophilus*). This area was popular for hunting during the fall with an annual average of 511 deer harvested in the wildlife management unit (Game Management Unit 22), which encompassed the entire study area (45). Mule deer in this area typically occupy their winter range between October and April of each year (39, 46) and migrate to several different summer ranges (46) located south and east of the winter range (Figure 4.1a). Individuals tend to migrate to the same summer range each year. Elevation on the winter study area ranged from 1,675 to 2,285 m and from 2,000 to 2,800 m on the summer study areas. We documented that body weight, hind leg length, chest girth and ingesta-free body fat percentage do not differ significantly between east-west and north-south migrating groups (47) and there is no apparent genetic subdivision within the population (39, 47).

Individual sampling and phenotypes

Adult (>1 year old) female mule deer were captured in either December or March from 2008–2015 using helicopter net gunning and fitted with store-on-board GPS radio collars (Advanced Telemetry Systems, Isanti MN, USA) with three different relocation schedules (5 hours, 60 minutes, and 30 minutes) depending on the individual. Deer were spotted visually by the helicopter capture crew and captured using a net gun. Deer were then blindfolded, hobbled, and administered 0.5 mg/kg of Midazolam and 0.25 mg/kg of Azaperone intramuscularly to alleviate capture-related stress (dose of both drugs based on an average weight of 75 kg). Deer were transported to a central processing site typically within 2 km of the capture site, where they were weighed, measured for chest girth and hind foot length, and blood samples were collected for genetic analysis. We estimated their age using tooth replacement and wear (48–50). We also obtained a body condition score by palpating the rump and measured the thickness of subcutaneous rump fat and the depth of the longissimus dorsi muscle using ultrasound (51–55). We used the body condition score and ultrasound measurements to estimate the percent ingesta-free body fat of each deer (52, 53). During late-winter captures, we assessed pregnancy using ultrasound and for does for which we did not detect a fetus, we confirmed pregnancy status using pregnancy-specific protein B from blood samples. Deer were released at the processing site immediately following blood sample collection and GPS collar attachment. All procedures were approved by the Colorado State University (protocol ID:

10-2350A) and Colorado Parks and Wildlife (protocol ID: 15-2008) Animal Care and Use Committees.

GPS locations were input into Migration Mapper v3.0 (56) where we removed erroneous locations, and then delineated migration routes visually for each individual using graphs of the individual's net-squared displacement. Some individuals were collared for more than one year, so we determined spring migrations for every year in which data were available. After migration routes had been determined, we recorded the start and end of spring migration in day of year, the duration of the migration in days, and calculated straight-line distance from the first GPS location of the migration route to the last GPS point. Movement rate was calculated per single step length, and then averaged across all step lengths for the entire route. To account for the three different relocation schedules, we rescaled relocations for all individuals to the coarsest (5-hour) interval before calculating movement rate. Habitat characteristics (i.e., vegetation type) occurring along the migratory paths of mule deer was similar across the study areas (57), however individuals that migrated east-west on average travelled greater distances than individuals migrating north-south (Figure 4.1a).

DNA extraction and library preparation for RAD sequencing

We extracted DNA from blood samples using the DNeasy Blood and Tissue Kit (Qiagen, Inc., Valencia, CA, USA), following the manufacturer's protocol. We generated restriction site-associated DNA sequencing (RADseq) libraries using an adapted protocol from Parchman et al. (58) and Peterson et al. (59) with Sbfl-HF and Msel restriction enzymes. Samples were incubated, digested overnight, and heat-inactivated in 96-well plates (see Haworth et al. (60) for reaction conditions and primer details). Each 96-well plate had UltraPure distilled water (Invitrogen, 1897011) as negative controls. Restriction-digested DNA was combined with 7 µl of ligation mixture and 3 µl of one of the 24 available Sbfl adapters (1.0 µM), and adapters were ligated at 16°C for 3 hours. We purified DNA fragments of artifacts following manufacturer protocol for AMPure XP beads (Beckman Coulter, A63880). Adapter-ligated fragments were amplified in four separate 10 µl reactions that incorporated barcodes. We pooled and purified samples following manufacturer protocol for QIAquick PCR Purification kit (Qiagen, 28106) for a final elution to 42 µl. We performed size selection between 450 bp to 700 bp on 80 µl purified libraries and performed gel purification following manufacturer protocol for QIAquick Gel Extraction kit (Qiagen, 28706) for a final elution to 60 µl. We validated the purified final libraries with a TapeStation D1000 kit (Agilent, 5067-5582). The libraries were sequenced at The Centre for Applied Genomics (TCAG) in The Hospital for Sick Children (SickKids, Toronto, Ontario, Canada) on an Illumina HiSeq 2500 to produce 2 × 126 base pair paired-end reads.

Bioinformatic pipeline for RADseq data

Fastq files were demultiplexed using process_radtags within the Stacks v2.3 module (61). Parameters within process_radtags included the removal of any read with an uncalled base and the discarding of reads with low-quality scores. The demultiplexed sample files were aligned against the white-tailed deer genome. Mule deer and white-tailed deer can hybridize (62) so we opted to use the long-read-based draft genome of white-tailed deer (*Odocoileus virginianus*) (Accession No. JAAVWD000000000) that was recently annotated (63); we note that the mule deer genome available at the time of analysis was simply a consensus sequence from reads mapped to earlier versions of the white-tailed reference (64). Mapped reads were sorted and indexed using SAMtools (65). We then ran the gstacks and populations program within STACKs, retaining loci found in at least 80% of samples (r = 0.80), with a minor allele frequency of 1% (min_maf = 0.01), and heterozygosity upper bound of 0.8 (max_het = 0.8) that produced a variant call format (VCF) file. We also only retained one single nucleotide polymorphism (SNP) per locus (--write_single_snp), to meet the assumptions of linkage equilibrium in subsequent analyses.

The VCF file was filtered using PLINK v.19 (66) to include only individuals with less than 10% missing data. Using VCFtools (67) we determined F_{IS} and observed and estimated homozygosity and removed outlier individuals with $F_{IS} < -0.1$ on the basis of excess heterozygosity (68, 69), which was visualized with a principal component analysis (Appendix III Figure S3.2) using PLINK and R v.4.2.1 (70). The VCF file was converted into a binary fileset using PLINK and that was used to generate the classic genomic relatedness matrix (GRM) in GCTA v1.92.4 (20). We examined the diagonal values of the GRM to identify potential problematic samples with inflated self-relatedness values and used this to further inform filtering. Highly related individuals were removed at two levels (r > 0.10 and r > 0.05) to reduce heterogeneity in the matrix using the grm-cutoff flag. All individuals were retained to generate the unfiltered GRM even if phenotypic data were missing as this improves relatedness estimates. All subsequent analyses were run using the unfiltered and filtered GRMs separately.

Quantitative analyses

We used the animal model approach to partition the phenotypic variance of migration and body size traits (V_P) into additive genetic variance (V_A), permanent environmental effects

(V_{PE}) and residual variance (V_R) such that $V_P = V_A + V_{PE} + V_R$ conditional on any fixed effects. In our models (Table 4.1) we included age and month of capture (December or March) as fixed effects in all body size models as body size may differ between life-history stages and time of year. There was little variation in pregnancy rates as 95% of the deer captured in March were pregnant at the time. We included age and log-transformed hind leg length in all the migration models; summer range was included as a fixed effect for start day, end day, distance, and duration models; log-transformed distance of migration route was included in the movement rate and duration models. To account for interannual differences in individual behaviour and environmental conditions, we included year as a random effect in all the models. Individual identity was included as a random effect in all the migration models to account for multiple migrations per individual. We included the GRMs in the models as a random effect as our measure of pairwise relatedness (Table 4.1). The unfiltered GRM was nonpositive definite but could nevertheless be implemented in an animal model by bending the matrix (71).

We fitted the animal models using a Markov Chain Monte Carlo for generalized linear mixed models with the MCMCglmm package in R (72). We ran the algorithm 4 times for each model, resulting in 4 chains, and thinned the chains at an interval of 100. We used a burn-in period of 10,000 iterations and a total of 500,000 iterations per chain to estimate the posterior distribution. We log-transformed traits with continuous distributions to ensure proper support. We ran the start day, end day, and duration models using a Poisson distribution. Narrow sense heritability (h^2) of the traits was estimated as $h^2 = V_A/(V_A + V_{PE} + V_R)$ and the permanent environmental effect (pe^2) as $pe^2 = V_{PE}/(V_A + V_{PE} + V_R)$. Individual repeatability (ind^2) was calculated as the ratio of among-individual variance (genetic and nongenetic) over the total phenotypic variance $ind^2 = V_A+V_{PE}/(V_A + V_{PE} + V_R)$ (73). For the models using the Poisson distribution we report the heritability and additive genetic variance on both the latent scale and true data scale which were determined using the R package QCglmm (74).

Results

Of the 242 individuals captured, 207 had sufficient GPS data to determine a spring migration for at least one year. The number of migrations per individual ranged from 1-4 with 256 animal-years total. Frequency plots of migration traits are illustrated in Figure 4.1. The average start of spring migration was May 2 (range March 8–June 1) and the average end was May 10 (range April 1–July 6). The average duration of migration was 7 days (range 2–67). The average distance of migrations to the eastern summer range was 39.8 km (range 14.2–94.9 km) and the average distance to the northern summer range was 31.1 km (range 14.7–58.2 km). The average movement rate for individuals was 327.1 m/h (range 41.3–1468.3 m/h). Density plots of body size traits are available in Figure S3.3.

After applying quality filtering 143 individuals were retained in the GRM. The genomic relatedness matrix included 10,097 SNPs and 20,306 pairwise relatedness coefficients, of which 104 pairs had a relatedness coefficient higher than 0.1 (Figure S3.4, Table S3.1). Here we present the results for the models that used the GRM with a relatedness cutoff of 0.1; this GRM included 109 individuals, had a mean diagonal of 1.02, and the total variance of the relatedness coefficient of the off-diagonal was 0.0001. For the model results using the unfiltered and 0.05 cutoff see Appendix III.

Narrow-sense heritability h^2 (95% CI) of body size traits ranged from $h^2 = 0.12$ (0.01-0.57) for ingesta-free body-fat to $h^2 = 0.27$ (0.06-0.53) for hind leg length. Permanent environmental effects pe^2 (95% CI) and repeatability (i.e., among-individual differences, ind^2 (95% CI)) were similarly low for ingesta-free body-fat $pe^2 = 0.07$ (0.01-0.31) and $ind^2 = 0.19$ (0.03-0.66). Permanent environmental effects for other body size traits ranged from $pe^2 = 0.22$ (0.05-0.63) for weight to $pe^2 = 0.45$ (0.17-0.84) for hind leg length. Repeatability estimates were all moderate for the remaining body size traits with $ind^2 = 0.42$ (0.14-0.86) for weight, $ind^2 = 0.56$ (0.27-0.88) for chest girth, and $ind^2 = 0.72$ (0.46-0.93) for hind leg length (Figure 4.2, Table 4.2).

Heritability for the dates marking the beginning and end of migration was low, for both the start day $h^2 = 0.04$ (0.01-0.11), and end day $h^2 = 0.05$ (0.01-0.14). Variation in migration start and end day was explained primarily by permanent environmental effects which were captured in the year-to-year variation (Figure 4.2, Table 4.2). Movement behaviours along the migration route ranged considerably, with distance $h^2 = 0.14$ (<0.01-0.66) and duration $h^2 = 0.10$ (<0.01-0.37) having lower heritability, while average movement rate was highly heritable $h^2 = 0.76$ (0.12-0.94). Variation in distance and duration was explained largely by individual identity (Figure 4.2).

Discussion

Migratory behaviour is a complex process that is thought to emerge from a combination of physiological, morphological, and cognitive traits (29, 30). This implies that genetics at least partially underpin the phenotypic variation of migratory traits. Knowing the general pattern of heritability of migration behaviour is important as inferences on the selection, evolution and maintenance of migration behaviour often assume that phenotypic differences among groups, whether age classes, sexes, populations, or species, are adaptive and driven by underlying genetic differences (i.e., the phenotypic gambit; (75)). However, whether this is true or not is unclear for many taxa yet critically important. The degree of heritability of different traits could help identify which traits are most plastic under ongoing global environmental change. Our study provides, to our knowledge, the first empirical evidence of heritability in migration behaviour in ungulates. For mule deer, we found low heritability for broad patterns of migration timing, distance, and duration, but high heritability for movement rate along the migratory route. Additionally, our heritability estimates of body size traits were comparable to the estimates of ungulate body size (e.g., (22, 76, 77)). Therefore, we are confident that our pedigree-free approach to estimating heritability of both body size and migration behaviours has likely captured a true signal. These findings have important implications for our understanding of the evolution of migration in ungulates and for how migration behaviours may be influenced by human-mediated environmental change.

High heritability of movement rate, low heritability of migration timing

Contrary to our prediction, we found high heritability for average movement rate during migration ($h^2 = 0.76$) after accounting for age, body size and distance migrated. Heritability of migration behaviour in ungulates has not been measured in other systems; for roe deer (*Capreolus capreolus*) heritability of movement rate and space-use behaviours within home ranges was measured, with moderate heritability for daily average movement speed ($h^2 = 0.21 \pm 0.08$) and high heritability of distance to roads ($h^2 = 0.70 \pm 0.11$; (14)). For racehorses, the genetic basis for speed and stamina has been well documented, with genome-wide scans identifying candidate loci correlating with speed (78, 79). Heritability estimates of speed in racehorses varies within the literature from low (h^2 range: 0.074 ± 0.012 – 0.124 ± 0.006; (80)) to moderate and high (h^2 range: 0.38 ± 0.03 – 0.68 ± 0.05; (81)). For mule deer a genetic basis for movement traits has been suggested as the escape gaits of mule deer, white-tailed deer, and their F1 hybrid crosses are highly consistent (82). Nevertheless, high heritability does not necessarily imply high evolvability, due to the lack of independence between additive genetic variance and environmental effects (83), and in the case of movement rate, physiological constraints and reduced selection pressure on movement rate as a trait are likely to limit evolvability and response to selection.

Low heritability can result from the erosion of additive genetic variance by stabilizing or directional selection (84) or from increased residual variance due to environment (85). Such residual variance can include variation due to year, which in our models explained the largest proportion of phenotypic variation for migration start and end day (Figure 4.2). Similarly, for these mule deer, spring migration tends to vary among years, in relation to snow depth, and plant phenology (38). For mule deer in the Sierra Nevada, the same patterns of year-to-year variation exist for migration timing, linked to southern oscillation index, snow depth and plant phenology (86). Plant phenology influences the migration timing of several ungulates – including elk (*Cervus elaphus canadensis*) (87), mule deer (38, 86), red deer (*Cervus elaphus*) (88), and roe deer (88, 89); such plasticity leads to improved foraging en route. Plant phenology is tightly linked to changes in temperature (90) which contribute to yearly variation in spring green-up. Such low heritability of migration timing is in line with our prediction that most of the phenotypic variation in migration timing is explained by environmental effects. Therefore, under rapid environmental change, mule deer may face detrimental fitness consequences with migrations that depend at least to a degree on predictable environmental conditions.

Individual repeatability of migration distance and duration

All heritability values that we estimated were substantially lower than our estimates of individual repeatability, which is assumed to set the upper bound for heritability (91, 92). High estimates of repeatability for migration behaviours fit with our prediction, given the large contribution of permanent environmental effects to phenotypic variance. Bell et al. (91) found in their meta-analysis the average measure of repeatability of behaviour was 0.37. Average repeatability across migration traits was 0.67, and individual identity largely explained variation in migration distance and duration. High repeatability of migration behaviours might be linked to strong spatial fidelity exhibited by mule deer (37, 93, 94). For example, Sawyer et al. (37) found high levels (>80%) of site fidelity in mule deer migration routes, regardless of age, reproductive status, or number of years monitored and Northrup et al. (94), working in our system, showed high year-to-year fidelity in summer and winter ranges indicating they migrate to and from the same locations annually. Similarly, Mahoney and Schaefer (95) found that rank order of caribou (*Rangifer tarandus*) migration was highly consistent among individuals, and independent of sex or age.

Studies reporting consistent among-individual differences in movement and space-use behaviours are becoming more prevalent across taxa (14, 96, 97), however the mechanisms underpinning individual repeatability of behaviours is still in need of exploration. Sawyer et al. (37) proposed that the high level of consistency in mule deer migration behaviour is due to the strong reliance on memory for navigation. Migrations shaped largely by memory and experience may be less flexible than those acquired by social learning from conspecifics (98, 99).

Implications for free-ranging populations

When estimating heritability using GRM-based approaches, sample size and variance in relatedness need to be considered. Small sample size can increase sampling variance, which biases V_A downwards, thereby decreasing heritability estimates (100). Our study and that of Gervais et al. (14) are two examples which demonstrate a GRM-based approach can be used to estimate heritability using small samples sizes of a few hundred unrelated individuals. The GRM variance of relatedness for our study was low, because like other studies of wild ungulates (e.g., (11, 14)) our GRM was skewed towards unrelated individuals. With SNP data, the GRM variance is inversely proportional to the variance of h^2 (101), however, by removing highly related individuals, we can reduce error resulting from the impracticality of sampling the full spectrum of relatives (102).

Linkage disequilibrium (LD) and genomic architecture may underly biases in heritability estimates using unrelated individuals. Regions along the genome with higher LD tend to overestimate heritability and regions of low LD tend to underestimate heritability (103, 104). In addition, due to the relationship between LD and allele frequency, if an individual has mostly low-frequency variants underlying a trait or mostly high-frequency variants, estimates of heritability will be biased. One way to account for the bias caused by LD would be to weight estimates of pairwise genetic similarity by LD with neighbouring SNPs when generating the GRM. Speed et al. (103) showed that this greatly reduced bias and increased precision of heritability estimates.

GRM-based approaches make estimating heritability of wild populations more accessible, however another challenge it presents is understanding the effect of heterogeneous landscapes on heritability estimates. Observed heritability of a trait may be partially due to related individuals sharing more similar habitats, which would result in the genetic and environmental sources of variation being potentially confounded (105). In our system relatives are more likely to share similar environments as offspring are philopatric to their mother's range. Environmental similarity affects heritability estimates in red deer populations (106) but did not have substantial effect in Soay sheep (*Ovis aries*; (107)). We assume environmental similarity has little effect for our study population.

Conclusion

Our study provides empirical demonstration of heritability of a migration trait. Broad patterns of migration timing have low heritability and are heavily influenced by year-to-year environmental variation, while migration speed is highly heritable and subject to individual differences in repeatability. Future studies should seek to quantify the heritability of more movement and space-use behaviours that affect fitness along the migration route, such as tracking forage, and habitat selection or avoidance of anthropogenic features. Changes to the landscape resulting from human activity are having a negative effect, even leading to the disappearance of migration routes (26, 28). Given that additive genetic variance of fitness may often be substantially underestimated

(4) suggests that the adaptive evolution may occur as rapidly as generation to generation. Our findings imply that wild mule deer populations have the potential to respond to selection pressure generated by human activity or global environmental changes through microevolutionary changes in migration behaviours.

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Tables and Figures

Table 4.1 Summary of fixed and random effect for each animal model.

Model	Response variable	Fixed effects	Random effects	Model distribution
1	Chest girth	age + month of capture	relatedness (GRM) + year	Normal
2	Hind leg length	age + month of capture	relatedness (GRM) + year	Normal
3	Ingest-free body-fat	age + month of capture	relatedness (GRM) + year	Normal
4	Weight	age + month of capture	relatedness (GRM) + year	Normal
5	Start day	age + summer range + log(hind leg length)	relatedness (GRM) + year + identity	Poisson
6	End day	age + summer range + log(hind leg length)	relatedness (GRM) + year + identity	Poisson
7	Distance	age + summer range + log(hind leg length)	relatedness (GRM) + year + identity	Normal
8	Duration	age + summer range + log(hind leg length) + log(distance)	relatedness (GRM) + year + identity	Poisson
9	Movement rate	age + log(hind leg length) + log(distance)	relatedness (GRM) + year + identity	Normal

Table 4.2 Variance component estimates and their associated ratios for body size and migration traits. h^2: heritability, pe^2: permanent environmental effects, ind^2: repeatability, V_A: additive genetic variance, V_{ID}: variance due individual identity, V_{YR}: variance due to year, V_R: residual variance.

Trait	**[1]h^2**	**pe^2**	**ind^2**	**[1]V_A**	**V_{ID}**	**V_{YR}**	**V_R**
Chest girth	0.25 (0.06-0.58)	0.30 (0.09-0.72)	0.56 (0.27-0.88)	0.001 (<0.001-0.002)	-	0.001 (<0.001-0.006)	0.001 (0.001-0.002)
Hind leg length	0.27 (0.06-0.53)	0.45 (0.17-0.84)	0.72 (0.46-0.93)	<0.001 (<0.001-0.001)	-	0.001 (<0.001-0.005)	<0.001 (<0.001-0.001)
Ingest-free body-fat	0.12 (0.01-0.57)	0.07 (0.01-0.31)	0.19 (0.03-0.66)	0.009 (0.001-0.044)	-	0.006 (<0.001-0.030)	0.060 (0.027-0.085)
Weight	0.20 (0.03-0.63)	0.22 (0.05-0.63)	0.42 (0.14-0.86)	0.002 (<0.001-0.007)	-	0.003 (<0.001-0.015)	0.007 (0.002-0.0100)
Start day	[a]0.08 (0.01-0.23) [b]0.04(0.01-0.11)	0.86 (0.62-0.98)	0.93 (0.78-0.99)	[a]0.001 (<0.001-0.002) [b]13.37 (3.82-33.96)	0.001 (<0.001-0.002)	0.017 (0.003-0.069)	0.001 (<0.001-0.002)
End day	[a]0.11 (0.01-0.32) [b]0.05 (0.01-0.14)	0.79 (0.51-0.97)	0.90 (0.71-0.99)	[a]0.001 (<0.001-0.002) [b]16.43 (4.49-41.56)	0.001 (<0.001-0.002)	0.011 (0.002-0.045)	0.001 (<0.001-0.002)
Distance	0.14 (<0.01-0.66)	0.55 (0.04-0.88)	0.68 (0.17-0.92)	0.017 (0.001-0.087)	0.063 (0.002-0.123)	0.005 (<0.001-0.027)	0.039 (0.011-0.104)
Duration	[a]0.25 (<0.01-0.94) [b]0.10 (<0.01-0.37)	0.51 (0.02-0.98)	0.76 (0.07-1.00)	[a]0.084 (0.001-0.347) [b]4.80 (0.04-20.86)	0.151 (0.001-3.88)	0.019 (0.001-0.113)	0.078 (0.001-0.321)
Movement rate	0.75 (0.11-0.94)	0.13 (0.01-0.72)	0.88 (0.64-0.97)	0.291 (0.045-0.444)	0.041 (0.001-0.276)	0.011 (0.001-0.062)	0.044 (0.012-0.137)

[1] For Poisson distributed traits (start day, end day, duration) heritability and additive genetic effect values are given in both the latent model state [a] and true data state [b].

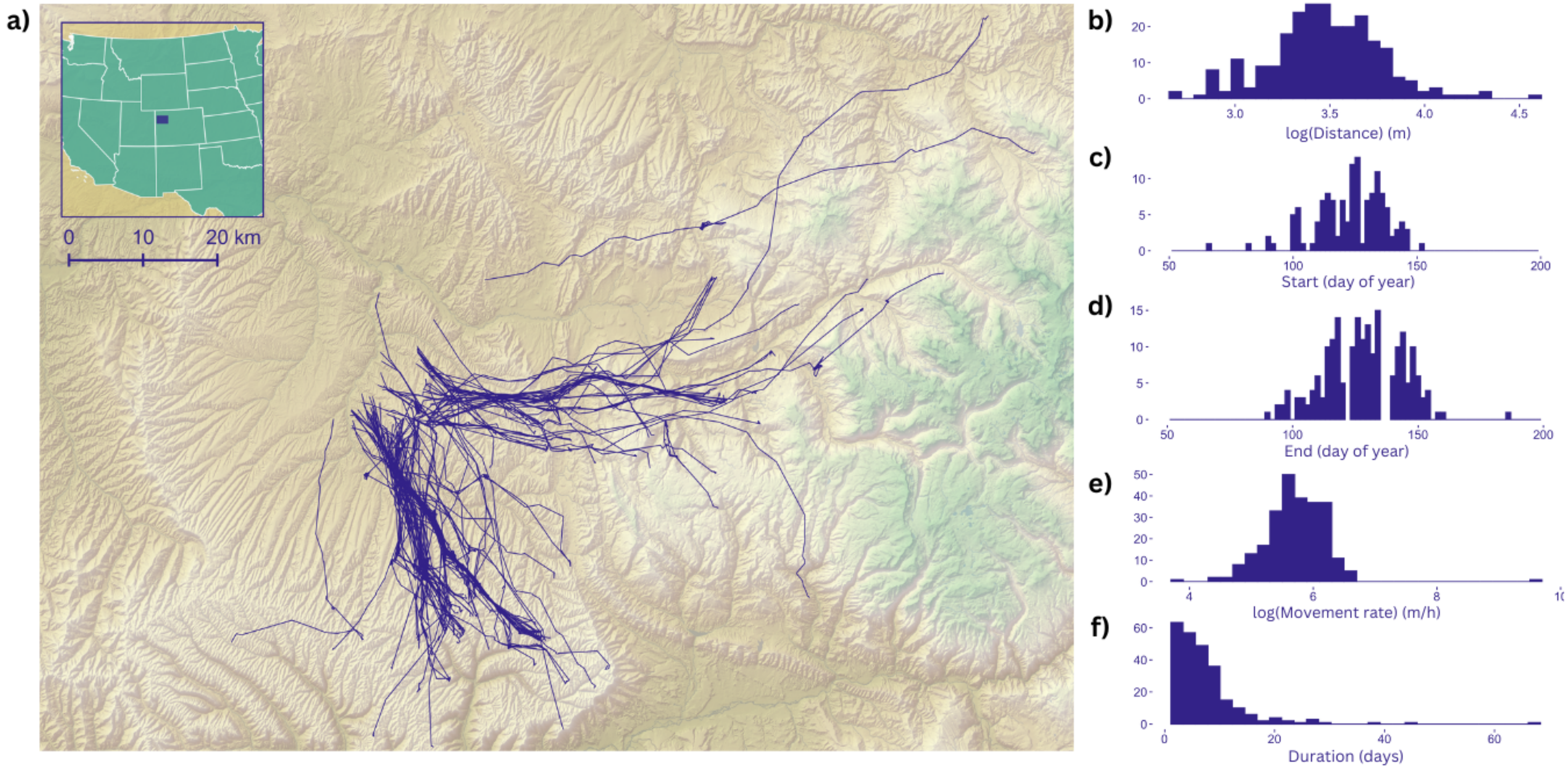

Figure 4.1 a) Mule deer migration routes for 256-animal years in the Piceance Basin, Colorado, USA. Frequency distributions of migratory traits for b) migration distance; c) migration start day; d) migration end day; e) average movement rate along the route; and f) duration of migration.

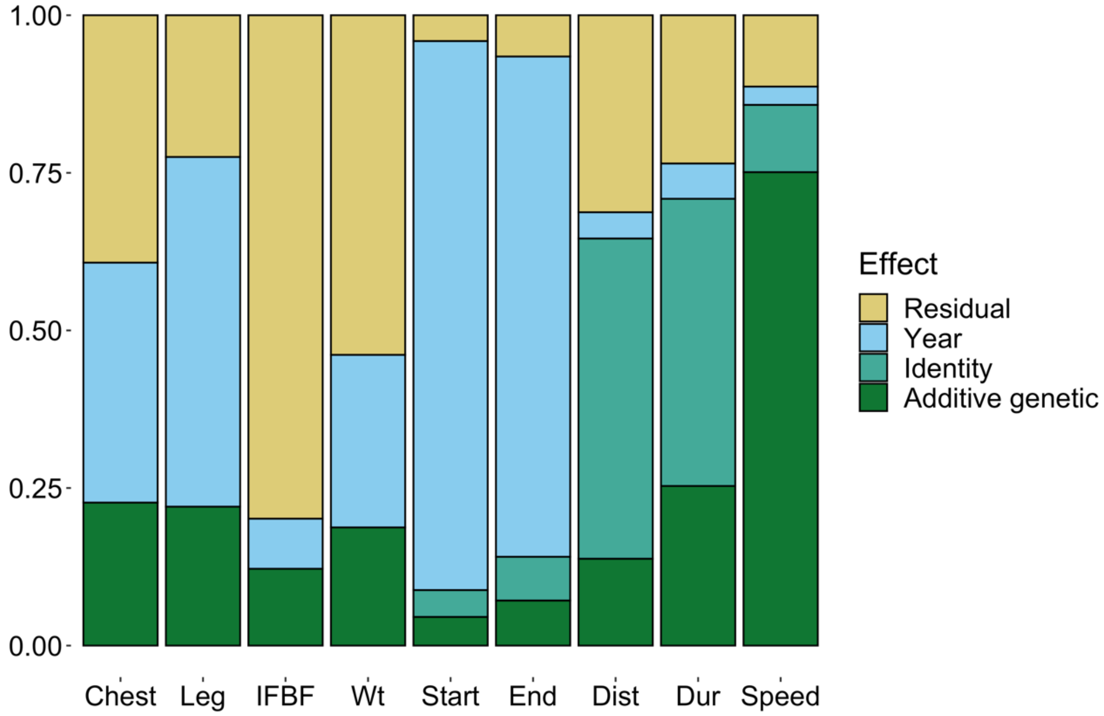

Figure 4.2 Variance partitioning of body size and migration behavioural traits. Proportion of phenotypic variance of body size traits (chest girth, hind leg length, ingesta-free body fat percentage, weight) and migration traits (start day, end day, distance, duration, and average speed) explained by additive genetic effects, permanent environmental effects (year and animal identity), and residual effects.

Chapter 5. General Discussion

The overarching goal of my doctoral thesis was to expand the understanding of ecology and evolution of animal migration by examining the drivers of phenotypic variation in migration behaviour. The complexity of migration behaviour can make it difficult to tease apart the underlying mechanisms contributing to its evolution. Such partitioning of underlying mechanisms is helpful for conservation of species whose migrations are considered vulnerable to environmental change. In **Chapter 2** I quantitatively reviewed the literature on partially migratory systems, to better characterize what drives migration and ultimately clarify the potential drivers for its evolution across systems. This chapter served as a foundation for improving our empirical understanding of factors driving the evolution of migration. Our findings support, in many ways, the current understanding of the drivers of migration propensity, such as the strong influence of predators and environmental variables, highlights the knowledge gap in our understanding of the genetic drivers of migration. Some of these gaps I addressed in subsequent chapters.

In **Chapter 3** I identified genomic regions associated with migration direction by undertaking pooled genome-wide scans on a natural population of mule deer. I identified distinct differences in the genomes of individuals who overlap in space on their winter range while migrating to two different summer ranges, demonstrating that genomic differentiation between migratory strategies is detectable at a fine scale. Such a genomic basis for a migratory trait improves our understanding of the adaptive potential of migration and the flexibility of individuals to change their behaviour in the face of stochastic, short-term changes to their environment and more permanent landscape changes that might make previous migration routes impenetrable. I continue to investigate the adaptive potential of migration behaviour in mule deer in **Chapter 4** where I used a pedigree-free quantitative genetic approach to quantify the proportion of phenotypic variance explained by additive genetic effects in spring migration behaviours in mule deer. I found low heritability for broad patterns of migration timing, and greater variation in heritability for behaviours during migration, with low heritability for distance and duration and high heritability for movement rate along the route. Changes to the landscape resulting from human activity can result in the disappearance of migration routes (Harris et al., 2009; Wilcove & Wikelski, 2008). My findings illustrate the adaptive potential of migration and imply that mule deer populations have the potential to adaptively respond to selection pressure generated by human activity or global environmental changes as rapidly as generation to generation.

Future directions for studies of the evolution of migration include the goals to: i) characterize the genetic architecture of migration in other species, with an emphasis on behavioural and physiological traits; ii) expand on our understanding of how the expression of genes associated with migration interact with environmental factors in a wider variety of taxa; iii) target investigations on the outlier regions identified in Chapter 3, for example screening for runs of homozygosity (Brüniche-Olsen et al., 2018) and assaying differential methylation (Hu & Barrett, 2017); and iv) quantify the heritability of more movement and space-use traits along the migration route, such as tracking forage, and habitat selection or avoidance of anthropogenic features. My thesis explored phenotypic variation in migration behaviour across species, populations, and individuals. In its chapters I have strived to provide a resource for future studies on migration in ungulates, and to broaden the understanding of ecology and evolution of this fascinating behaviour.

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Appendix I. Supplementary Material for Chapter 2

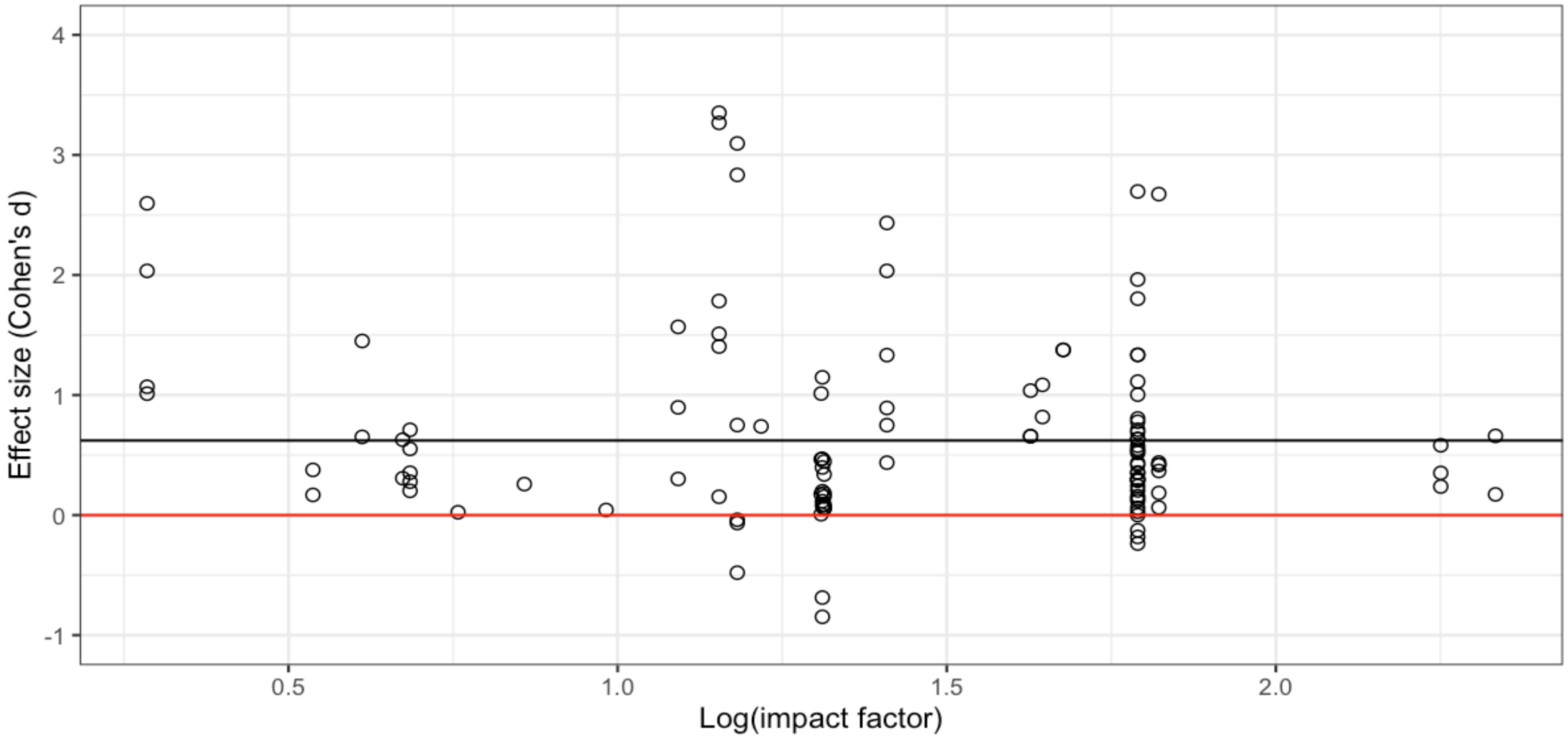

Figure S1.1. Potential bias of journal articles on migration depicted as Cohen’s d as a function of the log of impact factor. Black line mean Cohen’s *d* across studies, and red line is y = 0.

Table S1.1. Full list of articles on migration with exclusions from search criteria. All articles from the initial search were given a unique search ID and only those articles kept after immediate exclusion due to topic relevance were given a full article ID beginning with JN. Articles with a unique article ID were reviewed in full and excluded based on the criterial listed in the methods section of the Chapter 2. NA = not applicable, 0 = excluded 1 = included.

SearchUniqueID	Relevant Topic	FullArticleID	FullArticleKeep	ExclusionCriteria	Author	Title	Journal	Vol	Pages	Year
Able_Rapid 'evo_1998	1	JN1	0	2-Study does assess both migratory and non-migratory group within population	Able, K. P. and J. R. Belthoff	Rapid 'evolution' of migratory behaviour in the introduced house finch of eastern North America.	Proceedings of the Royal Society B-Biological Sciences 265(1410): 2063-2071.	265	2063-2071	1998
Acke_Episodes o_2021	1	JN138	0	4-Study did not apply frequentist statistical approach with effect size	Acker, P; et al.	Episodes of opposing survival and reproductive selection cause strong fluctuating selection on seasonal migration versus residence	PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	288		2021
Acke_Strong sur_2021	0	NA	NA	NA	Acker, P; et al.	Strong survival selection on seasonal migration versus residence induced by extreme climatic events	JOURNAL OF ANIMAL ECOLOGY	90	796-808	2021
Adri_POPULATION _1990	1	JN2	0	2-Study does assess both migratory and non-migratory group within population	Adriaensen, F. and A. A. Dhondt	POPULATION-DYNAMICS AND PARTIAL MIGRATION OF THE EUROPEAN ROBIN (ERITHACUS-RUBECULA) IN DIFFERENT HABITATS.	Journal of Animal Ecology 59(3): 1077-1090.	59	1077-1090	1990
Ahar_Why fly th_2016	0	NA	NA	NA	Aharon-Rotman, Y., et al.	Why fly the extra mile? Using stress biomarkers to assess wintering habitat quality in migratory shorebirds.	Oecologia 182(2): 385-395.	182	385-395	2016
Ahol_Variation _2004	0	NA	NA	NA	Ahola, M., et al.	Variation in climate warming along the migration route uncouples arrival and breeding dates.	Global Change Biology 10(9): 1610-1617.	10	1610-1617	2004
Akes_Bimodal or_1996	1	JN3	0	2-Study does assess both migratory and non-migratory group within population	Akesson, S., et al.	Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in south Scandinavia.	Behavioral Ecology and Sociobiology 38(5): 293-302.	38	293-302	1996

Akes_Wind selec_2000	0	NA	NA	NA	Akesson, S. and A. Hedenstrom	Wind selectivity of migratory flight departures in birds.	Behavioral Ecology and Sociobiology 47(3): 140-144.	47	140-144	2000
Aler_Bird orien_1999	0	NA	NA	NA	Alerstam, T. and G. A. Gudmundsson	Bird orientation at high latitudes: flight routes between Siberia and North America across the Arctic Ocean.	Proceedings of the Royal Society B-Biological Sciences 266(1437): 2499-2505.	266	2499-2505	1999
Alle_Scaling up_2016	1	JN4	0	2-Study does assess both migratory and non-migratory group within population	Allen, A. M., et al.	Scaling up movements: from individual space use to population patterns.	Ecosphere 7(10).	7		2016
Alon_Post-breed_2009	1	JN5	1	NA	Alonso, J. C., et al.	Post-breeding migration in male great bustards: low tolerance of the heaviest Palaearctic bird to summer heat.	Behavioral Ecology and Sociobiology 63(12): 1705-1715.	63	1705-1715	2009
Alva_Integrativ_2014	0	NA	NA	NA	Alvarado, A. H., et al.	Integrative tracking methods elucidate the evolutionary dynamics of a migratory divide.	Ecology and Evolution 4(17): 3456-3469.	4	3456-3469	2014
Alza_Old diverg_2019	0	NA	NA	NA	Alza, L; et al.	Old divergence and restricted gene flow between torrent duck (Merganetta armata) subspecies in the Central and Southern Andes	ECOLOGY AND EVOLUTION	9	9961-9976	2019
Ambr_Migratory_2016	1	JN6	1	NA	Ambrosini, R., et al.	Migratory connectivity and effects of winter temperatures on migratory behaviour of the European robin Erithacus rubecula: a continent-wide analysis.	Journal of Animal Ecology 85(3): 749-760.	85	749-760	2016
Anan_Formation_2020	0	NA	NA	NA	Ananin, AA	Formation and Analysis of Long-Term Series of Bird-Population Observations at Key Sites as Way to Study Biodiversity	CONTEMPORARY PROBLEMS OF ECOLOGY	13	382-390	2020
Andr_Ontogeneti_2020	0	NA	NA	NA	Andrade, H; et al.	Ontogenetic movements of cod in Arctic fjords and the Barents Sea as revealed by otolith microchemistry	POLAR BIOLOGY	43	409-421	2020
Anuf_Long-Term_2011	0	NA	NA	NA	Anufriev, V. V.	Long-Term Dynamics and Demographic Features of the Migration of Alopex lagopus	Contemporary Problems of	4	449-450	2011

						Linneaus in East European Tundras.	Ecology 4(4): 449-450.			
Arch_Associatio_2021	0	NA	NA	NA	Archer, LC; et al.	Associations between metabolic traits and growth rate in brown trout (Salmo trutta) depend on thermal regime	PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	288		2021
Arch_Food and t_2020	0	NA	NA	NA	Archer, LC; et al.	Food and temperature stressors have opposing effects in determining flexible migration decisions in brown trout (Salmo trutta)	GLOBAL CHANGE BIOLOGY	26	2878-2896	2020
Arch_Metabolic_2020	0	NA	NA	NA	Archer, LC; et al.	Metabolic traits in brown trout (Salmo trutta) vary in response to food restriction and intrinsic factors	CONSERVATION PHYSIOLOGY	8		2020
Arch_The Interp_2019	1	JN156	0	2-Study does assess both migratory and non-migratory group within population	Archer, LC; et al.	The Interplay Between Extrinsic and Intrinsic Factors in Determining Migration Decisions in Brown Trout (Salmo trutta): An Experimental Study	FRONTIERS IN ECOLOGY AND EVOLUTION	7		2019
Arna_New insigh_2020	0	NA	NA	NA	Arnaud-Haond, S; Stoeckel, S; Bailleul, D	New insights into the population genetics of partially clonal organisms: When seagrass data meet theoretical expectations	MOLECULAR ECOLOGY	29	3248-3260	2020
Aros_Ontogeneti_2019	1	JN165	0	2-Study does assess both migratory and non-migratory group within population	Arostegui, MC; Quinn, TP	Ontogenetic and ecotypic variation in the coloration and morphology of rainbow trout (Oncorhynchus mykiss) in a stream-lake system	BIOLOGICAL JOURNAL OF THE LINNEAN SOCIETY	128	681-699	2019
Arte_The influe_2013	0	NA	NA	NA	Artemyev, A. V.	The influence of climate change on the ecology of the Pied Flycatcher (Ficedula hypoleuca) in Southern Karelia.	Russian Journal of Ecology 44(3): 239-246.	44	239-246	2013
Arum_Persistenc_2020	0	NA	NA	NA	Arumugam, R; Guichard, F; Lutscher, F	Persistence and extinction dynamics driven by the rate of environmental change in a predator-prey metacommunity	THEORETICAL ECOLOGY	13	629-643	2020
Aust_Otolith mi_2019	0	NA	NA	NA	Austin, CS; et al.	Otolith microchemistry reveals partial migration and life history variation in a facultatively anadromous, iteroparous salmonid, bull	ENVIRONMENTAL BIOLOGY OF FISHES	102	95-104	2019

						trout (Salvelinus confluentus)				
Aust_Scaup migr_2002	0	NA	NA	NA	Austin, J. E., et al.	Scaup migration patterns in North Dakota relative to temperatures and water conditions.	Journal of Wildlife Management 66(3): 874-882.	66	874-882	2002
Baer_Migration-_2016	1	JN7	1	NA	Baerwald, M. R., et al.	Migration-related phenotypic divergence is associated with epigenetic modifications in rainbow trout.	Molecular Ecology 25(8): 1785-1800.	25	1785-1800	2016
Bai,_Mechanisms_2012	1	JN8	1	NA	Bai, M. L., et al.	Mechanisms underlying small-scale partial migration of a subtropical owl.	Behavioral Ecology 23(1): 153-159.	23	153-159	2012
Bail_Modeling i_2013	0	NA	NA	NA	Bailleul, F., et al.	Modeling implications of food resource aggregation on animal migration phenology.	Ecology and Evolution 3(8): 2535-2546.	3	2535-2546	2013
Balb_Individual_2009	0	NA	NA	NA	Balbontin, J., et al.	Individual responses in spring arrival date to ecological conditions during winter and migration in a migratory bird.	Journal of Animal Ecology 78(5): 981-989.	78	981-989	2009
Ball_Partial mi_2001	1	JN9	0	4-Study did not apply frequentist statistical approach with effect size	Ball, J. P., et al.	Partial migration by large ungulates: characteristics of seasonal moose Alces alces ranges in northern Sweden.	Wildlife Biology 7(1): 39-47.	7	39-47	2001
Ball_POPULATION_1991	0	NA	NA	NA	Ballard, W. B., et al.	POPULATION-DYNAMICS OF MOOSE IN SOUTH-CENTRAL ALASKA.	Wildlife Monographs(114): 1-49.		1-49	1991
Ball_Responding_2010	0	NA	NA	NA	Ballard, G., et al.	Responding to climate change: Adelie Penguins confront astronomical and ocean boundaries.	Ecology 91(7): 2056-2069.	91	2056-2069	2010
Bals_Parasite i_2021	0	NA	NA	NA	Balstad, LJ; et al.	Parasite intensity and the evolution of migratory behavior	ECOLOGY	102		2021
Barb_Organic ma_2021	0	NA	NA	NA	Barbaro, L; et al.	Organic management and landscape heterogeneity combine to sustain multifunctional bird communities in European vineyards	JOURNAL OF APPLIED ECOLOGY	58	1261-1271	2021
Bark_Land manag_2019	1	JN142	0	2-Study does assess both migratory and non-migratory group within population	Barker, KJ; et al.	Land management alters traditional nutritional benefits of migration for elk	JOURNAL OF WILDLIFE MANAGEMENT	83	167-174	2019

Bark_Native for_2019	1	JN141	0	4-Study did not apply frequentist statistical approach with effect size	Barker, KJ; Mitchell, MS; Proffitt, KM	Native forage mediates influence of irrigated agriculture on migratory behaviour of elk	JOURNAL OF ANIMAL ECOLOGY	88	1100-1110	2019
Barn_Social and_2013	1	JN10	1	NA	Barnowe-Meyer, K. K., et al.	Social and genetic structure associated with migration in pronghorn.	Biological Conservation 168: 108-115.	168	108-115	2013
Barr_Lifetime m_2021	1	JN164	0	4-Study did not apply frequentist statistical approach with effect size	Barrow, JS; et al.	Lifetime movement history is associated with variable growth of a potamodromous freshwater fish	JOURNAL OF ANIMAL ECOLOGY	90	2560-2572	2021
Barv_Life-histo_2016	1	JN11	0	2-Study does assess both migratory and non-migratory group within population	Barve, S., et al.	Life-history characteristics influence physiological strategies to cope with hypoxia in Himalayan birds.	Proceedings of the Royal Society B-Biological Sciences 283(1843).	283	NA	2016
Basi_Joint seas_2020	0	NA	NA	NA	Basille, M; et al.	Joint seasonality in geographic and ecological spaces, illustrated with a partially migratory bird	ECOSPHERE	11		2020
Bast_Animal mov_2017	1	JN12	0	2-Study does assess both migratory and non-migratory group within population	Bastille-Rousseau, G., et al.	Animal movement in the absence of predation: environmental drivers of movement strategies in a partial migration system.	Oikos 126(7): 1004-1019.	126	1004-1019	2017
Bast_Migration_2019	1	JN166	0	2-Study does assess both migratory and non-migratory group within population	Bastille-Rousseau, G; et al.	Migration triggers in a large herbivore: Galapagos giant tortoises navigating resource gradients on volcanoes	ECOLOGY	100		2019
Batt_Consistent_2006	0	NA	NA	NA	Battley, P. F.	Consistent annual schedules in a migratory shorebird.	Biology Letters 2(4): 517-520.	2	517-520	2006
Bazz_Adcyap1 po_2016	0	NA	NA	NA	Bazzi, G., et al.	Adcyap1 polymorphism covaries with breeding latitude in a Nearctic migratory songbird, the Wilson's warbler (Cardellina pusilla).	Ecology and Evolution 6(10): 3226-3239.	6	3226-3239	2016
Bear_Stable iso_2004	1	JN13	0	2-Study does assess both migratory and non-migratory group within population	Bearhop, S., et al.	Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat.	Proceedings of the Royal Society B-Biological Sciences 271: S215-S218.	271	S215-S218	2004
Bech_Spring hun_2003	0	NA	NA	NA	Bechet, A., et al.	Spring hunting changes the regional movements of migrating greater snow geese.	Journal of Applied Ecology 40(3): 553-564.	40	553-564	2003

Bens_Is the ran_1999	0	NA	NA	NA	Bensch, S.	Is the range size of migratory birds constrained by their migratory program?	Journal of Biogeography 26(6): 1225-1235.	26	1225-1235	1999
Berb_How the in_2012	1	JN14	0	5-Simulation study or systematic review	Berbert, J. M. and W. F. Fagan	How the interplay between individual spatial memory and landscape persistence can generate population distribution patterns.	Ecological Complexity 12: 1-12.	12	12-Jan	2012
Berg_Mothers' M_2021	1	JN131	0	2-Study does assess both migratory and non-migratory group within population	Berg, JE; et al.	Mothers' Movements: Shifts in Calving Area Selection by Partially Migratory Elk	JOURNAL OF WILDLIFE MANAGEMENT	85	1476-1489	2021
Bert_GENETIC-CO_1991	1	JN15	0	5-Simulation study or systematic review	Berthold, P.	GENETIC-CONTROL OF MIGRATORY BEHAVIOR IN BIRDS.	Trends in Ecology & Evolution 6(8): 254-257.	6	254-257	1991
Best_Integrativ_2013	0	NA	NA	NA	Bestley, S., et al.	Integrative modelling of animal movement: incorporating in situ habitat and behavioural information for a migratory marine predator.	Proceedings of the Royal Society B-Biological Sciences 280(1750).	280	NA	2013
Bety_Individual_2004	0	NA	NA	NA	Bety, J., et al.	Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (Anser caerulescens atlanticus).	Behavioral Ecology and Sociobiology 57(1): 1-8.	57	08-Jan	2004
Bhau_Dispersal_2020	0	NA	NA	NA	Bhaumik, V; Kunte, K	Dispersal and migration have contrasting effects on butterfly flight morphology and reproduction	BIOLOGY LETTERS	16		2020
Bish_An empiric_2021	0	NA	NA	NA	Bishop, MA; Bernard, JW	An empirical Bayesian approach to incorporate directional movement information from a forage fish into the Arnason-Schwarz mark-recapture model	MOVEMENT ECOLOGY	9		2021
Blak_Vegetation_2013	1	JN16	0	2-Study does assess both migratory and non-migratory group within population	Blake, S., et al.	Vegetation dynamics drive segregation by body size in Galapagos tortoises migrating across altitudinal gradients.	Journal of Animal Ecology 82(2): 310-321.	82	310-321	2013
Boel_Extreme sp_2017	0	NA	NA	NA	Boelman, N. T., et al.	Extreme spring conditions in the Arctic delay spring phenology of long-distance migratory songbirds.	Oecologia 185(1): 69-80.	185	69-80	2017

Bold_The Distri_2020	0	NA	NA	NA	Boldyrev, VS	The Distribution of Vimba Bream Vimba vimbavimba (Actinopterygii: Cyprinidae) in the Unregulated Section of the Lower Volga River	RUSSIAN JOURNAL OF BIOLOGICAL INVASIONS	11	301-309	2020
Bolu_Phylogeogr_2021	0	NA	NA	NA	Boluda, CG; et al.	Phylogeographic reconstructions can be biased by ancestral shared alleles: The case of the polymorphic lichen Bryoria fuscescens in Europe and North Africa	MOLECULAR ECOLOGY	30	4845-4865	2021
Bond_Beyond dic_2015	1	JN17	0	2-Study does assess both migratory and non-migratory group within population	Bond, M. H., et al.	Beyond dichotomous life histories in partially migrating populations: cessation of anadromy in a long-lived fish.	Ecology 96(7): 1899-1910.	96	1899-1910	2015
Bonn_Effects of_2020	1	JN139	1	NA	Bonnet-Lebrun, AS; Manica, A; Rodrigues, ASL	Effects of urbanization on bird migration	BIOLOGICAL CONSERVATION	244		2020
Bopp_Telemetry_2021	1	JN151	0	2-Study does assess both migratory and non-migratory group within population	Bopp, JJ; et al.	Telemetry reveals migratory drivers and disparate space use across seasons and age-groups in American horseshoe crabs	ECOSPHERE	12		2021
Borg_Diet of th_2019	0	NA	NA	NA	Borghello, P; et al.	Diet of the Brown Skua (Stercorarius antarcticus lonnbergi) at Hope Bay, Antarctic Peninsula: differences between breeders and non-breeders	POLAR BIOLOGY	42	385-394	2019
Boro_Annual mov_2021	1	JN173	0	4-Study did not apply frequentist statistical approach with effect size	Borowik, T; et al.	Annual movement strategy predicts within-season space use by moose	BEHAVIORAL ECOLOGY AND SOCIOBIOLOGY	75		2021
Boss_Gene expre_2016	0	NA	NA	NA	Boss, J., et al.	Gene expression in the brain of a migratory songbird during breeding and migration.	Movement Ecology 4.	4	NA	2016
Boul_Spatial gr_2020	0	NA	NA	NA	Boulanger, E; et al.	Spatial graphs highlight how multi-generational dispersal shapes landscape genetic patterns	ECOGRAPHY	43	1167-1179	2020
Boyl_Lekking bi_2011	1	JN21	0	2-Study does assess both migratory and non-migratory group within population	Boyle, W. A., et al.	Lekking birds in a tropical forest forego sex for migration.	Biology Letters 7(5): 661-663.	7	661-663	2011
Boyl_Partial mi_2008	1	JN18	0	4-Study did not apply frequentist statistical approach with effect size	Boyle, W. A.	Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore.	Journal of Animal Ecology 77(6): 1122-1128.	77	1122-1128	2008

Boyl_Short-dist_2011	1	JN19	0	2-Study does assess both migratory and non-migratory group within population	Boyle, W. A.	Short-distance partial migration of Neotropical birds: a community-level test of the foraging limitation hypothesis.	Oikos 120(12): 1803-1816.	120	1803-1816	2011
Boyl_Storms dri_2010	1	JN22	0	2-Study does assess both migratory and non-migratory group within population	Boyle, W. A., et al.	Storms drive altitudinal migration in a tropical bird.	Proceedings of the Royal Society B-Biological Sciences 277(1693): 2511-2519.	277	2511-2519	2010
Boyl_Why migrat_2007	1	JN20	0	2-Study does assess both migratory and non-migratory group within population	Boyle, W. A. and C. J. Conway	Why migrate? A test of the evolutionary precursor hypothesis.	American Naturalist 169(3): 344-359.	169	344-359	2007
Brac_Revisitati_2018	0	NA	NA	NA	Bracis, C; Bildstein, KL; Mueller, T	Revisitation analysis uncovers spatio-temporal patterns in animal movement data	ECOGRAPHY	41	1801-1811	2018
Brav_Fish passa_2021	0	NA	NA	NA	Bravo-Cordoba, FJ; et al.	Fish passage assessment in stepped fishways: Passage success and transit time as standardized metrics	ECOLOGICAL ENGINEERING	162		2021
Brav_Vertical s_2018	0	NA	NA	NA	Bravo-Cordoba, FJ; et al.	Vertical slot versus submerged notch with bottom orifice: Looking for the best technical fishway type for Mediterranean barbels	ECOLOGICAL ENGINEERING	122	120-125	2018
Brew_Perceived_2020	0	NA	NA	NA	Brewer, DE; McGill, CA; Fudickar, AM	Perceived wintering latitude determines timing of song output in a migratory bird	ECOLOGY AND EVOLUTION	10	748-755	2020
Brie_Cold spell_2017	0	NA	NA	NA	Briedis, M., et al.	Cold spell en route delays spring arrival and decreases apparent survival in a long-distance migratory songbird.	Bmc Ecology 17.	17	NA	2017
Brie_Integratio_2015	0	NA	NA	NA	Brieuc, M. S. O., et al.	Integration of Random Forest with population-based outlier analyses provides insight on the genomic basis and evolution of run timing in Chinook salmon (Oncorhynchus tshawytscha).	Molecular Ecology 24(11): 2729-2746.	24	2729-2746	2015
Brig_Demographi_2004	0	NA	NA	NA	Briggler, J. T., et al.	Demographics of a ringed salamander (Ambystoma annulatum) breeding migration.	Southwestern Naturalist 49(2): 209-217.	49	209-217	2004

Brin_Movemento_2005	1	JN23	0	2-Study does assess both migratory and non-migratory group within population	Brinkman, T. J., et al.	Movement of female white-tailed deer: Effects of climate and intensive row-crop agriculture.	Journal of Wildlife Management 69(3): 1099-1111.	69	1099-1111	2005
Brod_Condition-_2008	1	JN24	1	NA	Brodersen, J., et al.	Condition-dependent individual decision-making determines cyprinid partial migration.	Ecology 89(5): 1195-1200.	89	1195-1200	2008
Brod_Interplay_2011	1	JN25	0	2-Study does assess both migratory and non-migratory group within population	Brodersen, J., et al.	Interplay between temperature, fish partial migration and trophic dynamics.	Oikos 120(12): 1838-1846.	120	1838-1846	2011
Brow_Male-Biase_2020	1	JN130	0	2-Study does assess both migratory and non-migratory group within population	Brown, MB; Bolger, DT	Male-Biased Partial Migration in a Giraffe Population	FRONTIERS IN ECOLOGY AND EVOLUTION	7		2020
Brow_MOVEMENTA_1992	0	NA	NA	NA	Brown, C. G.	MOVEMENT AND MIGRATION PATTERNS OF MULE DEER IN SOUTHEASTERN IDAHO.	Journal of Wildlife Management 56(2): 246-253.	56	246-253	1992
Brya_Home range_2019	0	NA	NA	NA	Bryan, DR; et al.	Home range and spawning migration patterns of queen triggerfish Balistes vetula in St. Croix, US Virgin Islands	MARINE ECOLOGY PROGRESS SERIES	616	123-139	2019
Brya_Seasonalm_2021	0	NA	NA	NA	Bryan, DR; et al.	Seasonal migratory patterns of Pacific cod (Gadus macrocephalus) in the Aleutian Islands	ANIMAL BIOTELEMETRY	9		2021
Bunn_A model-dr_2011	0	NA	NA	NA	Bunnefeld, N., et al.	A model-driven approach to quantify migration patterns: individual, regional and yearly differences.	Journal of Animal Ecology 80(2): 466-476.	80	466-476	2011
Burn_Migratory_2020	0	NA	NA	NA	Burns, MD; Bloom, DD	Migratory lineages rapidly evolve larger body sizes than non-migratory relatives in ray-finned fishes	PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	287		2020
Cada_Advancemen_2017	0	NA	NA	NA	Cadahia, L., et al.	Advancement of spring arrival in a long-term study of a passerine bird: sex, age and environmental effects.	Oecologia 184(4): 917-929.	184	917-929	2017
Cagn_Partial mi_2011	1	JN26	1	NA	Cagnacci, F., et al.	Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors.	Oikos 120(12): 1790-1802.	120	1790-1802	2011

Camp_Assessing_2022	0	NA	NA	NA	Campo-Celada, M; et al.	Assessing short and long-term variations in diversity, timing and body condition of frugivorous birds	OIKOS			2022
Cand_Size-depen_2003	0	NA	NA	NA	Candolin, U. and H. R. Voigt	Size-dependent selection on arrival times in sticklebacks: Why small males arrive first.	Evolution 57(4): 862-871.	57	862-871	2003
Capo_Hypatia-tr_2019	0	NA	NA	NA	Capotosti, S; et al.	Hypatia-trackRadar: A software for animal tracking using marine surveillance radars	ECOLOGICAL INFORMATICS	53		2019
Care_Egg retent_2021	0	NA	NA	NA	Carey, MP; et al.	Egg retention of high-latitude sockeye salmon (Oncorhynchus nerka) in the Pilgrim River, Alaska, during the Pacific marine heatwave of 2014-2016	POLAR BIOLOGY	44	1643-1654	2021
Carn_Consistenc_2016	0	NA	NA	NA	Carneiro, A. P. B., et al.	Consistency in migration strategies and habitat preferences of brown skuas over two winters, a decade apart.	Marine Ecology Progress Series 553: 267-281.	553	267-281	2016
Caro_Sex steroi_2019	0	NA	NA	NA	Carone, E; et al.	Sex steroid hormones and behavior reveal seasonal reproduction in a resident fin whale population	CONSERVATION PHYSIOLOGY	7		2019
Carr_Genetic Di_2020	0	NA	NA	NA	Carroll, EL; et al.	Genetic Diversity and Connectivity of Southern Right Whales (Eubalaena australis) Found in the Brazil and Chile-Peru Wintering Grounds and the South Georgia (Islas Georgias del Sur) Feeding Ground	JOURNAL OF HEREDITY	111	263-276	2020
Cast_Spatio-Tem_2019	0	NA	NA	NA	Castaneda, S; et al.	Spatio-Temporal Distribution of Monarch Butterflies Along Their Migratory Route	FRONTIERS IN ECOLOGY AND EVOLUTION	7		2019
Catr_Carry-over_2013	1	JN27	0	2-Study does assess both migratory and non-migratory group within population	Catry, P., et al.	Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration.	Ecology 94(6): 1230-1235.	94	1230-1235	2013
Cava_Temporals_2020	0	NA	NA	NA	Cavalcante, G; et al.	Temporal streamflow reduction and impact on the salt dynamics of the Sao Francisco River Estuary	REGIONAL STUDIES IN MARINE SCIENCE	38		2020

						and adjacent coastal zone (NE/Brazil)				
Cave_Genomics,_2019	1	JN169	1	NA	Cavedon, M; et al.	Genomics, environment and balancing selection in behaviourally bimodal populations: The caribou case	MOLECULAR ECOLOGY	28	1946-1963	2019
Chai_Evolutiona_2019	0	NA	NA	NA	Chaintoutis, SC; et al.	Evolutionary dynamics of lineage 2 West Nile virus in Europe, 2004-2018: Phylogeny, selection pressure and phylogeography	MOLECULAR PHYLOGENETICS AND EVOLUTION	141		2019
Chal_The global_2019	0	NA	NA	NA	Chalant, A; et al.	The global geography of fish diadromy modes	GLOBAL ECOLOGY AND BIOGEOGRAPHY	28	1272-1282	2019
Cham_Australian_2010	0	NA	NA	NA	Chambers, L. E. and M. R. Keatley	Australian bird phenology: a search for climate signals.	Austral Ecology 35(8): 969-979.	35	969-979	2010
Chap_Density-de_2020	0	NA	NA	NA	Chaparro-Pedraza, PC; de Roos, AM	Density-dependent effects of mortality on the optimal body size to shift habitat: Why smaller is better despite increased mortality risk	EVOLUTION	74	831-841	2020
Chap_Latitudina_2019	1	JN175	0	2-Study does assess both migratory and non-migratory group within population	Chapa-Vargas, L; et al.	Latitudinal effects of anthropogenic factors driving raptor species richness across the American continent	JOURNAL OF BIOGEOGRAPHY	46	1948-1958	2019
Chap_Shape up o_2015	1	JN28	1	NA	Chapman, B. B., et al.	Shape up or ship out: migratory behaviour predicts morphology across spatial scale in a freshwater fish.	Journal of Animal Ecology 84(5): 1187-1193.	84	1187-1193	2015
Chap_To boldly _2011	1	JN29	1	NA	Chapman, B. B., et al.	To boldly go: individual differences in boldness influence migratory tendency.	Ecology Letters 14(9): 871-876.	14	871-876	2011
Char_Assisted s_2021	0	NA	NA	NA	Charles, KM; Stehlik, I	Assisted species migration and hybridization to conserve cold-adapted plants under climate change	CONSERVATION BIOLOGY	35	559-566	2021
Chen_DNA barcod_2021	0	NA	NA	NA	Chen, WT; et al.	DNA barcoding reveals the temporal community composition of drifting fish eggs in the lower Hongshui River, China	ECOLOGY AND EVOLUTION	11	11507-11514	2021

Cher_Habitat-me_2016	0	NA	NA	NA	Cherry, S. G., et al.	Habitat-mediated timing of migration in polar bears: an individual perspective.	Ecology and Evolution 6(14): 5032-5042.	6	5032-5042	2016
Cher_Migration _2013	0	NA	NA	NA	Cherry, S. G., et al.	Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics.	Journal of Animal Ecology 82(4): 912-921.	82	912-921	2013
Cher_Reproducti_2020	0	NA	NA	NA	Chero, G; et al.	Reproductive capacity of an endangered and recovering population of humpback whales in the Southern Hemisphere	MARINE ECOLOGY PROGRESS SERIES	643	219-227	2020
Chev_Influence _2010	0	NA	NA	NA	Chevallier, D., et al.	Influence of weather conditions on the flight of migrating black storks.	Proceedings of the Royal Society B-Biological Sciences 277(1695): 2755-2764.	277	2755-2764	2010
Clar_Generalize_2021	0	NA	NA	NA	Clare, JDJ; Townsend, PA; Zuckerberg, B	Generalized model-based solutions to false-positive error in species detection/nondetection data	ECOLOGY	102		2021
Clau_Earlier Ar_2013	0	NA	NA	NA	Clausen, K. K. and P. Clausen	Earlier Arctic springs cause phenological mismatch in long-distance migrants.	Oecologia 173(3): 1101-1112.	173	1101-1112	2013
Clau_Highly dyn_2018	0	NA	NA	NA	Clausen, K. K., et al.	Highly dynamic wintering strategies in migratory geese: Coping with environmental change.	Global Change Biology 24(7): 3214-3225.	24	3214-3225	2018
Clev_Aggregatio_2021	0	NA	NA	NA	Clevenstine, AJ; Lowe, CG	Aggregation site fidelity and movement patterns of the protected marine predator giant sea bass (Stereolepis gigas)	ENVIRONMENTAL BIOLOGY OF FISHES	104	401-417	2021
Colb_Groups of _2013	0	NA	NA	NA	Colbeck, G. J., et al.	Groups of related belugas (Delphinapterus leucas) travel together during their seasonal migrations in and around Hudson Bay.	Proceedings of the Royal Society B-Biological Sciences 280(1752).	280	NA	2013
Coll_Migration _2009	1	JN30	0	2-Study does assess both migratory and non-migratory group within population	Collins, S. A., et al.	Migration strategy and divergent sexual selection on bird song.	Proceedings of the Royal Society B-Biological Sciences 276(1656): 585-590.	276	585-590	2009

Coll_SEASONAL D_2016	0	NA	NA	NA	Collins, G. H.	SEASONAL DISTRIBUTION AND ROUTES OF PRONGHORN IN THE NORTHERN GREAT BASIN.	Western North American Naturalist 76(1): 101-112.	76	101-112	2016
Conk_Impacts of_2011	0	NA	NA	NA	Conklin, J. R. and P. F. Battley	Impacts of wind on individual migration schedules of New Zealand bar-tailed godwits.	Behavioral Ecology 22(4): 854-861.	22	854-861	2011
Conr_Carryover _2015	1	JN31	0	2-Study does assess both migratory and non-migratory group within population	Conroy, C. W., et al.	Carryover effects of early growth and river flow on partial migration in striped bass Morone saxatilis.	Marine Ecology Progress Series 541: 179-194.	541	179-194	2015
Cook_Physiologi_2 008	0	NA	NA	NA	Cooke, S. J., et al.	Physiological correlates of coastal arrival and river entry timing in late summer Fraser River sockeye salmon (Oncorhynchus nerka).	Behavioral Ecology 19(4): 747-758.	19	747-758	2008
Coop_Experiment_ 2015	0	NA	NA	NA	Cooper, N. W., et al.	Experimental reduction of winter food decreases body condition and delays migration in a long-distance migratory bird.	Ecology 96(7): 1933-1942.	96	1933-1942	2015
Corm_The nature_2014	0	NA	NA	NA	Corman, A. M., et al.	The nature of the migration route shapes physiological traits and aerodynamic properties in a migratory songbird.	Behavioral Ecology and Sociobiology 68(3): 391-402.	68	391-402	2014
Corn_Seasonal P_2021	0	NA	NA	NA	Cornelius, JM; et al.	Seasonal Patterns of Fat Deposits in Relation to Migratory Strategy in Facultative Migrants	FRONTIERS IN ECOLOGY AND EVOLUTION	9		2021
Cost_Razorbill _2019	0	NA	NA	NA	Costa, RA; et al.	Razorbill Alca torda mortality in the Portuguese west coast	EUROPEAN JOURNAL OF WILDLIFE RESEARCH	65		2019
Coul_Climatic N_2020	0	NA	NA	NA	Coulleri, JP; et al.	Climatic Niche Dynamics of Three Widespread Cardiospermum (Paullinieae, Sapindaceae) Species Revealed Possible Dispersal Pathways	SYSTEMATIC BOTANY	45	879-890	2020
Cour_Truly sede_2018	1	JN32	0	2-Study does assess both migratory and non-migratory group within population	Couriot, O., et al.	Truly sedentary? The multi-range tactic as a response to resource heterogeneity and unpredictability in a large herbivore.	Oecologia 187(1): 47-60.	187	47-60	2018

Cout_Body Size _2010	1	JN33	0	2-Study does assess both migratory and non-migratory group within population	Couturier, S., et al.	Body Size Variations in Caribou Ecotypes and Relationships With Demography.	Journal of Wildlife Management 74(3): 395-404.	74	395-404	2010
Covi_Spring mig_2020	0	NA	NA	NA	Covino, KM; et al.	Spring migration of Blackpoll Warblers across North America	AVIAN CONSERVATION AND ECOLOGY	15		2020
Croo_Environmen_2014	1	JN34	0	2-Study does assess both migratory and non-migratory group within population	Crook, D. A., et al.	Environmental cues and extended estuarine residence in seaward migrating eels (Anguilla australis).	Freshwater Biology 59(8): 1710-1720.	59	1710-1720	2014
Crys_Differenti_2016	0	NA	NA	NA	Crysler, Z. J., et al.	Differential fall migratory routes of adult and juvenile Ipswich Sparrows (Passerculus sandwichensis princeps).	Movement Ecology 4.	4	NA	2016
Cui,_The Pangea_2019	0	NA	NA	NA	Cui, YY; Ren, D; Bethoux, O	The Pangean journey of 'south forestflies' (Insecta: Plecoptera) revealed by their first fossils	JOURNAL OF SYSTEMATIC PALAEONTOLOGY	17	255-268	2019
Cusc_Inter-indi_2018	0	NA	NA	NA	Cusco, F; et al.	Inter-individual consistency in habitat selection patterns and spatial range constraints of female little bustards during the non-breeding season	BMC ECOLOGY	18		2018
Dall_Higher fli_2018	1	JN35	0	4-Study did not apply frequentist statistical approach with effect size	Dallenbach, L. J., et al.	Higher flight activity in the offspring of migrants compared to residents in a migratory insect.	Proceedings of the Royal Society B-Biological Sciences 285(1881).	285		2018
Dall_Lack of ge_2003	0	NA	NA	NA	Dallimer, M., et al.	Lack of genetic and plumage differentiation in the red-billed quelea Quelea quelea across a migratory divide in southern Africa.	Molecular Ecology 12(2): 345-353.	12	345-353	2003
Dani_ECOLOGY OF_1994	0	NA	NA	NA	Danilkin, A. A., et al.	ECOLOGY OF MIGRATING POPULATIONS OF SIBERIAN ROE DEER.	Russian Journal of Ecology 25(6): 452-458.	25	452-458	1994
Davi_Variable p_2020	0	NA	NA	NA	Davis, MJ; et al.	Variable prey consumption leads to distinct regional differences in Chinook salmon growth during the early marine critical period	MARINE ECOLOGY PROGRESS SERIES	640	147-169	2020
De C_Annelid po_2019	0	NA	NA	NA	De Cubber, L; et al.	Annelid polychaetes experience metabolic acceleration as other	ECOLOGICAL MODELLING	411		2019

						Lophotrochozoans: Inferences on the life cycle of Arenicola marina with a Dynamic Energy Budget model				
de l_Migratory _2009	1	JN36	0	4-Study did not apply frequentist statistical approach with effect size	de la Hera, I., et al.	Migratory behaviour affects the trade-off between feather growth rate and feather quality in a passerine bird.	Biological Journal of the Linnean Society 97(1): 98-105.	97	98-105	2009
De P_Searching _2021	0	NA	NA	NA	De Pascalis, F; et al.	Searching on the edge: dynamic oceanographic features increase foraging opportunities in a small pelagic seabird	MARINE ECOLOGY PROGRESS SERIES	668	121-132	2021
de Z_How migrat_2020	0	NA	NA	NA	de Zoeten, T; Pulido, F	How migratory populations become resident	PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	287		2020
Deak_Sex differ_2019	0	NA	NA	NA	Deakin, Z; et al.	Sex differences in migration and demography of a wide-ranging seabird, the northern gannet	MARINE ECOLOGY PROGRESS SERIES	622	191-201	2019
Debe_Genetic gr_2020	1	JN155	0	4-Study did not apply frequentist statistical approach with effect size	Debes, PV; et al.	Genetic growth potential, rather than phenotypic size, predicts migration phenotype in Atlantic salmon	PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	287		2020
Debe_Implicatio_2017	1	JN37	0	4-Study did not apply frequentist statistical approach with effect size	Debeffe, L., et al.	Implications of the forage maturation hypothesis for activity of partially migratory male and female deer.	Ecosphere 8(12).	8		2017
Dech_Determinan _2017	0	NA	NA	NA	Dechmann, D. K. N., et al.	Determinants of spring migration departure decision in a bat.	Biology Letters 13(9).	13	NA	2017
Deck_Predicting_2021	0	NA	NA	NA	Decker, C; et al.	Predicting uptake of a malignant catarrhal fever vaccine by pastoralists in northern Tanzania: Opportunities for improving livelihoods and ecosystem health	ECOLOGICAL ECONOMICS	190		2021
Delh_Partial or_2020	0	NA	NA	NA	Delhey, K; et al.	Partial or complete? The evolution of post-juvenile moult strategies in passerine birds	JOURNAL OF ANIMAL ECOLOGY	89	2896-2908	2020

Dell_Molecular_2019	0	NA	NA	NA	Della Rocca, G; et al.	Molecular analyses indicate that both native and exotic pathogen populations serve as sources of novel outbreaks of Cypress Canker Disease	BIOLOGICAL INVASIONS	21	2919-2932	2019
Delm_Hybridson_2014	0	NA	NA	NA	Delmore, K. E. and D. E. Irwin	Hybrid songbirds employ intermediate routes in a migratory divide.	Ecology Letters 17(10): 1211-1218.	17	1211-1218	2014
Derk_Avianpara_2021	0	NA	NA	NA	Derko, AA; et al.	Avian paramyxovirus 4 isolated from the mallard (Anas platyrhynchos, Linnaeus, 1758): the first case detected in the Western Caspian region	SOUTH OF RUSSIA-ECOLOGY DEVELOPMENT	16	81-87	2021
Desp_Linkingoc_2018	0	NA	NA	NA	Desprez, M., et al.	Linking oceanographic conditions, migratory schedules and foraging behaviour during the non-breeding season to reproductive performance in a long-lived seabird.	Functional Ecology 32(8): 2040-2053.	32	2040-2053	2018
Deut_Seasonalm_2003	0	NA	NA	NA	Deutsch, C. J., et al.	Seasonal movements, migratory behavior, and site fidelity of West Indian manatees along the Atlantic Coast of the United States.	Wildlife Monographs(151): 1-77.	NA	1-77	2003
Dias_Habitatus_2020	0	NA	NA	NA	Dias, E; et al.	Habitat use and food sources of European flounder larvae (Platichthys flesus, L. 1758) across the Minho River estuary salinity gradient (NW Iberian Peninsula)	REGIONAL STUDIES IN MARINE SCIENCE	34		2020
Dier_Stopoverb_2001	0	NA	NA	NA	Dierschke, V. and J. Delingat	Stopover behaviour and departure decision of northern wheatears, Oenanthe oenanthe, facing different onward non-stop flight distances.	Behavioral Ecology and Sociobiology 50(6): 535-545.	50	535-545	2001
Dixo_Cost of fl_1999	0	NA	NA	NA	Dixon, A. F. G. and P. Kindlmann	Cost of flight apparatus and optimum body size of aphid migrants.	Ecology 80(5): 1678-1690.	80	1678-1690	1999
Dosw_Potential_2009	1	JN38	0	2-Study does assess both migratory and non-migratory group within population	Doswald, N., et al.	Potential impacts of climatic change on the breeding and non-breeding ranges and	Journal of Biogeography 36(6): 1194-1208.	36	1194-1208	2009

						migration distance of European Sylvia warblers.				
Drak_Winter hab_2014	0	NA	NA	NA	Drake, A., et al.	Winter habitat use does not influence spring arrival dates or the reproductive success of Yellow Warblers breeding in the arctic.	Polar Biology 37(2): 181-191.	37	181-191	2014
Dren_Pay-offs a_2003	0	NA	NA	NA	Drent, R., et al.	Pay-offs and penalties of competing migratory schedules.	Oikos 103(2): 274-292.	103	274-292	2003
Duij_Body condi_2017	0	NA	NA	NA	Duijns, S., et al.	Body condition explains migratory performance of a long-distance migrant.	Proceedings of the Royal Society B-Biological Sciences 284(1866).	284	NA	2017
Dunl_Seasonal m_2021	1	JN174	0	2-Study does assess both migratory and non-migratory group within population	Dunlop, JN; Greenwell, CN	Seasonal movements and metapopulation structure of the Australian fairy tern in Western Australia	PACIFIC CONSERVATIO N BIOLOGY	27	47-60	2021
Dunn_Changes in_2014	0	NA	NA	NA	Dunn, P. O. and A. P. Moller	Changes in breeding phenology and population size of birds.	Journal of Animal Ecology 83(3): 729-739.	83	729-739	2014
Dur,_An individ_2021	0	NA	NA	NA	Dur, G; et al.	An individual-based model for evaluating post-exposure effects of UV-B radiation on zooplankton reproduction	ECOLOGICAL MODELLING	441		2021
Duri_What decis_2009	0	NA	NA	NA	Duriez, O., et al.	What decision rules might pink-footed geese use to depart on migration? An individual-based model.	Behavioral Ecology 20(3): 560-569.	20	560-569	2009
Dutr_Haemospori_2021	1	JN158	0	2-Study does assess both migratory and non-migratory group within population	Dutra, DD; Fecchio, A; Braga, EM; Poulin, R	Haemosporidian taxonomic composition, network centrality and partner fidelity between resident and migratory avian hosts	OECOLOGIA	197	501-509	2021
Duva_Long-term _2021	0	NA	NA	NA	Duval, E; Skaala, O; Quintela, M; Dahle, G; Delaval, A; Wennevik, V; Glover, KA; Hansen, MM	Long-term monitoring of a brown trout (Salmo trutta) population reveals kin-associated migration patterns and contributions by resident trout to the anadromous run	BMC ECOLOGY AND EVOLUTION	21		2021
Egge_Behavioura_2016	1	JN39	1	NA	Eggeman, S. L., et al.	Behavioural flexibility in migratory behaviour in a long-lived large herbivore.	Journal of Animal Ecology 85(3): 785-797.	85	785-797	2016

Eich_Restingme_2019	1	JN150	0	4-Study did not apply frequentist statistical approach with effect size	Eichhorn, G; Enstipp, MR; Georges, JY; Hasselquist, D; Nolet, BA	Resting metabolic rate in migratory and non-migratory geese following range expansion: go south, go low	OIKOS	128	1424-1434	2019
Eike_A hidden c_2018	1	JN40	0	4-Study did not apply frequentist statistical approach with effect size	Eikenaar, C., et al.	A hidden cost of migration? Innate immune function versus antioxidant defense.	Ecology and Evolution 8(5): 2721-2728.	8	2721-2728	2018
Eike_Migratory_2016	0	NA	NA	NA	Eikenaar, C. and A. Hegemann	Migratory common blackbirds have lower innate immune function during autumn migration than resident conspecifics.	Biology Letters 12(3).	12	NA	2016
Eina_Deep-divin_2018	0	NA	NA	NA	Einarsson, SM; Gudjonsson, S; Jonsson, IR; Gudbrandsson, J	Deep-diving of Atlantic salmon (Salmo salar) during their marine feeding migrations	ENVIRONMENTAL BIOLOGY OF FISHES	101	1707-1715	2018
Elli_Impacts of_2021	0	NA	NA	NA	Ellis, KS; et al.	Impacts of extreme environmental disturbances on piping plover survival are partially moderated by migratory connectivity	BIOLOGICAL CONSERVATION	264		2021
Ely,_Geographic_2013	0	NA	NA	NA	Ely, C. R., et al.	Geographic Variation in Migration Chronology and Winter Distribution of Midcontinent Greater White-Fronted Geese.	Journal of Wildlife Management 77(6): 1182-1191.	77	1182-1191	2013
Emme_Individual_2014	0	NA	NA	NA	Emmenegger, T., et al.	Individual migration timing of common nightingales is tuned with vegetation and prey phenology at breeding sites.	Bmc Ecology 14.	14	NA	2014
Esca_Revised sp_2021	0	NA	NA	NA	Escanez, A; Guerra, A; Riera, R; Rocha, FJ	Revised species records reveal the Canary Islands as a cephalopod biodiversity hotspot	REGIONAL STUDIES IN MARINE SCIENCE	41		2021
Ever_Speciation_2019	0	NA	NA	NA	Everson, KM; McLaughlin, JF; Cato, IA; Evans, MM; Gastaldi, AR; Mills, KK; Shink, KG; Wilbur, SM; Winker, K	Speciation, gene flow, and seasonal migration in Catharsis thrushes (Aves:Turdidae)	MOLECULAR PHYLOGENETICS AND EVOLUTION	139		2019
Faga_Leadership_2012	1	JN41	0	5-Simulation study or systematic review	Fagan, W. F., et al.	Leadership, social learning, and the maintenance (or collapse) of migratory populations.	Theoretical Ecology 5(2): 253-264.	5	253-264	2012

Fand_Seasonal n_2020	0	NA	NA	NA	Fandos, G; Rotics, S; Sapir, N; Fiedler, W; Kaatz, M; Wikelski, M; Nathan, R; Zurell, D	Seasonal niche tracking of climate emerges at the population level in a migratory bird	PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	287		2020
Fang_Worldwide _2018	0	NA	NA	NA	Fang, BH; Merila, J; Ribeiro, F; Alexandre, CM; Momigliano, P	Worldwide phylogeny of three-spined sticklebacks	MOLECULAR PHYLOGENETICS AND EVOLUTION	127	613-625	2018
Farl_Influence _2022	0	NA	NA	NA	Farley, EB; Schummer, ML; Leopold, DJ; Coluccy, JM; Tozer, DC	Influence of water level management on vegetation and bird use of restored wetlands in the Montezuma Wetlands Complex	WILDLIFE BIOLOGY			2022
Fauc_Density-de_2006	0	NA	NA	NA	Fauchald, P., et al.	Density-dependent migratory waves in the marine pelagic ecosystem.	Ecology 87(11): 2915-2924.	87	2915-2924	2006
Faye_Drivers an_2016	0	NA	NA	NA	Fayet, A. L., et al.	Drivers and fitness consequences of dispersive migration in a pelagic seabird.	Behavioral Ecology 27(4): 1061-1072.	27	1061-1072	2016
Fern_rWind: dow_2019	0	NA	NA	NA	Fernandez-Lopez, J; Schliep, K	rWind: download, edit and include wind data in ecological and evolutionary analysis	ECOGRAPHY	42	804-810	2019
Feut_Evolution _2013	1	JN42	0	2-Study does assess both migratory and non-migratory group within population	Feutry, P., et al.	Evolution of Diadromy in Fish: Insights from a Tropical Genus (Kuhlia Species).	American Naturalist 181(1): 52-63.	181	52-63	2013
Fieb_A hidden M_2014	1	JN43	0	2-Study does assess both migratory and non-migratory group within population	Fieberg, J. R. and P. B. Conn	A hidden Markov model to identify and adjust for selection bias: an example involving mixed migration strategies.	Ecology and Evolution 4(10): 1903-1912.	4	1903-1912	2014
Figu_Haematozoa_ 2000	1	JN44	0	2-Study does assess both migratory and non-migratory group within population	Figuerola, J. and A. J. Green	Haematozoan parasites and migratory behaviour in waterfowl.	Evolutionary Ecology 14(2): 143-153.	14	143-153	2000
Fing_Environmen_ 2016	0	NA	NA	NA	Finger, T. A., et al.	Environmental Factors Influence Lesser Scaup Migration Chronology and Population Monitoring.	Journal of Wildlife Management 80(8): 1437-1449.	80	1437-1449	2016
Fins_Migrate or_2012	1	JN45	0	2-Study does assess both migratory and non-migratory group within population	Finstad, A. G. and C. L. Hein	Migrate or stay: terrestrial primary productivity and climate drive anadromy in Arctic char.	Global Change Biology 18(8): 2487-2497.	18	2487-2497	2012

Flem_A latent p_2020	0	NA	NA	NA	Fleming, J; Sutherland, C; Sterrett, SC; Grant, EHC	A latent process model approach to improve the utility of indicator species	OIKOS	129	1753-1762	2020
Fokk_Ontogeneti_2020	1	JN148	0	5-Simulation study or systematic review	Fokkema, W; van der Jeugd, HP; Lameris, TK; Dokter, AM; Ebbinge, BS; de Roos, AM; Nolet, BA; Piersma, T; Olff, H	Ontogenetic niche shifts as a driver of seasonal migration	OECOLOGIA	193	285-297	2020
Forc_North Atla_2002	0	NA	NA	NA	Forchhammer, M. C., et al.	North Atlantic Oscillation timing of long- and short-distance migration.	Journal of Animal Ecology 71(6): 1002-1014.	71	1002-1014	2002
Fors_Juvenile m_1999	0	NA	NA	NA	Forseth, T., et al.	Juvenile migration in brown trout: a consequence of energetic state.	Journal of Animal Ecology 68(4): 783-793.	68	783-793	1999
Fort_Seasonal d_2020	0	NA	NA	NA	Fortune, SME; Ferguson, SH; Trites, AW; LeBlanc, B; LeMay, V; Hudson, JM; Baumgartner, MF	Seasonal diving and foraging behaviour of Eastern Canada-West Greenland bowhead whales	MARINE ECOLOGY PROGRESS SERIES	643	197-217	2020
Fran_Animal tra_2017	1	JN46	1	NA	Franchini, P., et al.	Animal tracking meets migration genomics: transcriptomic analysis of a partially migratory bird species.	Molecular Ecology 26(12): 3204-3216.	26	3204-3216	2017
Fray_Demographi_2021	0	NA	NA	NA	Frayer, ME; Payseur, BA	Demographic history shapes genomic ancestry in hybrid zones	ECOLOGY AND EVOLUTION	11	10290-10302	2021
Frei_Bio ecolog_2021	0	NA	NA	NA	Freitas, F; Schroeder, R; Hillesheim, JC; Wahrlich, R; Diehl, FL; Branco, JO	Bio ecology of the white shrimp Litopenaeus schmitti in Babitonga Bay. Do the current regulation of closed seasons is suitable to the lifecycle of this species?	REGIONAL STUDIES IN MARINE SCIENCE	46		2021
Fudi_Female-bia_2013	1	JN47	1	NA	Fudickar, A. M., et al.	Female-biased obligate strategies in a partially migratory population.	Journal of Animal Ecology 82(4): 863-871.	82	863-871	2013
Funn_Orientatio_2007	1	JN48	0	2-Study does assess both migratory and non-migratory group within population	Funnell, J. R. and U. Munro	Orientation in captive migratory and sedentary Australian silvereyes Zosterops lateralis (Zosteropidae).	Behavioral Ecology and Sociobiology 61(3): 337-345.	61	337-345	2007

Furu_Fin whale _2021	0	NA	NA	NA	Furumaki, S; Tsujii, K; Mitani, Y	Fin whale (Balaenoptera physalus) song pattern in the southern Chukchi Sea	POLAR BIOLOGY	44	1021-1027	2021
Futa_Size-depen_2022	1	JN163	0	4-Study did not apply frequentist statistical approach with effect size	Futamura, R; Morita, K; Kanno, Y; Kumikawa, S; Matsuoka, Y; Okuda, A; Sugiyama, H; Takahashi, H; Uchida, J; Kishida, O	Size-dependent growth tactics of a partially migratory fish before migration	OECOLOGIA			2022
Gaha_Partial mi_2015	1	JN49	0	2-Study does assess both migratory and non-migratory group within population	Gahagan, B. I., et al.	Partial migration of striped bass: revisiting the contingent hypothesis.	Marine Ecology Progress Series 525: 185-197.	525	185-197	2015
Gaid_Benefits o_2013	1	JN50	0	4-Study did not apply frequentist statistical approach with effect size	Gaidet, N. and P. Lecomte	Benefits of migration in a partially-migratory tropical ungulate.	Bmc Ecology 13.	13		2013
Gall_Seasonal d_2019	0	NA	NA	NA	Gallagher, CP; Guzzo, MM; Dick, TA	Seasonal depth and temperature use, and diel movements of lake trout (Salvelinus namaycush) in a subarctic lake	ARCTIC SCIENCE	5	71-89	2019
Gara_Latitudina_2008	0	NA	NA	NA	Garamszegi, L. Z., et al.	Latitudinal distribution, migration, and testosterone levels in birds.	American Naturalist 172(4): 533-546.	172	533-546	2008
Garc_Current la_2021	0	NA	NA	NA	Garcia, J; Moran-Ordonez, A; Garcia, JT; Calero-Riestra, M; Alda, F; Sanz, J; Suarez-Seoane, S	Current landscape attributes and landscape stability in breeding grounds explain genetic differentiation in a long-distance migratory bird	ANIMAL CONSERVATIO N	24	120-134	2021
Garc_Distributi_2020	0	NA	NA	NA	Garcia-Seoane, E; Vieira, RP; Moreno, A; Caldeira, RMA; Azevedo, CC; Gaudencio, MJ; dos Santos, A	Distribution and diversity of mesopelagic fauna on seamounts of the Madeira-Tore complex (Northeastern Atlantic)	REGIONAL STUDIES IN MARINE SCIENCE	39		2020
Garc_Influence _2018	0	NA	NA	NA	Garcia-Morales, E; Carrillo-Angeles, IG; Golubov, J; Pinero, D; Mandujano, MC	Influence of fruit dispersal on genotypic diversity and migration rates of a clonal cactus from the Chihuahuan Desert	ECOLOGY AND EVOLUTION	8	12559-12575	2018
Garc_Morphologi_2021	0	NA	NA	NA	Garcia, J; Arizaga, J; Rodriguez, JI;	Morphological differentiation in a migratory bird across geographic gradients in	JOURNAL OF BIOGEOGRAPH Y	48	2828-2838	2021

					Alonso, D; Suarez-Seoane, S	mountains of southern Europe				
Gatt_Costs of r_2021	1	JN161	0	4-Study did not apply frequentist statistical approach with effect size	Gatt, MC; Versteegh, M; Bauch, C; Tieleman, BI; Granadeiro, JP; Catry, P	Costs of reproduction and migration are paid in later return to the colony, not in physical condition, in a long-lived seabird	OECOLOGIA	195	287-297	2021
Gavr_The Long-T_2018	0	NA	NA	NA	Gavrilov, AL; Gos'kova, OA	The Long-Term Dynamics of Parasite Infection in Coregonids with Different Food Specializations	RUSSIAN JOURNAL OF ECOLOGY	49	548-553	2018
Geof_Functional_2021	0	NA	NA	NA	Geoffroy, C; Villard, MA; Belisle, M	Functional connectivity of managed forest landscapes for the Ovenbird: an experimental assessment of within-patch movement behavior	AVIAN CONSERVATION AND ECOLOGY	16		2021
Giar_Size-struc_2010	0	NA	NA	NA	Giarrizzo, T., et al.	Size-structured migration and feeding patterns in the banded puffer fish Colomesus psittacus (Tetraodontidae) from north Brazilian mangrove creeks.	Marine Ecology Progress Series 419: 157-170.	419	157-170	2010
Gibs_Where noth_2022	0	NA	NA	NA	Gibson, MR; Runge, CA; Stephens, PA; Fuller, RA; Willis, SG	Where nothing stands still: quantifying nomadism in Australian arid-zone birds	LANDSCAPE ECOLOGY			2022
Gill_Life histo_2008	1	JN52	0	4-Study did not apply frequentist statistical approach with effect size	Gillis, E. A., et al.	Life history correlates of alternative migratory strategies in American Dippers.	Ecology 89(6): 1687-1695.	89	1687-1695	2008
Gill_Partial mi_2015	1	JN51	1	NA	Gillanders, B. M., et al.	Partial migration: growth varies between resident and migratory fish.	Biology Letters 11(3).	11		2015
Gils_Timing of _2020	0	NA	NA	NA	Gilsenan, C; Valcu, M; Kempenaers, B	Timing of arrival in the breeding area is repeatable and affects reproductive success in a non-migratory population of blue tits	JOURNAL OF ANIMAL ECOLOGY	89	1017-1031	2020
Giro_Changes in_2016	0	NA	NA	NA	Giroux, J. F., et al.	Changes in spring arrival date and timing of breeding of Ring-billed Gulls in southern Quebec over four decades.	Avian Conservation and Ecology 11(1).	11	NA	2016
Goet_The timing_2021	0	NA	NA	NA	Goetz, FA; Beamer, E; Connor, EJ; Jeanes, E; Kinsel, C; Chamberlin, JW;	The timing of anadromous bull trout migrations in estuarine and marine	ENVIRONMENTAL BIOLOGY OF FISHES	104	1073-1088	2021

					Morello, C; Quinn, TP	waters of Puget Sound, Washington				
Gord_Do changes_2005	0	NA	NA	NA	Gordo, O., et al.	Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds?	Global Change Biology 11(1): 12-21.	11	21-Dec	2005
Gord_Phenology_2005	0	NA	NA	NA	Gordo, O. and J. J. Sanz	Phenology and climate change: a long-term study in a Mediterranean locality.	Oecologia 146(3): 484-495.	146	484-495	2005
Gray_Life histo_2011	1	JN54	0	2-Study does assess both migratory and non-migratory group within population	Grayson, K. L., et al.	Life history benefits of residency in a partially migrating pond-breeding amphibian.	Ecology 92(6): 1236-1246.	92	1236-1246	2011
Gray_Sex- and c_2009	1	JN53	1	NA	Grayson, K. L. and H. M. Wilbur	Sex- and context-dependent migration in a pond-breeding amphibian.	Ecology 90(2): 306-312.	90	306-312	2009
Gris_Reproducti_2017	1	JN55	0	4-Study did not apply frequentist statistical approach with effect size	Grist, H., et al.	Reproductive performance of resident and migrant males, females and pairs in a partially migratory bird.	Journal of Animal Ecology 86(5): 1010-1021.	86	1010-1021	2017
Gris_The equili_2011	1	JN56	0	5-Simulation study or systematic review	Griswold, C. K., et al.	The equilibrium population size of a partially migratory population and its response to environmental change.	Oikos 120(12): 1847-1859.	120	1847-1859	2011
Gris_The evolut_2010	1	JN57	0	5-Simulation study or systematic review	Griswold, C. K., et al.	The evolution of migration in a seasonal environment.	Proceedings of the Royal Society B-Biological Sciences 277(1694): 2711-2720.	277	2711-2720	2010
Guil_What type_2007	1	JN58	0	2-Study does assess both migratory and non-migratory group within population	Guillemain, M., et al.	What type of lean ducks do hunters kill? Weakest local ones rather than migrants.	Wildlife Biology 13(1): 102-107.	13	102-107	2007
Gunn_Population_2006	0	NA	NA	NA	Gunnarsson, T. G., et al.	Population-scale drivers of individual arrival times in migratory birds.	Journal of Animal Ecology 75(5): 1119-1127.	75	1119-1127	2006
Gura_A framewor_2017	1	JN59	0	2-Study does assess both migratory and non-migratory group within population	Gurarie, E., et al.	A framework for modelling range shifts and migrations: asking when, whither, whether and will it return.	Journal of Animal Ecology 86(4): 943-959.	86	943-959	2017
Gura_Memorieso_2021	0	NA	NA	NA	Gurarie, E; Potluri, S; Cosner, GC; Cantrell, RS; Fagan, WF	Memories of Migrations Past: Sociality and Cognition in Dynamic, Seasonal Environments	FRONTIERS IN ECOLOGY AND EVOLUTION	9		2021

Gura_Tactical d_2019	0	NA	NA	NA	Gurarie, E; et al.	Tactical departures and strategic arrivals: Divergent effects of climate and weather on caribou spring migrations	ECOSPHERE	10		2019
Guti_Migration _2017	0	NA	NA	NA	Gutierrez, J. S., et al.	Migration and parasitism: habitat use, not migration distance, influences helminth species richness in Charadriiform birds.	Journal of Biogeography 44(5): 1137-1147.	44	1137-1147	2017
Hahn_Longer win_2016	0	NA	NA	NA	Hahn, S., et al.	Longer wings for faster springs - wing length relates to spring phenology in a long-distance migrant across its range.	Ecology and Evolution 6(1): 68-77.	6	68-77	2016
Hake_Age-depend_2003	0	NA	NA	NA	Hake, M., et al.	Age-dependent migration strategy in honey buzzards Pernis apivorus tracked by satellite.	Oikos 103(2): 385-396.	103	385-396	2003
Hans_An unseen _2020	0	NA	NA	NA	Hansen, HH; Pegg, M; Van Den Broeke, M; Watkinson, D; Enders, EC	An unseen synchrony or recurrent resource pulse opportunity? linking fisheries with aeroecology	REMOTE SENSING IN ECOLOGY AND CONSERVATION	6	366-380	2020
Hans_Ecological_2020	0	NA	NA	NA	Hansen, JH; Skov, C; Baktoft, H; Bronmark, C; Chapman, B; Hulthen, K; Hansson, LA; Nilsson, PA; Brodersen, J	Ecological Consequences of Animal Migration: Prey Partial Migration Affects Predator Ecology and Prey Communities	ECOSYSTEMS	23	292-306	2020
Hans_Physiologi_2011	1	JN60	0	4-Study did not apply frequentist statistical approach with effect size	Hanson, K. C., et al.	Physiological Characterization of Hatchery-Origin Juvenile Steelhead Oncorhynchus mykiss Adopting Divergent Life-History Strategies.	Journal of Fish and Wildlife Management 2(1): 61-71.	2	61-71	2011
Hara_Patterns o_2021	0	NA	NA	NA	Haran, R; Kiat, Y; Izhaki, I	Patterns of partial migration of the Dead Sea Sparrow (Passer moabiticus) along the Great Rift Valley in Israel	JOURNAL OF ARID ENVIRONMENTS	192		2021
Haro_Global con_2021	0	NA	NA	NA	Haro-Bilbao, I; Riginos, C; Baldwin, JD; Zischke, M; Tibbetts, IR; Thia, JA	Global connections with some genomic differentiation occur between Indo-Pacific and Atlantic Ocean wahoo, a	JOURNAL OF BIOGEOGRAPHY	48	2053-2067	2021

						large circumtropical pelagic fish				
Haus_Decadal sh_2017	0	NA	NA	NA	Hauser, D. D. W., et al.	Decadal shifts in autumn migration timing by Pacific Arctic beluga whales are related to delayed annual sea ice formation.	Global Change Biology 23(6): 2206-2217.	23	2206-2217	2017
Haus_Unmasking _2020	0	NA	NA	NA	Hauser, M; et al.	Unmasking continental natal homing in goliath catfish from the upper Amazon	FRESHWATER BIOLOGY	65	325-336	2020
Hazr_Calendar-e_2012	0	NA	NA	NA	Hazra, P., et al.	Calendar-effects and temperature-impacts in migratory waterbirds at three tropical Indian wetlands.	Acta Oecologica-International Journal of Ecology 43: 60-71.	43	60-71	2012
Hebb_Demographi _2011	1	JN61	0	4-Study did not apply frequentist statistical approach with effect size	Hebblewhite, M. and E. H. Merrill	Demographic balancing of migrant and resident elk in a partially migratory population through forage-predation tradeoffs.	Oikos 120(12): 1860-1870.	120	1860-1870	2011
Hebb_Multiscale_2007	1	JN62	1	NA	Hebblewhite, M. and E. H. Merrill	Multiscale wolf predation risk for elk: does migration reduce risk?	Oecologia 152(2): 377-387.	152	377-387	2007
Hebb_Trade-offs_2009	1	JN63	1	NA	Hebblewhite, M. and E. H. Merrill	Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate.	Ecology 90(12): 3445-3454.	90	3445-3454	2009
Hege_Causes and_2015	1	JN64	1	NA	Hegemann, A., et al.	Causes and Consequences of Partial Migration in a Passerine Bird.	American Naturalist 186(4): 531-546.	186	531-546	2015
Hell_Population_2008	0	NA	NA	NA	Hellgren, O., et al.	Population structure and migratory directions of Scandinavian bluethroats Luscinia svecica - a molecular, morphological and stable isotope analysis.	Ecography 31(1): 95-103.	31	95-103	2008
Hess_Genetic ba_2016	0	NA	NA	NA	Hess, J. E., et al.	Genetic basis of adult migration timing in anadromous steelhead discovered through multivariate association testing.	Proceedings of the Royal Society B-Biological Sciences 283(1830).	283	NA	2016
Higu_Horizontal_2021	0	NA	NA	NA	Higuchi, T; Watanabe, S; Manabe, R;	Horizontal and vertical migration behavior of silver-phase Japanese eels in	JOURNAL OF EXPERIMENTAL MARINE	542		2021

					Tanimoto, A; Miller, MJ; Kojima, T; Tsukamoto, K	coastal, pelagic and spawning areas observed by pop-up satellite archival tags	BIOLOGY AND ECOLOGY			
Hild_Molecular_2019	0	NA	NA	NA	Hildebrand, J; Pyrka, E; Sitko, J; Jezewski, W; Zalesny, G; Tkach, VV; Laskowski, Z	Molecular phylogeny provides new insights on the taxonomy and composition of Lyperosomum Looss, 1899 (Digenea, Dicrocoeliidae) and related genera	INTERNATIONAL JOURNAL FOR PARASITOLOGY-PARASITES AND WILDLIFE	9	90-99	2019
Hill_Migration_2012	1	JN65	0	2-Study does assess both migratory and non-migratory group within population	Hill, N. J., et al.	Migration strategy affects avian influenza dynamics in mallards (Anas platyrhynchos).	Molecular Ecology 21(24): 5986-5999.	21	5986-5999	2012
Hill_Migratory_2019	0	NA	NA	NA	Hill, JM; Renfrew, RB	Migratory patterns and connectivity of two North American grassland bird species	ECOLOGY AND EVOLUTION	9	680-692	2019
Hoch_The Influe_2019	0	NA	NA	NA	Hoch, JM; Bermudez, AC; Coury, OS; Donahou, AS; Jeffers, CN; LaMartina, M; Ramsaran, D; Spadafore, S	The Influence of Personality on Small Fish Migration and Dispersal in the Everglades	WETLANDS	39	991-1002	2019
Hock_A geostati_2018	0	NA	NA	NA	Hocking, DJ; Thorson, JT; O'Neil, K; Letcher, BH	A geostatistical state-space model of animal densities for stream networks	ECOLOGICAL APPLICATIONS	28	1782-1796	2018
Hopc_Competitio_2014	0	NA	NA	NA	Hopcraft, J. G. C., et al.	Competition, predation, and migration: individual choice patterns of Serengeti migrants captured by hierarchical models.	Ecological Monographs 84(3): 355-372.	84	355-372	2014
Hota_Long-dista_2019	0	NA	NA	NA	Hotaling, S; Shain, DH; Lang, SA; Bagley, RK; Tronstad, LM; Weisrock, DW; Kelley, JL	Long-distance dispersal, ice sheet dynamics and mountaintop isolation underlie the genetic structure of glacier ice worms	PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	286		2019
Hube_Comparativ_2017	1	JN66	0	2-Study does assess both migratory and non-migratory group within population	Huber, G. H., et al.	Comparative analysis reveals migratory swallows (Hirundinidae) have less pointed wings than residents.	Biological Journal of the Linnean Society 120(1): 228-235.	120	228-235	2017

Huis_Palm Phyto_2018	0	NA	NA	NA	Huisman, SN; Raczka, MF; McMichael, CNH	Palm Phytoliths of Mid-Elevation Andean Forests	FRONTIERS IN ECOLOGY AND EVOLUTION	6		2018
Hult_Escaping p_2015	1	JN67	1	NA	Hulthen, K., et al.	Escaping peril: perceived predation risk affects migratory propensity.	Biology Letters 11(8).	11		2015
Hume_Push, pull_2020	0	NA	NA	NA	Hume, JB; Luhring, TM; Wagner, CM	Push, pull, or push-pull? An alarm cue better guides sea lamprey towards capture devices than a mating pheromone during the reproductive migration	BIOLOGICAL INVASIONS	22	2129-2142	2020
Iafr_Factors af_2008	0	NA	NA	NA	Iafrate, J. and K. Oliveira	Factors affecting migration patterns of juvenile river herring in a coastal Massachusetts stream.	Environmental Biology of Fishes 81(1): 101-110.	81	101-110	2008
Ibra_Land degra_2018	0	NA	NA	NA	Ibrahim, YZ; Balzter, H; Kaduk, J	Land degradation continues despite greening in the Nigeria-Niger border region	GLOBAL ECOLOGY AND CONSERVATION	16		2018
Igot_Seasonal m_2004	0	NA	NA	NA	Igota, H., et al.	Seasonal migration patterns of female sika deer in eastern Hokkaido, Japan.	Ecological Research 19(2): 169-178.	19	169-178	2004
Inum_First reco_2021	0	NA	NA	NA	Inumaru, M; Odaya, Y; Sato, Y; Marzal, A	First records of prevalence and diversity of avian haemosporidia in snipe species (genus Gallinago) of Japan	INTERNATIONAL JOURNAL FOR PARASITOLOGY-PARASITES AND WILDLIFE	16	5-17	2021
Irig_Habitat us_2019	0	NA	NA	NA	Irigoyen, AJ; Bovcon, N; Trobbiani, G; De Wysiecki, AM; Argemi, F; Jaureguizar, AJ	Habitat use, seasonality and demography of the broadnose sevengill shark Notorynchus cepedianus in central Patagonia: Another piece of the puzzle	AUSTRAL ECOLOGY	44	1463-1470	2019
Jaco_Recent evo_2019	0	NA	NA	NA	Jacob, J; Cravo, A	Recent evolution of the tidal prisms at the inlets of the western sector of the Ria Formosa, south coast of Portugal	REGIONAL STUDIES IN MARINE SCIENCE	31		2019
Jahn_Determinan_2010	1	JN68	0	4-Study did not apply frequentist statistical approach with effect size	Jahn, A. E., et al.	Determinants of partial bird migration in the Amazon Basin.	Journal of Animal Ecology 79(5): 983-992.	79	983-992	2010
Jake_Classifyin_2018	0	NA	NA	NA	Jakes, A. F., et al.	Classifying the migration behaviors of pronghorn on their northern range.	Journal of Wildlife Management 82(6): 1229-1242.	82	1229-1242	2018

Jens_Migrant bl_2020	1	JN171	0	4-Study did not apply frequentist statistical approach with effect size	Jensen, JK; Isaksson, C; Eikenaar, C; Andersson, MN	Migrant blackbirds,Turdus merula, have higher plasma levels of polyunsaturated fatty acids compared to residents, but not enhanced fatty acid unsaturation index	ECOLOGY AND EVOLUTION	10	10196-10206	2020
Jian_The import_2019	0	NA	NA	NA	Jiang, Y; Gao, M; Meng, Y; Wen, J; Ge, XJ; Nie, ZL	The importance of the North Atlantic land bridges and eastern Asia in the post-Boreotropical biogeography of the Northern Hemisphere as revealed from the poison ivy genus (Toxicodendron, Anacardiaceae)	MOLECULAR PHYLOGENETICS AND EVOLUTION	139		2019
Jiao_The impact_2020	0	NA	NA	NA	Jiao, J; Gilchrist, MA; Fefferman, NH	The impact of host metapopulation structure on short-term evolutionary rescue in the face of a novel pathogenic threat	GLOBAL ECOLOGY AND CONSERVATION	23		2020
Jone_Annual Pro_2020	0	NA	NA	NA	Jones, PF; Jakes, AF; Eacker, DR; Hebblewhite, M	Annual Pronghorn Survival of a Partially Migratory Population	JOURNAL OF WILDLIFE MANAGEMENT	84	1114-1126	2020
Jone_Fences red_2019	0	NA	NA	NA	Jones, PF; Jakes, AF; Telander, AC; Sawyer, H; Martin, BH; Hebblewhite, M	Fences reduce habitat for a partially migratory ungulate in the Northern Sagebrush Steppe	ECOSPHERE	10		2019
Jone_Individual_2014	0	NA	NA	NA	Jones, T. B., et al.	Individual quality explains association between plumage colouration, arrival dates and mate acquisition in yellow warblers (Setophaga petechia).	Bmc Ecology 14.	14	NA	2014
Jone_Supplement_2014	0	NA	NA	NA	Jones, J. D., et al.	Supplemental feeding alters migration of a temperate ungulate.	Ecological Applications 24(7): 1769-1779.	24	1769-1779	2014
Jonk_Genetic co_2013	1	JN69	0	2-Study does assess both migratory and non-migratory group within population	Jonker, R. M., et al.	Genetic consequences of breaking migratory traditions in barnacle geese Branta leucopsis.	Molecular Ecology 22(23): 5835-5847.	22	5835-5847	2013
Jons_Migration_2002	0	NA	NA	NA	Jonsson, N. and B. Jonsson	Migration of anadromous brown trout Salmo trutta in a Norwegian river.	Freshwater Biology 47(8): 1391-1401.	47	1391-1401	2002
Jord_Detecting_2007	0	NA	NA	NA	Jorde, P. E., et al.	Detecting genetic structure in migrating bowhead whales off the coast of Barrow, Alaska.	Molecular Ecology 16(10): 1993-2004.	16	1993-2004	2007

Jord_Ocean warm_2020	0	NA	NA	NA	Jorda, G; Marba, N; Bennett, S; Santana-Garcon, J; Agusti, S; Duarte, CM	Ocean warming compresses the three-dimensional habitat of marine life	NATURE ECOLOGY & EVOLUTION	4	109-+	2020
Jose_Independen_2003	1	JN70	0	2-Study does assess both migratory and non-migratory group within population	Joseph, L., et al.	Independent evolution of migration on the South American landscape in a long-distance temperate-tropical migratory bird, Swainson's flycatcher (Myiarchus swainsoni).	Journal of Biogeography 30(6): 925-937.	30	925-937	2003
Kark_Impact of _2019	0	NA	NA	NA	Karkkainen, T; Teerikorpi, P; Panda, B; Helle, S; Stier, A; Laaksonen, T	Impact of continuous predator threat on telomere dynamics in parent and nestling pied flycatchers	OECOLOGIA	191	757-766	2019
Karl_Genomic di_2013	1	JN71	1	NA	Karlsen, B. O., et al.	Genomic divergence between the migratory and stationary ecotypes of Atlantic cod.	Molecular Ecology 22(20): 5098-5111.	22	5098-5111	2013
Keef_Variabilit_2009	0	NA	NA	NA	Keefer, M. L., et al.	Variability in migration timing of adult Pacific lamprey (Lampetra tridentata) in the Columbia River, USA.	Environmental Biology of Fishes 85(3): 253-264.	85	253-264	2009
Kell_Insights i_2002	0	NA	NA	NA	Kelly, J. F., et al.	Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios.	Oecologia 130(2): 216-+.	130	216-+	2002
Kell_Novel meas_2016	0	NA	NA	NA	Kelly, J. F., et al.	Novel measures of continental-scale avian migration phenology related to proximate environmental cues.	Ecosphere 7(9).	7	NA	2016
Kell_Seasonal m_2016	0	NA	NA	NA	Kelly, T. R., et al.	Seasonal migration distance varies with natal dispersal and predicts parasitic infection in song sparrows.	Behavioral Ecology and Sociobiology 70(11): 1857-1866.	70	1857-1866	2016
Kels_Days to vi_2021	0	NA	NA	NA	Kelsey, NA; Huppop, O; Bairlein, F	Days to visit an offshore island: effect of weather conditions on arrival fuel load and potential flight range for common blackbirds Turdus merula migrating over the North Sea	MOVEMENT ECOLOGY	9		2021

Kels_Do precipi_2019	0	NA	NA	NA	Kelson, SJ; Carlson, SM	Do precipitation extremes drive growth and migration timing of a Pacific salmonid fish in Mediterranean-climate streams?	ECOSPHERE	10		2019
Kels_Indirect g_2020	1	JN154	1	NA	Kelson, SJ; Carlson, SM; Miller, MR	Indirect genetic control of migration in a salmonid fish	BIOLOGY LETTERS	16		2020
Kels_Partial mi_2020	0	NA	NA	NA	Kelson, SJ; Power, ME; Finlay, JC; Carlson, SM	Partial migration alters population ecology and food chain length: evidence from a salmonid fish	ECOSPHERE	11		2020
Kels_Temporal d_2020	0	NA	NA	NA	Kelson, SJ; Miller, MR; Thompson, TQ; O'Rourke, SM; Carlson, SM	Temporal dynamics of migration-linked genetic variation are driven by streamflows and riverscape permeability	MOLECULAR ECOLOGY	29	870-885	2020
Kemp_The Biogeo_2018	0	NA	NA	NA	Kemp, BL; Tabish, EM; Wolford, AJ; Jones, DL; Butler, JK; Baxter, BK	The Biogeography of Great Salt Lake Halophilic Archaea: Testing the Hypothesis of Avian Mechanical Carriers	DIVERSITY-BASEL	10		2018
Kent_Does winte_2017	0	NA	NA	NA	Kentie, R., et al.	Does wintering north or south of the Sahara correlate with timing and breeding performance in black-tailed godwits?	Ecology and Evolution 7(8): 2812-2820.	7	2812-2820	2017
Kerr_Latent eff_2010	1	JN72	0	2-Study does assess both migratory and non-migratory group within population	Kerr, L. A. and D. H. Secor	Latent effects of early life history on partial migration for an estuarine-dependent fish.	Environmental Biology of Fishes 89(3-4): 479-492.	89	479-492	2010
Kess_Predictabl_2014	1	JN73	0	2-Study does assess both migratory and non-migratory group within population	Kessel, S. T., et al.	Predictable temperature-regulated residency, movement and migration in a large, highly mobile marine predator (Negaprion brevirostris).	Marine Ecology Progress Series 514: 175-190.	514	175-190	2014
Kett_Fine-scale_2019	0	NA	NA	NA	Kettenring, KM; Mossman, BN; Downard, R; Mock, KE	Fine-scale genetic diversity and landscape-scale genetic structuring in three foundational bulrush species: implications for wetland revegetation	RESTORATION ECOLOGY	27	408-420	2019
Kiel_Can Disrup_2020	0	NA	NA	NA	Kiel, NG; Griffiths, GR; Mcgee, GG	Can Disruption of an Ant-Plant Mutualism Explain a Lack of Recovery of Forest Herbs in Post-agricultural Forests of New York?	NORTHEASTERN NATURALIST	27	215-228	2020

Kim,_Migration_2021	0	NA	NA	NA	Kim, DM; Shaw, AK	Migration and tolerance shape host behaviour and response to parasite infection	JOURNAL OF ANIMAL ECOLOGY	90	2315-2324	2021
Kinn_Common thr_2020	1	JN172	0	2-Study does assess both migratory and non-migratory group within population	Kinney, MJ; Kacev, D; Sippel, T; Dewar, H; Eguchi, T	Common thresher shark Alopias vulpinus movement: Bayesian inference on a data-limited species	MARINE ECOLOGY PROGRESS SERIES	639	155-167	2020
Kish_Population_2021	0	NA	NA	NA	Kishida, T; Toda, M; Go, Y; Tatsumoto, S; Sasai, T; Hikida, T	Population history and genomic admixture of sea snakes of the genus Laticauda in the West Pacific	MOLECULAR PHYLOGENETICS AND EVOLUTION	155		2021
Kiss_Sexual siz_2003	0	NA	NA	NA	Kissner, K. J., et al.	Sexual size dimorphism and timing of spring migration in birds.	Journal of Evolutionary Biology 16(1): 154-162.	16	154-162	2003
Kley_A Comprehe_2019	0	NA	NA	NA	Kleyheeg, E; Fiedler, W; Safi, K; Waldenstrom, J; Wikelski, M; van Toor, ML	A Comprehensive Model for the Quantitative Estimation of Seed Dispersal by Migratory Mallards	FRONTIERS IN ECOLOGY AND EVOLUTION	7		2019
Kobo_The effect_2012	0	NA	NA	NA	Kobori, H., et al.	The effects of climate change on the phenology of winter birds in Yokohama, Japan.	Ecological Research 27(1): 173-180.	27	173-180	2012
Kokk_Directions_2011	1	JN74	0	5-Simulation study or systematic review	Kokko, H.	Directions in modelling partial migration: how adaptation can cause a population decline and why the rules of territory acquisition matter.	Oikos 120(12): 1826-1837.	120	1826-1837	2011
Kova_Genetic ch_2012	0	NA	NA	NA	Kovach, R. P., et al.	Genetic change for earlier migration timing in a pink salmon population.	Proceedings of the Royal Society B-Biological Sciences 279(1743): 3870-3878.	279	3870-3878	2012
Kova_Temporal p_2013	0	NA	NA	NA	Kovach, R. P., et al.	Temporal patterns of genetic variation in a salmon population undergoing rapid change in migration timing.	Evolutionary Applications 6(5): 795-807.	6	795-807	2013
Kova_Temporal p_2015	0	NA	NA	NA	Kovach, R. P., et al.	Temporal patterns in adult salmon migration timing across southeast Alaska.	Global Change Biology 21(5): 1821-1833.	21	1821-1833	2015
Krem_Spring Mig_2011	0	NA	NA	NA	Krementz, D. G., et al.	Spring Migration of Mallards from Arkansas as Determined by Satellite Telemetry.	Journal of Fish and Wildlife Management 2(2): 156-168.	2	156-168	2011

Kris_Matrilinea_2021	0	NA	NA	NA	Kristjansson, D; Bohlin, J; Jugessur, A; Schurr, TG	Matrilineal diversity and population history of Norwegians	AMERICAN JOURNAL OF PHYSICAL ANTHROPOLOGY	176	120-133	2021
Krop_Home range_2015	1	JN75	1	NA	Kropil, R., et al.	Home range and migration patterns of male red deer Cervus elaphus in Western Carpathians.	European Journal of Wildlife Research 61(1): 63-72.	61	63-72	2015
Kuce_INFLUENCES_1992	0	NA	NA	NA	Kucera, T. E.	INFLUENCES OF SEX AND WEATHER ON MIGRATION OF MULE DEER IN CALIFORNIA.	Great Basin Naturalist 52(2): 122-130.	52	122-130	1992
Kunz_Mitochondr_2019	0	NA	NA	NA	Kunz, F; Gamauf, A; Zachos, FE; Haring, E	Mitochondrial phylogenetics of the goshawk Accipiter [gentilis] superspecies	JOURNAL OF ZOOLOGICAL SYSTEMATICS AND EVOLUTIONARY RESEARCH	57	942-958	2019
Kurt_Migratory_2013	1	JN76	1	NA	Kurth, R.	Migratory patterns of lower Feather River natural and hatchery-origin Oncorhynchus mykiss.	Environmental Biology of Fishes 96(2-3): 355-362.	96	355-362	2013
La S_Migration_2015	0	NA	NA	NA	La Sorte, F. A., et al.	Migration timing and its determinants for nocturnal migratory birds during autumn migration.	Journal of Animal Ecology 84(5): 1202-1212.	84	1202-1212	2015
La S_Migration_2017	0	NA	NA	NA	La Sorte, F. A. and D. Fink	Migration distance, ecological barriers and en-route variation in the migratory behaviour of terrestrial bird populations.	Global Ecology and Biogeography 26(2): 216-227.	26	216-227	2017
Laho_Where do t_2021	0	NA	NA	NA	Lahournat, M; Jiguet, F; Villers, A; Eraud, C; Henry, PY	Where do thrushes migrating to France come from? Within-France distribution and temporal changes over 70 years	EUROPEAN JOURNAL OF WILDLIFE RESEARCH	67		2021
Lai,_Movement t_2017	1	JN77	0	4-Study did not apply frequentist statistical approach with effect size	Lai, S., et al.	Movement tactics of a mobile predator in a meta-ecosystem with fluctuating resources: the arctic fox in the High Arctic.	Oikos 126(7): 937-947.	126	937-947	2017
Lamb_Influence_2017	0	NA	NA	NA	Lamb, J. S., et al.	Influence of density-dependent competition on foraging and migratory behavior of a subtropical colonial seabird.	Ecology and Evolution 7(16): 6469-6481.	7	6469-6481	2017
Lant_Restoring_2020	0	NA	NA	NA	Lanta, V; Mudrak, O; Liancourt, P; Dvorsky, M; Bartos,	Restoring diversity of thermophilous oak forests:	BIODIVERSITY AND	29	3411-3427	2020

					M; Chlumska, Z; Sebek, P; Cizek, L; Dolezal, J	connectivity and proximity to existing habitats matter	CONSERVATION			
Lars_Characteri_2020	0	NA	NA	NA	Larsen, T; Hansen, T; Dierking, J	Characterizing niche differentiation among marine consumers with amino acid delta C-13 fingerprinting	ECOLOGY AND EVOLUTION	10	7768-7782	2020
Laug_Quantifyin_2016	0	NA	NA	NA	Laughlin, A. J., et al.	Quantifying non-breeding season occupancy patterns and the timing and drivers of autumn migration for a migratory songbird using Doppler radar.	Ecography 39(10): 1017-1024.	39	1017-1024	2016
Leac_Brood Size_2019	0	NA	NA	NA	Leach, AG; Sedinger, JS; Riecke, TV; Van Dellen, AW; Ward, DH; Boyd, WS	Brood Size Affects Future Reproduction in a Long-Lived Bird with Precocial Young	AMERICAN NATURALIST	193	458-471	2019
Lee,_Late-arriv_2011	0	NA	NA	NA	Lee, S. D., et al.	Late-arriving barn swallows linked to population declines.	Biological Conservation 144(9): 2182-2187.	144	2182-2187	2011
Lehn_Variabilit_2018	1	JN143	0	4-Study did not apply frequentist statistical approach with effect size	Lehnert, LS; et al.	Variability and repeatability of noctule bat migration in Central Europe: evidence for partial and differential migration	PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	285		2018
Leit_Adaptation_2019	0	NA	NA	NA	Leites, LP; Rehfeldt, GE; Steiner, KC	Adaptation to climate in five eastern North America broadleaf deciduous species: Growth clines and evidence of the growth-cold tolerance trade-off	PERSPECTIVES IN PLANT ECOLOGY EVOLUTION AND SYSTEMATICS	37	64-72	2019
Leop_Corridor-_2014	0	NA	NA	NA	Leopold, C. R. and S. C. Hess	Corridor- and stopover-use of the Hawaiian goose (Branta sandvicensis), an intratropical altitudinal migrant.	Journal of Tropical Ecology 30: 67-78.	30	67-78	2014
Lewi_Effects of_1998	0	NA	NA	NA	Lewis, T. L. and O. J. Rongstad	Effects of supplemental feeding on white-tailed deer, Odocoileus virginianus, migration and survival in Northern Wisconsin.	Canadian Field-Naturalist 112(1): 75-81.	112	75-81	1998
Li, _River Vall_2019	0	NA	NA	NA	Li, YC; Ye, WJ; Jiang, CG; Zeng, Z; Tian, JY; Yang, LQ; Liu, KJ; Kong, QP	River Valleys Shaped the Maternal Genetic Landscape of Han Chinese	MOLECULAR BIOLOGY AND EVOLUTION	36	1643-1652	2019

Lian_A multi-lo_2019	0	NA	NA	NA	Lian, L; Xiang, KL; Ortiz, RD; Wang, W	A multi-locus phylogeny for the Neotropical Anomospermeae (Menispermaceae): Implications for taxonomy and biogeography	MOLECULAR PHYLOGENETICS AND EVOLUTION	136	44-52	2019
Liao_Climate ch_2020	0	NA	NA	NA	Liao, ZY; Zhang, L; Nobis, MP; Wu, XG; Pan, KW; Wang, KQ; Dakhil, MA; Du, MX; Xiong, QL; Pandey, B; Tian, XL	Climate change jointly with migration ability affect future range shifts of dominant fir species in Southwest China	DIVERSITY AND DISTRIBUTIONS	26	352-367	2020
Linc_Optimal fo_2019	0	NA	NA	NA	Lincoln, AE; Quinn, TP	Optimal foraging or surplus killing: selective consumption and discarding of salmon by brown bears	BEHAVIORAL ECOLOGY	30	202-212	2019
Lind_Do migrato_2019	1	JN168	0	2-Study does assess both migratory and non-migratory group within population	Lindenmayer, DB; Lane, P; Foster, CN; Westgate, MJ; Sato, C; Ikin, K; Crane, M; Michael, D; Florance, D; Scheele, B	Do migratory and resident birds differ in their responses to interacting effects of climate, weather and vegetation?	DIVERSITY AND DISTRIBUTIONS	25	449-461	2019
Line_A partial _2021	0	NA	NA	NA	Linek, N; et al.	A partial migrant relies upon a range-wide cue set but uses population-specific weighting for migratory timing	MOVEMENT ECOLOGY	9		2021
Lino_Acoustic b_2016	1	JN78	1	NA	Linossier, J., et al.	Acoustic but no genetic divergence in migratory and sedentary populations of blackcaps, Sylvia atricapilla.	Biological Journal of the Linnean Society 119(1): 68-79.	119	68-79	2016
Liso_Sex-Specif_2016	0	NA	NA	NA	Lisovski, S., et al.	Sex-Specific Arrival Times on the Breeding Grounds: Hybridizing Migratory Skuas Provide Empirical Support for the Role of Sex Ratios.	American Naturalist 187(4): 532-539.	187	532-539	2016
Liso_The roles _2018	0	NA	NA	NA	Lisovski, S; van Dijk, JGB; Klinkenberg, D; Nolet, BA; Fouchier, RAM; Klaassen, M	The roles of migratory and resident birds in local avian influenza infection dynamics	JOURNAL OF APPLIED ECOLOGY	55	2963-2975	2018
Liu,_EFFECT OF _2021	0	NA	NA	NA	Liu, JH; Geng, YH; Li, J; Cao, GJ; Zhang, ZQ	EFFECT OF STRAW SUBSTITUTING PARTIAL MINERAL N FERTILIZER ON N DISTRIBUTION OF	APPLIED ECOLOGY AND ENVIRONMENTAL RESEARCH	19	625-639	2021

						MAIZE PLANTS AND SOIL IN NORTHEAST CHINA				
Liu,_Meta-barco_2018	1	JN79	0	2-Study does assess both migratory and non-migratory group within population	Liu, G., et al.	Meta-barcoding insights into the spatial and temporal dietary patterns of the threatened Asian Great Bustard (Otis tarda dybowskii) with potential implications for diverging migratory strategies.	Ecology and Evolution 8(3): 1736-1745.	8	1736-1745	2018
Liu,_The gut mi_2021	1	JN159	0	4-Study did not apply frequentist statistical approach with effect size	Liu, YQ; Li, XH; Li, J; Chen, WT	The gut microbiome composition and degradation enzymes activity of black Amur bream (Megalobrama terminalis) in response to breeding migratory behavior	ECOLOGY AND EVOLUTION	11	5150-5163	2021
Liu,_The tetrap_2021	0	NA	NA	NA	Liu, J; Chen, JY	The tetrapod fauna of the upper Permian Naobaogou Formation of China: 7. Laosuchus hun sp. nov. (Chroniosuchia) and interrelationships of chroniosuchians	JOURNAL OF SYSTEMATIC PALAEONTOLOGY	18	2043-2058	2021
Live_Causation_2021	0	NA	NA	NA	Lively, CM; Xu, JL; Ben-Ami, F	Causation without correlation: parasite-mediated frequency-dependent selection and infection prevalence	BIOLOGY LETTERS	17		2021
Lowr_Behavior-s_2021	1	JN170	0	4-Study did not apply frequentist statistical approach with effect size	Lowrey, B; DeVoe, JD; Proffitt, KM; Garrott, RA	Behavior-specific habitat models as a tool to inform ungulate restoration	ECOSPHERE	12		2021
Lowr_Individual_2020	1	JN162	0	2-Study does assess both migratory and non-migratory group within population	Lowrey, B; McWhirter, DE; Proffitt, KM; Monteith, KL; Courtemanch, AB; White, PJ; Paterson, JT; Dewey, SR; Garrott, RA	Individual variation creates diverse migratory portfolios in native populations of a mountain ungulate	ECOLOGICAL APPLICATIONS	30		2020
Luca_Seasonalm_1996	0	NA	NA	NA	Lucas, M. C. and E. Batley	Seasonal movements and behaviour of adult barbel Barbus barbus, a riverine cyprinid fish: Implications for river management.	Journal of Applied Ecology 33(6): 1345-1358.	33	1345-1358	1996

Lund_DOMINANCE_1985	1	JN80	0	2-Study does assess both migratory and non-migratory group within population	Lundberg, P.	DOMINANCE BEHAVIOR, BODY-WEIGHT AND FAT VARIATIONS, AND PARTIAL MIGRATION IN EUROPEAN BLACKBIRDS TURDUS-MERULA.	Behavioral Ecology and Sociobiology 17(2): 185-189.	17	185-189	1985
Lund_Testing fo_2020	1	JN134	0	2-Study does assess both migratory and non-migratory group within population	Lundblad, CG; Conway, CJ	Testing four hypotheses to explain partial migration: balancing reproductive benefits with limits to fasting endurance	BEHAVIORAL ECOLOGY AND SOCIOBIOLOGY	74		2020
Lund_Variation_2020	1	JN149	0	2-Study does assess both migratory and non-migratory group within population	Lundblad, CG; Conway, CJ	Variation in selective regimes drives intraspecific variation in life-history traits and migratory behaviour along an elevational gradient	JOURNAL OF ANIMAL ECOLOGY	89	397-411	2020
Lyle_The spawni_1997	0	NA	NA	NA	Lyle, A. A. and P. S. Maitland	The spawning migration and conservation of smelt Osmerus eperlanus in the River Cree, southwest Scotland.	Biological Conservation 80(3): 303-311.	80	303-311	1997
Macm_Changes in_2007	0	NA	NA	NA	Macmynowski, D. P., et al.	Changes in spring arrival of Nearctic-Neotropical migrants attributed to multiscalar climate.	Global Change Biology 13(11): 2239-2251.	13	2239-2251	2007
MacN_Plankton c_2021	0	NA	NA	NA	MacNeil, L; Missan, S; Luo, J; Trappenberg, T; LaRoche, J	Plankton classification with high-throughput submersible holographic microscopy and transfer learning	BMC ECOLOGY AND EVOLUTION	21		2021
Macp_Morphology_2022	0	NA	NA	NA	Macpherson, MP; Jahn, AE; Mason, NA	Morphology of migration: associations between wing shape, bill morphology and migration in kingbirds (Tyrannus)	BIOLOGICAL JOURNAL OF THE LINNEAN SOCIETY	135	71-83	2022
Magg_Should I s_2019	1	JN167	0	2-Study does assess both migratory and non-migratory group within population	Maggs, JQ; Cowley, PD; Porter, SN; Childs, AR	Should I stay or should I go? Intra-population variability in movement behaviour of wide-ranging and resident coastal fishes	MARINE ECOLOGY PROGRESS SERIES	619	111-124	2019
Mall_Leucocyte_2015	0	NA	NA	NA	Mallory, M. L., et al.	Leucocyte profiles of Arctic marine birds: correlates of migration and breeding phenology.	Conservation Physiology 3.	3	NA	2015
Malp_Postglacia_2014	1	JN81	1	NA	Malpica, A. and J. F. Ornelas	Postglacial northward expansion and genetic differentiation between	Molecular Ecology 23(2): 435-452.	23	435-452	2014

						migratory and sedentary populations of the broad-tailed hummingbird (Selasphorus platycercus).				
Mani_Hidden lek_2020	0	NA	NA	NA	Manica, LT; Graves, JA; Podos, J; Macedo, RH	Hidden leks in a migratory songbird: mating advantages for earlier and more attractive males	BEHAVIORAL ECOLOGY	31	1180-1191	2020
Mann_Potential _2021	0	NA	NA	NA	Manning, FS; Curtis, PJ; Walker, IR; Pither, J	Potential long-distance dispersal of freshwater diatoms adhering to waterfowl plumage	FRESHWATER BIOLOGY	66	1136-1148	2021
Manr_Interpopul_ 2020	0	NA	NA	NA	Manrique-Poyato, MI; Cabrero, J; Lopez-Leon, MD; Perfectti, F; Gomez, R; Camacho, JPM	Interpopulation spread of a parasitic B chromosome is unlikely through males in the grasshopper Eyprepocnemis plorans	HEREDITY	124	197-206	2020
Marr_The influe_2005	0	NA	NA	NA	Marra, P. P., et al.	The influence of climate on the timing and rate of spring bird migration.	Oecologia 142(2): 307-315.	142	307-315	2005
Masl_Assessing _2020	0	NA	NA	NA	Maslo, B; Burkhalter, JC; Bushek, D; Yuhas, T; Schumm, B; Burger, J; Lockwood, JL	Assessing conservation conflict: Does intertidal oyster aquaculture inhibit foraging behavior of migratory shorebirds?	ECOSPHERE	11		2020
Matt_Direct est_2020	0	NA	NA	NA	Matter, SF; Goff, J; Keyghobadi, N; Roland, J	Direct estimates of metapopulation capacity from dispersal show high interannual variability, but little effect of recent forest encroachment on network persistence	LANDSCAPE ECOLOGY	35	675-688	2020
Maty_Timing of _2013	0	NA	NA	NA	Matyjasiak, P.	Timing of arrival from spring migration is associated with flight performance in the migratory barn swallow.	Behavioral Ecology and Sociobiology 67(1): 91-100.	67	91-100	2013
May,_Spatio-tem_2020	0	NA	NA	NA	May, C; Burness, G; Morrison, B; Fox, MG	Spatio-temporal patterns of occupation and density by an invasive fish in streams	BIOLOGICAL INVASIONS	22	2143-2161	2020
Maze_Interannua_ 2011	0	NA	NA	NA	Mazerolle, D. F., et al.	Interannual flexibility in breeding phenology of a Neotropical migrant songbird in response to weather conditions at breeding and wintering areas.	Ecoscience 18(1): 18-25.	18	18-25	2011

McCl_Energetic_2019	0	NA	NA	NA	McClain, SE; Hagy, HM; Hine, CS; Yetter, AP; Jacques, CN; Simpson, JW	Energetic implications of floodplain wetland restoration strategies for waterfowl	RESTORATION ECOLOGY	27	168-177	2019
McCl_MIGRATION_1994	0	NA	NA	NA	McClelland, B. R., et al.	MIGRATION ECOLOGY OF BALD EAGLES FROM AUTUMN CONCENTRATIONS IN GLACIER NATIONAL-PARK, MONTANA.	Wildlife Monographs(125): 5-61.	NA	5-61	1994
McGu_Light enou_2011	1	JN82	0	2-Study does assess both migratory and non-migratory group within population	McGuire, L. P. and J. M. Ratcliffe	Light enough to travel: migratory bats have smaller brains, but not larger hippocampi, than sedentary species.	Biology Letters 7(2): 233-236.	7	233-236	2011
McKe_Winter rai_2013	0	NA	NA	NA	McKellar, A. E., et al.	Winter rainfall predicts phenology in widely separated populations of a migrant songbird.	Oecologia 172(2): 595-605.	172	595-605	2013
McKi_Ontogeneti_2015	1	JN83	1	NA	McKinney, G. J., et al.	Ontogenetic changes in embryonic and brain gene expression in progeny produced from migratory and resident Oncorhynchus mykiss.	Molecular Ecology 24(8): 1792-1809.	24	1792-1809	2015
Meed_Changes in_2021	0	NA	NA	NA	Meeder, JF; Parkinson, RW; Ogurcak, D; Ross, MS; Kominoski, JS	Changes in Sediment Organic Carbon Accumulation under Conditions of Historical Sea-Level Rise, Southeast Saline Everglades, Florida, USA	WETLANDS	41		2021
Meis_Spatial mi_2018	0	NA	NA	NA	Meisingset, E. L., et al.	Spatial mismatch between management units and movement ecology of a partially migratory ungulate.	Journal of Applied Ecology 55(2): 745-753.	55	745-753	2018
Mell_Interannua_2016	1	JN84	0	2-Study does assess both migratory and non-migratory group within population	Meller, K., et al.	Interannual variation and long-term trends in proportions of resident individuals in partially migratory birds.	Journal of Animal Ecology 85(2): 570-580.	85	570-580	2016
Mell_Seasonal d_2015	0	NA	NA	NA	Mellone, U., et al.	Seasonal differences in migration patterns of a soaring bird in relation to environmental conditions: a multi-scale approach.	Behavioral Ecology and Sociobiology 69(1): 75-82.	69	75-82	2015
Menc_Conservati_2020	0	NA	NA	NA	Menchaca, A; Arteaga, MC;	Conservation units and historical matrilineal structure in the tequila bat	GLOBAL ECOLOGY AND	23		2020

					Medellin, RA; Jones, G	(Leptonycteris yerbabuenae)	CONSERVATION			
Mend_Individual_2020	1	JN135	0	4-Study did not apply frequentist statistical approach with effect size	Mendez, V; Alves, JA; Porisson, B; Marca, A; Gunnarsson, TG; Gill, JA	Individual variation in migratory behavior in a subarctic partial migrant shorebird	BEHAVIORAL ECOLOGY	31	672-679	2020
Merr_Density-De_2020	1	JN132	0	4-Study did not apply frequentist statistical approach with effect size	Merrill, E; Killeen, J; Pettit, J; Trottier, M; Martin, H; Berg, J; Bohm, H; Eggeman, S; Hebblewhite, M	Density-Dependent Foraging Behaviors on Sympatric Winter Ranges in a Partially Migratory Elk Population	FRONTIERS IN ECOLOGY AND EVOLUTION	8		2020
Meun_Proximate_2008	0	NA	NA	NA	Meunier, J., et al.	Proximate cues for a short-distance migratory species: an application of survival analysis.	Journal of Wildlife Management 72(2): 440-448.	72	440-448	2008
Mich_Distinctm_2008	1	JN85	1	NA	Michel, C., et al.	Distinct migratory and non-migratory ecotypes of an endemic New Zealand eleotrid (Gobiomorphus cotidianus) - implications for incipient speciation in island freshwater fish species.	Bmc Evolutionary Biology 8.	8		2008
Mikh_Geomorphol_2020	0	NA	NA	NA	Mikheev, PB; Jarvis, MG; Matthaei, CD; Ingram, T; Nikiforov, AI; Closs, GP	Geomorphological features drive spatiotemporal dynamics of young-of-the-year brown trout populations in a large New Zealand river catchment	FRESHWATER BIOLOGY	65	1392-1400	2020
Mila_Seasonalo_2021	0	NA	NA	NA	Milankovic, HR; Ray, ND; Gentle, LK; Kruger, C; Jacobs, E; Ferreira, CJ	Seasonal occurrence and sexual segregation of great white sharks Carcharodon carcharias in Mossel Bay, South Africa	ENVIRONMENTAL BIOLOGY OF FISHES	104	555-568	2021
Mill_Bird migra_2008	0	NA	NA	NA	Miller-Rushing, A. J., et al.	Bird migration times, climate change, and changing population sizes.	Global Change Biology 14(9): 1959-1972.	14	1959-1972	2008
Mill_Variation_2012	1	JN86	1	NA	Miller, M. P., et al.	Variation in Migratory Behavior Influences Regional Genetic Diversity and Structure among American Kestrel Populations (Falco sparverius) in North America.	Journal of Heredity 103(4): 503-514.	103	503-514	2012
Mini_Leukocyte_2018	0	NA	NA	NA	Minias, P., et al.	Leukocyte profiles are associated with longevity and survival, but not migratory	Functional Ecology 32(2): 369-378.	32	369-378	2018

						effort: A comparative analysis of shorebirds.				
Misu_Distributi_1998	0	NA	NA	NA	Misund, O. A., et al.	Distribution, migration and abundance of Norwegian spring spawning herring in relation to the temperature and zooplankton biomass in the Norwegian Sea as recorded by coordinated surveys in spring and summer 1996.	Sarsia 83: 117-127.	83	117-127	1998
Mitc_Automated _2015	0	NA	NA	NA	Mitchell, G. W., et al.	Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird.	Movement Ecology 3.	3	NA	2015
Mitc_Timing of _2012	0	NA	NA	NA	Mitchell, G. W., et al.	Timing of breeding carries over to influence migratory departure in a songbird: an automated radiotracking study.	Journal of Animal Ecology 81(5): 1024-1033.	81	1024-1033	2012
Mitr_The influe_2006	0	NA	NA	NA	Mitrus, C.	The influence of male age and phenology on reproductive success of the red-breasted flycatcher (Ficedula parva Bechst.).	Annales Zoologici Fennici 43(4): 358-365.	43	358-365	2006
Moe,_Twilight f_2021	0	NA	NA	NA	Moe, B; et al.	Twilight foraging enables European shags to survive the winter across their latitudinal range	MARINE ECOLOGY PROGRESS SERIES	676	145-157	2021
Moll_Extrapair _2003	0	NA	NA	NA	Moller, A. P., et al.	Extrapair paternity in relation to sexual ornamentation, arrival date, and condition in a migratory bird.	Behavioral Ecology 14(5): 707-712.	14	707-712	2003
Moll_Heritabili_2001	0	NA	NA	NA	Moller, A. P.	Heritability of arrival date in a migratory bird.	Proceedings of the Royal Society B-Biological Sciences 268(1463): 203-206.	268	203-206	2001
Moll_Loss of mi_2014	1	JN87	0	4-Study did not apply frequentist statistical approach with effect size	Moller, A. P., et al.	Loss of migration and urbanization in birds: a case study of the blackbird (Turdus merula).	Oecologia 175(3): 1019-1027.	175	1019-1027	2014

Moll_Morphologi_2017	0	NA	NA	NA	Moller, A. P., et al.	Morphological constraints on changing avian migration phenology.	Journal of Evolutionary Biology 30(6): 1177-1184.	30	1177-1184	2017
Moll_Parasitism_2004	0	NA	NA	NA	Moller, A. P., et al.	Parasitism, immunity, and arrival date in a migratory bird, the barn swallow.	Ecology 85(1): 206-219.	17	603-612	2004
Moll_PHENOTYPE-_1994	0	NA	NA	NA	Moller, A. P.	PHENOTYPE-DEPENDENT ARRIVAL TIME AND ITS CONSEQUENCES IN A MIGRATORY BIRD.	Behavioral Ecology and Sociobiology 35(2): 115-122.	35	115-122	1994
Moll_Repeatedi_2020	0	NA	NA	NA	Moller, M; Liu, J; Li, Y; Li, JH; Ye, LJ; Mill, R; Thomas, P; Li, DZ; Gao, LM	Repeated intercontinental migrations and recurring hybridizations characterise the evolutionary history of yew (Taxus L.)	MOLECULAR PHYLOGENETICS AND EVOLUTION	153		2020
Moll_Tardy fema_2007	0	NA	NA	NA	Moller, A. P.	Tardy females, impatient males: protandry and divergent selection on arrival date in the two sexes of the barn swallow.	Behavioral Ecology and Sociobiology 61(8): 1311-1319.	61	1311-1319	2007
Mona_Population_2021	0	NA	NA	NA	Monakhov, VG; Ranyuk, MN; Modorov, MV	Population Structure of Sable in the Baikal Mountain Land: Analysis of Genetic and Phenotypic Traits	RUSSIAN JOURNAL OF ECOLOGY	52	155-164	2021
Monk_DO MIGRANT_1995	0	NA	NA	NA	Monkkonen, M.	DO MIGRANT BIRDS HAVE MORE POINTED WINGS - A COMPARATIVE-STUDY.	Evolutionary Ecology 9(5): 520-528.	9	520-528	1995
Mont_Timing of_2011	0	NA	NA	NA	Monteith, K. L., et al.	Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics.	Ecosphere 2(4).	2		2011
Moor_Genomicsa_2017	0	NA	NA	NA	Moore, J. S., et al.	Genomics and telemetry suggest a role for migration harshness in determining overwintering habitat choice, but not gene flow, in anadromous Arctic Char.	Molecular Ecology 26(24): 6784-6800.	26	6784-6800	2017
Mora_Out of sig_2018	0	NA	NA	NA	Morant, J; Zabala, J; Martinez, JE; Zuberogoitia, I	Out of sight, out of mind? Testing the effects of overwinter habitat alterations on breeding territories of a migratory endangered species	ANIMAL CONSERVATION	21	465-473	2018
Mori_Intra-and_2020	0	NA	NA	NA	Morita, K; Fukuwaka, MA	Intra- and interspecific density-dependent growth	ECOLOGICAL RESEARCH	35	106-112	2020

						and maturation of Pacific salmon in the Bering Sea				
Mori_Temperatur_2014	1	JN88	0	5-Simulation study or systematic review	Morita, K., et al.	Temperature-dependent variation in alternative migratory tactics and its implications for fitness and population dynamics in a salmonid fish.	Journal of Animal Ecology 83(6): 1268-1278.	83	1268-1278	2014
Morr_Environmen_2020	0	NA	NA	NA	Morrice, KJ; Baptista, AM; Burke, BJ	Environmental and behavioral controls on juvenile Chinook salmon migration pathways in the Columbia River estuary	ECOLOGICAL MODELLING	427		2020
Morr_Freshwater_2021	1	JN128	0	2-Study does assess both migratory and non-migratory group within population	Morrison, CM; Gallagher, CP; Tierney, KB; Howland, KL	Freshwater early life growth influences partial migration in populations of Dolly Varden (Salvelinus malma malma)	POLAR BIOLOGY	44	1353-1364	2021
Moun_Vireo song_2001	0	NA	NA	NA	Mountjoy, J. and D. W. Leger	Vireo song repertoires and migratory distance: three sexual selection hypotheses fail to explain the correlation.	Behavioral Ecology 12(1): 98-102.	12	98-102	2001
Mour_Pliocene O_2019	0	NA	NA	NA	Moura, CCD; Bastian, HV; Bastian, A; Wang, EJ; Wang, XJ; Wink, M	Pliocene Origin, Ice Ages and Postglacial Population Expansion Have Influenced a Panmictic Phylogeography of the European Bee-Eater Merops apiaster	DIVERSITY-BASEL	11		2019
Mull_Nocturnal_2018	0	NA	NA	NA	Muller, F., et al.	Nocturnal departure timing in songbirds facing distinct migratory challenges.	Journal of Animal Ecology 87(4): 1102-1115.	87	1102-1115	2018
Myst_Parasite l_2016	1	JN89	0	4-Study did not apply frequentist statistical approach with effect size	Mysterud, A., et al.	Parasite load and seasonal migration in red deer.	Oecologia 180(2): 401-407.	180	401-407	2016
Myst_Partial mi_2011	1	JN90	1	NA	Mysterud, A., et al.	Partial migration in expanding red deer populations at northern latitudes - a role for density dependence?	Oikos 120(12): 1817-1825.	120	1817-1825	2011
Myst_Plant phen_2001	0	NA	NA	NA	Mysterud, A., et al.	Plant phenology, migration and geographical variation in body weight of a large herbivore: the effect of a variable topography.	Journal of Animal Ecology 70(6): 915-923.	70	915-923	2001
Myst_The role o_2017	1	JN91	0	4-Study did not apply frequentist statistical approach with effect size	Mysterud, A., et al.	The role of landscape characteristics for forage maturation and nutritional	Ecology and Evolution 7(12): 4448-4455.	7	4448-4455	2017

						benefits of migration in red deer.				
Myst_Ungulatem_2013	0	NA	NA	NA	Mysterud, A.	Ungulate migration, plant phenology, and large carnivores: The times they are a-changin'.	Ecology 94(6): 1257-1261.	94	1257-1261	2013
Nagy_Uniqueness_2019	0	NA	NA	NA	Nagylaki, T; Su, LL; Dupont, TF	Uniqueness and multiplicity of clines in an environmental pocket	THEORETICAL POPULATION BIOLOGY	130	106-131	2019
Nana_Estimation_2015	0	NA	NA	NA	Nanami, A., et al.	Estimation of spawning migration distance of the white-streaked grouper (Epinephelus ongus) in an Okinawan coral reef system using conventional tag-and-release.	Environmental Biology of Fishes 98(5): 1387-1397.	98	1387-1397	2015
Nasl_IMPORTANCE_1993	1	JN93	0	2-Study does assess both migratory and non-migratory group within population	Naslund, I., et al.	IMPORTANCE OF HABITAT PRODUCTIVITY DIFFERENCES, COMPETITION AND PREDATION FOR THE MIGRATORY BEHAVIOR OF ARCTIC CHARR.	Oikos 66(3): 538-546.	66	538-546	1993
Nasl_UPSTREAMM_1992	1	JN92	0	2-Study does assess both migratory and non-migratory group within population	Naslund, I.	UPSTREAM MIGRATORY BEHAVIOR IN LANDLOCKED ARCTIC CHARR.	Environmental Biology of Fishes 33(3): 265-274.	33	265-274	1992
Naum_Investigat_2021	0	NA	NA	NA	Naumova, EY; Rzhepka, TP; Makarov, MM; Olshukov, AS; Kucher, KM; Magomedova, MZ; Troitskaya, ES	Investigation of the ecology of winter plankton of Lake Baikal using complex instrumental methods	SOUTH OF RUSSIA-ECOLOGY DEVELOPMENT	16	59-67	2021
Nave_Infection_2020	0	NA	NA	NA	Naven Narayanan; Binning, SA; Shaw, AK	Infection state can affect host migratory decisions	OIKOS	129	1493-1503	2020
Nedz_Solublecu_2021	0	NA	NA	NA	Nedzvetsky, VS; Gasso, VY; Agca, CA; Sukharenko, EV	Soluble curcumin ameliorates motility, adhesiveness and abrogate parthanatos in cadmium-exposed retinal pigment epithelial cells	BIOSYSTEMS DIVERSITY	29	235-243	2021
Newt_LongestSa_2017	0	NA	NA	NA	Newton, R. E., et al.	Longest Sage-Grouse Migratory Behavior Sustained by Intact Pathways.	Journal of Wildlife Management 81(6): 962-972.	81	962-972	2017
Nieh_Ecological_2006	0	NA	NA	NA	Niehaus, A. C. and R. C. Ydenberg	Ecological factors associated with the breeding and	Polar Biology 30(1): 11-17.	30	17-Nov	2006

						migratory phenology of high-latitude breeding western sandpipers.				
Niel_Forecastin_2022	0	NA	NA	NA	Niella, Y; Butcher, P; Holmes, B; Barnett, A; Harcourt, R	Forecasting intraspecific changes in distribution of a wide-ranging marine predator under climate change	OECOLOGIA			2022
Nils_Basal meta_2011	1	JN94	1	NA	Nilsson, A. L. K., et al.	Basal metabolic rate and energetic cost of thermoregulation among migratory and resident blue tits.	Oikos 120(12): 1784-1789.	120	1784-1789	2011
Nils_Difference_2013	0	NA	NA	NA	Nilsson, C., et al.	Differences in Speed and Duration of Bird Migration between Spring and Autumn.	American Naturalist 181(6): 837-845.	181	837-845	2013
Nils_The effect_2006	1	JN95	0	2-Study does assess both migratory and non-migratory group within population	Nilsson, A. L. K., et al.	The effect of climate change on partial migration - the blue tit paradox.	Global Change Biology 12(10): 2014-2022.	12	2014-2022	2006
Norb_Partial al_2017	1	JN96	0	2-Study does assess both migratory and non-migratory group within population	Norbu, N., et al.	Partial altitudinal migration of the Near Threatened satyr tragopan Tragopan satyra in the Bhutan Himalayas: implications for conservation in mountainous environments.	Oryx 51(1): 166-173.	51	166-173	2017
Nore_Wind-assoc_2020	0	NA	NA	NA	Norevik, G; Akesson, S; Artois, T; Beenaerts, N; Conway, G; Cresswell, B; Evens, R; Henderson, I; Jiguet, F; Hedenstrom, A	Wind-associated detours promote seasonal migratory connectivity in a flapping flying long-distance avian migrant	JOURNAL OF ANIMAL ECOLOGY	89	635-646	2020
Norm_Living wit_2020	0	NA	NA	NA	Normandeau, J; Kutz, SJ; Hebblewhite, M; Merrill, EH	Living with liver flukes: Does migration matter?	INTERNATIONAL JOURNAL FOR PARASITOLOGY-PARASITES AND WILDLIFE	12	76-84	2020
Noro_Post-depos_2020	0	NA	NA	NA	Noro, K; Takenaka, N	Post-depositional loss of nitrate and chloride in Antarctic snow by photolysis and sublimation: a field investigation	POLAR RESEARCH	39		2020

Nort_Fine-scale_2014	0	NA	NA	NA	Northrup, J. M., et al.	Fine-scale genetic correlates to condition and migration in a wild cervid.	Evolutionary Applications 7(8): 937-948.	7	937-948	2014
Nosa_Movemente_2019	0	NA	NA	NA	Nosal, AP; Cartamil, DP; Wegner, NC; Lam, CH; Hastings, PA	Movement ecology of young-of-the-year blue sharks Prionace glauca and shortfin makos Isurus oxyrinchus within a putative binational nursery area	MARINE ECOLOGY PROGRESS SERIES	623	99-115	2019
Noyc_Seasonalm_2011	0	NA	NA	NA	Noyce, K. V. and D. L. Garshelis	Seasonal migrations of black bears (Ursus americanus): causes and consequences.	Behavioral Ecology and Sociobiology 65(4): 823-835.	65	823-835	2011
Nune_Potential_2019	0	NA	NA	NA	Nunez-Penichet, C; Cobos, ME; Barro, A; Soberon, J	Potential migratory routes of Urania boisduvalii (Lepidoptera: Uraniidae) among host plant populations	DIVERSITY AND DISTRIBUTIONS	25	478-488	2019
O'Ma_A latitudi_2008	0	NA	NA	NA	O'Malley, K. G. and M. A. Banks	A latitudinal cline in the Chinook salmon (Oncorhynchus tshawytscha) Clock gene: evidence for selection on PolyQ length variants.	Proceedings of the Royal Society B-Biological Sciences 275(1653): 2813-2821.	275	2813-2821	2008
O'Ma_Candidate_2007	0	NA	NA	NA	O'Malley, K. G., et al.	Candidate loci reveal genetic differentiation between temporally divergent migratory runs of Chinook salmon (Oncorhynchus tshawytscha).	Molecular Ecology 16(23): 4930-4941.	16	4930-4941	2007
O'Ma_Diel feedi_2019	0	NA	NA	NA	O'Malley, BP; Stockwell, JD	Diel feeding behavior in a partially migrant Mysis population: A benthic-pelagic comparison	FOOD WEBS	20		2019
O'Ne_The effect_2018	0	NA	NA	NA	O'Neal, BJ; Stafford, JD; Larkin, RP; Michel, ES	The effect of weather on the decision to migrate from stopover sites by autumn-migrating ducks	MOVEMENT ECOLOGY	6		2018
Ogon_Migratory_2009	1	JN97	0	4-Study did not apply frequentist statistical approach with effect size	Ogonowski, M. S. and C. J. Conway	Migratory decisions in birds: extent of genetic versus environmental control.	Oecologia 161(1): 199-207.	161	199-207	2009
Ohms_The evolut_2019	0	NA	NA	NA	Ohms, HA; Mohapatra, A; Lytle, DA; De Leenheer, P	The evolutionary stability of partial migration under different forms of competition	THEORETICAL ECOLOGY	12	347-363	2019

Oliv_Impact of _2020	1	JN176	0	2-Study does assess both migratory and non-migratory group within population	Oliveira, IC; Alexandre, CM; Quintella, BR; Almeida, PR	Impact of flow regulation for hydroelectric production in the movement patterns, growth and condition of a potamodromous fish species	ECOHYDROLOGY	13		2020
Olss_Environmen_2006	1	JN98	1	NA	Olsson, I. C., et al.	Environmentally induced migration: the importance of food.	Ecology Letters 9(6): 645-651.	9	645-651	2006
Oppe_Does winte_2009	0	NA	NA	NA	Oppel, S. and A. N. Powell	Does winter region affect spring arrival time and body mass of king eiders in northern Alaska?	Polar Biology 32(8): 1203-1209.	32	1203-1209	2009
Orne_Tracking H_2019	0	NA	NA	NA	Ornelas, JF; Garcia, JM; Ortiz-Rodriguez, AE; Licona-Vera, Y; Gandara, E; Molina-Freaner, F; Vasquez-Aguilar, AA	Tracking Host Trees: The Phylogeography of Endemic Psittacanthus sonorae (Loranthaceae) Mistletoe in the Sonoran Desert	JOURNAL OF HEREDITY	110	229-246	2019
Osor_Relationsh_2020	0	NA	NA	NA	Osorio-Olvera, L; Yanez-Arenas, C; Martinez-Meyer, E; Peterson, T	Relationships between population densities and niche-centroid distances in North American birds	ECOLOGY LETTERS	23	555-564	2020
Oter_Basin-scal_2014	0	NA	NA	NA	Otero, J., et al.	Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (Salmo salar).	Global Change Biology 20(1): 61-75.	20	61-75	2014
Ouwe_African de_2017	0	NA	NA	NA	Ouwehand, J. and C. Both	African departure rather than migration speed determines variation in spring arrival in pied flycatchers.	Journal of Animal Ecology 86(1): 88-97.	86	88-97	2017
Ouwe_Shifts in _2017	0	NA	NA	NA	Ouwehand, J., et al.	Shifts in hatch dates do not provide pied flycatchers with a rapid ontogenetic route to adjust offspring time schedules to climate change.	Functional Ecology 31(11): 2087-2097.	31	2087-2097	2017
Padi_Gastrointe_2020	0	NA	NA	NA	Padilla-Aguilar, P; et al.	Gastrointestinal helminths of waterfowl (Anatidae: Anatinae) in the Lerma marshes of central Mexico: Some pathological aspects	INTERNATIONAL JOURNAL FOR PARASITOLOGY-PARASITES AND WILDLIFE	13	72-79	2020

Pala_Changes in_2017	1	JN99	0	4-Study did not apply frequentist statistical approach with effect size	Palacin, C., et al.	Changes in bird-migration patterns associated with human-induced mortality.	Conservation Biology 31(1): 106-115.	31	106-115	2017
Papa_Telemetry _2013	1	JN100	0	2-Study does assess both migratory and non-migratory group within population	Papastamatiou, Y. P., et al.	Telemetry and random-walk models reveal complex patterns of partial migration in a large marine predator.	Ecology 94(11): 2595-2606.	94	2595-2606	2013
Pars_Maladaptiv_2020	0	NA	NA	NA	Parssinen, V; Hulthen, K; Bronmark, C; Skov, C; Brodersen, J; Baktoft, H; Chapman, B; Hansson, LA; Nilsson, PA	Maladaptive migration behaviour in hybrids links to predator-mediated ecological selection	JOURNAL OF ANIMAL ECOLOGY	89	2596-2604	2020
Pass_Roads cons_2021	1	JN144	0	2-Study does assess both migratory and non-migratory group within population	Passoni, G; et al.	Roads constrain movement across behavioural processes in a partially migratory ungulate	MOVEMENT ECOLOGY	9		2021
Pati_Identifyin_2020	0	NA	NA	NA	Patin, R; Etienne, MP; Lebarbier, E; Chamaille-Jammes, S; Benhamou, S	Identifying stationary phases in multivariate time series for highlighting behavioural modes and home range settlements	JOURNAL OF ANIMAL ECOLOGY	89	44-56	2020
Payt_Measuring _2020	0	NA	NA	NA	Payton, Q; Evans, AF; Hostetter, NJ; Roby, DD; Cramer, B; Collis, K	Measuring the additive effects of predation on prey survival across spatial scales	ECOLOGICAL APPLICATIONS	30		2020
Peco_Using citi_2019	0	NA	NA	NA	Pecorelli, JP; Macphie, KH; Hebditch, C; Clifton-Dey, DRJ; Thornhill, I; Debney, AJ	Using citizen science to improve the conservation of the European Eel (Anguilla anguilla) in the Thames River Basin District	FRESHWATER SCIENCE	38	281-291	2019
Pede_Full-year _2018	0	NA	NA	NA	Pedersen, L., et al.	Full-year tracking suggests endogenous control of migration timing in a long-distance migratory songbird.	Behavioral Ecology and Sociobiology 72(8).	72	NA	2018
Peim_If and whe_2017	1	JN101	0	4-Study did not apply frequentist statistical approach with effect size	Peiman, K. S., et al.	If and when: intrinsic differences and environmental stressors influence migration in brown trout (Salmo trutta).	Oecologia 184(2): 375-384.	184	375-384	2017
Pena_Noteworthy _2020	0	NA	NA	NA	Pena-Peniche, A; Ruvalcaba-Ortega, I; Canales-Del-Castillo, R	Noteworthy Wintering Records and Habitat of LeConte's Sparrow (Ammospiza leconteii) in	AMERICAN MIDLAND NATURALIST	184	123-127	2020

						Grasslands of Coahuila, Northern Mexico				
Pere_Historical_2004	1	JN102	1	NA	Perez-Tris, J., et al.	Historical diversification of migration patterns in a passerine bird.	Evolution 58(8): 1819-1832.	58	1819-1832	2004
Pere_When males_2014	1	JN103	0	4-Study did not apply frequentist statistical approach with effect size	Perez, C., et al.	When males are more inclined to stay at home: insights into the partial migration of a pelagic seabird provided by geolocators and isotopes.	Behavioral Ecology 25(2): 313-319.	25	313-319	2014
Perr_Maternal g_2005	1	JN104	1	NA	Perry, G. M. L., et al.	Maternal genetic effects on adaptive divergence between anadromous and resident brook charr during early life history.	Journal of Evolutionary Biology 18(5): 1348-1361.	18	1348-1361	2005
Pete_Consequenc_2021	1	JN136	0	2-Study does assess both migratory and non-migratory group within population	Peterson, CJ; DeCesare, NJ; Hayes, TA; Bishop, CJ; Mitchell, MS	Consequences of migratory strategy on habitat selection by mule deer	JOURNAL OF WILDLIFE MANAGEMENT			2021
Pete_Large herb_2019	1	JN146	0	2-Study does assess both migratory and non-migratory group within population	Peters, W; et al.	Large herbivore migration plasticity along environmental gradients in Europe: life-history traits modulate forage effects	OIKOS	128	416-429	2019
Pete_Migration_2017	1	JN105	1	NA	Peters, W., et al.	Migration in geographic and ecological space by a large herbivore.	Ecological Monographs 87(2): 297-320.	87	297-320	2017
Peti_Susceptibi_2021	0	NA	NA	NA	Petit, G; Bleve, G; Gallo, A; Mita, G; Montanaro, G; Nuzzo, V; Zambonini, D; Pitacco, A	Susceptibility to Xylella fastidiosa and functional xylem anatomy in Olea europaea: revisiting a tale of plant-pathogen interaction	AOB PLANTS	13		2021
Phil_Shifting T_2016	1	JN106	0	2-Study does assess both migratory and non-migratory group within population	Phillis, C. C., et al.	Shifting Thresholds: Rapid Evolution of Migratory Life Histories in Steelhead/Rainbow Trout, Oncorhynchus mykiss.	Journal of Heredity 107(1): 51-60.	107	51-60	2016
Phil_Summer dis_2005	0	NA	NA	NA	Phillips, R. A., et al.	Summer distribution and migration of nonbreeding albatrosses: Individual consistencies and implications for conservation.	Ecology 86(9): 2386-2396.	86	2386-2396	2005

Pica_Movementr_2019	0	NA	NA	NA	Picardi, S; Basille, M; Peters, W; Ponciano, JM; Boitani, L; Cagnacci, F	Movement responses of roe deer to hunting risk	JOURNAL OF WILDLIFE MANAGEMENT	83	43-51	2019
Pica_Partialmi_2020	0	NA	NA	NA	Picardi, S; Frederick, PC; Borkhataria, RR; Basille, M	Partial migration in a subtropical wading bird in the southeastern United States	ECOSPHERE	11		2020
Pine_Migration,_2011	0	NA	NA	NA	Pinet, P., et al.	Migration, wintering distribution and habitat use of an endangered tropical seabird, Barau's petrel Pterodroma baraui.	Marine Ecology Progress Series 423: 291-302.	423	291-302	2011
Plum_Is supplem_2015	0	NA	NA	NA	Plummer, K. E., et al.	Is supplementary feeding in gardens a driver of evolutionary change in a migratory bird species?	Global Change Biology 21(12): 4353-4363.	21	4353-4363	2015
Pola_TIMING OF _2012	0	NA	NA	NA	Polakowski, M. and L. Jankowiak	TIMING OF AUTUMN MIGRATION AND BIOMETRIC CHARACTERISTICS OF MIGRATING POPULATIONS OF EUROPEAN ROBIN (ERITHACUS RUBECULA L., 1758) IN NORTH-EASTERN POLAND.	Polish Journal of Ecology 60(4): 797-804.	60	797-804	2012
Ponc_Similar at_2021	0	NA	NA	NA	Ponchon, A; Gamble, A; Tornos, J; Delord, K; Barbraud, C; Travis, JMJ; Weimerskirch, H; Boulinier, T	Similar at-sea behaviour but different habitat use between failed and successful breeding albatrosses	MARINE ECOLOGY PROGRESS SERIES	678	183-196	2021
Powe_Biases in _2021	0	NA	NA	NA	Powers, KE; Burroughs, LA; Harris, NI; Harris, RC	Biases in Bird-window Collisions: A Focus on Scavengers and Detection Rates by Observers	SOUTHEASTERN NATURALIST	20	293-307	2021
Pras_Ecological_2021	0	NA	NA	NA	Prasad, A; Leites, L	Ecological analysis of intraspecific variability of eastern white pine (Pinus strobus) under climate change by combining provenance and demographic data	LANDSCAPE ECOLOGY			2021
Prat_Prioritizi_2019	0	NA	NA	NA	Pratt, AC; Smith, KT; Beck, JL	Prioritizing seasonal habitats for comprehensive conservation of a partially migratory species	GLOBAL ECOLOGY AND CONSERVATION	17		2019

Prav_The relati_2006	1	JN107	0	4-Study did not apply frequentist statistical approach with effect size	Pravosudov, V. V., et al.	The relationship between migratory behaviour, memory and the hippocampus: an intraspecific comparison.	Proceedings of the Royal Society B-Biological Sciences 273(1601): 2641-2649.	273	2641-2649	2006
Pret_Movement p_2020	0	NA	NA	NA	Pretorius, MD; Leeuwner, L; Tate, GJ; Botha, A; Michael, MD; Durgapersad, K; Chetty, K	Movement patterns of lesser flamingos Phoeniconaias minor: nomadism or partial migration?	WILDLIFE BIOLOGY	2020		2020
Prod_A reversal_2017	0	NA	NA	NA	Prodon, R., et al.	A reversal of the shift towards earlier spring phenology in several Mediterranean reptiles and amphibians during the 1998-2013 warming slowdown.	Global Change Biology 23(12): 5481-5491.	23	5481-5491	2017
Prov_Drivers of_2018	0	NA	NA	NA	Provinciato, I. C. C., et al.	Drivers of wing shape in a widespread Neotropical bird: a dual role of sex-specific and migration-related functions.	Evolutionary Ecology 32(4): 379-393.	32	379-393	2018
Qiu,_Niche Shif_2021	0	NA	NA	NA	Qiu, T; Sharma, S; Woodall, CW; Clark, JS	Niche Shifts From Trees to Fecundity to Recruitment That Determine Species Response to Climate Change	FRONTIERS IN ECOLOGY AND EVOLUTION	9		2021
Quin_Environmen_1996	0	NA	NA	NA	Quinn, T. P. and D. J. Adams	Environmental changes affecting the migratory timing of American shad and sockeye salmon.	Ecology 77(4): 1151-1162.	77	1151-1162	1996
Ramo_Evaluating_2021	0	NA	NA	NA	Ramos-Jiliberto, R; Herrera, RJ	Evaluating Social Policy Scenarios for Tourism Development of Baru Island (Colombia) Using Structural Qualitative Modeling	FRONTIERS IN ECOLOGY AND EVOLUTION	9		2021
Raut_Genomic Ad_2021	0	NA	NA	NA	Rautsaw, RM; et al.	Genomic Adaptations to Salinity Resist Gene Flow in the Evolution of Floridian watersnakes	MOLECULAR BIOLOGY AND EVOLUTION	38	745-760	2021
Ravi_Patterns o_2021	0	NA	NA	NA	Ravinet, M; Kume, M; Ishikawa, A; Kitano, J	Patterns of genomic divergence and introgression between Japanese stickleback species with overlapping breeding habitats	JOURNAL OF EVOLUTIONARY BIOLOGY	34	114-127	2021

Rayl_Elk migrat_2021	1	JN152	0	4-Study did not apply frequentist statistical approach with effect size	Rayl, ND; Merkle, JA; Proffitt, KM; Almberg, ES; Jones, JD; Gude, JA; Cross, PC	Elk migration influences the risk of disease spillover in the Greater Yellowstone Ecosystem	JOURNAL OF ANIMAL ECOLOGY	90	1264-1275	2021
Read_The effect_1998	0	NA	NA	NA	Reading, C. J.	The effect of winter temperatures on the timing of breeding activity in the common toad Bufo bufo.	Oecologia 117(4): 469-475.	117	469-475	1998
Reid_Among-indi_2020	1	JN133	0	2-Study does assess both migratory and non-migratory group within population	Reid, JM; Souter, M; Fenn, SR; Acker, P; Payo-Payo, A; Burthe, SJ; Wanless, S; Daunt, F	Among-individual and within-individual variation in seasonal migration covaries with subsequent reproductive success in a partially migratory bird	PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	287		2020
Resa_Partial mi_2020	1	JN129	1	NA	Resano-Mayor, J; et al.	Partial migration of White-winged snowfinches is correlated with winter weather conditions	GLOBAL ECOLOGY AND CONSERVATION	24		2020
Rese_Consequenc_2020	0	NA	NA	NA	Resendiz-Infante, C; Gauthier, G; Souchay, G	Consequences of a changing environment on the breeding phenology and reproductive success components in a long-distance migratory bird	POPULATION ECOLOGY	62	284-296	2020
Rich_Serial int_2019	0	NA	NA	NA	Richardson, DC; Bruno, EC; Edwards, HL; Green, DM; Hollander, AJ; McFadden, SR; Reid, KA; Wander, HL	Serial introductions modify a trophic cascade and partially mitigate changes in lake ecosystem structure	FRESHWATER SCIENCE	38	642-653	2019
Ride_Multi-year_2021	0	NA	NA	NA	Rider, MJ; McDonnell, LH; Hammerschlag, N	Multi-year movements of adult and subadult bull sharks (Carcharhinus leucas): philopatry, connectivity, and environmental influences	AQUATIC ECOLOGY	55	559-577	2021
Ridg_Isotopic n_2020	0	NA	NA	NA	Ridgway, MS; Piette-Lauziere, G; Bell, AH; Turgeon, J	Isotopic niche size ofCoregonus artedi(sensu lato) Increases in the presence ofMysis diluviana, expanded habitat use and phenotypic diversity	ECOLOGY AND EVOLUTION	10	11713-11726	2020

Riou_Genetic Di_2012	1	JN108	0	2-Study does assess both migratory and non-migratory group within population	Riou, S., et al.	Genetic Differentiation among Migrant and Resident Populations of the Threatened Asian Houbara Bustard.	Journal of Heredity 103(1): 64-70.	103	64-70	2012
Rise_Active mig_2018	1	JN109	1	NA	Risely, A., et al.	Active migration is associated with specific and consistent changes to gut microbiota in Calidris shorebirds.	Journal of Animal Ecology 87(2): 428-437.	87	428-437	2018
Riva_Contrastin_2007	1	JN110	0	2-Study does assess both migratory and non-migratory group within population	Rivalan, P., et al.	Contrasting responses of migration strategies in two European thrushes to climate change.	Global Change Biology 13(1): 275-287.	13	275-287	2007
Rivr_Future sui_2019	0	NA	NA	NA	Rivrud, IM; Meisingset, EL; Loe, LE; Mysterud, A	Future suitability of habitat in a migratory ungulate under climate change	PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES	286		2019
Rivr_Leave befo_2016	0	NA	NA	NA	Rivrud, I. M., et al.	Leave before it's too late: anthropogenic and environmental triggers of autumn migration in a hunted ungulate population.	Ecology 97(4): 1058-1068.	97	1058-1068	2016
Robe_Migration_2019	0	NA	NA	NA	Roberts, BH; Morrongiello, JR; King, AJ; Morgan, DL; Saunders, TM; Woodhead, J; Crook, DA	Migration to freshwater increases growth rates in a facultatively catadromous tropical fish	OECOLOGIA	191	253-260	2019
Robs_Ecological_2011	0	NA	NA	NA	Robson, D. and C. Barriocanal	Ecological conditions in wintering and passage areas as determinants of timing of spring migration in trans-Saharan migratory birds.	Journal of Animal Ecology 80(2): 320-331.	80	320-331	2011
Rodr_Coastal ch_2021	0	NA	NA	NA	Rodriguez-Santalla, I; Roca, M; Martinez-Clavel, B; Pablo, M; Moreno-Blasco, L; Blaquez, AM	Coastal changes between the harbours of Castellon and Sagunto (Spain) from the mid-twentieth century to present	REGIONAL STUDIES IN MARINE SCIENCE	46		2021
Rola_On fitness_2017	1	JN111	1	NA	Rolandsen, C. M., et al.	On fitness and partial migration in a large herbivore - migratory moose have higher reproductive performance than residents.	Oikos 126(4): 547-555.	126	547-555	2017
Rols_Individual_2013	0	NA	NA	NA	Rolshausen, G., et al.	Individual differences in migratory behavior shape population genetic structure	Ecology and Evolution 3(12): 4278-4289.	3	4278-4289	2013

						and microhabitat choice in sympatric blackcaps (Sylvia atricapilla).				
Rols_Spring arr_2010	0	NA	NA	NA	Rolshausen, G., et al.	Spring arrival along a migratory divide of sympatric blackcaps (Sylvia atricapilla).	Oecologia 162(1): 175-183.	162	175-183	2010
Rose_Diet and b_2020	0	NA	NA	NA	Roseman, EF; Riley, SC; Tucker, TR; Farha, SA; Jackson, SA; Bowser, DA	Diet and bathymetric distribution of juvenile Lake Trout Salvelinus namaycush in Lake Huron	AQUATIC ECOSYSTEM HEALTH & MANAGEMENT	23	350-365	2020
Rose_Proportion_2021	0	NA	NA	NA	Rosenberger, K; Schumacher, E; Brown, A; Hoban, S	Proportional sampling strategy often captures more genetic diversity when population sizes vary	BIOLOGICAL CONSERVATION	261		2021
Roth_Timing and_2017	0	NA	NA	NA	Roth, T., et al.	Timing and body condition of dichromatic Black Redstarts during autumn migration.	Ecology and Evolution 7(10): 3567-3573.	7	3567-3573	2017
Roug_Long-dista_2022	0	NA	NA	NA	Rougemont, Q; et al.	Long-distance migration is a major factor driving local adaptation at continental scale in Coho salmon	MOLECULAR ECOLOGY			2022
Rubo_Correlates_2005	0	NA	NA	NA	Rubolini, D., et al.	Correlates of timing of spring migration in birds: a comparative study of trans-Saharan migrants.	Biological Journal of the Linnean Society 85(2): 199-210.	85	199-210	2005
Rush_Empirical_2021	0	NA	NA	NA	Rushing, CS; Ryder, TB; Valente, JJ; Sillett, TS; Marra, PP	Empirical tests of habitat selection theory reveal that conspecific density and patch quality, but not habitat amount, drive long-distance immigration in a wild bird	ECOLOGY LETTERS	24	1167-1177	2021
Ruta_Multiple I_2019	0	NA	NA	NA	Rutaihwa, LK; et al.	Multiple Introductions of Mycobacterium tuberculosis Lineage 2-Beijing Into Africa Over Centuries	FRONTIERS IN ECOLOGY AND EVOLUTION	7		2019
Rybi_The more t_2021	0	NA	NA	NA	Rybicki, S; Hamon, KG; Simons, S; Temming, A	The more the merrier? Testing spatial resolution to simulate area closure effects on the pelagic North Sea autumn spawning herring stock and fishery	REGIONAL STUDIES IN MARINE SCIENCE	48		2021
Sabi_Migration_2002	1	JN112	0	2-Study does assess both migratory and non-migratory group within population	Sabine, D. L., et al.	Migration behavior of white-tailed deer under varying winter climate regimes in New Brunswick.	Journal of Wildlife Management 66(3): 718-728.	66	718-728	2002
Sabo_Carryover_2019	0	NA	NA	NA	Saboret, G; Ingram, T	Carryover effects of larval environment on individual	ECOLOGY AND EVOLUTION	9	10630-10643	2019

						variation in a facultatively diadromous fish				
Saha_Adoptiono_2018	1	JN113	0	2-Study does assess both migratory and non-migratory group within population	Sahashi, G. and K. Morita	Adoption of alternative migratory tactics: a view from the ultimate mechanism and threshold trait changes in a salmonid fish.	Oikos 127(2): 239-251.	127	239-251	2018
Saha_Migration_2013	1	JN114	0	2-Study does assess both migratory and non-migratory group within population	Sahashi, G. and K. Morita	Migration costs drive convergence of threshold traits for migratory tactics.	Proceedings of the Royal Society B-Biological Sciences 280(1773).	280		2013
Sain_Climatewa_2011	0	NA	NA	NA	Saino, N., et al.	Climate warming, ecological mismatch at arrival and population decline in migratory birds.	Proceedings of the Royal Society B-Biological Sciences 278(1707): 835-842.	278	835-842	2011
Sain_Climaticc_2008	0	NA	NA	NA	Saino, N. and R. Ambrosini	Climatic connectivity between Africa and Europe may serve as a basis for phenotypic adjustment of migration schedules of trans-Saharan migratory birds.	Global Change Biology 14(2): 250-263.	14	250-263	2008
Sain_Ecological_2004	0	NA	NA	NA	Saino, N., et al.	Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird.	Ecology Letters 7(1): 21-25.	7	21-25	2004
Sain_Light-leve_2015	0	NA	NA	NA	Saino, N., et al.	Light-level geolocators reveal covariation between winter plumage molt and phenology in a trans-Saharan migratory bird.	Oecologia 178(4): 1105-1112.	178	1105-1112	2015
Sain_Polymorphi_2015	0	NA	NA	NA	Saino, N., et al.	Polymorphism at the Clock gene predicts phenology of long-distance migration in birds.	Molecular Ecology 24(8): 1758-1773.	24	1758-1773	2015
Sain_Sex-depend_2017	0	NA	NA	NA	Saino, N., et al.	Sex-dependent carry-over effects on timing of reproduction and fecundity of a migratory bird.	Journal of Animal Ecology 86(2): 239-249.	86	239-249	2017
Saku_Benefitof_2003	1	JN115	0	2-Study does assess both migratory and non-migratory group within population	Sakuragi, M., et al.	Benefit of migration in a female sika deer population in eastern Hokkaido, Japan.	Ecological Research 18(4): 347-354.	18	347-354	2003

Sanc_Brachyuran_2020	0	NA	NA	NA	Sanchez-Latorre, C; Triay-Portella, R; Cosme, M; Tuya, F; Otero-Ferrer, F	Brachyuran Crabs (Decapoda) Associated with Rhodolith Beds: Spatio-Temporal Variability at Gran Canaria Island	DIVERSITY-BASEL	12		2020
Sand_Timing and_2017	0	NA	NA	NA	Sandlund, O. T., et al.	Timing and pattern of annual silver eel migration in two European watersheds are determined by similar cues.	Ecology and Evolution 7(15): 5956-5966.	7	5956-5966	2017
Sapi_Timing and_2011	0	NA	NA	NA	Sapir, N., et al.	Timing and flight mode of departure in migrating European bee-eaters in relation to multi-scale meteorological processes.	Behavioral Ecology and Sociobiology 65(7): 1353-1365.	65	1353-1365	2011
Sato_Positive a_2018	0	NA	NA	NA	Sato, DX; Kawata, M	Positive and balancing selection on SLC18A1 gene associated with psychiatric disorders and human-unique personality traits	EVOLUTION LETTERS	2	499-510	2018
Satt_Migratory _2018	1	JN147	0	4-Study did not apply frequentist statistical approach with effect size	Satterfield, DA; Maerz, JC; Hunter, MD; Flockhart, DTT; Hobson, KA; Norris, DR; Streit, H; de Roode, JC; Altizer, S	Migratory monarchs that encounter resident monarchs show life-history differences and higher rates of parasite infection	ECOLOGY LETTERS	21	1670-1680	2018
Sawy_Migratory _2019	1	JN157	0	2-Study does assess both migratory and non-migratory group within population	Sawyer, H; Merkle, JA; Middleton, AD; Dwinnell, SPH; Monteith, KL	Migratory plasticity is not ubiquitous among large herbivores	JOURNAL OF ANIMAL ECOLOGY	88	450-460	2019
Sawy_The extra _2016	1	JN116	0	2-Study does assess both migratory and non-migratory group within population	Sawyer, H., et al.	The extra mile: Ungulate migration distance alters the use of seasonal range and exposure to anthropogenic risk.	Ecosphere 7(10).	7		2016
Scha_Delineatio_2004	0	NA	NA	NA	Schabetsberger, R., et al.	Delineation of terrestrial reserves for amphibians: post-breeding migrations of Italian crested newts (Triturus c. carnifex) at high altitude.	Biological Conservation 117(1): 95-104.	117	95-104	2004
Scha_Demographi _2011	0	NA	NA	NA	Schaub, M., et al.	Demographic response to environmental variation in breeding, stopover and non-breeding areas in a migratory passerine.	Oecologia 167(2): 445-459.	167	445-459	2011

Schm_Body condi_2011	0	NA	NA	NA	Schmaljohann, H. and B. Naef-Daenzer	Body condition and wind support initiate the shift of migratory direction and timing of nocturnal departure in a songbird.	Journal of Animal Ecology 80(6): 1115-1122.	80	1115-1122	2011
Schm_Proximate _2016	0	NA	NA	NA	Schmaljohann, H., et al.	Proximate causes of avian protandry differ between subspecies with contrasting migration challenges.	Behavioral Ecology 27(1): 321-331.	27	321-331	2016
Schu_Forage Qua_2021	1	JN137	0	4-Study did not apply frequentist statistical approach with effect size	Schuyler, EM; Ellsworth, LM; Sanchez, DM; Whittaker, DG	Forage Quality and Quantity in Migratory and Resident Mule Deer Summer Ranges	RANGELAND ECOLOGY & MANAGEMENT	79	43-52	2021
Seba_Functional_2021	0	NA	NA	NA	Sebastian-Gonzalez, E; et al.	Functional traits driving species role in the structure of terrestrial vertebrate scavenger networks	ECOLOGY	102		2021
Seba_Network st_2020	0	NA	NA	NA	Sebastian-Gonzalez, E; et al.	Network structure of vertebrate scavenger assemblages at the global scale: drivers and ecosystem functioning implications	ECOGRAPHY	43	1143-1155	2020
Sedi_Dynamics o_2020	0	NA	NA	NA	Sedinger, JS; Riecke, TV; Street, PA; Fischer, JB	Dynamics of Dispersed-Nesting Black Brant on the Yukon-Kuskokwim Delta	JOURNAL OF FISH AND WILDLIFE MANAGEMENT	11	112-120	2020
Seml_PHENOTYPIC _1993	0	NA	NA	NA	Semlitsch, R. D., et al.	PHENOTYPIC VARIATION IN THE ARRIVAL TIME OF BREEDING SALAMANDERS - INDIVIDUAL REPEATABILITY AND ENVIRONMENTAL-INFLUENCES.	Journal of Animal Ecology 62(2): 334-340.	62	334-340	1993
Serg_Predator-p_2015	0	NA	NA	NA	Sergeant, C. J., et al.	Predator-prey migration phenologies remain synchronised in a warming catchment.	Freshwater Biology 60(4): 724-732.	60	724-732	2015
Serr_Non-tidal _2021	0	NA	NA	NA	Serrano, MA; Diez-Minguito, M; Valle-Levinson, A; Ortega-Sanchez, M	Non-tidal superinertial internal waves in a short microtidal submarine canyon	REGIONAL STUDIES IN MARINE SCIENCE	44		2021
Serv_The evolut_2020	0	NA	NA	NA	Servedio, MR; Hermisson, J	The evolution of partial reproductive isolation as an adaptive optimum	EVOLUTION	74	4-14	2020
Seta_Nest Site _2020	0	NA	NA	NA	Setash, CM; Kendall, WL; Olson, D	Nest Site Selection Influences Cinnamon Teal Nest Survival in Colorado	JOURNAL OF WILDLIFE MANAGEMENT	84	542-552	2020

Shah_Do fishway_2021	0	NA	NA	NA	Shahabi, M; Ghomeshi, M; Ahadiyan, J; Mohammadian, T; Katopodis, C	Do fishways stress fish? Assessment of physiological and hydraulic parameters of rainbow trout navigating a novel W-weir fishway	ECOLOGICAL ENGINEERING	169		2021
Shak_Phylogeogr_2021	0	NA	NA	NA	Shakya, SK; et al.	Phylogeography of the wide-host range panglobal plant pathogen Phytophthora cinnamomi	MOLECULAR ECOLOGY	30	5164-5178	2021
Sham_Is there a_2006	0	NA	NA	NA	Shamoun-Baranes, J., et al.	Is there a connection between weather at departure sites, onset of migration and timing of soaring-bird autumn migration in Israel?	Global Ecology and Biogeography 15(6): 541-552.	15	541-552	2006
Shaw_Host migra_2019	0	NA	NA	NA	Shaw, AK; Craft, ME; Zuk, M; Binning, SA	Host migration strategy is shaped by forms of parasite transmission and infection cost	JOURNAL OF ANIMAL ECOLOGY	88	1601-1612	2019
Shaw_Linking El_2013	0	NA	NA	NA	Shaw, A. K. and K. A. Kelly	Linking El Nino, local rainfall, and migration timing in a tropical migratory species.	Global Change Biology 19(11): 3283-3290.	19	3283-3290	2013
Shel_Environmen_2019	0	NA	NA	NA	Shelton, AO; Kelly, RP; O'Donnell, JL; Park, L; Schwenke, P; Greene, C; Henderson, RA; Beamer, EM	Environmental DNA provides quantitative estimates of a threatened salmon species	BIOLOGICAL CONSERVATION	237	383-391	2019
Sher_Migration_2008	0	NA	NA	NA	Sherrill-Mix, S. A., et al.	Migration cues and timing in leatherback sea turtles.	Behavioral Ecology 19(2): 231-236.	19	231-236	2008
Shim_Optimising_2021	0	NA	NA	NA	Shimada, T; Thums, M; Hamann, M; Limpus, CJ; Hays, GC; FitzSimmons, NN; Wildermann, NE; Duarte, CM; Meekan, MG	Optimising sample sizes for animal distribution analysis using tracking data	METHODS IN ECOLOGY AND EVOLUTION	12	288-297	2021
Silv_Bayesian e_2018	0	NA	NA	NA	Silva, NM; Rio, J; Kreutzer, S; Papageorgopoulou, C; Currat, M	Bayesian estimation of partial population continuity using ancient DNA and spatially explicit simulations	EVOLUTIONARY APPLICATIONS	11	1642-1655	2018
Sims_Low-temper_2004	0	NA	NA	NA	Sims, D. W., et al.	Low-temperature-driven early spawning migration of a temperate marine fish.	Journal of Animal Ecology 73(2): 333-341.	73	333-341	2004

Sims_Spatial re_2022	0	NA	NA	NA	Simsek, E; Dawson, E; Rather, PN; Kim, M	Spatial regulation of cell motility and its fitness effect in a surface-attached bacterial community	ISME JOURNAL			2022
Sing_From migra_2012	0	NA	NA	NA	Singh, N. J., et al.	From migration to nomadism: movement variability in a northern ungulate across its latitudinal range.	Ecological Applications 22(7): 2007-2020.	22	2007-2020	2012
Skov_Sizing up _2011	1	JN117	1	NA	Skov, C., et al.	Sizing up your enemy: individual predation vulnerability predicts migratory probability.	Proceedings of the Royal Society B-Biological Sciences 278(1710): 1414-1418.	278	1414-1418	2011
Smal_Tits on th_2010	0	NA	NA	NA	Smallegange, I. M., et al.	Tits on the move: exploring the impact of environmental change on blue tit and great tit migration distance.	Journal of Animal Ecology 79(2): 350-357.	79	350-357	2010
Smit_Arrival ti_2005	0	NA	NA	NA	Smith, R. J. and F. R. Moore	Arrival timing and seasonal reproductive performance in a long-distance migratory landbird.	Behavioral Ecology and Sociobiology 57(3): 231-239.	57	231-239	2005
Smit_Migratory _2007	0	NA	NA	NA	Smith, B. L.	Migratory Behavior of hunted elk.	Northwest Science 81(4): 251-264.	81	251-264	2007
Smol_Factors in_2013	0	NA	NA	NA	Smolinsky, J. A., et al.	Factors influencing the movement biology of migrant songbirds confronted with an ecological barrier.	Behavioral Ecology and Sociobiology 67(12): 2041-2051.	67	2041-2051	2013
Soko_Has recent_2008	0	NA	NA	NA	Sokolov, L. V. and N. S. Gordienko	Has recent climate warming affected the dates of bird arrival to the Il'men Reserve in the Southern Urals?	Russian Journal of Ecology 39(1): 56-62.	39	56-62	2008
Sote_Mesoscale _2018	0	NA	NA	NA	Sotelo, I; Thompson, G; Sabatini, M; Reta, R; Daponte, MC	Mesoscale distribution and population structure of the chaetognath Serratosagitta tasmanica (Thomson, 1947) from Southwestern Atlantic Ocean	MARINE BIOLOGY RESEARCH	14	945-960	2018
Spar_Examining _2005	0	NA	NA	NA	Sparks, T. H., et al.	Examining the total arrival distribution of migratory birds.	Global Change Biology 11(1): 22-30.	11	22-30	2005
Spit_Habitat pr_2020	1	JN140	0	4-Study did not apply frequentist statistical approach with effect size	Spitz, DB; Hebblewhite, M; Stephenson, TR	Habitat predicts local prevalence of migratory behaviour in an alpine ungulate	JOURNAL OF ANIMAL ECOLOGY	89	1032-1044	2020

Sple_Life histo_2020	0	NA	NA	NA	Splendiani, A; et al.	Life history and genetic characterisation of sea trout Salmo trutta in the Adriatic Sea	FRESHWATER BIOLOGY	65	460-473	2020
Spot_Sexual sel_2006	0	NA	NA	NA	Spottiswoode, C. N., et al.	Sexual selection predicts advancement of avian spring migration in response to climate change.	Proceedings of the Royal Society B-Biological Sciences 273(1605): 3023-3029.	273	3023-3029	2006
Srih_Phylodynam_2021	0	NA	NA	NA	Srihi, H; Chatti, N; Ben Mhadheb, M; Gharbi, J; Abid, N	Phylodynamic and phylogeographic analysis of the complete genome of the West Nile virus lineage 2 (WNV-2) in the Mediterranean basin	BMC ECOLOGY AND EVOLUTION	21		2021
Stee_Applying t_2020	0	NA	NA	NA	Steel, AE; Anderson, JJ; Mulvey, B; Smith, DL	Applying the mean free-path length model to juvenile Chinook salmon migrating in the Sacramento River, California	ENVIRONMENTAL BIOLOGY OF FISHES	103	1603-1617	2020
Step_Ongoing ch_2018	0	NA	NA	NA	Stepanian, P. M. and C. E. Wainwright	Ongoing changes in migration phenology and winter residency at Bracken Bat Cave.	Global Change Biology 24(7): 3266-3275.	24	3266-3275	2018
Stie_The potent_2020	0	NA	NA	NA	Stieglitz, TC; Dujon, AM; Peel, JR; Amice, E	The potential of marginal coastal nursery habitats for the conservation of a culturally important Caribbean marine species	DIVERSITY AND DISTRIBUTIONS	26	565-574	2020
Stra_Factors in_2013	0	NA	NA	NA	Strange, J. S.	Factors influencing the behavior and duration of residence of adult Chinook salmon in a stratified estuary.	Environmental Biology of Fishes 96(2-3): 225-243.	96	225-243	2013
Stra_Hybridizat_2021	1	JN160	1	NA	Strait, JT; Eby, LA; Kovach, RP; Muhlfeld, CC; Boyer, MC; Amish, SJ; Smith, S; Lowe, WH; Luikart, G	Hybridization alters growth and migratory life-history expression of native trout	EVOLUTIONARY APPLICATIONS	14	821-833	2021
Stre_What trigg_2006	1	JN118	0	4-Study did not apply frequentist statistical approach with effect size	Streich, W. J., et al.	What triggers facultative winter migration of Great Bustard (Otis tarda) in Central Europe?	European Journal of Wildlife Research 52(1): 48-53.	52	48-53	2006
Stud_Rainfall-i_2011	0	NA	NA	NA	Studds, C. E. and P. P. Marra	Rainfall-induced changes in food availability modify the spring departure programme of a migratory bird.	Proceedings of the Royal Society B-Biological Sciences	278	3437-3443	2011

							278(1723): 3437-3443.			
Stud_Year-round_2019	0	NA	NA	NA	Studholme, KR; Hipfner, JM; Domalik, AD; Iverson, SJ; Crossin, GT	Year-round tracking reveals multiple migratory tactics in a sentinel North Pacific seabird, Cassin's auklet	MARINE ECOLOGY PROGRESS SERIES	619	169-185	2019
Stut_Effects of_2011	0	NA	NA	NA	Stutchbury, B. J. M., et al.	Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics.	Proceedings of the Royal Society B-Biological Sciences 278(1702): 131-137.	278	131-137	2011
Sudo_Environmen_2017	0	NA	NA	NA	Sudo, R., et al.	Environmental factors affecting the onset of spawning migrations of Japanese eels (Anguilla japonica) in Mikawa Bay Japan.	Environmental Biology of Fishes 100(3): 237-249.	100	237-249	2017
Suho_Temporally_2019	0	NA	NA	NA	Suhonen, J; Jokimaki, J	Temporally Stable Species Occupancy Frequency Distribution and Abundance-Occupancy Relationship Patterns in Urban Wintering Bird Assemblages	FRONTIERS IN ECOLOGY AND EVOLUTION	7		2019
Supp_Citizen-sc_2015	0	NA	NA	NA	Supp, S. R., et al.	Citizen-science data provides new insight into annual and seasonal variation in migration patterns.	Ecosphere 6(1).	6	NA	2015
Sved_Migratory_2007	1	JN119	1	NA	Svedang, H., et al.	Migratory behaviour of Atlantic cod Gadus morhua: natal homing is the prime stock-separating mechanism.	Marine Ecology Progress Series 345: 1-12.	345	12-Jan	2007
Svin_Genetic st_2021	0	NA	NA	NA	Svinin, AO; et al.	Genetic structure, morphological variation, and gametogenic peculiarities in water frogs (Pelophylax) from northeastern European Russia	JOURNAL OF ZOOLOGICAL SYSTEMATICS AND EVOLUTIONARY RESEARCH	59	646-662	2021
Szpi_Applicatio_2021	0	NA	NA	NA	Szpiech, ZA; Novak, TE; Bailey, NP; Stevison, LS	Application of a novel haplotype-based scan for local adaptation to study high-altitude adaptation in rhesus macaques	EVOLUTION LETTERS	5	408-421	2021

Tacc_Seasonal p_2021	0	NA	NA	NA	Taccardi, EY; Bricknell, IR; Hamlin, HJ	Seasonal progression of embryo size and lipid reserves in sea lice Lepeophtheirus salmonis collected from salmon farms	MARINE ECOLOGY PROGRESS SERIES	664	79-86	2021
Taka_Comparison_2020	0	NA	NA	NA	Takahara, T; Iwai, N; Yasumiba, K; Igawa, T	Comparison of the detection of 3 endangered frog species by eDNA and acoustic surveys across 3 seasons	FRESHWATER SCIENCE	39	18-27	2020
Taka_Long-Term_2021	0	NA	NA	NA	Takashina, N	Long-Term Conservation Effects of Protected Areas in Stochastic Population Dynamics	FRONTIERS IN ECOLOGY AND EVOLUTION	9		2021
Taka_Migratory_2015	0	NA	NA	NA	Takahashi, A., et al.	Migratory movements of rhinoceros auklets in the northwestern Pacific: connecting seasonal productivities.	Marine Ecology Progress Series 525: 229-243.	525	229-243	2015
Take_First use_2019	0	NA	NA	NA	Takeuchi, A; et al.	First use of oceanic environmental DNA to study the spawning ecology of the Japanese eel Anguilla japonica	MARINE ECOLOGY PROGRESS SERIES	609	187-196	2019
Tana_Captive-br_2021	0	NA	NA	NA	Tanaka, T; Ueda, R; Sato, T	Captive-bred populations of a partially migratory salmonid fish are unlikely to maintain migratory polymorphism in natural habitats	BIOLOGY LETTERS	17		2021
Tark_Selection_2015	0	NA	NA	NA	Tarka, M., et al.	Selection and evolutionary potential of spring arrival phenology in males and females of a migratory songbird.	Journal of Evolutionary Biology 28(5): 1024-1038.	28	1024-1038	2015
Tayl_Climate wa_2008	0	NA	NA	NA	Taylor, S. G.	Climate warming causes phenological shift in Pink Salmon, Oncorhynchus gorbuscha, behavior at Auke Creek, Alaska.	Global Change Biology 14(2): 229-235.	14	229-235	2008
Tayl_Predicting_2007	1	JN120	0	5-Simulation study or systematic review	Taylor, C. M. and D. R. Norris	Predicting conditions for migration: effects of density dependence and habitat quality.	Biology Letters 3(3): 280-283.	3	280-283	2007
Tepl_Quantitati_2011	0	NA	NA	NA	Teplitsky, C., et al.	Quantitative genetics of migration syndromes: a study of two barn swallow populations.	Journal of Evolutionary Biology 24(9): 2025-2039.	24	2025-2039	2011

Ther_Mating sys_2007	1	JN121	1	NA	Theriault, V., et al.	Mating system and individual reproductive success of sympatric anadromous and resident brook charr, Salvelinus fontinalis, under natural conditions.	Behavioral Ecology and Sociobiology 62(1): 51-65.	62	51-65	2007
Thom_Natal disp_2021	0	NA	NA	NA	Thompson, HL; Caven, AJ; Hayes, MA; Lacy, AE	Natal dispersal of Whooping Cranes in the reintroduced Eastern Migratory Population	ECOLOGY AND EVOLUTION	11	12630-12638	2021
Thor_Ontogeneti_2019	0	NA	NA	NA	Thorburn, J; Neat, F; Burrett, I; Henry, LA; Bailey, DM; Jones, CS; Noble, LR	Ontogenetic Variation in Movements and Depth Use, and Evidence of Partial Migration in a Benthopelagic Elasmobranch	FRONTIERS IN ECOLOGY AND EVOLUTION	7		2019
Tibb_Causes and_2016	0	NA	NA	NA	Tibblin, P., et al.	Causes and consequences of repeatability, flexibility and individual fine-tuning of migratory timing in pike.	Journal of Animal Ecology 85(1): 136-145.	85	136-145	2016
Till_Artificial_2019	0	NA	NA	NA	Tillotson, MD; Barnett, HK; Bhuthimethee, M; Koehler, ME; Quinn, TP	Artificial selection on reproductive timing in hatchery salmon drives a phenological shift and potential maladaptation to climate change	EVOLUTIONARY APPLICATIONS	12	1344-1359	2019
Toko_Breeding p_2011	0	NA	NA	NA	Tokolyi, J. and Z. Barta	Breeding phenology determines evolutionary transitions in migratory behaviour in finches and allies.	Oikos 120(2): 184-193.	120	184-193	2011
Toku_Seasonal p_2019	0	NA	NA	NA	Tokuhiro, K; Abe, Y; Matsuno, K; Onodera, J; Fujiwara, A; Harada, N; Hirawake, T; Yamaguchi, A	Seasonal phenology of four dominant copepods in the Pacific sector of the Arctic Ocean: Insights from statistical analyses of sediment trap data	POLAR SCIENCE	19	94-111	2019
Tomo_Climate ch_2018	0	NA	NA	NA	Tomotani, B. M., et al.	Climate change leads to differential shifts in the timing of annual cycle stages in a migratory bird.	Global Change Biology 24(2): 823-835.	24	823-835	2018
Tonr_Remote est_2019	0	NA	NA	NA	Tonra, CM; Wright, JR; Matthews, SN	Remote estimation of overwintering home ranges in an elusive, migratory nocturnal bird	ECOLOGY AND EVOLUTION	9	12586-12599	2019
Torr_Temperatur_2020	0	NA	NA	NA	Torres, G; Gimenez, L	Temperature modulates compensatory responses to	FUNCTIONAL ECOLOGY	34	1564-1576	2020

						food limitation at metamorphosis in a marine invertebrate				
Tott_Avian migr_2008	0	NA	NA	NA	Tottrup, A. P., et al.	Avian migrants adjust migration in response to environmental conditions en route.	Biology Letters 4(6): 685-688.	4	685-688	2008
Tott_The annual_2012	0	NA	NA	NA	Tottrup, A. P., et al.	The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration.	Proceedings of the Royal Society B-Biological Sciences 279(1730): 1008-1016.	279	1008-1016	2012
Tsai_New insigh_2021	0	NA	NA	NA	Tsai, PY; Ko, CJ; Chia, SY; Lu, YJ; Tuanmu, MN	New insights into the patterns and drivers of avian altitudinal migration from a growing crowdsourcing data source	ECOGRAPHY	44	75-86	2021
Tshi_Partial mi_2017	1	JN122	0	2-Study does assess both migratory and non-migratory group within population	Tshipa, A., et al.	Partial migration links local surface-water management to large-scale elephant conservation in the world's largest transfrontier conservation area.	Biological Conservation 215: 46-50.	215	46-50	2017
Tsuj_Annual var_2021	0	NA	NA	NA	Tsujii, K; Otsuki, M; Akamatsu, T; Amakasu, K; Kitamura, M; Kikuchi, T; Fujiwara, A; Shirakawa, H; Miyashita, K; Mitani, Y	Annual variation of oceanographic conditions changed migration timing of bowhead whales Balaena mysticetus in the southern Chukchi Sea	POLAR BIOLOGY	44	2289-2298	2021
Tsur_Evidence f_2019	0	NA	NA	NA	Tsurui-Sato, K; Sato, Y; Kato, E; Katoh, M; Kimura, R; Tatsuta, H; Tsuji, K	Evidence for frequency-dependent selection maintaining polymorphism in the Batesian mimic Papilio polytes in multiple islands in the Ryukyus, Japan	ECOLOGY AND EVOLUTION	9	5991-6002	2019
Turj_Migration,_2020	1	JN153	1	NA	Turjeman, S; Corl, A; Wolfenden, A; Tsalyuk, M; Lublin, A; Choi, O; Kamath, PL; Getz, WM; Bowie, RCK; Nathan, R	Migration, pathogens and the avian microbiome: A comparative study in sympatric migrants and residents	MOLECULAR ECOLOGY	29	4706-4720	2020

Uyen_Allele fre_2020	0	NA	NA	NA	Uyenoyama, MK; Takebayashi, N; Kumagai, S	Allele frequency spectra in structured populations: Novel-allele probabilities under the labelled coalescent	THEORETICAL POPULATION BIOLOGY	133	130-140	2020
Vaha_Temporally_ 2011	0	NA	NA	NA	Vaha, J. P., et al.	Temporally stable population-specific differences in run timing of one-sea-winter Atlantic salmon returning to a large river system.	Evolutionary Applications 4(1): 39-53.	4	39-53	2011
Vali_Genetic de_2018	0	NA	NA	NA	Vali, U., et al.	Genetic determination of migration strategies in large soaring birds: evidence from hybrid eagles.	Proceedings of the Royal Society B-Biological Sciences 285(1884).	285	NA	2018
Van _Bioscatter_2022	0	NA	NA	NA	Van den Broeke, MS	Bioscatter transport by tropical cyclones: insights from 10 years in the Atlantic basin	REMOTE SENSING IN ECOLOGY AND CONSERVATION			2022
Van _Migration _1998	0	NA	NA	NA	Van Deelen, T. R., et al.	Migration and seasonal range dynamics of deer using adjacent deeryards in northern Michigan.	Journal of Wildlife Management 62(1): 205-213.	62	205-213	1998
van _Mismatch b_2016	0	NA	NA	NA	van Leeuwen, C. H. A., et al.	Mismatch between fishway operation and timing of fish movements: a risk for cascading effects in partial migration systems.	Ecology and Evolution 6(8): 2414-2425.	6	2414-2425	2016
Van _Phenotypic_2012	0	NA	NA	NA	Van Buskirk, J., et al.	Phenotypic plasticity alone cannot explain climate-induced change in avian migration timing.	Ecology and Evolution 2(10): 2430-2437.	2	2430-2437	2012
Van _Radar quan_2019	0	NA	NA	NA	Van den Broeke, MS	Radar quantification, temporal analysis and influence of atmospheric conditions on a roost of American Robins (Turdus migratorius) in Oklahoma	REMOTE SENSING IN ECOLOGY AND CONSERVATION	5	193-204	2019
Van _Resource a_2016	1	JN123	0	2-Study does assess both migratory and non-migratory group within population	Van Leeuwen, T. E., et al.	Resource availability and life-history origin affect competitive behavior in territorial disputes.	Behavioral Ecology 27(2): 385-392.	27	385-392	2016
van _Seasonal r_2021	1	JN145	1	NA	van Moorter, B; et al.	Seasonal release from competition explains partial migration in European moose	OIKOS	130	1548-1561	2021

Van _The influe_2021	0	NA	NA	NA	Van Den Broeke, MS; Gunkel, TJ	The influence of isolated thunderstorms and the low-level wind field on nocturnally migrating birds in central North America	REMOTE SENSING IN ECOLOGY AND CONSERVATIO N	7	187-197	2021
Van _Variable s_2009	0	NA	NA	NA	Van Buskirk, J., et al.	Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change.	Global Change Biology 15(3): 760-771.	15	760-771	2009
Vegv_Life histo_2010	0	NA	NA	NA	Vegvari, Z., et al.	Life history predicts advancement of avian spring migration in response to climate change.	Global Change Biology 16(1): 1-11.	16	11-Jan	2010
Vele_Ecological_2013	1	JN124	0	5-Simulation study or systematic review	Velez-Espino, L. A., et al.	Ecological advantages of partial migration as a conditional strategy.	Theoretical Population Biology 85: 1-11.	85	11-Jan	2013
Vilk_Changes in_2016	0	NA	NA	NA	Vilkov, E. V.	Changes in the strategy of migration of gulls (Laridae) along the western coast of the Caspian Sea as a result of environmental changes in space and time.	Contemporary Problems of Ecology 9(3): 233-253.	9	233-253	2016
Vill_Global war_2020	0	NA	NA	NA	Villen-Perez, S; Heikkinen, J; Salemaa, M; Makipaa, R	Global warming will affect the maximum potential abundance of boreal plant species	ECOGRAPHY	43	801-811	2020
Vinc_Brain regi_2015	0	NA	NA	NA	Vincze, O., et al.	Brain regions associated with visual cues are important for bird migration.	Biology Letters 11(11).	11	NA	2015
Vinc_Light enou_2016	1	JN125	0	2-Study does assess both migratory and non-migratory group within population	Vincze, O.	Light enough to travel or wise enough to stay? Brain size evolution and migratory behavior in birds.	Evolution 70(9): 2123-2133.	70	2123-2133	2016
Viss_Climate ch_2009	0	NA	NA	NA	Visser, M. E., et al.	Climate change leads to decreasing bird migration distances.	Global Change Biology 15(8): 1859-1865.	15	1859-1865	2009
Voel_Morphologi_2001	0	NA	NA	NA	Voelker, G.	Morphological correlates of migratory distance and flight display in the avian genus Anthus.	Biological Journal of the Linnean Society 73(4): 425-435.	73	425-435	2001
von _Disruptive_2016	0	NA	NA	NA	von Ronn, J. A. C., et al.	Disruptive selection without genome-wide evolution across a migratory divide.	Molecular Ecology 25(11): 2529-2541.	25	2529-2541	2016

Vu, _Population_2021	0	NA	NA	NA	Vu, NTT; Zenger, KR; Silva, CNS; Guppy, JL; Jerry, DR	Population Structure, Genetic Connectivity, and Signatures of Local Adaptation of the Giant Black Tiger Shrimp (Penaeus monodon) throughout the Indo-Pacific Region	GENOME BIOLOGY AND EVOLUTION	13		2021
Walt_Implicatio_2019	0	NA	NA	NA	Walters, RJ; Berger, D	Implications of existing local (mal)adaptations for ecological forecasting under environmental change	EVOLUTIONARY APPLICATIONS	12	1487-1502	2019
Wang_Experiment_2019	0	NA	NA	NA	Wang, YZ; Pedersen, JLM; Macdonald, SE; Nielsen, SE; Zhang, J	Experimental test of assisted migration for conservation of locally range-restricted plants in Alberta, Canada	GLOBAL ECOLOGY AND CONSERVATION	17		2019
Wata_Flight mod_2016	0	NA	NA	NA	Watanabe, Y. Y.	Flight mode affects allometry of migration range in birds.	Ecology Letters 19(8): 907-914.	19	907-914	2016
Wats_Freshwater_2021	0	NA	NA	NA	Watson, AS; Hickford, MJH; Schiel, DR	Freshwater reserves for fisheries conservation and enhancement of a widespread migratory fish	JOURNAL OF APPLIED ECOLOGY	58	2135-2145	2021
Watt_Host funct_2018	0	NA	NA	NA	Watts, AG; Saura, S; Jardine, C; Leighton, P; Werden, L; Fortin, MJ	Host functional connectivity and the spread potential of Lyme disease	LANDSCAPE ECOLOGY	33	1925-1938	2018
Webb_An Empiric_2019	0	NA	NA	NA	Webb, MH; Heinsohn, R; Sutherland, WJ; Stojanovic, D; Terauds, A	An Empirical and Mechanistic Explanation of Abundance-Occupancy Relationships for a Critically Endangered Nomadic Migrant	AMERICAN NATURALIST	193	59-69	2019
Webe_Strontium_2020	0	NA	NA	NA	Weber, M; Tacail, T; Lugli, F; Clauss, M; Weber, K; Leichliter, J; Winkler, DE; Mertz-Kraus, R; Tutken, T	Strontium Uptake and Intra-Population Sr-87/Sr-86 Variability of Bones and Teeth-Controlled Feeding Experiments With Rodents (Rattus norvegicus, Cavia porcellus)	FRONTIERS IN ECOLOGY AND EVOLUTION	8		2020
Wei,_Plant evol_2021	0	NA	NA	NA	Wei, CQ; Gao, LL; Tang, XF; Lu, XM	Plant evolution overwhelms geographical origin in shaping rhizosphere fungi across latitudes	GLOBAL CHANGE BIOLOGY	27	3911-3922	2021
Well_Intensive_2020	0	NA	NA	NA	Wells, CR; Lethbridge, M	Intensive and extensive movements of feral camels in central Australia	RANGELAND JOURNAL	42	195-210	2020

Whit_A novel qu_2020	0	NA	NA	NA	White, SL; Hanks, EM; Wagner, T	A novel quantitative framework for riverscape genetics	ECOLOGICAL APPLICATIONS	30		2020
Whit_Benefits o_2014	1	JN126	0	2-Study does assess both migratory and non-migratory group within population	White, K. S., et al.	Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population.	Ecology 95(1): 225-237.	95	225-237	2014
Wies_Pollen tra_2020	0	NA	NA	NA	Wiesenborn, WD	Pollen transport to Lycium cooperi (Solanaceae flowers by flies and moths	WESTERN NORTH AMERICAN NATURALIST	80	359-368	2020
Wilk_Migration _1996	0	NA	NA	NA	Wilkinson, G. S. and T. H. Fleming	Migration and evolution of lesser long-nosed bats Leptonycteris curasoae, inferred from mitochondrial DNA.	Molecular Ecology 5(3): 329-339.	5	329-339	1996
Will_Genomic re_2021	0	NA	NA	NA	Willis, SC; Hess, JE; Fryer, JK; Whiteaker, JM; Narum, SR	Genomic region associated with run timing has similar haplotypes and phenotypic effects across three lineages of Chinook salmon	EVOLUTIONARY APPLICATIONS	14	2273-2285	2021
Will_Rapid gene_2018	0	NA	NA	NA	Willoughby, JR; Harder, AM; Tennessen, JA; Scribner, KT; Christie, MR	Rapid genetic adaptation to a novel environment despite a genome-wide reduction in genetic diversity	MOLECULAR ECOLOGY	27	4041-4051	2018
Wils_Coastal ma_2014	0	NA	NA	NA	Wilson, S. M., et al.	Coastal marine and in-river migration behaviour of adult sockeye salmon en route to spawning grounds.	Marine Ecology Progress Series 496: 71-84.	496	71-84	2014
Wint_Movements _2021	0	NA	NA	NA	Winter, ER; Hindes, AM; Lane, S; Britton, JR	Movements of common bream Abramis brama in a highly connected, lowland wetland reveal sub-populations with diverse migration strategies	FRESHWATER BIOLOGY	66	1410-1422	2021
Wobk_Sex, age, _2021	0	NA	NA	NA	Wobker, J; Heim, W; Schmaljohann, H	Sex, age, molt strategy, and migration distance explain the phenology of songbirds at a stopover along the East Asian flyway	BEHAVIORAL ECOLOGY AND SOCIOBIOLOGY	75		2021
Wood_Differenti_2016	0	NA	NA	NA	Woodworth, B. K., et al.	Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird.	Oecologia 181(2): 413-422.	181	413-422	2016

Wood_Extreme va_2015	0	NA	NA	NA	Wood, E. M. and A. M. Pidgeon	Extreme variations in spring temperature affect ecosystem regulating services provided by birds during migration.	Ecosphere 6(11).	6	NA	2015
Wrig_Comparing _2020	0	NA	NA	NA	Wright, CA; Adams, IT; Stent, P; Ford, AT	Comparing Survival and Movements of Non-Urban and Urban Translocated Mule Deer	JOURNAL OF WILDLIFE MANAGEMENT	84	1457-1472	2020
Wyck_Evaluating_ 2018	0	NA	NA	NA	Wyckoff, T. B., et al.	Evaluating the influence of energy and residential development on the migratory behavior of mule deer.	Ecosphere 9(2).	9	NA	2018
Xu, _Migration _2021	0	NA	NA	NA	Xu, YC; Zhang, YQ; Chen, JQ	Migration under economic transition and changing climate in Mongolia	JOURNAL OF ARID ENVIRONMENTS	185		2021
Xu, _The Effect_2021	0	NA	NA	NA	Xu, Y; Shen, ZH; Zhang, JL; Zang, RG; Jiang, YX	The Effects of Multi-Scale Climate Variability on Biodiversity Patterns of Chinese Evergreen Broad-Leaved Woody Plants: Growth Form Matters	FRONTIERS IN ECOLOGY AND EVOLUTION	8		2021
Yasu_Quaternary_ 2019	0	NA	NA	NA	Yasuhara, M; Hunt, G; Okahashi, H	Quaternary deep-sea ostracods from the north-western Pacific Ocean: global biogeography and Drake-Passage, Tethyan, Central American and Arctic pathways	JOURNAL OF SYSTEMATIC PALAEONTOLOGY	17	91-110	2019
Youn_Spatiotemp_ 2014	0	NA	NA	NA	Young, J. M., et al.	Spatiotemporal dynamics of spawning aggregations of common snook on the east coast of Florida.	Marine Ecology Progress Series 505: 227-240.	505	227-240	2014
Zamp_Multiscale_ 2018	0	NA	NA	NA	Zampatti, BP; Leigh, SJ; Bice, CM; Rogers, PJ	Multiscale movements of golden perch (Percichthyidae: Macquaria ambigua) in the River Murray, Australia	AUSTRAL ECOLOGY	43	763-774	2018
Zenz_Temporal m_2018	0	NA	NA	NA	Zenzal, T. J., et al.	Temporal migration patterns between natal locations of ruby-throated hummingbirds (Archilochus colubris) and their Gulf Coast stopover site.	Movement Ecology 6.	6	NA	2018
Zhan_Effect of _2020	0	NA	NA	NA	Zhang, B; DeAngelis, DL; Ni, WM; Wang, YS; Zhai, L; Kula, A; Xu, S; Van Dyken, JD	Effect of Stressors on the Carrying Capacity of Spatially Distributed Metapopulations	AMERICAN NATURALIST	196	E46-E60	2020

Zhan_Morphologi_2019	0	NA	NA	NA	Zhang, SD; Ma, ZJ; Choi, CY; Peng, HB; Melville, DS; Zhao, TT; Bai, QQ; Liu, WL; Chan, YC; van Gils, JA; Piersma, T	Morphological and digestive adjustments buffer performance: How staging shorebirds cope with severe food declines	ECOLOGY AND EVOLUTION	9	3868-3878	2019
Zhao_Time versu_2017	0	NA	NA	NA	Zhao, M. J., et al.	Time versus energy minimization migration strategy varies with body size and season in long-distance migratory shorebirds.	Movement Ecology 5.	5	NA	2017
Zido_Zebra migr_2017	1	JN127	1	NA	Zidon, R., et al.	Zebra migration strategies and anthrax in Etosha National Park, Namibia.	Ecosphere 8(8).	8		2017
Zrin_Does hydro_2021	0	NA	NA	NA	Zrini, ZA; Sandrelli, RM; Gamperl, AK	Does hydrostatic pressure influence lumpfish (Cyclopterus lumpus) heart rate and its response to environmental challenges?	CONSERVATION PHYSIOLOGY	9		2021

Appendix II. Supplementary Material for Chapter 3

Additional information on study area

We used high-resolution GPS data from 233 adult female mule deer from four areas in the Piceance Basin of northwestern Colorado: North Ridge (53 km^2); North Magnolia (79 km^2); South Magnolia (83 km^2); and Ryan Gulch (141 km^2) (Figure S2.1). Climate in the region is characterized by warm dry summers and cold winters (Western Regional Climate Centre). Vegetation on the winter range is dominated by Pinion pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*), with the summer range being characterized by quaking aspen (*Populus tremuloides*), Douglas-fir (*Pseudotsuga menziesii*) forest, and Engelmann spruce (*Picea engelmannii*) subalpine fir (*Abies lasiocarpa*) forest at higher elevations (Garrott, White, Bartmann, Carpenter, & Alldredge, 1987; Northrup et al., 2014).

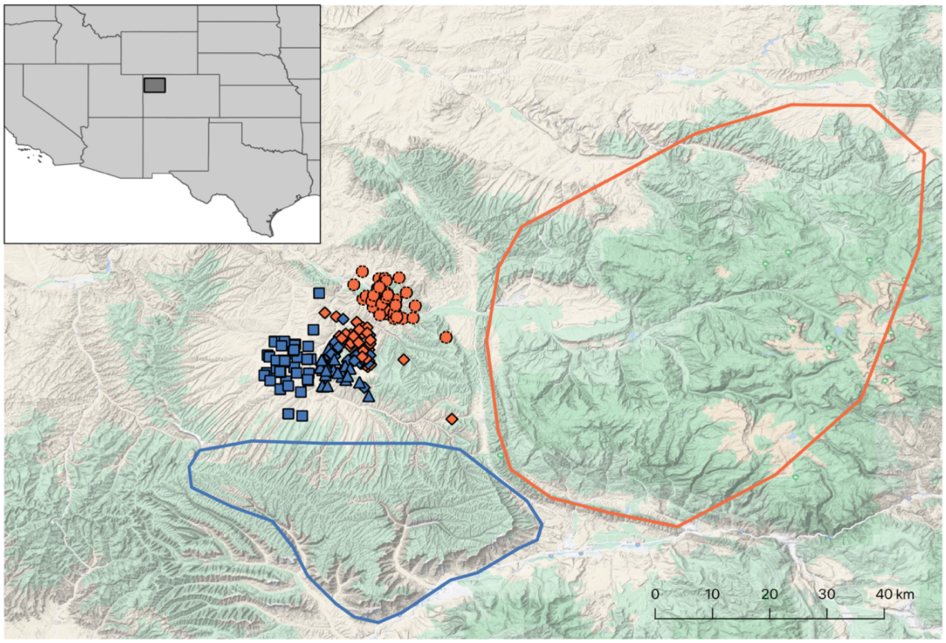

Figure S2.1. Study areas in the Piceance Basin of northwestern Colorado, USA: North Ridge (●, 53 km^2); North Magnolia (◆, 79 km^2); South Magnolia (▲, 83 km^2); and Ryan Gulch (■, 141 km^2). Symbols represent study group and colour represents migratory direction with blue indicating north-south migration and orange indicating east-west migration. Points shown are the centroid of all GPS locations per individual while on the winter range. Eastern and southern summer ranges are designated by the orange and blue outlines respectively.

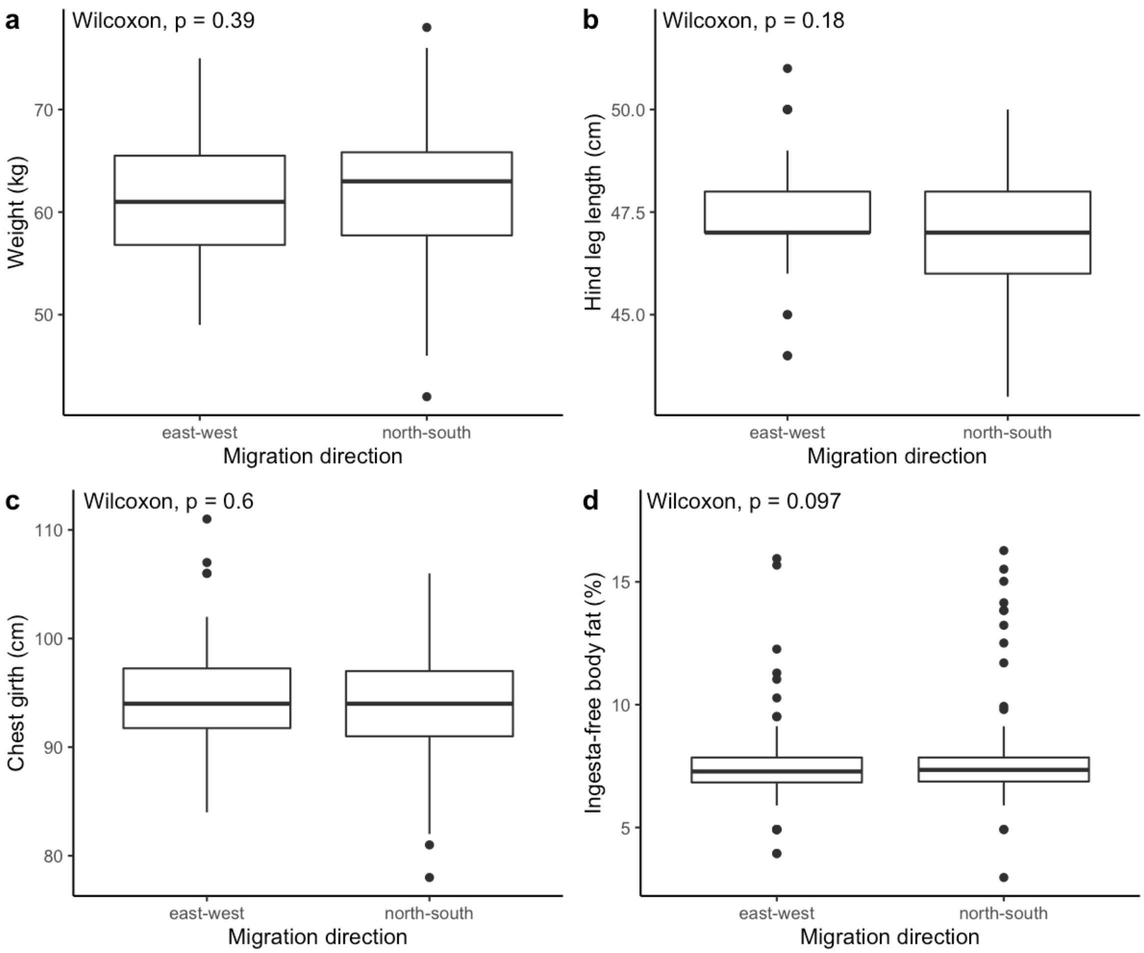

Figure S2.2. Box plot of body size traits a) weight, b) hind leg length, c) chest girth, d) ingesta-free body fat percentage for mule deer in the Piceance Basin, Colorado, USA. Wilcoxon t-test was used to compare means between east-west and north-south migrating groups, and p-value for each comparison is shown.

Sequencing information

Table S2.1. Number of reads remaining after each filtering step and final genome wide coverage for each pool.

	Initial	**Deduplicateded**	**Unique**	**Coverage**
North Magnolia	885,404,886	790,433,632	648,399,900	35.6
North Magnolia (South)	685,338,615	770,955,285	631,223,528	34.6
North Ridge	890,861,042	633,029,250	649,381,675	35.6
Ryan Gulch	879,559,090	785,577,726	514,932,256	35.4
South Magnolia	848,004,029	752,455,051	616,581,653	33.8

Genome scan for population differentiation in migratory direction using less conservative outlier criteria

We repeated the analysis explained in the main text using the same empirical F_{ST} approach (Akey et al., 2010; Cavedon et al., 2019) to identify potential SNPs relating to migratory phenotype between north-migrating and south-migrating pools, but with a less conservative outlier selection criteria. We defined an outlier window as one that was within the top 1% of F_{ST} values in at least 3/6 of the opposite phenotype comparisons and was not within the top 1% of F_{ST} values in all 4 of the same phenotype comparisons (Cavedon et al., 2019).

The analysis was identical as outlined in the main text of Chapter 3. For all outlier windows, we examined the proximity to genic regions for all SNPs identified within outlier regions using SnpEff v4.3t (Cingolani et al., 2012). We evaluated genetic differentiation between east-west-migrating and north-south-migrating pools by conducting a principal component analysis (PCA) using allele frequencies for the SNPs within outlier regions. And finally identify shared gene pathways among outlier SNPs we used an analysis of gene ontology (GO) terms. We used the program Gowinda v1.12 (Kofler & Schlötterer, 2012) to determine GO term enrichment, while also accounting for biases in gene length.

Detecting genetic variants and their genomic regions

Based on our pairwise comparisons we identified 113 windows that were within the 99th percentile in at least 3/6 pairwise comparisons of opposite migratory types and not within the 99th percentile in the 4 same migratory type comparisons (Figure S2.3). The average

F_{ST} for these windows was 0.063 in the opposite migratory type comparisons and 0.027 in the same migratory type comparisons.

Within the 113 outlier windows, 13,416 SNPs were identified as on or within 25kbp of genic regions. 551 on Exons, 3495 introns, 2294 25kbp downstream, 7076 25kbp upstream (Figure S3). These 13,416 SNPs were found on or near 26 genes. The PCA analysis using allele frequencies from the whole genome and outlier SNPs revealed separation of the migratory groups along the PC2 axis (Figure S2.4).

Gene Ontology Annotations

The results from GOWINDA on the 13,416 non-intergenic SNPs found on 26 genes, yielded 267 GO terms which were classified into 76 functional groups belonging to three functional categories: cellular component (26 groups), molecular function (26 groups), and biological process (24 groups) (Figure S5, Table S3). Some genes belonged to more than one functional group (e.g., protein binding and cell differentiation), which sometimes resulted in a sum exceeding 100% in a category (e.g., cellular component). Among the genes categorized as cellular components, 100 % were classified as cell parts. Most of the genes with molecular functions were associated with protein binding (92.3 %), and most of the genes categorized as having biological processes were involved in cellular processes (88.5 %), biological regulation (80.8%) and metabolic processes (76.9 %).

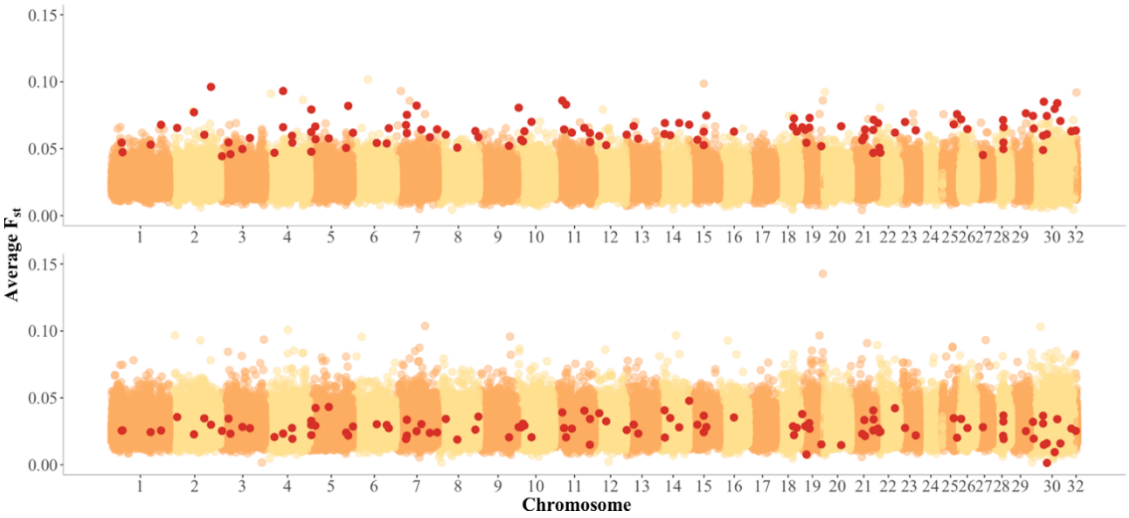

Figure S2.3. Manhattan plot for average F_{ST} values across the whole genome, for all opposite migration comparisons (top) and same migration comparisons (bottom). Each point represents a 2500kbp window, and points highlighted in red indicate outlier windows associated with migratory direction, determined to have high levels of differentiation in at least 3/6 of the opposite migration comparisons and low levels of differentiation in all same migration comparisons.

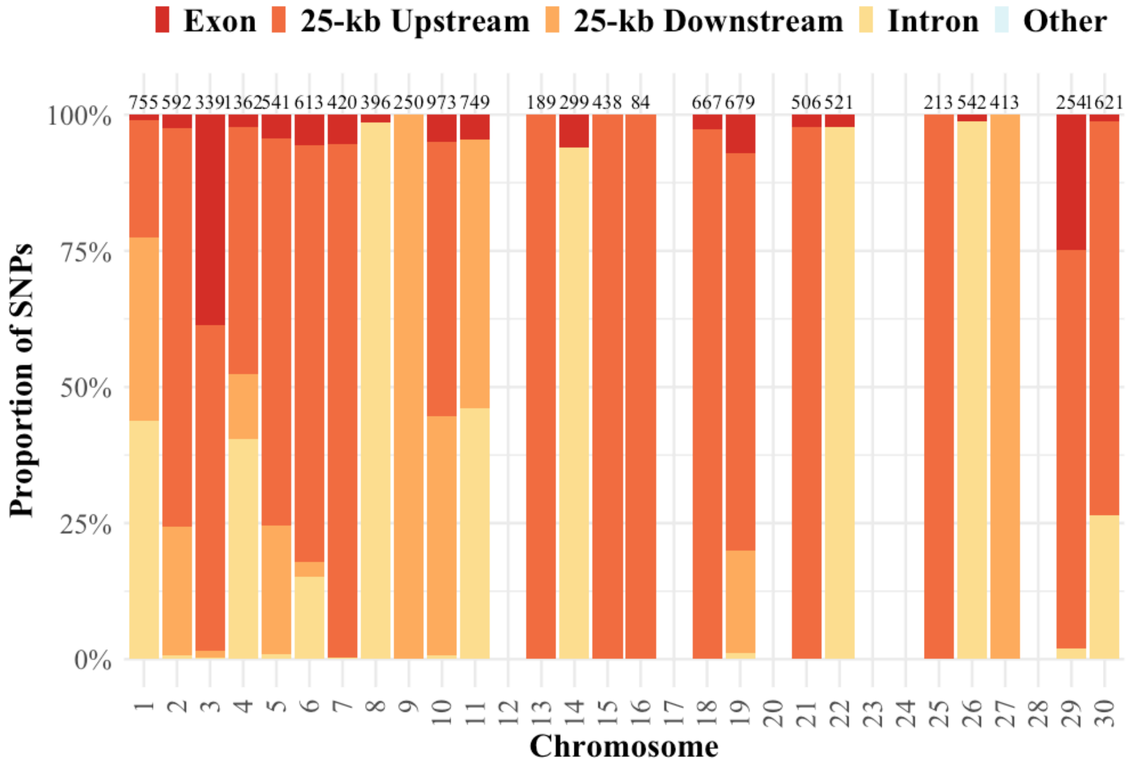

Figure S2.4. Distribution of 13,416 outlier SNPs across chromosomes identified as being on or within 25kbp of genic regions. Bars indicate the proportion of SNPs found on each chromosome distributed between exons, introns, 25kbp up- and downstream cites, and all other genic cites. Numbers above bars indicate the total number of outlier SNPs found on each chromosome.

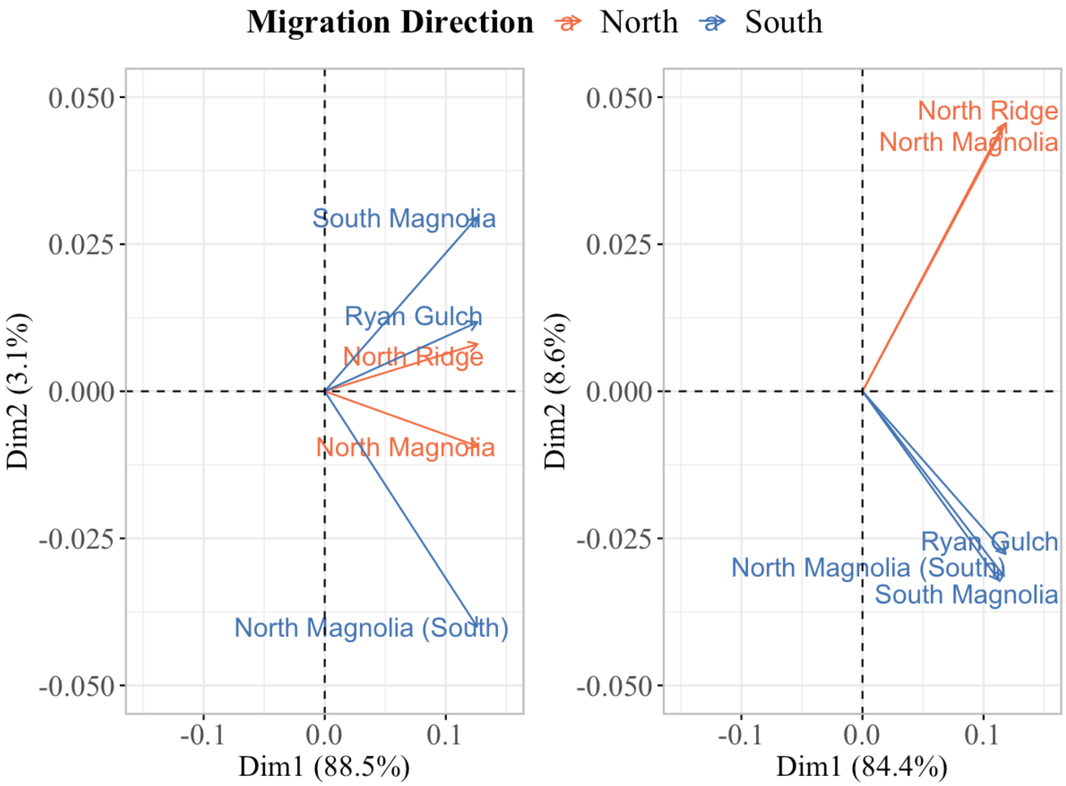

Figure S2.5. Principal component analysis plot of major allele frequency values across 21,944,208 biallelic SNPs on the whole genome (I) and 2935 biallelic outlier SNPs that are differentiated based on migratory direction (II). Arrows represent the 5 study group-migration direction groups with east-west migrators shown in orange and north-south migrators shown in blue.

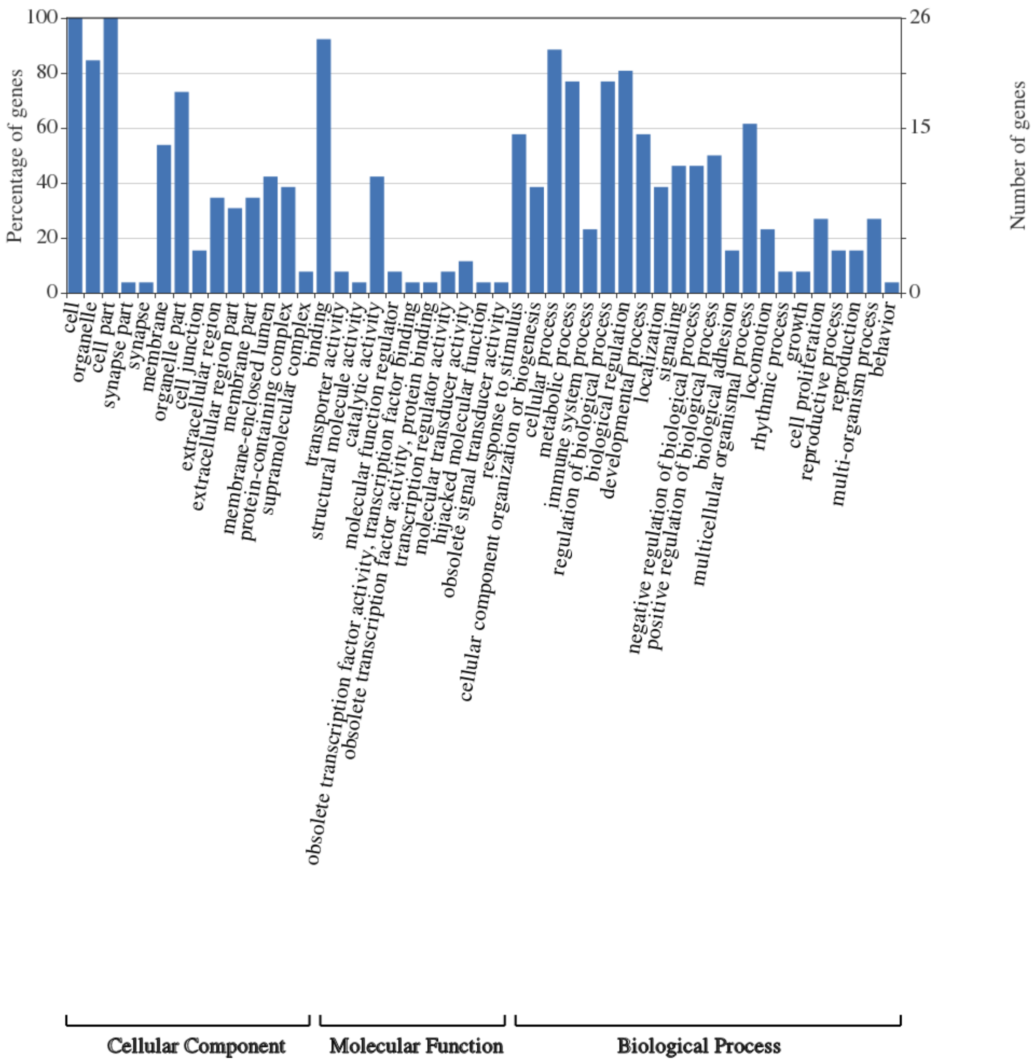

Figure S2.6. Gene ontology assignment plots based on white-tailed deer annotations. Functional groups (x-axis) were in three functional categories: cellular component, molecular function, and biological process. Number and percent of genes within a given functional category performing a specific function are indicated on the y-axis. Some genes belong to more than one functional group, which may result in a sum exceeding 100% in a category.

Gene ontology analysis

Table S2.2. Gene ontology (GO) tree showing the hierarchical breakdown of GO terms for SNPs within outlier windows found on genic regions. We defined an outlier window as one that was within the top 1% of F_{ST} values in at least 4/6 of the opposite phenotype comparisons and was not within the top 1% of F_{ST} values in all 4 of the same phenotype comparisons.

GO term	Gene No.	Gene % of the GO term	GO term description	Functional group	Functional category
GO:0044464	11	100	cell part	cell	Cellular component
GO:0099572	1	9.1	postsynaptic specialization	organelle	Cellular component
GO:0043227	10	90.9	membrane-bounded organelle	organelle	Cellular component
GO:0043230	3	27.3	extracellular organelle	organelle	Cellular component
GO:0043229	10	90.9	intracellular organelle	organelle	Cellular component
GO:0044422	9	81.8	organelle part	organelle	Cellular component
GO:0043228	2	18.2	non-membrane-bounded organelle	organelle	Cellular component
GO:0099572	1	9.1	postsynaptic specialization	cell part	Cellular component
GO:0098794	1	9.1	postsynapse	cell part	Cellular component
GO:0097458	2	18.2	neuron part	cell part	Cellular component
GO:0044424	11	100	intracellular part	cell part	Cellular component
GO:0005622	11	100	intracellular	cell part	Cellular component
GO:0097223	1	9.1	sperm part	cell part	Cellular component
GO:0012505	4	36.4	endomembrane system	cell part	Cellular component
GO:0042175	2	18.2	nuclear outer membrane-endoplasmic reticulum membrane network	cell part	Cellular component
GO:0042995	2	18.2	cell projection	cell part	Cellular component
GO:0030427	1	9.1	site of polarized growth	cell part	Cellular component
GO:0044463	2	18.2	cell projection part	cell part	Cellular component

GO:0005886	3	27.3	plasma membrane	cell part	Cellular component
GO:0071944	3	27.3	cell periphery	cell part	Cellular component
GO:0044459	2	18.2	plasma membrane part	cell part	Cellular component
GO:0098794	1	9.1	postsynapse	synapse part	Cellular component
GO:0099572	1	9.1	postsynaptic specialization	synapse part	Cellular component
GO:0097060	1	9.1	synaptic membrane	synapse part	Cellular component
GO:0098984	1	9.1	neuron to neuron synapse	synapse	Cellular component
GO:0044456	1	9.1	synapse part	synapse	Cellular component
GO:0043230	3	27.3	extracellular organelle	extracellular region part	Cellular component
GO:0045171	1	9.1	intercellular bridge	extracellular region part	Cellular component
GO:0005615	4	36.4	extracellular space	extracellular region part	Cellular component
GO:0044421	5	45.5	extracellular region part	extracellular region	Cellular component
GO:0044446	9	81.8	intracellular organelle part	organelle part	Cellular component
GO:0043233	4	36.4	organelle lumen	organelle part	Cellular component
GO:0031090	3	27.3	organelle membrane	organelle part	Cellular component
GO:0043233	4	36.4	organelle lumen	membrane enclosed lumen	Cellular component
GO:0031090	3	27.3	organelle membrane	membrane	Cellular component
GO:0098805	2	18.2	whole membrane	membrane	Cellular component
GO:0042175	2	18.2	nuclear outer membrane-endoplasmic reticulum membrane network	membrane	Cellular component
GO:0044425	5	45.5	membrane part	membrane	Cellular component
GO:0005789	2	18.2	endoplasmic reticulum membrane	membrane	Cellular component
GO:0098590	1	9.1	plasma membrane region	membrane	Cellular component
GO:0005886	3	27.3	plasma membrane	membrane	Cellular component
GO:0098589	2	18.2	membrane region	membrane	Cellular component
GO:0005789	2	18.2	endoplasmic reticulum membrane	membrane part	Cellular component
GO:0044459	2	18.2	plasma membrane part	membrane part	Cellular component
GO:0098796	1	9.1	membrane protein complex	membrane part	Cellular component

GO:0031224	4	36.4	intrinsic component of membrane	membrane part	Cellular component
GO:0098589	2	18.2	membrane region	membrane part	Cellular component
GO:0070161	2	18.2	anchoring junction	cell junction	Cellular component
GO:0005911	1	9.1	cell-cell junction	cell junction	Cellular component
GO:0030055	2	18.2	cell-substrate junction	cell junction	Cellular component
GO:0098796	1	9.1	membrane protein complex	protein-containing complex	Cellular component
GO:1902494	1	9.1	catalytic complex	protein-containing complex	Cellular component
GO:0008537	1	9.1	proteasome activator complex	protein-containing complex	Cellular component
GO:0022624	1	9.1	proteasome accessory complex	protein-containing complex	Cellular component
GO:0038023	1	9.1	signaling receptor activity	molecular transducer activity	Molecular function
GO:0060090	1	9.1	molecular adaptor activity	binding	Molecular function
GO:0005515	9	81.8	protein binding	binding	Molecular function
GO:1901363	2	18.2	heterocyclic compound binding	binding	Molecular function
GO:0097159	2	18.2	organic cyclic compound binding	binding	Molecular function
GO:0036094	3	27.3	small molecule binding	binding	Molecular function
GO:0072341	1	9.1	modified amino acid binding	binding	Molecular function
GO:0043167	6	54.5	ion binding	binding	Molecular function
GO:0008289	1	9.1	lipid binding	binding	Molecular function
GO:0097367	2	18.2	carbohydrate derivative binding	binding	Molecular function
GO:0030246	2	18.2	carbohydrate binding	binding	Molecular function
GO:0008144	1	9.1	drug binding	binding	Molecular function
GO:0016787	2	18.2	hydrolase activity	catalytic activity	Molecular function
GO:0140096	1	9.1	catalytic activity, acting on a protein	catalytic activity	Molecular function
GO:0016740	1	9.1	transferase activity	catalytic activity	Molecular function
GO:0140097	1	9.1	catalytic activity, acting on DNA	catalytic activity	Molecular function
GO:0005085	1	9.1	guanyl-nucleotide exchange factor activity	molecular function regulator	Molecular function
GO:0022857	1	9.1	transmembrane transporter activity	transporter activity	Molecular function

GO:0003700	1	9.1	DNA-binding transcription factor activity	transcription regulator activity	Molecular function
GO:0051093	1	9.1	negative regulation of developmental process	developmental process	Biological process
GO:0048856	7	63.6	anatomical structure development	developmental process	Biological process
GO:0050793	5	45.5	regulation of developmental process	developmental process	Biological process
GO:0009653	4	36.4	anatomical structure morphogenesis	developmental process	Biological process
GO:0048646	1	9.1	anatomical structure formation involved in morphogenesis	developmental process	Biological process
GO:0051094	3	27.3	positive regulation of developmental process	developmental process	Biological process
GO:0048869	5	45.5	cellular developmental process	developmental process	Biological process
GO:0003006	1	9.1	developmental process involved in reproduction	developmental process	Biological process
GO:0048589	1	9.1	developmental growth	developmental process	Biological process
GO:0050789	9	81.8	regulation of biological process	biological regulation	Biological process
GO:0065009	2	18.2	regulation of molecular function	biological regulation	Biological process
GO:0065008	3	27.3	regulation of biological quality	biological regulation	Biological process
GO:0007275	7	63.6	multicellular organism development	multicellular organismal process	Biological process
GO:0051239	6	54.5	regulation of multicellular organismal process	multicellular organismal process	Biological process
GO:0051241	2	18.2	negative regulation of multicellular organismal process	multicellular organismal process	Biological process
GO:0051240	3	27.3	positive regulation of multicellular organismal process	multicellular organismal process	Biological process
GO:0032504	2	18.2	multicellular organism reproduction	multicellular organismal process	Biological process
GO:0001816	1	9.1	cytokine production	multicellular organismal process	Biological process

GO:0044706	1	9.1	multi-multicellular organism process	multicellular organismal process	Biological process
GO:0090130	1	9.1	tissue migration	multicellular organismal process	Biological process
GO:0050793	5	45.5	regulation of developmental process	regulation of biological process	Biological process
GO:0051239	6	54.5	regulation of multicellular organismal process	regulation of biological process	Biological process
GO:0048519	5	45.5	negative regulation of biological process	regulation of biological process	Biological process
GO:0043900	1	9.1	regulation of multi-organism process	regulation of biological process	Biological process
GO:0050794	7	63.6	regulation of cellular process	regulation of biological process	Biological process
GO:0002682	3	27.3	regulation of immune system process	regulation of biological process	Biological process
GO:0019222	5	45.5	regulation of metabolic process	regulation of biological process	Biological process
GO:0048518	5	45.5	positive regulation of biological process	regulation of biological process	Biological process
GO:0048583	3	27.3	regulation of response to stimulus	regulation of biological process	Biological process
GO:0023051	3	27.3	regulation of signaling	regulation of biological process	Biological process
GO:0044087	2	18.2	regulation of cellular component biogenesis	regulation of biological process	Biological process
GO:0032879	2	18.2	regulation of localization	regulation of biological process	Biological process
GO:0040012	1	9.1	regulation of locomotion	regulation of biological process	Biological process
GO:0040008	1	9.1	regulation of growth	regulation of biological process	Biological process

GO:0051241	2	18.2	negative regulation of multicellular organismal process	negative regulation of multicellular organismal process	Biological process
GO:0051093	1	9.1	negative regulation of developmental process	negative regulation of multicellular organismal process	Biological process
GO:0023057	1	9.1	negative regulation of signaling	negative regulation of multicellular organismal process	Biological process
GO:0040013	1	9.1	negative regulation of locomotion	negative regulation of multicellular organismal process	Biological process
GO:0048523	4	36.4	negative regulation of cellular process	negative regulation of multicellular organismal process	Biological process
GO:0048585	1	9.1	negative regulation of response to stimulus	negative regulation of multicellular organismal process	Biological process
GO:0009892	3	27.3	negative regulation of metabolic process	negative regulation of multicellular organismal process	Biological process
GO:0043900	1	9.1	regulation of multi-organism process	multi-organism process	Biological process
GO:0051707	2	18.2	response to other organism	multi-organism process	Biological process
GO:0044703	2	18.2	multi-organism reproductive process	multi-organism process	Biological process
GO:0044419	1	9.1	interspecies interaction between organisms	multi-organism process	Biological process
GO:0044706	1	9.1	multi-multicellular organism process	multi-organism process	Biological process
GO:0044764	1	9.1	multi-organism cellular process	multi-organism process	Biological process
GO:0019882	1	9.1	antigen processing and presentation	immune system process	Biological process

GO:0006955	2	18.2	immune response	immune system process	Biological process
GO:0002682	3	27.3	regulation of immune system process	immune system process	Biological process
GO:0045321	1	9.1	leukocyte activation	immune system process	Biological process
GO:0002684	1	9.1	positive regulation of immune system process	immune system process	Biological process
GO:0002253	1	9.1	activation of immune response	immune system process	Biological process
GO:0002252	1	9.1	immune effector process	immune system process	Biological process
GO:0002520	2	18.2	immune system development	immune system process	Biological process
GO:0050900	1	9.1	leukocyte migration	immune system process	Biological process
GO:0050794	7	63.6	regulation of cellular process	cellular process	Biological process
GO:0001775	1	9.1	cell activation	cellular process	Biological process
GO:0044237	8	72.7	cellular metabolic process	cellular process	Biological process
GO:0048522	4	36.4	positive regulation of cellular process	cellular process	Biological process
GO:0051716	5	45.5	cellular response to stimulus	cellular process	Biological process
GO:0006949	1	9.1	syncytium formation	cellular process	Biological process
GO:0016043	6	54.5	cellular component organization	cellular process	Biological process
GO:0140253	1	9.1	cell-cell fusion	cellular process	Biological process
GO:0007154	5	45.5	cell communication	cellular process	Biological process
GO:0007165	5	45.5	signal transduction	cellular process	Biological process
GO:0048869	5	45.5	cellular developmental process	cellular process	Biological process
GO:0006928	2	18.2	movement of cell or subcellular component	cellular process	Biological process
GO:0048523	4	36.4	negative regulation of cellular process	cellular process	Biological process
GO:0007049	1	9.1	cell cycle	cellular process	Biological process
GO:0022402	1	9.1	cell cycle process	cellular process	Biological process
GO:0016049	1	9.1	cell growth	cellular process	Biological process
GO:0008219	3	27.3	cell death	cellular process	Biological process

GO:0008037	1	9.1	cell recognition	cellular process	Biological process
GO:0044764	1	9.1	multi-organism cellular process	cellular process	Biological process
GO:0051641	1	9.1	cellular localization	localization	Biological process
GO:0051234	4	36.4	establishment of localization	localization	Biological process
GO:0032879	2	18.2	regulation of localization	localization	Biological process
GO:0051674	2	18.2	localization of cell	localization	Biological process
GO:0033036	2	18.2	macromolecule localization	localization	Biological process
GO:0051235	1	9.1	maintenance of location	localization	Biological process
GO:0006955	2	18.2	immune response	response to stimulus	Biological process
GO:0009719	2	18.2	response to endogenous stimulus	response to stimulus	Biological process
GO:0048583	3	27.3	regulation of response to stimulus	response to stimulus	Biological process
GO:0048584	2	18.2	positive regulation of response to stimulus	response to stimulus	Biological process
GO:0051716	5	45.5	cellular response to stimulus	response to stimulus	Biological process
GO:0006950	4	36.4	response to stress	response to stimulus	Biological process
GO:0042221	3	27.3	response to chemical	response to stimulus	Biological process
GO:0009605	2	18.2	response to external stimulus	response to stimulus	Biological process
GO:0009607	2	18.2	response to biotic stimulus	response to stimulus	Biological process
GO:0009628	1	9.1	response to abiotic stimulus	response to stimulus	Biological process
GO:0048585	1	9.1	negative regulation of response to stimulus	response to stimulus	Biological process
GO:0070661	1	9.1	leukocyte proliferation	cell proliferation	Biological process
GO:0042127	2	18.2	regulation of cell proliferation	cell proliferation	Biological process
GO:0008285	1	9.1	negative regulation of cell proliferation	cell proliferation	Biological process
GO:0009058	5	45.5	biosynthetic process	metabolic process	Biological process
GO:0019222	5	45.5	regulation of metabolic process	metabolic process	Biological process
GO:0044237	8	72.7	cellular metabolic process	metabolic process	Biological process
GO:0071704	8	72.7	organic substance metabolic process	metabolic process	Biological process

GO:0006807	7	63.6	nitrogen compound metabolic process	metabolic process	Biological process
GO:0044238	7	63.6	primary metabolic process	metabolic process	Biological process
GO:0009893	3	27.3	positive regulation of metabolic process	metabolic process	Biological process
GO:0044281	2	18.2	small molecule metabolic process	metabolic process	Biological process
GO:0009056	3	27.3	catabolic process	metabolic process	Biological process
GO:0009892	3	27.3	negative regulation of metabolic process	metabolic process	Biological process
GO:0032259	1	9.1	methylation	metabolic process	Biological process
GO:0070085	1	9.1	glycosylation	metabolic process	Biological process
GO:0070988	1	9.1	demethylation	metabolic process	Biological process
GO:0009893	3	27.3	positive regulation of metabolic process	positive regulation of biological process	Biological process
GO:0048522	4	36.4	positive regulation of cellular process	positive regulation of biological process	Biological process
GO:0002684	1	9.1	positive regulation of immune system process	positive regulation of biological process	Biological process
GO:0048584	2	18.2	positive regulation of response to stimulus	positive regulation of biological process	Biological process
GO:0023056	2	18.2	positive regulation of signaling	positive regulation of biological process	Biological process
GO:0051094	3	27.3	positive regulation of developmental process	positive regulation of biological process	Biological process
GO:0044089	2	18.2	positive regulation of cellular component biogenesis	positive regulation of biological process	Biological process
GO:0051240	3	27.3	positive regulation of multicellular organismal process	positive regulation of biological process	Biological process
GO:0045927	1	9.1	positive regulation of growth	positive regulation of biological process	Biological process
GO:1905954	1	9.1	positive regulation of lipid localization	positive regulation of biological process	Biological process

GO:0023057	1	9.1	negative regulation of signaling	signaling	Biological process
GO:0023051	3	27.3	regulation of signaling	signaling	Biological process
GO:0023056	2	18.2	positive regulation of signaling	signaling	Biological process
GO:0007165	5	45.5	signal transduction	signaling	Biological process
GO:0007267	2	18.2	cell-cell signaling	signaling	Biological process
GO:0016043	6	54.5	cellular component organization	cellular component organization or biogenesis	Biological process
GO:0044085	2	18.2	cellular component biogenesis	cellular component organization or biogenesis	Biological process
GO:0040012	1	9.1	regulation of locomotion	locomotion	Biological process
GO:0048870	2	18.2	cell motility	locomotion	Biological process
GO:0040013	1	9.1	negative regulation of locomotion	locomotion	Biological process
GO:0003006	1	9.1	developmental process involved in reproduction	reproductive process	Biological process
GO:0044703	2	18.2	multi-organism reproductive process	reproductive process	Biological process
GO:0048609	2	18.2	multicellular organismal reproductive process	reproductive process	Biological process
GO:0007566	1	9.1	embryo implantation	reproductive process	Biological process
GO:0022414	2	18.2	reproductive process	reproduction	Biological process
GO:0032504	2	18.2	multicellular organism reproduction	reproduction	Biological process
GO:0019953	1	9.1	sexual reproduction	reproduction	Biological process
GO:0007623	1	9.1	circadian rhythm	rhythmic process	Biological process
GO:0040008	1	9.1	regulation of growth	growth	Biological process
GO:0048589	1	9.1	developmental growth	growth	Biological process
GO:0016049	1	9.1	cell growth	growth	Biological process
GO:0045927	1	9.1	positive regulation of growth	growth	Biological process
GO:0007155	1	9.1	cell adhesion	biological adhesion	Biological process

Table S2.3. Gene ontology (GO) tree showing the hierarchical breakdown of GO terms for SNPs within outlier windows found on genic regions. We defined an outlier window as one that was within the top 1% of F_{ST} values in at least 3/6 of the opposite phenotype comparisons and was not within the top 1% of F_{ST} values in all 4 of the same phenotype comparisons.

Go term	Gene No.	Gene % of the GO term	GO term description	Functional group	Functional category
GO:0044464	26	100	cell part	cell	Cellular component
GO:0099572	1	3.8	postsynaptic specialization	organelle	Cellular component
GO:0043229	21	80.8	intracellular organelle	organelle	Cellular component
GO:0043227	20	76.9	membrane-bounded organelle	organelle	Cellular component
GO:0044422	19	73.1	organelle part	organelle	Cellular component
GO:0043228	9	34.6	non-membrane-bounded organelle	organelle	Cellular component
GO:0043230	5	19.2	extracellular organelle	organelle	Cellular component
GO:0099572	1	3.8	postsynaptic specialization	cell part	Cellular component
GO:0098794	1	3.8	postsynapse	cell part	Cellular component
GO:0097458	3	11.5	neuron part	cell part	Cellular component
GO:0044424	24	92.3	intracellular part	cell part	Cellular component
GO:0005622	24	92.3	intracellular	cell part	Cellular component
GO:0097223	1	3.8	sperm part	cell part	Cellular component
GO:0012505	7	26.9	endomembrane system	cell part	Cellular component
GO:0042995	4	15.4	cell projection	cell part	Cellular component
GO:0030427	1	3.8	site of polarized growth	cell part	Cellular component
GO:0044463	3	11.5	cell projection part	cell part	Cellular component
GO:0071944	9	34.6	cell periphery	cell part	Cellular component
GO:0005886	8	30.8	plasma membrane	cell part	Cellular component
GO:0031252	1	3.8	cell leading edge	cell part	Cellular component
GO:0044459	5	19.2	plasma membrane part	cell part	Cellular component
GO:0009986	1	3.8	cell surface	cell part	Cellular component

GO:1990204	1	3.8	oxidoreductase complex	cell part	Cellular component
GO:0042175	1	3.8	nuclear outer membrane-endoplasmic reticulum membrane network	cell part	Cellular component
GO:0043209	1	3.8	myelin sheath	cell part	Cellular component
GO:0044297	1	3.8	cell body	cell part	Cellular component
GO:0098794	1	3.8	postsynapse	synapse part	Cellular component
GO:0099572	1	3.8	postsynaptic specialization	synapse part	Cellular component
GO:0097060	1	3.8	synaptic membrane	synapse part	Cellular component
GO:0098984	1	3.8	neuron to neuron synapse	synapse	Cellular component
GO:0044456	1	3.8	synapse part	synapse	Cellular component
GO:0031090	4	15.4	organelle membrane	membrane	Cellular component
GO:0098805	5	19.2	whole membrane	membrane	Cellular component
GO:0005886	8	30.8	plasma membrane	membrane	Cellular component
GO:0044425	9	34.6	membrane part	membrane	Cellular component
GO:0098589	4	15.4	membrane region	membrane	Cellular component
GO:0098590	1	3.8	plasma membrane region	membrane	Cellular component
GO:0042175	1	3.8	nuclear outer membrane-endoplasmic reticulum membrane network	membrane	Cellular component
GO:0005789	1	3.8	endoplasmic reticulum membrane	membrane	Cellular component
GO:0044446	19	73.1	intracellular organelle part	organelle part	Cellular component
GO:0031090	4	15.4	organelle membrane	organelle part	Cellular component
GO:0043233	11	42.3	organelle lumen	organelle part	Cellular component
GO:0005911	3	11.5	cell-cell junction	cell junction	Cellular component
GO:0070161	2	7.7	anchoring junction	cell junction	Cellular component
GO:0030055	2	7.7	cell-substrate junction	cell junction	Cellular component
GO:0044421	8	30.8	extracellular region part	extracellular region	Cellular component
GO:0043230	5	19.2	extracellular organelle	extracellular region part	Cellular component
GO:0031012	1	3.8	extracellular matrix	extracellular region part	Cellular component
GO:0005615	6	23.1	extracellular space	extracellular region part	Cellular component
GO:0045171	1	3.8	intercellular bridge	extracellular region part	Cellular component

GO:0044420	1	3.8	extracellular matrix component	extracellular region part	Cellular component
GO:0098589	4	15.4	membrane region	membrane part	Cellular component
GO:0044459	5	19.2	plasma membrane part	membrane part	Cellular component
GO:0031224	6	23.1	intrinsic component of membrane	membrane part	Cellular component
GO:0098552	1	3.8	side of membrane	membrane part	Cellular component
GO:0098796	2	7.7	membrane protein complex	membrane part	Cellular component
GO:0005789	1	3.8	endoplasmic reticulum membrane	membrane part	Cellular component
GO:0043233	11	42.3	organelle lumen	membrane enclosed lumen	Cellular component
GO:1902494	3	11.5	catalytic complex	protein-containing complex	Cellular component
GO:0017053	1	3.8	transcriptional repressor complex	protein-containing complex	Cellular component
GO:0098796	2	7.7	membrane protein complex	protein-containing complex	Cellular component
GO:0036452	1	3.8	ESCRT complex	protein-containing complex	Cellular component
GO:0005667	1	3.8	transcription factor complex	protein-containing complex	Cellular component
GO:0016281	1	3.8	eukaryotic translation initiation factor 4F complex	protein-containing complex	Cellular component
GO:0008537	1	3.8	proteasome activator complex	protein-containing complex	Cellular component
GO:0022624	1	3.8	proteasome accessory complex	protein-containing complex	Cellular component
GO:0099081	2	7.7	supramolecular polymer	supramolecular complex	Cellular component
GO:0060090	1	3.8	molecular adaptor activity	binding	Molecular function
GO:0005515	21	80.8	protein binding	binding	Molecular function
GO:1901363	7	26.9	heterocyclic compound binding	binding	Molecular function
GO:0097159	7	26.9	organic cyclic compound binding	binding	Molecular function
GO:0072341	1	3.8	modified amino acid binding	binding	Molecular function
GO:0043167	13	50	ion binding	binding	Molecular function
GO:0048037	2	7.7	cofactor binding	binding	Molecular function
GO:0008144	3	11.5	drug binding	binding	Molecular function
GO:0036094	6	23.1	small molecule binding	binding	Molecular function
GO:0097367	4	15.4	carbohydrate derivative binding	binding	Molecular function
GO:0030246	3	11.5	carbohydrate binding	binding	Molecular function

GO:0044877	2	7.7	protein-containing complex binding	binding	Molecular function
GO:0008289	1	3.8	lipid binding	binding	Molecular function
GO:0042165	1	3.8	neurotransmitter binding	binding	Molecular function
GO:0022857	2	7.7	transmembrane transporter activity	transporter activity	Molecular function
GO:0140096	6	23.1	catalytic activity, acting on a protein	catalytic activity	Molecular function
GO:0016740	2	7.7	transferase activity	catalytic activity	Molecular function
GO:0016491	2	7.7	oxidoreductase activity	catalytic activity	Molecular function
GO:0016787	8	30.8	hydrolase activity	catalytic activity	Molecular function
GO:0140097	1	3.8	catalytic activity, acting on DNA	catalytic activity	Molecular function
GO:0016829	1	3.8	lyase activity	catalytic activity	Molecular function
GO:0005085	2	7.7	guanyl-nucleotide exchange factor activity	molecular function regulator	Molecular function
GO:0003700	2	7.7	DNA-binding transcription factor activity	transcription regulator activity	Molecular function
GO:0038023	1	3.8	signaling receptor activity	molecular transducer activity	Molecular function
GO:0001618	1	3.8	virus receptor activity	hijacked molecular function	Molecular function
GO:0042221	8	30.8	response to chemical	response to stimulus	Biological process
GO:0048583	8	30.8	regulation of response to stimulus	response to stimulus	Biological process
GO:0051716	13	50	cellular response to stimulus	response to stimulus	Biological process
GO:0009719	3	11.5	response to endogenous stimulus	response to stimulus	Biological process
GO:0048585	2	7.7	negative regulation of response to stimulus	response to stimulus	Biological process
GO:0006955	4	15.4	immune response	response to stimulus	Biological process
GO:0048584	4	15.4	positive regulation of response to stimulus	response to stimulus	Biological process
GO:0006950	6	23.1	response to stress	response to stimulus	Biological process
GO:0009628	2	7.7	response to abiotic stimulus	response to stimulus	Biological process
GO:0051606	1	3.8	detection of stimulus	response to stimulus	Biological process
GO:0009607	2	7.7	response to biotic stimulus	response to stimulus	Biological process
GO:0009605	5	19.2	response to external stimulus	response to stimulus	Biological process

GO:0016043	10	38.5	cellular component organization	cellular component organization or biogenesis	Biological process
GO:0044085	5	19.2	cellular component biogenesis	cellular component organization or biogenesis	Biological process
GO:0016043	10	38.5	cellular component organization	cellular process	Biological process
GO:0044237	19	73.1	cellular metabolic process	cellular process	Biological process
GO:0050794	19	73.1	regulation of cellular process	cellular process	Biological process
GO:0007154	12	46.2	cell communication	cellular process	Biological process
GO:0051716	13	50	cellular response to stimulus	cellular process	Biological process
GO:0007165	11	42.3	signal transduction	cellular process	Biological process
GO:0048523	10	38.5	negative regulation of cellular process	cellular process	Biological process
GO:0048522	12	46.2	positive regulation of cellular process	cellular process	Biological process
GO:0006949	1	3.8	syncytium formation	cellular process	Biological process
GO:0140253	1	3.8	cell-cell fusion	cellular process	Biological process
GO:0001775	3	11.5	cell activation	cellular process	Biological process
GO:0007049	4	15.4	cell cycle	cellular process	Biological process
GO:0022402	3	11.5	cell cycle process	cellular process	Biological process
GO:0008219	4	15.4	cell death	cellular process	Biological process
GO:0048869	9	34.6	cellular developmental process	cellular process	Biological process
GO:0006928	5	19.2	movement of cell or subcellular component	cellular process	Biological process
GO:0019725	1	3.8	cellular homeostasis	cellular process	Biological process
GO:0032940	2	7.7	secretion by cell	cellular process	Biological process
GO:0016049	1	3.8	cell growth	cellular process	Biological process
GO:0007163	1	3.8	establishment or maintenance of cell polarity	cellular process	Biological process
GO:0061919	1	3.8	process utilizing autophagic mechanism	cellular process	Biological process
GO:0030029	1	3.8	actin filament-based process	cellular process	Biological process
GO:0007059	1	3.8	chromosome segregation	cellular process	Biological process
GO:0051301	1	3.8	cell division	cellular process	Biological process
GO:0008037	1	3.8	cell recognition	cellular process	Biological process

GO:0044764	1	3.8	multi-organism cellular process	cellular process	Biological process
GO:0022412	1	3.8	cellular process involved in reproduction in multicellular organism	cellular process	Biological process
GO:0071704	19	73.1	organic substance metabolic process	metabolic process	Biological process
GO:0006807	18	69.2	nitrogen compound metabolic process	metabolic process	Biological process
GO:0044238	18	69.2	primary metabolic process	metabolic process	Biological process
GO:0044237	19	73.1	cellular metabolic process	metabolic process	Biological process
GO:0032259	3	11.5	methylation	metabolic process	Biological process
GO:0019222	15	57.7	regulation of metabolic process	metabolic process	Biological process
GO:0009058	10	38.5	biosynthetic process	metabolic process	Biological process
GO:0009892	7	26.9	negative regulation of metabolic process	metabolic process	Biological process
GO:0009893	7	26.9	positive regulation of metabolic process	metabolic process	Biological process
GO:0009056	7	26.9	catabolic process	metabolic process	Biological process
GO:0032963	1	3.8	collagen metabolic process	metabolic process	Biological process
GO:0044281	4	15.4	small molecule metabolic process	metabolic process	Biological process
GO:0055114	2	7.7	oxidation-reduction process	metabolic process	Biological process
GO:0070085	1	3.8	glycosylation	metabolic process	Biological process
GO:0070988	1	3.8	demethylation	metabolic process	Biological process
GO:0019882	1	3.8	antigen processing and presentation	immune system process	Biological process
GO:0002252	2	7.7	immune effector process	immune system process	Biological process
GO:0006955	4	15.4	immune response	immune system process	Biological process
GO:0002684	2	7.7	positive regulation of immune system process	immune system process	Biological process
GO:0002253	2	7.7	activation of immune response	immune system process	Biological process
GO:0002682	3	11.5	regulation of immune system process	immune system process	Biological process
GO:0045321	3	11.5	leukocyte activation	immune system process	Biological process
GO:0002520	3	11.5	immune system development	immune system process	Biological process
GO:0050900	2	7.7	leukocyte migration	immune system process	Biological process
GO:0031294	1	3.8	lymphocyte costimulation	immune system process	Biological process

GO:0050793	9	34.6	regulation of developmental process	regulation of biological process	Biological process
GO:0050794	19	73.1	regulation of cellular process	regulation of biological process	Biological process
GO:0023051	9	34.6	regulation of signaling	regulation of biological process	Biological process
GO:0048583	8	30.8	regulation of response to stimulus	regulation of biological process	Biological process
GO:0048519	12	46.2	negative regulation of biological process	regulation of biological process	Biological process
GO:0019222	15	57.7	regulation of metabolic process	regulation of biological process	Biological process
GO:0002682	3	11.5	regulation of immune system process	regulation of biological process	Biological process
GO:0048518	13	50	positive regulation of biological process	regulation of biological process	Biological process
GO:0044087	3	11.5	regulation of cellular component biogenesis	regulation of biological process	Biological process
GO:0051239	9	34.6	regulation of multicellular organismal process	regulation of biological process	Biological process
GO:0032879	6	23.1	regulation of localization	regulation of biological process	Biological process
GO:0040012	3	11.5	regulation of locomotion	regulation of biological process	Biological process
GO:0040008	1	3.8	regulation of growth	regulation of biological process	Biological process
GO:0030155	1	3.8	regulation of cell adhesion	regulation of biological process	Biological process
GO:0042752	1	3.8	regulation of circadian rhythm	regulation of biological process	Biological process
GO:0043900	1	3.8	regulation of multi-organism process	regulation of biological process	Biological process
GO:1900046	1	3.8	regulation of hemostasis	regulation of biological process	Biological process
GO:0050789	20	76.9	regulation of biological process	biological regulation	Biological process
GO:0065009	7	26.9	regulation of molecular function	biological regulation	Biological process
GO:0065008	7	26.9	regulation of biological quality	biological regulation	Biological process

GO:0050793	9	34.6	regulation of developmental process	developmental process	Biological process
GO:0009653	8	30.8	anatomical structure morphogenesis	developmental process	Biological process
GO:0048646	4	15.4	anatomical structure formation involved in morphogenesis	developmental process	Biological process
GO:0048856	14	53.8	anatomical structure development	developmental process	Biological process
GO:0051094	6	23.1	positive regulation of developmental process	developmental process	Biological process
GO:0048869	9	34.6	cellular developmental process	developmental process	Biological process
GO:0048589	2	7.7	developmental growth	developmental process	Biological process
GO:0051093	3	11.5	negative regulation of developmental process	developmental process	Biological process
GO:0003006	2	7.7	developmental process involved in reproduction	developmental process	Biological process
GO:0051641	5	19.2	cellular localization	localization	Biological process
GO:0051234	8	30.8	establishment of localization	localization	Biological process
GO:0033036	3	11.5	macromolecule localization	localization	Biological process
GO:0032879	6	23.1	regulation of localization	localization	Biological process
GO:0051674	5	19.2	localization of cell	localization	Biological process
GO:0051235	1	3.8	maintenance of location	localization	Biological process
GO:0007165	11	42.3	signal transduction	signaling	Biological process
GO:0023051	9	34.6	regulation of signaling	signaling	Biological process
GO:0023057	2	7.7	negative regulation of signaling	signaling	Biological process
GO:0023056	4	15.4	positive regulation of signaling	signaling	Biological process
GO:0007267	3	11.5	cell-cell signaling	signaling	Biological process
GO:0023057	2	7.7	negative regulation of signaling	negative regulation of biological process	Biological process
GO:0048585	2	7.7	negative regulation of response to stimulus	negative regulation of biological process	Biological process
GO:0048523	10	38.5	negative regulation of cellular process	negative regulation of biological process	Biological process
GO:0009892	7	26.9	negative regulation of metabolic process	negative regulation of biological process	Biological process

GO:0040013	1	3.8	negative regulation of locomotion	negative regulation of biological process	Biological process
GO:0051093	3	11.5	negative regulation of developmental process	negative regulation of biological process	Biological process
GO:0051241	3	11.5	negative regulation of multicellular organismal process	negative regulation of biological process	Biological process
GO:0034260	1	3.8	negative regulation of GTPase activity	negative regulation of biological process	Biological process
GO:0002684	2	7.7	positive regulation of immune system process	positive regulation of biological process	Biological process
GO:0048584	4	15.4	positive regulation of response to stimulus	positive regulation of biological process	Biological process
GO:0048522	12	46.2	positive regulation of cellular process	positive regulation of biological process	Biological process
GO:0023056	4	15.4	positive regulation of signaling	positive regulation of biological process	Biological process
GO:0051094	6	23.1	positive regulation of developmental process	positive regulation of biological process	Biological process
GO:0009893	7	26.9	positive regulation of metabolic process	positive regulation of biological process	Biological process
GO:0044089	3	11.5	positive regulation of cellular component biogenesis	positive regulation of biological process	Biological process
GO:0051240	6	23.1	positive regulation of multicellular organismal process	positive regulation of biological process	Biological process
GO:0045927	1	3.8	positive regulation of growth	positive regulation of biological process	Biological process
GO:0045785	1	3.8	positive regulation of cell adhesion	positive regulation of biological process	Biological process
GO:0051050	2	7.7	positive regulation of transport	positive regulation of biological process	Biological process
GO:1900048	1	3.8	positive regulation of hemostasis	positive regulation of biological process	Biological process
GO:0007155	4	15.4	cell adhesion	biological adhesion	Biological process
GO:0007275	14	53.8	multicellular organism development	multicellular organismal process	Biological process
GO:0051239	9	34.6	regulation of multicellular organismal process	multicellular organismal process	Biological process

GO:0032922	1	3.8	circadian regulation of gene expression	multicellular organismal process	Biological process
GO:0051240	6	23.1	positive regulation of multicellular organismal process	multicellular organismal process	Biological process
GO:0051241	3	11.5	negative regulation of multicellular organismal process	multicellular organismal process	Biological process
GO:0032504	4	15.4	multicellular organism reproduction	multicellular organismal process	Biological process
GO:0044706	1	3.8	multi-multicellular organism process	multicellular organismal process	Biological process
GO:0090130	2	7.7	tissue migration	multicellular organismal process	Biological process
GO:0035264	1	3.8	multicellular organism growth	multicellular organismal process	Biological process
GO:0022404	1	3.8	molting cycle process	multicellular organismal process	Biological process
GO:0042303	1	3.8	molting cycle	multicellular organismal process	Biological process
GO:0001816	1	3.8	cytokine production	multicellular organismal process	Biological process
GO:0050817	2	7.7	coagulation	multicellular organismal process	Biological process
GO:0040012	3	11.5	regulation of locomotion	locomotion	Biological process
GO:0048870	5	19.2	cell motility	locomotion	Biological process
GO:0040013	1	3.8	negative regulation of locomotion	locomotion	Biological process
GO:0052192	1	3.8	movement in environment of other organism involved in symbiotic interaction	locomotion	Biological process
GO:0042330	1	3.8	taxis	locomotion	Biological process
GO:0007623	2	7.7	circadian rhythm	rhythmic process	Biological process
GO:0007622	1	3.8	rhythmic behavior	rhythmic process	Biological process
GO:0040008	1	3.8	regulation of growth	growth	Biological process
GO:0048589	2	7.7	developmental growth	growth	Biological process
GO:0016049	1	3.8	cell growth	growth	Biological process
GO:0045927	1	3.8	positive regulation of growth	growth	Biological process
GO:0061351	1	3.8	neural precursor cell proliferation	cell proliferation	Biological process

GO:0042127	7	26.9	regulation of cell proliferation	cell proliferation	Biological process
GO:0008284	3	11.5	positive regulation of cell proliferation	cell proliferation	Biological process
GO:0070661	1	3.8	leukocyte proliferation	cell proliferation	Biological process
GO:0050673	1	3.8	epithelial cell proliferation	cell proliferation	Biological process
GO:0033687	1	3.8	osteoblast proliferation	cell proliferation	Biological process
GO:0008285	3	11.5	negative regulation of cell proliferation	cell proliferation	Biological process
GO:0044703	4	15.4	multi-organism reproductive process	reproductive process	Biological process
GO:0048609	4	15.4	multicellular organismal reproductive process	reproductive process	Biological process
GO:0009566	1	3.8	fertilization	reproductive process	Biological process
GO:0007566	1	3.8	embryo implantation	reproductive process	Biological process
GO:0003006	2	7.7	developmental process involved in reproduction	reproductive process	Biological process
GO:0022412	1	3.8	cellular process involved in reproduction in multicellular organism	reproductive process	Biological process
GO:0032504	4	15.4	multicellular organism reproduction	reproduction	Biological process
GO:0022414	4	15.4	reproductive process	reproduction	Biological process
GO:0019953	3	11.5	sexual reproduction	reproduction	Biological process
GO:0044703	4	15.4	multi-organism reproductive process	multiorganism process	Biological process
GO:0044419	3	11.5	interspecies interaction between organisms	multiorganism process	Biological process
GO:0051707	2	7.7	response to other organism	multiorganism process	Biological process
GO:0044706	1	3.8	multi-multicellular organism process	multiorganism process	Biological process
GO:0043900	1	3.8	regulation of multi-organism process	multiorganism process	Biological process
GO:0044764	1	3.8	multi-organism cellular process	multiorganism process	Biological process
GO:0007622	1	3.8	rhythmic behavior	behavior	Biological process
GO:0007626	1	3.8	locomotory behavior	behavior	Biological process

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Appendix III. Supplementary Material for Chapter 4

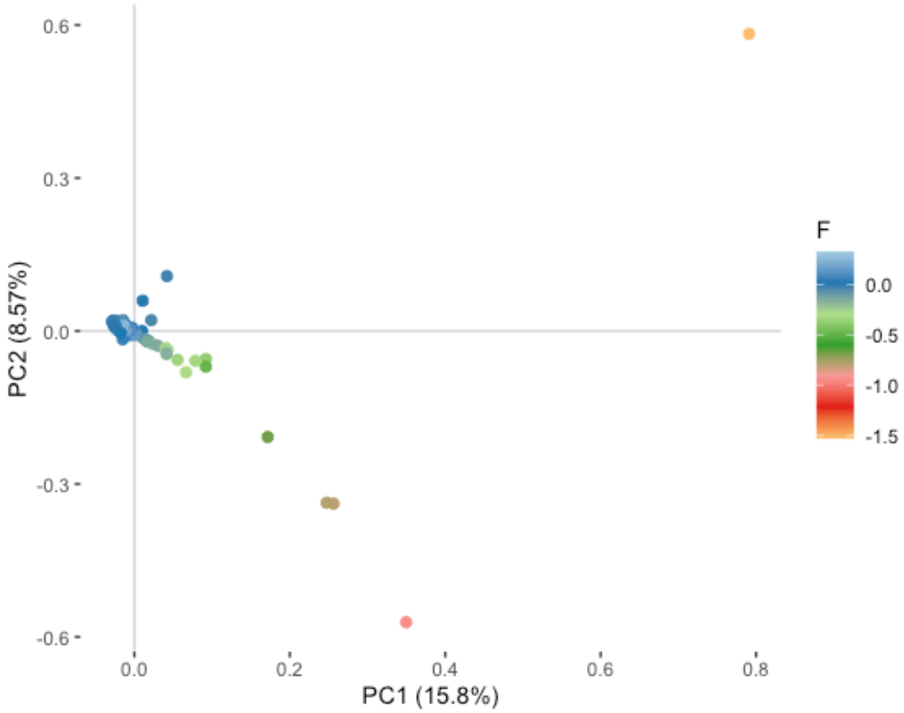

Figure S3.1. Principal coordinate analysis of individuals by F_{IS} coefficient, prior to removal based on excess heterozygosity (n = 155).

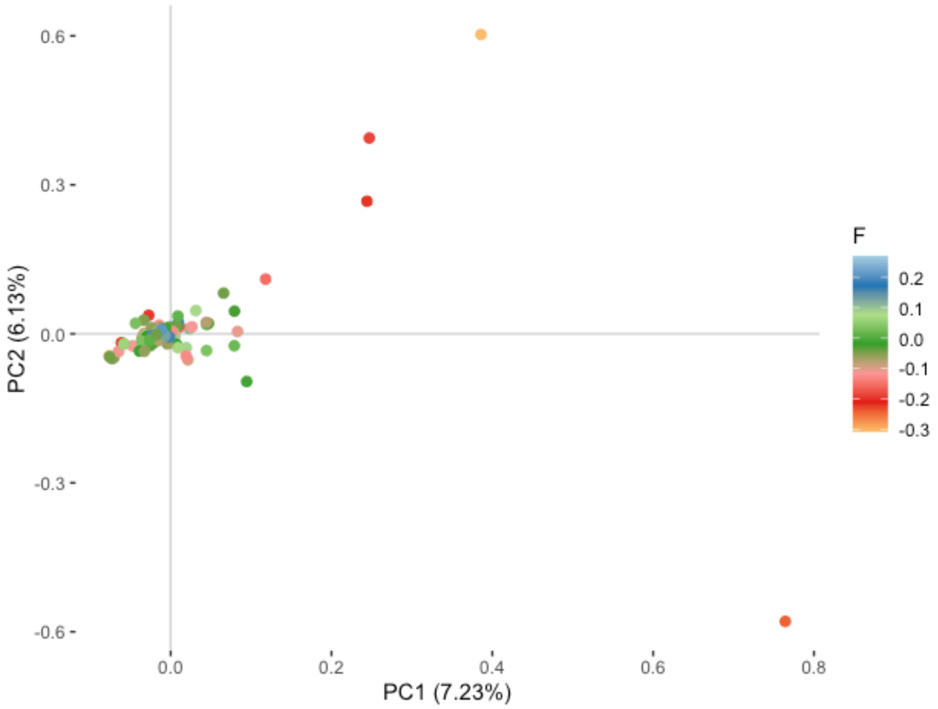

Figure S3.2. Principal coordinate analysis of individuals by F_{IS} coefficient, after removal based on excess heterozygosity (n = 143).

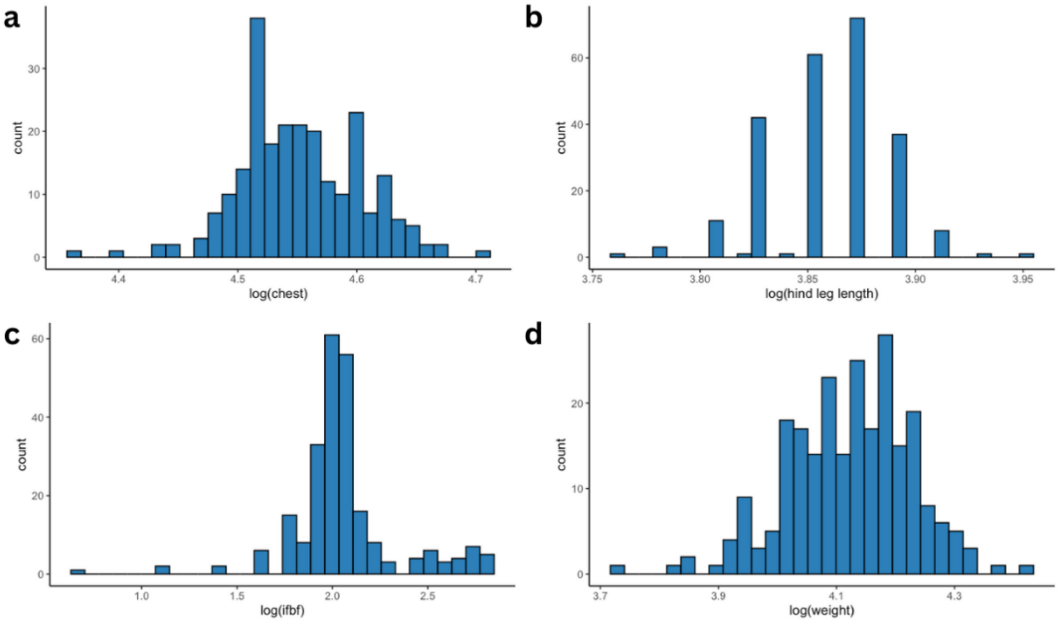

Figure S3.3. Frequency distributions of body size traits for 242 individuals. Body size traits are a) chest girth (cm); b) hind leg length (cm); c) ingesta-free body fat (%); and d) weight (kg).

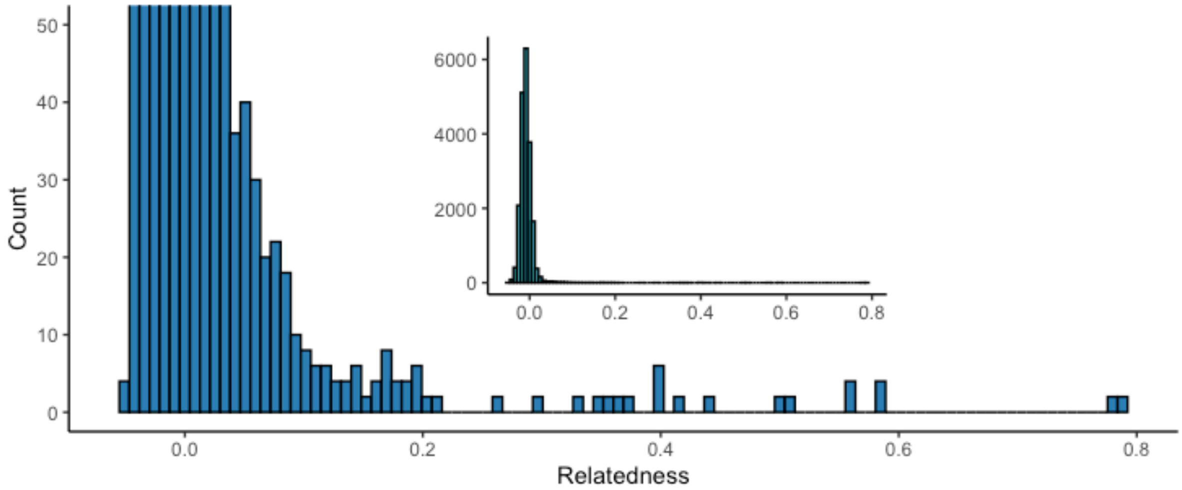

Figure S3.4. Distribution of pairwise genomic relatedness coefficients (n = 20,306).

Table S3.1. Summary data for unfiltered and filtered genomic relatedness matrices (GRM). The GRM was filtered based on two relatedness coefficient cut-offs, 0.1 and 0.05.

GRM	N	SNPs	mean off-diagonal	var off-diagonal	mean diagonal	var diagonal
unfiltered	143	10,097	-0.0071543	0.00072768	0.9904386	0.06703364
0.1 cutoff	109	10,097	-0.0074564	0.0001735	1.0177661	0.08338047
0.05 cutoff	88	10,097	-0.0072232	0.00012267	0.9916709	0.05397322

Table S3.2. Variance component estimates and their associated ratios for body size and migration traits using the unfiltered GRM. h^2: heritability, pe^2: permanent environmental effects, ind^2: repeatability, V_A: additive genetic variance, V_{ID}: variance due individual identity, V_{YR}: variance due to year, V_R: residual variance.

Trait	[1]h^2	pe^2	ind^2	[1]V_A	V_{ID}	V_{YR}	V_R
Chest girth	0.28 (0.07-0.60)	0.32 (0.10-0.73)	0.60 (0.30-0.89)	0.001 (<0.001-0.002)		0.001 (<0.001-0.006)	0.001 (<0.001-0.002)
Hind leg length	0.27 (0.07-0.51)	0.47 (0.19-0.85)	0.74 (0.50-0.94)	<0.001 (<0.001-0.001)		0.001 (<0.001-0.005)	<0.001 (<0.001-0.001)
Ingest-free body-fat	0.13 (0.01-0.60)	0.06 (0.01-0.26)	0.19 (0.03-0.67)	0.008 (0.001-0.039)		0.004 (<0.001-0.020)	0.049 (0.022-0.067)
Weight	0.23 (0.03-0.65)	0.20 (0.04-0.60)	0.43 (0.11-0.85)	0.002 (<0.001-0.007)		0.003 (<0.001-0.012)	0.006 (0.002-0.009)
Start day	[a]0.06 (0.01-0.20) [b]0.03 (0.01-0.09)	0.88 (0.68-0.98)	0.94 (0.82-0.99)	[a]0.001 (<0.001-0.002) [b]11.16 (3.5-26.87)	0.001 (<0.001-0.073)	0.018 (0.003-0.073)	0.001 (<0.001-0.002)
End day	[a]0.09 (0.01-0.26) [b]0.04 (0.01-0.11)	0.83 (0.59-0.98)	0.92 (0.77-0.99)	[a]0.001 (<0.001-0.002) b13.63 (4.16-32.69)	0.001 (<0.001-0.002)	0.012 (0.002-0.051)	0.001 (<0.001-0.002)
Distance	0.13 (0.01-0.56)	0.56 (0.06-0.87)	0.70 (0.24-0.91)	0.014 (0.001-0.062)	0.056 (0.003-0.099)	0.004 (<0.001-0.022)	0.032 (0.010-0.081)
Duration	[a]0.17 (<0.01-0.83) [b]0.07 (<0.01-0.34)	0.49 (0.02-0.98)	0.66 (0.05-1.00)	[a]0.049 (0.001-0.249) [b]2.5 (0.04-13.4)	0.123 (0.001-0.308)	0.012 (0.001-0.071)	0.093 (0.001-0.288)
Movement rate	0.75 (0.37-0.92)	0.10 (0.01-0.45)	0.86 (0.64-0.95)	0.243 (0.117-0.350)	0.024 (0.001-0.133)	0.001 (<0.001-0.051)	0.045 (0.016-0.111)

[1]For Poisson distributed traits (start day, end day, duration) heritability and additive genetic effect values are given in both the latent model state [a] and true data state [b]

Table S3.3. Variance component estimates and their associated ratios for body size and migration traits using the GRM with 0.05 relatedness cut-off. h^2: heritability, pe^2: permanent environmental effects, ind^2: repeatability, V_A: additive genetic variance, V_{ID}: variance due individual identity, V_{YR}: variance due to year, V_R: residual variance.

Trait	[1]h^2	pe^2	ind^2	[1]V_A	V_{ID}	V_{YR}	V_R
Chest girth	0.30 (0.07-0.65)	0.28 (0.08-0.69)	0.59 (0.28-0.89)	0.001 (<0.001-0.002)		0.001 (<0.001-0.006)	0.002 (<0.001-0.003)
Hind leg length	0.28 (0.07-0.54)	0.44 (0.17-0.83)	0.72 (0.45-0.93)	<0.001 (<0.001-0.001)		0.001 (<0.001-0.005)	0.001 (<0.001-0.001)
Ingest-free body-fat	0.17 (0.01-0.81)	0.06 (0.01-0.27)	0.23 (0.03-0.87)	0.014 (0.001-0.067)		0.005 (<0.001-0.027)	0.061 (0.011-0.093)
Weight	0.23 (0.03-0.72)	0.20 (0.04-0.59)	0.43 (0.13-0.89)	0.003 (<0.001-0.001)		0.003 (<0.001-0.013)	0.007 (0.001-0.011)
Start day	[a]0.07 (0.01-0.21) [b]0.04 (0.01-0.10)	0.87 (0.65-0.98)	0.94 (0.80-0.99)	[a]0.001 (<0.001-0.002) [b]13.37 (3.83-34.53)	0.001 (<0.001-0.002)	0.019 (0.003-0.081)	0.001 (<0.001-0.002)
End day	[a]0.10 (0.01-0.31) [b]0.05 (0.01-0.14)	0.79 (0.50-0.97)	0.90 (0.70-0.99)	[a]0.001 (<0.001-0.003) [b]17.49 (4.53-46.58)	0.001 (<0.001-0.003)	0.011 (0.002-0.048)	0.001 (<0.001-0.002)
Distance	0.19 (0.01-0.73)	0.47 (0.03-0.87)	0.66 (0.17-0.91)	0.023 (0.001-0.095)	0.051 (0.001-0.115)	0.006 (<0.001-0.033)	0.040 (0.011-0.102)
Duration	[a]0.30 (<0.01-0.93) [b]0.10 (<0.01-0.31)	0.45 (0.02-0.98)	0.75 (0.08-1.00)	[a]0.083 (0.001-0.302) [b]1.48 (0.05-19.44)	0.104 (0.001-0.315)	0.024 (0.001-0.132)	0.067 (0.001-0.265)
Movement rate	0.76 (0.24-0.94)	0.12 (0.01-0.58)	0.89 (0.65-0.97)	0.287 (0.092-0.443)	0.016 (0.001-0.206)	0.016 (0.001-0.085)	0.042 (0.012-0.130)

[1] For Poisson distributed traits (start day, end day, duration) heritability and additive genetic effect values are given in both the latent model state [a] and true data state [b]