

Original Article

Moving to mate? Migration strategy does not predict genetic structure or diversity in bats (Chiroptera)

Alicia M. Korpach^{1,2,3,*}, Evelien de Greef¹, Levi Newediuk¹, Chloé Schmidt⁴, Colin J. Garroway¹, Matt J. Thorstensen¹ 

¹Department of Biological Sciences, University of Manitoba, Winnipeg, MB, Canada

²Department of Biology, University of Winnipeg, Winnipeg, MB, Canada

³Department of Biology, University of Regina, Regina, SK, Canada

⁴German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

*Corresponding author. Department of Biological Sciences, University of Manitoba, R3T 2N2, Winnipeg, Canada; Department of Biology, University of Winnipeg, R3B 2E9, Winnipeg, Canada; Department of Biology, University of Regina, S4S 0A2, Regina, Canada. E-mail: alicia.korpach@gmail.com

ABSTRACT

How, when, and where animals move during mating periods directs gene-flow patterns across landscapes. Traits associated with movement, such as movement ability and migratory behaviour, are sometimes correlated with population genetic structure, but this relationship depends on where and when mating occurs relative to annual movements. With their wide diversity in behaviours and life-history strategies, bats provide a testing ground for hypotheses about population structure related to migration and mating. We used a global sample of microsatellite data ($N = 233$ sampling locations from 17 bat species) associated with published studies to examine links between genetic variation and short-distance, long-distance, or non-migratory strategies that also relate to varied mating strategies. The genetic measures we tested were population-specific differentiation, gene diversity, and allelic richness. Using Bayesian models that accounted for phylogenetic distances among species and spatial autocorrelation, we identified no correlations between migration strategy and genetic variation. Our results suggest that hypotheses about genetic structure being mediated by migration might not hold, in general, for bat species. We discuss the need for continued research into the complex association of ecological, biogeographical, and behavioural factors that facilitate gene flow among populations, especially in species with diverse movement patterns.

Keywords: allelic richness; movement; gene diversity; genetic variation; life-history trait; macrogenetics; mammal; population-specific F_{ST}

INTRODUCTION

Geographical, ecological, and behavioural barriers to movement can shape patterns of gene flow and generate structured populations (Coulon *et al.* 2006, Kekkonen *et al.* 2011). Movement ability (the capacity to fly, swim, or move across potential barriers) generally exhibits a negative correlation with genetic structure, because reproductive individuals from populations of highly motile species are more able to interact and exchange genetic material (Bohonak 1999, Bradbury *et al.* 2008). However, such movement can also promote genetic differentiation by increasing the rates at which novel habitats are encountered (Phillimore *et al.* 2006).

As the only flying mammals, bats (Order Chiroptera) are an interesting group to study connections between movement, mating, and genetic patterns because there is wide variation in the distances that bat species travel to mate. Migratory behaviour

(the round-trip, seasonal movement of organisms between locations) has been related to increased genetic diversity in taxa as diverse as butterflies (García-Berro *et al.* 2023), mammals (Gustafson *et al.* 2017), and fish (Kovach *et al.* 2013). In bats, migration has been correlated with population structure (Burland and Worthington Wilmer 2001, Olival 2012, Taylor *et al.* 2012, Moussy *et al.* 2013, Burns and Broders 2014). However, migration as a predictor of genetic structure could be improved by explicitly taking into account the social structures of where and when mating occurs (Heckel and Von Helversen 2003, D'Urban Jackson *et al.* 2017).

Bat species that migrate long distances, i.e. outside of the region where they were born, are likely to mate during autumn migration or winter (Cryan and Brown 2007, Lausen *et al.* 2023) or even during spring migration (Clerc, Rogers and McGuire 2021). There is little evidence of population structure in several

North American and European long-distance migratory bat species, suggesting that migratory routes are not distinct unless there are geographical barriers and that species form single, panmictic populations (Petit and Mayer 2000, Korstian *et al.* 2015, Vohnhof and Russell 2015, Sovic *et al.* 2016). Bat species that migrate over shorter distances, within the breeding range, often mate at swarming sites or hibernacula (Fenton 1969, van Schaik *et al.* 2015). Swarming behaviour can maintain gene flow between genetically differentiated populations of temperate bat species, although levels of gene flow can vary, possibly with regional physiography (Kerth *et al.* 2003, Miller-Butterworth *et al.* 2003, Furmankiewicz and Altringham 2007, Davy *et al.* 2015). Population structure in non-migratory, or sedentary, bats varies greatly with sex-biased dispersal, mating behaviours, and movement ability (as a result of lower flight capability and geographical barriers to movement), but in general there is evidence that structure is greater in non-migratory than in migratory bats (Burland and Worthington Wilmer 2001, Moussy *et al.* 2013). Relatively limited movements to mate can limit gene flow among populations and lead to significant isolation by distance and genetic differentiation at small geographical scales (Wright *et al.* 2018, Budinski *et al.* 2019).

Not all research supports this general pattern, however, because migratory and non-migratory populations within species of birds and bats can be genetically indistinct (Buerkle 1999, Russell *et al.* 2005). The reason for inconsistent conclusions about the association between migratory behaviour and genetic structure is unclear, but the results of previous review studies are difficult to compare because of varying types of markers, measures of genetic variation (Moussy *et al.* 2013), a lack of phylogenetic control (Olival 2012) or statistical treatment (Burland and Worthington Wilmer 2001, Moussy *et al.* 2013), or a disregard of mating behaviour. Regardless of the distance that a population migrates, a key assumption about gene flow is that the migration movement results in breeding (Petit and Mayer 2000); if strongly migratory species mate on the summer breeding grounds, as non-migrants do, their genetic structure would not be expected to differ from that of non-migrants (Moussy *et al.* 2013). A new standardized examination of potential interplay between migration and mating, hence gene flow, can provide additional insight into how these behavioural traits interact with genetic variation in bat species or populations (Olival 2012, Papadopoulou and Knowles 2016).

Bats also vary widely in other ecological, morphological, and behavioural traits, and hypotheses about order-wide trends in population structure become complicated when certain species exhibit traits that support conflicting hypotheses. Predictions of degrees of genetic subdivision are usually based on wing morphology or body size, migratory behaviour, monogamous vs. polygynous breeding systems, roost selection, and fruit- or nectar-based diets (McCracken and Wilkinson 2000, Fleming and Martino 2020). But polygynous bat species can be migratory or non-migratory, frugivorous or insectivorous (McCracken and Wilkinson 2000). Random or promiscuous mating reduces relatedness in family groups and increases genetic diversity (McCauley and O'Donnell 1984, Gohli *et al.* 2013); therefore, an effect attributed to migration could potentially be confounded by the mating strategy. Bat species worldwide face threats related to climate change, habitat loss, overhunting, and, in North

America, novel fungal pathogens (Lorch *et al.* 2011, Frick *et al.* 2020). Identifying traits that directly affect genetic structure can help to identify groups of bats that might be at greater risk of loss of genetic variation, thereby requiring enhanced monitoring or protection.

Our goal was to leverage publicly available genetic data to revisit the question of how well migratory behaviour predicts genetic variation in bats, particularly where migration might facilitate mating activity, hence gene flow among populations. We hypothesized that the weakest population-specific genetic differentiation (Weir and Goudet 2017) would occur in bats that migrate the furthest and for which there is evidence of mating during migration. We classified bat species into three migration classes (long-distance, regional, and non-migrant) to test an association between migration distance and genetic differentiation. We also classified species into two mating classes (single male/multi-female and multi-male/multi-female) to examine the association between migration distance, mating strategy, and genetic differentiation and to examine whether our interpretation of migration effects could be confounded by potential effects of mating strategy. To provide a genetic context for these models of population genetics and behavioural traits, we assessed differences in three genetic measures (genetic differentiation, gene diversity, and allelic richness) at a species level.

MATERIALS AND METHODS

Genetic measurement collection methods

The microsatellite data used in the present genetic analyses were compiled in previously published work (Schmidt *et al.* 2020). They were originally published in multiple research articles (Buchalski *et al.* 2014, Burns and Broders 2014, Baird *et al.* 2015, Boston *et al.* 2015b, Johnson *et al.* 2015, Moussy *et al.* 2015b, Razgour *et al.* 2015b, Witsenburg *et al.* 2015b, Günther *et al.* 2016b, Vesterinen *et al.* 2016b: p. 20; Afonso *et al.* 2017b, Cleary *et al.* 2017b, Davy *et al.* 2017, Lausen *et al.* 2019) and several online repositories (Buchalski *et al.* 2013, Boston *et al.* 2015a, Burns, Frasier and Broders 2015, Moussy *et al.* 2015a, Razgour *et al.* 2015a, Witsenburg *et al.* 2015a, Baerwald and Barclay 2016, Günther *et al.* 2016a, Johnson *et al.* 2016, Vesterinen *et al.* 2016a, Afonso *et al.* 2017a, Cleary *et al.* 2017a, Santos and Meyer 2017, Davy *et al.* 2018, Lausen *et al.* 2018). In total, we attained data from 17 bat species, representing 233 populations and 8095 individuals (Supporting Information, Table S1). We used all individuals for gene diversity and allelic richness metrics, and owing to one population for some groups, we used a subset of samples to estimate genetic differentiation, which included 12 species (228 populations with 7618 individuals) (Fig. 1; Supporting Information, Table S2). Gene diversity was calculated with ADEGENET v.2.1.5 (Jombart 2008), and genetic differentiation and allelic richness were calculated with HIERFSTAT v.0.5.7 (Goudet 2005).

Behaviour classification methods

We used data from primary literature and online species accounts to classify each species into discrete migration and mating classes (Davis and Hitchcock 1965, Bradbury and Vehrencamp 1977, Leu 2000, McCracken and Wilkinson 2000, Vingiello 2002, Keinath 2004, Wohlgenuth *et al.* 2004, Cryan and Brown 2007,

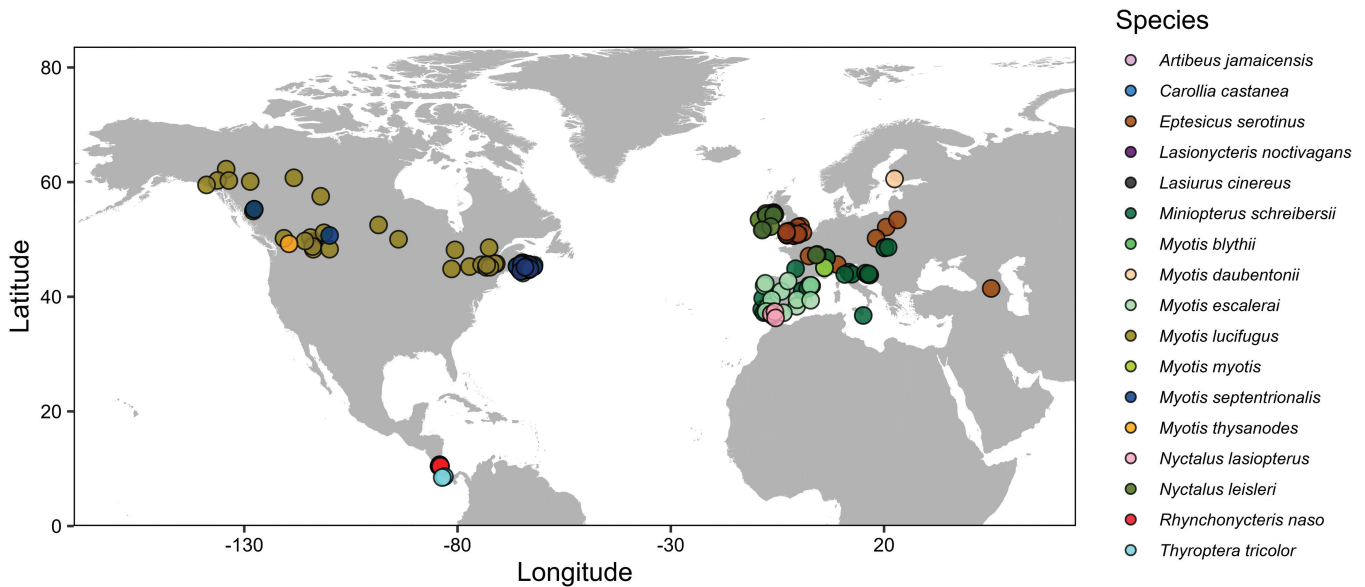


Figure 1. Map of bat genetic data-sampling locations. Sampling locations are coloured by species. A total of 12 species, 228 sampling groups, and 7618 individuals were used for analyses of genetic differentiation, and 17 species, 233 sampling groups, and 8095 individuals were used for analyses of gene diversity and allelic richness.

Ibáñez *et al.* 2009, Dondini and Vergari 2010, Morrison 2011, McGuire *et al.* 2012, Hans 2013: p. 201; Moussy *et al.* 2013, Cryan *et al.* 2014, Bentley 2017, Fraser *et al.* 2017, Taylor and Tuttle 2019, Encarnação and Becker 2020, Martinoli *et al.* 2020, Ruedi 2020, Godlevska *et al.* 2021, GBIF Secretariat 2022a, b, c, d, 2023, Ibáñez and Juste 2022, Lausen *et al.* 2022, Jarso 2023, UNEP/EUROBATS Secretariat 2023).

Species were classified into three distance-based migration classes (Supporting Information, Table S3), following the guidelines of Fleming (2019), and generally corresponding to the distance categories used in other work (Burns and Broders 2014). Species that are thought to remain within a 50 km radius year-round were classified as non-migratory. Species that are known to migrate 100–500 km between summer and winter roosts within the same region were considered regional migrants, and species that migrate seasonally ≥ 1000 km between different regions were considered long-distance migrants. Although there was only partial overlap in species between the current and previous studies (Olival 2012, Moussy *et al.* 2013, Burns and Broders 2014), our classifications generally agreed. In rare cases of disagreement (i.e. we classified *Myotis blythii* as non-migratory, whereas Moussy *et al.* (2013) classified it as migratory, and *Miniopterus schreibersii* was a long-distance migrant in the work of Burns and Broder (2014), whereas we initially considered it a regional migrant), we repeated the analysis using the alternative classification.

Species were also classified by mating strategy (Supporting Information, Table S3), in groupings of single male/single female (i.e. monogamy), single male/multi-female (i.e. harem), and multi-male/multi-female (i.e. both sexes mate promiscuously) used in other work (McCracken and Wilkinson 2000). These are simplistic categories, because harem-forming species can exhibit varying degrees of promiscuity, but they provide the most comparable classification to previous research (Olival 2012). Where there was a lack of information about the mating

strategy of a species, we either did not include that species in the analysis (e.g. *Myotis thysanodes*) or made an assumption based on the behaviour of a close congener (e.g. *Carollia castanea* is assumed to have a similar mating strategy to its well-studied relative *Carollia perspicillata*, and *Nyctalus lasiopterus* is assumed to be similar to other noctules). As with the migration class-based models, we repeated the analysis with the alternative classification to examine the possibility that ambiguous classifications might have biased our results.

Population genetics across species

We first examined differences in population genetic measures among species without modelling other variables. In the statistical computing environment R v.4.2.1, the packages TIDYVERSE v.2.0.0, TIDYBAYES v.3.0.3, GGBEESWARM v.0.7.1, and PATCHWORK v.1.1.2 were useful for data management and model visualization (Bürkner 2018, Wickham *et al.* 2019, Pedersen 2022, R Core Team 2022, Kay 2023). The package BRMS v.2.18.0 was used for all Bayesian modelling (Bürkner 2018).

We then examined differences in population genetic measures across species by fitting a series of models with species identity as a fixed effect. The three population genetic measures used were genetic differentiation, gene diversity (also called expected heterozygosity), and allelic richness (Nei and Chesser 1983, Weir and Goudet 2017). Each Bayesian model was fitted with a Gaussian distribution, using four independent Hamiltonian Monte Carlo chains across 5000 warm-up and 15 000 sampling iterations each (60 000 sampling iterations total). For the models analysing genetic differentiation or gene diversity, normal priors of mean zero and standard deviation one were used for global intercepts and model coefficients. For the model analysing allelic richness, we used normal priors of mean zero and standard deviation five. A different standard deviation was used for allelic richness because it had a wider numerical range than each of genetic differentiation and gene diversity. In all

models, adapt delta was raised to 0.99 and maximum tree depth raised to 16 to achieve sufficient sampling of the posterior distribution. Model fit was assessed with the potential scale reduction statistic \hat{R} , visual inspection of trace plots, and visual inspection of posterior predictive checks over 100 draws in each model. Models were accepted only if \hat{R} was 1.00 for all parameters. The R package *EMMEANS* v.1.8.4-1 (Searle *et al.* 1980) was used to gather posterior draws for visualization and for estimating marginal means to compare 95% highest posterior density in a pairwise manner between species.

Correlations between genetic and life-history traits

We used a Bayesian approach to model potential relationships between migration or mating strategy and population genetic measures. The same statistical programs and packages were used for these models as in the models of population genetics across species. Bayesian models were fitted with the following model structure in R:

```
population genetic measure ~
(migration strategy or mating system)
+ (1 | species)
+ (1 | phylogenetic correlation matrix)
+ (spatial simultaneous autoregressive structure)
```

Here, genetic differentiation, gene diversity, and allelic richness were each used as population genetic measures. Six models were thus run: three population genetic measures compared against migration strategy and three against mating strategy.

Both migration and mating strategy were modelled as fixed effects. Species was included as a random intercept to address factors independent of phylogenetic relatedness that might cause differences in species means for each genetic metric, such as niche or environmental effects (Hadfield and Nakagawa 2010). A phylogenetic correlation matrix was also included as a random effect to address evolutionary relatedness among the bat species used in the present analyses. This phylogeny was created by using the R package *TAXIZE* v.0.9.00 to retrieve the taxonomic classifications and hierarchy for the list of species from the National Center for Biotechnology Information database using the functions *classification* and *class2tree* (Supporting Information, Fig. S1) (Chamberlain and Szöcs 2013). With this taxonomic tree, the R package *APE* v.5.7 was used to calculate the phylogenetic correlation matrix used in each model with *vcv.phylo* (Paradis and Schliep 2019). Model priors, distributions, sampling parameters, and contrasts were set and assessed with the same methods as in the models of population genetic measures across species. We initially constructed models without spatial autoregressive terms and used the package *DHARMA* v.0.4.6 to identify weak spatial autocorrelation among sample sites in some models (0.05–0.12 Moran's *I*) (Hartig 2022). To address the potential for spatial autocorrelation to affect the results, we used spatial autoregressive terms in *BRMS* with the *sar* function in all models. Specifically, $K = 4$ nearest neighbours for each point were used in a connection network of sampling locations in the R package *ADESPATIAL* v.0.3-21, as a balance between connectivity at local and regional scales. This network was used for specifying the spatial weighting matrix in the spatial simultaneous autoregressive structure, with type 'lag' chosen to model response variables.

RESULTS

We identified six non-migratory, seven regional, and three long-distance migrants in our dataset (Fig. 2). Of these, most non-migratory bats had a single male/multi-female mating system, whereas more regional and long-distance species had multi-male/multi female mating systems (Fig. 2). Across species, the serotine bat (*Eptesicus serotinus*) and common bent-wing bat (*Miniopterus schreibersii*) tended to have higher genetic differentiation and lower gene diversity and allelic richness than certain other species, such as the Jamaican fruit bat (*Artibeus jamaicensis*) or chestnut short-tailed bat (*C. castanea*) (Fig. 2; Supporting Information, Tables S4–S6). Overall, these results revealed species-specific differences in population-specific differentiation and genetic variation. We observed no differences in any comparison between migration or mating strategies using 95% highest posterior density intervals (Fig. 3; Supporting Information, Tables S7 and S8). Results from models using alternative mating and migration strategy classifications were consistent with the original models (Supporting Information, Fig. S2).

DISCUSSION

Despite species-level differences in population genetic measures, our results do not support the hypothesis that a long-distance migratory tendency leads to more genetic mixing than other migration strategies, even for species that are expected to mate during migration (Fig. 3). This result remains consistent when using an alternative migration classification for *Myotis blythii* (following the classification by Moussy *et al.* 2013). In analyses using all accessible microsatellite data, it appears that bats maintain genetic variation despite differences in these behaviours and that the high mobility of bats in general is sufficient to maintain genetic connectivity for most species. These results are consistent with conclusion drawn by Fleming and Martino (2020) that bat species, assuming sufficiently large populations, are likely to have ample genetic variation.

Given the evidence in the literature that suggests a causal link between migratory behaviour and genetic variation in bats (Bryja *et al.* 2008, Olival 2012, Moussy *et al.* 2013, Burns and Broders 2014), we had expected populations of species with longer migration distances and more promiscuous mating behaviour to mix more, resulting in weaker population structure. It is possible that high correlation between migratory behaviour and mating strategy (as reported in this study) could have led past researchers to attribute genetic structure to movement characteristics instead of promiscuity during mating (e.g. all long-distance migratory species in our study were also classified as having promiscuous [multi-male/multi-female] mating strategies). It is also possible that migration distance is generally a weak predictor of population mixing, even in species that are known to mate during migration. Measures of high dispersal ability (e.g. wing morphology designed for fast and efficient flight) have been better predictors of low population structure in bats (Burland and Worthington Wilmer 2001, Olival 2012, Taylor *et al.* 2012, Moussy *et al.* 2013, Burns and Broders 2014), although long-distance migrants and high dispersers tend to share similar morphological characteristics, and migration has sometimes been described as a form

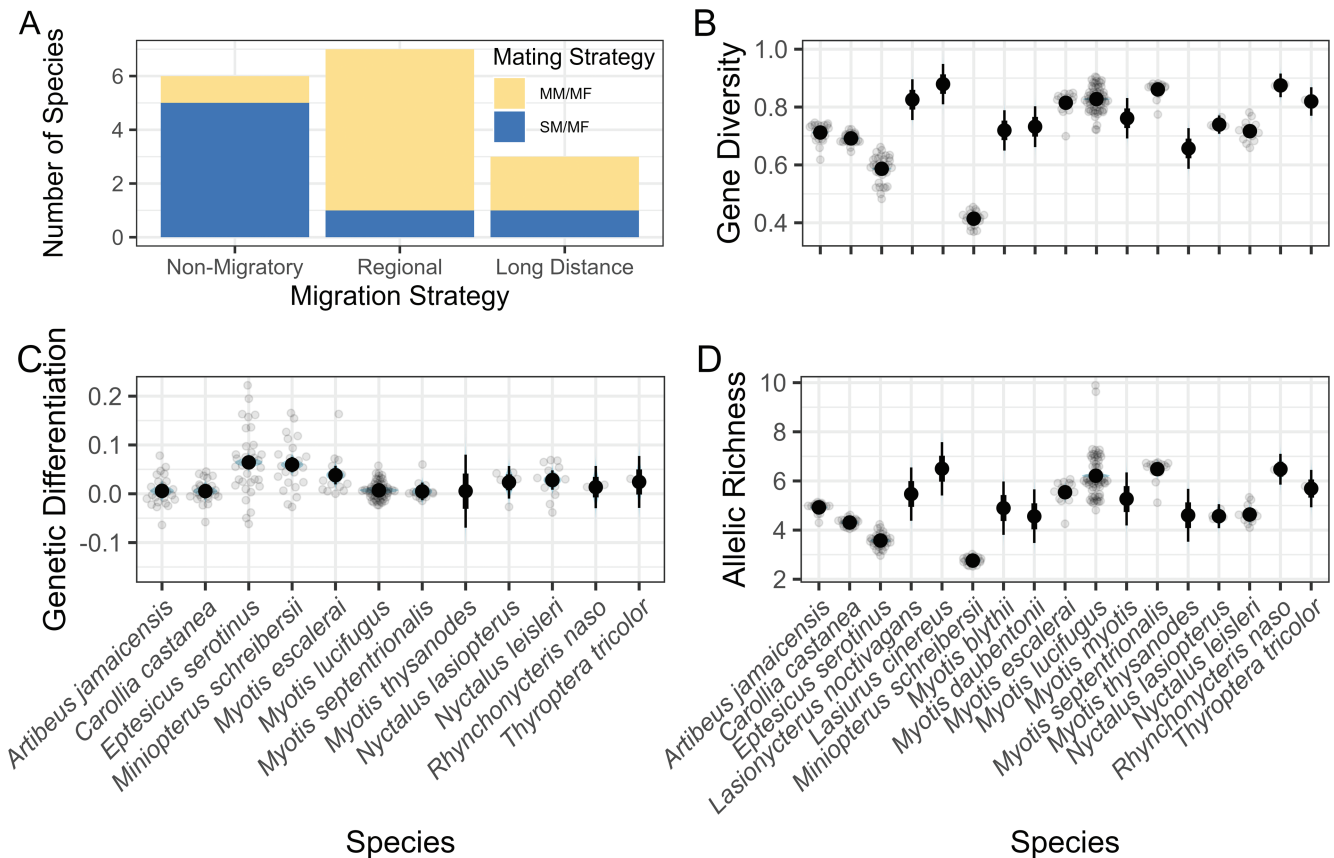


Figure 2. A, bar plot of migration and mating strategies across the bat species used in the present study. B–D, estimates of gene diversity (B), genetic differentiation (C), and allelic richness (D) across species. Posterior distributions are in blue, 95% credible intervals are indicated by thin black lines, and 66% credible intervals by thick black lines. Group-level data points used for modelling genetic measures across species are in light grey, and species labels are consistent on the x -axis for B and D.

of dispersal in bat species that mate during migration (Popa-Lisseanu and Voigt 2009, Burns and Broders 2014). Bat species with morphological features designed for fast and efficient flights would be able to mix far and wide at mating sites, whether they are migrants or non-migrants, which could explain the stronger correlation between dispersal ability (wing morphology) and population genetic structure than between migration distance and population genetic structure.

It is unclear why we did not find any difference in genetic measures between species that mate in single male/multi-female groups and species where both species are promiscuous. Of the six non-migratory species in our study, two were classified to have multi-male/multi-female mating systems, and of the nine migratory species, one was classified with a single male/multi-female mating system. These three species with anomalous behaviours (i.e. migration and mating systems did not follow the general trend) did not differ in genetic structure when compared with the rest of the species in the dataset, and reclassifying them to the alternative mating system did not change our results. An association between mating system and genetic structure is not straightforward, because some bat species that form harems exhibit higher-than-expected levels of promiscuity (Heckel and Von Helversen 2003, Garg *et al.* 2012), which could lead to weakened genetic structure among populations (Olival 2012). For example, in bats with polygynous harem-based mating systems, extra-harem mating can account for 70% of paternity (Heckel

and Von Helversen 2003). Therefore, clear-cut genetic structure in bat populations might defy the simple mating strategy classifications that we used.

Migration strategies are also not easily categorized, because many species are partial migrants, with some populations migrating in a different manner to others. For example, stable isotope analysis revealed high variation in the migratory movements of *Lasionycterus noctivagans* (Fraser *et al.* 2017). Within partially migratory species, non-migratory populations can have greater genetic structure (e.g. *Eidolon helvum*) (Juste, Ibáñez and Machordom 2000, Peel *et al.* 2013), but this is not always the case (e.g. *Tadarida brasiliensis Mexicana*) (Russell *et al.* 2005). In species where all populations are migratory, those populations with low migratory connectivity can have greater genetic structure, possibly reflecting genetic isolation by distance (e.g. *Myotis lucifugus*) (Vanhof and Russell 2015, Wilder *et al.* 2015). Nevertheless, the migration classes we used are likely to be useful for the purposes of general classification to investigate broad trends. Non-migratory bat species (e.g. *A. jamaicensis* and *C. castanea*) are obviously highly vagile, as are all bats, but they undeniably move much shorter annual distances than long-distance migrants (e.g. *Lasionycterus noctivagans* and *Lasiurus cinereus*). Studies that track migration movements directly and discern the mating locations and promiscuity of specific populations are required to reconcile fully the influences of those movement-related behavioural traits on genetic structure.

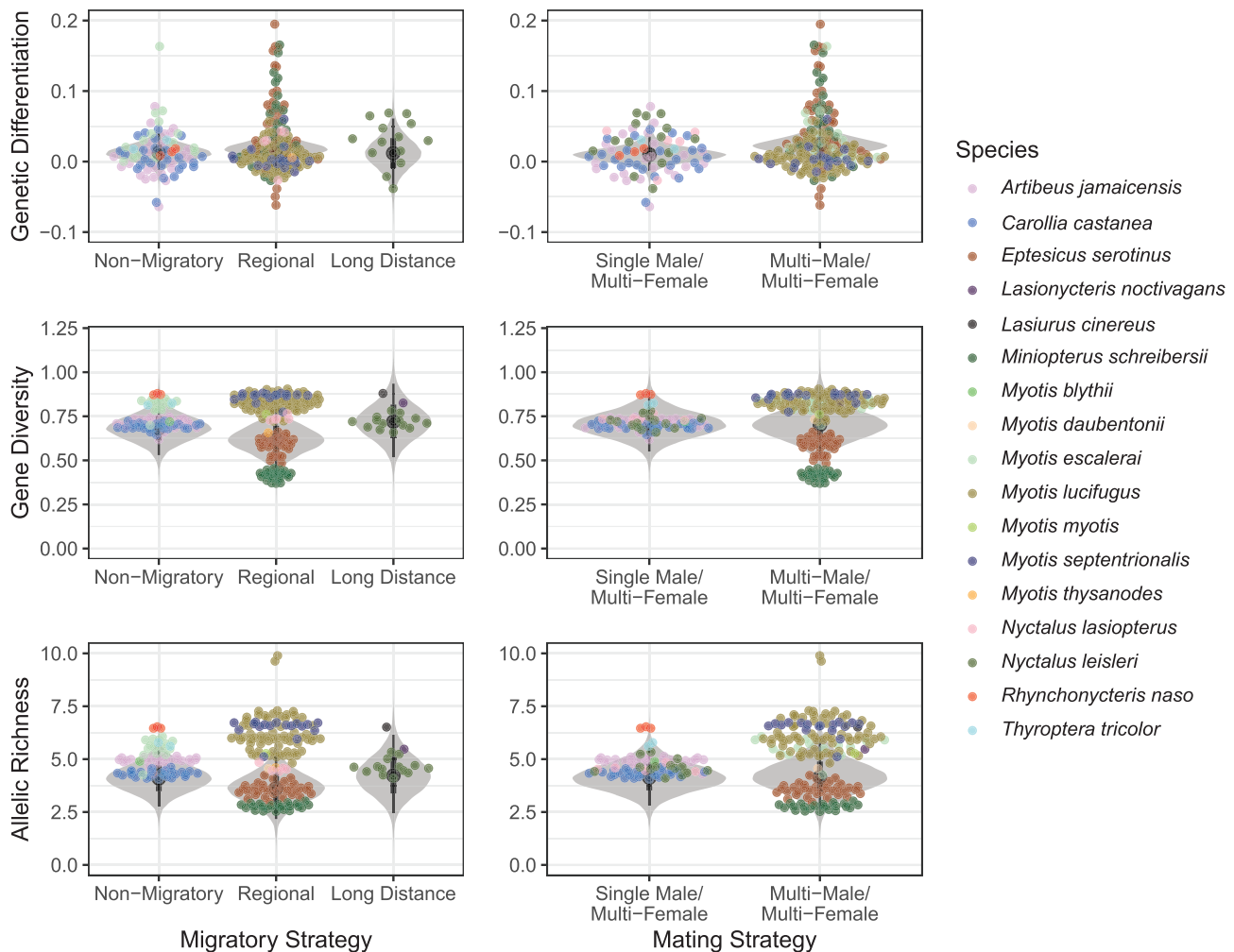


Figure 3. Estimates of population genetic differentiation, gene diversity, and allelic richness compared between migration strategies (non-migratory, regional, or long-distance) and mating strategies (single male/multi-female or multi-male/multi-female) in bats. Posterior distributions are in grey, 95% credible intervals are indicated by thin black lines, 66% credible intervals are indicated by thick black lines, and group-level data points used for modelling genetic measures are coloured by species.

Some disparities in the migratory classification of species could, hypothetically, explain the difference between our results and previous studies, but the species composition of our dataset had little overlap with those previous studies. Where there was overlap, there were only two cases where our classifications did not agree. We classified *Myotis blythii* as non-migratory, whereas [Moussy et al. \(2013\)](#) classified it as migratory. This disparity could be attributable to the latter's liberal definitions of "migratory" to include all facultative and partial migration and "non-migratory" to include seasonal relocations typically <100 km. Although we used similar classification guidelines to [Burns and Broder \(2014\)](#), those authors classified *Miniopterus schreibersii* as a long-distance migrant, whereas we classified it as a regional migrant; [Olivall \(2012\)](#) and [Moussy et al. \(2013\)](#) simply classified it as migratory. In the case of *Miniopterus schreibersii*, bats at mating roosts are more likely to mate with individuals from outside their own colony and populations are significantly differentiated, but how nursing, mating, and hibernation roosts are linked to migration patterns is still unclear ([Ramos Pereira et al.](#)

[2009](#)). Reanalyses of our dataset that excluded or reassigned species with uncertainty surrounding their behavioural classification showed that the uncertainty did not change our results. We were unable to detect differences in genetic measures between migratory or mating classes regardless of how those species were classified.

Several factors could be responsible for the measurable genetic variation among species that could not be explained by migratory or mating behaviour in our study. Availability of food resources might influence short-term movement patterns on the breeding grounds; for instance, frugivorous or nectivorous bats might need to move further or more frequently than insectivorous bats, because insects are typically a more stable food source ([Webb and Tidemann 1996](#), [Moreno-Valdez et al. 2004](#), [Bontadina et al. 2008](#)). Thus, for two species with similar mating strategies, frugivorous bats might incidentally have more genetic mixing because they are exposed to more individuals outside their populations while moving around to find food. However, species with lower tolerance to human disturbance or

with more specialized diets could have more limited movements across the landscape, hence reduced gene flow (Ripperger *et al.* 2014, McCulloch and Waters 2023). Finally, historical events can confound landscape-level effects that we might be tempted to attribute to ecology or behaviours such as migration or social structure (Hewitt 2000).

The variability in sample distribution and quantity across species in our study could affect the representation of different types of migration or mating strategies. For example, some species were sampled much more than others (ranging from 3104 bats from 66 sample sites [*Myotis lucifugus*] to six bats from one sample site [*Myotis thysanodes*]). If the full spatial extents of respective ranges of each species are not sampled, measures of genetic differentiation could be reduced artificially. We also assumed that distances moved during migration relative to range sizes did not affect the categorization of migratory strategies. Additionally, describing spatial genetic structure in populations requires consideration of multiple seasons, such as summer maternity roosts, swarming sites, and hibernacula (Davy *et al.* 2015). Variation in the timing of sampling collection across species made it difficult to parse out seasonal effects on population structure overall, and we assumed that samples came from genetic populations based on sampling sites. However, we can at least conclude that site-specific genetic differentiation and variation were not associated with migration or breeding strategy.

Genetics might, nevertheless, be related to migration or mating strategies, even if the relationship is weak in bats. Genetic variation was found to have a small to moderate influence on variance in migration timing in purple martins (*Progne subis*), with a particularly strong signal on one chromosome (de Greef *et al.* 2023). Therefore, a locus-specific analysis (such as a large genome-wide association study) might have been necessary to establish individual-level connections between the observed traits and genetics. Rather, we show that there is a minimal effect of the migration or mating strategy on neutral variation and population structure in bats. Widespread phenotypic shifts might have induced prior shifts in gene flow or related processes in bats because of environmental change (Smeraldo *et al.* 2021), which might have altered the dynamics of how genotypes reflect phenotypes.

Genetic variation and connectivity underlie adaptive potential and thus population resilience to future environmental change, which bodes well for maintaining genetic connectivity and minimizing genetic diversity losses in recovering bat populations. In birds, long-distance migrants are especially vulnerable to global change and human land use, and climate change can restrict long-distance migratory behaviours (Visser *et al.* 2009, Zurell *et al.* 2018). The dynamics of evolution are context specific, and our data highlight gaps in our understanding about the circumstances in which a trait or behaviour becomes a driver of genetic diversity. A greater understanding of the push and pull between traits (such as specific behaviours), genetic diversity, and gene flow across a landscape would provide substantial power for explaining and conserving biodiversity worldwide.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

ACKNOWLEDGEMENTS

We thank Quinn Fletcher for helpful conversations when designing this study. The present study would not have been possible without the work of numerous researchers in collecting, publishing, and making available the data used here.

AUTHOR CONTRIBUTION

AMK, EG, CS, CJG, and MJT conceived of and designed the study. EG, LN, and CS collected and organized data. MJT performed formal analyses. EG, LN, and MJT created visualizations. AMK and MJT wrote the original draft of the manuscript, which all authors reviewed and edited.

CONFLICT OF INTEREST

None declared.

FUNDING

A Natural Sciences and Engineering Research Council of Canada Discovery Grant (05972) awarded to C.J.G supported this work.

DATA AVAILABILITY

All data used in the present study were downloaded from publicly available resources detailed in the Materials and methods, with specific repositories listed in the references as data citations.

REFERENCES

- Afonso E, Goydadin AC, Giraudoux P *et al.* 2017a. Investigating hybridization between the two sibling bat species *Myotis myotis* and *M. blythii* from guano in a natural mixed maternity colony. *Dryad, Dataset*. <https://doi.org/10.5061/dryad.g53d0>
- Afonso E, Goydadin AC, Giraudoux P *et al.* Investigating hybridization between the two sibling bat species *Myotis myotis* and *M. blythii* from guano in a natural mixed maternity colony. *PLoS One* 2017b;12:e0170534. <https://doi.org/10.1371/journal.pone.0170534>
- Baerwald EF, Barclay RMR. Are migratory behaviours of bats socially transmitted? 2016. *Dryad, Dataset*. <https://doi.org/10.5061/dryad.4d3n1>
- Baird AB, Braun JK, Mares MA *et al.* Molecular systematic revision of tree bats (Lasiurini): doubling the native mammals of the Hawaiian Islands. *Journal of Mammalogy* 2015;96:1255–74. <https://doi.org/10.1093/jmammal/gyv135>
- Bentley J. *Lasionycteris noctivagans* (silver-haired bat). *Animal Diversity Web*. 2017. https://animaldiversity.org/accounts/Lasionycteris_noctivagans (8 July 2024, date last accessed)
- Bohonak AJ. Dispersal, gene flow, and population structure. *The Quarterly Review of Biology* 1999;74:21–45. <https://doi.org/10.1086/392950>
- Bontadina F, Schmied SF, Beck A *et al.* Changes in prey abundance unlikely to explain the demography of a critically endangered Central European bat. *Journal of Applied Ecology* 2008;45:641–8. <https://doi.org/10.1111/j.1365-2664.2007.01417.x>
- Boston ESM, Montgomery WI, Hynes R *et al.* 2015a. New insights on postglacial colonisation in Western Europe: the phylogeography of the Leisler's bat (*Nyctalus leisleri*). *Dryad, Dataset*. <https://doi.org/10.5061/dryad.6g6r6>
- Boston ESM, Montgomery WI, Hynes R *et al.* New insights on postglacial colonization in western Europe: the phylogeography of the Leisler's bat (*Nyctalus leisleri*). *Proceedings Biological Sciences* 2015b;282:20142605. <https://doi.org/10.1098/rspb.2014.2605>

- Bradbury IR, Laurel B, Snelgrove PVR et al. Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. *Proceedings Biological Sciences* 2008;275:1803–9. <https://doi.org/10.1098/rspb.2008.0216>
- Bradbury JW, Vehrencamp SL. Social organization and foraging in emballonurid bats. *Behavioral Ecology and Sociobiology* 1977;2:19–29. <https://doi.org/10.1007/bf00299285>
- Bryja J, Kaňuch P, Fornůsková A et al. Low population genetic structuring of two cryptic bat species suggests their migratory behaviour in continental Europe: genetic structure of cryptic pipistrelles. *Biological Journal of the Linnean Society* 2008;96:103–14. <https://doi.org/10.1111/j.1095-8312.2008.01093.x>
- Buchalski MR, Chaverri G, Vonhof MJ. 2013. When genes move farther than offspring: gene flow by male gamete dispersal in the highly philopatric bat species *Thyroptera tricolor*. *Dryad, Dataset*. <https://doi.org/10.5061/dryad.46h6j>
- Buchalski MR, Chaverri G, Vonhof MJ. When genes move farther than offspring: gene flow by male gamete dispersal in the highly philopatric bat species *Thyroptera tricolor*. *Molecular Ecology* 2014;23:464–80. <https://doi.org/10.1111/mec.12593>
- Budinski I, Blagojević J, Jovanović VM et al. Population genetic structure of the Mediterranean horseshoe bat *Rhinolophus euryale* in the central Balkans. *PLoS One* 2019;14:e0210321. <https://doi.org/10.1371/journal.pone.0210321>
- Buerkle CA. The historical pattern of gene flow among migratory and nonmigratory populations of prairie warblers (Aves: Parulinae). *Evolution* 1999;53:1915–24. <https://doi.org/10.1111/j.1558-5646.1999.tb04572.x>
- Bürkner PC. Advanced Bayesian multilevel modeling with the R package brms. *The R Journal* 2018;10:395. <https://doi.org/10.32614/rj-2018-017>
- Burland TM, Worthington Wilmer J. Seeing in the dark: molecular approaches to the study of bat populations. *Biological Reviews* 2001;76:389–409.
- Burns LE, Broders HG. Correlates of dispersal extent predict the degree of population genetic structuring in bats. *Conservation Genetics* 2014;15:1371–9. <https://doi.org/10.1007/s10592-014-0623-y>
- Burns LE, Frasier TR, Broders HG. 2015. Genetic connectivity among swarming sites in the wide ranging and recently declining little brown bat (*Myotis lucifugus*). *Dryad, Dataset*. <https://doi.org/10.5061/dryad.hs37s>
- Chamberlain SA, Szöcs E. taxize: taxonomic search and retrieval in R. *F1000Research* 2013;2:191. <https://doi.org/10.12688/f1000research.2-191.v2>
- Cleary KA, Waits LP, Finegan B. 2017a. Comparative landscape genetics of two frugivorous bats in a biological corridor undergoing agricultural intensification. *Dryad, Dataset*. <https://doi.org/10.5061/dryad.nv92q>
- Cleary KA, Waits LP, Finegan B. Comparative landscape genetics of two frugivorous bats in a biological corridor undergoing agricultural intensification. *Molecular Ecology* 2017b;26:4603–17. <https://doi.org/10.1111/mec.14230>
- Clerc J, Rogers EJ, McGuire LP. Testing predictions of optimal migration theory in migratory bats. *Frontiers in Ecology and Evolution* 2021;9:1–10. <https://doi.org/10.3389/fevo.2021.686379>
- Coulon A, Guillot G, Cosson J-F et al. Genetic structure is influenced by landscape features: empirical evidence from a roe deer population. *Molecular Ecology* 2006;15:1669–79.
- Cryan PM, Brown AC. Migration of bats past a remote island offers clues toward the problem of bat fatalities at wind turbines. *Biological Conservation* 2007;139:1–11. <https://doi.org/10.1016/j.biocon.2007.05.019>
- Cryan PM, Stricker CA, Wunder MB. Continental-scale, seasonal movements of a heterothermic migratory tree bat. *Ecological Applications* 2014;24:602–16. <https://doi.org/10.1890/13-0752.1>
- Davis WH, Hitchcock HB. Biology and migration of the bat, *Myotis lucifugus*, in New England. *Journal of Mammalogy* 1965;46:296–313. <https://doi.org/10.2307/1377850>
- Davy CM, Donaldson ME, Rico Y et al. Prelude to a panzootic: gene flow and immunogenetic variation in northern little brown myotis vulnerable to bat white-nose syndrome. *FACETS* 2017;2:690–714. <https://doi.org/10.1139/facets-2017-0022>
- Davy CM, Donaldson ME, Rico Y et al. 2018. Prelude to a panzootic: gene flow and immunogenetic variation in northern little brown myotis vulnerable to bat white-nose syndrome. *Dryad, Dataset*. <https://doi.org/10.5061/dryad.h7n25>
- Davy CM, Martinez-Nunez F, Willis CKR et al. Spatial genetic structure among bat hibernacula along the leading edge of a rapidly spreading pathogen. *Conservation Genetics* 2015;16:1013–24. <https://doi.org/10.1007/s10592-015-0719-z>
- de Greef E, Suh A, Thorstensen MJ et al. Genomic architecture of migration timing in a long-distance migratory songbird. *Scientific Reports* 2023;13:2437. <https://doi.org/10.1038/s41598-023-29470-7>
- Dondini G, Vergari S. Harem size and male mating tactics in *Nyctalus leisleri* (Kuhl, 1817) (Chiroptera: Vespertilionidae). *Hystrix, the Italian Journal of Mammalogy* 2010;20:147–54. <https://doi.org/10.4404/hystrix-20.2-4445>
- D'Urban Jackson J, Dos Remedios N, Maher KH et al. Polygamy slows down population divergence in shorebirds: mating systems and diversification in shorebirds. *Evolution* 2017;71:1313–26. <https://doi.org/10.1111/evo.13212>
- Encarnação JA, Becker NI. Daubenton's bat *Myotis daubentonii* (Kuhl, 1817). In: Hackländer K, Zacos FE, (eds.). *Handbook of the Mammals of Europe*. Cham: Springer International, 2020, 1–31.
- Fenton MB. Summer activity of *Myotis lucifugus* (Chiroptera: Vespertilionidae) at hibernacula in Ontario and Quebec. *Canadian Journal of Zoology* 1969;47:597–602. <https://doi.org/10.1139/z69-103>
- Fleming TH. Bat migration. In: *Encyclopedia of Animal Behavior*. Elsevier, 2019, 605–610.
- Fleming TH, Martino AMG. Population biology. In: Fleming TH, Dávalos LM, Mello MAR, (eds.), *Phyllostomid Bats: A Unique Mammalian Radiation*. Chicago and London: The University of Chicago Press, 2020.
- Fraser EE, Brooks D, Longstaffe FJ. Stable isotope investigation of the migratory behavior of silver-haired bats (*Lasiurus noctivagans*) in eastern North America. *Journal of Mammalogy* 2017;98:1225–35.
- Frick WF, Kingston T, Flanders J. A review of the major threats and challenges to global bat conservation. *Annals of the New York Academy of Sciences* 2020;1469:5–25. <https://doi.org/10.1111/nyas.14045>
- Furmankiewicz J, Altringham J. Genetic structure in a swarming brown long-eared bat (*Plecotus auritus*) population: evidence for mating at swarming sites. *Conservation Genetics* 2007;8:913–23. <https://doi.org/10.1007/s10592-006-9246-2>
- García-Berro A, Talla V, Vila R et al. Migratory behaviour is positively associated with genetic diversity in butterflies. *Molecular Ecology* 2023;32:560–74. <https://doi.org/10.1111/mec.16770>
- Garg KM, Chattopadhyay B, Doss D et al. Promiscuous mating in the harem-roosting fruit bat, *Cynopterus sphinx*. *Molecular Ecology* 2012;21:4093–105.
- GBIF Secretariat. 2022a. *Myotis blythii* (Tomes, 1857). <https://www.gbif.org/species/2432414> (8 July 2024, date last accessed).
- GBIF Secretariat. 2022b. *Myotis daubentonii* (Kuhl, 1817). <https://www.gbif.org/species/195628195> (8 July 2024, date last accessed).
- GBIF Secretariat. 2022c. *Myotis escaleraei* Cabrera, 1904. <https://www.gbif.org/species/8181305> (8 July 2024, date last accessed).
- GBIF Secretariat. 2022d. *Nyctalus lasiopterus* (Schreber, 1780). <https://www.gbif.org/species/5218525> (8 July 2024, date last accessed).
- GBIF Secretariat. *Carollia castanea* (H. Allen, 1890). *GBIF Backbone Taxonomy* 2023. <https://www.gbif.org/species/2433178> (8 July 2024, date last accessed).
- Godlevska L, Gazaryan S, Kruskop SV. *Eptesicus serotinus* (amended version of 2020 assessment). *IUCN Red List of Threatened Species* 2021. <https://www.iucnredlist.org/species/85199559/195834153> (8 July 2024, date last accessed).
- Gohli J, Anmarkrud JA, Johnsen A et al. Female promiscuity is positively associated with neutral and selected genetic diversity in passerine birds. *Evolution* 2013;67:1406–19. <https://doi.org/10.1111/evo.12045>

- Goudet J. HIERFSTAT, a package for R to compute and test hierarchical *F*-statistics. *Molecular Ecology Notes* 2005;5:184–6.
- Günther L, Lopez MD, Knörnschild M *et al.* 2016a. From resource to female defence: the impact of roosting ecology on a bat's mating strategy. *Dryad, Dataset*. <https://doi.org/10.5061/dryad.df878>
- Günther L, Lopez MD, Knörnschild M *et al.* From resource to female defence: the impact of roosting ecology on a bat's mating strategy. *Royal Society Open Science* 2016b;3:160503. <https://doi.org/10.1098/rsos.160503>
- Gustafson KD, Vickers TW, Boyce WM *et al.* A single migrant enhances the genetic diversity of an inbred puma population. *Royal Society Open Science* 2017;4:170115. <https://doi.org/10.1098/rsos.170115>
- Hadfield JD, Nakagawa S. General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology* 2010;23:494–508. <https://doi.org/10.1111/j.1420-9101.2009.01915.x>
- Hans S. *Rhynchonycteris naso*. *Global Biodiversity Information Facility* 2013. https://animaldiversity.org/accounts/Rhynchonycteris_naso/ (8 July 2024, date last accessed).
- Hartig F. 2022. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.6. <https://CRAN.R-project.org/package=DHARMA> (8 July 2024, date last accessed).
- Heckel G, Von Helversen O. Genetic mating system and the significance of harem associations in the bat *Saccopteryx bilineata*. *Molecular Ecology* 2003;12:219–27. <https://doi.org/10.1046/j.1365-294x.2003.01722.x>
- Hewitt G. The genetic legacy of the Quaternary ice ages. *Nature* 2000;405:907–13. <https://doi.org/10.1038/35016000>
- Ibáñez C, Guillén A, Agirre-Mendi PT *et al.* Sexual segregation in Iberian noctule bats. *Journal of Mammalogy* 2009;90:235–43. <https://doi.org/10.1644/08-mamm-a-037.1>
- Ibáñez C, Juste J. Greater noctule bat *Nyctalus lasiopterus* (Schreber, 1780). In: Hackländer K, Zachos FE, (eds.), *Handbook of the Mammals of Europe*. Cham: Springer International, 2022, 1–24.
- Jarso W. *Thyroptera tricolor* (Spix's disk-winged bat). *Animal Diversity Web* 2023. https://animaldiversity.org/accounts/Thyroptera_tricolor/ (8 July 2024, date last accessed).
- Johnson LNL, McLeod BA, Burns LE *et al.* Population genetic structure within and among seasonal site types in the little brown bat (*Myotis lucifugus*) and the northern long-eared bat (*M. septentrionalis*). *PLoS One* 2015;10:e0126309. <https://doi.org/10.1371/journal.pone.0126309>
- Johnson LNL, McLeod BA, Burns LE *et al.* 2016. Population genetic structure within and among seasonal site types in the little brown bat (*Myotis lucifugus*) and the northern long-eared bat (*M. septentrionalis*). *Dryad, Dataset*. <https://doi.org/10.5061/dryad.47nm0>
- Jombart T. ADEGENET: a R package for the multivariate analysis of genetic markers. *Bioinformatics* 2008;24:1403–5. <https://doi.org/10.1093/bioinformatics/btn129>
- Juste J, Ibáñez C, Machordom A. Morphological and allozyme variation of *Eidolon helvum* (Mammalia: Megachiroptera) in the islands of the Gulf of Guinea. *Biological Journal of the Linnean Society* 2000;71:359–78.
- Kay M. 2023. tidybayes: tidy data and geoms for Bayesian models. *Zenodo*. <https://doi.org/10.5281/zenodo.8242124> (8 July 2024, date last accessed).
- Keinath DA. Fringed Myotis (*Myotis thysanodes*): a technical conservation assessment. *USDA Forest Service, Rocky Mountain Region* 2004:1–63.
- Kekkonen J, Seppä P, Hanski IK *et al.* Low genetic differentiation in a sedentary bird: house sparrow population genetics in a contiguous landscape. *Heredity* 2011;106:183–90. <https://doi.org/10.1038/hdy.2010.32>
- Kerth G, Kiefer A, Trappmann C *et al.* High gene diversity at swarming sites suggest hot spots for gene flow in the endangered Bechstein's bat. *Conservation Genetics* 2003;4:491–9.
- Korstian JM, Hale AM, Williams DA. Genetic diversity, historic population size, and population structure in 2 North American tree bats. *Journal of Mammalogy* 2015;96:972–80. <https://doi.org/10.1093/jmammal/gyv101>
- Kovach RP, Gharrett AJ, Tallmon DA. Temporal patterns of genetic variation in a salmon population undergoing rapid change in migration timing. *Evolutionary Applications* 2013;6:795–807. <https://doi.org/10.1111/eva.12066>
- Lausen C, Proctor MF, Nagorsen D *et al.* 2018. Population genetics reveal *Myotis keenii* (Keen's myotis) and *Myotis evotis* (long-eared myotis) to be a single species. *Dryad, Dataset*. <https://doi.org/10.5061/dryad.h9b3d30>
- Lausen CL, Falxa GA, Solick DI *et al.* Singing silver-haired bats (*Lasionycteris noctivagans*). *Wildlife Society Bulletin* 2023;47:e1500.
- Lausen C, Nagorsen D, Brigham M *et al.* 2022. *Bats of British Columbia*. Place of publication not identified: Independent Publishers Group: The Royal British Columbia Museum.
- Lausen CL, Proctor M, Nagorsen DW *et al.* Population genetics reveal *Myotis keenii* (Keen's myotis) and *Myotis evotis* (long-eared myotis) to be a single species. *Canadian Journal of Zoology* 2019;97:267–79. <https://doi.org/10.1139/cjz-2018-0113>
- Leu H. *Miniopterus schreibersii* (Schreibers's long-fingered bat). *Animal Diversity Web* 2000. https://animaldiversity.org/accounts/Miniopterus_schreibersii/ (8 July 2024, date last accessed).
- Lorch JM, Meteyer CU, Behr MJ *et al.* Experimental infection of bats with *Geomyces destructans* causes white-nose syndrome. *Nature* 2011;480:376–8. <https://doi.org/10.1038/nature10590>
- Martinoli A, Mazzamuto MV, Spada M. Serotine *Eptesicus serotinus* (Schreber, 1774). In: Hackländer K, Zachos FE, (eds.), *Handbook of the Mammals of Europe*. Cham: Springer International, 2020, 1–17.
- McCauley DE, O'Donnell R. The effect of multiple mating on genetic relatedness in larval aggregations of the imported willow leaf beetle (*Plagioderma versicolora*, Coleoptera: Chrysomelidae). *Behavioral Ecology and Sociobiology* 1984;15:287–91. <https://doi.org/10.1007/bf00292991>
- McCracken GF, Wilkinson GS. Bat mating systems. In: Crichton EG, Krutzsch PH (eds.), *Reproductive Biology of Bats*. Amsterdam: Elsevier, 2000, 321–62.
- McCulloch GA, Waters JM. Rapid adaptation in a fast-changing world: emerging insights from insect genomics. *Global Change Biology* 2023;29:943–54. <https://doi.org/10.1111/gcb.16512>
- McGuire LP, Guglielmo CG, Mackenzie SA *et al.* Migratory stopover in the long-distance migrant silver-haired bat, *Lasionycteris noctivagans*. *The Journal of Animal Ecology* 2012;81:377–85. <https://doi.org/10.1111/j.1365-2656.2011.01912.x>
- Miller-Butterworth CM, Jacobs DS, Harley EH. Strong population substructure is correlated with morphology and ecology in a migratory bat. *Nature* 2003;424:187–91. <https://doi.org/10.1038/nature01742>
- Moreno-Valdez A, Honeycutt RL, Grant WE. Colony dynamics of *Leptonycteris nivalis* (Mexican long-nosed bat) related to flowering agave in northern Mexico. *Journal of Mammalogy* 2004;85:453–9.
- Morrison P. *Artibeus jamaicensis*. *Animal Diversity Web* 2011. https://animaldiversity.org/accounts/Artibeus_jamaicensis/ (8 July 2024, date last accessed).
- Moussy C, Atterby H, Griffiths AGF *et al.* 2015a. Population genetic structure of serotine bats (*Eptesicus serotinus*) across Europe and implications for the potential spread of bat rabies (European bat lyssavirus EBLV-1). *Dryad, Dataset*. <https://doi.org/10.5061/dryad.665np>
- Moussy C, Atterby H, Griffiths AGF *et al.* Population genetic structure of serotine bats (*Eptesicus serotinus*) across Europe and implications for the potential spread of bat rabies (European bat lyssavirus EBLV-1). *Heredity* 2015b;115:83–92. <https://doi.org/10.1038/hdy.2015.20>
- Moussy C, Hosken DJ, Mathews F *et al.* Migration and dispersal patterns of bats and their influence on genetic structure. *Mammal Review* 2013;43:183–95. <https://doi.org/10.1111/j.1365-2907.2012.00218.x>

- Nei M, Chesser RK. Estimation of fixation indices and gene diversities. *Annals of Human Genetics* 1983;**47**:253–9. <https://doi.org/10.1111/j.1469-1809.1983.tb00993.x>
- Olival K. Evolutionary and ecological correlates of population genetic structure in bats. In: Gunnell GF, Simmons NB (eds.), *Evolutionary History of Bats: Fossils, Molecules and Morphology*. Cambridge: Cambridge University Press, 2012, 267–316.
- Papadopoulou A, Knowles LL. Toward a paradigm shift in comparative phylogeography driven by trait-based hypotheses. *Proceedings of the National Academy of Sciences of the United States of America* 2016;**113**:8018–24. <https://doi.org/10.1073/pnas.1601069113>
- Paradis E, Schliep K. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 2019;**35**:526–8. <https://doi.org/10.1093/bioinformatics/bty633>
- Pedersen TL. 2022. patchwork: the composer of plots. <https://patchwork.data-imaginist.com/> (8 July 2024, date last accessed).
- Peel AJ, Sargan DR, Baker KS et al. Continent-wide panmixia of an African fruit bat facilitates transmission of potentially zoonotic viruses. *Nature Communications* 2013;**4**:2770. <https://doi.org/10.1038/ncomms3770>
- Petit E, Mayer F. A population genetic analysis of migration: the case of the noctule bat (*Nyctalus noctula*). *Molecular Ecology* 2000;**9**:683–90. <https://doi.org/10.1046/j.1365-294x.2000.00896.x>
- Phillimore AB, Freckleton RP, Orme CDL et al. Ecology predicts large-scale patterns of phylogenetic diversification in birds. *The American Naturalist* 2006;**168**:220–9. <https://doi.org/10.1086/505763>
- Popa-Lisseanu AG, Voigt CC. Bats on the move. *Journal of Mammalogy* 2009;**90**:1283–9. <https://doi.org/10.1644/09-mamm-s-130r.2.1>
- Ramos Pereira MJ, Salgueiro P, Rodrigues L et al. Population structure of a cave-dwelling bat, *Miniopterus schreibersii*: does it reflect history and social organization? *The Journal of Heredity* 2009;**100**:533–44. <https://doi.org/10.1093/jhered/esp032>
- Razgour O, Salicini I, Ibáñez C et al. 2015a. Unravelling the evolutionary history and future prospects of endemic species restricted to former glacial refugia. *Dryad, Dataset*. <https://doi.org/10.5061/dryad.v1v47>
- Razgour O, Salicini I, Ibáñez C et al. Unravelling the evolutionary history and future prospects of endemic species restricted to former glacial refugia. *Molecular Ecology* 2015b;**24**:5267–83. <https://doi.org/10.1111/mec.13379>
- R Core Team. *R: a Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing, 2022.
- Ripperger SP, Tschapka M, Kalko EKV et al. Resisting habitat fragmentation: high genetic connectivity among populations of the frugivorous bat *Carollia castanea* in an agricultural landscape. *Agriculture, Ecosystems & Environment* 2014;**185**:9–15.
- Ruedi M. Lesser mouse-eared bat *Myotis blythii* (Tomes, 1857). In: Hackländer K, Zacos FE, (eds.), *Handbook of the Mammals of Europe*. Cham: Springer International, 2020, 1–24.
- Russell AL, Medellín RA, Mccracken GF. Genetic variation and migration in the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*). *Molecular Ecology* 2005;**14**:2207–22. <https://doi.org/10.1111/j.1365-294X.2005.02552.x>
- Santos JD, Meyer CFJ. 2017. Dispersal and group formation dynamics in a rare and endangered temperate forest bat (*Nyctalus lasiopterus*, Chiroptera: Vespertilionidae). *Dryad, Dataset*. <https://doi.org/10.5061/dryad.rc504>
- Schmidt C, Domaratzki M, Kinnunen RP et al. Continent-wide effects of urbanization on bird and mammal genetic diversity. *Proceedings Biological Sciences* 2020;**287**:20192497. <https://doi.org/10.1098/rspb.2019.2497>
- Searle SR, Speed FM, Milliken GA. Population marginal means in the linear model: an alternative to least squares means. *The American Statistician* 1980;**34**:216–21. <https://doi.org/10.2307/2684063>
- Smeraldo S, Bosso L, Salinas-Ramos VB et al. Generalists yet different: distributional responses to climate change may vary in opportunistic bat species sharing similar ecological traits. *Mammal Review* 2021;**51**:571–84. <https://doi.org/10.1111/mam.12247>
- Sovic MG, Carstens BC, Gibbs HL. Genetic diversity in migratory bats: results from RADseq data for three tree bat species at an Ohio windfarm. *PeerJ* 2016;**4**:e1647. <https://doi.org/10.7717/peerj.1647>
- Taylor P, Goodman S, Schoeman M et al. Wing loading correlates negatively with genetic structuring of eight Afro-Malagasy bat species (Molossidae). *Acta Chiropterologica* 2012;**14**:53–62.
- Taylor M, Tuttle M. *Bats: an Illustrated Guide to all Species*. Washington: Smithsonian Books, 2019.
- UNEP/EUROBATS Secretariat. *Myotis myotis*. UNEP/EUROBATS 2023. https://www.eurobats.org/about_eurobats/protected_bat_species/myotis_myotis (8 July 2024, date last accessed).
- van Schaik J, Janssen R, Bosch T et al. Bats swarm where they hibernate: compositional similarity between autumn swarming and winter hibernation assemblages at five underground sites. *PLoS One* 2015;**10**:e0130850. <https://doi.org/10.1371/journal.pone.0130850>
- Vesterinen EJ, Ruokolainen L, Wahlberg N et al. 2016a. What you need is what you eat? Prey selection by the bat *Myotis daubentonii*. *Dryad, Dataset*. <https://doi.org/10.5061/dryad.343nd>
- Vesterinen EJ, Ruokolainen L, Wahlberg N et al. What you need is what you eat? Prey selection by the bat *Myotis daubentonii*. *Molecular Ecology* 2016b;**25**:1581–94. <https://doi.org/10.1111/mec.13564>
- Vingiello S. *Myotis thysanodes* (fringed myotis). *Animal Diversity Web* 2002. https://animaldiversity.org/accounts/Myotis_thysanodes/ (8 July 2024, date last accessed).
- VisserME, PerdeckAC, VanBalenJH et al. Climate change leads to decreasing bird migration distances. *Global Change Biology* 2009;**15**:1859–65. <https://doi.org/10.1111/j.1365-2486.2009.01865.x>
- Vonhof MJ, Russell AL. Genetic approaches to the conservation of migratory bats: a study of the eastern red bat (*Lasiurus borealis*). *PeerJ* 2015;**3**:e983. <https://doi.org/10.7717/peerj.983>
- Webb NJ, Tidemann CR. Mobility of Australian flying-foxes, *Pteropus* spp. (Megachiroptera): evidence from genetic variation. *Proceedings: Biological Sciences* 1996;**263**:497–502.
- Weir BS, Goudet J. A unified characterization of population structure and relatedness. *Genetics* 2017;**206**:2085–103. <https://doi.org/10.1534/genetics.116.198424>
- Wickham H, Averick M, Bryan J et al. Welcome to the Tidyverse. *Journal of Open Source Software* 2019;**4**:1686. <https://doi.org/10.21105/joss.01686>
- Wilder AP, Kunz TH, Sorenson MD. Population genetic structure of a common host predicts the spread of white-nose syndrome, an emerging infectious disease in bats. *Molecular Ecology* 2015;**24**:5495–506. <https://doi.org/10.1111/mec.13396>
- Witsenburg F, Clément L, Dutoit L et al. 2015a. How a haemosporidian parasite of bats gets around: the genetic structure of a parasite, vector and host compared. *Dryad, Dataset*. <https://doi.org/10.5061/dryad.2m1p0>
- Witsenburg F, Clément L, López-Baucells A et al. How a haemosporidian parasite of bats gets around: the genetic structure of a parasite, vector and host compared. *Molecular Ecology* 2015b;**24**:926–40. <https://doi.org/10.1111/mec.13071>
- Wohlgemuth R, Devrient I, García A et al. Long-distance flight of a lesser noctule (*Nyctalus leisleri*) after rehabilitation. *Myotis* 2004;**41**–42:69–73.
- Wright PGR, Hamilton PB, Schofield H et al. Genetic structure and diversity of a rare woodland bat, *Myotis bechsteini*: comparison of continental Europe and Britain. *Conservation Genetics* 2018;**19**:777–87. <https://doi.org/10.1007/s10592-018-1053-z>
- Zurell D, Graham CH, Gallien L et al. Long-distance migratory birds threatened by multiple independent risks from global change. *Nature Climate Change* 2018;**8**:992–6. <https://doi.org/10.1038/s41558-018-0312-9>