Predicting migration routes for three species of migratory bats using species distribution models

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Understanding seasonal variation in the distribution and movement patterns of migratory species is essential to their monitoring and conservation. While there are many species of migratory bats little is known about their seasonal movements in North America. This is important because the bat fatalities from wind energy turbines are significant and may fluctuate seasonally. Here we describe accurate seasonally resolved distributions for the three species that are most impacted by wind farms (*Lasiurus borealis* [eastern red bat], *L. cinereus* [hoary bat], and *Lasionycteris noctivagans* [silver-haired bat]) that were used to infer migratory pathways. To accomplish this, we used 2880 occurrence points collected from the Global Biodiversity Information Facility over five decades in North America to model species distributions on a seasonal basis and used an ensemble approach for modeling distributions. The results suggest that all three species exhibit variation in distributions from north to south depending on season, with each species showing potential migratory pathways during the fall migration that follow linear features. Finally, we describe proposed migratory pathways for these three species that can be used to identify stop-over sites, assessing small-scale migration, and highlight areas that should be prioritized to reduce the effects of wind farm mortality.

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9 **Abstract**

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13 bat fatalities from wind energy turbines are significant and may fluctuate seasonally. Here we

14 describe accurate seasonally resolved distributions for the three species that are most impacted

15 by wind farms (*Lasiurus borealis* [eastern red bat], *L. cinereus* [hoary bat], and *Lasionycteris*

16 *noctivagans* [silver-haired bat]) that were used to infer migratory pathways. To accomplish this,

17 we used 2880 occurrence points collected from the Global Biodiversity Information Facility over

18 five decades in North America to model species distributions on a seasonal basis and used an

19 ensemble approach for modeling distributions. The results suggest that all three species exhibit

20 variation in distributions from north to south depending on season, with each species showing

21 potential migratory pathways during the fall migration that follow linear features. Finally, we

22 describe proposed migratory pathways for these three species that can be used to identify stop-

23 over sites, assessing small-scale migration, and highlight areas that should be prioritized to

24 reduce the effects of wind farm mortality.

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28

29   **Introduction**

30   Conservation and management of migratory animals requires knowledge about their seasonal

31   movements across space and time (Webster et al. 2002). In a wide variety of taxa, species

32   migrate when resources vary seasonally (Shaw & Couzin 2013) or temperature variation results

33   in thermal stress (Fleming & Eby 2003). Due to small body sizes it is difficult to track long

34   distance movements of many taxa such as species of bats, birds, and insects reducing our

35   understanding of their migratory behavior. While some progress has been made using light-level

36   geolocators (Åkesson et al. 2012) and various biomarkers (e.g. Hobson & Wassner 2018), these

37   methods have limitations such as requiring recapture and low precision, respectively and as a

38   result are limited in their impact. This is particularly true for bats, small-bodied nocturnal

39   mammals capable of true flight.

40   Although only 12 of 500 Vespertilionid bats undertake long-distance migration,

41   understanding their migration is vital to the conservation of these species (Fleming & Eby 2003;

42   Simmons & Cirranello 2020; Welbergen et al. 2020). By understanding migration of these

43   species we can better inform the pressures an individual will face during migration or at home

44   ranges during non-migratory time periods. However, we currently know little about the long-

45   distance migration of bats in North America; for most species all that is known is approximate

46   direction (North/South), time of year, a few environmental variables, and some rough estimates

47   of distances travelled (Fleming & Eby 2003; Pettit & O'Keefe 2019). While the information is

48   lacking for North America, more is known from Europe and other regions. Previous studies in

49   bats have shown repeated and partial migration (Lehnert et al. 2018), and that bats showed site

50   fidelity at stop-over sites during migration (Giavi et al. 2014). In addition, others have suggested

51   the tracking of linear features for bat migration (e.g. Voigt et al. 2016; Ahlén et al. 2009),

52   although others have challenged this aspect of migration (Krauel et al. 2018). Human activities

53   have the potential to disrupt bat migration via mechanisms such as interfering with magnetic

54   navigation (Voigt et al. 2017), increasing light pollution (Lacoeuilhe et al. 2014), developing

55   wind farms along migration corridors (Hayes, Cryan, & Wunder 2015), or reducing stop-over

56   sites and food availability through deforestation and habitat destruction. To mitigate these

57   effects, a better understanding of migration in bats is needed.

58   Latitudinal migratory bats are particularly vulnerable to these effects as compared to

59   other species of bats because they roost in trees which provide less protection from seasonal

60   changes through increased exposure to the elements, likely influencing the tendency of certain

61   species to migrate longer distances (>1,000 km) between summer and winter habitats (Hayes,

62   Cryan, & Wunder 2015). A few of these species such as *Lasiurus borealis* (Eastern Red bat), *L.*

63   *cinereus* (Hoary bat), and *Lasionycteris noctivagans* (Silver-haired bat) have been a focus of

64   understanding these behaviors in North America due to their high mortality at wind farms, with

65   some estimates predicting a 90% species population decline within 50 years due to wind farm

66   interactions (Frick et al. 2017). In terms of impact, bats are the most common animal found dead

67   beneath wind turbines in North America (Kunz et al. 2007) with the majority (~80%) of bats

68   consisting of just the three species of latitudinal migratory bats listed above (Arnett & Baerwald

69   2013). Most of the fatalities for these species occur during a period of time coinciding with

70   autumn migration (Kunz et al. 2007), but data concretely linking the act of migration and

71   mortality is lacking. Overall, a more precise delineation of possible migratory corridors and how

72   these influence wind farm interactions could help to minimize impacts of wind facilities on these

73   species.

74   One reason for why long-distance migratory pathways of migratory bats are poorly

75   known is the lack of data on spatial locations through time, particularly in comparison to better-

76   studied migratory species such as birds. In particular, observational data on birds can come from

77   a variety of Citizen Science initiatives such as the Breeding Bird and Christmas Bird Surveys

78   and eBird (National Audubon Society 2010; Sullivan et al. 2009) whereas no such sources of

79   information are available for bats. The difference in data quantity is large. For example, a

80   common migratory bird, the yellow warbler (*Setophaga petechia*) has 2.39 million occurrences

81   the Global Biodiversity Information Facility (GBIF; checked 11 Dec 2019) whereas the entire

82   family of Vespertilionidae bats consisting of >400 species have only 1.49 million occurrences

83   recorded. This is largely due to the nocturnal behavior of bats which makes them more difficult

84   to observe and identify, and difficulty associated with capturing them. While efforts are

85   happening to change this trend, it has not caught up to the scale of more commonly known taxa.

86   All of this has led to a lack of broad scale data on bat migration.

87   One approach to better understand seasonal distributions and identify migratory corridors

88   is to generate seasonally explicit species distribution models (SDMs; Fink et al. 2010, Hayes,

89   Cryan, & Wunder 2015; Smeraldo et al. 2018) and use these to infer movement patterns. This

90   approach has been successful in other migratory species, such as birds (e.g. Reynolds et al.

91   2017). While other studies have attempted to explore this approach with these species (see

92   Findley & Jones 1964; Cryan 2003; Hayes, Cryan, & Wunder 2015), with the advent of the

93   Worldclim 2.0 database there are now more data sets available that will allow better seasonal

94   resolution than has been previously possible. As a result, monthly models can be generated that

95   provide information more explicit seasonal variation to be visualized, while allowing them to be

96   combined to allow for migration modeling during various seasons or times or year. In addition,

97   the use of monthly models allows for possible variation and adapting the models as we learn

98   more about the timing of bat migration in North America.

99   Our objective was to identify possible migratory corridors utilized by migratory bat

100   species (*L. borealis*, *L. cinereus*, and *L. noctivagans*) by modelling their monthly distributions

101   using SDMs. The models generated in this study shed light on the seasonal dynamics for these

102   three species, and highlight areas of interest for further study of migratory corridors that could be

103   used to investigate stop-over sites, small scale migration, and be used as a starting point for

104   designing methods to mitigate wind farm mortality.

105   **Methods**

106   *Occurrence data from GBIF*

107   Figure 1 shows an overview of the steps involved in data collection and analysis; more detailed

108   methods are described on Supplemental Material. To begin, all available occurrence data were

109   downloaded for *L. borealis, L. cinereus*, and *L. noctivagans* through the GBIF data portal

110   (http://www.gbif.org) on 11 March 2019 using only 'Preserved Specimens', 'Human

111   Observations', and 'Material Sample' keywords for data from the past 50 years

112   (https://doi.org/10.15468/dl.dpiwzi, https://doi.org/10.15468/dl.irfol0, and

113   https://doi.org/10.15468/dl.viiyt5, respectively). This 50-year period was selected as it allows for

114   more confidence in the call of a species and its locality. Older records are more likely to be

115   unreliable and it's possible that species are now extirpated from regions they once occupied. All

116   downloaded records were then screened using several filters (described below) as recommended

117   by others (Feeley & Silman 2011; Carstens et al. 2018). Once data sets were filtered using these

118   criteria, we corrected for over sampling within a 1° region following guidelines given by

119   Hijmans and Elith (2017). In brief, we created a grid of 1º resolution and subsampled our

120   occurrence data to one occurrence per grid cell. This was done to reduce the possibility of

121   sampling bias in our data.

122   *Predictor environmental variables*

123   WorldClim version 2 monthly climatic data were used at 2.5-minute resolution (Fick & Hijmans

124   2017) for our species distribution models and included the following variables: precipitation,

125   solar radiation, average temperature, maximum temperature, minimum temperature, vapor

126   pressure, and wind speed (downloaded on 03 June 2019 from worldclim.org). Additionally,

127   elevation maps (Tachikawa et al. 2011; 11 March 2019), and the human influence index

128   (CIESIN, 2005; 11 March 2019) for North America were also downloaded as Jung and Threlfall

129   (2016) showed a negative response to urbanization in the Americas in insectivorous bats in the

130   family Vespertilionidae. Human influence was determined by combining population density,

131   human land use and infrastructure, and human access (WCS, 2005). Following Hayes et al.

132   (2015), we also included MODIS Normalized Difference Vegetative Index (Didan et al. 2015)

133   and Global Tree Coverage 2010 (Hansen et al. 2013) as metrics of seasonality and leaf growth,

134   which could impact prey abundance, and be a metric of available roost sites in trees, downloaded

135   on 04 June 2019 and 05 June 2019, respectively. Prior to final selection of predictor variables,

136   correlations between each possible pair of predictor variables was determined and one variable

137   from each pair that was strongly correlated with the other was removed ($r > 0.8$; Mateo et al.

138   2013). Any removal of a variable was determined based on biological relevance and previous

139   uses in literature.

140   *Species distribution modeling*

141   Species distribution models were generated for each species using five different methods: four

142   specific model algorithms and an ensemble approach (see below). Specific algorithms included:

143   generalized linear model (GLM), BIOCLIM model (BC), random forest (RF), and maximum

144   entropy (MaxEnt; Phillips, Dudik, & Schapire 2017). These four approaches, while good

145   predictors in their own right, can be made more effective through an ensemble method. This

146   approach accounts for the problems of each model and can allow for better performing models

147   (Araújo & New, 2006; Marmion et al. 2009) and is becoming more common (Razgour et al.

148   2016). Due to this and preliminary results, we used the ensemble models for all analyses.

149   All SDM analyses were carried out in R using the packages "randomForest" (Liaw &

150   Wiener 2018), "raster" (Hijmans et al., 2019), "rgeos" (Bivand et al. 2019), "maptools" (Bivand

151   et al. 2019), "dismo" (Hijmans et al. 2017), "sp" (Pebesma, Bivand, & Pebesm, 2012),

152   "ecospat" (Di Cola et al. 2016), and "rJava" (Urbanek 2019). We created 1000 pseudo absence

153   points for each month from random points in the background layers and partitioned the model

154   into testing (80%) and training data (20%) using the "kfold" function.

155   Each model was then assessed using: 1) Area under the ROC (receiver operating

156   characteristic) curve (AUC) and 2) True Skill Statistic (TSS). These values were then used to

157   weigh each layer and were then combined into a single comprehensive SDM. Following

158   generation of our ensemble models, they were assessed using the same AUC and TSS metrics as

159   outlined above and data points used for all other models for comparison to determine which

160   model to use for further analysis. These layers were used to predict migratory pathways.

161   The importance of individual variables was assessed using different methods for each

162   model. For RF we used the 'importance' function in the "randomForest" R package to measure

163   the importance of a variable in a given model. With MaxEnt, variable importance was assessed

164   using 'var.importance' function in "ENMeval" to determine the importance of each variable

165   (Muscarella et al., 2014). For the GLM model, we used the 'varImp' function present in "caret"

166   (Kuhn et al., 2020).

167   *Migratory pathways*

168   To identify migratory pathways using SDMs we used three complementary methods: circuit

169   theory (McRae & Beier 2007; Shah & McRae 2008), 95th percentile suitability (Poor et al. 2012),

170   and least cost path analyses (LCP; Howey 2011). Since each of these methods have advantages

171   and disadvantages, results from these three methods were compared to generate a consensus

172   delineation of possible corridors (Bond et al. 2017; Marrotte & Bowman 2017). While some

173   authors have argued for selecting the single best hypothesized approach (Marrotte & Bowman

174   2017), as we do not know if these species follow linear features as has been observed in some

175   species (Ahlén et al. 2009) or exhibit more erratic movements, we could not confidently select a

176   single approach.

177   For circuit theory, the protocol of Burke et al. (2019) was followed. In brief, we

178   aggregated our winter month occurrences (December – February) into a single dataset and did

179   the same for summer months (June-July), using Hayes et al., (2015) to determine the appropriate

180   months for each season. As SDMs can be interpreted as conductance maps, we used an average

181   of both spring and fall months (March, April, May; and August, September, October,

182   respectively) to assess potential corridors between winter and summer occurrences. These time

183   periods are based on previously published distributions of occurrences (Cryan 2003), previous

184   SDM modeling (Hayes, Cryan, & Wunder 2015), wind farm fatality data (Arnett et al. 2008),

185   radio telemetry (Walters et al. 2006), and acoustic data (Muthersbaugh et al. 2019). Using

186   Circuitscape (Shah & McRae 2008), we set our start ("source") and end ("ground") points based

187   on the hypothesized direction of migration. To identify patterns of spring migration, we set our

188   start as winter occurrences and end as summer points, with the Spring SDMs as the conductance

189   raster; and summer as start and winter as end with Fall SDMs as the fall migration conductance

190   raster; this was repeated for each species.

191   To use least cost path analysis to predict migratory pathways we used the R function

192   'shortestPath' implemented in 'gdistance' (Van Etten 2017). The analysis was done iteratively

193   between all points previously designated as "Winter" and "Summer" points for Circuitscape, and

194   Spring/Fall conductance surfaces for cost determination. As single pathways are not informative

195   for species-wide migratory pathways, we combined each least cost path to create a density of

196   pathways. A high density of overlapping paths was used to identify a migratory pathway.

197   Additionally, while we are unable to infer if a proposed path is true, we used Moran's I (Moran

198   1950) and Geary's C (Geary 1954) to quantify if these proposed pathways are positively

199   clustered, as would be expected in a migratory corridor. We also quantified the distance traveled

200   compared to straight-line distance to determine if the proposed pathways would be biologically

201   relevant (i.e. if not following straight line, other factors influence where bats migrate through).

202   Next, binary rasters identifying potential migratory pathways using the 95th percentile

203   approach was generated to identify areas where bats are more likely to be concentrated compared

204   to background (Poor et al. 2012). This was to identify areas where bats suitability is higher and

205   therefore a potential migratory pathway. Finally, overlaps between Circuitscape, least cost path,

206   and 95th percentile approaches were identified to highlight locations where they agreed and those

207   were assessed to be potential migratory pathways.

208   To ensure we are tracking migration and not simply sampling bias, a comparison between

209   the results for migratory pathways above and those from two non-long-distance migratory

210 species (*Myotis lucifugus* and *Eptesicus fuscus*) following the same methods above was carried

211 out. If the pathways are similar to those from these two species it is possible that we are tracking

212 the ability to capture bats during the winter instead of actual movement. On the other hand, if

213 pathways are different, then it is more likely that we are identifying true pathways. Occurrence

214 data for these additional species were collected from GBIF on 31 January 2020

215 (https://doi.org/10.15468/dl.fphagx) and filtered the same way as previous species, followed by

216 SDM generation and pathway analysis following the same steps and procedures used for the

217 three migratory species.

218 **Results**

219 *GBIF Occurrence Data*

220 A total of 20,697 occurrences were downloaded from the GBIF database: 8,362 for *L. borealis*,

221 7,649 for *L. cinereus*, and 4,686 for *L. noctivagans*. After filtering, there were 10,743 data points

222 remaining: 4,380 for *L. borealis*, 3,736 for *L. cinereus*, and 2,627 for *L. noctivagans*. Finally,

223 after accounting for sampling bias there were 1,129 data points for *L. borealis*, 917 for *L.*

224 *cinereus*, and 834 for *L. noctivagans*. For each month numbers of data points ranged between 21

225 and 205 (Table 1). All months were above the minimum of 13 observations suggested by van

226 Proosdij et al. (2016) (based on simulated data) as necessary for SDM analyses for wide ranging

227 species. Further, only December for two species had occurrences below a higher secondary the

228 minimum threshold of 25 data points (per van Proosdij et al. 2016). SDM analyses were

229 conducted with each subset of data using each of the 5 modeling approaches: GLM, BC, RF,

230 MaxEnt, and ensemble, for a total of 60 model runs for each species. While we acknowledge the

231 presence of other datasets (see NABat [https://www.nabatmonitoring.org/] and/or American

232 Wind/Wildlife Institute [https://awwi.org/]), we found that we had sufficient data available via

233   GBIF for all months given that we had over 25 occurrences for 11 months, and the only month

234   below this threshold is also deficient in other datasets. Further these other datasets are not

235   comprehensive across North American for all months and/or are not readily available to the

236   public.

237   *Predictor variables*

238   Following removal of variables that were highly correlated (r>0.8), eight variables were retained:

239   elevation, forest coverage, NDVI, precipitation, solar radiation, average temperature, vapor

240   pressure and wind speed. The variables that were removed were minimum and maximum

241   temperature which were highly correlated with average temperature (r=0.98 and 0.99,

242   respectively). Average temperature was selected due to the ability of bats to regulate their body

243   temperature and energy expenditure through torpor (Baloun & Guglielmo 2019). While relative

244   importance of variables fluctuated between the four original models implemented (GLM,

245   MaxEnt, RF, and BC), in general, average temperature, solar radiation, and vapor pressure were

246   the most important variables (Table 2; specific weights Table S1). In contrast, NDVI, percent

247   forest, wind, and precipitation were consistently the least important variables.

248   *Species distribution models*

249   AUC scores range from 0.50 to 0.99, while TSS values range from 0.44 to 0.95 across all 5 types

250   of models. When evaluated by both AUC and TSS, the consistently best performing species

251   distribution model was the TSS weighted ensemble model (Figure S1), with this model having a

252   minimum AUC of 0.94 and TSS of 0.78 (Table S2), indicating a high predictive performance

253   (e.g. Smeraldo et al., 2018). With the exception of the model for *L. borealis* for July, our TSS

254   weighted ensemble model was always determined to be the best model by both AUC and TSS.

255   As a result of the ensemble models consistently high performance, it was used for all subsequent

256   analyses. We now describe the results for each of the three species.

257   While we did not explicitly explore the seasonal variations present in each species

258   generated SDM's, they are presented in Figure 2 (each species detailed in Figure S2-4). In short,

259   based on wind turbine mortality and previous studies, we observe expected trends (e.g. Baerwald

260   & Barclay 2011; Johnson et al. 2011; Hayes, Cryan, & Wunder 2015). For *L. borealis* and *L.*

261   *cinereus* we observe concentration of habitat suitability in the southern portions of their range

262   during winter months with a northward movement during the summer into early fall. This is

263   followed by a contraction again to the south. On the other hand, *L. noctivagans* does not exhibit

264   this same pattern as it has suitable habitat further north during the winter, and while expanding

265   northward it doesn't appear to do so to the same extend of the other two species.

266   *Potential migratory pathways*

267   Using three methods (Circuitscape, LCP, and 95th percentile), we find potential migratory

268   pathways for each species that vary between the Spring and Fall seasons (Figure 3; Circuitscape

269   maps are shown in Figure S5). In terms of spring migration patterns, *L. borealis* shows highest

270   density of LCP along the Eastern coast of the US and near the Mississippi River suggesting an

271   avoidance of the Appalachian Mountains and using coasts and rivers as guidance during

272   migration (Figure 3). This pattern is also present in the 95th percentile maps. For *L. cinereus*,

273   higher LCP densities occur along Western Mexico into the Southern US, after which the higher

274   probability pathways lie on either side of the Rocky Mountains pattern and along the Atlantic

275   coast suggesting a lack of resolved pathway during this time period (Figure 3). This is also

276   supported by the 95th percentile map showing higher suitability scores being present in both

277   these regions before the paths would extend further north. Finally, *L. noctivagans* shows two

278   different patterns: LCP maps suggest movement from South to North in the Western US along

279   the Pacific coast and along the western edge of the Rocky Mountains (Figure 3). In the Eastern

280   U.S. there appears to be more of an East/West movement during which individuals would split

281   off to move North or South, likely indicating a partial or incomplete migration in this species.

282   For each of these species we see significant positive clustering in our pathways when using both

283   Moran's I and Geary's C (Table 3). We can also observe that these potential pathways are

284   significantly longer than straight distance by hundreds of kilometers meaning these pathways

285   would be biologically important.

286   In terms of fall patterns, *L. borealis* show*s* two apparent migration paths: one along the

287   East coast, and the other near the Mississippi River and into the Southern plains (Figure 3).

288   These paths are supported by the 95th percentile map, which shows suitable habitat in these areas

289   at the same time of year. These two paths again indicate a potential following of coastline and

290   rivers as guides during migration. *L. cinereus* shows evidence for multiple pathways (Figure 3).

291   Two possible pathways are present along the coasts of the Atlantic and Pacific, again indicating a

292   possible following of coastlines during migration. While the Pacific is the clearer pathway of the

293   two there is still a high density of lines along the Atlantic, which could be a minor pathway for

294   those individuals navigating around the Appalachian Mountains. In addition, a pathway appears

295   in our LCP map and is supported by the 95th percentile map along the Mississippi River. There is

296   also evidence for movement through the Great Plains between the Rocky Mountains and the

297   interior highlands near Missouri and Arkansas. Finally, *L. noctivagans* shows similar patterns for

298   Fall as those observed during Spring migration periods (Figure 3). We see a North/South

299   pathway west of the Rocky Mountains, and east of those, a more east/west pathway is observed,

300   with movements extending North or South, which again potentially indicates a partial or

301 incomplete migration. With fall migration, we also observe positively clustered pathways that are

302 significantly longer than Euclidean distance (Table 3).

303   The two bats that are not long-distance migrants show less variation in seasonal

304 distribution as compared to the three migrant species discussed earlier (Figure 3). In particular,

305 both *E. fuscus* and *M. lucifugus* show a consistent East/West distribution pattern that does not

306 change throughout the year. This supports the idea that changes in distributions likely reflect

307 migratory behavior. Of interest is that the pathways determined by LCP for *E. fuscus* are similar

308 to *L. noctivagans,* providing additional support that silver-haired bats undergo only a partial

309 migration, that being some individual migrant while others overwinter in northern portions of the

310 range. This seems possible as it has been documented silver-haired bats can overwinter at

311 Northern latitudes (Cryan, 2003).

312 **Discussion**

313 Other studies have used SDMs and occurrence distributions to model seasonal distributions of

314 wide-ranging migratory bats (e.g. Hayes, Cryan, & Wunder 2015). This study extends this

315 general approach by using SDMs to predict migratory corridors. Understanding these migratory

316 pathways is vital to the conservation of these three species. Below we discuss limitations of our

317 analyses and then expand on the implications of our results.

318 *Analysis limitations*

319 Using species occurrence data to generate species distribution models can be impacted by

320 sampling biases present in the data (Feng et al. 2019). We attempted to minimize these biases by

321 following guidelines described in Feng et al. (2019). Specifically, we took steps to reduce

322 oversampling of regions by subsampling our dataset to 1 point per 1º grid cell. Additionally,

323   because occurrence records only representing presence points, and not true absences, we

324   included models that require only presence data or can be adapted for use with presence only

325   data. Despite these measures, it is possible biases remain in our models and so we stress that our

326   models represent hypothetical species distributions and migratory pathways for any point in

327   time.

328   *Migratory Pathways*

329   Our analyses identify potential migratory pathways across modelling approaches, although we

330   observed some differences that likely result from features of the data that are given different

331   weight by different methods (McClure, Hansen, & Inman 2016). For example, we lacked clear

332   pathways using Circuitscape. While we attempted to correct this using multiple transformations

333   of the data (square root, log, natural log, and cube-root transformations), none were able to

334   adequately correct for this. Regardless, it is still evident in the current maps that the areas of

335   higher possible movement are also predicted by the LCP and 95th percentile threshold methods,

336   providing support for those proposed pathways. The lack of clear paths using Circuitscape is a

337   possible indication of a lack of clear migratory pathways and they may in fact be more dispersed,

338   while still following the general patterns presented in the other methods. This is supported by the

339   least cost path analysis, as while the figures present the most common paths, many other paths

340   were evident. However, while pathways used may not be the same for every individual the other

341   methods provide the most likely pathways that should be tested further

342   The pathways are summarized in Figure 4 and reflect migratory patterns of many other

343   species in North America including waterfowl and insects (e.g. Lincoln 1935; Westbrook et al.

344   2016; Tracy et al. 2019). Of interest is the relation to insect migrations which is consistent with

345   an idea proposed by Rydell et al. (2010) that bat deaths at wind farms may be related to feeding

346   on migratory insects near turbines. Bats may be tracking the migration of insects to determine

347   their pathways and are feeding on them during migration leading to turbine mortality of bats (but

348   see Reimer, Baerwald, & Barclay 2018).

349   Another possibility is the use of linear features, such as rivers and mountain ranges, as

350   guides during migration (Wang et al. 2007; Ijäs et al. 2017; but see Weller et al. 2016; Krauel,

351   McGuire & Boyles 2018; Cortes & Gillam, 2020). The proposed pathways observed in our data

352   support the idea of bats using linear bodies of water as guides during migration, especially for

353   the two species of *Lasiurus*. In *L. borealis* we observe apparent tracking of the Mississippi river

354   and Atlantic Coast/eastern edge of Appalachian Mountains, while *L. cinereus* tracks the previous

355   two mentioned and the Pacific Coast. One proposed rationale for the tracking of water bodies is

356   that there exists higher abundance of prey to feed upon during migration, allowing for faster

357   overall travel (Furmankiewicz & Kucharska 2009).

358   The last possibility for the apparent tracking of linear features is that increased tree cover

359   also tends to follow these same features (i.e. near river = more trees; as observed in tree cover

360   maps from Hansen et al. 2013). While this is not universally true, it is possible these species are

361   using the linear features to guide them, while the proximity to water provide increased foraging

362   and tree cover provides roosts. Finally, the last possibility is some varied combination of all the

363   previous presented hypotheses that should be investigated further. These types of insights have

364   the ability to inform further study and impact conservation efforts.

365   Conservation for migratory bat species needs to be politically and geographically broad

366   in order to be effective (Fleming 2019). Conservation plans need to include protecting roost sites

367   (during all stages of life), stop-over sites, and conserving foraging habitat around these sites

368   (Fleming 2019). In aid of this goal, our results give direction on where to look for stopover sites

369 during migration, provide a starting point to identify areas where protecting habitat for migration

370 is needed, and gives information as to where to best implement smart-curtailment during fall

371 migration (Hayes et al. 2019).

372   Additionally, there has been a recent effort by bat researchers to focus on small-scale

373 migration of these species (e.g. Baerwald, Patterson, & Barclay 2014). The goal of these types of

374 studies is to understand the local migration that occurs during long distance migration, with the

375 hope that these types of data can compel wildlife managers and/or wind energy industry to

376 implement best practices for the species included in this study, and others. While this has been

377 challenging, the results presented here again give a hypothesis with which to begin future studies

378 that focus on small-scale migration. This can inform researchers on where to focus efforts on

379 implementing these types of questions, and areas where it would likely have the largest impact

380 through reduction of mortality. The results we present cannot definitely answer these types of

381 question, but instead they provide a framework for where to begin and provide a methodology

382 that can be implemented as more data become available.

383 *Conclusions*

384 Due to the seasonality of bat fatalities at wind farms, it is imperative that more research toward

385 understanding the migratory movements of bats be done. This study provides a framework with

386 which to start understanding migratory corridors for these species that could be used in a variety

387 of ways toward reducing mortality. Additionally, while not explored here, for some types of

388 studies such as biomarker migration studies, the SDMs created can be used as priors to better

389 inform probabilistic models for assignment to a location and could be used in conjunction to

390 improve isotopic or other biomarker models for determining movement.

391   Developing better understanding on how these species move to and from summer habitat may be

392   key in reducing the number of bats killed at wind farms. With bats making significant

393   contributions to the economy of the United States through ecosystem services (Boyles et al.

394   2011) and provide valuable ecological services (Ghanem & Voigt 2012) effective and practical

395   measures are necessary to reduce the number of bat deaths annually at wind farms (Frick et al.

396   2017). By understanding migration, we can better mitigate and conserve species that are

397   currently of concern in many states (e.g. Ohio Division of Wildlife 2015). Our study provides a

398   proof of concept of how SDMs can be used to predict migratory pathways, thereby informing

399   researchers on where to focus our efforts toward the goal of reducing bat mortality due to wind

400   farms.

401

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405

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616

Table 1(on next page)

GBIF Occurrence Data

Number of GBIF occurrence points per month for each species analyzed after filtering

	January	February	March	April	May	June	July	August	September	October	November	December
L. borealis	45	33	44	75	99	151	205	192	123	86	49	27
L. cinereus	29	38	44	80	99	108	125	138	110	86	36	24
L. noctivagans	25	24	28	62	110	111	104	131	106	74	38	21
Total	99	95	116	217	308	370	434	461	339	246	123	72

1

Table 2 (on next page)

Variable Importance

Variable importance rank for three of the four SDM models implemented in these analyses. 1 – indicates the most important variable, while 9 – represents the least important. Each importance was found by the following: RF we used the 'importance' function in the "randomForest" R package, MaxEnt, variable importance was assessed using 'var.importance' function in "ENMeval", GLM model, we used the 'varImp' function present in "caret".

	Precipitation	Solar Radiation	Temperature	Vapor Pressure	Wind Speed	Human Influence	Elevation	NDVI	Forest Cover
Random Forest	5	2	1	3	8	7	4	6	9
MaxENT	6	2	1	3	8	4	5	7	9
GLM	6	1	2	3	7	4	5	8	9

1

Table 3 (on next page)

Spatial Clustering of Paths

Moran's I and Geary's C to determine if clustering among potential migratory pathways is present. For Moran's I, values range between -1 and 1, with values above 1 indicating positive clustering. Geary's C values range between 0 and 2, with values below 1 indicating positive clustering. Results given for paired t-tests comparing Euclidean and Least-Cost distances.

	Spring						Fall					
	Moran's I		Geary's C		Paired t-test		Moran's I		Geary's C		Paired t-test	
	I	p-value	C	p-value	Mean Increase	p-value	I	p-value	C	p-value	Mean Increase	p-value
L. noctivagans	0.39	0.01	0.60	0.01	880.40	<0.001	0.34	0.01	0.67	0.01	767.16	<0.001
L. borealis	0.45	0.01	0.54	0.01	348.33	<0.001	0.42	0.01	0.56	0.01	325.39	<0.001
L. cinereus	0.36	0.01	0.65	0.01	721.51	<0.001	0.37	0.01	0.63	0.01	526.85	<0.001

1

Figure 1

Methods Overview

Flowchart showing how occurrence data were analyzed and used to infer migratory pathways for each bat species.
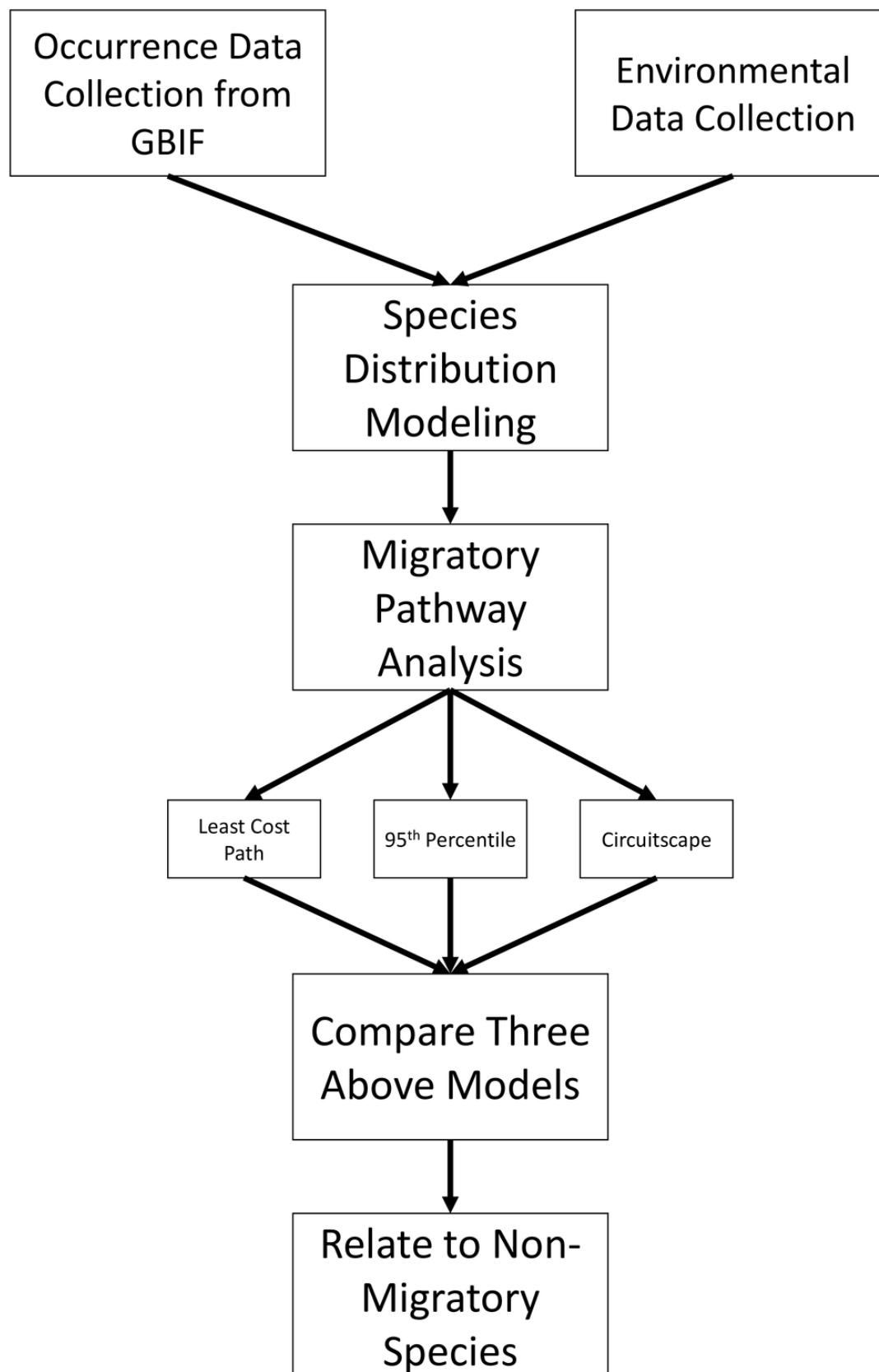
Figure 2

Seasonal Suitability for Three Species of Migratory Bat Species

Seasonal SDMs for all three species (*L. borealis*, *L. cinereus*, and *L. noctivagans*). Colors identify either individual species or groups of species that occur in a given area. For more detailed figures for each species, see supplemental Figures S2-S4.
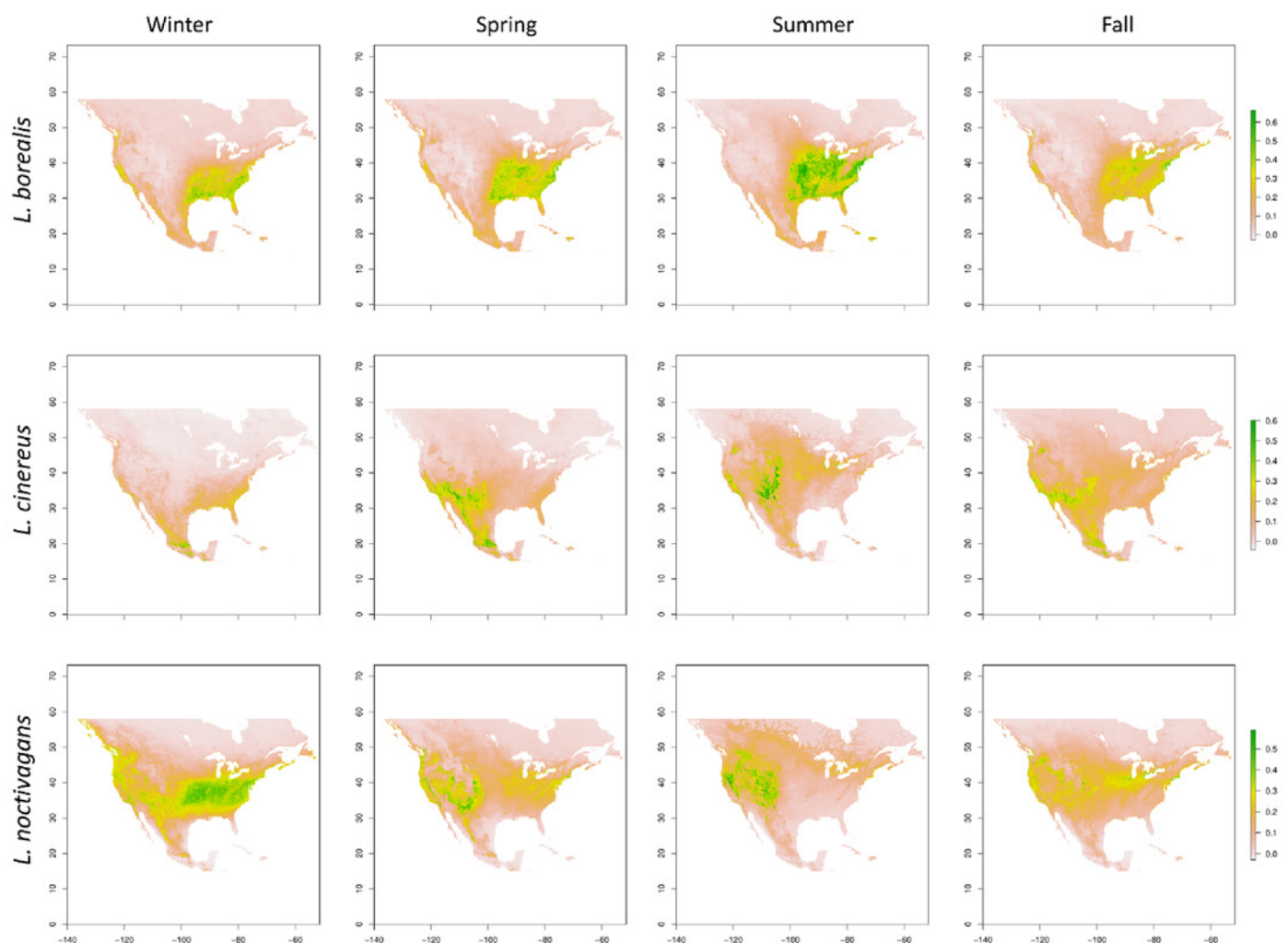
Figure 3

Potential Migratory Pathways

Migration pathways determined using two approaches: binary models determined from TSS

weighted ensemble model using 95th percentile threshold determined for each species

(shown in grey and white), and least-cost-path density (shown as color gradient) for *L.*

borealis, *L. cinereus*, and *L. noctivagans, M. lucifugus*, and *E. fuscus*.
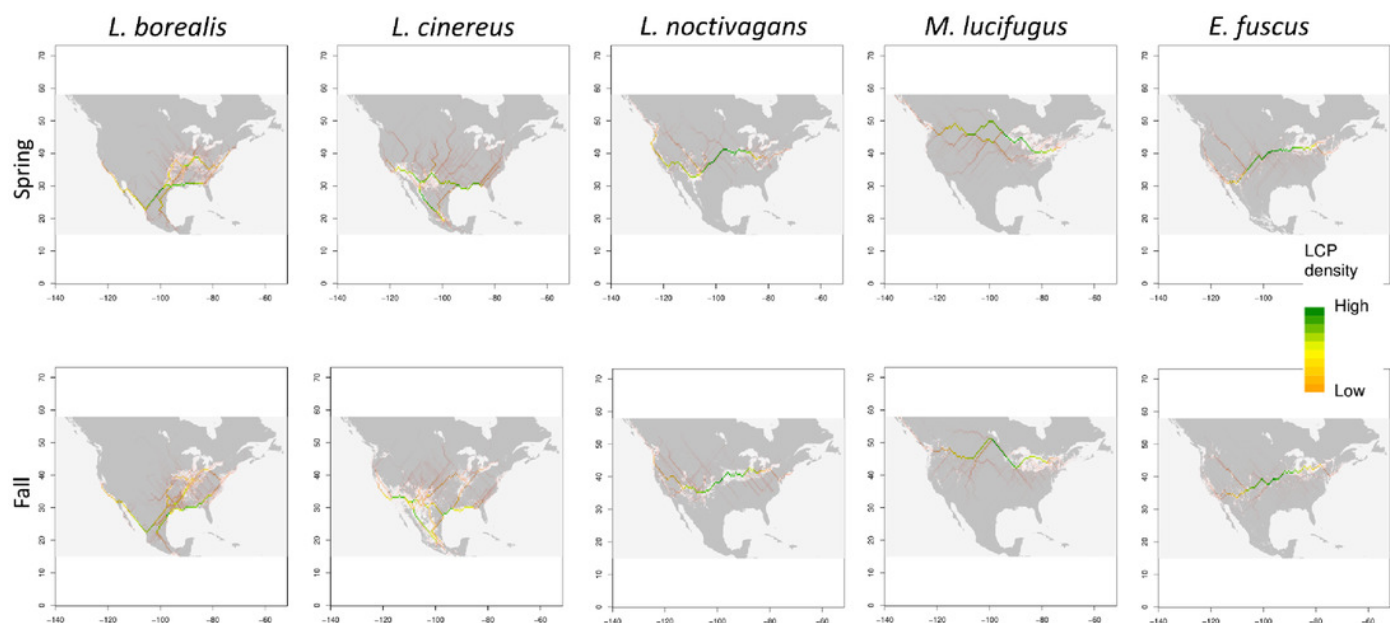
Figure 4

Pathway Summary

Summary of proposed migratory pathways used by two species (*L. borealis* and *L. cinereus*) of migratory tree bats. Due to the more limited range, eastern red bats, are proposed to use the yellow and blue portions, while hoary bats use all four.