1 **Title**

2 Retreat, detour, or advance? Understanding the movements of birds confronting

3 the Gulf of Mexico

4 **Author Information**

5 Theodore J. Zenzal Jr.[1,2,3]*, Michael P. Ward[3], Robert H. Diehl[4], Jeffrey J. Buler[5],

6 Jaclyn Smolinsky[5‡], Jill L. Deppe[6], Rachel T. Bolus[7], Antonio Celis-Murillo[8], and

7 Frank R. Moore[2]

8 [1]U.S. Geological Survey, Wetland and Aquatic Research Center, Lafayette, LA

9 [2]School of Biological, Environmental, and Earth Sciences, University of Southern

10 Mississippi, Hattiesburg, MS

11 [3]Department of Natural Resources and Environmental Sciences, University of

12 Illinois, Urbana, IL

13 [4]U.S. Geological Survey, Northern Rocky Mountain Science Center, Bozeman,

14 MT

15 [5]Department of Entomology and Wildlife Ecology, University of Delaware,

16 Newark, DE

17 [6]National Audubon Society, Washington, D.C.

18 [7]Department of Biology, Southern Utah University, Cedar City, UT

19 [8]U.S. Geological Survey, Patuxent Wildlife Research Center, Laurel, MD

20 *Corresponding author: 700 Cajundome Blvd., Lafayette, LA 70526; 337-266-

21 8645; tzenzal@usgs.gov

22 ‡Current address: Cherokee Nation System Solutions, contracted to the U.S.

23 Geological Survey, Wetland and Aquatic Research Center, Lafayette, LA

24

Abstract

26   During migration, birds must locate stopover habitats that provide

27 sufficient resources to rest and refuel while *en route* to the breeding or non-

28 breeding area. Long-distance migrants invariably encounter inhospitable

29 geographic features, the edges of which are often characterized by habitat

30 limited in food and safety. In response, they often depart in directions

31 inconsistent with reaching their destination, presumably searching for better

32 habitat. We used automated radio telemetry to track 442 individuals of five

33 species to investigate the behavior of migratory birds as they departed edge

34 habitat along the northern Gulf of Mexico coast during autumn from 2008-2014.

35 Most migrants (75%) retreated inland or detoured around rather than advanced

36 across the Gulf, but this depended on bird species and fat-based energy stores.

37 Most individuals in lean condition or of smaller bodied species tended to retreat

38 or detour, rather than advance, when departing from the coast. Twenty-one

39 percent of all birds that departed the coast in 2013-2014 were redetected over 45

40 km inland, providing a unique opportunity to compare stopover duration,

departure times, and travel speeds between migrants that retreat away from the

coast and those that continue to advance toward their destination. Individuals

that retreated the coast and were redetected inland spent ~1 day on the coast

before retreating inland, where they spent 11 days before resuming migration.

Further when those same individuals retreated from the coast, they departed

around evening civil twilight, whereas those that advanced from inland habitats

departed after evening civil twilight. Travel speeds were slower for individuals

retreating inland compared to those advancing towards the coast from inland

habitats. The differences between retreating and advancing individuals suggest

how an individual's drive to feed or fly influences behavior. Our study illustrates

how the sum of individual decisions can shape habitat use, landscape-scale

movements, and migration strategies.

61

62

Introduction

Most birds that migrate thousands of kilometers between their breeding and non-breeding areas must stopover *en route,* where they rest and refuel to survive the journey. Locating habitat where migrants can safely and efficiently sustain or gain a favorable energetic state (i.e., increase fat stores) needed to resume migration in a timely fashion is critical but challenging, especially along the edge of a large geographical feature (e.g., oceans, mountains, or deserts) where opportunities to stopover are limited (Brooks 1952, Alerstam and Lindström 1990, Sandberg and Moore 1996, Strandberg et al. 2009, Alerstam 2011, Deppe et al. 2015, Moore 2018, Ward et al. 2018). Depending on the direction of travel, habitat at the edge of inhospitable geographic features (hereafter "edge sites") represent the last possible place to stopover before an individual must negotiate a crossing of the non-habitat feature or the first possible landfall after a non-stop flight. Migrants departing edge sites often select departure directions inconsistent with progress toward their breeding or non-breeding destination (Alerstam 1978, Åkesson et al. 1996, Åkesson 1999, Smolinsky et al. 2013, Woodworth et al. 2014, Deppe et al. 2015, Nilsson and Sjöberg 2016). Coastlines, for example, are often characterized as habitat-poor landscapes with high concentrations of migrants, which leads to reduced habitat

82   quality (Abdollahi et al. 2005, Mehlman et al. 2005, Schaub et al. 2008, Buler and

83   Moore 2011, Lain et al. 2017) in terms of increased predation pressure (Aborn

84   1994, Cimprich et al. 2005, Woodworth et al. 2014) and competition for food

85   (Moore and Yong 1991, Zenzal and Moore 2019). Ultimately, if individuals are

86   unable to adequately prepare for a long distance flight in edge habitats, then they

87   will have a lower survival probability when attempting to cross the potential

88   barrier (Erni et al. 2003, Ward et al. 2018). Individuals unable to directly advance

89   (i.e., move directly towards the final migration destination) from the edge site

90   must either retreat from (i.e., move away from the edge) or detour around (i.e.,

91   move parallel to the edge) the inhospitable geographic feature.

92   Decisions about when and in what direction to leave a stopover site reflect

93   an individual's readiness to resume migration and are often influenced by

94   extrinsic factors, such as habitat described above and weather, or intrinsic

95   factors such as energetic condition, species, and age (Hake et al. 2003,

96   Smolinsky et al. 2013, Sjöberg et al. 2015, Deppe et al. 2015, Dossman et al.

97   2016, Nilsson and Sjöberg 2016; but see Zenzal et al. 2018a). In terms of

98   energetic condition, individuals with substantial fat stores orient in an advancing

99   direction (i.e., south), consistent with migrating to their non-breeding range, while

100   lean individuals tend to orient in directions indicative of detouring or retreating

101   (i.e., east/west or north, respectively; Sandberg and Moore, 1996; Sandberg et

102   al., 2002; Nilsson and Sjöberg 2016). Species-dependent decisions may also

103   occur considering poorer flight performance related to smaller body size allows

5

104 for a lower margin of error when negotiating long-distance, non-stop flights (Buler

105 et al. 2017), which may suggest that smaller bodied species would choose to

106 detour or retreat. Age-dependent migratory decisions reveal that young birds

107 tend to show more variation in migratory routes compared to adults (Hake et al.

108 2003, Agostini 2004) and tend to be less efficient at foraging, impacting energetic

109 condition (Gauthreaux 1978, Burger 1988, Wunderle 1991, Woodrey 2000, but

110 see Moore et al. 2003). While intrinsic factors that describe an individual's

111 disposition (e.g., age, species) are generally inflexible within a season, other

112 factors, such as energetic condition and habitat quality, allow individuals to

113 change the circumstances (e.g., find nearby habitat with more food) and increase

114 their readiness to resume migration and advance.

115   Readiness is especially evident at an edge of inhospitable features and

116 can be described as a dichotomy between states of feeding or flying (i.e.,

117 *Zugdisposition* or *Zugstimmung*; *sensu* Groebbels 1928, Rappole and Warner

118 1976, Schaub et al. 2008, Mills et al. 2011, Taylor et al. 2011, Chernetsov 2012,

119 Cohen et al. 2014, Woodworth et al. 2014). The feeding state is characterized by

120 habitat assessment, longer stopover duration at a landscape scale, diurnal fat

121 deposition, slower travel speeds, and departure in a direction inconsistent with

122 advancing while searching for additional foraging opportunities at a landscape

123 scale (Alerstam 1978, Sandberg and Moore 1996, Moore and Aborn 2000,

124 Chernetsov 2006, Mills et al. 2011, Taylor et al. 2011, Cohen et al. 2012,

125 Smolinsky et al. 2013, Woodworth et al. 2014, Dossman et al. 2016, 2018,

126   Ferretti et al. 2019, Schmaljohann and Klinner 2020). Feeders eventually

127   transition to a state of migratory flight, which is characterized by higher travel

128   speed, minimal stopover duration, advancing directly towards the final migration

129   destination, especially when weather conditions are supportive (Rappole and

130   Warner 1976, Dingle 1996, Bruderer and Liechti 1998, Smolinsky et al. 2013,

131   Deppe et al. 2015, Dossman et al. 2016, 2018, Nilsson and Sjöberg 2016,

132   Packmor et al. 2020, Schmaljohann and Klinner 2020). Moreover, nocturnally

133   migrating flyers are: 1) less likely to move during the day (i.e., sleep instead of

134   forage), 2) engage in quiescence and orientation behaviors before departing, and

135   3) depart stopover sites early at night between sunset and astronomical twilight

136   to take advantage of improved directional information, atmospheric stability, and

137   lower predation risk (Moore 1987, 2018, Kerlinger and Moore 1989, Moore and

138   Aborn 2000, Newton 2008, Németh 2009, Cohen et al. 2012, Covino and Cooney

139   2015, Dossman et al. 2016, 2018, Schofield et al. 2018a, b, Packmor et al.

140   2020).

141   Transitions between feeder and flyer, which occur throughout migration,

142   are likely attributed to the cyclical interplay between circumstance, condition,

143   state, and behavior, which can be magnified or diminished by context. For

144   example, circumstance may place an individual in lean condition at a food poor,

145   edge site with high competition and predation risk. The internal state of this lean

146   individual is to feed but circumstances may prevent or limit foraging opportunities

147   and so the individual changes its behavior to relocate to a higher quality stopover

148   site, which may be inconsistent with advancing. Now with circumstances

149   changed, the lean bird is at a food rich, interior stopover site with lower

150   competition and predation risk relative to the edge site. The bird, now able to

151   satisfy the need to feed, changes condition by increasing fuel stores and in turn

152   becomes motivated to fly and advance towards the migratory destination. While

153   this process occurs continually throughout migration, the context of being at an

154   edge site paired with inflexible internal factors, such as age or species, can

155   exacerbate all aspects of this cycle given the high energy demand for flight

156   across the inhospitable landscape.

157   We radio-tagged 5 species of migratory bird at an edge site to investigate

158   decisions related to the internal states of feeding and flying during autumn

159   migration by tracking behaviors with an array of automated radio telemetry (ART)

160   systems on the northern coast of the Gulf of Mexico. We hypothesize that

161   departure decisions are influenced by species, age, and fat load. We predict

162   smaller species, individuals carrying lower fuel stores, or those on their first

163   migration are not ready to resume migration from an edge site and will tend to

164   retreat or detour rather than advance (i.e., transition to migratory flight). We also

165   hypothesize that feeders retreating lower quality, edge sites differ from flyers

166   advancing from higher quality, interior sites with respect to departure time, travel

167   speed, and stopover duration. We predict feeders retreating from edge sites will

168   depart later in the evening, travel slower (i.e., a more tortuous route), and have

169   stopped over for shorter compared to flyers advancing from interior sites. We

170   also test the underlying assumption that interior habitats are higher quality than

171   edge habitat by predicting that food resources are higher at interior sites.

172

173   **Materials and Methods**

174   *Study sites*

175   Edge site – Our edge site was at the Bon Secour National Wildlife Refuge

176   (30° 10'N, 88° 00'W; Figure 1C) located approximately 2 km from the end of the

177   Fort Morgan Peninsula, Alabama, USA in coastal dune-forest habitat. The Fort

178   Morgan Peninsula, which is a 1 km wide strip of land between Mobile Bay and

179   the Gulf of Mexico, represents the last stopover habitat before some individuals

180   advance across the Gulf of Mexico during autumn. The site is composed

181   primarily of oaks (*Quercus sp.*), hollies (*Ilex sp.*), greenbrier (*Smilax* spp.),

182   grapevine (*Vitis sp.*), wax myrtle (*Myrica cerifera*), bay (*Persea sp.*), saw

183   palmetto (*Serenoa repens*), sand heath (*Ceratiola ericoides*), and pines (*Pinus*

184   *sp.;* see Zenzal et al. 2013 for a complete description of the habitat). Many

185   migrants at this site tend to have short stopover durations and do not

186   substantially refuel on the available fruit and arthropod resources (Woodrey and

187   Moore 1997, Smolinsky et al. 2013, Deppe et al. 2015, Zenzal and Moore 2016,

188   Zenzal et al. 2018a).

189   Interior site – Our interior site was in the Jacinto Port Wildlife Management

190   Area (30° 48'N, 88° 02'W: at Tower 6 in Figure 1B) just east of Saraland,

9

191   Alabama, USA. The extensive, contiguous upland and bottomland hardwood

192   forests located in the Five Rivers Delta area is ~50 km north of the Gulf of Mexico

193   and where the Mobile, Spanish, Tensaw, Apalachee, and Blakeley Rivers flow

194   into Mobile Bay. This site is dominated by sweetgum (*Liquidambar styraciflua*),

195   American beautyberry (*Callicarpa americana*), pines, oaks, hollies, grapevine,

196   greenbrier, and dwarf palmetto (*Sabal minor*). Similar habitats harbor large

197   numbers of migrants and are rich in food resources (Buler et al. 2007),

198   suggesting it is a potentially high-quality site.

199   *Bird captures*

200   We captured birds at a long-term migration monitoring station located at

201   our edge site during autumn (25 August to 1 November) 2008 to 2014, except

202   temporarily during a U.S. government shutdown (1-13 October 2013) which

203   precluded access to our study site (we were also unable to sample fruit and

204   arthropods, see below, at this site during the same period). We operated a

205   station of 30 nylon mist nets (12 or 6 m x 2.6 m with 30mm mesh) from just

206   before sunrise until approximately noon (Central Daylight Time [CDT]), barring

207   unfavorable weather that might prevent the safe operation of nets. We banded

208   each individual with a unique U.S. Geological Survey metal band, aged

209   individuals as hatch-year (HY; hatched that summer) or after hatch-year (AHY;

210   hatched a previous year) according to Pyle (1997), assessed muscle and fat

211   (Helms and Drury 1960, Bairlein 1995), and measured unflattened wing chord

212   (0.5 mm) and mass (nearest 0.1 g with an electronic balance). We classified

213 visible subcutaneous fat in individuals based on a 0-5 fat scoring system (Helms

214 and Drury 1960).

215   We affixed a small radio transmitter to 473 individuals from the following

216 five species: indigo bunting (*Passerina cyanea*, n = 39; 97% HY), red-eyed vireo

217 (*Vireo olivaceus*, n = 151; 63% HY), ruby-throated hummingbird (*Archilochus*

218 *colubris*, n = 55; 100% HY), Swainson's thrush (*Catharus ustulatus*, n = 177;

219 65% HY), and wood thrush (*Hylocichla mustelina*, n = 51; 88% HY). We assume

220 all individuals were captured the day of arrival due to the high turnover rate of

221 migrants previously described at this site (Woodrey and Moore 1997, Smolinsky

222 et al. 2013, Deppe et al. 2015, Zenzal and Moore 2016, Zenzal et al. 2018a). All

223 species are considered long-distance, neotropical migrants (*sensu* Carlisle et al.

224 2004, DeGraaf and Rappole 1995, Zenzal et al. 2018b) that breed in temperate

225 North America and winter primarily south of the Tropic of Cancer (for more

226 details see: Cimprich et al. 2018, Evans et al. 2011, Mack and Yong 2000, Payne

227 1992, Weidensaul et al. 2019). All animal research activities were approved by

228 the University of Southern Mississippi institutional animal care and use

229 committee (IACUC; protocol number 11092210), University of Illinois IACUC

230 (protocol number 15154), U.S. Geological Survey Bird Banding Laboratory

231 (permit number 21221), and the Bon Secour National Wildlife Refuge.

232 *Automated radio telemetry, transmitters, and telemetry data*

233   We established a network of automated radio telemetry (ART) systems

234   using automated receiving units from JDJC Corp (Fisher, Illinois, USA). We used

235   the signal strength, noise, pulse width, and pulse interval data to determine the

236   departure and arrival behavior of radio-tagged individuals. The transmitters used

237   on the five focal species varied in weight, battery life, and were made by different

238   companies (see Supplementary Information for details). We do not suspect the

239   weight of the transmitter to significantly impact the behaviors observed given that

240   flight behaviors of the smallest species tagged, ruby-throated hummingbirds, did

241   not differ in an aviary with or without the transmitters we used in this study

242   (Zenzal et al. 2014). The automated system along the Gulf's edge used different

243   antennas than the interior system. The two systems were thus slightly different in

244   terms of the resolution of the bearing estimates and gain of the antennas. While

245   we could triangulate and estimate the tracts of departing individuals, for the

246   purpose of this study we used vanishing bearing as the metric to determine if an

247   individual was advancing, detouring, or retreating. As an example, we

248   triangulated a few individuals to provide a visual representation of the departure

249   behavior and their "retreat" north (Figure 1B; see supplementary information for

250   further details).

251   *Food Sampling*

252   In 2013 and 2014, we sampled fruit and arthropods along transect(s)

253   within the telemetry detection area of each site (interior site: one transect totaling

254   375 m in length to sample the bottomland forested habitat [located near "Tower

255 6" in Figure 1B]; edge site: two transects totaling 725 m in length to sample the

256 scrub and pine habitats [located at "Banding Station" in Figure 1C]). Once a

257 transect was established we marked all plants that were within 2 m of the

258 transect center line and fruiting between 25 August and 9 September at the start

259 of each season. Fruit sampling involved counting all the ripe fruit once a week

260 between 2 September and 28 October on the marked plants. Marked plants

261 included: 1) peppervine (*Ampelopsis arborea*), dahoon holly (*Ilex cassine*),

262 inkberry (*I. glabra*), yaupon holly (*I. vomitoria*), gopher apple (*Licania michauxii*),

263 wax myrtle, red bay (*P. borbonia*), chokecherry (*Prunus virginiana*), winged

264 sumac (*Rhus copallinum*), saw palmetto, greenbrier, and blueberry (*Vaccinium*

265 *sp.*) at the edge site and 2) American beautyberry, American holly (*I. opaca*),

266 yaupon holly, dwarf palmetto (*Sabal minor*), and sparkleberry (*Vaccinium*

267 *arboreum*) at the interior site. Arthropod sampling took place at 8 points, spaced

268 50 m apart, along each transect (n = 16 points at the coastal site; n = 8 points at

269 the inland site). Every three days between 3 September and 30 October we

270 surveyed arthropods at each location once in the afternoon (~15:00 CDT); if high

271 winds or precipitation interfered with sampling we conducted surveys on the next

272 available day. At the start of the season, we selected similarly sized oak tree

273 branches from the nearest oak tree at each point along the transect from which

274 to sample arthropods throughout the season. We carefully covered the branch

275 with a pillowcase, closed the end around the branch, shook the branch vigorously

276 for approximately 30 seconds, and then counted the arthropods inside the

277   pillowcase classifying them by taxonomic order and 1 mm size class before

278   releasing them alive. We then used previously published length-weight

279   regression equations to calculate arthropod biomass (see Johnson and Strong

280   2000, Strong and Sherry 2000).

281   *Statistics*

282   <u>*Departing the Edge*</u>

283   To test the prediction of our first hypothesis related to how conditions such

284   as species, age, and fat load influence behavior when circumstance places an

285   individual at an edge site within the context of negotiating a 1,000 km, non-stop

286   flight, we classified departure directions from the edge site into three discreet

287   groups: advancing (south = 135 – 224°), detouring (east = 45 – 134° or west =

288   225 – 314°; i.e. individuals were roughly following the coast), and retreating

289   (north = ≥315° or <45°; Figure S1). Individuals advancing upon departure

290   illustrate the flyer state (i.e., resuming migration), individuals retreating upon

291   departure are considered to be in a feeder state, and those detouring upon

292   departure have discontinued the direct route to the non-breeding grounds but

293   may be exhibiting either the feeder or flyer state. For all tagged individuals, we

294   analyzed departure group membership using an information theoretic approach

295   to determine which factors influence departure direction. We used Akaike's

296   information criterion (AIC$_c$; Burnham and Anderson 2002) with a multinomial

297   logistic regression to determine if age (HY or AHY), fat score (0-5), or bird

298   species, factors typically related to departure decisions (e.g., Deppe et al. 2015,

299   Nilsson and Sjöberg 2016, Sandberg and Moore 1996, but see Zenzal et al.

300   2018a), influenced departure direction. We created 14 candidate models (Table

301   1), all of which, excluding the null model, included year as a random factor. We

302   tested the null model (no variables), single-variable models, global models (all

303   variables, additive and interactive), as well as specific variable combinations in

304   additive and interactive models (see Table 1). We considered models with a

305    $\Delta AIC_c \leq 2$ as receiving the strongest support based on the data and determined

306   the best model based on the calculated weight and parsimony of each model

307   (Burnham and Anderson 2002).

308   *Comparing Retreating to Advancing*

309   To test the prediction of our second hypothesis comparing behaviors of feeders

310   and flyers, we analyzed data on individuals tagged at the edge site and later

311   detected at an ART system north of Mobile Bay. For any individual detected by

312   an ART system at the interior site (hereafter "redetected individuals", n = 42), we

313   calculated departure time (defined as the number of hours before or after civil

314   twilight based on expected departure times; Deppe et al. [2015], Moore and

315   Kerlinger [1992], and Smolinsky et al. [2013]), northbound and southbound travel

316   speed (meters per second [m/s]), as well as the number of days (stopover

317   duration) at the edge and interior sites when possible. We estimated travel speed

318   by determining the time when the signal strength indicated the bird was directly

319   east or west of the tower and dividing the amount of time it took for an individual

320   to move in an assumed straight path between the coastal towers and either tower

15

321   5 or 6 (see Figure 1B). We pooled data across species for analyses of redetected

322   individuals in order to maximize our sample size. Two variables did not conform

323   to a normal distribution based on a Shapiro-Wilk Test ($p < 0.05$), therefore we

324   transformed departure time (paired samples only) and travel speed (independent

325   samples only) of redetected individuals with the natural logarithm (natural

326   logarithm + 1 for departure time) in order to fit the data to a normal distribution.

327   Stopover duration of redetected individuals did not conform to a normal

328   distribution after performing log and square root transformations, necessitating

329   the use of non-parametric statistics. We used a paired t-test or Wilcoxon signed-

330   rank test to determine if the response variable changed between sites. However,

331   given the low sample sizes of pairwise data captured by our ART network (range

332   of n = 9 – 20), we also performed an independent t-test or Mann Whitney U test

333   to characterize differences between individuals at the two sites. The independent

334   test is likely to be more conservative in its test of significant differences between

335   sites.

336   Given the possibility that detected differences in travel speeds between

337   northbound and southbound flights could be due to wind conditions aloft, we

338   analyzed wind speed and direction of redetected individuals with data on flights

339   north and south (n = 20). We used this approach rather than assessing flow

340   assistance (e.g., Kemp et al. 2012) as we cannot predict the desired bearing of

341   retreating individuals and do not know where individuals outside of our detection

342   area originate from, but rather simply illustrate that wind conditions aloft are not

343   different between advancing and retreating flights. We obtained weather data

344   from Dauphin Island, AL (ID: 994420; 30°15'N, 88°4'W) and averaged conditions

345   from within 2 hours of an individual's departure time (hour of departure ± 1 hour).

346   We used a generalized linear model (GLM) with a binomial distribution and

347   selected flight direction (retreat or advance) as the response variable; fixed

348   factors included speed (m/s) and cardinal direction (as defined above) of surface

349   winds as well as their interaction. We determined significant differences between

350   flight directions using a Wald test.

351   *Food Abundance*

352   We tested the expected difference in food abundance by recording the

353   weekly mean number of ripe fruit/m or mean arthropod biomass at each sampling

354   period, between sites using generalized linear mixed models (GLMMs). For each

355   response variable, we used a Gaussian distribution and selected site as a fixed

356   factor; day of year nested within year was a random factor. We determined

357   significance of variables in our GLMMs using a Wald test and 95% confidence

358   intervals. We followed up our analysis of arthropod biomass with a Hedge's g test

359   to determine differences in magnitude (i.e., the effective difference) between the

360   two sites.

361   *Software*

362   We performed all statistics in the R statistical language (version 3.5.1; R

363   Core Team 2018). To run multinomial regression models, we used package

364 "nnet" (Venables and Ripley 2002) and then calculated ΔAIC$_c$ and AIC$_c$ weights

365 using package "AICcmodavg" (Mazerolle 2017). For linear models (GLMM/GLM),

366 we used packages: "MASS" (Venables and Ripley 2002), "nlme" (Pinheiro et al.

367 2018), "car" (Fox and Weisberg 2011), and "gmodels" (Warnes et al. 2018). We

368 used package "effsize" to perform the Hedge's g test (Torchiano 2017).

369 **Results**

370 *Departing from the Edge*

371   We found that of all the radio-tagged individuals (n=442), most (75%) did

372 not advance when departing the edge site. The majority of individuals (n = 184;

373 42%) departed in a direction parallel to the Gulf of Mexico consistent with

374 detouring (i.e., east or west). The second most frequent departure direction was

375 retreating from the Gulf of Mexico (i.e., north; n = 146; 33%). The least number of

376 individuals (n = 112; 25%) departed over the Gulf of Mexico consistent with

377 advancing toward the non-breeding grounds (i.e., south). We were unable to

378 estimate the departure direction for 31 (5 indigo buntings, 6 red-eyed vireos, 3

379 ruby-throated hummingbirds, 16 Swainson's thrushes, and 1 wood thrush) of the

380 473 radio-tagged individuals due to transmitter failures and errors in programing

381 the ARTs to search for a specific frequency.

382   Results from our AIC$_c$ approach to test the prediction of our first

383 hypothesis related to the conditions of age, species, and fat load on departure

384 direction found one model with sufficient support (ΔAIC$_c$ < 2; w_i = 0.86), which

385   was the additive model between bird species and fat score (Table 1). From a

386   species standpoint, detouring along the coast was the most frequent departure

387   direction for the two smallest species examined, indigo buntings (74%) and ruby-

388   throated hummingbirds (77%), and the least frequent direction for wood thrush

389   (22%). Individuals retreating toward inland habitat was most common for red-

390   eyed vireos (47%) and wood thrush (42%) and the least frequent direction

391   among indigo buntings (12%) and Swainson's thrush (29%). Southbound

392   departures over the Gulf by advancing individuals were most frequent for

393   Swainson's thrush (38%) and the least frequent direction in red-eyed vireos

394   (16%) and ruby-throated hummingbirds (10%; Figure 2).

395   Considering an individual's fat score in relation to departure decisions,

396   fewer than 10% of those individuals with lower fat stores (scored 1-3) advanced

397   south over the Gulf of Mexico. The majority of individuals with lower fat scores (0-

398   3) detoured (48-58%), followed closely by retreating (37-45%). The majority of

399   individuals (41%) with a fat score of 4 also detoured, followed by fairly similar

400   numbers advancing (31%) and retreating (28%). Almost half of individuals with

401   the highest fat score (5) advanced over the Gulf of Mexico (47%) and less than a

402   quarter retreated towards interior sites (22%; Figure 3).

403   *Comparing Retreating to Advancing*

404   We tested the prediction of our second hypothesis by comparing

405   behaviors of feeders retreating from our edge site to flyers advancing from our

inland site. Retreating individuals departed the edge site earlier in the day (1.60 ±

1.75 hours after evening civil twilight, n = 42) than when advancing from the

interior site (2.51 ± 1.20 hours after civil twilight, n = 20; repeated measures

approach: t = -4.076, df = 19, p-value < 0.001; independent samples approach: t

= -4.129, df = 23.797, p-value < 0.001), although departures from the edge site

showed more variation compared to interior departures. Moreover, half of the

interior-departing individuals included in the analysis resumed migration outside

of our inland detection areas (likely north of the site; see below), which means

they departed earlier in the day than when we detected them on the interior ART

network. Between edge and interior ART networks, travel speed was greater for

individuals advancing (15.12 ± 5.03 m/s, n = 9) compared to those retreating

(9.45 ± 3.65 m/s, n = 34; repeated measures approach: t = -4.633, df = 5, p-value

= 0.006; independent samples approach: t = -3.112, df = 8.431, p-value = 0.014;

Figure 4). For both retreating and advancing flights, winds were from the south

and wind speeds were similar (retreating: 4.65 ± 2.31 m/s; advancing: 6.06 ±

2.45; all p > 0.25). Wind speed and direction results suggest retreating

individuals experienced wind assistance, while advancing individuals flew into

headwinds at departure. Individuals had a longer stopover duration at interior

habitats compared to the edge site in both analyses. In the pairwise analysis,

individuals spent significantly less time at the edge site (0.08 ± 0.29 days)

compared to interior sites (11.67 ± 4.69 days, n = 12; V = 0, p = 0.002). The

independent samples test also showed redetected individuals spent significantly

428   less time at the edge site (0.67 ± 1.96 days, n = 42) compared to interior habitats

429   (11.67 ± 4.96 days, n = 12; W = 7, p < 0.001). Furthermore, mean stopover

430   duration of all radio-tagged individuals at the edge site was short (1.21 ± 2.62

431   days, n = 442), with most individuals (82%; n = 362) departing within 24 hours of

432   capture.

433   *Interior Flights*

434   During 2013 and 2014, we redetected 21% of all tagged individuals which

435   comprised 62% of retreating individuals flying near the interior ART network after

436   departing from the edge site. Wood thrush was the most common species

437   redetected at the inland site (42% of all tagged wood thrushes), whereas we

438   never redetected ruby-throated hummingbirds at the inland site. The remaining

439   species each had ~15-24% of individuals redetected inland (Table 2). We found

440   that 8 of the 33 redetected individuals landed and stopped over in the detection

441   area of our inland receivers: one indigo bunting, two red-eyed vireos, and five

442   wood thrushes (examples of wood thrush movements illustrated in Figure 1B).

443   Based on the 8 individuals that landed in the inland detection area, the average

444   distance from the location where they were tagged was 57.4 km (± 9.43 km;

445   range: 45-70 km) and the individuals that continued north (n= 27) likely stopped

446   at least 72 km (i.e., the edge of the detection area) from where they were tagged.

447   Of the 33 individuals that retreated to stopover at an interior site, we

448   redetected 14 individuals departing south, of which seven individuals departed

449   locally (within the detection area of the receivers) from bottomland forests; the

450   remaining seven departed from interior habitats outside the detection area. While

451   we found no evidence that the 14 individuals moving south from interior habitats

452   made landfall again near the edge site, 9 individuals were detected aloft passing

453   by the ART network at the edge site. Four of the 14 southbound birds not

454   detected by our ART network on the coast were heading in a west-southwesterly

455   direction when passing the interior ART network and were likely out of range of

456   the coastal ART network. The last southbound individual not redetected, a red-

457   eyed vireo, turned sharply to the east and likely passed to the east out of range

458   of the coastal ART network.

459   *Food Abundance*

460   To test our underlying assumption of habitat quality, we compared

461   arthropod and fruit resources between out edge and interior sites. Arthropod

462   biomass was greater at the interior site (0.17 ± 0.38 mg/sampling period; n = 18)

463   compared to the edge site (0.05 ± 0.03 mg/sampling period; n = 20). While the

464   difference in arthropod biomass was not significant ($F_{1,8}$ = 2.46, p = 0.16, 95% CI

465   = -0.06 to 0.30), we did find a difference in the magnitude of arthropod biomass

466   between sites (|g| = 0.44). The moderate difference in magnitude or effect size

467   suggests that observed values at the interior site are greater despite the large

468   amount of temporal variation at the interior site (range: 0.005 – 1.560 g/sampling

469   period). The number of ripe fruit counted each week was over 3x greater at the

470   interior site (43.23 ± 10.48 ripe fruit/m) compared to the edge site (13.04 ± 4.07

471   ripe fruit/m; $F_{1,14}$ = 163.33, p < 0.0001, 95% CI = 1.01 to 1.41).

472   **Discussion**

473   *Departing the Edge*

474   We found partial support of our hypothesis that departure decisions are

475   influenced by species, age, and fat load. As predicted, species of smaller body

476   size (e.g., hummingbirds, buntings, and vireos) and birds in lean condition (fat

477   score < 4; Helms and Drury 1960) were more likely to discontinue a direct route

478   to the migratory destination. Age was not important in explaining flight direction,

479   despite the tight interplay typically found between age and foraging efficiency

480   (Gauthreaux 1978, Burger 1988, Wunderle 1991, Woodrey 2000, but see Moore

481   et al. 2003). Despite smaller-bodied species having higher fuel deposition rates

482   (Lindström 2003) and the ability to carry more fat relative to their fat-free mass

483   (Hedenström and Alerstam 1992), they are more affected by turbulent conditions

484   aloft (e.g., Ravi et al., 2015) and have higher metabolic costs (Vogel 1988) that

485   reduce their margin of safety during long flights over large geographic features.

486   This trade-off may explain why smaller-bodied species are more selective when

487   attempting to advance from edge habitats or detour around the perceived barrier

488   (Deppe et al. 2015, Zenzal et al. 2018a). While we know detouring individuals

489   discontinued the direct route to their migratory destination when departing the

490   edge site, tracking whether they made additional stopovers within the landscape

491   or resumed migratory flight by circumventing the Gulf of Mexico is beyond the

492   scope of our study.

493   Regardless of departure direction, most individuals left our edge

494   site within 24 hours of capture and, with our underlying assumption of less food

495   at edge sites confirmed, individuals seeking to replenish energy stores would be

496   more food limited and likely face increased competitor and predation pressure if

497   remaining on the coast (Moore and Yong 1991, Aborn 1994, Woodrey and Moore

498   1997, Kelly et al. 2002, Cimprich et al. 2005, Cimprich and Moore 2006, Moore et

499   al. 2017, Zenzal and Moore 2019). A third of the departing individuals engaged in

500   retreating movements consistent with locating more suitable stopover habitat,

501   based on our food data - a behavior associated with the feeding state. This

502   finding is similar to other studies where migrants stop at the edge of an

503   inhospitable landscape and retreat instead of advancing (Baird and Nisbet 1960,

504   Alerstam 1978, Woodworth et al. 2014, Nilsson and Sjöberg 2016), and it is

505   assumed that retreating individuals were unable to meet the necessary departure

506   fuel load to resume migration. Our ART network confirms that individuals in a

507   feeding state retreated to interior habitats with greater forest cover and food

508   resources (Buler et al. 2007; this study), as well as presumably lower predation

509   risk (*sensu* Lindström, 1990). While retreating over 45 km from the coast to

510   another unfamiliar stopover site may result in extra energy expenditure and

511   uncertainty compared to remaining at the current site, for lean individuals, the

512 cost appears to be outweighed by successful transition to the flyer state and

513 associated advancing flight that we observed.

514 *Advancing versus Retreating Flights*

515   The positioning of our ART network allowed us to test the prediction of our

516 second hypothesis by directly comparing the decisions of birds retreating to

517 interior habitats and then advancing after presumably refueling (i.e., transition

518 from feeding to flying). We detected differences in departure time, stopover

519 duration, and travel speed as hypothesized between retreating and advancing

520 migrants. While stopover duration and travel speed were in the predicted

521 direction, departure time results were opposite of what we expected. This may be

522 an artifact of processing departures from edge sites versus interior sites. All

523 retreating individuals departed from known locations within our detection area,

524 whereas half the individuals advancing from inland sites departed outside the

525 detection area and were detected when already aloft. Individuals retreating inland

526 showed greater variation in departure time and may be flexible in departure time

527 since they are moving a relatively short distance (45-72+ km) that may take 2-3

528 hours based on our calculated travel speeds, as opposed to advancing over the

529 Gulf of Mexico for a sustained flight of 1,000 km lasting an average of 22 hours

530 (Deppe et al. 2015). Given the more demanding flight, birds advancing and

531 engaging in trans-Gulf flights should show higher consistency in departure times

532 to take advantage of orientation cues available at twilight and nocturnal flight

533 conditions (Kerlinger and Moore 1989, Newton 2008, Schofield et al. 2018a).

534   While individuals retreated from our edge site shortly after arrival, they

535   spent an average of 11 days at the higher-quality inland site presumably

536   refueling and waiting for appropriate atmospheric conditions (Able 1973,

537   Richardson 1978, Åkesson and Hedenström 2000, Liechti 2006, Buler et al.

538   2007, Shamoun-Baranes and van Gasteren 2011, Deppe et al. 2015, Bolus et al.

539   2017). The contrast in stopover duration between locations supports the

540   hypothesis that migrants unable to refuel at a stopover site will quickly leave,

541   while those gaining mass should remain until they achieve the necessary

542   departure fuel load to be in the flyer state (Mehlman et al. 2005, Schaub et al.

543   2008). For example, thrushes in our study tended to be fairly inactive at the edge

544   site, did not significantly gain mass, and departed the day of first capture – an

545   indication they are likely not foraging and attempting to reduce the threat of

546   predation in the open coastal habitat (Woodrey and Moore 1997, Cimprich et al.

547   2005, Cimprich and Moore 2006, Schofield et al. 2018b). The longer stopovers at

548   interior sites paired with advancing departures suggests that thrushes were able

549   to change their condition and internal state by taking advantage of the greater

550   food abundance and presumably lower competition and predation pressure.

551   In addition to longer stopover durations, retreating migrants exhibited

552   slower travel speeds despite generally experiencing supportive tailwinds, which

553   is consistent with the feeder state. When migrants resume migration, they should

554   not respond to habitat quality or resource availability (Dingle 1996, Chernetsov

555   2006, Cohen et al. 2012). Migrants retreating from edge habitats had slower

26

556   travel speeds compared to when they later advanced from interior habitats

557   toward the Gulf of Mexico (see also Bruderer and Liechti 1998, Nilsson and

558   Sjöberg 2016). While it may seem surprising that advancing migrants flew into

559   headwinds, this has been found previously for Swainson's thrush departing from

560   our edge site (see Bolus et al. 2017). Typically, those advancing should make

561   decisions aloft to maximize a successful trans-Gulf flight, such as selecting

562   altitudes that reduce time and energy expenditure, as opposed to retreating,

563   which should focus on identifying high-quality stopover habitat by flying slower, at

564   lower altitudes to seek and assess habitats (Cochran and Kjos 1986, Kerlinger

565   and Moore 1989).

566   *Conclusion*

567   The ability for migrating birds to stop *en route* and locate habitat where

568   they can quickly transition from feeders to flyers is critical for a successful

569   migration. In our study, most migrants stopping along the edge of the Gulf of

570   Mexico departed shortly after arrival but discontinued the direct route to the

571   migratory destination. A third of the tagged individuals did not appear to find the

572   resources needed to resume migration and instead relocated a considerable

573   distance inland before advancing. Based on our observations, retreating

574   individuals were likely able to relocate to relatively higher quality habitat and

575   subsequently advance across the Gulf of Mexico after a substantial stopover

576   duration. Nearly half of the tagged individuals departed our edge site parallel to

577   the coast, but it is not clear if detouring individuals are selecting to feed, resume

578   migratory flight, or employ an intermediate strategy (i.e., fly and forage). The

579   decision-making process we observed occurs throughout the migratory period

580   based on the circumstances and conditions migrants experience, yet the context

581   of being at the edge of an expansive, inhospitable landscape causes the

582   decision-making process to carry greater consequences given that a

583   miscalculation could be fatal (Ward et al. 2018).

584   **Speculations**

585   We suspect the feeder/flyer dichotomy influenced behaviors we did not measure,

586   and was influenced by weather conditions and migration timing:

587   - We hypothesize that the individuals in this study also displayed

588   differences in foraging behavior, daytime sleep, and general activity

589   consistent with the feeder/flyer dichotomy. We predict that flyers foraged

590   less and were risk averse if foraging, slept more during the day, and were

591   less active (i.e., sit and wait to advance) compared to feeders.

592   - Prevailing weather conditions are known to influence departure decisions,

593   including in our system, and likely adds a consequential circumstance to

594   the feeder/flyer dichotomy. While individuals advancing from the interior

595   site generally flew into headwinds upon departure, we suspect longer

596   stopover durations at the interior site could also be due to some

597   individuals attempting to await favorable weather conditions – delaying the

598   transition from feeder to flyer.

- A migrant's spatiotemporal context can influence decisions (e.g., a late bird minimizing time) and circumstances (e.g., more favorable weather later in the season). We hypothesize that we would see less retreating movements and other behaviors associated with feeders later in the season compared to earlier in the season as migrants may need to minimize time as *en route* resources diminish.

Declarations

628 **Data Accessibility Statement**

629 Data presented in this paper will be uploaded to the University of Illinois

630 Databank upon acceptance.

631 **Literature Cited**

632 Abdollahi, K. K. et al. 2005. Urban forest ecosystem structure and the function of
633   the gulf coastal communities in the United States. - In: Tiezzi, E. et al.
634   (eds), Ecosystems and Sustainable Development V. Southampton, pp.
635   605–614.

636 Able, K. P. 1973. The role of weather variables and flight direction in determining
637   the magnitude of nocturnal bird migration. - Ecology 54: 1031–1041.

638 Aborn, D. A. 1994. Correlation between raptor and songbird numbers at a
639   migratory stopover site. - The Wilson Bulletin: 150–154.

640 Agostini, N. 2004. Additional observations of age-dependent migration behaviour
641   in western honey buzzards Pernis apivorus. - Journal of Avian Biology 35:
642   469–470.

643 Åkesson, S. 1999. Do passerine migrants captured at an inland site perform
644   temporary reverse migration in autumn? - Ardea 87: 129–137.

645 Åkesson, S. and Hedenström, A. 2000. Wind selectivity of migratory flight
646   departures in birds. - Behav Ecol Sociobiol 47: 140–144.

647 Åkesson, S. et al. 1996. Bimodal orientation and the occurrence of temporary
648   reverse bird migration during autumn in south Scandinavia. - Behav Ecol
649   Sociobiol 38: 293–302.

650 Alerstam, T. 1978. Reoriented bird migration in coastal areas: dispersal to
651   suitable resting grounds? - Oikos 30: 405–408.

652 Alerstam, T. 2011. Optimal bird migration revisited. - Journal of Ornithology 152:
653   5–23.

654 Alerstam, T. and Lindström, Å. 1990. Optimal Bird Migration: The Relative
655   Importance of Time, Energy, and Safety. - In: Gwinner, P. D. E. (ed), Bird
656   Migration. Springer Berlin Heidelberg, pp. 331–351.

657 Baird, J. and Nisbet, I. C. T. 1960. Northward fall migration on the Atlantic coast
658   and its relation to offshore drift. - Auk 77: 119–149.

659 Bairlein, F. 1995. Manual of field methods, European-African songbird migration
660   network. - Institut für Vogelforschung/ Vogelwarte Helgoland.

661 Bolus, R. T. et al. 2017. Swainson's Thrushes do not show strong wind selectivity
662   prior to crossing the Gulf of Mexico. - Scientific reports 7: 14280.

663 Brooks, M. 1952. The Allegheny Mountains as a Barrier to bird movement. - Auk
664   69: 192–198.

665 Bruderer, B. and Liechti, F. 1998. Flight behaviour of nocturnally migrating birds
666   in coastal areas: crossing or coasting. - Journal of Avian Biology: 499–
667   507.

668 Buler, J. J. and Moore, F. R. 2011. Migrant–habitat relationships during stopover
669   along an ecological barrier: extrinsic constraints and conservation
670   implications. - J Ornithol 152: 101–112.

671 Buler, J. J. et al. 2007. A Multi-Scale Examination of Stopover Habitat Use by
672   Birds. - Ecology 88: 1789–1802.

673 Buler, J. J. et al. 2017. Body mass and wing shape explain variability in broad-
674   scale bird species distributions of migratory passerines along an
675   ecological barrier during stopover. - Oecologia 185: 205–212.

676 Burger, J. 1988. Effects of age on foraging in birds. - Proceedings of the
677   International Ornithological Congress 19: 1127–1140.

678 Burnham, K. P. and Anderson, D. R. 2002. Model Selection and Multimodel
679   Inference: A Practical Information-Theoretic Approach. - Springer.

Carlisle, J. D. et al. 2004. Habitat Associations, Relative Abundance, and Species Richness of Autumn Landbird Migrants in Southwestern Idaho. - The Condor 106: 549–566.

Chernetsov, N. 2006. Habitat selection by nocturnal passerine migrants en route: mechanisms and results. - J Ornithol 147: 185–191.

Chernetsov, N. 2012. Passerine Migration: Stopovers and Flight. - Springer Science & Business Media.

Cimprich, D. A. and Moore, F. R. 2006. Fat affects predator-avoidance behavior in Gray Catbirds (Dumetella carolinensis) during migratory stopover. - The Auk 123: 1069–1076.

Cimprich, D. A. et al. 2005. Passerine migrants respond to variation in predation risk during stopover. - Animal Behaviour 69: 1173–1179.

Cimprich, D. A. et al. 2018. Red-eyed Vireo (Vireo olivaceus). - In: Rodewald, P. G. (ed), The Birds of North America Online. 2nd ed.n. Cornell Lab of Ornithology, in press.

Cochran, W. W. and Kjos, C. G. 1986. Wind drift and migration of thrushes: A telemetry study. - Illinois Natural History Bulletin 33: 297–330.

Cohen, E. B. et al. 2012. Experimental Evidence for the Interplay of Exogenous and Endogenous Factors on the Movement Ecology of a Migrating Songbird. - PLOS ONE 7: e41818.

Cohen, E. B. et al. 2014. Fuel stores, time of spring, and movement behavior influence stopover duration of Red-eyed Vireo Vireo olivaceus. - Journal of Ornithology 155: 785–792.

Covino, K. M. and Cooney, B. 2015. Daytime sleeping behavior observed in a Black-and-white Warbler during spring stopover. - Animal Migration 2: 44–46.

DeGraaf, R. M. and Rappole, J. H. 1995. Neotropical Migratory Birds: Natural History, Distribution, and Population Change. - Cornell University Press.

Deppe, J. L. et al. 2015. Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. - PNAS 112: E6331–E6338.

Dingle, H. 1996. Migration: The Biology of Life on the Move. - Oxford University Press.

713   Dossman, B. C. et al. 2016. The effects of wind and fuel stores on stopover
714   departure behavior across a migratory barrier. - Behavioral Ecology 27:
715   567–574.

716   Dossman, B. C. et al. 2018. An experimental examination of the influence of
717   energetic condition on the stopover behavior of a Nearctic–Neotropical
718   migratory songbird, the American Redstart (Setophaga ruticilla). - Auk
719   135: 91–100.

720   Erni, B. et al. 2003. How does a first year passerine migrant find its way?
721   Simulating migration mechanisms and behavioural adaptations. - Oikos
722   103: 333–340.

723   Evans, M. et al. 2011. Wood Thrush (Hylocichla mustelina). - In: Poole, A. F.
724   (ed), The Birds of North America Online. 2nd ed.n. Cornell Lab of
725   Ornithology, in press.

726   Ferretti, A. et al. 2019. The amount of available food affects diurnal locomotor
727   activity in migratory songbirds during stopover. - Sci Rep 9: 1–9.

728   Fox, J. and Weisberg, S. 2011. An R companion to applied regression. - Sage.

729   Gauthreaux, S. A. 1978. The Ecological Significance of Behavioral Dominance. -
730   In: Bateson, P. P. G. and Klopfer, P. H. (eds), Social Behavior.
731   Perspectives in Ethology. Springer US, pp. 17–54.

732   Groebbels, F. 1928. Zur Physiologie des Vogelzuges. - Verhandlungen der
733   Ornithologischen Gesellschaft in Bayern 18: 44–74.

734   Hake, M. et al. 2003. Age-dependent migration strategy in honey buzzards
735   Pernis apivorus tracked by satellite. - Oikos 103: 385–396.

736   Hedenström, A. and Alerstam, T. 1992. Climbing Performance of migrating birds
737   as a basis for estimating limits for fuel-carrying capacity and muscle work.
738   - Journal of Experimental Biology 164: 19–38.

739   Helms, C. W. and Drury, W. H. 1960. Winter and migratory weight and fat field
740   studies on some North American buntings. - Bird-Banding 31: 1–40.

741   Johnson, M. D. and Strong, A. M. 2000. Length-weight relationships of Jamaican
742   arthropods. - Entomological News 111: 270–281.

743   Kelly, J. F. et al. 2002. Density-dependent mass gain by Wilson's Warblers
744   during stopover. - The Auk 119: 210–213.

745   Kemp, M. U. et al. 2012. Quantifying flow-assistance and implications for
746   movement research. - Journal of Theoretical Biology 308: 56–67.

747   Kerlinger, P. and Moore, F. R. 1989. Atmospheric structure and avian migration. -
748   In: Current ornithology. Springer, pp. 109–142.

749   Lain, E. J. et al. 2017. Songbirds are resilient to hurricane disturbed habitats
750   during spring migration. - Journal of Avian Biology 48: 815–826.

751   Liechti, F. 2006. Birds: blowin'by the wind? - Journal of Ornithology 147: 202–
752   211.

753   Lindström, Å. 1990. The role of predation risk in stopover habitat selection in
754   migrating bramblings, Fringilla montifringilla. - Behav Ecol 1: 102–106.

755   Lindström, Å. 2003. Fuel deposition rates in migrating birds: causes, constraints
756   and consequences. - In: Berthold, P. et al. (eds), Avian migration.
757   Springer-Verlag, pp. 307–320.

758   Mack, D. E. and Yong, W. 2000. Swainson's Thrush (Catharus ustulatus). - In:
759   Rodewald, P. G. (ed), The Birds of North America. 2nd ed.n. Cornell Lab
760   of Ornithology, in press.

761   Mazerolle, M. J. 2017. AICcmodavg: Model selection and multimodel inference
762   based on (Q)AIC(c). R package version 2.1-1.

763   Mehlman, D. W. et al. 2005. Conserving stopover sites for forest-dwelling
764   migratory landbirds. - The Auk 122: 1281–1290.

765   Mills, A. M. et al. 2011. Passerines use Nocturnal Flights for Landscape-Scale
766   Movements during Migration Stopover. - The Condor 113: 597–607.

767   Moore, F. R. 1987. Sunset and the orientation behaviour of migrating birds. -
768   Biological Reviews 62: 65–86.

769   Moore, F. R. 2018. Biology of landbird migrants: a stopover perspective. - The
770   Wilson Journal of Ornithology 130: 1–12.

771   Moore, F. R. and Yong, W. 1991. Evidence of food-based competition among
772   passerine migrants during stopover. - Behavioral Ecology and
773   Sociobiology 28: 85–90.

774   Moore, F. R. and Kerlinger, P. 1992. Nocturnality, long-distance migration, and
775   ecological barriers. - Proceedings of the 20th International Ornithological
776   Congress 1990: 1122–1129.

777   Moore, F. R. and Aborn, D. A. 2000. Mechanisms of en route habitat selection:
778   How do migrants make habitat decisions during stopover? - Studies in
779   Avian Biology 20: 34–42.

780   Moore, F. R. et al. 2003. Priority Access to Food in Migratory Birds: Age, Sex and
781   Motivational Asymmetries. - In: Berthold, P. D. P. et al. (eds), Avian
782   Migration. Springer Berlin Heidelberg, pp. 281–292.

783   Moore, F. R. et al. 2017. Effect of fuel deposition rate on departure fuel load of
784   migratory songbirds during spring stopover along the northern coast of the
785   Gulf of Mexico. - J Avian Biol 48: 123–132.

786   National Oceanic and Atmospheric Administration, Office for Coastal
787   Management 2010. 2010 C-CAP Regional Land Cover. - In: Coastal
788   Change Analysis Program (C-CAP) Regional Land Cover. NOAA Office
789   for Coastal Management, in press.

790   Németh, Z. 2009. Observation of daytime sleep-like behavior in a migratory
791   songbird during stopover. - wils 121: 644–646.

792   Newton, I. 2008. The Migration Ecology of Birds. - Academic Press.

793   Nilsson, C. and Sjöberg, S. 2016. Causes and characteristics of reverse bird
794   migration: an analysis based on radar, radio tracking and ringing at
795   Falsterbo, Sweden. - Journal of Avian Biology 47: 354–362.

796   Packmor, F. et al. 2020. Stopover departure decisions in songbirds: do long-
797   distance migrants depart earlier and more independently of weather
798   conditions than medium-distance migrants? - Mov Ecol 8: 6.

799   Payne, R. B. 1992. Indigo Bunting (Passerina cyanea). - In: Poole, A. et al. (eds),
800   The Birds of North America Online. 2nd ed.n. Cornell Lab of Ornithology,
801   in press.

802   Pinheiro, J. et al. 2018. nlme: Linear and Nonlinear Mixed Effects Models. - The
803   R Foundation for Statistical Computing, Vienna http://cran. r-project. org

804   Pyle, P. 1997. Identification guide to North American birds: Columbidae to
805   Ploceidae. - Slate Creek Press.

806   R Core Team 2018. R: A language and environment for statistical computing. - R
807   Foundation for Statistical Computing.

808 Rappole, J. H. and Warner, D. W. 1976. Relationships between behavior,
809   physiology and weather in avian transients at a migration stopover site. -
810   Oecologia 26: 193–212.

811 Ravi, S. et al. 2015. Hummingbird flight stability and control in freestream
812   turbulent winds. - Journal of Experimental Biology 218: 1444–1452.

813 Richardson, W. J. 1978. Timing and amount of bird migration in relation to
814   weather: a review. - Oikos: 224–272.

815 Sandberg, R. and Moore, F. R. 1996. Migratory orientation of red-eyed vireos,
816   Vireo olivaceus, in relation to energetic condition and ecological context. -
817   Behavioral Ecology and Sociobiology 39: 1–10.

818 Sandberg, R. et al. 2002. Orientation of nocturnally migrating Swainson's thrush
819   at dawn and dusk: importance of energetic condition and geomagnetic
820   cues. - The Auk 119: 201–209.

821 Schaub, M. et al. 2008. Fuel stores, fuel accumulation, and the decision to depart
822   from a migration stopover site. - Behav Ecol 19: 657–666.

823 Schmaljohann, H. and Klinner, T. 2020. A quasi-experimental approach using
824   telemetry to assess migration-strategy-specific differences in the decision-
825   making processes at stopover. - BMC Ecology 20: 36.

826 Schofield, L. N. et al. 2018a. Occurrence of quiescence in free-ranging migratory
827   songbirds. - Behav Ecol Sociobiol 72: 36.

828 Schofield, L. N. et al. 2018b. Using automated radio telemetry to quantify activity
829   patterns of songbirds during stopover. - Auk 135: 949–963.

830 Shamoun-Baranes, J. and van Gasteren, H. 2011. Atmospheric conditions
831   facilitate mass migration events across the North Sea. - Animal Behaviour
832   81: 691–704.

833 Sjöberg, S. et al. 2015. Weather and fuel reserves determine departure and flight
834   decisions in passerines migrating across the Baltic Sea. - Animal
835   Behaviour 104: 59–68.

836 Smolinsky, J. A. et al. 2013. Factors influencing the movement biology of migrant
837   songbirds confronted with an ecological barrier. - Behavioral Ecology and
838   Sociobiology 67: 2041–2051.

839   Strandberg, R. et al. 2009. How hazardous is the Sahara Desert crossing for
840   migratory birds? Indications from satellite tracking of raptors. - Biology
841   Letters: rsbl20090785.

842   Strong, A. M. and Sherry, T. W. 2000. Habitat-specific effects of food abundance
843   on the condition of ovenbirds wintering in Jamaica. - Journal of Animal
844   Ecology 69: 883–895.

845   Taylor, P. D. et al. 2011. Landscape Movements of Migratory Birds and Bats
846   Reveal an Expanded Scale of Stopover. - PLOS ONE 6: e27054.

847   Torchiano, M. 2017. effsize: Efficient Effect Size Computation. R package
848   version 0.7.1.

849   Venables, W. N. and Ripley, B. D. 2002. Modern Applied Statistics with S. -
850   Springer.

851   Vogel, S. 1988. Life's Devices: The Physical World of Animals and Plants. -
852   Princeton University Press.

853   Ward, M. P. et al. 2018. Estimating apparent survival of songbirds crossing the
854   Gulf of Mexico during autumn migration. - Proc. R. Soc. B 285: 20181747.

855   Warnes, G. R. et al. 2018. gmodels: Various R Programming Tools for Model
856   Fitting.

857   Weidensaul, S. et al. 2019. Ruby-throated Hummingbird (Archilochus colubris). -
858   In: Rodewald, P. G. (ed), The Birds of North America Online. 2nd ed.n.
859   Cornell Lab of Ornithology, in press.

860   Woodrey, M. S. 2000. Age-dependent aspects of stopover biology of passerine
861   migrants. - Studies in Avian Biology 20: 43–52.

862   Woodrey, M. S. and Moore, F. R. 1997. Age-Related Differences in the Stopover
863   of Fall Landbird Migrants on the Coast of Alabama. - The Auk 114: 695–
864   707.

865   Woodworth, B. K. et al. 2014. Inland flights of young red-eyed vireos Vireo
866   olivaceus in relation to survival and habitat in a coastal stopover
867   landscape. - Journal of avian biology 45: 387–395.

868   Wunderle, J. M. 1991. Age-specific foraging proficiency in birds. - Current
869   Ornithology 8: 273–324.

870 Zenzal, T. J. and Moore, F. R. 2016. Stopover biology of Ruby-throated
871   Hummingbirds (Archilochus colubris) during autumn migration. - The Auk
872   133: 237–250.

873 Zenzal, T. J. and Moore, F. R. 2019. Resource use and defence by Ruby-
874   throated Hummingbirds during stopover. - Behaviour 156: 131–153.

875 Zenzal, T. J. et al. 2013. Observations of predation and anti-predator behavior of
876   Ruby-throated Hummingbirds during migratory stopover. - Southeastern
877   Naturalist 12: N21–N25.

878 Zenzal, T. J. et al. 2014. The impact of radio-tags on Ruby-throated
879   Hummingbirds (Archilochus colubris). - The Condor 116: 518–526.

880 Zenzal, T. J. et al. 2018. Migratory hummingbirds make their own rules: the
881   decision to resume migration along a barrier. - Animal Behaviour 137:
882   215–224.

883 Zenzal, T. J. et al. 2018. Fine-scale heterogeneity drives forest use by spring
884   migrant landbirds across a broad, contiguous forest matrix. - The Condor
885   120: 166–184.

886

887 **Figure Legends**

888

889 Figure 1. A) Gulf of Mexico region with study area outlined in black. B) The

890 Mobile Bay region with telemetry tower locations shown. Tower 4 was operated

891 from 2012-2014, Tower 5 from 2013-2014, and Tower 6 in 2014 only. Resource

892 sampling at the inland site occurred near Tower 6. An example of tower tracking

893 is shown by dots indicating the inland flight tracks of three individual wood thrush;

894 red circles: hatch-year, female in lean condition that departed the coastal site on

895 9/25/14, white circles: hatch-year female in fat condition that departed the coastal

896 site on 9/22/14, gold circles: hatch-year female in fat condition that departed the

897 coastal site on 9/23/14. C) Fort Morgan Peninsula (coastal site) with locations of

898 banding station and telemetry towers shown. Towers 1 and 2 operated from

899 2009-2014, Tower 3A from 2009-2011, and Tower 3B from 2012-2014. Land

900 cover is based on a modified version of NOAA's Coastal Change Analysis

901 Program land cover atlas (National Oceanic and Atmospheric Administration,

902 Office for Coastal Management 2010).

903 Figure 2. A) Departure directions of radio-tagged individuals by species from the

904 coastal site on Fort Morgan, AL. Departures are categorized as Detouring (east-

905 west), Retreating (north), or Advancing (south). Species include ruby-throated

906 hummingbird (n = 52), indigo bunting (n = 34), red-eyed vireo (n = 145),

907 Swainson's thrush (n = 161), and wood thrush (n = 50). B) Circular histograms of

908 departure directions per species, binned to five degrees. Some individuals of

909 each species had departure directions that were not resolved (i.e., range of

910 possible directions within each category: detouring, retreating, or advancing; see

911 text) and were not included in this figure. Species include: Ruby-throated

912 hummingbird (n = 44), Indigo bunting (n = 34), Red-eyed vireo (n = 145),

913 Swainson's thrush (n = 161), and Wood thrush (n = 50).

914 Figure 3. Departure directions of radio-tagged individuals by fat score from the

915 coastal site on Fort Morgan, AL. Departures are categorized as Detouring (east-

916 west), Retreating (north), or Advancing (south). Fat scores are based on Helms &

917 Drury (1960) and include zero (n = 19), one (n = 45), two (n = 66), three (n = 58),

918 four (n = 127), and five (n = 127).

919 Figure 4. Travel speed of radio-tagged individuals by direction between the

920 coastal site and inland site. Directions include advance (south; n = 9) and retreat

921 (north, n = 31). Central black line indicates median, top and bottom of box

922 indicate interquartile range, and whiskers indicate total range.

923 **Tables**

924 Table1. AIC_C model selection analysis of departure directions (retreat, detour, or

925 advance) of indigo buntings (n = 34), ruby-throated hummingbirds (n = 52),

926 Swainson's thrush (n = 161), wood thrush (n = 50), and red-eyed vireo (n = 145)

927 from Fort Morgan, Alabama, U.S.A during 2008-2014.

Candidate Model	w_i	Log-likelihood	ΔAICc	AICc	K
Species + Fat Score	0.86	-399.51	0.00	823.74	12
Species * Fat Score	0.06	-393.56	5.38	829.12	20
Age + Fat Score + Species	0.06	-397.92	5.39	829.13	16
Age * Fat Score + Species	0.02	-396.78	7.43	831.17	18
Age + Fat Score * Species	0.00	392.05	11.24	834.98	24

Age * Condition * Species	0.00	-386.75	28.35	852.09	36
Fat Score	0.00	-441.97	68.30	892.04	4
Age + Fat Score	0.00	-438.41	69.41	893.15	8
Age * Fat Score	0.00	-437.28	71.33	895.06	10
Species + Age	0.00	-433.69	72.63	896.37	14
Species	0.00	-438.33	73.44	897.18	10
Species * Age	0.00	-430.65	79.56	903.30	20
Age	0.00	-469.55	127.56	951.30	6
Null	0.00	-476.73	133.75	957.49	2

928 Table 2. The number of individuals radio-tagged at an edge site in Fort Morgan,

929 AL and subsequently detected retreating north of Mobile Bay during 2013 and

930 2014 by the interior ART network.

Species	Tagged at Fort Morgan	Detection of retreating individuals at interior ART network
Indigo Bunting	10	2 (20%)
Red-eyed Vireo	88	14 (15%)
Ruby-throated Hummingbird	23	0 (0%)
Swainson's Thrush	37	9 (24%)
Wood Thrush	40	17 (42%)

931 Percentages of individuals detected inland provided in parentheses.

932

933

934