

1 Migratory hummingbirds make their own rules: the decision to resume migration along a
2 barrier

3 Theodore J. Zenzal Jr.,^{a,b*} Frank R. Moore,^a Robert H. Diehl,^c Michael P. Ward,^b and Jill
4 L. Deppe^d

5 ^aDepartment of Biological Sciences, University of Southern Mississippi, Hattiesburg

6 ^bDepartment of Natural Resources and Environmental Sciences, University of Illinois,
7 Urbana

8 ^cUS Geological Survey, Northern Rocky Mountain Science Center, Bozeman, MT

9 ^dDepartment of Biological Sciences, Eastern Illinois University, Charleston

10 *Corresponding author:

11 Department of Natural Resources and Environmental Sciences

12 University of Illinois, Urbana-Champaign

13 1102 S. Goodwin Ave.

14 Urbana, IL USA 61801

15 Phone: 1-217-300-3095

16 Fax: 1-217-244-3219

17 E-mail: tjenzal@gmail.com

18 Word Count: 9,029

19 Knowing how naïve migrants respond to intrinsic and extrinsic factors experienced *en*
20 *route* will allow a more thorough understanding of the endogenous migratory program.
21 To understand how inexperienced individuals respond to ecological features, we
22 tracked the migratory departures of juvenile *Archilochus colubris* (ruby-throated
23 hummingbird), one of the smallest (~ 3 grams) and least-studied migrants, along the
24 Gulf of Mexico during southbound migration using an international automated radio-
25 telemetry system. The recent miniaturization of radio-tags provides a novel method to
26 track one of the smallest migratory birds, rendering the first information on departure
27 decisions of known hummingbirds in relation an ecological barrier. Using weather
28 conditions and individual attributes, we also determined which factors influenced the
29 time and direction of departure from a coastal stopover site. Most migrants (83%)
30 departed in the morning, and daily departure time was only influenced by stopover
31 duration, the amount of time spent at a stopover site. The majority (77%) of departure
32 orientations paralleled the coastline, and we found little influence of any factor on
33 departure direction. Our results reveal that: 1) juvenile hummingbirds departing coastal
34 Alabama move in a direction indicative of a circum-Gulf path during southbound
35 migration; and 2) departure decisions support a fly-and-forage strategy, hummingbirds
36 likely take advantage of resources along the coast while moving towards their
37 destination.

38 KEYWORDS: Migration, Gulf of Mexico, Stopover, ruby-throated hummingbird, Radio
39 telemetry, Fly-and-forage strategy, *Archilochus colubris*, extrinsic, intrinsic, Alabama

40

41 HIGHLIGHTS

- 42 • Migratory animals often need to traverse large ecological features *en route*
- 43 • We examine decisions of young hummingbirds departing a coastal stopover site
- 44 • Young hummingbirds do not cross the Gulf of Mexico during autumn migration
- 45 • Young hummingbirds departed in the morning parallel with the coastline

46

47 Many migratory animals face at least one barrier during migration (e.g.,
48 Rittenhouse & Semlitsch, 2006; Marschall, Mather, Parrish, Allison, & McMenemy,
49 2011; Deppe et al., 2015), with migratory birds negotiating large inhospitable ecological
50 features, such as oceans and deserts, to reach breeding or wintering locations (e.g.,
51 Biebach et al., 2000; Gill, Piersma, Hufford, Servranckx, & Riegen, 2005; Deppe et al.,
52 2015). In eastern North America, the majority of breeding birds that winter in the tropics
53 must make a critically important decision when arriving at the Gulf of Mexico: fly across
54 or around this feature. Birds that fly across the Gulf of Mexico require stores of fat
55 sufficient to meet the energetic demands of a trans-Gulf flight (Sandberg & Moore,
56 1996; Smolinsky, Diehl, Radzio, Delaney, & Moore, 2013; Deppe et al., 2015) and those
57 reserves are largely obtained during stopovers (e.g. Woodrey & Moore, 1997; Zenzal &
58 Moore, 2016). Habitats along the northern coast of the Gulf of Mexico provide the last
59 possible stopover before migrants engage in a non-stop flight of ~900 km, and evidence
60 suggests that landbird migrants may not begin to build large fuel loads until they
61 encounter barriers (Odum, Connell, & Stoddard, 1961; Caldwell, Odum, & Marshall,
62 1963; but see Hou & Welch, 2016). Alternatively, individuals may move along the

63 coastline in a circum-Gulf flight (Sandberg & Moore, 1996; Alerstam, 2001). Whether
64 migrants fly around or over the Gulf, they face important decisions (Deppe et al., 2015):
65 when to depart and in what direction to travel, and each will have repercussions for a
66 successful migration. Both intrinsic and extrinsic factors, which can influence the
67 endogenous program that governs migratory behaviour, have been found to impact
68 these decisions (e.g. Sandberg & Moore, 1996; Smolinsky et al., 2013, Deppe et al.,
69 2015; Müller et al., 2016).

70 Intrinsic factors (age, sex, and fuel load) influence the decision to depart as well
71 as departure direction (e.g., Thorup, Alerstam, Hake, & Kjellén, 2003; Smolinsky et al.,
72 2013; McKinnon, Fraser, Stanley, & Stutchbury, 2014; Deppe et al., 2015; Dossman et
73 al., 2016; Müller et al., 2016). Less experienced juvenile (hatching year) birds on their
74 first migration may be inadequately prepared to negotiate the Gulf of Mexico (Woodrey,
75 2000) and/or more prone to orientation errors (Ralph, 1978; Moore, 1984; Able &
76 Bingman, 1987). The role of sex on departure decisions has received less attention.
77 Although Helbig (1991) found no differences in migratory directions between male and
78 female *Sylvia atricapilla* (blackcaps), sex can influence access to resources (Moore,
79 Mabey, & Woodrey, 2003) and wing morphology (Stiles, Altshuler, & Dudley, 2005),
80 both of which may influence an individual's departure decisions (e.g., Sandberg &
81 Moore, 1996; Bowlin, 2007). Fuel stores have the strongest influence on the departure
82 decisions of migrants since it determines the distance a bird can travel (Pennycuick,
83 2008), which in turn influences how an individual negotiates ecological features
84 (Sandberg & Moore, 1996; Smolinsky et al., 2013, Deppe et al., 2015; Sjöberg et al.,
85 2015; Dossman et al., 2016). Individuals with sufficient fuel stores are able to traverse

86 inhospitable ecological features, while individuals with insufficient fuel stores may
87 choose to spend time fueling on stopover, reorient in search of better habitat, or if
88 possible, circumnavigate the feature (Nilsson & Sjöberg, 2015; Deppe et al., 2015).
89 Rarely do intrinsic factors act alone; young migrants, for example, are often in leaner
90 condition compared to adult birds (Woodrey & Moore, 1997; Zenzal & Moore, 2016).

91 Extrinsic factors, specifically atmospheric conditions, can influence the
92 endogenous program governing the departure decisions of migrants along the northern
93 Gulf of Mexico coast (Able, 1972; Deppe et al., 2015; Müller et al., 2016), especially for
94 individuals preparing for overwater flights (Richardson, 1978, 1990; Deppe et al., 2015;
95 Kranstauber, Weinzierl, Wikelski, & Safi, 2015). Supportive winds decrease the
96 energetic cost of transport and allow a higher migration speed (Liechti & Brunderer,
97 1998; Kranstauber et al., 2015), while opposing winds, turbulence, or low visibility from
98 cloud cover or precipitation increase transport costs and may cause orientation
99 problems (e.g. Richardson, 1978; Able, 1982; Liechti & Brunderer, 1998; Åkesson,
100 Walinder, Karlsson, & Ehnbohm, 2001; Ravi et al., 2015). Migrants experiencing
101 unfavorable weather conditions may delay their departure until conditions are favorable,
102 depart in a non-preferred direction, or attempt to compensate for unfavorable wind
103 conditions by altering flight direction to maintain progress towards the destination
104 (Mueller & Berger, 1967; Åkesson & Hedenström 2000; Schaub, Liechti, & Jenni, 2004;
105 Schmaljohann & Naef-Daenzer, 2011), all of which can have negative carryover effects
106 (e.g., Smith & Moore, 2003; Norris & Marra, 2007; Drake, Rock, Quinlan, Martin, &
107 Green, 2014).

108 *Archilochus colubris* (ruby-throated hummingbird; hereafter “hummingbirds”) is
109 the smallest (~3 g) migratory bird in eastern North America, travelling between
110 temperate breeding grounds in the United States and Canada and wintering grounds in
111 Mexico and Central America (Weidensaul, Robinson, Sargent, & Sargent, 2013). While
112 thought to be the only hummingbird that crosses the Gulf of Mexico (e.g., Osborne,
113 1998; Sargent, 1999), there is no evidence supporting this hypothesis. We suspect that
114 the Gulf of Mexico presents a barrier to hummingbirds because their small size
115 increases susceptibility to unfavorable weather aloft (Ravi et al., 2015). Flight range
116 estimates based on oxygen consumption of hovering flight suggest that a hummingbird
117 with 2 g of fat could fly 1050 km (Lasiewski, 1962), and hummingbirds carry enough
118 fuel, primarily derived from nectar, to cross the Gulf of Mexico under still air conditions
119 (Zenzal & Moore, 2016). However, unfavorable atmospheric conditions, particularly
120 head- or crosswinds and turbulence, would necessarily decrease the probability of a
121 successful crossing. Given that hummingbirds increase wing beat frequency in turbulent
122 conditions (Ravi et al., 2015), encountering unfavorable winds over the Gulf of Mexico
123 would dangerously increase the energetic cost of flight. The departure decisions of
124 hummingbirds at a coastal stopover site may depend on precisely estimating internal
125 energetic state and prevailing weather conditions. Moreover, our understanding of
126 hummingbird migration, especially in relation to departure decisions from a stopover
127 site, pales in comparison to what is known about other landbird migrants.

128 In this study, we are the first to examine how intrinsic and extrinsic factors impact
129 the departure decisions, and hence the endogenous program, of hummingbirds on their
130 first migration. The miniaturization of radio tags and an international automated radio-

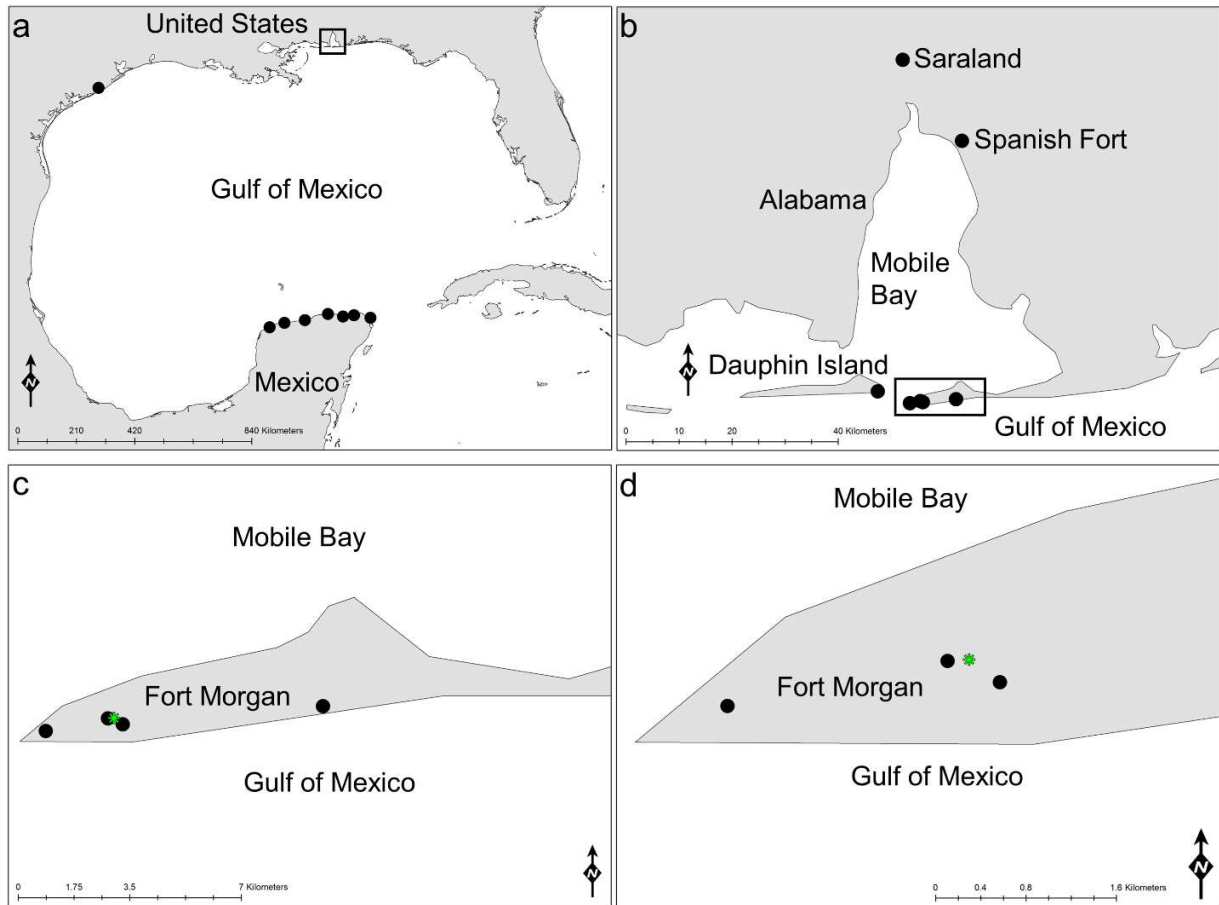
131 tracking network provide a novel way to understand the movements of known
132 individuals during stopover as they negotiate crossing the Gulf of Mexico. We focus on
133 juvenile birds for three main reasons: 1) the U.S. Bird Banding Laboratory only
134 approved tagging of juveniles, 2) large numbers of juvenile birds were captured at our
135 study site compared to adult birds (see Zenzal & Moore, 2016) ensuring adequate
136 sample sizes, and 3) studying departure decisions made by young migrants should
137 improve our understanding of migratory strategies based on endogenous programming
138 or factors experienced *en route*, especially considering no prior experience with
139 negotiating ecological features. We hypothesized that hummingbirds would behave
140 similarly to songbirds moving along the Gulf coast (Sandberg & Moore, 1996, Smolinsky
141 et al., 2013, Deppe et al., 2015), that is: (1) departure direction – trans-Gulf (south),
142 circum-Gulf (east or west), or reverse movement (north) – depends on energetic
143 condition as well as weather variables, and (2) the time of departure depends on
144 weather conditions, specifically individuals should depart during days and times when
145 weather is most favorable for migration. A secondary objective of this study is to
146 determine the extent to which we can generalize what we know about songbird
147 migration to hummingbirds.

148 METHODS

149 *Study Site and Capture Methods*

150 Ruby-throated hummingbirds were captured at a long-term migration station
151 (30°10'N, 88°00'W; Figure 1) on the Bon Secour National Wildlife Refuge (NWR) in Fort
152 Morgan, Alabama, USA. The site was composed of scrub-shrub habitat and pine forest
153 with *Pinus elliottii*, *Quercus* spp., *Ilex* spp., *Smilax* spp., and *Serenoa repens* as the

154 dominant species (for a complete description see Zenzal, Fish, Jones, Ospina, &
155 Moore, 2013). Autumn migrants that stopover at this site are immediately confronted
156 with a departure decision in relation to the Gulf of Mexico.
157



158
159 Figure 1. Automated radio telemetry system (ARTS) network around the Gulf of Mexico.
160 (a) Locations of ARTS (circles) around the Gulf of Mexico and the study site (box). (b)
161 The ARTS network around Mobile Bay in Alabama, USA; box indicates Fort Morgan
162 Peninsula. (c) ARTS (circles) and banding station (green asterisk) on the Fort Morgan
163 Peninsula in Alabama. (d) West end of the Fort Morgan Peninsula with ARTS (circles)
164 and banding station (green asterisk).

165 We captured hummingbirds using nylon mist nets (n = 29-32; 12 meters or 6
166 meters x 2.6 meters with 30 millimeter mesh) from approximately 25 August to 1
167 November 2011-2014 (see Zenzal & Moore, 2016). We typically operated mist nets
168 from sunrise until noon (Central Daylight Time [CDT]), depending on weather conditions
169 and capture rates. We supplemented resources in the study site with 14 artificial
170 feeders. Ten of the feeders were part of a separate study and not associated with
171 netting locations; the remaining four were used to increase hummingbird capture
172 probability; the majority of the netting effort was passive. We banded hummingbirds with
173 U.S. Geological Survey aluminum leg bands, aged (juvenile/hatch year or adult/after
174 hatch year) and sexed them according to Pyle (1997), estimated visible subcutaneous
175 fat (Helms & Drury, 1960), and measured natural wing chord (0.01 mm) and mass
176 (nearest 0.01 gram using an electronic balance). Given the high turnover rate of
177 hummingbirds at this study site (see Zenzal & Moore, 2016), we assume birds arrived
178 on the day of capture.

179 *Radio Tag Attachment*

180 A subsample of juvenile hummingbirds ($N = 55$) received a small, pulsed radio-
181 tag (0.28 ± 0.06 g with glue and cloth [all results are presented as mean \pm standard
182 deviation]; ~ 10 day lifespan; JDJC Corp. Fisher, USA) which was 6.9% of the average
183 total body mass for the birds used in this study (4.14 ± 0.61 g). We used radio-tags
184 because: 1) they were not found to have a significant influence on hummingbirds in an
185 aviary during autumn migration (Zenzal, Diehl, & Moore, 2014), and 2) we were able to
186 take advantage of an existing international automated radio-tracking network (Deppe et
187 al., 2015; see below). Each radio-tag had a unique frequency between 163.929-165.297

188 MHz with pulse intervals that ranged between 525 - 836 ms and pulse widths that
189 ranged from 14 - 16 ms. We attached radio-tags using a method modified from Raim
190 (1978) that was developed by Smolinsky et al. (2013), which allows radio-tags to fall off
191 the bird in three to four weeks. Once a hummingbird was selected, we cut feathers on
192 the dorsal side to reveal a patch of skin and feather stubble then affixed the radio-tag to
193 this patch using eyelash adhesive (Revlon, New York, USA) and a small amount of
194 cyanoacrylate glue (Loctite, Düsseldorf, Germany) at the bird's approximate center of
195 gravity. Birds were held for ~5 minutes after attachment to allow the adhesive to dry and
196 to ensure that tag attachment did not impede movement. All research activities were
197 approved by the University of Southern Mississippi Institutional Animal Care and Use
198 Committee (Protocol #11092210), U.S. Geological Survey Bird Banding Laboratory
199 (Permit #21221), and the Bon Secour National Wildlife Refuge.

200 *Radio Telemetry Network*

201 We used a network of automated radio telemetry systems (ARTS) similar to that
202 described by Deppe et al. (2015), to track hummingbirds in Alabama, USA as well as
203 the Yucatan Peninsula, Mexico (Figure 1). In Alabama, we operated three ARTS on the
204 Fort Morgan Peninsula to estimate the date, time, and direction of departures. Over the
205 course of the study we changed the location of one ARTS prior to data collection in
206 2012, moving it ~ 1.5 km east, in order to obtain better departure direction estimates.
207 We expanded the Alabama tracking network over the course of the study; we added
208 ARTS in: 2012 on Dauphin Island, Alabama (7.5 km west of the study site), 2013 on
209 Spanish Fort, Alabama (50 km north of the study site) where the Mobile-Tensaw Delta
210 enters Mobile Bay, and in 2014 near Saraland, Alabama along the Mobile-Tensaw Delta

211 (65 km north of the study site; Figure 1a). In 2011, we equipped all ARTS with six three-
212 element directional Yagi folded-dipole antennas (JDJC Corp., Fisher, USA). From 2012-
213 2014 we equipped the eastern ARTS on Fort Morgan as well as the two ARTS north of
214 Mobile Bay with four high-gain stacked directional antennas (designed by W.W.
215 Cochran) to increase the detection probability of tagged birds passing through the array;
216 all other ARTS used the directional Yagis described above. To continuously monitor
217 radio-tagged birds we used automated receiving units (ARU; JDJC Corp., Fisher, USA)
218 programmed to search each tag frequency at 2.5 - 6 minute intervals. At each search
219 interval the pulse width, pulse interval, noise, and signal strength of each radio-tag was
220 recorded from each antenna by the ARU.

221 We used stacked high-gain antennas on ARTS (similar to those described
222 above) distributed across the northern coast of the Yucatan Peninsula to establish a
223 “telemetry fence” in order to detect the arrival of hummingbirds after trans-Gulf flight
224 (Figure 1a). In 2011, each ARTS (n = 7) was equipped with two sets of stacked
225 antennas parallel to the coast, whereas from 2012-2014 each ARTS was equipped with
226 a stacked antenna in each cardinal direction. In 2014 we added an additional ARTS with
227 four high-gain stacked antennas near Cedar Lake, Texas to detect hummingbirds
228 engaged in circum-Gulf movements. The ARU search interval for the Yucatan and
229 Texas ARTS was 4.25 - 6 minutes and recorded the same variables (pulse width, pulse
230 interval, noise, and signal strength) for each radio-tag on each antenna (see Deppe et
231 al., 2015 for a complete description of the telemetry network).

232 *Radio Telemetry Data Processing*

233 We followed data processing methods described by Deppe et al. (2015) to
234 determine departure time and direction. To process the automated radio telemetry data,
235 we used R (R Core Team 2016) and Python scripts to detect radio-tagged individuals
236 based on six criteria: 1) the individual had to be detected during at least three
237 successive sampling periods, 2) detected frequency (MHz) had to be within two one-
238 thousandths of the known radio-tag frequency, 3) pulse interval had to be within 50 ms
239 of the radio-tag's interval or a multiple thereof, 4) pulse width had to be within 2 ms of
240 the radio-tag's width provided by the manufacturer, 5) noise level under -130 dBm, and
241 6) signal strength over -122 dBm. See Deppe et al. (2015) for a complete description of
242 scripts and data processing techniques.

243 To determine departure track and direction of an individual with signals > -122
244 dBm from the closest ARTS, we followed the approach used by Smolinsky et al. (2013)
245 and Deppe et al. (2015) that estimated a bird's departure track and direction through
246 biangulation or triangulation. The last five predicted coordinates of the track determined
247 the bird's departure time and bearing. We also estimated departure direction based on
248 vanishing bearings, which is when we determined departure time, according to data
249 from the ARTS receiving the strongest signal. Along the Yucatan Peninsula we
250 searched for signals on the east/west oriented antennas.

251 We were unable to obtain data on three tagged individuals due to problems with
252 radio tags, ARTS, or electromagnetic noise. Also, we were unable to determine exact
253 departure bearings on eleven other tagged birds due to electromagnetic noise or low
254 flight altitude reducing the number of predicted coordinates required to obtain a precise
255 estimate; however, we were able to determine their general (cardinal) departure

256 direction (e.g., north) as well as time of departure based on a spike in signal strength
257 that steadily decreased as the bird moved away from the ARTS. We excluded these
258 latter birds from circular statistics that required precise departure bearings.

259 *Weather Variables*

260 Weather data were obtained from two nearby weather stations since we were
261 unable to gather all variables of interest from a single station. From the Bon Secour
262 NWR station (ID: BONA1; 30° 15' N, 87° 48' W) we obtained relative humidity (%) and
263 precipitation (presence/absence). From the Dauphin Island station (ID: 994420; 30° 15'
264 N, 88° 4' W) we obtained wind direction, wind speed ($\text{m}\cdot\text{s}^{-1}$), temperature ($^{\circ}\text{C}$), and
265 barometric pressure (hPa). We selected data within an hour of the bird's departure to
266 relate atmospheric conditions to departure decisions. All variables were attained from
267 surface level readings since hummingbirds are thought to fly at low altitudes (Kerlinger
268 & Moore, 1989).

269 *Statistical Analysis*

270 We used descriptive and information theoretic approaches to understand the
271 departure decisions of hummingbirds. First, we used circular statistics to calculate the
272 mean direction and resultant length (r), which represents the concentration of data,
273 followed by a Rayleigh test of uniformity on departure time ($N = 52$) and direction ($N =$
274 41 ; Fisher, 1993; Pewsey, Neuhäuser, & Ruxton, 2013). Second, we selected Akaike's
275 information criterion corrected for small sample sizes (AIC_c ; $n = 52$; Burnham &
276 Anderson, 2002) to determine which variables might influence an individual's departure
277 time and direction. We performed the following data transformations to fit circular
278 variables to logistic (departure direction) or linear (departure time) models: 1) We

279 transformed departure and wind direction bearings into four discrete categories
280 centered on cardinal directions (north: $\geq 315^\circ$ or $< 45^\circ$; east: $\geq 45^\circ$ and $< 135^\circ$; south: \geq
281 135° and $< 225^\circ$; west: $\geq 225^\circ$ and $< 315^\circ$); these directions were informed by
282 departures from other radio-tagged birds departing our study site (Smolinsky et al.,
283 2013, Deppe et al., 2015) and the geography of the coastline (Figure 1). 2) Categories
284 for wind direction were the same as bird departure categories since we expected birds
285 to use wind assistance during migration (Alerstam, 1979a; Åkesson & Hedenström,
286 2000). 3) We transformed departure time to hours after local sunrise based on Kerlinger
287 & Moore (1989).

288 We selected two response variables, departure direction and departure time, for
289 use within a multinomial logistic regression or linear regression framework, respectively,
290 and created a number of candidate models for each response variable. We looked for
291 relationships between our response variables and the following predictor variables: fuel
292 load at capture, sex, stopover duration, density of hummingbirds at our study site on the
293 day of departure, wind direction, wind speed, temperature, barometric pressure, relative
294 humidity, and precipitation; departure day was included in all models, except the null, to
295 control for timing of season. Departure direction and departure time exchanged roles as
296 response and predictor variables between the two regression models (Table 1).

297 Stopover duration is calculated from the time of capture and the last detection of an
298 individual's unique radio-tag frequency; considering most hummingbirds (89%) at our
299 study site are never redetected after initial capture based on various marking
300 techniques (see Zenzal & Moore, 2016) we assume we captured birds the day they
301 arrived at our site. All weather parameters were obtained for the time closest to

302 departure. We tested all single variable models, a null model (no variables), global
303 model (all variables) as well as a number of specific additive and interactive models,
304 including those testing hypotheses related to weather, energy, intrinsic factors, and
305 extrinsic factors, based on the biology of the species and what is known about factors
306 that influence the departure decisions of other avian migrants (see Tables 2, 3). We
307 interpreted models with a $\Delta AIC_c \leq 2$ to be the strongest supported model(s) based on
308 the data and determined the top supported model based on the calculated weight of
309 each model (Burnham and Anderson 2002).

310 **Table 1.** Description of predictor variables used in model selection. We provide a
 311 measure of each continuous (mean \pm standard deviation) and categorical (sample size
 312 per group) variable.

Variable	Description	Measure
Fuel load	Grams of mass over lean body mass following methods from Zenzal and Moore (2016)	1.17 ± 0.58 g
Sex	The sex of the bird based on Pyle (1997)	Male = 27 Female = 25
Stopover duration	Number of hours spent on stopover (based on telemetry detections)	31.00 ± 43.17 hr
Departure day	Ordinal date of final detection from telemetry	270 ± 12
Density	Number of hummingbirds captured on the day of departure	10 ± 9
Wind direction	Direction from which the wind originates nearest to time of departure	North = 22 South = 3 East = 22 West = 5
Wind Speed	The velocity of the wind in m/s nearest to time of departure	5.51 ± 2.35 m/s
Temperature	Temperature ($^{\circ}$ C) nearest to time of departure	23.82 ± 3.46 $^{\circ}$ C
Barometric Pressure	Air pressure (hPa) nearest to time of departure	1016.48 ± 4.08

Relative humidity	Measure of humidity (%) nearest to time of departure	78.21 ± 16.56 %
Precipitation	Presence or absence of precipitation occurring nearest to time of departure	Presence = 1 Absence = 51
Departure direction ^a	The cardinal direction of a bird at final telemetry detection	North = 8 South = 4 East = 11 West = 29
Departure time ^b	Number of hours since local sunrise of a bird's final telemetry detection	3.05 ± 3.00

313 ^aPredictor variables used for the response variable “departure time”

314 ^bPredictor variables used for the response variable “departure direction”

315

316

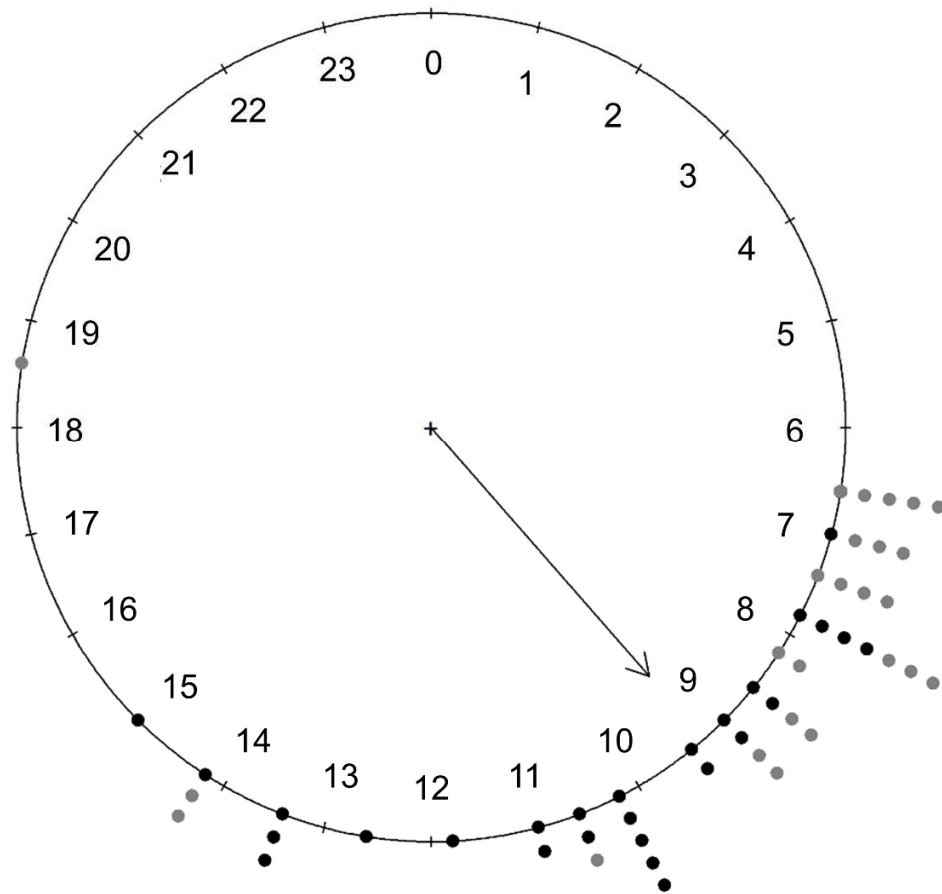
317 We used the R statistical language (R Core Team, 2016) to perform all statistical
318 analyses. For analysis of circular data, we used package “circular” (Agostinelli & Lund,
319 2013) and “CircStats” (Lund & Agostinelli, 2012). We used package “nnet” (Venables &
320 Ripley, 2002) to perform multinomial logistic regressions (function: multinom). To
321 calculate ΔAIC_c and AIC_c weights we used package “AICcmodavg” (Mazerolle, 2015).

322 RESULTS

323 *Departure Time*

324 Most hummingbirds (83%, $N = 43$) departed Fort Morgan between sunrise and
325 noon (mean: 9:15 CDT, $r = 0.80$, $P < 0.001$; Figure 2). The best supported candidate
326 model contained stopover duration and departure day ($\Delta AIC_c = 0.00$, AIC_c weight =
327 0.25; Table 2), although departure time did not appear to be influenced by departure
328 day (coefficient = -0.03, SE = 0.03). Over half the individuals with departures between
329 sunrise and noon tended to spend the night at the study site before departing (mean:
330 33.19 ± 45.60 hours, median 22.25 hours), whereas those departing between noon and
331 civil twilight ($N = 9$) often departed the evening of capture and hence had much shorter
332 stopover durations (mean: 20.32 ± 28.48 hours, median: 5.97 hours; Figure 3). The next
333 best model was the null model ($\Delta AIC_c = 0.33$, AIC_c weight = 0.21), while the remainder
334 of candidate models received weaker support according to model selection results
335 ($\Delta AIC_c > 1.59$; AIC_c weight < 0.12).

336



337

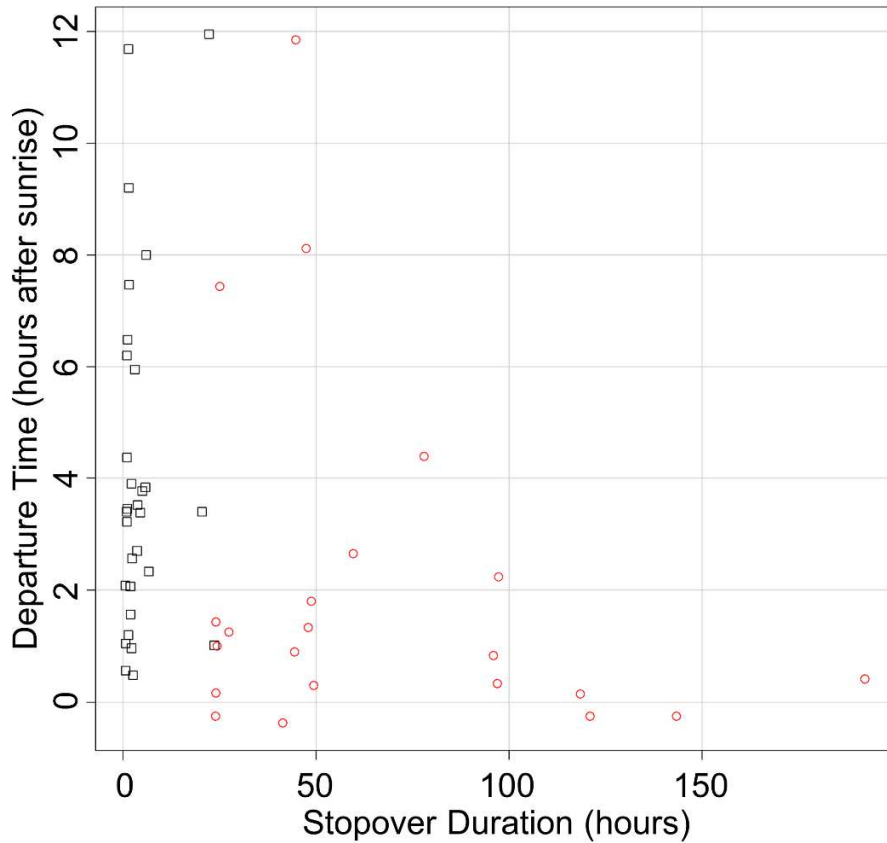
338 Figure 2. Departure times of ruby-throated hummingbirds from coastal Alabama, USA.
 339 Individual birds that departed the day they were tagged ($N = 27$) are represented by
 340 black dots and individuals that departed a subsequent day after tagging ($n = 25$) are
 341 represented by gray dots. The arrow represents the mean departure time (9:15) and the
 342 length of the arrow indicates the vector length (0.80). Local sunrise and sunset spanned
 343 between 6:32-7:01 and 19:03-18:09 (CDT), respectively, over the course of the study.

344 **Table 2.** Model selection analysis of departure times of ruby-throated hummingbirds
 345 from Fort Morgan, Alabama, 2011-2014. Only the top six models are shown.

Model	K	AIC _c	ΔAIC _c	w _i	Log-likelihood
Stopover duration + departure day	4	264.57	0.00	0.25	-127.86
Null model	2	264.90	0.33	0.21	-130.33
Wind speed + departure day	4	266.16	1.60	0.11	-128.66
Departure day	3	266.78	2.21	0.08	-130.14
Temperature + departure day	4	267.59	3.03	0.06	-129.37
Density + departure day	4	268.20	3.63	0.04	-129.68

346

347



349

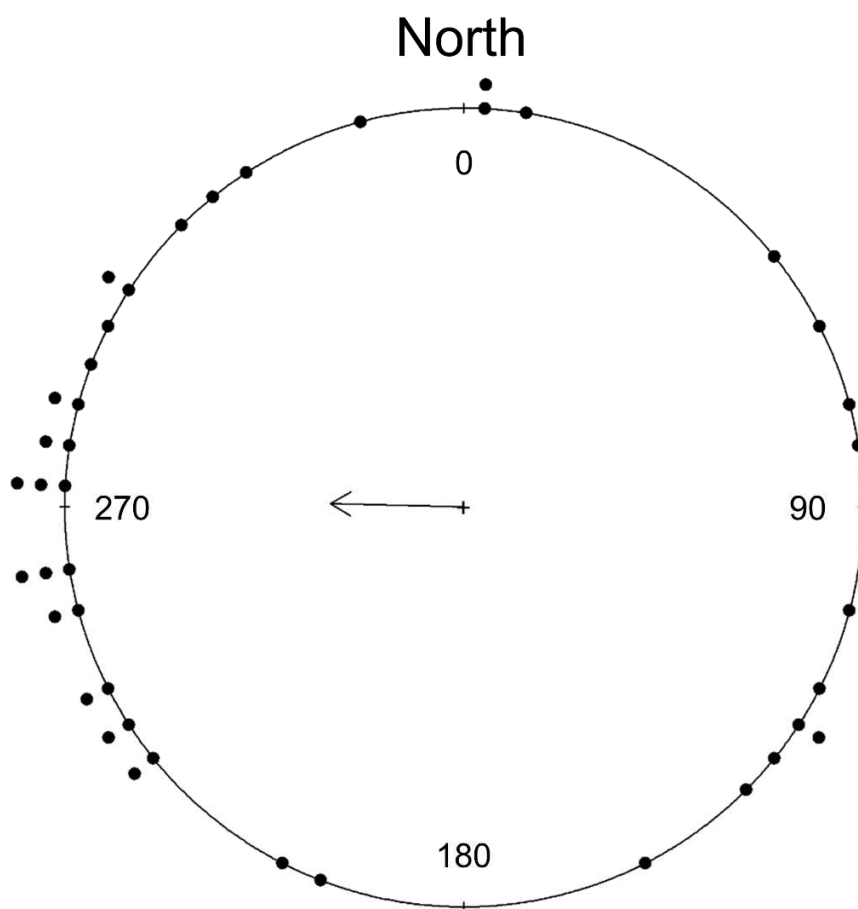
350 Figure 3. The relationship between departure time (hours after sunrise) and stopover
 351 duration, the number of hours between initial capture and last detection. Individuals
 352 departing the same day of capture are indicated by black squares and individuals
 353 departing a subsequent day are indicated by red circles.

354 *Departure Direction*

355 Most birds (77%, $N = 40$) departed parallel (east-west) with the coastline when
 356 resuming migration from our study site (mean: 272° , $r = 0.34$, $p = 0.008$), in line with a
 357 circum-Gulf migration strategy (Figure 4). While we investigated a number of
 358 parameters associated with the departure direction of songbird migrants (Table 1), we

359 found no support for the effect of any predictor variable on direction (null model: $\Delta AIC_c =$
360 0.00, AIC_c weight = 0.94; Table 3). This result suggest that the endogenous migratory
361 program is not related to weather or fuel load, factors that influence songbird migrants,
362 rather their migration may be affected by foraging strategy or resource availability. All
363 other candidate models received weak support ($\Delta AIC_c > 7.04$, AIC_c weight < 0.04).

364



365

366 Figure 4. Departure directions of ruby-throated hummingbirds from coastal Alabama,
367 USA. Individual birds ($N = 42$) are represented by black dots, the arrow represents the
368 mean departure angle (272°), and the length of the arrow indicates the vector length
369 (0.34).

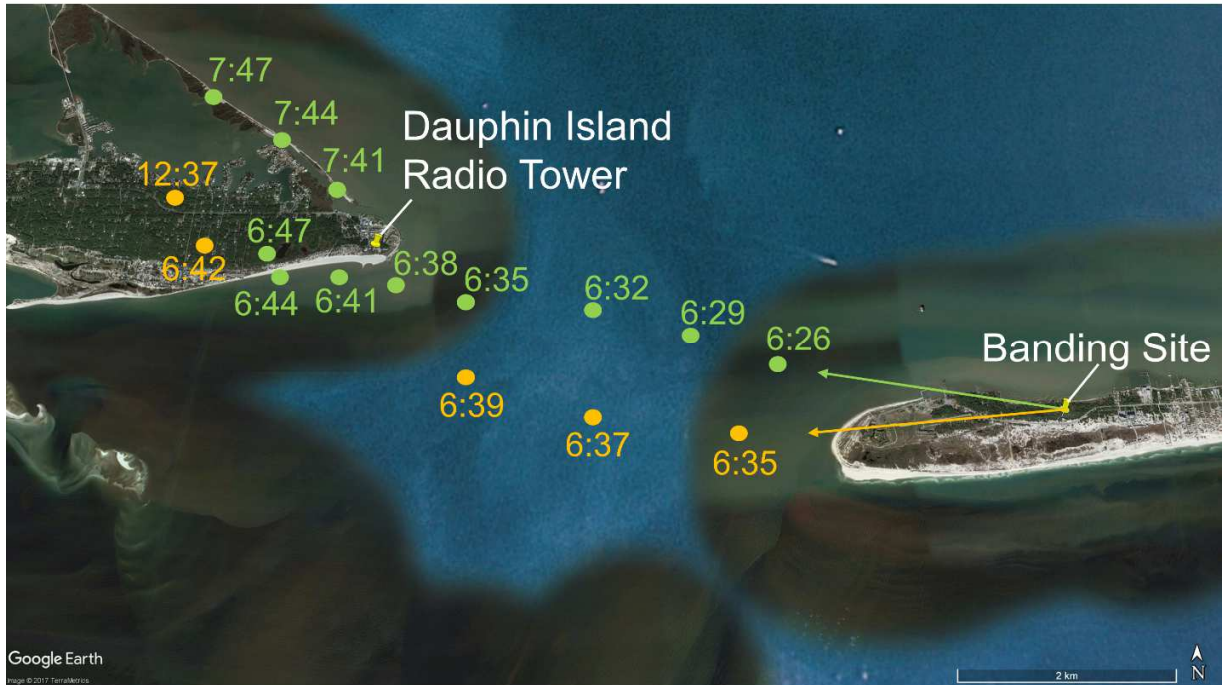
370 **Table 3.** Model selection analysis of departure directions of ruby-throated hummingbirds
 371 from Fort Morgan, Alabama, USA, 2011-2014. Only the top six models are shown.

Model	K	AIC _c	ΔAIC _c	w _i	Log-likelihood
Null model	3	125.01	0.00	0.94	-59.26
Departure day	6	132.06	7.05	0.03	-59.10
Sex+ departure day	9	132.40	7.39	0.02	-55.06
Stopover duration + departure day	9	135.80	10.79	0.00	-56.76
Precipitation + departure day	9	137.33	12.32	0.00	-57.52
Barometric Pressure + departure day	9	138.21	13.20	0.00	-57.96

372

373 *En Route Detections*

374 After hummingbirds departed Fort Morgan, we only detected 15 individuals on
375 ARTS located off the peninsula. We detected three birds from our ARTS on the north
376 shore of Mobile Bay (Spanish Fort, ~50 km north of the study site) and on our Dauphin
377 Island ARTS, west of the Fort Morgan Peninsula (~10 km west of the study site; Figure
378 1b). Three individuals made reverse movements from Fort Morgan. One individual
379 detected by the Spanish Fort ARTS was redetected on Fort Morgan one day later
380 before departing to the southwest; the two other individuals detected by the Spanish
381 Fort ARTS were never redetected on Fort Morgan. Birds flying west over Dauphin
382 Island tended to fly more slowly (6.53 ± 5.05 km/hr; $N = 6$) compared to individuals
383 departing overwater off the Dauphin Island coast (34.94 ± 7.23 km/hr; $N = 23$), even
384 landing on the island presumably to feed, after departing the Fort Morgan Peninsula
385 (Figure 5). We never detected radio-tagged hummingbirds within the Tensas River
386 Delta, on the Yucatan Peninsula, or on the Texas coast, despite detecting other radio
387 tagged songbird migrants (Deppe et al. 2015). Although we acknowledge that the
388 probability of detecting hummingbirds outside of Alabama was lower than that for other
389 tagged migrants due to the transmitter itself, the lower power output of the transmitter
390 would have reduced the range of the ARTS. Furthermore, the transmitter battery, which
391 had a short life (~10 days), could have died before the bird reached the next ARTS
392 located >700 km away. As an example, in 2013 one radio-tagged Hummingbird was
393 observed in Corpus Christi, Texas (~ 1,000 km west of the study site) at a hummingbird
394 feeder two weeks after departing the Fort Morgan Peninsula (USGS Bird Banding Lab,
395 Personal Communication), beyond a transmitter's expected lifespan.



396

397 Figure 5. The estimated location of ruby-throated hummingbirds engaged in the fly-and-
 398 forage migration strategy. Yellow dots indicate estimated locations of a male, hatch-year
 399 hummingbird that departed the Fort Morgan banding site on 9/18/2012 at 6:30 and was
 400 detected by an ARU from the Dauphin Island ARTS. The bird was not detected between
 401 6:42 and 12:37 likely because it was feeding in a residential area of the island where the
 402 signal was blocked from the ARU. Green dots indicate estimated locations of a female,
 403 hatch-year hummingbird that departed on 10/9/2012 at 6:25. This individual
 404 disappeared from the ARU from 6:47 to 7:41 and then appeared to depart the island to
 405 the northwest.

406 DISCUSSION

407 A variety of factors are purported to influence the departure time (Müller et al.
408 2016) and direction (e.g., Deppe et al., 2015) of migrating animals, with foraging
409 ecology and atmospheric conditions the likely primary selective forces on the
410 endogenous migratory program (Kerlinger & Moore, 1989). In our study, young
411 hummingbirds generally departed the Fort Morgan Peninsula in the morning, consistent
412 with the observations of migrating hummingbirds in the northeastern United States (Hall
413 & Bell, 1981) and the behaviour of other diurnal landbird migrants (Kerlinger & Moore,
414 1989; Strandberg & Alerstam, 2007; Ward & Raim, 2011). Most radio-tagged
415 hummingbirds assumed a westerly heading while many others departed toward the east
416 when leaving the Fort Morgan Peninsula, coinciding with the east-west orientation of the
417 coastline and a circum-Gulf route. In contrast to juvenile hummingbirds, many
418 intercontinental migratory songbirds that were radio-tagged on Fort Morgan in autumn
419 departed the coast heading south out over the Gulf of Mexico after sunset (Smolinsky et
420 al., 2013; Deppe et al., 2015), behaviour consistent with a trans-Gulf route (see also
421 Sandberg & Moore, 1996). The short stopover duration (< 24 hours) in the majority of
422 hummingbirds (58%), the departure direction, and similarities in the movement ecology
423 of other diurnal migrants suggests a fly-and-forage migration strategy.

424 Migrating birds often alternate between periods of flight, usually at night when
425 distance is covered and energy utilized, and stopover periods of one to several days,
426 when they rest and restore energy reserves. Some migrants, however, forage while
427 making progress towards their destination; this fly-and-forage migration strategy is used
428 mainly by diurnal migratory birds and some bats that hunt or locate prey *en route*
429 (Strandberg & Alerstam, 2007; Ward & Raim, 2011; Åkesson, Klaassen, Holmgren, Fox,

430 & Hedenström, 2012; Šuba, Petersons, & Rydell, 2012). We detected several
431 hummingbirds either landing on or moving slowly over Dauphin Island compared to
432 birds flying overwater, suggesting that those flying overland were using the habitat
433 they encountered. Although many birds encountered during stopover carry fuel loads
434 sufficient for a trans-Gulf flight (Zenzal & Moore, 2016), hummingbirds may elect to
435 make short stopovers throughout the day in food patches to meet energetic demands as
436 they migrate, rather than allocating extended periods of time to deposit fuel before and
437 after migratory flights, as is the case for most nocturnal migrants. The hummingbirds'
438 primary food source, nectar, is widely available throughout their migratory range (Bertin,
439 1982), supporting the benefits of a fly-and-forage strategy. While sources of nectar for
440 hummingbirds can be widely available, they are often temporally as well as spatially
441 ephemeral and do not often occur at our study site during autumn migration (TJZ,
442 personal observation). A lack of natural nectar sources may explain why some of our
443 radio-tagged birds ($N = 7$) were observed, as part of a separate study, visiting artificial
444 feeders on site (see Zenzal, 2016). These individuals observed at artificial feeders had
445 stopover durations of at least one day, which is not surprising given that artificial feeders
446 represent a reliable and essentially inexhaustible resource (Zenzal & Moore,
447 unpublished data). Further, birds that did spend the night usually departed the next
448 morning, which 1) coincides with replenishment of inflorescence nectaries (e.g.,
449 Feinsinger, 1978; Bertin, 1982; Galetto & Bernardello, 2004), 2) allows birds to identify
450 resource patches, and 3) provides more time for birds to migrate throughout the day.

451 A circum-Gulf route, consistent with the fly-and-forage strategy, has advantages
452 and disadvantages compared to moving across the Gulf of Mexico. The major

453 disadvantage is a longer migration distance, translating to longer transit times,
454 increased exposure to hazards such as predation risk (Cimprich & Moore, 1999),
455 competition for resources (Lindström, Hasselquist, Bensch, & Grahn, 1990),
456 unpredictable habitats and resources (Németh & Moore, 2007), and later arrival to the
457 destination (Kokko, 1999). However, these disadvantages are likely minimal for
458 hummingbirds during autumn. Although a longer migration distance takes more time,
459 detours around ecological barriers may reduce transport cost of fuel or may result in
460 higher fueling rates (Alerstam, 2001; Lindström et al., 2011). A circum-Gulf route may
461 explain why fuel load did not explain departure decisions, contrary to songbird migrants
462 striking out over the Gulf of Mexico from Fort Morgan (Deppe et al., 2015). The cost of a
463 fly-and-forage, circum-Gulf strategy may be reduced because hummingbirds are
464 generalist feeders, which lessens the need to find specific resources *en route*, and time
465 their migration with flowering phenology (Bertin, 1982). Moreover, hummingbirds have
466 less pressure to arrive early on the wintering grounds due to fluxes in resource density
467 in the tropics (Lara, 2006). Finally, hummingbirds are not thought to be under significant
468 predation risk (Miller & Gass, 1985; but see Zenzal et al., 2013).

469 While some hummingbirds arrive on the Alabama coast with fat reserves
470 theoretically capable of making a trans-Gulf flight (Zenzal & Moore, 2016), other factors
471 may explain why individuals did not appear to cross the Gulf when departing coastal
472 Alabama. Even though a trans-Gulf flight may be the quickest and most direct route to
473 their destination, there can be considerable risk when crossing an ecological barrier –
474 especially for a small bird. Aside from obtaining enough fuel, other factors such as
475 atmospheric conditions (Richardson, 1978), wind drift (Alerstam, 1979b), disorientation

476 (reviewed by Alerstam, 1990), and the cost of transport (Alerstam, 2001) can influence
477 the ability to make a successful barrier crossing. Hummingbirds, for example, may not
478 be able to successfully compensate for wind drift due to their small size. Furthermore, a
479 hummingbirds' small size seems to increase susceptibility to atmospheric turbulence,
480 causing increased energy expenditure during flight (Ravi et al., 2015). While some
481 hummingbirds may elect to make a trans-Gulf flight, this route seems to have
482 considerably more risk when compared an overland route.

483 Adopting a risk averse strategy, such as a circum-Gulf fly-and-forage migration,
484 allows naïve hummingbirds to reduce dependency on weather or fuel load as is the
485 case with the departure decisions of nocturnally migrating songbirds at Fort Morgan
486 (Sandberg & Moore, 1996; Smolinsky et al., 2013; Deppe et al., 2015). Young
487 inexperienced hummingbirds, the subjects of this study, likely follow their endogenous
488 program (e.g., Gwinner & Wiltschko, 1978) to migrate in a southerly direction in fall, and
489 then adopt a circum-Gulf strategy when encountering the Gulf of Mexico. While it is
490 possible that individuals moving parallel with the coast when departing our site may be
491 making relocation type movements (*sensu* Mills, Thurber, Mackenzie, & Taylor, 2011;
492 Taylor et al., 2011; Sjöberg et al., 2015) before making a trans-Gulf crossing from
493 another location, it would be difficult to disentangle the fly-and-forage strategy from a
494 landscape-scale relocation event. The future miniaturization of GPS tags or the
495 expansion of automated radio telemetry networks have the potential to better
496 understand these large scale movements.

497 We captured few adult hummingbirds at our site (see Zenzal & Moore, 2016 for
498 possible explanations), which may indicate that adults initiate a trans-Gulf flight or turn

499 to move along the coast further inland. While young migrants are often found to be
500 concentrated in coastal areas (Ralph, 1971; 1978, 1981; Zenzal & Moore, 2016),
501 juvenile hummingbirds may take advantage of the coast as a leading line (*sensu*
502 Mueller & Berger, 1967) that parallels the direction of travel and separates suitable and
503 unsuitable habitat. If young hummingbirds are moving around the Gulf of Mexico in a fly-
504 and-forage strategy, then individuals should turn south as soon as feasible which would
505 be in east Texas or peninsular Florida. Citizen science data (eBird) reveals that
506 hummingbird passage in the fall is moderate in south Florida and heavy along the
507 Texas coast (Sullivan et al., 2009), which is consistent with the direction and magnitude
508 of departures from Fort Morgan. Interestingly, banding data along the northern Yucatan
509 Peninsula coast suggest that hummingbirds are a fairly common fall migrant, in which
510 the majority (82%) are juveniles (JLD, unpublished data). However, the mean passage
511 date of hummingbirds on the Yucatan Peninsula is more than a month later than mean
512 passage date along the Alabama coast (Deppe & Rotenberry, 2005; Zenzal & Moore,
513 2016), more in line with movement around the Gulf of Mexico than across the Gulf of
514 Mexico. Moreover, banding records from Cuba and Isla Contoy, located off the coast of
515 northeastern Quintana Roo, Mexico, affirmed few hummingbirds during autumn
516 migration (JLD, unpublished data), suggesting that a Caribbean migration route is
517 uncommon.

518 The miniaturization of radio tags allowed use of a novel method to collect data on
519 the movement ecology of eastern North America's smallest migratory bird. We provide
520 the first, direct evidence on the movement ecology of hummingbirds in relation to the
521 Gulf of Mexico and show that the migration of young hummingbirds differs from that of

522 songbirds. Departure time of juvenile hummingbirds is linked to stopover length, likely
523 influenced by food availability, their foraging ecology, and possibly energetic
524 constraints. Morning departure times may also allow hummingbirds to identify stopover
525 locations with available resources so they might forage while they migrate, increasing
526 the probability of a successful migration. Departure direction was not influenced by
527 intrinsic or extrinsic factors, which is consistent with a fly-and-forage, circum-Gulf
528 migration strategy. A circum-Gulf strategy in young hummingbirds is further supported
529 by an absence of detections from the automated radio telemetry network in the Yucatan
530 and Texas, mismatches in the phenology of arrival through banding data between the
531 northern and southern Gulf of Mexico coast, and observations from citizen scientists
532 around the Gulf of Mexico. While more study is needed to determine if adult males and
533 females make the same decisions as juvenile hummingbirds, our results have
534 implications that impact all individuals stopping over along the Gulf coast. Notably, a
535 circum-Gulf route necessitates the availability of high-quality stopover sites along the
536 coast, requiring a deeper understanding of resource use for proper management,
537 conservation and restoration efforts, which is especially critical in relation to
538 encroaching development as well as natural and anthropogenic change (Hutto, 2000;
539 Abdollahi, Ning, & Stubblefield, 2005; Buler & Moore, 2011).

540 ACKNOWLEDGEMENTS

541 We thank the 2011-2014 Fort Morgan banding station field technicians, M. Tabasco and
542 W. Santamaria for assistance in the Yucatan Peninsula, R. Bolus, L. Schofield, E.
543 Swenson, A. Celis-Murillo, W. Cochran, and J. Cochran for assistance with telemetry
544 aspects of the project, J. Schaefer and C. Qualls for statistical advice, the 2011-2015

545 radio tower crews, as well as members of the Migratory Bird Research Group for their
546 support. We also thank the Bon Secour National Wildlife Refuge, Fort Morgan State
547 Historic Site, and many site partners around the Gulf for assistance and permission to
548 use their properties. This work was supported by the National Science Foundation
549 (NSF) (IOS Awards 1146832, 1147096, 1145952, and 1147022; GK-12 0947944);
550 National Geographic Committee on Research and Exploration (Awards 8971-11 and
551 9155-12); Birmingham Audubon Society; Alabama Ornithological Society; Wilson
552 Ornithological Society; Louisiana Ornithological Society; and the Eastern Bird Banding
553 Association. T.J.Z. was supported by a NSF GK-12 Program Award (0947944) and the
554 Mississippi-Alabama Sea Grant Consortium (NA14OAR4170089). We thank the
555 University of Southern Mississippi, University of Illinois at Urbana-Champaign, and
556 Eastern Illinois University for support, computing time, and copy services. This
557 manuscript was greatly improved through comments and critiques from Å Lindström, J.
558 Jawor, C. Qualls, and anonymous reviewers. Any use of trade, firm, or product names is
559 for descriptive purposes only and does not imply endorsement by the US Government.

560

561 REFERENCES

- 562 Abdollahi, K. K., Ning, Z. H., & Stubblefield, M. (2005). Urban forest ecosystem
563 structure and the function of the gulf coastal communities in the United States. In E.
564 Tiezzi, C. A. Brebbia, S. Jorgensen, & D. Almorza Gomar (Eds.), *Ecosystems and*
565 *Sustainable Development V* (pp. 605-614). Boston: Southampton.
- 566 Able, K. P. (1972). Fall migration in coastal Louisiana and the evolution of migration
567 patterns in the Gulf region. *Wilson Bulletin*, 84,231-242.

568 Able, K. P. (1982). The effects of overcast skies on the orientation of free-flying
569 nocturnal migrants. In F. Papi, & H. G. Wallraff (Eds.), *Avian Navigation* (pp. 38-49).
570 Berlin: Springer.

571 Able, K. P., & Bingman, V. P. (1987). The development of orientation and navigation
572 behavior in birds. *Quarterly Review of Biology*, 62,1-29.

573 Agostinelli, C., & Lund, U. (2013). R package 'circular': Circular statistics, version 0.4-7.
574 Available from: <https://r-forge.r-project.org/projects/circular/>

575 Åkesson, S., & Hedenström, A. (2000). Wind selectivity of migratory flight departures in
576 birds. *Behavioral Ecology and Sociobiology*, 47,140-144.

577 Åkesson, S., Klaassen, R., Holmgren, J., Fox, J.W., & Hedenström, A. (2012). Migration
578 routes and strategies in a highly aerial migrant, the common swift *Apus apus*, revealed
579 by light-level geolocators. *PLoS ONE*, 7, e41195.

580 Åkesson, S., Walinder, G., Karlsson, L., & Ehnbohm, S. (2001). Reed warbler orientation:
581 initiation of nocturnal migratory flights in relation to visibility of celestial cues at dusk.
582 *Animal Behaviour*, 61,181-189.

583 Alerstam, T. (1979a). Wind as a selective agent in bird migration. *Ornis Scandinavica*,
584 10,76-93.

585 Alerstam, T. (1979b). Optimal use of wind by migrating birds: Combined drift and
586 overcompensation. *Journal of Theoretical Biology*, 79,341-353.

587 Alerstam, T. (1990). Ecological causes and consequences of bird orientation.
588 *Experientia*, 46, 405-415

589 Alerstam, T. (2001). Detours in bird migration. *Journal of Theoretical Biology*, 209,319-
590 331.

591 Bertin, R. I. (1982). The Ruby-throated Hummingbird and its major food plants: ranges,
592 flowering phenology, and migration. *Canadian Journal of Zoology*, 60,210-219.

593 Biebach, H., Biebach, I., Friedrich, W., Heine, G., Partecke, J., & Schmidl, D. (2000).
594 Strategies of passerine migration across the Mediterranean Sea and the Sahara Desert:
595 A radar study. *Ibis*, 142, 623-634.

596 Bowlin, M. S. (2007). Sex, wingtip shape, and wing-loading predict arrival date at a
597 stopover site in the Swainson's Thrush. *The Auk*, 124,1388-1396.

598 Buler, J.J., & Moore, F.R. (2011). Migrant-habitat relationships during stopover along an
599 ecological barrier: extrinsic constraints and conservation implications. *Journal of*
600 *Ornithology*, 152, S101-S112.

601 Burnham, K.P., & Anderson, D.R. (2002). *Model selection and multimodel inference: A*
602 *practical information-theoretic approach*. (2nd ed.).New York: Springer.

603 Caldwell, L. D., Odum, E. P., & Marshall, S. G. (1963). Comparison of fat levels in
604 migrating birds killed at a Central Michigan and a Florida Gulf coast television tower.
605 *Wilson Bulletin*, 75, 428-434.

606 Cimprich, D. A., & Moore, F. R. (1999). Energetic constraints and predation pressure
607 during stopover. *Proceedings of the International Ornithological Congress*, 22, 834-846.

608 Deppe, J. L., & Rotenberry, J. T. (2005). Temporal patterns in fall migrant communities
609 in Yucatan, Mexico. *The Condor*, 107, 228-243.

610 Deppe, J. L., Ward, M. P., Bolus, R. T., Diehl, R. H., Celis-Murillo, A., Zenzal, T. J., Jr.,
611 Moore, F. R., Benson, T. J., Smolinsky, J. A., Schofield, L. N., Enstrom, D. A., Paxton,
612 E. H., Bohrer, G., Beveroth, T. A., Raim, A., Obringer, R. L., Delaney, D., & Cochran, W.
613 W. (2015). Fat, weather, and date affect migratory songbirds' departure decisions,

614 routes, and time it takes to cross the Gulf of Mexico. *Proceedings of the National*
615 *Academy of Sciences*, 112, E6331-E6338.

616 Dossman, B. C., Mitchell, G. W., Norris, D. R., Taylor, P. D., Gugliemo, C. G.,
617 Matthews, S. N., & Rodewald, P. G. (2016). The effects of wind and fuel stores on
618 stopover departure behavior across a migratory barrier. *Behavioral Ecology*, 27, 567-
619 574.

620 Drake, A., Rock, C. A., Quinlan, S. P., Martin, M., & Green, D. J. (2014). Wind speed
621 during migration influences the survival, timing of breeding, and productivity of a
622 Neotropical migrant, *Setophaga petechia*. *PLoS ONE*, 9, e97152.

623 Feinsinger, P. (1978). Ecological interactions between plants and hummingbirds in a
624 successional tropical community. *Ecological Monographs*, 48, 269-287.

625 Fisher, N. I. (1993). *Statistical analysis of circular data*. Cambridge: Cambridge
626 University Press.

627 Galetto, L., & Bernardello, G. (2004). Floral nectaries, nectar production dynamics, and
628 chemical composition in six *Ipomoea* species (Convolvilaceae) in relation to pollinators.
629 *Annals of Botany*, 94, 269-280.

630 Gill, R. E., Jr., Piersma, T., Hufford, G., Servranckx, R., & Riegen, A. (2005). Crossing
631 the ultimate ecological barrier: Evidence for an 11000-km-long nonstop flight from
632 Alaska to New Zealand and Eastern Australia by bar-tailed godwits. *The Condor*, 107,
633 1-20.

634 Gwinner, E., & Wiltschko, W. (1978). Endogenously controlled changes in migratory
635 direction of the garden warbler, *Sylvia borin*. *Journal of Comparative Physiology A:*
636 *Neuroethology, Sensory, Neural, and Behavioral Physiology*, 125, 267-273.

637 Hall, G. A., & Bell, R. K. (1981). The diurnal migration of passerines along an
638 Appalachian ridge. *American Birds*, 35, 135-138.

639 Helbig, A. J. (1991). Inheritance of migratory direction in a bird species: A cross-
640 breeding experiment with SE- and SW-migrating blackcaps (*Sylvia atricapilla*).
641 *Behavioral Ecology and Sociobiology*, 28, 9-12.

642 Helms, C. W., & Drury, W. H. (1960). Winter and migratory weight and fat field study on
643 some North American bunting. *Bird-banding*, 31, 1-40.

644 Hou, L., & Welch, K. C., Jr. (2016). Premigratory ruby-throated hummingbirds,
645 *Archilochus colubris*, exhibit multiple strategies for fueling migration. *Animal Behaviour*,
646 121, 87-99.

647 Hutto, R. L. (2000). On the importance of en route periods to the conservation of
648 migratory landbirds. *Studies in Avian Biology*, 20, 109-114.

649 Kerlinger, P., & Moore, F. R. (1989). Atmospheric structure and avian migration. In D.
650 M. Power (Ed.), *Current Ornithology* 6 (pp. 109-142). New York: Plenum Press.

651 Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal*
652 *Ecology*, 68, 940-950.

653 Kranstauber, B., Weinzierl, R., Wikelski, M., & Safi, K. (2015). Global aerial flyways
654 allow efficient travelling. *Ecology Letters*, 18, 1338-1345.

655 Lara, C. (2006). Temporal dynamics of flower use by hummingbirds in a highland
656 temperate forest in Mexico. *Ecoscience*, 13, 23-29.

657 Lasiewski, R. C. (1962). The energetics of migrating hummingbirds. *The Condor*, 64,
658 324.

659 Liechti, F., & Bruderer, B. (1998). The relevance of wind for optimal migration theory.
660 *Journal of Avian Biology*, 29, 561-568.

661 Lindström, Å., Gill, R. E., Jr., Jamieson, S. E., McCaffery, B., Wennerberg, L., Wikelski,
662 M., & Klaassen, M. (2011). A puzzling migratory detour: are fueling conditions in Alaska
663 driving the movement of juvenile Sharp-tailed Sandpipers? *The Condor*, 113, 129-139.

664 Lindström, Å., Hasselquist, D., Bensch, S., & Grahn, M. (1990). Asymmetric contests
665 over resources for survival and migration: A field experiment with bluethroats. *Animal*
666 *Behaviour*, 40, 453-461.

667 Lund, U., & Agostinelli, C. (2012). S-plus original by Ulric Lund and R port by Claudio
668 Agostinelli. CircStats: Circular Statistics, from "Topics in circular Statistics" (2001). R
669 package version 0.2-4. <http://CRAN.R-project.org/package=CircStats>

670 Marschall, E. A., Mather, M. E., Parrish, D. L., Allison, G. W., & McMenemy, J. R.
671 (2011). Migration delays caused by anthropogenic barriers: modeling dams,
672 temperature, and success of migrating salmon smolts. *Ecological Applications*, 21,
673 3014-3031.

674 Mazerolle, M. J. (2015). AICcmodavg: Model selection and multimodel inference based
675 on (Q)AIC(c), R package version 2.0-3

676 McKinnon, E. A., Fraser, K. C., Stanley, C. Q., & Stutchbury, B. J. M. (2014). Tracking
677 from the tropics reveals behavior of juvenile songbirds on their first spring migration.
678 *PLoS ONE*, 9, e105605.

679 Miller, R. S., & Gass, C. L. (1985). Survivorship in hummingbirds: Is predation
680 important? *The Auk*, 102, 175-178.

681 Mills, A. M., Thurber, B. G., Mackenzie, S. A., & Taylor, P. D. (2011). Passerines use
682 nocturnal flights for landscape-scale movements during migration stopover. *The*
683 *Condor*, 113, 597-607.

684 Moore, F. R. (1984). Age-dependent variability in the migratory orientation of the
685 savannah sparrow (*Passerculus sandwichensis*). *The Auk*, 101, 875-880.

686 Moore, F. R., Mabey, S., & Woodrey, M. (2003). Priority access to food in migratory
687 birds: age, sex and motivational asymmetries. In P. Berthold, E. Gwinner, & E.
688 Sonnenschein (Eds.), *Avian Migration* (pp. 281-292). Berlin: Springer Verlag.

689 Mueller, H. C., & Berger, D. D. (1967). Wind drift, leading lines, and diurnal migration.
690 *Wilson Bulletin*, 79, 50-63.

691 Müller, F., Taylor, P. D., Sjöberg, S., Muheim, R., Tsvery, A., Mackenzie, S. A., &
692 Schmaljohann, H. (2016). Towards a conceptual framework for explaining variation in
693 nocturnal departure time of songbird migrants. *Movement Ecology*, 4, 24.

694 Németh, Z., & Moore FR (2007). Unfamiliar stopover sites and the value of social
695 information during migration. *Journal of Field Ornithology*, 148, S369-S376.

696 Nilsson, C., & Sjöberg, S. (2015). Causes and characteristics of reverse bird migration:
697 an analysis based on radar, radio tracking, and ringing at Falsterbo, Sweden. *Journal of*
698 *Avian Biology*, 47, 354-362.

699 Norris, D. R., & Marra, P. P. (2007). Seasonal interactions, habitat quality, and
700 population dynamics in migratory birds. *The Condor*, 109, 535-547.

701 Odum, E. P., Connell, C. E., & Stoddard, H. L. (1961). Flight energy and estimated flight
702 ranges of some migratory birds. *The Auk*, 78, 515-527.

703 Osborne, J. (1998). *The Ruby-throated Hummingbird*. Austin: University of Texas Press.

704 Pennycuick, C. J. (2008). *Modelling the flying bird*. Boston: Academic Press.

705 Pewsey, A., Neuhäuser, M., & Ruxton, G. D. (2013). *Circular Statistics in R*. Oxford:
706 Oxford University Press.

707 Pyle, P. (1997). *Identification Guide to North American Birds, Part 1*. Bolinas: Slate
708 Creek Press.

709 R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna:
710 R Foundation for Statistical Computing.

711 Raim, A. (1978). A radio transmitter attachment for small passerine birds. *Bird-banding*,
712 49, 326-332.

713 Ralph, C. J. (1971). An age differential of migrants in coastal California. *The Condor*,
714 73, 243-246.

715 Ralph, C. J. (1978). Disorientation and possible fate of young passerine coastal
716 migrants. *Bird-banding*, 49, 237-247.

717 Ralph, C. J. (1981). Age ratios and their possible use in determining autumn routes of
718 passerine migrants. *Wilson Bulletin*, 93, 164-188.

719 Ravi, S., Crall, J. D., McNeilly, L., Gagliardi, S. F., Biewener, A. A., & Combes, S. A.
720 (2015). Hummingbird flight stability and control in freestream turbulent winds. *Journal of*
721 *Experimental Biology*, 218, 1444-1452.

722 Richardson, W. J. (1978). Timing and amount of bird migration in relation to weather: A
723 review. *Oikos*, 30, 224-272.

724 Richardson, W. J. (1990). Timing of bird migration in relation to weather: Updated
725 review. In E. Gwinner (Ed.), *Bird Migration: Physiology and Ecophysiology* (pp. 78-101).
726 Berlin: Springer.

727 Rittenhouse, T. A. G., & Semlitsch, R. D. (2006). Grasslands as movement barriers for a
728 forest-associated salamander: Migration behavior of adult and juvenile salamanders at
729 a distinct habitat edge. *Biological Conservation*, 131, 14-22.

730 Sandberg, R., & Moore, F. R. (1996). Migratory orientation of Red-eyed Vireos, *Vireo*
731 *olivaceus*, in relation to energetic condition and ecological context. *Behavioral Ecology*
732 *and Sociobiology*, 39, 1-10.

733 Sargent, R. R. (1999). *Ruby-throated hummingbird*. Mechanicsburg: Stackpole Books.

734 Schaub, M., Liechti, F., & Jenni, L. (2004). Departure of migrating European robins,
735 *Erithacus rubecula*, from a stopover site in relation to wind and rain. *Animal Behaviour*,
736 67, 229-237.

737 Schmaljohann, H., & Naef-Daenzer, B. (2011). Body condition and wind support initiate
738 the shift of migratory direction and timing of nocturnal departure in a songbird. *Journal*
739 *of Animal Ecology*, 80, 1115-1122.

740 Sjöberg, S., Alerstam, T., Åkesson, S., Schulz, A., Weidauer, A., Coppack, & T.,
741 Muheim, R. (2015). Weather and fuel reserves determine departure and flight decisions
742 in passerines migrating across the Baltic Sea. *Animal Behaviour*, 104, 56-68.

743 Smith, R. J., & Moore, F. R. (2003). Arrival fat and reproductive performance in a long-
744 distance passerine migrant. *Oecologia*, 134, 325-331.

745 Smolinsky, J. A., Diehl, R. H., Radzio, T. A., Delaney, D. K., & Moore, F. R. (2013).
746 Factors influencing the movement biology of migrant songbirds confronted with an
747 ecological barrier. *Behavioral Ecology and Sociobiology* 67, 2041-2051.

748 Stiles, F. G., Altshuler, D. L., & Dudley, R. (2005). Wing morphology and flight behavior
749 of some North American hummingbird species. *The Auk*, 122, 872-886.

750 Strandberg, R., & Alerstam, T. (2007). The strategy of fly-and-forage migration,
751 illustrated for the osprey (*Pandion haliaetus*). *Behavioral Ecology and Sociobiology*, 61,
752 1865-1875.

753 Šuba, J., Petersons, G., & Rydell, J. (2012). Fly-and-forage strategy in the bat
754 *Pipistrellus nathusii* during autumn migration. *Acta Chiropterologica*, 14, 379-385.

755 Sullivan, B. L., Wood, C. L., Iliff, M. J., Bonney, R. E., Fink, D., & Kelling, S. (2009).
756 eBird: a citizen-based bird observation network in the biological sciences. *Biological*
757 *Conservation*, 142, 2282-2292.

758 Taylor, P. D., Mackenzie, S. A., Thurber, B. G., Calvert, A. M., Mills, A. M., McGuire, L.
759 P., & Guglielmo, C. G. (2011). Landscape movements of migratory birds and bats
760 reveal an expanded scale of stopover. *PLOS One*, 6, e27054.

761 Thorup, K., Alerstam, T., Hake, M., & Kjellén, N. (2003). Bird orientation: Compensation
762 for wind drift in migrating raptors is age dependent. *Proceedings of the Royal Society B:*
763 *Biological Sciences*, 270, S8-S11.

764 Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S*. (4th ed.) New
765 York: Springer.

766 Ward, M. P., & Raim, A. (2011). The fly-and-social foraging hypothesis for diurnal
767 migration: Why American crows migrate during the day. *Behavioral Ecology and*
768 *Sociobiology*, 65, 1411-1418.

769 Weidensaul, S. T., Robinson, T. R., Sargent, R. R., & Sargent, M. B. (2013). Ruby-
770 throated hummingbird (*Archilochus colubris*). In A. Poole, & F. B. Gill (Eds.), *The Birds*
771 *of North America*. Ithaca: Cornell Laboratory of Ornithology.

772 Woodrey, M. S. (2000). Age-dependent aspects of stopover biology of passerine
773 migrants. *Studies in Avian Biology*, 20, 43-52.

774 Woodrey, M. S., & Moore, F. R. (1997). Age-related differences in the stopover of fall
775 landbird migrants on the coast of Alabama. *The Auk*, 114, 695–707.

776 Zenzal, T. J., Jr. (2016). *Stopover ecology of ruby-throated hummingbirds (Archilochus*
777 *colubris) during autumn migration* (Doctoral dissertation). Hattiesburg, MS: University of
778 Southern Mississippi.

779 Zenzal, T. J., Jr., & Moore, F. R. (2016). Stopover biology of ruby-throated
780 hummingbirds (*Archilochus colubris*) during autumn migration. *The Auk: Ornithological*
781 *Advances*, 133, 237-250.

782 Zenzal, T. J., Jr., Diehl, R. H., & Moore, F. R. (2014). The impact of radio-tags on ruby-
783 throated hummingbirds (*Archilochus colubris*). *The Condor: Ornithological Applications*,
784 116, 518-526.

785 Zenzal, T. J., Jr., Fish, A. C., Jones, T. M., Ospina, E. A., & Moore, F. R. (2013).
786 Observations of mortality and anti-predator behavior of Ruby-throated Hummingbirds
787 (*Archilocus colubris*) during migratory stopover. *Southeastern Naturalist*, 12, N21-N25.
788