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Running head: Geographic convergence during stopover

Range-wide populations of a long-distance migratory songbird converge during stopover in the tropics

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9   **Abstract.**

10 Geographic convergence during migration influences the extent to which animal populations

11 may experience carry-over effects across periods of the annual cycle. When most individuals of a

12 population share geographic areas during a given period, carry-over effects are likely stronger

13 than when individuals occupy multiple areas. We used genetic data and stable isotope (δ^2H)

14 measurements from feathers and claws to describe the likely breeding and wintering geographic

15 origins of a long-distance migratory songbird (Gray-cheeked Thrush, *Catharus minimus*) moving

16 through northern Colombia in spring and fall migration. Furthermore, we used these data

17 coupled with regional occupancy surveys to assess whether individuals from various breeding

18 populations converge during migration, and evaluated whether geographic origin, age, or sex

19 affected stopover strategies. We found that range-wide breeding populations of Gray-cheeked

20 Thrush converged in northern Colombia in an area spanning less than 1% of the breeding range,

21 especially during a prolonged spring stopover in the Sierra Nevada de Santa Marta. Breeding

22 (but not winter) origin, sex, and age, influenced arrival date and body condition upon arrival at

23 stopover sites where populations converged. Birds from more northerly breeding latitudes, males

24 and adults generally arrived earlier and in lower body condition than those with more southerly

25 breeding origins, females and juveniles. Our work and other studies suggest that areas in

26 northern Colombia may function as ecological bottlenecks for Gray-cheeked Thrush because

27 they concentrate individuals from across the breeding range, provide critical resources, and

28 impose constraints during migration. Future studies quantifying the effects of high-convergence

29 areas on fitness and survival of individuals and their demographic consequences are required to

30 assess their roles as ecological bottlenecks.

31 *Key words.-* Bottleneck*, Catharus minimus,* Colombia, deuterium, migratory connectivity, ND2,

32 occupancy, South America, stable isotopes.

33

Migratory animals show high geographic convergence when large proportions of populations

concentrate in the same area during periods of their annual cycle (Iwamura et al. 2013). For

example, geographical constraints may result in large numbers of individuals travelling through

and stopping over in certain regions (e.g. small or narrow land masses, low mountain passes), or

spatial variation in resource availability may force animals to concentrate in a few high-quality

areas to fuel (Buehler and Piersma 2008, Bayly et al. 2017, Cohen et al. 2017). Within these

restricted areas, which may be obligatory stopovers, there may be access to high-quality

resources or safe flyways, but there may also be heightened competition, predation risk, or

exposure to diseases (Buehler and Piersma 2008, Bauer et al. 2016). Therefore, opportunities and

constraints at high-convergence areas may enhance positive or negative carry-over effects,

significantly influencing individual fitness and population dynamics (Webster and Marra 2005,

Boulet and Norris 2006, Betini et al. 2015, Cohen et al. 2018)

In areas of high geographic convergence, spatial constraints may act simultaneously with

temporal constraints. For instance, during spring migration, animals experience strong time

constraints if they are to reach their breeding grounds on time to obtain the best territories and

mates (Velmala et al. 2015). Yet, migrants must also invest sufficient time accumulating fuel at

stopovers to safely reach their next destination (Hedenström and Alerstam 1997), not become so

heavy that mass hinders their ability to avoid predators (Pomeroy 2006), and not arrive too early

so as to risk starvation in potentially barren breeding areas (Piersma 2002, Alerstam 2011).

Furthermore, because constraints may change over time in relation to food availability or

climate, the timing of passage through a convergence area could be limiting for some

populations but not for others depending on their migratory strategy (Bauer et al. 2016). Any

change disrupting the delicate equilibrium of adaptations involved in migration (e.g. protection

or degradation of a high-convergence area imposing multiple selection pressures on individuals)

could therefore result in a significant boost or toll on survival through carry-over effects on

arrival time to breeding grounds and breeding success (Buehler and Piersma 2008, Iwamura et al.

2013, Piersma et al. 2016, Studds et al. 2017). Determining whether species show high

geographic convergence in their annual cycle is thus an essential first step to identify potential

63 ecological bottlenecks for populations, and is central to understanding the ecology and guiding

64 the conservation of migratory species.

65

66 In birds, high convergence during migration is common among shorebirds (Rogers et al.

67 2010, Iwamura et al. 2013, Piersma et al. 2016, Studds et al. 2017) and waterfowl (Drent et al.

68 2007, Hübner et al. 2010), with major consequences for population dynamics via carry-over

69 effects (Rogers et al. 2010, Iwamura et al. 2013, Piersma et al. 2016, Studds et al. 2017). For

70 most songbirds, however, we lack information about the range-wide connectivity of populations

71 (Faaborg et al. 2010, Cresswell 2014, O'Connor et al. 2014) and thus we know little about the

72 extent to which periods of the annual cycle may represent bottlenecks resulting from high

73 convergence in particular areas (Rodenhouse et al. 2003, Leyrer et al. 2013, Rockwell et al.

74 2016, Bayly et al. 2017). Not only do we lack knowledge about geographic convergence, but

75 also about the constraints that individuals face in areas of high convergence when they exist.

76

77 Because the distance to be travelled and the time spent fueling largely determine the

78 duration of migration in birds (Alerstam and Lindström 1990, Cohen et al. 2014, Schmaljohann

79 and Eikenaar 2017), stopover behavior is intricately related to migratory ecology (Alerstam et al.

80 2003, Alerstam 2011). Depending on total migration distance, the quality and availability of

81 food, and the energy required to complete migratory flights, birds may attempt either long

82 stopovers and extensive fueling followed by long flights, or short stopovers with minimal fuel

83 replenishment followed by shorter flights (Tsipoura and Burger 1999, Buler et al. 2007,

84 Seewagen et al. 2013). Therefore, individuals from different populations may show different

85 stopover strategies when they converge in particular areas depending on breeding origin or

86 wintering destination (Paxton and Moore 2017). Such differences may be temporal, if individuals

87 from certain populations arrive or leave the stopover before others (Warnock et al. 2004, Bauer

88 et al. 2016). Alternatively, differences in stopover strategy may have a physiological basis, such

89 that individuals from different populations differ in body condition on arrival and in their

90 subsequent fueling behavior (how fast and for how long they gain fuel during stopover) due to

91 conditions experienced on their breeding or wintering grounds (Battley et al. 2012, Paxton and

92 Moore 2017).

93

94   Fuel load on arrival (i.e. the stored energy possessed by birds on arrival at a stopover site)

95   also likely influences the stopover strategy that individuals adopt (Weber and Houston 1997,

96   Alerstam 2011). For instance, birds with low fuel on arrival have likely made longer flights and

97   will require longer stopovers to prepare for the next leg of their journey (Alerstam 2011).

98   Differences in stopover strategies may also exist between males and females or between adults

99   and immature birds given that individuals of different sex or age may face dissimilar constraints

100   or may use areas differing in quality during migration (Cooper et al. 2009, 2011).

101

102   We used an integrative approach to examine geographic convergence of populations

103   across the annual cycle of the Gray-cheeked Thrush (*Catharus minimus*), a Nearctic-Neotropical

104   long-distance migratory songbird in which at least some populations have declined precipitously.

105   Populations of the western breeding subspecies *C. m. aliciae* appear stable whereas populations

106   of the eastern subspecies *C. m. minimus* have shown recent, drastic declines (Whitaker et al.

107   2015, FitzGerald 2017, FitzGerald et al. 2017). We combined regional estimates of occupancy

108   rates based on field surveys with genetic and stable-isotope (δ^2H) analyses of tissue samples

109   collected at spring and fall stopover sites in northern Colombia to determine the extent of

110   geographic convergence at previously identified stopover sites (Bayly et al. 2013, Gomez et al.

111   2013), and to test the hypothesis that birds may adopt different stopover strategies depending on

112   their breeding origin and wintering destinations. As with other recent studies unraveling

113   connections among populations of migratory species (e.g. Norris et al., 2006; Rushing et al.,

114   2013; Stanley et al., 2014; Hostetler et al., 2015), we used stable isotopes and genes to infer

115   breeding and wintering origins of individuals and then examined potential links between such

116   origins and the stopover behavior of birds.

117   **Methods**

118   *Study system.-* Gray-cheeked Thrush breed in high-latitude taiga and tundra from eastern Siberia

119   to Newfoundland in Canada (Lowther et al. 2001, FitzGerald 2017). Subspecies *C. m. minimus*

120   breeds in Newfoundland and southeastern Labrador and is listed as threatened under the

121   Newfoundland and Labrador Endangered Species Act because of precipitous population declines

122   in recent decades (SSAC 2010, Environment Canada 2014, Whitaker et al. 2015, FitzGerald et

123   al. 2017). In contrast, *C. m. aliciae* breeds from Siberia across North America to central Labrador

124 and is not known to be declining. Gray-cheeked Thrush follow a loop migration, entering South

125 America in the fall mainly via the Isthmus of Panama and the Darién region in the north west,

126 and leaving South America in the spring by crossing the Caribbean Sea from the Sierra Nevada

127 de Santa Marta (Bayly et al. 2013, Gómez et al. 2013, 2014, 2017). Evidence exists for multi-day

128 stopovers in both regions and energy accumulated at spring stopovers in northern Colombia fuels

129 flights in excess of 3000 km (Bayly et al. 2013, Gómez et al. 2017). The winter range of the

130 species is poorly known, but most available records show birds wintering mainly in Amazonia

131 and in the northern Andes (Lowther et al. 2001, eBird 2014, Ungvari-Martin et al. 2016).

132 Furthermore, during 10 years of research along the length of the northern coast of Colombia, we

133 have not had any records of wintering Gray-cheeked Thrush in that region. However, a recent

134 tracking study suggests some individuals from Newfoundland spent the winter in northern

135 Colombia, probably at very low densities (Whitaker et al. *in press*). There is low but significant

136 mitochondrial DNA differentiation between subspecies (Topp et al. 2013, FitzGerald et al.

137 2017), but there is no information regarding potential differences between them in migratory

138 routes, wintering, or stopover areas.

139 *Fieldwork and sample collection. -* We captured several Gray-cheeked Thrush during fall

140 migration (September – October 2014 and 2015, n = 499) in the Darién region near the

141 Colombia-Panama border (Reserva Natural Tacarcuna, 08°39′44″N, 77°21′48″W) and during

142 spring migration (April – May 2015 and 2016, n = 877) in the Sierra Nevada de Santa Marta,

143 northern Colombia (Hacienda La Victoria, 11°7′19.84″N, 74°5′34.14″W). All birds were banded

144 and aged according to plumage characteristics as either adult or immature (Pyle 1997, Johnson et

145 al. 2011). We also measured the wing chord (± 1 mm) and body mass (± 0.1 g) of each

146 individual to assess body condition.

147   We used values of stable-hydrogen isotope analyses (δ^2H) from feathers and claws to

148 infer the breeding and wintering origins of birds migrating through northern Colombia. During

149 spring migration, we clipped the distal ends (~ 1 cm) of the first primary feather (P1) and

150 (~2mm) of both hallux claws from a subset of captured individuals (n = 326). Because P1 is the

151 first feather to be molted by adult Gray-cheeked Thrush during the pre-basic molt after the

152 breeding season (Pyle 1997), it contains the isotopic signature most representative of the

153 breeding grounds in North America (Hobson et al. 2014). Bird claws grow continuously and tips

154 contain the combined isotopic information of the previous 2-4 months pre-capture (Hahn et al.

155 2014); the claw samples from Gray-cheeked Thrush captured during spring migration were

156 therefore expected to contain the isotopic signature of the wintering grounds occupied prior to

157 migration. All isotopic data are available through Dryad (doi:10.5061/dryad.7hk6523).

158   During both migration periods we also collected ~20 µl of blood from the brachial vein of

159 birds and stored samples on filter paper prior to genetic analyses (see below). Because Gray-

160 cheeked Thrush cannot be reliably sexed in the hand outside of the breeding period, blood

161 samples were also used for molecular sex determination (Griffiths et al., 1998; see Appendix S1:

162 Supplementary Methods for details).

163 *Occupancy surveys during spring and fall migration.-* A first step to evaluate whether a region

164 represents a high-convergence area is to determine whether most individuals concentrate in

165 restricted geographic areas or if they are widely spread across the landscape. To examine this, we

166 carried out repeated surveys for Gray-cheeked Thrush across northern Colombia during the

167 spring and fall migrations of 2016. Repeated surveys (>4 per transect) were carried out every 10

168 days during two months in 200 transects, each 100 m long, spread across 17 sites spanning c.700

169 km from east to west (Fig. 1), for a total effort of 400 person/hours. We analyzed survey data in a

170 dynamic occupancy modelling framework (Fiske and Chandler 2011, Guillera-Arroita 2017)

171 allowing us to estimate the probability of occurrence of Gray-cheeked Thrush throughout the

172 region and to examine the influence of variables such as vegetation cover, precipitation and

173 elevation on the detectability and occupancy rate of the species during both migration seasons.

174 Detailed methods of data collection and occupancy modelling are described in Appendix S1.

175 *Linking birds from the breeding range and stopover areas using genetics.-* To infer

176 connectivity of Gray-cheeked Thrush populations, we assessed the genetic similarity of birds

177 captured during migration in northern Colombia with individuals from known breeding

178 populations in North America. We compared sequences of the NADH dehydrogenase subunit 2

179 (ND2) gene obtained for 150 individuals captured at our field sites in Colombia with published

180 sequences from breeding areas in Siberia (n = 3), Alaska (n = 7), Quebec (n = 3), southern

181 Labrador (n = 12), western Labrador (n = 11), and Newfoundland (n = 39; FitzGerald et al. 2017;

182 see Appendix S1: Supplementary Methods and Table S1). Sequences were aligned using

183 Geneious version R7.1 (Kearse et al. 2012) and polymorphisms confirmed from the

184 chromatograms. We used two complementary methods to characterize genetic differences

185 between populations. Haplotype networks and pairwise population comparisons were used to

186 assess variation along the entire ND2 sequence (Bandelt et al. 1999), while presence of private

187 alleles was used to identify variation in unique positions among populations (Kekkonen et al.

188 2011).

189   We used POPART (Leigh and Bryant 2015) to estimate a minimum spanning network

190 depicting relationships among haplotypes (Bandelt et al. 1999). In addition, we used estimates of

191 pairwise population differentiation (φ_{st}) calculated using the Kimura 2P substitution model

192 (identified as the best fit to the data; FitzGerald et al. 2017) with 1000 permutations of the

193 haplotype matrix in Arlequin v. 3.5 (Excoffier et al. 2005), to evaluate similarities between

194 breeding regions (Newfoundland/southern Labrador [subspecies *C. m. minimus*], western

195 Labrador/Quebec [subspecies *C. m. aliciae*], Alaska/Siberia [subspecies *C. m .aliciae*]) and

196 stopover locations (Darién [fall] and Sierra Nevada de Santa Marta [spring]). We evaluated

197 whether the genetic composition of birds captured in Colombia differed by year or migration

198 period by employing a hierarchical analysis of molecular variance (AMOVA) to assess how

199 much genetic variation was attributed to stopover groupings (i.e. spring vs. fall and 2014 vs.

200 2015) from 20,000 permutations of the dataset. We also estimated allelic frequencies, identified

201 parsimony-informative alleles, and calculated the number of geographic regions in the breeding

202 range where alleles occurred. We then examined whether individuals captured in Colombia

203 shared any private alleles (i.e. those found only in 1-2 breeding regions) with birds of known

204 breeding origin. An assumption of this method is that a random sample of individuals from a

205 population will be roughly representative of the frequency of alleles present in that population

206 (Kekkonen et al. 2011). If most members of a population share a private allele, then it should

207 likely be detected even with relatively small sample sizes. Sharing of private alleles between

208 birds captured in Colombia and the breeding range was therefore taken as an indication of

209 linkage between populations (Kekkonen et al. 2011).

210 ***Assigning individuals to breeding and wintering grounds with stable-isotope analysis of***

211 ***feathers and claws.-*** Stable-isotope analyses were carried out at the Stable Isotope Laboratory of

212 Environment and Climate Change Canada, Saskatoon, Canada. Feathers and claws were cleaned

213 of external oils and debris before analysis using a 2:1 chloroform:methanol soak and rinse.

214   Measurements of δ^2H in feather (δ^2H$_f$) and claw (δ^2H$_c$) were obtained through continuous-flow

215   isotope-ratio mass spectrometry (CF-IRMS) following the 'comparative equilibration' method

216   which uses calibrated keratin reference materials to correct for exchangeable hydrogen using the

217   keratin standards CBS (-197 ‰) and KHS (-54 ‰; Wassenaar and Hobson 2003). We report δ^2H

218   values in standard delta (δ) notation, in parts per thousand (‰) relative to Vienna Standard Mean

219   Ocean Water (VSMOW). Based on within-run replicates (n=6) of calibration standards, we

220   estimate analytical error to be of the order of ±2 ‰.

221   Employing data on species abundance in space and potential distribution models as

222   geographic priors may improve geographic assignments based on stable isotopes (Chabot et al.

223   2012, Fournier et al. 2017, Rushing et al. 2017b). For species like the Gray-cheeked Thrush,

224   which breed and winter in remote locations seldom visited by people, there is considerable

225   uncertainty about true distribution ranges and more so about patterns of spatial abundance. We

226   therefore combined tissue δ^2H data with a 'spatiotemporal exploratory model' (STEM; Fink et

227   al., 2010) showing relative abundance of Gray-cheeked Thrush during the breeding period based

228   on field observations and, separately with a season-specific (breeding and winter) species

229   distribution model (SDM) generated from field records and climatic variables (FitzGerald 2017,

230   Fournier et al. 2017). Abundance and probability of occurrence estimated by distribution models

231   are usually correlated and considered good proxies for predicting species presence (Weber et al.

232   2016). We evaluated the similarity between geographic assignments based on STEM and SDM

233   priors by estimating the spatial correlation between them. Methods for the construction of the

234   STEM and SDM models are in the Appendix S1. We also present assignments based only on δ^2H

235   values to assess any biases derived from the priors (Rushing et al. 2017b).

236   ***Surfaces of likely origin based on stable isotopes.-*** Isotopic data were used to derive δ^2H$_f$ and

237   δ^2H$_c$ isoscapes based on δ^2H$_p$ during the growing season (Bowen et al. 2005), and a calibration

238   equation estimated for feathers of ground-foraging Neotropical migrants (Hobson et al. 2012):

239     $\delta^2 H_f = 27.09 + 0.95 \left(\delta^2 H_p\right)$. Prior to modeling, we removed outliers with δ^2H values more

240   than three standard deviations from the mean (feathers = 3, claws = 2; Chabot et al., 2012). Claw

241   δ^2H values are closely correlated with feather values but they require a slightly different

242   conversion factor varying by age (Hobson, *unpubl. data*). Therefore, to generate the claw

243   isoscape we first expressed δ^2H$_c$ values in terms of equivalent expected δ^2H$_f$ values using age-

244 specific claw-to-feather conversion equations derived for *Catharus* thrushes: for immature birds

245 SY: $\delta^2H_f = -15.7 + 0.94\,(\delta^2H_c)$, and for adults ASY: $\delta^2H_f = 24.1 + 1.3\,(\delta^2H_c)$ (Hobson,

246 *unpubl. data*). In addition, we needed to account for the fact that the winter of 2015/2016

247 coincided with one of the strongest El Niño events ever recorded (Jiménez-Muñoz et al. 2016).

248 This event produced anomalous droughts in the Amazon, where Gray-cheeked Thrush are

249 expected to winter, giving rise to δ^2H values enriched by ~16‰ above the long-term average

250 (Srygley et al. 2010, Brienen et al. 2012, Jiménez-Muñoz et al. 2016). To use our data with the

251 available long-term δ^2H$_p$ isoscape for the Amazon region (Bowen et al. 2005) while correcting

252 for the effect of El Niño in 2015, we subtracted 16‰ from our measured δ^2H$_c$ values before

253 undertaking spatial assignments.

254   The probability of each individual originating from any given ~ 1 km^2 cell on the

255 breeding or wintering grounds was estimated based on a normal probability density function:

256 $f(y^*|\mu_i, \sigma) = \frac{1}{\sqrt{2\pi\sigma}} exp\left[-\frac{1}{2\sigma^2}(y^* - \mu_i)^2\right]$, where $f(y^*|\mu_i, \sigma)$ is the likelihood that an individual

257 with feather isotopic values $\delta^2H_f = y^*$ originated from cell i. μ_i is the predicted δ^2H$_f$ value for cell

258 i, and σ is the standard deviation of the δ^2H$_f$ values within a breeding or wintering site, which

259 was set at 10.8‰ (Hobson et al. 2012). Likelihood values were transformed into a probability

260 surface by dividing each likelihood by the total sum of likelihoods (Hobson et al. 2012). A cutoff

261 of the upper 67% of the probability was defined as the likely area of origin for each individual

262 (Hobson et al. 2012, Chabot et al. 2012) and cells with values equal to or above this cutoff were

263 set a probability value of 1 (likely origin), whereas those with lower values were set to 0

264 (unlikely origin). The 67% cutoff provides a good compromise between assignment precision

265 and overestimation error (Hobson et al. 2012, Chabot et al. 2012). Finally, using Bayes rule,

266 $f(b|y) = \frac{f(y|b)f(b)}{\sum_b^B f(y|b)f(b)}$, we estimated the posterior probability $f(b/y)$ that any 1 km^2 cell on the

267 map represented the origin of a bird, given $f(b)$, the prior probability of occurrence based on the

268 abundance (STEM) or the distribution model (SDM), and $f(y/b)$, the likelihood of the δ^2H

269 assignment surface (Chabot et al. 2012, Fournier et al. 2017). We finally overlaid the likely

270 origins of all birds and obtained a cumulative surface for all the individuals in our sample.

271 ***Assessing the influence of breeding and wintering origins on stopover strategies.-*** To evaluate

272 whether stopover strategies of Gray-cheeked Thrushes were related to breeding or wintering

273   origin, we examined how fuel load on arrival to the stopover site varied as a function of date of

274   arrival, breeding or winter origin isotopic values (δ^2H_f and δ^2H_c), age, and sex. We estimated

275   fuel load on arrival as the mass (g) above lean body mass (LBM) of each individual on its first

276   capture: $Fuel\ load\ on\ arrival = Mass\ on\ first\ capture - LBM$. Lean body mass was

277   estimated by regressing wing chords and body masses of all captured individuals with a fat score

278   of 0 (n = 135), which resulted in the equation $LBM = 0.33 \times wing\ length - 4.63$ (Gómez et

279   al. 2017). We used AIC values (Burnham and Anderson 2002) to evaluate 15 candidate models

280   plus a null model in which none of the independent variables influenced fuel load on arrival

281   (Table 1). To evaluate whether observed differences in breeding and wintering origin between

282   age and sex classes were significant, we carried out randomization tests, where the observed

283   difference in means between each group (males vs. females or adults vs. immatures) was

284   compared to a random distribution of 999 differences of equivalent datasets selected regardless

285   of age or sex.

286   **Results**

287   ***Occupancy rates during spring and fall migration.-*** Occupancy surveys resulted in 159 and 264

288   presence records of Gray-cheeked Thrush during fall and spring migration, respectively, across

289   the 17 sites sampled along the Caribbean coast of Colombia. Spatial predictions of occupancy

290   rates of Gray-cheeked Thrush during spring and fall migration revealed marked concentrations of

291   individuals in the Darién region during fall (sum of area of grid cells with occupancy ≥ 0.5 =

292   80,045 km^2, Fig. 1A) and on the northern and western slopes of the Sierra Nevada de Santa

293   Marta in spring (12,963 km^2, Fig. 1B), with intermediate areas showing very low probabilities of

294   occupancy. These two areas span only 5% and 0.8%, respectively, of areas occupied by Gray-

295   cheeked Thrush during the breeding season (1,587,463 km^2, according to our isotopic

296   assignments). During fall migration, occupancy increased towards the west, in areas with low-

297   mid elevations, high canopy cover and a dense understory (Appendix S1: Table S2A). During

298   spring, occupancy was predicted to be highest in regions where intermediate levels of annual

299   precipitation coincided with elevations below < 1700 m in northernmost Colombia, which

300   largely correspond to the mountain slopes of the Sierra Nevada de Santa Marta (Appendix S1:

301   Table S2B).

302   *Linking birds from the breeding range and stopover areas using genetics.-*We found no

303   significant difference in the genetic composition of birds captured in Colombia between years

304   (φ_{st} = 0.010, P = 0.073), with most of the genetic variation (96.6%) found within years (P =

305   0.667). Very low but significant differentiation was found between migration seasons (i.e. fall vs.

306   spring φ_{st} = 0.047, P < 0.001), yet most of the variation (94.8%) existed within seasons (P =

307   0.330). ND2 φ_{st} pairwise population comparisons showed that most fall and spring birds in

308   Colombia were more genetically similar to individuals from subspecies *C. m. aliciae* (breeding

309   in Alaska/Siberia) than to *C. m. minimus* (Newfoundland/ S Labrador; Table 2). However, birds

310   captured in Colombia shared at least some haplotypes with birds from throughout the breeding

311   range (Fig. 2A). All Alaska haplotypes and most haplotypes from western Labrador and Quebec

312   were found in Colombia. Conversely, fewer of Newfoundland/S Labrador haplotypes were found

313   in Colombia. A large number of haplotypes found in birds captured in Colombia were not

314   observed in any of the birds of known breeding origin (Fig. 2A), likely reflecting a lack of

315   sampling in north-central Canada and low sample sizes in some of the other breeding areas.

316   However, of those haplotypes shared among birds from Colombia and the breeding grounds,

317   there were 24 informative sites and 14 of these corresponded to private alleles restricted to

318   individuals from only one or two of the sampled breeding populations. Furthermore, 119 out of

319   150 individuals from Colombia had alleles private to birds from all 6 breeding regions; out of

320   these, 8 individuals had alleles private to breeding sites in Newfoundland and southern Labrador

321   (Fig. 2B). Overall, this suggests that although most birds sampled in Colombia were more

322   genetically similar to birds from the western subspecies *C. m. aliciae*, individuals from most

323   breeding regions and both subspecies likely converged in Colombia.

324   *Geographic assignment through stable isotopes and geographic priors.-* In agreement with the

325   genetic data, geographic assignments based on δ^2H values and distribution and abundance

326   models suggested that Gray-cheeked Thrush migrating through northern Colombia likely

327   originated from multiple breeding populations (Fig. 3). Geographic assignment of breeding

328   origin using the STEM model as a prior showed a 60% correlation with that based on the species

329   distribution model (SDM), suggesting relatively close agreement between predictions

330   considering geographic variation in abundance and habitat suitability (Weber et al. 2016). The

331   two models predicted high numbers of individuals originating from Alaska and north-central

332   Canada, but the STEM model did not predict as many as the SDM from the eastern extreme of

333   the breeding range. Given the agreement between models, we present only the assignments based

334   on the SDM because they were available for both the breeding and the winter periods.

335   Geographic assignments to breeding areas based solely on isotopes predicted a high probability

336   of origin from three main regions: (1) Alaska, (2) an area bordering Hudson Bay in the provinces

337   of Nunavut and Manitoba, and (3) northern Quebec and Labrador (Appendix S1: Fig. S1).

338   Similarly, isotopic analyses predicted individuals originating from a wide range of

339   wintering locations mostly concentrated in northern Amazonia including portions of Ecuador,

340   Peru, Colombia, Venezuela, and Brazil. A smaller proportion of birds were also predicted to

341   have wintered at mid-elevations in the Andes of Colombia (Fig. 3).

342   ***Effect of date, age, sex and geographic origin, on stopover strategies.-*** We found no spatial

343   differences in the inferred breeding or winter origin between adult and immature birds stopping

344   over in northern Colombia (97% and 100% Pearson correlation of breeding and winter surfaces,

345   respectively). However, adults had significantly higher δ^2H_f values compared to immature birds

346   (Appendix S1: Fig. S2, P = 0.02), suggesting a slightly more southerly breeding/molting origin

347   compared to immature birds. Adults also showed slightly lower values of δ^2H_c than immature

348   birds (Appendix S1: Fig. S2, P = 0.03). There were no obvious differences in breeding or

349   wintering origin between sexes (97% and 98% Pearson correlation of breeding and wintering

350   surfaces, respectively) although females showed slightly higher values of δ^2H_f than males

351   (Appendix S1: Fig. S3, P = 0.06), and both sexes showed equivalent winter ranges and values of

352   δ^2H_c (Appendix S1: Fig. S3, P = 0.12).

353   Date of arrival at the spring stopover site in Colombia varied as a function of breeding

354   but not winter origin (Fig. 4A-B. $\beta_{breeding}$ = 0.16 ± 0.03, P <0.001; β_{winter} = -0.05 ± 0.04, P =

355   0.22), with birds that bred at more northerly latitudes arriving ~10 days earlier on average.

356   Additionally, males arrived in Colombia significantly earlier than females (~5-10 days), during

357   both spring (Fig. 4C, P = 0.001) and fall migration (Fig. 4D, P = 0.01); similarly, adults arrived

358   in northern Colombia significantly earlier than immature birds during both migration periods

359   (Figs 4E-F, Spring: P = 0.003; Fall: P < 0.001).

360   Two candidate models explained 84% of the variation in fuel load on arrival at the spring

361   stopover site. Contributing variables included date of arrival, breeding origin, sex, and an

362   interaction between sex and breeding origin (Table 1). Both males and females arriving earlier

363 did so in lower body condition than birds arriving later in the season (Fig 5A, $\beta_{male} = 0.26 \pm 0.02$,

364 $P < 0.001$; $\beta_{female} = 0.21 \pm 0.03$, $P < 0.001$). In addition, males with lower δ^2H_f values (i.e. those

365 with more northerly breeding origin) arrived earlier and in lower body condition than those from

366 more southerly origins (Fig 5B, $\beta_{males} = 0.09 \pm 0.04$, $P = 0.02$). This association between

367 breeding origin on fuel loads was not significant for females (Fig 4B, $\beta_{females} = -0.03 \pm 0.06$, $P =$

368 0.56) and, if anything, showed the opposite tendency than that observed in males.

369 **Discussion**

370 Our occupancy surveys, genetic comparisons, and stable-isotope analyses suggest that Gray-

371 cheeked Thrush from across the breeding and wintering range funnel through two regions of

372 northern Colombia during migration: the Darién in the fall and the Sierra Nevada de Santa Marta

373 in the spring. Geographic convergence is particularly strong in spring, when individuals from

374 most of the breeding range appear to stopover exclusively in the Sierra Nevada de Santa Marta

375 prior to undertaking non-stop flights (>2500 km) across the Caribbean Sea and Gulf of Mexico

376 (Fig. 1; Bayly et al. 2013, Gómez et al. 2017). Regions occupied in northern Colombia during

377 fall and spring had areas equivalent to only 5% and 0.8%, respectively, of the area used during

378 the breeding season, highlighting the extreme degree of convergence.

379

380   Based on the above results, we hypothesize that the high-convergence area in the Sierra

381 Nevada de Santa Marta likely functions as an ecological bottleneck for populations of the Gray-

382 cheeked Thrush. Given that fat gained in the region may fuel 40% of total migration distance

383 covered by Gray-cheeked Thrush (Bayly et al. 2013) and that events at this spring stopover site

384 carry-over to influence the pace of migration and potentially breeding success (Gómez et al.

385 2017), it is likely that there are fitness and survival consequences associated to a successful

386 spring stopover in northern Colombia (Bayly et al. 2012, 2013, Gómez et al. 2017). Future

387 research should verify whether this is the case for Gray-cheeked Thrushes as well as other

388 migratory species.

389

390   Because our work and other studies (e.g. González-Prieto et al., 2011; Fraser et al., 2013)

391 suggest that stopover regions where range-wide populations converge have the potential to

392   function as ecological bottlenecks, a priority for the conservation of populations of migrants

393   worldwide would be to identify and protect such areas. Most studies on migratory connectivity to

394   date have addressed connections between the breeding and wintering grounds (e.g. Rushing et

395   al., 2013; Hobson et al., 2014; Fraser et al., 2017), and a recent meta-analysis suggested that low

396   migratory connectivity between breeding and wintering populations is common among long-

397   distance migrants (Finch et al. 2017). Fewer studies have examined connectivity during

398   migration (e.g. Hübner et al., 2010; Laughlin et al., 2013; Andueza et al., 2014; Stanley et al.,

399   2014), but these studies consistently found high convergence of populations, particularly at

400   stopover sites before barriers or at obligatory flyways within narrow land masses (Buehler and

401   Piersma 2008, Fort et al. 2009, Piersma et al. 2016). Furthermore, for a few songbird species,

402   mortality rates are known to be higher during migration than any other phase of the annual cycle

403   (Sillett and Holmes 2002, Rockwell et al. 2016, Paxton et al. 2017, Rushing et al. 2017a). This,

404   combined with the recent finding that multi-day stopovers occur in just a few key regions in

405   many species (Bonter et al. 2009, Stanley et al. 2014), means that migration is probably the most

406   vulnerable period in the annual cycle across a range of taxa (Faaborg et al. 2010). Therefore,

407   more research effort should be directed to identify convergence areas during migration and

408   assess their demographic effects on the populations of migrants worldwide.

409

410   A question arising from our study is whether differences in population declines between

411   *C. m. aliciae* and the endangered *C. m. minimus* may be connected with events taking place in

412   the high-convergence area we identified. Given that most variation in $\delta^2 H_f$ values in the Northern

413   Hemisphere is described by latitude, breeding origin isotopic assignments based on hydrogen

414   have low longitudinal precision (Hobson et al. 2012). It is therefore difficult to discriminate with

415   certainty individuals originating from eastern and western populations in northern North

416   America based solely on $\delta^2 H_f$ values (Appendix S1: Fig. S2, but see Cárdenas-Ortiz et al., 2017).

417   However, by combining isotopic assignments with genetic information, we confirmed that birds

418   captured in northern Colombia have likely origins from across the breeding range of the Gray-

419   cheeked Thrush, with most individuals probably belonging to populations of *C. m. aliciae*. The

420   apparently lower proportion of *C. m. minimus* in our samples may reflect either a differential

421   migratory strategy between subspecies, that the range of *C. m. minimus* is smaller, or that there

422   are fewer *C. m. minimus* due to population declines (Whitaker et al. 2015, FitzGerald et al.

423   2017). Spatial or temporal differences in migratory strategy between populations may determine

424   whether a high-convergence site is also a bottleneck for some or all populations (Iwamura et al.

425   2013, Bauer et al. 2016). Tracking of individuals from different subspecies and using genomics

426   to more finely characterize population structure and hence map geographic origins with greater

427   resolution, are promising avenues of research to start testing these hypotheses.

428   Differences in population dynamics may not be related to events occurring on migration

429   but instead depend more on conditions experienced during the winter (Wilson et al. 2011, 2018,

430   Rockwell et al. 2016). We found that breeding but not winter (isotopic) origin influenced the

431   spring migratory strategies of individuals: birds that bred further north migrated earlier and

432   arrived at the spring stopover site in poorer body condition than those from more southern

433   breeding origins. This may reflect chain migration, a pattern where migration occurs in a

434   latitudinal sequence between populations (Lundberg and Alerstam 1986, Kelly 2006, González-

435   Prieto et al. 2011). However, because the isotopic uniformity of Amazonia limits the resolution

436   with which latitudinal patterns can be detected in that region (Bowen et al. 2005), we could not

437   determine whether northern breeding populations indeed winter in more northerly regions.

438   Although our results did not show an effect of winter origin, we cannot rule out that it exists.

439   Other studies have consistently shown that winter habitat use has significant carry-over effects

440   on breeding success by affecting behavior during migration and date of arrival to the breeding

441   grounds (Marra and Holmes 2001, Norris et al. 2004, Norris and Marra 2007, McKinnon et al.

442   2015). Furthermore, given that we only made inferences of likely geographic origin and not of

443   variation in winter habitat quality, we cannot rule out that winter habitat may affect individual

444   performance during stopover in Gray-cheeked Thrush.

445

446   We also documented differences in migration timing between age classes, with adult

447   thrushes migrating earlier than immatures during both fall and spring. Moreover, adults had less

448   negative breeding ground values of $\delta^2 H_f$ than immature birds, suggesting that age classes have

449   either different hydrogen isotope precipitation-to-feather discrimination factors (Hobson and

450   Clark 1992, Rushing et al. 2013) or that Gray-cheeked Thrush exhibit a molt-migration whereby

451   adults disperse from their breeding sites prior to molting – a pattern primarily known for

452   migratory birds from western North America (Rohwer et al. 2005). Differences between age

453   classes in migration phenology have been linked to individual experience because adults may

454   navigate more accurately (Mitchell et al. 2015), fuel up faster (Yong and Moore 1994), make

455   fewer stopovers along the way, or take riskier routes (McKinnon et al. 2014, Dossman et al.

456   2016) than first-year birds. Alternatively, first-year birds may migrate more slowly because they

457   do not benefit from early arrival to the breeding grounds to the same extent as adults (Stewart et

458   al. 2002, Cooper et al. 2009). Even if young birds arrive early they are likely to be outcompeted

459   by adults and still face the perils of variable climatic conditions and increased risk from agonistic

460   interactions with adults early in the season (Cooper et al. 2009). A recent study on Gray-cheeked

461   Thrush found no effect of age on fueling rates (Gómez et al. 2017), but more study is needed to

462   evaluate age differences in navigation skills or route use in this species.

463   We found differences in migration phenology between sexes, with males migrating

464   earlier than females in the spring. Such differences in other species have been attributed to a

465   stronger selection pressure acting on males to arrive earlier than females to the breeding grounds

466   (Kokko et al. 2006, Cooper et al. 2009, 2011, Coppack and Pulido 2009, Schmaljohann et al.

467   2015), such that males that migrate faster arrive earlier and therefore settle in better territories

468   and get the best mates. The 'mate opportunity hypothesis' posits that early arrival improves the

469   probability of mate acquisition for males more so than for females, given that most females will

470   breed regardless of arrival date, whereas late-arriving males will likely fail to breed in a given

471   year (Kokko et al. 2006, Cooper et al. 2009, 2011). More study is needed to evaluate sex ratios of

472   Gray-cheeked Thrush on the breeding grounds as well as the strength of sexual selection to see

473   whether this hypothesis is a plausible explanation for our observations. Segregation of sexes by

474   latitude on the winter grounds may also contribute to protandry, when males winter closer to the

475   breeding grounds (Woodworth et al. 2016), yet we did not detect any geographical differences in

476   wintering origin between sexes.

477   Overall, our study emphasizes the importance of northern Colombia and particularly of

478   the Sierra Nevada de Santa Marta for Gray-cheeked Thrush during migration given that

479   individuals from throughout the breeding range converge there during a critical period of the

480   annual cycle. Furthermore, we showed how breeding geographic origin, age and sex influence

481   the migratory strategies of individual Gray-cheeked Thrush during stopover. Verifying whether

482   this high geographic convergence area functions as an ecological bottleneck for Gray-cheeked

483   Thrush populations and potentially other species, should be a research priority (Bayly et al. 2014,

484   Gómez et al. 2015). We thus highlight the need to identify and study other high-convergence

485   regions for migratory songbirds and to quantify their impact on fitness and survival. In areas of

486   high geographic convergence the effects of habitat loss or change may be magnified, potentially

487   making a large contribution to the pronounced population declines recorded in many Neotropical

488   migrants (Robbins et al. 1989, Sauer et al. 2013), or indeed, to the reversal of such long term

489   declines in the future.

490

506   **Author's contributions**.- CG, DC and KH conceived the study; CG and NB collected the data;

507   CG, SG, AF and NB analyzed the data; KH provided stable isotope analyses. CG led the writing

508   of the manuscript. All authors contributed critically to the drafts and gave final approval for

509   publication.

510

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Tables.

Table 1. Fuel load on arrival of Gray-cheeked Thrush at a spring stopover site in northern
Colombia varied as a function of date of arrival, breeding origin (δ^2H values of feathers), and
sex. The first two models were equally likely and overall explained 84% of the variation in fuel
on arrival. Models including age did not rank among the top two.

Model	AICc	ΔAICc	wi
Fuel ~ Date + δ^2H feather + δ^2H feather:Sex	**357.57**	**0.00**	**0.54**
Fuel ~ Date + δ^2H feather + Sex	**358.73**	**1.16**	**0.30**
Fuel ~ Date + δ^2H feather + Sex + Age	361.04	3.47	0.09
Fuel ~ Date + δ^2H feather + δ^2H feather:Sex + δ^2H feather:Age	361.70	4.12	0.07
Fuel ~ δ^2H feather + Sex	378.30	20.73	0.00
Fuel ~ δ^2H feather + Sex + Age	380.37	22.80	0.00
Fuel ~ Date + δ^2H feather	1636.68	1279.11	0.00
Fuel ~ Date + δ^2H feather + δ^2H feather:Age	1640.52	1282.95	0.00
Fuel ~ δ^2H feather	1714.82	1357.25	0.00
Fuel ~ Date + Sex	2898.49	2540.92	0.00
Fuel ~ Sex + Age	3015.04	2657.46	0.00
Fuel ~ Sex	3022.43	2664.86	0.00
Fuel ~ Date + Age	8772.38	8414.81	0.00
Fuel ~ Date	8821.76	8464.19	0.00
Fuel ~ Age	9060.65	8703.08	0.00

Table 2. Pairwise φ_{st} comparisons between breeding populations and stopover localities, based on mitochondrial ND2. Note that birds from 'Newfoundland/s. Labrador' are all designated *C. m. minimus* whereas birds from 'w. Labrador/Quebec' and 'Alaska/Siberia' are of subspecies *C. m. aliciae*. Significance (p < 0.05) is denoted with *.

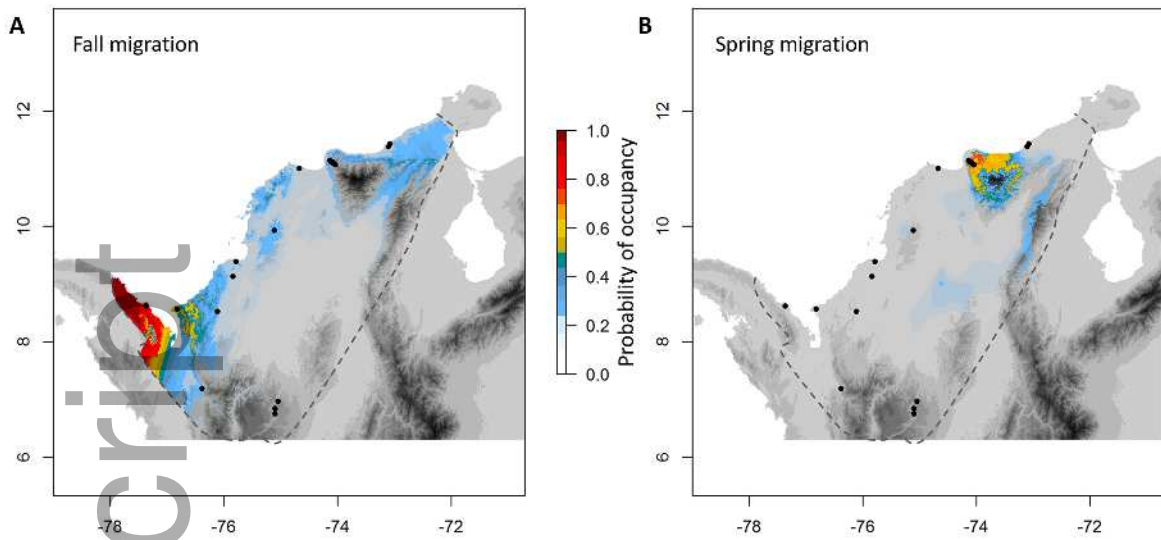|		Fall stopover	Spring stopover	Newfoundland/ s. Labrador	w. Labrador/ Quebec	Alaska/ Siberia
C.m.minimus	Fall stopover	-				
	Spring stopover	0.047*	-			
	Newfoundland/ s. Labrador	0.384*	0.330*	-		
C.m.aliciae	w. Labrador / Quebec	0.381*	0.327*	0.293*	-	
	Alaska / Siberia	0.072*	0.066*	0.301*	0.319*	-

Figure Legends

Figure 1. Occupancy surveys carried out at 17 sites (black dots on maps) across the northern coast of Colombia were used to predict probability of occurrence of Gray-cheeked Thrush during fall and spring migration. The dashed lines show the area to which occupancy predictions were limited (see suppl. material for details). High occupancy rates in the Darién in the fall (**A**) and in the Sierra Nevada de Santa Marta in the spring (**B**), suggest a funneling effect where most Gray-cheeked Thrush entering and leaving South America concentrate in these two regions during migration.

Figure 2. A. Low population structure of ND2 among populations of Gray-cheeked Thrush was found, however, birds captured in Colombia (n = 150) shared haplotypes with individuals from throughout the breeding range. The number of individuals sampled from each breeding region are shown on the map, as well as the subspecies to which each population belongs. The dashed line shows the approximate geographic division between subspecies breeding ranges. **B.** 14 out of 24 informative sites within the Gray-cheeked Thrush ND2, were private alleles restricted to individuals from one or two breeding populations. Birds captured in Colombia shared private alleles with all of the sampled breeding regions.

Figure 3A. Temporally explicit breeding and wintering distribution models of the Gray-cheeked Thrush based on monthly climatic variables and presence records. Surfaces reflect the probability of presence based on a maximum entropy algorithm. **B.** Likely breeding and wintering geographic origins of Gray-cheeked Thrush captured during spring migration in northern Colombia based on a species distribution model and on δ^2H values of feathers (breeding) and claws (winter). In agreement with genetic data, our assignment suggests that range-wide populations of Gray-cheeked Thrush converge in northern Colombia during stopover. Colored surfaces represent the sum of the upper 67% likelihood probability (2:1 odds) of origin for each bird.
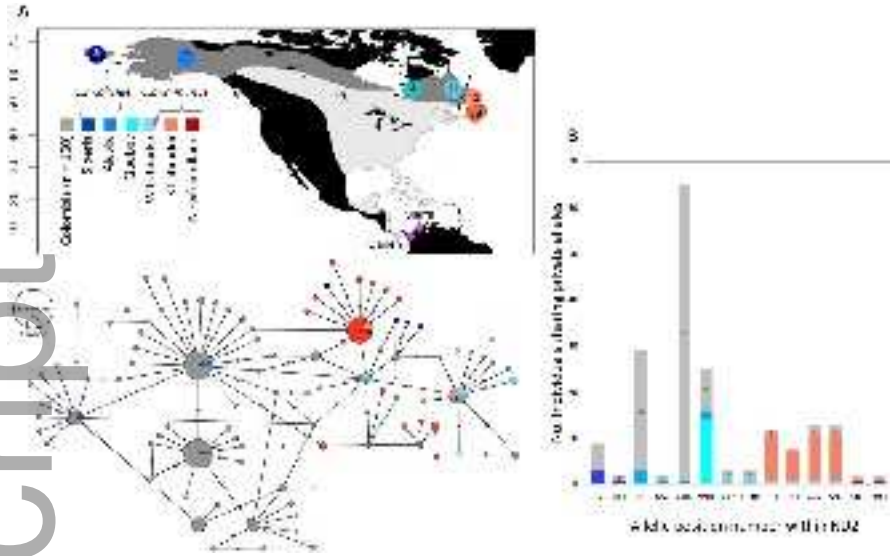
Figure 4. There was a significant effect of breeding origin (δ^2H$_f$ values) (**A**) but not of winter origin (δ^2H$_c$ values) (**B**) on date of arrival of Gray-cheeked Thrush to the spring stopover in northern Colombia. Males arrived significantly earlier than females both to the spring (**C**) and fall (**D**) stopover sites, and adults arrived significantly earlier than immature birds during spring (**E**) and especially during fall (**F**).

Figure 5. Fuel load on arrival to a spring stopover site for Gray-cheeked Thrush varied as a function of date, breeding origin and sex. **A.** Both males and females captured earlier in the season were in poorer body condition than those that arrived later. **B.** There was no difference in fuel on arrival between females of different breeding origins but males from more northerly breeding origin (more negative δ^2H$_f$ values) arrived with lower fuel stores than those from more southerly breeding origins.
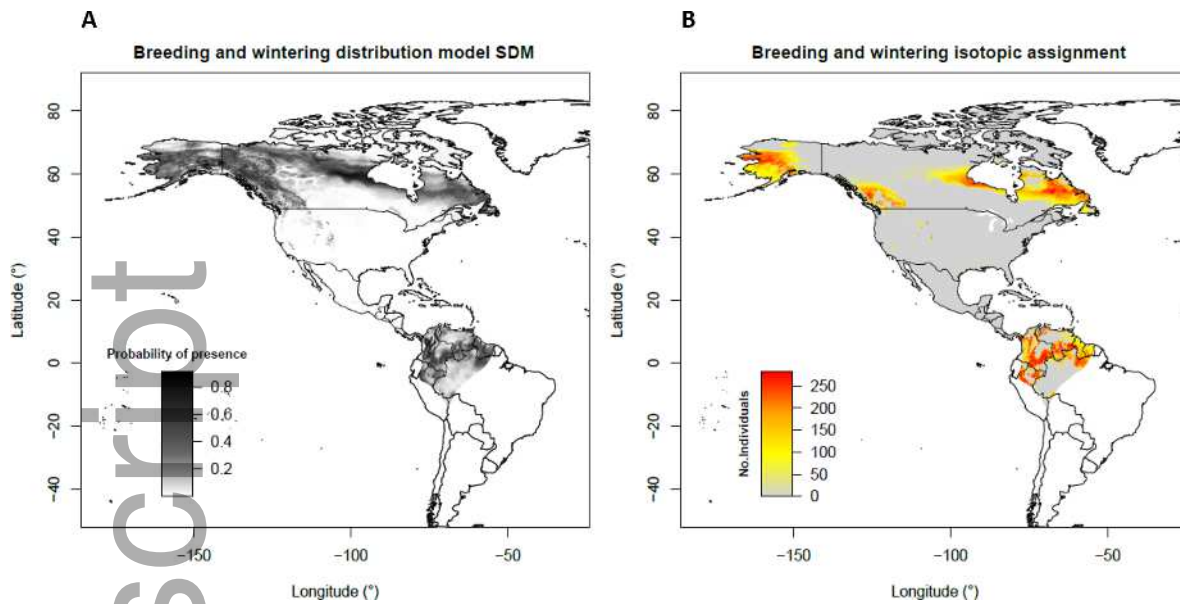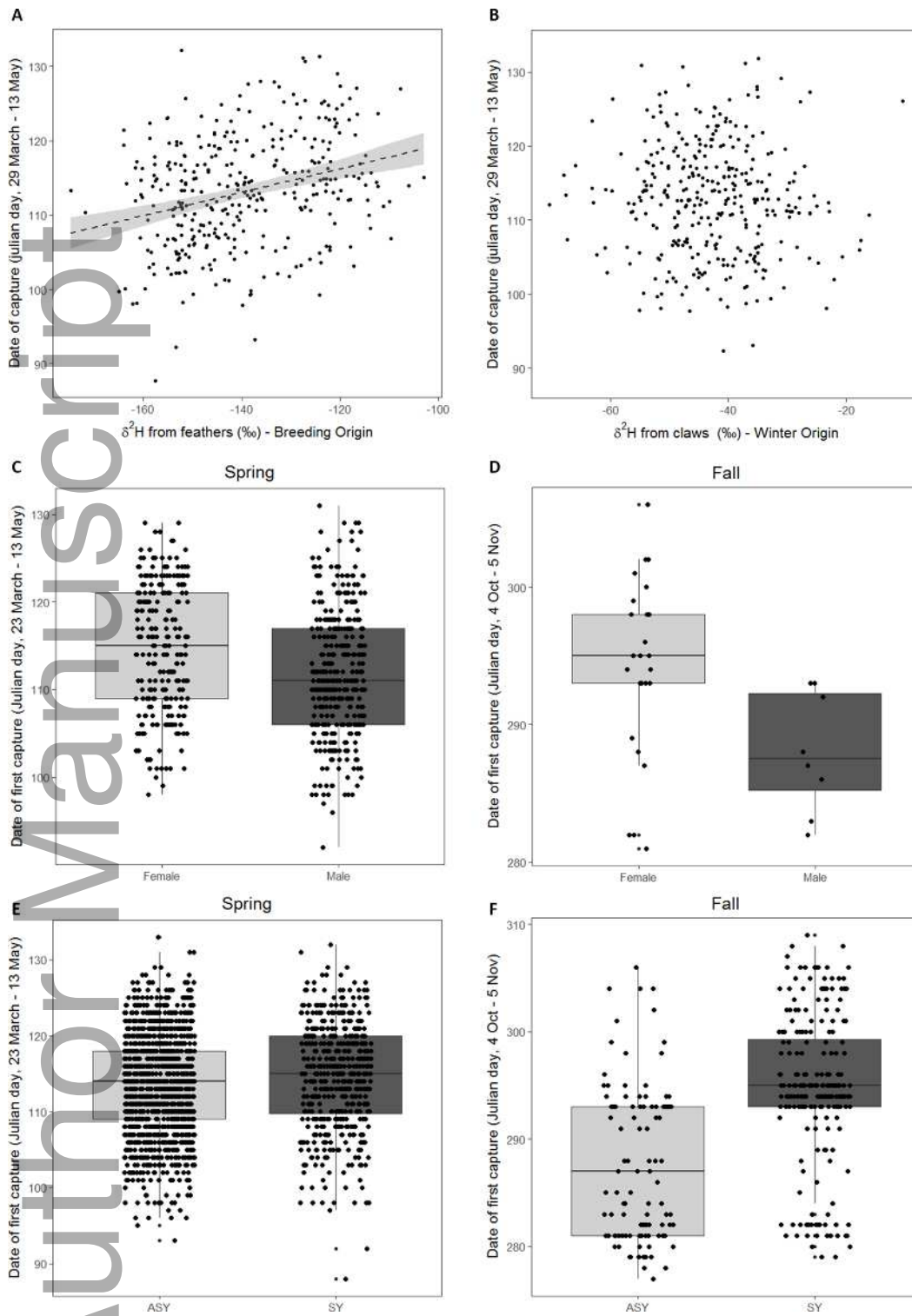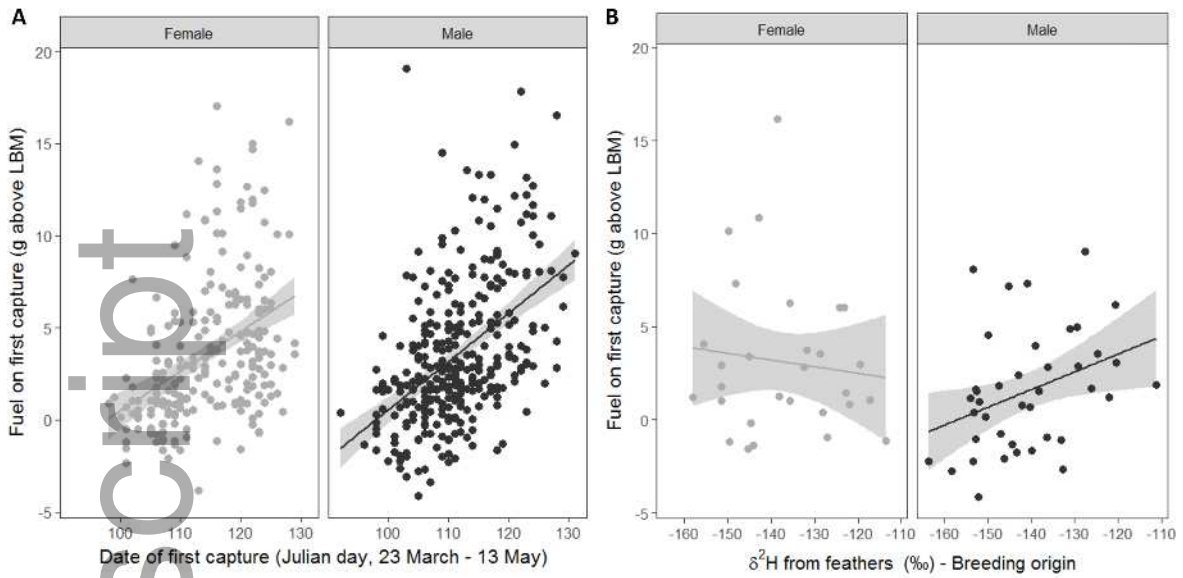
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A Breeding and wintering distribution model SDM

B Breeding and wintering isotopic assignment

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