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1 **Spring and autumn movements of an Arctic bird in relation to temperature and**

2 **primary production**

3

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15

16 **Abstract**

17 It is increasingly important to understand animal migratory movements because

18 climate disruption is shifting plant and animal phenology at different rates across the

19 world. We applied a Markov state-switching model to telemetry data of a long-

20 distance migrant, the barnacle goose, to detect migratory movement and relate it to

21 three proximate environmental factors: photoperiod, daily mean temperature and

22 forage plant phenology. Spring migratory movements towards the breeding grounds

23 were most closely related to forage plant phenology (measured by accumulated

24 growing degree days, GDDs); high GDDs values were associated with a greater

25 probability of transiting to a more northerly site, suggesting that spring migration is

closely aligned with primary productivity. Autumn migration from the breeding

grounds was most closely related to temperature; higher temperature values were

associated with a greater probability of remaining settled at the current site,

suggesting that autumn migration is closely aligned with atmospheric conditions.

Understanding the relative influence of different environmental factors on migratory

patterns may in turn provide us with insight into how continued climate disruption

could influence northern migratory systems.

Introduction

Long-range animal movement during spring and autumn migration is regulated by a complex combination of internal and external factors, varying widely across geographic regions, ecosystems and even within species (Alerstam et al. 2003, Shaw 2016). External factors may include, for example, seasonal changes in photoperiod (Dechmann et al. 2017, Robart et al. 2018), atmospheric/aquatic conditions (Singh et al. 2010, Harvey et al. 2020) and primary productivity (Singh et al. 2010). The relative importance of different external factors and the importance of internal and external factors can also vary over the course of migration (Bauer et al. 2008, Duriez et al. 2009). As such, the factors regulating migration in a given species is often obscured, limiting our potential to predict how some migratory systems may be affected by global climate disruption.

Many animal species breed at high Arctic latitudes to take advantage of high summer productivity and extended daylength, with reduced competition, predation and pathogen exposure, then migrate south to avoid the harsh conditions of winter (Somveille et al. 2015). In recent times, seasonal phenological synchrony between the Arctic and temperate/tropical regions has been deteriorating due to climate disruption, in turn disrupting synchrony between animal migratory movements and external environmental factors (Bekryaev et al. 2010, Lameris et al. 2017, Praetorius et al. 2018). Such phenological mismatches in synchrony have been observed in the barnacle goose *Branta leucopsis*, a long-distance migrant with three distinct flyways between the Arctic and temperate Europe (Jensen et al. 2018), termed herein as the Greenland, Svalbard and Russian flyways. As spring primary production advances in the Russian Arctic, hatch dates of Russian barnacle geese appear to be advancing

60 to maintain synchrony between peak nutrient requirements and availability. Although

61 the geese have successfully advanced their arrival to the breeding grounds by

62 skipping refuelling stopovers, the timing of egg laying is still constrained by the need

63 to acquire local resources prior to breeding. Therefore, the geese still face a

64 phenological mismatch between chick hatching and nutrient availability (Lameris et

65 al. 2018). Gosling survival within the first month following hatching is reduced in

66 years with a large phenological mismatch. This highlights the importance of

67 understanding how migratory movements in Arctic fauna relate to environmental

68 factors as the world's climate changes at an unprecedented rate, especially in the

69 Arctic.

70

71 As with a number of goose species, the timing of barnacle goose migration to the

72 Arctic breeding grounds has been closely linked to the northward flush of nutrient-

73 rich forage plant growth (the "green wave") as spring progresses (van der Graaf et

74 al. 2006, Kölzsch et al. 2015, Najafabadi et al. 2015, Si et al. 2015, Shariati-

75 Najafabadi et al. 2016, Wang et al. 2019). However, the phenology of migration on

76 the Greenland flyway appears to differ from the other flyways (Shariatinajafabadi et

77 al. 2014, Wang et al. 2019). Shariatinajafabadi et al. (2014) found that the

78 relationship between migration and forage plant phenology on the Greenland flyway

79 was much weaker than that observed on the Russian and Svalbard flyways. This

80 may be related to findings by Kölzsch et al. (2015), who found that the long sea

81 crossing from Iceland to Greenland reduced the bird's ability to predict foraging

82 conditions in Greenland and suggested that photoperiod may play a role at this point

83 of migration. Therefore, it is still unclear whether barnacle geese on the Greenland

84 flyway align their spring migration more closely with primary productivity or

85 photoperiod or some other environmental factor. Furthermore, environmental factors

86 influencing migratory movements are likely to differ between spring and autumn:

87 Arctic-breeding white-fronted goose *Anser albifrons* spring migration is most closely

88 associated with the green wave as the birds aim to acquire breeding capital,

89 whereas autumn migration is most closely associated with wind conditions as the

90 birds aim to fly quickly to the wintering grounds (Kölzsch et al. 2016). The timing of

91 barnacle goose autumn migration has not been linked to particular environmental

92 factors on any flyway, although Shariatinajafabadi et al. (2014) suggest it could be

93 related to atmospheric conditions.

94

95 Satellite telemetry is an excellent tool to study migratory movements in animals

96 where direct observation is unfeasible (Wilmers et al. 2015). Previous studies have

97 assessed the relationship between migratory movements of barnacle geese tracked

98 by satellite telemetry and satellite imagery of the green wave to link migratory

99 movements to environmental factors (e.g. Najafabadi et al. 2015). Here, we expand

100 on previous studies using a novel approach: we applied a Markov state-switching

101 model to telemetry data to relate behaviour – rather than location – to environmental

102 factors. This model identifies patterns of movement characteristics in telemetry time

103 series that represent discrete behavioural states, as well as time-dependent changes

104 in behavioural state. We can then test how various environmental factors influence

105 the probability of switching behavioural state. Using this technique, we aim to test the

106 relative importance of three environmental factors associated with migratory

107 movements in Greenland barnacle geese: photoperiod, air temperature and forage

108 plant phenology. We expect that spring movements from the wintering grounds to

109 the breeding grounds, including main spring staging and other shorter stopovers, will

110 be associated with some or all of lengthening days, rising air temperatures and

111 forage plant growth. Conversely, we expect that autumn movements from the

112 breeding grounds to the wintering grounds, including main autumn staging and other

113 shorter stopovers, will be associated with some or all of shortening days, falling air

114 temperatures and forage plant senescence. Our results demonstrate how state-

115 switching models can provide further insight into seasonal movements of a long-

116 distance Arctic migrant.

117

118 **Methods**

119 <u>Transmitter tag deployment</u>

120 Greenland barnacle geese winter on the north-west coasts of Ireland and Scotland

121 and migrate via Iceland to breed in north-east Greenland. A total of 28 tags were

122 deployed on barnacle geese in Ireland between 2008 and 2019: $n = 5$ (2008), $n = 2$

123 (2009) and $n = 2$ (2010) on the Inishkea Islands, Mayo, $n = 8$ (2018) and $n = 5$

124 (2019) on the Inishowen Peninsula, Donegal, and $n = 6$ (2019) in Lisadell, Sligo (Fig.

125 1a). Geese were captured using cannon nets and released immediately after tag

126 deployment. Tags from 2008-2010 comprised a 30-45g GPS-ARGOS platform

127 transmitter terminal (Microwave Telemetry Inc, Columbia MD) with an elastic body

128 harness attachment (final fitted weight of 45-65g respectively). Tags from 2018-2019

129 comprised a nanoFix® GEO+RF (Pathtrack Ltd, Otley, UK) on a neck collar

130 attachment (21mm high with an adjustable internal diameter of 36-44mm) with a final

131 fitted weight of ~15g and typical final internal diameter of 38-44mm. Tags from 2008-

132 2010 collected a geographical coordinate fix at 2 hour intervals (including night time)

133 and transmitted data via the Argos system almost daily. Tags from 2018-2019

134 collected a fix at 6 hour intervals and transmitted these data via ultra-high frequency

radio to base stations on the wintering grounds. Both tag types were solar powered, but the interval time between fixes was varied due to differing battery power and the programmed intervals for data transfer varied with daylength to optimise battery levels. Data was collected from deployment until the tag no longer transmitted data (generally between 12 and 24 months). All birds with tags were also fitted with individually inscribed legrings so that their survival could be monitored during winter and staging in subsequent years. Records of legrings were submitted by volunteers conducting routine monitoring of barnacle geese in Ireland, Scotland and Iceland.

Data were received from 19 of the 28 deployed tags, 18 of which yielded near-complete time series for spring (1 March to 31 May, i.e. beginning of spring to beginning of nesting) or autumn (14 August to 31 October, i.e. end of breeding/moulting to beginning of winter). In spring, geese departed their primary winter homerange as early as mid-March. Generally, they travelled from the north-west coast of Ireland, along the Outer Hebrides of Scotland to the Southern Region of Iceland (some flew directly from Ireland to Iceland), then through the Northeastern/Northwestern Regions of Iceland, over the Savoia Peninsula of Greenland and along the east Greenland coast and islands as far north as Danmarkshavn (Fig. 1c). In autumn, geese departed their primary summer homerange by the end of August. Generally, they travelled south along the east Greenland coast to Jamesonland or the Savoia Peninsula before crossing to the Westfjords of Iceland, through the Southern Region of Iceland and along the Outer Hebrides as far south as Islay or north-western Ireland (again, some flew directly from Iceland to Ireland) (Fig. 1d). During spring, geese moved northward on short journeys punctuated with relatively regular and short stopovers (generally less than 2

160   weeks) in the Outer Hebrides, the south coast of Iceland and north Iceland. Most

161   stopped at their "main" spring staging grounds near the north coast of Iceland (the

162   Vatnsdalsá, Huseyjarkvisl and Héraðsvötn rivers) for 3 to 4 weeks, before continuing

163   on short journeys and stopovers on the Savoia Peninsula and east Greenland

164   islands. In contrast, during autumn, geese moved southward over longer journeys

165   with relatively fewer but longer stopovers (generally between 1 and 3 weeks) on the

166   east Greenland islands and the Icelandic Westfjords. Most stopped at their "main"

167   autumn staging grounds on the south coast of Iceland (Skeiðarársandur and

168   Kúðafljót) for 3 to 4 weeks, before flying almost directly to Islay or the north-west

169   coast of Ireland

170

171   <u>Environmental data</u>

172   Daily photoperiod was defined as hours between sunrise and sunset at the latitude

173   at which the bird was present at the time of the fix. Daily mean temperature (°C) was

174   sourced from the closest of six weather stations across the flyway at the time of the

175   fix (Fig. 1b and see Supplementary Information S1). Accumulated growing and

176   cooling degree days (GDDs and CDDs, based on the concept outlined by Burke,

177   1968) were used as a proxy for forage plant phenology in spring and autumn

178   respectively. The degree day (DD) was calculated as $\mathrm{DD} = \mathrm{MeanT} - \mathrm{BaseT}$, where

179   MeanT is the daily mean temperature and BaseT is 5.5°C, the lowest temperature at

180   which forage plants generally grow (Burke 1968). The accumulated DDs for each

181   day were summed to provide a daily value, starting in February for spring and

182   August for autumn. For GDDs in spring, if BaseT was greater than MeanT (i.e. too

183   cold for growth), the DD value was zero, thus providing heat accumulation above the

184   base temperature. For the complementary CDDs in autumn, if BaseT was greater

than MeanT (i.e. too warm for senescence), the DD value was zero and if BaseT was less than MeanT (i.e. cold enough for senescence), the DD value was one, thus calculating accumulated days below the base temperature. All environmental data were scaled to the same index by subtracting the mean and dividing by the standard deviation to standardise measurements on different scales before analysis.

State-switching model

Telemetry data was analysed using Hidden Markov models (Langrock et al. 2012), implemented using the moveHMM package (Michelot et al. 2016) in the R statistical language and environment 3.5.1 (R Core Team 2018). Hidden Markov models are a widely accepted method of inferring behavioural states from quantifiable telemetry data such as distance travelled ("step length") and direction travelled ("turning angle"), and have been utilised in a variety of studies, including data from terrestrial mammals, marine animals, insects and birds (Langrock et al. 2012, Patterson et al. 2017). Our spring and autumn data were analysed in separate models. From the 18 near-complete datasets, 14 contained a complete spring and 11 contained a complete autumn time series.

The time series of positions for each goose was decomposed into discrete behavioural states defined according to step length (Euclidean distance) and turning angle (degrees) between successive fixes (Michelot et al. 2016). We compared models with two, three or four behavioural states. The three state and four state models produced extra step length and turning angles for states which were not meaningful (see Supplementary Information S2), therefore the two state model was considered to most adequately capture barnacle goose behaviour and movement

210 and did not result in any residual autocorrelation. We termed these two behavioural

211 states (i) settled and (ii) transiting. For the initial parameter value estimation, we

212 characterised the settled state as sequences of short steps (mean length of 10km)

213 and an equal likelihood of turning in any direction (mean angle of 0° at a

214 concentration of 0.1, where minimum concentration is zero), i.e. goose moving

215 slowly and undirected. We characterised the transiting state as sequences of long

216 steps (mean length of 100km) and a lower likelihood of directional change (mean

217 angle of 0° at a concentration of 1), i.e. goose moving quickly in one direction.

218 Because step lengths are extremely variable and to capture step lengths between

219 the values defined above, we specified a large standard deviation for step length (15

220 and 150km respectively). A gamma distribution was specified for step length, as all

221 values were positive but right skewed, and a von Mises distribution for turning angle,

222 as the data were circular and normal. To ensure there was no influence of different

223 sampling frequencies, we compared a model with 2-hour interval data removed and

224 a model with 6-hour interval data removed to a model containing all data. The

225 behavioural states identified by each model were comparable in terms of the ratio of

226 state 1 to state 2 and the proportion of time steps in state 1 and state 2, indicating

227 consistency between all data (see Supplementary Information S2 for model output).

228

229 Between each time step in the time series, the individual can either remain in its

230 current behavioural state or switch to a new state. Switching from a settled to

231 transiting state was taken to represent the beginning of a journey and, likewise,

232 switching from a transiting to settled state was taken to represent the end of a

233 journey. The resolution of our data could detect state switching at the principle

234 wintering/breeding grounds, at the "main" staging grounds and at shorter stopovers

235 along the way. The probability of switching state was tested in relation to

236 photoperiod, daily mean temperature and accumulated GDDs in spring or CDDs in

237 autumn. A full model containing pairwise synergistic interactions was compared to a

238 model containing all three covariates additively and models containing each

239 covariate individually, as well as a null model containing no covariates (a three-way

240 interaction was not included as a candidate due to variance inflation). The best

241 supported model was identified using the Akaike Information Criterion (AIC); the

242 model with the lowest AIC value was selected (Akaike 1974). Model fit was assessed

243 by examining time series and auto-correlation functions of pseudo-residuals for

244 residual patterns and plots of pseudo-residuals against standard normal quantiles for

245 deviation from normality. The pseudo-residuals from our model followed a standard

246 normal distribution, indicating the model described the data well.

247

248 **Results**

249 <u>Spring migration</u>

250 The best supported spring model included the covariate GDDs (Table 1). The settled

251 state had a median step length of 0.17km (lower quartile 0.06km, upper quartile

252 0.62km) and a mean turning angle of -3.11° with a concentration of 0.44 and the

253 transiting state had a median step length of 8.61km (lower quartile 2.19km, upper

254 quartile 47.77km) and a mean turning angle of 0.16° with a concentration of 0.68

255 (Fig. 2a, b). There was a significant effect of GDDs on state-switching probability: as

256 GDDs increased, the probability of switching from a transiting state to a settled state

257 decreased by -0.99 (95% CI -1.38 – -0.60). High GDDs values were associated with

258 a greater probability of being or remaining in a transiting state and a lower probability

259 of being in a settled state, suggesting that geese are more likely to journey between

260 sites as GDDs increase (Fig. 3a). Geese typically departed for Iceland when GDDs

261 at winter sites was at least 45, but on average 110, and departed for Greenland

262 when average GDDs at staging sites reached 45. We further compared early spring

263 (1 March to 14 April) and late spring (14 April to 31 May) and found that the effect

264 was stronger in late spring (β = -0.68, 95% CI -1.07 – -0.29) compared to early

265 spring (confidence intervals approaching the null value). Uncertainty around the

266 mean also increased as spring progressed (possibly as other factors, e.g. individual

267 internal state, act).

268

269 <u>Autumn migration</u>

270 The best supported autumn model included the covariate daily mean air temperature

271 (Table 1). The settled state had a median step length of 0.91km (lower quartile

272 0.27km, upper quartile 2.67km) and a mean turning angle of 3.14° with a

273 concentration of 0.21 and the transiting state had a median step length of 91.67km

274 (lower quartile 27.39km, upper quartile 195.46) and a mean turning angle of 0.01°

275 with a concentration of 1.36 (Fig. 2c, d). There was a significant effect of temperature

276 on state-switching probability: as mean temperature increased, the probability of

277 switching from a settled state to a transiting state decreased by -0.48 (95% CI -0.77 -

278 -0.20). High mean temperature values were associated with a greater probability of

279 being in a settled state and a lower probability of being or remaining in a transiting

280 state, suggesting that geese are more likely to journey between sites as

281 temperatures decrease (Fig. 3b). Birds typically departed their primary breeding

282 grounds at temperatures between 1.5˚C and 5.5˚C (mean 3.8˚C) and crossed from

283 Greenland to Iceland when temperatures fell to between -1.2˚C and 2.9˚C (mean

284 1.6˚C).

286 **Discussion**

287 Our hidden Markov model successfully identified two discrete behavioural states in

288 barnacle goose GPS time series. The results reveal that the Greenland barnacle

289 goose spring movements are most strongly associated with GDDs. This suggests

290 that the timing of spring migration is closely aligned with primary production, as

291 observed in the Russian and Svalbard populations (van der Graaf et al. 2006, Si et

292 al. 2015, Shariati-Najafabadi et al. 2016). Because barnacle geese are a capital

293 breeding species, acquiring the majority of breeding reserves before arriving at the

294 breeding grounds, increased forage availability may allow them to acquire the

295 necessary fuel reserves to proceed to the breeding grounds. The timing of autumn

296 movements are most strongly associated with daily mean air temperature. This

297 suggests that autumn migration is closely aligned with atmospheric conditions, as

298 suggested by Shariatinajafabadi et al. (2014). As temperatures fall, the increased

299 thermoregulatory costs and relative inaccessibility of forage may limit the geese's

300 ability to persist in northerly sites.

301

302 <u>Phenological changes</u>

303 Climate disruption may have significant consequences for species that align their

304 spring movements closely with primary productivity (Howard et al. 2020). In seasonal

305 environments, migratory animals time their reproduction to coincide with the annual

306 peak of primary productivity, which in turn is governed by climate. Emerging

307 phenological mismatches between reproduction and primary productivity in both

308 marine and terrestrial environments due to amplified climate warming rates in the

309 Arctic is widely documented in the literature (e.g. Edwards and Richardson 2004,

Jones and Cresswell 2010, Lameris et al. 2017, Mayor et al. 2017). For example, light-bellied brent geese *Branta bernicla hrota* experience reduced breeding success when there is a mismatch between chick hatching and peak plant nutrient availability (Clausen and Clausen 2013). Mismatches are becoming more frequent because plant phenology is advancing faster in their Arctic Svalbard breeding grounds than in their temperate Danish staging grounds. Breeding success of caribou *Rangifer tarandus* in Greenland is adversely impacted due to a mismatch between calving and peak forage availability (Post and Forchhammer 2008). The mismatch occurs because the timing of spring migration to summer ranges for calving depends on photoperiod, which remains fixed, while plant phenology depends on temperature and is advancing. In marine environments, little auks *Alle alle* and Brünnich's guillemots *Uria lomvia* experienced reduced breeding success as the mismatch between hatching and phytoplankton productivity increased (Ramírez et al. 2017). The pulses of phytoplankton productivity advanced due to earlier sea ice melt, while bird breeding activity did not. An uncoupling of plant phenology between temperate Ireland/Scotland and Arctic Iceland/Greenland could have similar consequences for reproduction in barnacle geese in the future.

The consequences of climate disruption for autumn migration has received less attention than spring, despite notable changes to the plant growth period, leaf-senescence date and arrival of frost and snow (Gallinat et al. 2015). Passerine birds breeding in Europe and wintering south of the Sahara have advanced their autumn migration, possibly due to pressure to cross the Sahel before the dry period (Jenni and Kéry 2003). In contrast, beluga whales *Delphinapterus leucas* delay autumn migration due to later sea ice freeze (Hauser et al. 2017). Barnacle geese could

335 similarly be able to delay departing their summer homerange if falling temperatures

336 are delayed. This may have particular implications for juveniles gaining extra time to

337 develop before their first full migration. However, to date, we do not have evidence of

338 a long term delay in the time of southerly post-breeding movements from Greenland.

339

340 <u>Model performance and impact of telemetry tags on geese</u>

341 For each bird, we compared the behavioural state estimated by the model with its

342 position on a geographic map and found that the two behavioural states identified in

343 our model correlated coherently with the individual's geographic location and

344 movements, suggesting that they were appropriately identified. Transiting behaviour

345 tended to be observed in unsuitable habitat or sea crossings and correlated with

346 known migration dates, while settled behaviour tended to be observed in suitable

347 and known forage or roosting habitat. Of nine geese carrying harness tags between

348 2008 and 2010, all tags successfully transmitted data and seven birds were known to

349 be alive the following year with their tags still attached, suggesting a survival rate of

350 >75%. Two birds were assumed lost at sea during migration; the contribution of the

351 tag to this is unknown, but one bird is known to have encountered strong headwinds

352 during the sea crossing. Of eight geese carrying neck collar tags in 2018, five tags

353 successfully transmitted data and seven geese were known to be alive the following

354 year (one having lost its tag but retained its legring), suggesting a survival rate of

355 >85%, which is similar to the 87% average survival rate of uninstrumented birds

356 reported by Doyle et al. (2020). Although 4 data series were obtained, data retrieval

357 and legring recording from the 11 geese tagged in 2019 was interrupted by the

358 COVID-19 pandemic from March until migration to Greenland (after which the geese

359 become inaccessible), therefore conclusions on the effect of tags on this cohort

360 remained unknown at the time of writing.

361

362 Conclusion

363 This study successfully applied a Markov state-switching model to GPS time series

364 data of barnacle geese to detect migratory behaviour and examine the relationship

365 between the timing of changes in behavioural state and photoperiod, air temperature

366 and forage plant phenology. Like the Russian and Svalbard populations, the

367 Greenland population spring migratory movements were more closely associated

368 with forage plant phenology than with temperature or photoperiod. Autumn migratory

369 movements were more closely associated with temperature than plant phenology or

370 photoperiod. Increasing temperatures in the Arctic associated with climate disruption

371 is likely to advance forage plant growth in spring and extend summer temperatures

372 in autumn, therefore there is potential for continued climate disruption to alter the

373 traditional timing of barnacle goose and other Arctic bird migration.

374

383

Author contributions

SD, DC and BJM conceived ideas and designed the project. SD, DC, LG, KC and SB deployed tags and retrieved data. SD modelled the data with assistance from AK and BJM. SD led writing of the manuscript, with contribution to drafts from all authors.

Conflict of Interest

The authors declare that they have no conflict of interest.

Permits

Capture and tagging of geese was conducted under licence from the National Parks and Wildlife Service of the Government of Ireland and a special methods permit from the British Trust of Ornithology.

Data availability statement

Data supporting this paper is available in Movebank (https://www.movebank.org/cms/movebank-main)

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Table 1. The AIC for each model is presented, along with the difference between each model and the lowest AIC (ΔAIC). Models include additive (+), synergistic (*) or null (~1) effects.

	model	AIC	ΔAIC
spring migration	~GDDS	27535.89	0.00
	~temperature * daylength + GDDS	27536.32	0.44
	~temperature + GDDS + daylength	27537.74	1.86
	~temperature + GDDS * daylength	27538.04	2.15
	~temperature * GDDS + daylength	27539.12	3.23
	~daylength	27551.29	15.40
	~temperature	27558.56	22.67
	~1	27630.79	94.91
autumn migration	~temperature	24598.07	0.00
	~temperature * daylength + CDDS	24600.68	2.61
	~temperature + CDDS + daylength	24601.37	3.31
	~temperature + CDDS * daylength	24602.63	4.56
	~CDDS	24604.18	6.11
	~temperature * GDDS + daylength	24604.99	6.92
	~daylength	24610.11	12.04
	~1	24663.49	65.42

GDDs: accumulated growing degrees of the year
CDDs: accumulated cool days of the year
temperature: daily mean air temperature recorded (°C)
daylength: hours between sunrise and sunset
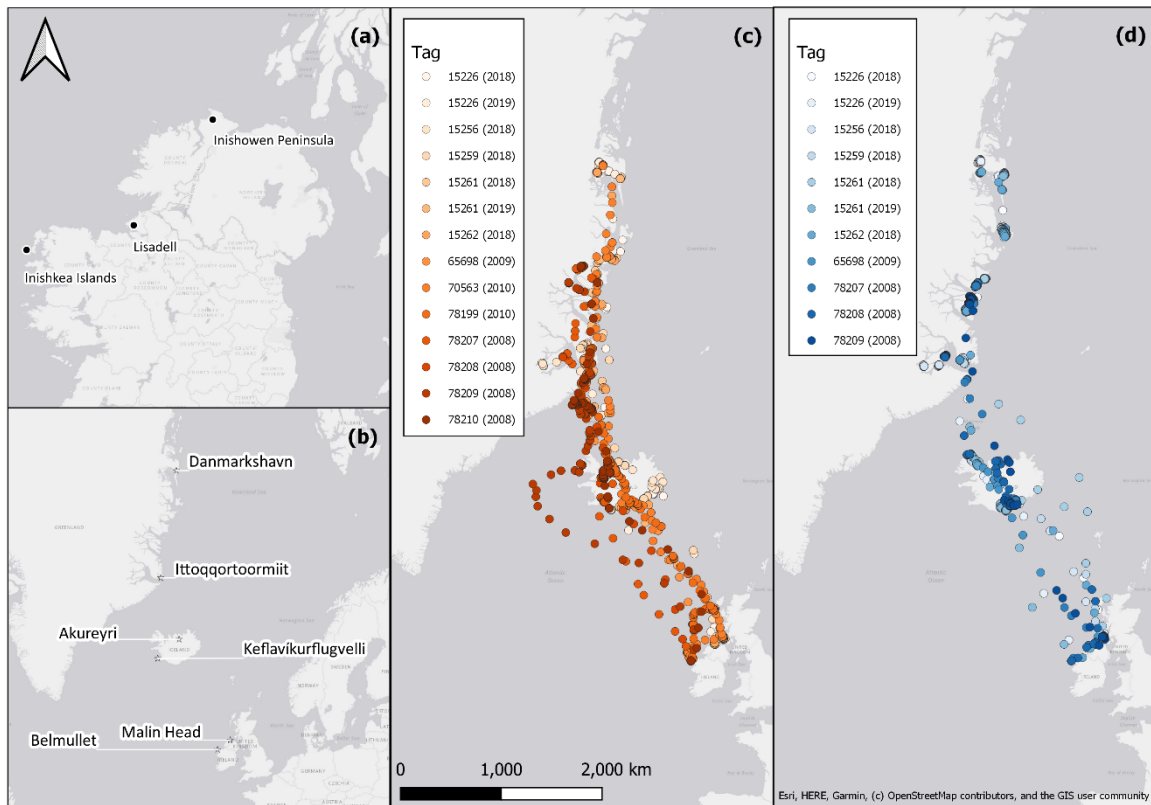
538
539 Figure 1. (a) Tagging locations of barnacle geese on the Greenland flyway. (b)
540 Location of the six weather stations along the Greenland flyway. (c) Tracking data
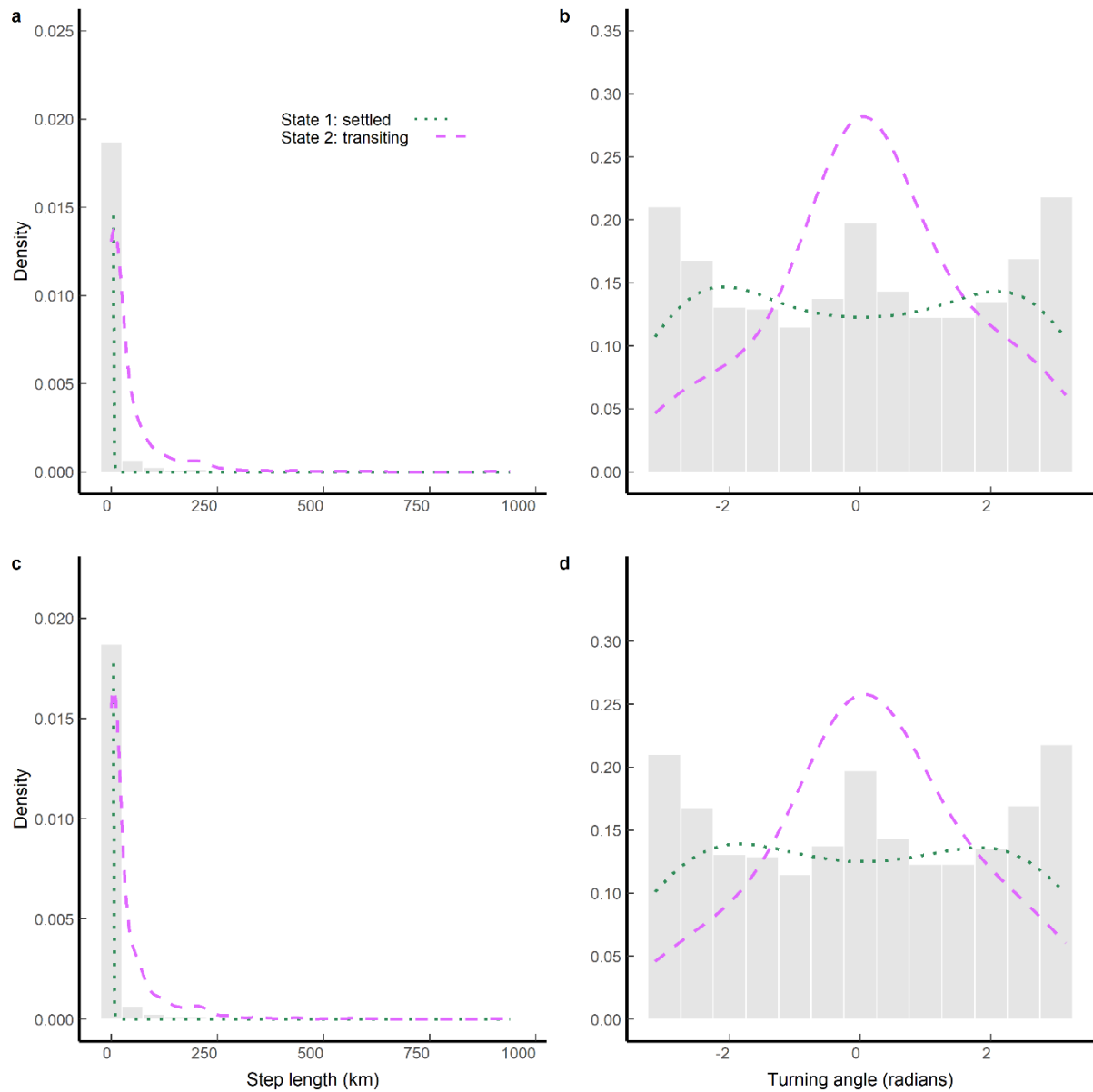541 recovered from tags in spring and (d) autumn.

Figure 2. Step length and turning angles classified into settled and transiting states: (a) spring step length, (b) spring turning angle, (c) autumn step length, (d) autumn turning angle.
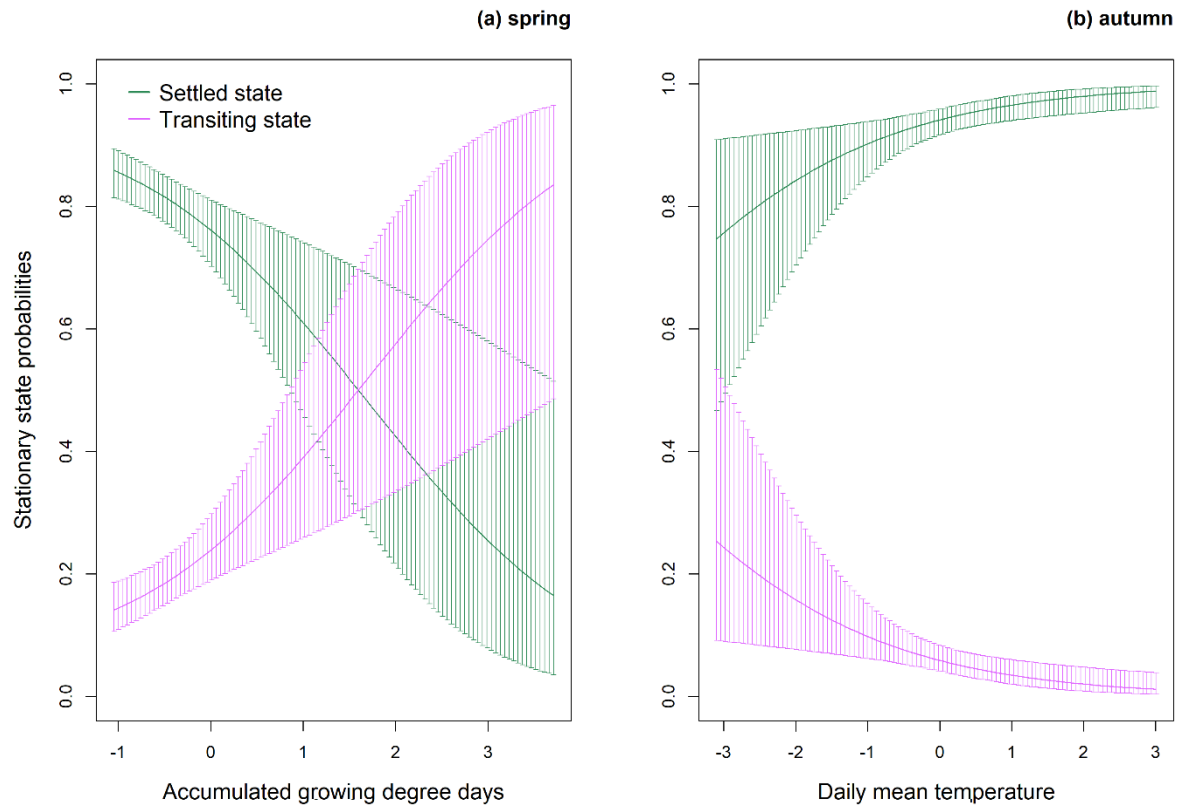
(a) spring
(b) autumn

546
547 Figure 3. The long-term probability of being in a settled state or a transiting state at
548 different values of (a) accumulated growing degree days and (b) daily mean air
549 temperature. Shaded area around the line represents 95% confidence intervals.
550 Note, covariate values are scaled and centred to mean zero and standard deviation
551 1.

Supplementary Information S1

Table 1. Weather station data.

Institution	Source and data extracted
Met Éireann	Source: www.met.ie/climate/available-data/historical-data Daily values for Station 2375 (Belmullet, Co. Mayo) apply to latitudes between 50.00 and 54.49. Daily values for Station 1575 (Malin Head, Co. Donegal) apply to latitudes between 54.50 and 60.49. Parameters max and min air temperature (°C) were extracted and consolidated to produce mean.
Veðurstofa Íslands	Source: https://www.vedur.is/vedur/vedurfar/daglegt/ Daily values for Station 990 (Keflavíkurflugvelli) apply to latitudes between 60.50 and 64.49. Daily values for Station 422 (Akureyri) apply to latitudes between 64.50 and 68.49. Parameter mean air temperature (meðalhiti; °C) was extracted.
Danmarks Meteorologiske Institut	Source: www.dmi.dk/publikationer/ Data pertaining to DMI Report No. 20-08 'Weather observations from Greenland 1958-2019'. Hourly values for Station 4339 (Ittoqqortoormiit) apply to latitudes between 68.50 and 73.49. Hourly values for Station 4320 (Danmarkshavn) apply to latitudes between 73.50 and 78.50. Parameter last hour mean air temperature (101; dry bulb temperature) was extracted and consolidated to produce daily values.

Supplementary Information S2

Table 1. Comparison of step length and turning angles in two- three- and four-state models for spring migration data. The mean (μ) is provided, along with the standard deviation (σ) for step length and the concentration (conc.) for turning angle.

Model	State	Step Length		Turning Angle	
		μ	σ	μ	conc.
2-state	State 1	0.49	0.64	-3.11	0.45
	State 2	38.03	65.51	0.15	0.66
		μ	σ	μ	conc.
3-state	State 1	0.11	0.10	-3.04	0.37
	State 2	1.43	1.77	3.04	0.45
	State 3	63.98	91.92	0.03	1.53
		μ	σ	μ	conc.
4-state	State 1	0.08	0.07	-3.10	0.34
	State 2	0.81	0.78	-3.11	0.57
	State 3	100.75	9.80	0.04	2.35
	State 4	4.37	6.41	1.21	0.10

Table 2. Comparison of step length and turning angles in two- three- and four-state models for autumn migration data. The mean (μ) is provided, along with the standard deviation (σ) for step length and the concentration (conc.) for turning angle.

Model	State	Step Length		Turning Angle	
		μ	σ	μ	conc.
2-state	State 1	2.17	2.70	3.14	0.21
	State 2	136.94	185.80	0.01	1.35
		μ	σ	μ	conc.
3-state	State 1	0.86	0.89	-3.12	0.22
	State 2	3.27	4.09	3.10	0.20
	State 3	137.57	188.00	-0.01	1.35
		μ	σ	μ	conc.
4-state	State 1	0.86	0.89	-3.10	0.22
	State 2	3.26	4.08	3.08	0.19
	State 3	96.66	157.49	-0.03	0.66
	State 4	201.88	145.16	-0.01	6.58

Table 3. Comparison of step length and turning angles in models with 2-hour frequency data, 6-hour frequency data and all data for spring migration. The mean (μ) is provided, along with the standard deviation (σ) for step length and the concentration (conc.) for turning angle.

Model	State	Step Length		Turning Angle	
		μ	σ	μ	conc.
2-hour	State 1	0.34	0.45	-3.07	0.37
	State 2	39.62	55.75	0.003	1.58
		μ	σ	μ	conc.
6-hour	State 1	1.63	2.10	3.00	0.58
	State 2	106.57	163.50	0.17	1.03
		μ	σ	μ	conc.
all	State 1	0.49	0.64	-3.11	0.44
	State 2	38.03	65.51	0.15	0.66

Table 4. Comparison of step length and turning angles in models with 2-hour frequency data, 6-hour frequency data and all data for autumn migration. The mean (μ) is provided, along with the standard deviation (σ) for step length and the concentration (conc.) for turning angle.

Model	State	Step Length		Turning Angle	
		μ	σ	μ	conc.
2-hour	State 1	1.15	1.37	-3.02	0.21
	State 2	95.38	144.93	0.10	1.42
		μ	σ	μ	conc.
6-hour	State 1	2.81	3.51	2.98	0.17
	State 2	192.04	152.57	-0.07	1.42
		μ	σ	μ	conc.
all	State 1	2.10	2.67	3.10	0.21
	State 2	129.02	177.41	0.02	1.40