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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

26 closely aligned with primary productivity. Autumn migration from the breeding
27 grounds was most closely related to temperature; higher temperature values were
28 associated with a greater probability of remaining settled at the current site,
29 suggesting that autumn migration is closely aligned with atmospheric conditions.
30 Understanding the relative influence of different environmental factors on migratory
31 patterns may in turn provide us with insight into how continued climate disruption
32 could influence northern migratory systems.

33

34 **Keywords:** animal migration, Arctic herbivore, phenological mismatch

35 **Introduction**

36 Long-range animal movement during spring and autumn migration is regulated by a
37 complex combination of internal and external factors, varying widely across
38 geographic regions, ecosystems and even within species (Alerstam et al. 2003,
39 Shaw 2016). External factors may include, for example, seasonal changes in
40 photoperiod (Dechmann et al. 2017, Robart et al. 2018), atmospheric/aquatic
41 conditions (Singh et al. 2010, Harvey et al. 2020) and primary productivity (Singh et
42 al. 2010). The relative importance of different external factors and the importance of
43 internal and external factors can also vary over the course of migration (Bauer et al.
44 2008, Duriez et al. 2009). As such, the factors regulating migration in a given species
45 is often obscured, limiting our potential to predict how some migratory systems may
46 be affected by global climate disruption.

47

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

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

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

143

144 Data were received from 19 of the 28 deployed tags, 18 of which yielded near-
145 complete time series for spring (1 March to 31 May, i.e. beginning of spring to
146 beginning of nesting) or autumn (14 August to 31 October, i.e. end of
147 breeding/moulting to beginning of winter). In spring, geese departed their primary
148 winter homerange as early as mid-March. Generally, they travelled from the north-
149 west coast of Ireland, along the Outer Hebrides of Scotland to the Southern Region
150 of Iceland (some flew directly from Ireland to Iceland), then through the
151 Northeastern/Northwestern Regions of Iceland, over the Savoia Peninsula of
152 Greenland and along the east Greenland coast and islands as far north as
153 Danmarkshavn (Fig. 1c). In autumn, geese departed their primary summer
154 homerange by the end of August. Generally, they travelled south along the east
155 Greenland coast to Jamesonland or the Savoia Peninsula before crossing to the
156 Westfjords of Iceland, through the Southern Region of Iceland and along the Outer
157 Hebrides as far south as Islay or north-western Ireland (again, some flew directly
158 from Iceland to Ireland) (Fig. 1d). During spring, geese moved northward on short
159 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 Kúðafliót) for 3 to 4 weeks, before flying almost directly to Islay or the north-west
169 coast of Ireland

170

171 Environmental data

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 $DD = \text{MeanT} - \text{BaseT}$, 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

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

190

191 State-switching model

192 Telemetry data was analysed using Hidden Markov models (Langrock et al. 2012),
193 implemented using the moveHMM package (Michelot et al. 2016) in the R statistical
194 language and environment 3.5.1 (R Core Team 2018). Hidden Markov models are a
195 widely accepted method of inferring behavioural states from quantifiable telemetry
196 data such as distance travelled (“step length”) and direction travelled (“turning
197 angle”), and have been utilised in a variety of studies, including data from terrestrial
198 mammals, marine animals, insects and birds (Langrock et al. 2012, Patterson et al.
199 2017). Our spring and autumn data were analysed in separate models. From the 18
200 near-complete datasets, 14 contained a complete spring and 11 contained a
201 complete autumn time series.

202

203 The time series of positions for each goose was decomposed into discrete
204 behavioural states defined according to step length (Euclidean distance) and turning
205 angle (degrees) between successive fixes (Michelot et al. 2016). We compared
206 models with two, three or four behavioural states. The three state and four state
207 models produced extra step length and turning angles for states which were not
208 meaningful (see Supplementary Information S2), therefore the two state model was
209 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 Spring migration

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 ($\beta = -0.68$, 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 Autumn migration

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).

285

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 Phenological changes

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,

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

327

328 The consequences of climate disruption for autumn migration has received less
329 attention than spring, despite notable changes to the plant growth period, leaf-
330 senescence date and arrival of frost and snow (Gallinat et al. 2015). Passerine birds
331 breeding in Europe and wintering south of the Sahara have advanced their autumn
332 migration, possibly due to pressure to cross the Sahel before the dry period (Jenni
333 and Kéry 2003). In contrast, beluga whales *Delphinapterus leucas* delay autumn
334 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 Model performance and impact of telemetry tags on geese

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 legging), 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 legging 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

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389

390 **Author contributions**

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

395

396 **Conflict of Interest**

397 The authors declare that they have no conflict of interest.

398

399 **Permits**

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

403

404 **Data availability statement**

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

407

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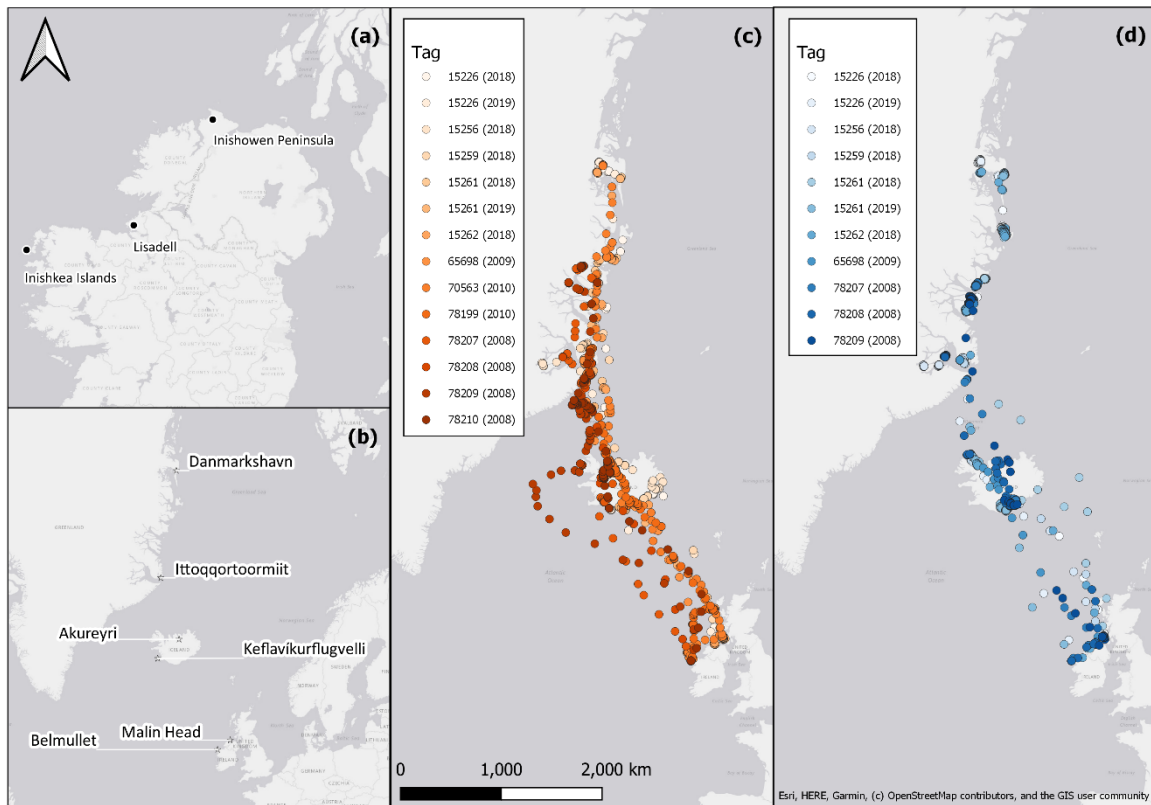
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535 Table 1. The AIC for each model is presented, along with the difference between
 536 each model and the lowest AIC (Δ AIC). Models include additive (+), synergistic (*) or
 537 null (~1) effects.

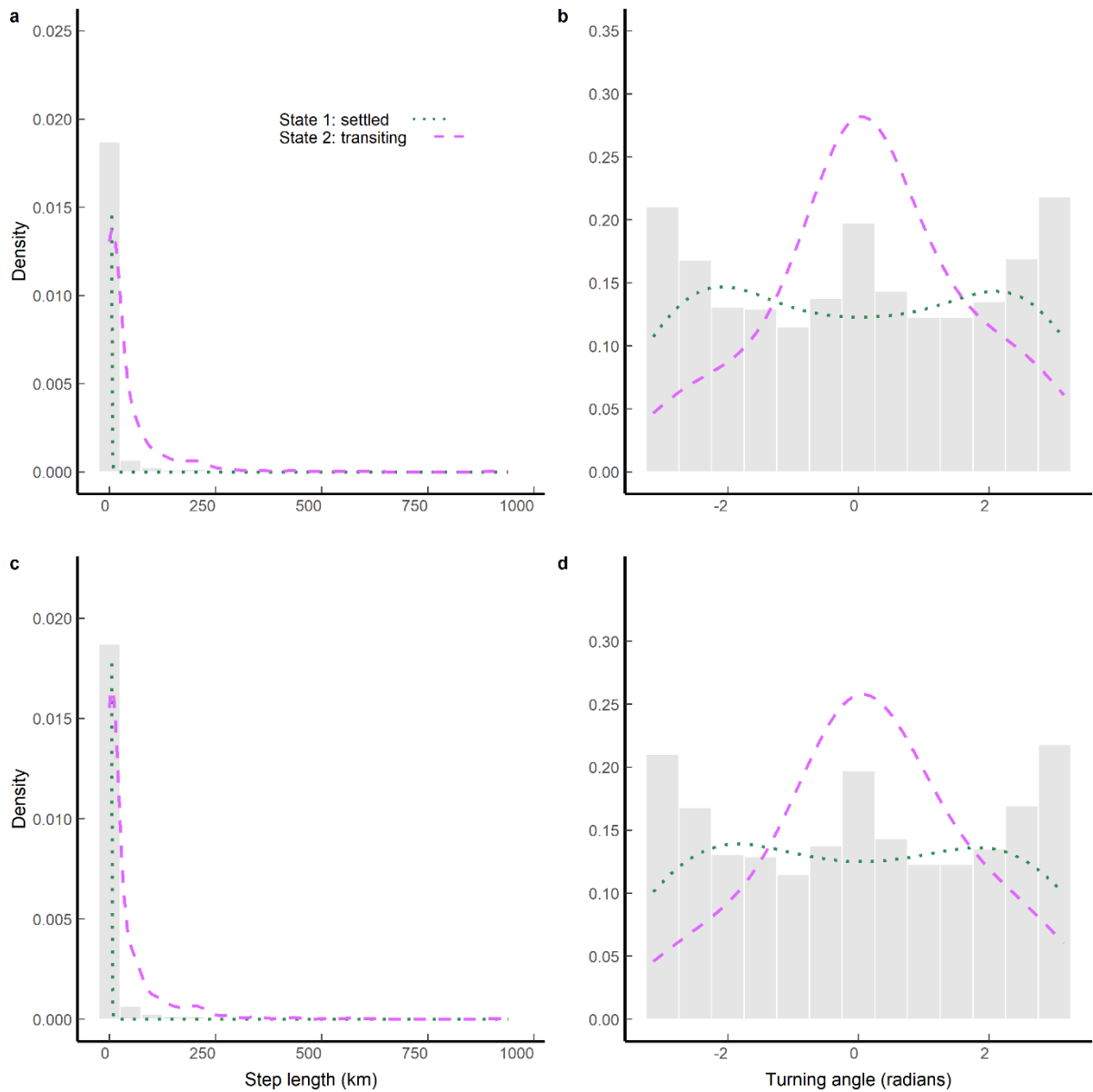
| | model | AIC | ΔAIC |
|---------------------|---------------------------------|------------|-------------------------------|
| spring migration | ~GDDS | 27535.89 | 0.00 |
| | ~temperature * daylength + GDDS | 27536.32 | 0.44 |
| | ~temperature + GDDS + daylength | 27537.74 | 1.86 |
| | ~temperature + 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 ($^{\circ}$ C)
daylength: hours between sunrise and sunset



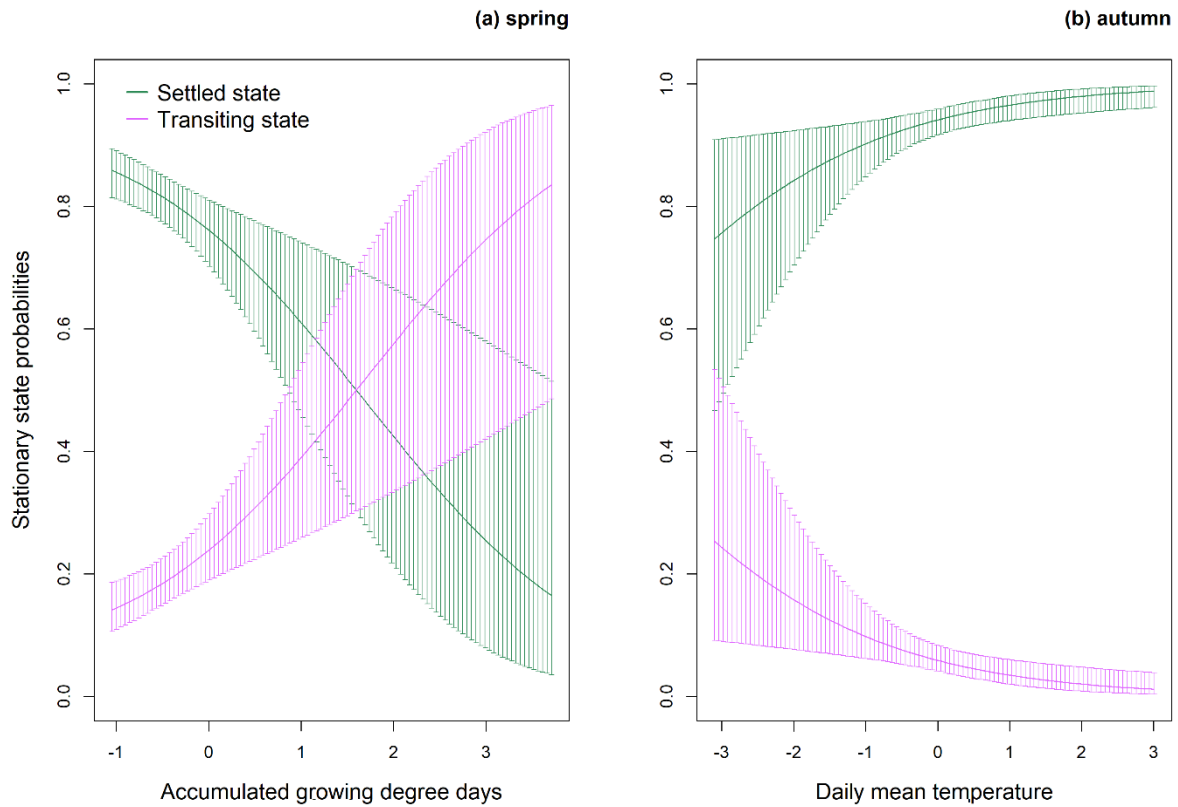
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Figure 1. (a) Tagging locations of barnacle geese on the Greenland flyway. (b) Location of the six weather stations along the Greenland flyway. (c) Tracking data recovered from tags in spring and (d) autumn.



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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.



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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 |
|---|---|
| | Source: www.met.ie/climate/available-data/historical-data |
| Met Éireann | 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. Source: https://www.vedur.is/vedur/vedurfar/daglegt/ |
| Veðurstofa Íslands | Daily values for Station 990 (Keflavíkurlugvelli) 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. Source: www.dmi.dk/publikationer/ |
| Danmarks Meteorologiske Institut | 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 |
| 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 |
| 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 |
| 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 |
| 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 |
| 6-hour | State 1 | 1.63 | 2.10 | 3.00 | 0.58 |
| | State 2 | 106.57 | 163.50 | 0.17 | 1.03 |
| 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 |
| 6-hour | State 1 | 2.81 | 3.51 | 2.98 | 0.17 |
| | State 2 | 192.04 | 152.57 | -0.07 | 1.42 |
| all | State 1 | 2.10 | 2.67 | 3.10 | 0.21 |
| | State 2 | 129.02 | 177.41 | 0.02 | 1.40 |