

Title	Spring and autumn movements of an Arctic bird in relation to temperature and primary production
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Publication date	2021-10-01
Original Citation	Doyle, S., Cabot, D., Griffin, L., Kane, A., Colhoun, K., Bearhop, S. and McMahon, B. J. (2021) 'Spring and autumn movements of an Arctic bird in relation to temperature and primary production', Journal of Avian Biology. doi: 10.1111/jav.02830
Type of publication	Article (peer-reviewed)
Link to publisher's version	10.1111/jav.02830
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Download date	2025-02-05 09:55:54
ltem downloaded from	https://hdl.handle.net/10468/12110



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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

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

Long-range animal movement during spring and autumn migration is regulated by a 36 complex combination of internal and external factors, varying widely across 37 geographic regions, ecosystems and even within species (Alerstam et al. 2003, 38 Shaw 2016). External factors may include, for example, seasonal changes in 39 photoperiod (Dechmann et al. 2017, Robart et al. 2018), atmospheric/aquatic 40 41 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 42 43 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 44 is often obscured, limiting our potential to predict how some migratory systems may 45 be affected by global climate disruption. 46

47

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

to maintain synchrony between peak nutrient requirements and availability. Although 60 the geese have successfully advanced their arrival to the breeding grounds by 61 skipping refuelling stopovers, the timing of egg laying is still constrained by the need 62 to acquire local resources prior to breeding. Therefore, the geese still face a 63 phenological mismatch between chick hatching and nutrient availability (Lameris et 64 al. 2018). Gosling survival within the first month following hatching is reduced in 65 66 years with a large phenological mismatch. This highlights the importance of understanding how migratory movements in Arctic fauna relate to environmental 67 68 factors as the world's climate changes at an unprecedented rate, especially in the Arctic. 69

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As with a number of goose species, the timing of barnacle goose migration to the 71 Arctic breeding grounds has been closely linked to the northward flush of nutrient-72 rich forage plant growth (the "green wave") as spring progresses (van der Graaf et 73 al. 2006, Kölzsch et al. 2015, Najafabadi et al. 2015, Si et al. 2015, Shariati-74 Najafabadi et al. 2016, Wang et al. 2019). However, the phenology of migration on 75 the Greenland flyway appears to differ from the other flyways (Shariatinajafabadi et 76 al. 2014, Wang et al. 2019). Shariatinajafabadi et al. (2014) found that the 77 relationship between migration and forage plant phenology on the Greenland flyway 78 79 was much weaker than that observed on the Russian and Svalbard flyways. This may be related to findings by Kölzsch et al. (2015), who found that the long sea 80 crossing from Iceland to Greenland reduced the bird's ability to predict foraging 81 82 conditions in Greenland and suggested that photoperiod may play a role at this point of migration. Therefore, it is still unclear whether barnacle geese on the Greenland 83 flyway align their spring migration more closely with primary productivity or 84

photoperiod or some other environmental factor. Furthermore, environmental factors 85 influencing migratory movements are likely to differ between spring and autumn: 86 Arctic-breeding white-fronted goose Anser albifrons spring migration is most closely 87 associated with the green wave as the birds aim to acquire breeding capital, 88 whereas autumn migration is most closely associated with wind conditions as the 89 birds aim to fly quickly to the wintering grounds (Kölzsch et al. 2016). The timing of 90 91 barnacle goose autumn migration has not been linked to particular environmental factors on any flyway, although Shariatinajafabadi et al. (2014) suggest it could be 92 93 related to atmospheric conditions.

94

Satellite telemetry is an excellent tool to study migratory movements in animals 95 where direct observation is unfeasible (Wilmers et al. 2015). Previous studies have 96 assessed the relationship between migratory movements of barnacle geese tracked 97 by satellite telemetry and satellite imagery of the green wave to link migratory 98 movements to environmental factors (e.g. Najafabadi et al. 2015). Here, we expand 99 on previous studies using a novel approach: we applied a Markov state-switching 100 model to telemetry data to relate behaviour - rather than location - to environmental 101 factors. This model identifies patterns of movement characteristics in telemetry time 102 series that represent discrete behavioural states, as well as time-dependent changes 103 104 in behavioural state. We can then test how various environmental factors influence the probability of switching behavioural state. Using this technique, we aim to test the 105 relative importance of three environmental factors associated with migratory 106 movements in Greenland barnacle geese: photoperiod, air temperature and forage 107 plant phenology. We expect that spring movements from the wintering grounds to 108 the breeding grounds, including main spring staging and other shorter stopovers, will 109

be associated with some or all of lengthening days, rising air temperatures and
forage plant growth. Conversely, we expect that autumn movements from the
breeding grounds to the wintering grounds, including main autumn staging and other
shorter stopovers, will be associated with some or all of shortening days, falling air
temperatures and forage plant senescence. Our results demonstrate how stateswitching models can provide further insight into seasonal movements of a longdistance Arctic migrant.

117

118 Methods

119 Transmitter tag deployment

Greenland barnacle geese winter on the north-west coasts of Ireland and Scotland 120 and migrate via Iceland to breed in north-east Greenland. A total of 28 tags were 121 deployed on barnacle geese in Ireland between 2008 and 2019: n = 5 (2008), n = 2122 (2009) and n = 2 (2010) on the Inishkea Islands, Mayo, n = 8 (2018) and n = 5123 (2019) on the Inishowen Peninsula, Donegal, and n = 6 (2019) in Lisadell, Sligo (Fig. 124 1a). Geese were captured using cannon nets and released immediately after tag 125 deployment. Tags from 2008-2010 comprised a 30-45g GPS-ARGOS platform 126 transmitter terminal (Microwave Telemetry Inc, Columbia MD) with an elastic body 127 harness attachment (final fitted weight of 45-65g respectively). Tags from 2018-2019 128 comprised a nanoFix® GEO+RF (Pathtrack Ltd, Otley, UK) on a neck collar 129 attachment (21mm high with an adjustable internal diameter of 36-44mm) with a final 130 fitted weight of ~15g and typical final internal diameter of 38-44mm. Tags from 2008-131 2010 collected a geographical coordinate fix at 2 hour intervals (including night time) 132 and transmitted data via the Argos system almost daily. Tags from 2018-2019 133 collected a fix at 6 hour intervals and transmitted these data via ultra-high frequency 134

radio to base stations on the wintering grounds. Both tag types were solar powered, 135 but the interval time between fixes was varied due to differing battery power and the 136 programmed intervals for data transfer varied with daylength to optimise battery 137 levels. Data was collected from deployment until the tag no longer transmitted data 138 (generally between 12 and 24 months). All birds with tags were also fitted with 139 individually inscribed legrings so that their survival could be monitored during winter 140 141 and staging in subsequent years. Records of legrings were submitted by volunteers conducting routine monitoring of barnacle geese in Ireland, Scotland and Iceland. 142 143

Data were received from 19 of the 28 deployed tags, 18 of which yielded near-144 complete time series for spring (1 March to 31 May, i.e. beginning of spring to 145 beginning of nesting) or autumn (14 August to 31 October, i.e. end of 146 breeding/moulting to beginning of winter). In spring, geese departed their primary 147 winter homerange as early as mid-March. Generally, they travelled from the north-148 west coast of Ireland, along the Outer Hebrides of Scotland to the Southern Region 149 of Iceland (some flew directly from Ireland to Iceland), then through the 150 Northeastern/Northwestern Regions of Iceland, over the Savoia Peninsula of 151 Greenland and along the east Greenland coast and islands as far north as 152 Danmarkshavn (Fig. 1c). In autumn, geese departed their primary summer 153 154 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 155 Westfjords of Iceland, through the Southern Region of Iceland and along the Outer 156 Hebrides as far south as Islay or north-western Ireland (again, some flew directly 157 from Iceland to Ireland) (Fig. 1d). During spring, geese moved northward on short 158 journeys punctuated with relatively regular and short stopovers (generally less than 2) 159

weeks) in the Outer Hebrides, the south coast of Iceland and north Iceland. Most 160 stopped at their "main" spring staging grounds near the north coast of Iceland (the 161 Vatnsdalsá, Huseyjarkvisl and Héraðsvötn rivers) for 3 to 4 weeks, before continuing 162 on short journeys and stopovers on the Savoia Peninsula and east Greenland 163 islands. In contrast, during autumn, geese moved southward over longer journeys 164 with relatively fewer but longer stopovers (generally between 1 and 3 weeks) on the 165 166 east Greenland islands and the Icelandic Westfjords. Most stopped at their "main" autumn staging grounds on the south coast of Iceland (Skeiðarársandur and 167 168 Kúðafljót) for 3 to 4 weeks, before flying almost directly to Islay or the north-west coast of Ireland 169

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171 <u>Environmental data</u>

Daily photoperiod was defined as hours between sunrise and sunset at the latitude 172 at which the bird was present at the time of the fix. Daily mean temperature (°C) was 173 sourced from the closest of six weather stations across the flyway at the time of the 174 fix (Fig. 1b and see Supplementary Information S1). Accumulated growing and 175 cooling degree days (GDDs and CDDs, based on the concept outlined by Burke, 176 1968) were used as a proxy for forage plant phenology in spring and autumn 177 respectively. The degree day (DD) was calculated as DD = MeanT - BaseT, where 178 MeanT is the daily mean temperature and BaseT is 5.5°C, the lowest temperature at 179 which forage plants generally grow (Burke 1968). The accumulated DDs for each 180 day were summed to provide a daily value, starting in February for spring and 181 August for autumn. For GDDs in spring, if BaseT was greater than MeanT (i.e. too 182 cold for growth), the DD value was zero, thus providing heat accumulation above the 183 base temperature. For the complementary CDDs in autumn, if BaseT was greater 184

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.

190

191 <u>State-switching model</u>

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

202

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

and did not result in any residual autocorrelation. We termed these two behavioural 210 states (i) settled and (ii) transiting. For the initial parameter value estimation, we 211 characterised the settled state as sequences of short steps (mean length of 10km) 212 and an equal likelihood of turning in any direction (mean angle of 0° at a 213 concentration of 0.1, where minimum concentration is zero), i.e. goose moving 214 slowly and undirected. We characterised the transiting state as sequences of long 215 216 steps (mean length of 100km) and a lower likelihood of directional change (mean angle of 0° at a concentration of 1), i.e. goose moving guickly in one direction. 217 218 Because step lengths are extremely variable and to capture step lengths between the values defined above, we specified a large standard deviation for step length (15 219 and 150km respectively). A gamma distribution was specified for step length, as all 220 values were positive but right skewed, and a von Mises distribution for turning angle, 221 as the data were circular and normal. To ensure there was no influence of different 222 sampling frequencies, we compared a model with 2-hour interval data removed and 223 a model with 6-hour interval data removed to a model containing all data. The 224 behavioural states identified by each model were comparable in terms of the ratio of 225 state 1 to state 2 and the proportion of time steps in state 1 and state 2, indicating 226 consistency between all data (see Supplementary Information S2 for model output). 227 228

Between each time step in the time series, the individual can either remain in its
current behavioural state or switch to a new state. Switching from a settled to
transiting state was taken to represent the beginning of a journey and, likewise,
switching from a transiting to settled state was taken to represent the end of a
journey. The resolution of our data could detect state switching at the principle
wintering/breeding grounds, at the "main" staging grounds and at shorter stopovers

along the way. The probability of switching state was tested in relation to 235 photoperiod, daily mean temperature and accumulated GDDs in spring or CDDs in 236 autumn. A full model containing pairwise synergistic interactions was compared to a 237 model containing all three covariates additively and models containing each 238 covariate individually, as well as a null model containing no covariates (a three-way 239 interaction was not included as a candidate due to variance inflation). The best 240 241 supported model was identified using the Akaike Information Criterion (AIC); the model with the lowest AIC value was selected (Akaike 1974). Model fit was assessed 242 243 by examining time series and auto-correlation functions of pseudo-residuals for residual patterns and plots of pseudo-residuals against standard normal quantiles for 244 deviation from normality. The pseudo-residuals from our model followed a standard 245 normal distribution, indicating the model described the data well. 246

247

248 **Results**

249 Spring migration

The best supported spring model included the covariate GDDs (Table 1). The settled 250 state had a median step length of 0.17km (lower quartile 0.06km, upper quartile 251 0.62km) and a mean turning angle of -3.11° with a concentration of 0.44 and the 252 transiting state had a median step length of 8.61km (lower quartile 2.19km, upper 253 quartile 47.77km) and a mean turning angle of 0.16° with a concentration of 0.68 254 (Fig. 2a, b). There was a significant effect of GDDs on state-switching probability: as 255 GDDs increased, the probability of switching from a transiting state to a settled state 256 decreased by -0.99 (95% CI -1.38 – -0.60). High GDDs values were associated with 257 a greater probability of being or remaining in a transiting state and a lower probability 258 of being in a settled state, suggesting that geese are more likely to journey between 259

sites as GDDs increase (Fig. 3a). Geese typically departed for Iceland when GDDs 260 at winter sites was at least 45, but on average 110, and departed for Greenland 261 when average GDDs at staging sites reached 45. We further compared early spring 262 (1 March to 14 April) and late spring (14 April to 31 May) and found that the effect 263 was stronger in late spring (β = -0.68, 95% CI -1.07 – -0.29) compared to early 264 spring (confidence intervals approaching the null value). Uncertainty around the 265 266 mean also increased as spring progressed (possibly as other factors, e.g. individual 267 internal state, act).

268

269 <u>Autumn migration</u>

The best supported autumn model included the covariate daily mean air temperature 270 (Table 1). The settled state had a median step length of 0.91km (lower quartile 271 0.27km, upper guartile 2.67km) and a mean turning angle of 3.14° with a 272 concentration of 0.21 and the transiting state had a median step length of 91.67km 273 (lower quartile 27.39km, upper quartile 195.46) and a mean turning angle of 0.01° 274 with a concentration of 1.36 (Fig. 2c, d). There was a significant effect of temperature 275 on state-switching probability: as mean temperature increased, the probability of 276 switching from a settled state to a transiting state decreased by -0.48 (95% CI -0.77 -277 -0.20). High mean temperature values were associated with a greater probability of 278 279 being in a settled state and a lower probability of being or remaining in a transiting state, suggesting that geese are more likely to journey between sites as 280 temperatures decrease (Fig. 3b). Birds typically departed their primary breeding 281 grounds at temperatures between 1.5°C and 5.5°C (mean 3.8°C) and crossed from 282 Greenland to Iceland when temperatures fell to between -1.2°C and 2.9°C (mean 283 1.6°C). 284

285

286 **Discussion**

Our hidden Markov model successfully identified two discrete behavioural states in 287 barnacle goose GPS time series. The results reveal that the Greenland barnacle 288 goose spring movements are most strongly associated with GDDs. This suggests 289 that the timing of spring migration is closely aligned with primary production, as 290 291 observed in the Russian and Svalbard populations (van der Graaf et al. 2006, Si et al. 2015, Shariati-Najafabadi et al. 2016). Because barnacle geese are a capital 292 293 breeding species, acquiring the majority of breeding reserves before arriving at the breeding grounds, increased forage availability may allow them to acquire the 294 necessary fuel reserves to proceed to the breeding grounds. The timing of autumn 295 296 movements are most strongly associated with daily mean air temperature. This suggests that autumn migration is closely aligned with atmospheric conditions, as 297 suggested by Shariatinajafabadi et al. (2014). As temperatures fall, the increased 298 thermoregulatory costs and relative inaccessibility of forage may limit the geese's 299 ability to persist in northerly sites. 300

301

302 <u>Phenological changes</u>

Climate disruption may have significant consequences for species that align their spring movements closely with primary productivity (Howard et al. 2020). In seasonal environments, migratory animals time their reproduction to coincide with the annual peak of primary productivity, which in turn is governed by climate. Emerging phenological mismatches between reproduction and primary productivity in both marine and terrestrial environments due to amplified climate warming rates in the 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, 310 light-bellied brent geese Branta bernicla hrota experience reduced breeding success 311 when there is a mismatch between chick hatching and peak plant nutrient availability 312 (Clausen and Clausen 2013). Mismatches are becoming more frequent because 313 plant phenology is advancing faster in their Arctic Svalbard breeding grounds than in 314 their temperate Danish staging grounds. Breeding success of caribou Rangifer 315 316 tarandus in Greenland is adversely impacted due to a mismatch between calving and peak forage availability (Post and Forchhammer 2008). The mismatch occurs 317 318 because the timing of spring migration to summer ranges for calving depends on photoperiod, which remains fixed, while plant phenology depends on temperature 319 and is advancing. In marine environments, little auks Alle alle and Brünnich's 320 guillemots Uria lomvia experienced reduced breeding success as the mismatch 321 between hatching and phytoplankton productivity increased (Ramírez et al. 2017). 322 The pulses of phytoplankton productivity advanced due to earlier sea ice melt, while 323 bird breeding activity did not. An uncoupling of plant phenology between temperate 324 Ireland/Scotland and Arctic Iceland/Greenland could have similar consequences for 325 reproduction in barnacle geese in the future. 326

327

The consequences of climate disruption for autumn migration has received less attention than spring, despite notable changes to the plant growth period, leafsenescence 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

similarly be able to delay departing their summer homerange if falling temperatures
are delayed. This may have particular implications for juveniles gaining extra time to
develop before their first full migration. However, to date, we do not have evidence of
a long term delay in the time of southerly post-breeding movements from Greenland.

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 position on a geographic map and found that the two behavioural states identified in 342 343 our model correlated coherently with the individual's geographic location and movements, suggesting that they were appropriately identified. Transiting behaviour 344 tended to be observed in unsuitable habitat or sea crossings and correlated with 345 known migration dates, while settled behaviour tended to be observed in suitable 346 and known forage or roosting habitat. Of nine geese carrying harness tags between 347 2008 and 2010, all tags successfully transmitted data and seven birds were known to 348 be alive the following year with their tags still attached, suggesting a survival rate of 349 >75%. Two birds were assumed lost at sea during migration; the contribution of the 350 tag to this is unknown, but one bird is known to have encountered strong headwinds 351 during the sea crossing. Of eight geese carrying neck collar tags in 2018, five tags 352 successfully transmitted data and seven geese were known to be alive the following 353 year (one having lost its tag but retained its legring), suggesting a survival rate of 354 >85%, which is similar to the 87% average survival rate of uninstrumented birds 355 reported by Doyle et al. (2020). Although 4 data series were obtained, data retrieval 356 and legring recording from the 11 geese tagged in 2019 was interrupted by the 357 COVID-19 pandemic from March until migration to Greenland (after which the geese 358

become inaccessible), therefore conclusions on the effect of tags on this cohortremained unknown at the time of writing.

361

362 <u>Conclusion</u>

This study successfully applied a Markov state-switching model to GPS time series 363 data of barnacle geese to detect migratory behaviour and examine the relationship 364 365 between the timing of changes in behavioural state and photoperiod, air temperature and forage plant phenology. Like the Russian and Svalbard populations, the 366 367 Greenland population spring migratory movements were more closely associated with forage plant phenology than with temperature or photoperiod. Autumn migratory 368 movements were more closely associated with temperature than plant phenology or 369 photoperiod. Increasing temperatures in the Arctic associated with climate disruption 370 is likely to advance forage plant growth in spring and extend summer temperatures 371 in autumn, therefore there is potential for continued climate disruption to alter the 372 traditional timing of barnacle goose and other Arctic bird migration. 373

374

375 Acknowledgements

We are grateful to David Tierney and Sean Kelly of the National Parks and Wildlife Service for their significant contribution to this research. We are also grateful to the Bryan Guinness Charitable Trust for their support. We extend our thanks to Daniel Moloney and Martin Enright for invaluable technical and field support and we thank Helen Boland, Olivia Crowe, Miriam Crowley, Kerry Mackie, Gerry Murphy, Patrick Manley, Barbara McInerney, Tim Roderick, Gerard Scott and family, Alyn Walsh and Ewan Weston for all their assistance with a challenging catching operation.

383

384	Funding
385	Our research was funded by an Irish Research Council Government of Ireland
386	Postgraduate Scholarship. Additional funding was also received from the National
387	Parks and Wildlife Service of the Government of Ireland and the Bryan Guinness
388	Charitable Trust.
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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Table 1. The AIC for each model is presented, along with the difference between 535

each model and the lowest AIC ($\triangle AIC$). Models include additive (+), synergistic (*) or 536 null (~1) effects. 537

	model	AIC	∆AIC
	~GDDS	27535.89	0.00
	~temperature * daylength + GDDS	27536.32	0.44
	~temperature + GDDS + daylength	27537.74	1.86
spring	~temperature + GDDS * daylength	27538.04	2.15
migration	~temperature * GDDS + daylength	27539.12	3.23
	~daylength	27551.29	15.40
	~temperature	27558.56	22.67
	~1	27630.79	94.91
	~temperature	24598.07	0.00
	~temperature * daylength + CDDS	24600.68	2.61
	~temperature + CDDS + daylength	24601.37	3.31
autumn	~temperature + CDDS * daylength	24602.63	4.56
migration	~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)

Location of the six weather stations along the Greenland flyway. (c) Tracking data 540 recovered from tags in spring and (d) autumn. 541



- 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.



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

Model	State	Step Length		Turning	g 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 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.

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	g 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	g 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	g 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