

Ocean-wide drivers of migration strategies and their influence on population breeding performance in a declining seabird

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Keywords: Atlantic puffin, competition, density-dependence, migratory connectivity, migration, seabirds, seasonal interactions

This is a pre-copyedited, author-produced PDF of an article accepted for publication in the journal Seabird following peer review. The version of record can be found here:

[http://www.cell.com/current-biology/fulltext/S0960-9822\(17\)31454-9](http://www.cell.com/current-biology/fulltext/S0960-9822(17)31454-9)

Full citation: Fayet, A. L., Freeman, R., Anker-Nilssen, T., Diamond, A., Erikstad, K. E., Fifield, D., ...

Guilford, T. (2017). Ocean-wide Drivers of Migration Strategies and Their Influence on Population Breeding Performance in a Declining Seabird. *Current Biology*, <https://doi.org/10.1016/j.cub.2017.11.009>

40 **Summary**

41 Which factors shape animals' migration movements across large geographical scales, how different
42 migratory strategies emerge between populations, and how these may affect population dynamics, are central
43 questions in the field of animal migration [1], which only large-scale studies of migration patterns across a
44 species' range can answer [2]. To address these questions we track the migration of 270 Atlantic
45 puffins *Fratercula arctica*, a red-listed, declining seabird, across their entire breeding range. We investigate
46 the role of demographic, geographical, and environmental variables in driving spatial and behavioural
47 differences on an ocean-basin scale, by measuring puffins' among-colony differences in migratory routes
48 and day-to-day behaviour (estimated with individual daily activity budgets and energy expenditure). We
49 show that competition and local winter resource availability are important drivers of migratory movements,
50 with birds from larger colonies or with poorer local winter conditions migrating further and visiting less
51 productive waters; this in turn led to differences in flight activity and energy expenditure. Other behavioural
52 differences emerge with latitude, with foraging effort and energy expenditure increasing when birds winter
53 further north in colder waters. Importantly, these ocean-wide migration patterns can ultimately be linked
54 with breeding performance: colony productivity is negatively associated with wintering latitude, population
55 size and migration distance, which demonstrates the cost of competition and migration on future breeding,
56 and the link between non-breeding and breeding periods. Our results help understand the drivers of animal
57 migration and have important implications for population dynamics and the conservation of migratory
58 species.

59 **Results**

60 The drivers of animal migration across large geographical scales are poorly understood. Tracking studies
61 have started to reveal the diversity of long-distance migration strategies, and the need to broaden the usual
62 definition - a long return journey to a specific overwintering destination following the breeding season [3] -
63 to encompass a larger range of migration patterns, including journeys to a single [4] or multiple [5,6] areas,
64 sometimes using various routes to get there [7]. Studies examining species' migration patterns across
65 multiple populations have increased, but few are sufficiently large-scale to reveal the migration landscape of
66 entire species, and those which remain largely descriptive [2,8]. Therefore our understanding of which
67 factors shape species' migration movements, how different migration strategies emerge between populations,
68 and whether these affect population dynamics, remains poor [1]. Potential drivers of migration include
69 competition, leading to density-dependent migratory distance (animals from large populations migrating
70 further [9]) or quality-dependent migratory distance (sub-dominant, low quality individuals migrating further
71 [10]), as well as winter resource availability close to the breeding grounds (animals in low quality habitat are
72 more likely to migrate [11]). Differences could have a genetic basis, resulting in closely-related colonies
73 following similar migration patterns [12]. Whether such mechanisms drive intraspecific differential
74 migratory strategies across large scales, and whether these may affect populations' fitness, is unknown.
75 These questions are particularly important for species with high migratory connectivity, where different
76 populations migrate to distinct areas [13], as they could help understand how different populations may be
77 under different selective pressures due to migratory differences, as shown in invertebrates [14], fish [15] and
78 birds [16]. This could also have important implications for conservation by making specific species or
79 populations more vulnerable to changes in their winter habitat [17,18]. Breeding and migration are linked
80 throughout annual cycles [19], and fitness differences between populations or individuals migrating to
81 different destinations have been found in multiple species [20-22]. Determining how differences in migration
82 strategies can shape fitness landscapes across multiple populations and perhaps even across an entire species'
83 range is therefore paramount to understanding migratory species' population dynamics.

84 We address these questions in an unprecedented large-scale and in-depth study of the migration strategies of
85 a long-distance migrant, the Atlantic puffin *Fratercula arctica*, across its entire range. Puffins around the

86 British Isles show considerable variation in migration strategy [23-25], and there is evidence from a single-
87 colony study that breeding success varies among migratory routes [26]. Whether this diversity of migration
88 strategies exists across the species' range, and whether it has fitness consequences, are particularly important
89 questions to answer, because some puffin populations (but not all) have dramatically declined in the last few
90 decades [27-29], and the species is now endangered in Europe [30]. This apparent variability in migratory
91 strategies and population trends among populations makes puffins an ideal species to investigate species-
92 wide drivers of migration and the potential fitness consequences of different migration strategies. We track
93 the migration of 270 adult puffins from 13 populations covering all major breeding grounds across the North
94 Atlantic, including novel data from 12 populations in Canada, Iceland, Ireland, Norway, UK and USA. We
95 combine spatial, behavioural, and environmental data to: (i) determine puffins' full non-breeding
96 distribution, their migratory connectivity between colonies, and assess spatial and behavioural differences
97 between colonies; (ii) investigate ocean-wide migration strategies and the role of geographical,
98 environmental and demographic variables on shaping these spatial and behavioural patterns; (iii) test the
99 potential consequences of different migration strategies on colony productivity.

100 Distributions differed substantially between colonies (Figure 1, Figure S1). No colony was totally spatially
101 segregated; all 90% occupancy kernels overlapped with 2-4 other colonies (Table S2), but overlap decreased
102 with distance between colonies (LM, $n=28$, $F_{1,26}=11.45$, $P=0.002$). Wintering hotspots were found around and
103 south of Ireland, south west of Iceland, at the entrance of the Labrador Sea and near the Charlie-Gibbs
104 Fracture Zone in the mid-North Atlantic (Figure 1c). Segregation was high between core utilisation areas
105 (50% kernels), most colonies overlapping by <3% (Table S2). Most birds wintered in multiple locations and
106 so distributions varied throughout the winter (Figure S1). Colonies differed in the total distance covered
107 overwinter, with birds from some colonies covering thousands of km more than others (LMM, $n=215$,
108 $\chi^2=80.5$, $P<0.001$; Table 1; Table S3), and in the birds' average distance from the colony, ranging from
109 <250km to >1,700km ($n=215$, $\chi^2=261.8$, $P<0.001$; Table 1; Table S4). These spatial differences led birds
110 from different colonies to experience different environmental conditions overwinter (Table 1), both in terms
111 of temperature and water productivity ($n=190$, SST: $\chi^2=301.3$, $P<0.001$; chlorophyll-a: $\chi^2=118.6$, $P<0.001$).
112 The SST experienced by puffins was bimodal, with peaks around 6 °C and 11 °C (Figure S2).

113 Colonies also differed behaviourally (Table 1), with different flight and foraging effort ($n=162$, flight:
114 $\chi^2=72.8$, $P<0.001$; foraging: $\chi^2=49.7$, $P<0.001$). Exposure to different day lengths at different latitudes
115 (Table 1, $n=190$, $\chi^2=70.2$, $P<0.001$) presumably affected the opportunity to engage in flight and foraging
116 (puffins do not dive at night [31]) and their intensity. To account for this we compared the proportion of
117 daylight hours spent flying and foraging between colonies (“intensity”). Flight and foraging intensity
118 differed between colonies ($n=190$, sustained flight: $\chi^2=95.5$, $P<0.001$; foraging: $\chi^2=69.0$, $P<0.001$).
119 Sustained flight was the least frequent behaviour (0.6-4.9% of daylight hours) but varied greatly between
120 colonies, with birds spending 17-102h in flight (5-29min/day). Puffins spent 15-35% of daylight hours
121 foraging, or 385-753h in total (1.8-3.5h/day). Therefore all birds spent the majority of daylight hours sitting
122 on the water. Daily and total energy expenditure varied significantly among colonies (DEE: $n=190$,
123 $\chi^2=367.4$, $P<0.001$; total EE: $n=168$, $\chi^2=252.5$, $P<0.001$).

124 We tested whether geographical (latitude), environmental (SST and chlorophyll-a) and demographic
125 (population size) variables drive migratory behaviour. We found ocean-wide migration patterns, mainly
126 driven by colony size and wintering latitude, and mediated by environmental factors (Figure 2a). A first key
127 finding is that puffins from larger colonies, and where local winter conditions were poorer, migrated further
128 (LM, $n=12$, $R^2=0.63$, colony size: p.e.= 0.15 ± 0.08 , $F_{1,9}=14.7$, $P=0.004$; chlorophyll-a: p.e.= -0.53 ± 0.22 ,
129 $F_{1,9}=6.1$, $P=0.036$, Figure S3), which supports competition as a driver of migration. These birds spent more
130 time in flight (p.e.= 0.03 ± 0.01 , $F_{1,9}=6.7$, $R^2=0.36$, $P=0.029$) and consequently increased their DEE
131 (p.e.= 1.0 ± 0.4 , $F_{1,9}=5.8$, $R^2=0.33$, $P=0.038$); interestingly they also visited waters with lower chlorophyll-a
132 (p.e.= $-5.9e^{-4}\pm 9.9e^{-5}$, $F_{1,10}=34.5$, $R^2=0.75$, $P<0.001$, Figure 2b). Latitude, strongly linked with temperature,
133 also drove ocean-wide migration patterns. Puffins wintering at higher latitudes spent more time foraging
134 (p.e.= 0.25 ± 0.09 , $F_{1,9}=7.4$, $R^2=0.39$, $P=0.024$), experienced colder waters (p.e.= -0.03 ± 0.009 , $F_{1,10}=13.7$,
135 $R^2=0.53$, $P=0.004$), and had higher DEE than birds wintering further south (p.e.= -32.9 ± 6.9 , $F_{1,9}=22.9$,
136 $R^2=0.69$, $P<0.001$, Figure 2c). How far from the colony birds migrated was unrelated to latitude
137 (p.e.= 0.03 ± 0.03 , $F_{1,10}=2.2$, $R^2=0.09$, $P=0.171$), so these two patterns occurred in parallel.

138 A second key finding is that these ocean-wide patterns were related to colony productivity. More
139 specifically, colony productivity was best predicted by a combination of winter latitude, colony size, average

140 distance from the colony, and winter chlorophyll-a levels (overall additive model compared to the null
141 model: LM, $n=11$, $F_{4,6}=13.6$, $R^2=0.84$, $P=0.004$, $\Delta AIC=-17.4$, Figure 3). In this model, all explanatory
142 variables were negatively correlated with colony productivity but with only marginal significance for
143 chlorophyll-a (latitude: residual p.e. $=-1.8e^{-2}\pm 4.8e^{-3}$, $t_9=-3.7$, $P=0.009$; colony size: residual p.e. $=-5.8e^{-7}\pm 1.6e^{-7}$,
144 $t_9=-3.6$, $P=0.011$; distance from colony: residual p.e. $=-2.8e^{-4}\pm 1.1e^{-4}$, $t_9=-2.6$, $P=0.039$; chlorophyll-a :
145 residual p.e. $=-0.3\pm 0.1$, $t_9=-2.3$, $P=0.061$ – where residual p.e. represents the effect of a single predictor on the
146 residual variation in productivity after taking into account the other three predictors). These relationships
147 occurred together and not separately, therefore latitude, colony size and migration distance all explained a
148 significant amount of variation in colony productivity not explained by the other three (see STAR Methods
149 for details). In other words, high winter latitude, large colony size and long migration distance (and to a
150 marginal extent, low ocean productivity at the wintering grounds) were all associated with low colony
151 productivity.

152 **Discussion**

153 We investigated the role of environmental, geographical and demographic factors as large-scale drivers of
154 migration strategies across a species' range. We found that colony size, local winter resource availability,
155 and latitude drive large-scale spatial and behavioural migratory patterns, and that these patterns are
156 ultimately linked with colony breeding productivity.

157 The overall winter distribution, likely representative of the puffin world population, covers most of the
158 winter range known from ringing recoveries [32], across the North Atlantic from the 30° parallel to north of
159 the Arctic Circle. During breeding, puffins forage close to their colony [32] and our study populations should
160 be completely segregated. This segregation stops during non-breeding, with some limited migratory
161 connectivity evident, as distributions of all colonies overlap with one to three others. Some of the areas
162 visited by multiple colonies are known hotspots for other marine species [7,33-36], most likely because of
163 highly productive waters [37].

164 Migration routes varied strikingly between colonies, some birds migrating >1700 km away while others
165 stayed within <250km from their colony. These complex patterns do not fit the well-known “leap-frog” or

166 “chain” migration patterns often observed in species breeding across a wide latitudinal range [3,38], and are
167 unusual. Species often share one wintering site (European rollers *Coracias garrulus* [8]) or a few (black-
168 legged kittiwakes *Rissa tridactyla* [2], Monarch butterflies *Danaus plexippus* [5], bobolinks *Dolichonyx*
169 *oryzivorus* [39], with the exception of a few (mostly marine) species such as Atlantic cod *Gadus morhua*
170 [40] and leatherback turtles *Dermochelys coriacea* [6]. The drivers of such complex migratory patterns are
171 unclear. In cod, there is evidence for the role of quality-dependent competition, with only large, strong
172 individuals going on long migrations; however industrial fishing seems to have changed the selection
173 pressures on migratory distance [41]. There is evidence in puffins from the Celtic Sea that individuals taking
174 the longest migration route to the Mediterranean Sea breed more successfully [26]. This however remains to
175 be shown for other colonies.

176 Distance from the colony was unrelated to colony latitude, suggesting that all birds did not search for the
177 same environmental conditions. In fact, puffins from different colonies experienced different day length,
178 temperature and water productivity, which led to different behavioural patterns and energy expenditures.
179 This may result different populations being under different selective pressures, as occurs in thrushes [16] or
180 salmon [15]. We identified multiple ocean-wide patterns in migratory strategies, driven by three main
181 variables. One was colony size, a good predictor of migration distance. Density-dependent competition is
182 therefore likely to be an important driver of migration. Larger populations may deplete resources near
183 colonies and lead birds to exploit more distant areas and spread more [42]. This is an adaptation of
184 Ashmole’s hypothesis for migratory behaviour [9,43]. Supporting theoretical predictions, local winter
185 resource availability also plays a role. Models of partial migration predict increasing migrants to residents
186 ratios when the relative difference in habitat quality between breeding and wintering site increases [11,44].
187 Support for this hypothesis has been found in multiple taxa, including birds [45], mammals [46], and
188 amphibians [47]. While most puffin populations seem to be fully migratory, our finding that individuals from
189 colonies with poorer local winter water productivity migrate further implies a similar process. In other
190 words, birds migrate further from the colony both when local habitat quality is poor and intra-specific
191 competition (mediated by colony size) is high.

192 Birds migrating further spent more time in flight, leading to higher DEE (flight is costly in auks [48]).
193 Puffins migrating to higher latitudes visited colder waters and, despite experiencing shorter days, spent more
194 time foraging, which also resulted in higher DEE. Higher foraging effort at high latitudes may not reflect
195 lower resource availability (we found no correlation between chlorophyll-a and SST) but increased calorific
196 requirements, due to the larger mass of birds further north and lower temperatures requiring additional
197 thermoregulation [49]. Therefore, we show that geographical and environmental parameters and
198 demographics shape the wintering behaviour and energy expenditure of a migratory species at a population
199 level across its entire range. A key result is that these ocean-wide patterns are linked with population
200 productivity across the species' range. Although qualitative, the first link between wintering area and
201 breeding success at a similar scale was found in thick-billed murre *Uria lomvia*, with stable populations
202 mostly wintering near Canada and declining populations mostly wintering east of Greenland [33]. Here we
203 found three predictors of colony productivity: colony size, wintering latitude and migratory distance (and, to
204 a lesser extent, water productivity at the wintering grounds). Larger colonies where birds migrated further, to
205 higher latitudes and poorer waters, had lower productivity, which demonstrates a cost of migration at a
206 species' range level. These birds spent more time engaged in energy-demanding activities such as flight and
207 foraging, experienced colder temperatures, and consequently had higher winter energy expenditure. Whilst
208 only experimental studies can definitively identify causal processes, one consistent mechanism could be that
209 because of increased energy expenditure overwinter birds may return to the colony in poorer condition,
210 which is known to delay breeding and reduce breeding success in many species. Winter habitat quality
211 affects arrival time at the breeding grounds, body condition, and subsequent breeding performance in many
212 migratory terrestrial species [50]. In marine species, SST can affect subsequent breeding success in a colony
213 [51,52]. We show that this is true across a much larger scale. Spring or summer environmental conditions
214 have been linked to breeding performance in several seabirds, probably by affecting prey availability during
215 chick-provisioning [27,53,54]. Reproductive performance is therefore likely to be affected by a combination
216 of prey availability during breeding (itself affected by colony size through density-dependent competition),
217 and adult body condition related to previous winter conditions. The negative relationship between colony
218 size and productivity raises questions about the origin and maintenance of large colonies. The answer
219 presumably relates to food availability near the colony during breeding [27]. While we cannot investigate
220 changes in migratory paths, environmental conditions and breeding productivity over time with our current

221 dataset, our findings suggest that large puffin colonies may not be sustainable anymore, perhaps because of
222 long-term changes in environmental conditions near the breeding [55] or wintering grounds [56], affecting
223 both the birds' ability to refuel in winter and feed their offspring in summer. This is also likely to be the case
224 for other species which have undergone similar declines in large northern colonies [57].

225 Our study provides unprecedented insight into the spatial and behavioural migration patterns of an avian
226 species. It reveals how competition, geographical and environmental parameters drive a species' migratory
227 strategies across its range, and how migration patterns are reflected in population-level breeding
228 performance. This study starts to uncover these important relationships and warrants further research into the
229 species-wide drivers and fitness consequences of migration, with important points such as the effect of
230 migration strategies on survival and the consistency of these patterns over time waiting to be explored. Our
231 findings highlight the need for, and benefits of, large-scale collaborative studies to help understand the
232 mechanisms behind the development of animals' migratory routes and determine which factors most
233 influence breeding performance and population dynamics. Such knowledge is also invaluable to understand
234 and tackle widespread population declines in migratory species, with marine species especially under threat
235 by fisheries, pollution and climate change.

236 **Author Contributions**

237 ALF and TG conceived the study, all authors collected data, ALF, RF and GJR analysed the data. All authors
238 critically discussed the results. ALF wrote the manuscript with the help of all authors.

239 **Acknowledgements**

240 We thank the many people who helped with fieldwork on all the different colonies, with special gratitude to
241 Dave Boyle (Skomer), Francis Daunt (Isle of May), Jeremy Tornøse and Tanguy Deville (Hornøya) and
242 Stefanie Collar (Machias Seal Island). ALF is funded by a Browne Junior Research Fellowship at The
243 Queen's College (Oxford). AS is supported by a JSPS Fellowship for Young Scientists. This work was
244 supported by Microsoft Research Cambridge, the Department of Zoology of Oxford University, the Mary

245 Griffiths Fund, the RSPB, the Wilson Ornithological Society, the Welsh Ornithological Society (Skomer), by
246 The Natural Environment Research Council and Scottish Natural Heritage (Isle of May), the Norwegian
247 Research Council (project 216547 to KEE) and the SEAPOP programme (Hornøya and Røst, Norway),
248 Science Foundation Ireland and the Zoological Society of London Good Gifts Programme (Ireland),
249 Canadian Wildlife Service, Environment and Climate Change Canada, New Brunswick Wildlife Trust Fund,
250 with logistic support by Canadian Wildlife Service and Canadian Coastguard (Machias Seal Island).

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382

383 **Figure & Table Legends**

384 **Figure 1. Winter distribution of Atlantic puffins across their range.** (A) Density distribution of puffins
385 from all study colonies across the non-breeding season, obtained by weighting occupancy kernels by colony
386 size (colony or archipelago sizes are indicated with circles of different size). *Italic names after each colony's*
387 name represent the name used to describe the colony in the main text. The unit of the grey parallels and
388 meridians is 5°. The blue parallels indicate the approximate latitudinal breeding range of puffins. (B)
389 Occupancy kernels for each colony across the non-breeding season, with each colony in a different colour
390 (the kernel for the Irish colony is contoured in green for clarity). (C) Overlap between the 90% occupancy
391 kernels of 2 to 4 different colonies. On the lower panels, colonies are indicated with black squares. The light
392 blue shade represents the approximate ice edge at its mid-winter level. See also Figure S1 and Table S2.
393 (photo: A. Fayet).

394 **Figure 2. Ocean-wide patterns of puffins' migratory strategies.** (A) Summary of the ocean-wide patterns
395 of migratory strategies driven by colony size, winter latitude and environmental variables at the whole
396 population level. Arrows indicate significant relationships between variables (see main text for statistics). (B-
397 C) Graphical representations of some of the relationships from the summary figure (A), more specifically the
398 association between (B) winter chlorophyll-a and distance from the colony and between (C) winter DEE and
399 winter SST. Regression lines, 95% confidence intervals (grey areas), R^2 and P values are obtained from
400 linear models. See also Figure S3.

401 **Figure 3. Relationship between ocean-wide patterns and colony productivity.** Effect size plots for the
402 model of colony productivity as a function of winter latitude, colony size, distance from colony and
403 chlorophyll-a, obtained from the best model of colony productivity. Each plot represents the effect of a
404 single predictor on the residual variation in colony productivity after the variation explained by the other
405 three variables was taken into account. The slope of the relationship is represented by a black line, with the
406 95% confidence intervals in grey. All values are obtained from the LM of colony productivity. See also
407 Figure S4.

408 **Table 1. Spatial, behavioural and environmental characteristics of puffin migratory routes from**
409 **different colonies.** The “intensity” values of time represents the percentage of daylight hours spent engaged
410 in a particular behaviour, while total time represents the number of hours spent in this behaviour over the
411 whole non-breeding season (mean±SE). See also Figure S2, Table S3 and S4.

412 **STAR Methods**

413 *Contact for Reagent and Resource Sharing*

414 Further information and requests for resources should be directed to and will be fulfilled by the Lead
415 Contact, Annette Fayet (annette.fayet@gmail.com).

416 *Experimental Model and Subject Details*

417 Between 2007 and 2015, adult Atlantic puffins *Fratercula arctica* were caught on 13 colonies across their
418 breeding range (Table S1). Birds were caught at the nest (all colonies) or in a mist net (Røst only) during the
419 chick-rearing period in June-July, between 2007 and 2015. Birds were ringed using a metal ring, and a
420 geolocator was attached either to the metal ring or an additional plastic ring (models Mk13, Mk14, Mk18 -
421 British Antarctic Survey, Mk4083, Mk4093 or Mk3005 – Biotrack, C65 – Migrate Technology, or LAT2900
422 - Lotek). Birds were recaptured in subsequent years using the same technique to remove or replace the
423 device. All work was conducted after ethical approval from the appropriate organisation from each
424 respective country. To avoid disturbance, handling was kept to a minimum. Recapture rate was high (>70%
425 on average) and when it was possible to compare survival of manipulated and control birds no detectable
426 difference was found [23,26].

427 *Method Details*

428 **Study sites**

429 Puffins breed across the North Atlantic, approximately between 42° and 80° latitudes and -70° and 65°
430 longitudes. Our study colonies include all major breeding areas across this range (Figure 1a), except
431 Svalbard (< 10,000 pairs, often inaccessible) and the Faroe Islands (~400,000 pairs). While colonies vary in
432 size from a few hundred to several hundred thousand pairs, most are part of archipelagos and we used the
433 total population of the archipelago as a measure of population size. Because the definition of archipelago can
434 vary among archipelagos and sometime includes extremely distant islands, we only included population
435 estimates from islands located within 100km of each study colony, well over the distance where puffins from

436 distinct colonies would be expected to overlap during breeding, as they are thought to forage within ~30km
437 of the colony during breeding. A list of the archipelagos used is available in Table S1.

438 **Spatial data**

439 In total 270 migration tracks (including 240 complete ones) were collected, representing 270 different
440 individuals (Table S1). Light data were decompressed and processed using the BASTrack software suite
441 (British Antarctic Survey) and MatLab R2010b (MathWorks Inc.). Data were filtered using speed and
442 equinox filters identical to those used in [26], and data corresponding to the breeding season were removed
443 (15 March – 15 August – a wide window chosen to encompass breeding across all colonies). We calculated
444 2-day median positions for all tracks and filtered out those with high standard error ($SE_{\text{longitude}} > 150$ km,
445 $SE_{\text{latitude}} > 150$ km) or unrealistic locations (longitude $> 65^\circ$ or $< -73^\circ$, latitude $< 30^\circ$ or $> 80^\circ$). After filtering
446 the average latitudinal range used by birds was 3007 ± 247 km, and the average longitudinal range was
447 3108 ± 435 km (Table S1). The range was not simply proportional to the number of birds tracked from each
448 colony (LMs, latitudinal range: p.e. = 0.2 ± 0.2 , $t_6 = 1.4$, $P = 0.215$; longitudinal range: p.e. = 0.5 ± 0.9 , $t_6 =$
449 0.6 , $P = 0.576$); for example the latitudinal range of birds from the North Sea (55 birds) was ~ 2.5 smaller
450 than the one of birds from the Icelandic colony of Stórhöfði (8 birds). Average winter latitude reflected
451 colony latitude (LM, p.e.= 0.9 ± 0.1 , $F_{1,6} = 47.6$, $P < 0.001$). Spatial occupancy kernels were calculated with
452 ArcGIS 10.0 (ESRI) and Geospatial Modelling Environment 0.7.2 (Spatial Ecology LLC) (parameters:
453 bandwidth ~275km, resolution ~20km) and the overlap between colonies was calculated with the
454 `{adehabitat}` package in R. We estimated distance from the colony as the great-circle distance between the
455 colony and each position. To account for the flight around the Iberian Peninsula for birds visiting the
456 Mediterranean Sea (puffins do not fly far over land), distance from the colony was calculated as the distance
457 between the actual position and the Strait of Gibraltar, and added to the shortest distance between the Strait
458 and the colony. A similar correction was applied to birds flying from the North Sea around the north of
459 Scotland into the Atlantic. Daily average distance and total distance covered were calculated for each track
460 by averaging or summing the great-circle distances between each 10-day median from 15 August to 15
461 March.

462 **Activity budgets and energy expenditure**

463 We estimated at-sea activity budgets using the same method as in [26], using salt-water immersion data
464 collected by geolocators. Briefly, each 10-minute interval during daylight (defined as with light levels >15%
465 of the maximum light level recorded by the geocator) between mid-August and mid-March was allocated
466 one of three categories: mostly ($\geq 98\%$) dry, mostly ($\geq 98\%$) wet and intermediate ($> 2\%$ dry and $> 2\%$ wet).
467 These have been shown to represent 3 main classes of behaviour (sustained flight, sitting on the water, and
468 foraging-related activity, respectively) by other studies using additional GPS, dive loggers and automated
469 classification methods (e.g. Hidden Markov Models) in a shearwater species [58]. The 98% threshold-based
470 classification leads to very similar results to automated classification [59]. For each behaviour two daily
471 variables were calculated: the proportion of time spent in the behaviour per total amount of daylight
472 available (flight or foraging “intensity”); and the total amount of time spent in this behaviour (flight or
473 foraging “effort”). These daily measures were then averaged (proportions of time) or added (total amount of
474 time) over the entire non-breeding period. On some occasions saltwater-immersion loggers stopped before
475 birds returned to the colony, and so only tracks for which saltwater-immersion data were available for at
476 least 70% of the non-breeding season were included in this analysis, and only complete or nearly-complete
477 tracks ($> 75\%$ complete, adjusted to the total non-breeding duration) were used to calculate cumulative
478 variables over the whole winter (by “winter” we mean the entire non-breeding season, as there was no
479 obvious migration-wintering-migration pattern but rather multiple bouts of movements alternated with bouts
480 of “stopover” throughout the whole non-breeding period). We estimated daily energy expenditure (DEE)
481 with the same method as in [26]. Briefly, we used day-time and night-time activity budgets (night-time
482 behaviour was classified into sitting on the water and sleep, with sleep periods identified by long dry bouts
483 when birds tuck one leg under their wing) and DEE and allometric equations from physiological studies of
484 free-living auks [48,60]. The birds’ mass used in the allometric equation was the average mass measured at
485 each colony during breeding, using a sample of > 10 birds (Table S1). More details on the activity budget
486 classification and the estimation of DEE can be found in [26]. As the 3 classes of behaviour are
487 complementary (the 3 proportions adding to 1), we only included time in flight and foraging activity in our
488 analysis to avoid using variables constrained by each other. We considered flight and foraging to be the most
489 relevant variables on account of being more energy consuming, more directly related to energy intake, and
490 potentially more likely to be related to overall body condition.

491 **Environmental data**

492 Sea-surface temperature (SST, °C) and chlorophyll-a concentrations (mg/m³, a proxy for ocean productivity)
493 were extracted from the NASA OceanColor website using data from the MODIS Terra and Aqua satellites,
494 using a spatial resolution of 50 km (~ the maximum resolution of geolocation data) and a temporal resolution
495 of 8 days (to limit gaps in the data due to cloud cover), and were smoothed over a 350 km-grid (~ twice the
496 average resolution of geolocation data). Each location from the dataset was assigned an SST and
497 chlorophyll-a value. To test whether environmental conditions were potential drivers of at-sea behaviour and
498 explain inter-colony differences in spatial and behavioural migratory strategies, each track was assigned an
499 SST and chlorophyll-a value averaged over the whole track, and average values were calculated for each
500 colony. To estimate local winter habitat quality near the colony, chlorophyll-a was extracted at regular 0.1°
501 longitude and latitude intervals within a 250km radius around each colony (points on land were excluded)
502 from September to February, on the year corresponding to the tracking period, and averaged for each colony.

503 **Colony productivity**

504 It was not possible to collect individual breeding success data of tracked birds at all colonies (birds were not
505 always caught at their nest), and so colony productivity was used instead to allow consistency of
506 measurements across colonies. Productivity was measured at all but one colony (only qualitative data were
507 available for Ireland and so were not included, Table S1). Note that the productivity at Hornøya may have
508 been affected by mink predation, which occurred concurrently with the tracking study. The methods were
509 comparable across all colonies (see [26,53,61] for examples of published protocols) and are briefly described
510 here. Each year a set number of burrows were observed at regular intervals during the breeding season to
511 determine occupancy. Occupied burrows were checked later in the season to determine the proportion which
512 hatched chicks, and later on the proportion of nests whose chick (i) had fledged or (ii) survived long enough
513 to be very likely to fledge successfully (chick mortality is high in the first week but chicks which survive
514 their first 2-3 weeks are very likely to fledge successfully). The observation methods varied slightly between
515 colonies, and were done either by direct observation of the nest (by hand or with an infrared endoscope) or
516 by repeated observations of puffin activity at the nest (e.g. regular 24h watches looking for parents bringing
517 fish to the burrow, an unmistakable sign of chick provisioning). Colony productivity was calculated as the

518 average number of chicks fledged per occupied burrow at each colony (maximum one chick per nest per
519 year). In this study we averaged the productivity of each colony over the tracking period or as close to the
520 tracking period as possible, to reflect the productivity of the colony at the time the birds were tracked.

521 *Quantification and Statistical Analysis*

522 Some colonies were pooled for the spatial analyses because of small sample sizes, their proximity to others,
523 and the lack of major differences between tracks. The 4 Icelandic colonies (~ 300 km apart) were pooled as
524 one “Iceland” group, the two colonies from Maine and the colony from the Bay of Fundy (< 150 km apart)
525 were pooled as one “Gulf of Maine” group, resulting in 8 principal colonies. For readability, all colonies or
526 groups of colonies in the main text are called by the name of the body of water they represent (or, when not
527 possible, their country). The 8 principal colonies are therefore hereafter referred to as Barents Sea, Celtic
528 Sea, Gulf of Maine, Iceland, Ireland, Newfoundland, North Sea and Norwegian Sea (Figure 1a). When
529 investigating potential relationships between behaviour, latitude and environmental conditions, all colonies
530 were counted separately (n=12, with the two very close Maine colonies remaining pooled together) but
531 sample sizes vary depending on the variables included in the model (colony productivity is only available for
532 11 colonies, and immersion data for 10).

533 Linear Mixed-Effects Models (LMMs) including year as a random effect (*lme4* package in R) were used to
534 test for among-colony differences in spatial characteristics (total distance covered, average distance from the
535 colony), activity budgets (proportion of time and total amount of time spent in different behavioural states),
536 energy expenditure, and environmental conditions. For analyses including population size, the population
537 size of the entire archipelago was taken for colonies within an archipelago (Table S1). Although study year
538 varied between colonies, we did not include it in the models for lack of degrees of freedom and because
539 evidence suggests puffins are repeatable in their migration route [26] and large scale environmental changes
540 usually take place over longer periods, hence our metrics are unlikely to vary significantly over the duration
541 of our study. Posthoc pairwise comparisons between colonies were realised with *lsmeans* in R (with
542 adjustment for multiple comparisons). Relationships between at-sea behaviour and environmental factors
543 were tested with LMMs with year and colony as random effects. Linear models (LM) were used in R to test
544 for relationships between behaviour, latitude and environmental conditions across colonies. To determine

545 whether ocean-wide patterns could help predict colony productivity, we used Akaike Information Criteria
546 and R^2 to select the best model predicting colony productivity (using additive models without interaction
547 between variables given our limited degrees of freedom). Data were log-, arcsin- or sqrt-transformed to meet
548 parametric assumptions when necessary (residuals were checked for normality). Means expressed in the text
549 are \pm SE unless stated otherwise. Significance was defined at the 5% level. All statistical details for each test
550 (e.g. sample size, parameter estimates, degrees of freedom, test statistics, P-value) can be found in the
551 Results section. Note that in the first part of the Results the sample size n refers to the number of birds (or
552 migration tracks), while in the second part, when we investigate ocean-wide patterns, it refers to the number
553 of populations.

554 **Model of colony productivity**

555 Colony productivity was best predicted by four variables, and covariance analyses were run on these
556 variables. Out of the four predictors of colony productivity (winter latitude, colony size, distance from
557 colony and chlorophyll-a), chlorophyll-a decreased with distance from the colony (p.e. = $-5.9e^{-4} \pm 9.9e^{-5}$,
558 $F_{1,10}=34.5$, $R^2=0.75$, $P < 0.001$) which itself increased with colony size (p.e. = 0.26 ± 0.08 , $F_{1,10}=9.8$, $R^2=0.44$,
559 $P=0.011$). All other predictors were not correlated with each other. Chlorophyll-a was not correlated with
560 winter latitude (p.e. = -0.02 ± 0.02 , $F_{1,10}=2.4$, $R^2=0.11$, $P=0.150$) or with colony size (p.e. = $-7.3e^{-7} \pm 5.5e^{-7}$, $F_{1,10}$
561 = 1.7 , $R^2=0.06$, $P=0.216$). Colony size was not correlated with winter latitude (p.e. = 4295 ± 10128 , $F_{1,1}=0.2$,
562 $R^2=0.08$, $P=0.681$), and distance from the colony was not correlated with winter latitude (p.e. = 0.03 ± 0.03 ,
563 $F_{1,10}=2.2$, $R^2=0.09$, $P=0.171$). Despite the covariance between chlorophyll-a and migration distance, and
564 migration distance and colony size, the relationships between these variables and colony productivity still
565 held after the variation explained by their covariates was taken into account (as illustrated on Figure 3). In
566 other words, the effect of each of the four predictors on colony productivity remains significant (or
567 marginally significant, for chlorophyll-a), even after the variation explained by the other three variables has
568 been taken into account. Therefore, these relationships are not artefacts of the covariance between
569 explanatory variables. For example, this means that migration distance explains a significant amount of
570 variation in colony productivity once the variation caused by colony size has been removed. Therefore at
571 least some variation in productivity must be controlled by migration distance independently of a direct effect
572 of colony size. Our findings suggest that long migration movements arise from both higher density-

573 dependent competition (driven by larger colony size) and from poor local conditions. These long
574 movements, which we show result in higher energy expenditure, combined with the relatively lower resource
575 availability at the wintering grounds, may lead birds to return to the colony in reduced body condition, which
576 may affect their chance to breed early or rear a chick successfully. These processes do not exclude additional
577 effects on productivity related to colony size during breeding.