

Current Biology

Ocean-wide Drivers of Migration Strategies and Their Influence on Population Breeding Performance in a Declining Seabird

Highlights

- Competition and local winter resource availability drive migratory movements
- Foraging effort and energy expenditure increase as puffins winter further north
- Ocean-wide migration patterns are reflected in populations' breeding performance
- Breeding productivity decreases with population size, migration distance, and latitude

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In Brief

To investigate the species-wide drivers and fitness consequences of animal migration, Fayet et al. tracked 270 puffins across the North Atlantic. They show that competition and geographical and environmental factors drive a species' migration movements across its range and that these migration patterns are reflected in population breeding performance.

Ocean-wide Drivers of Migration Strategies and Their Influence on Population Breeding Performance in a Declining Seabird

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SUMMARY

Which factors shape animals' migration movements across large geographical scales, how different migratory strategies emerge between populations, and how these may affect population dynamics are central questions in the field of animal migration [1] that only large-scale studies of migration patterns across a species' range can answer [2]. To address these questions, we track the migration of 270 Atlantic puffins *Fratercula arctica*, a red-listed, declining seabird, across their entire breeding range. We investigate the role of demographic, geographical, and environmental variables in driving spatial and behavioral differences on an ocean-basin scale by measuring puffins' among-colony differences in migratory routes and day-to-day behavior (estimated with individual daily activity budgets and energy expenditure). We show that competition and local winter resource availability are important drivers of migratory movements, with birds from larger colonies or with poorer local winter conditions migrating further and visiting less-productive waters; this in turn led to differences in flight activity and energy expenditure. Other behavioral differences emerge with latitude, with foraging effort and energy expenditure increasing when birds winter further north in

colder waters. Importantly, these ocean-wide migration patterns can ultimately be linked with breeding performance: colony productivity is negatively associated with wintering latitude, population size, and migration distance, which demonstrates the cost of competition and migration on future breeding and the link between non-breeding and breeding periods. Our results help us to understand the drivers of animal migration and have important implications for population dynamics and the conservation of migratory species.

RESULTS

The drivers of animal migration across large geographical scales are poorly understood. Tracking studies have started to reveal the diversity of long-distance migration strategies, as well as the need to broaden the usual definition—a long return journey to a specific overwintering destination after the breeding season [3]—to encompass a larger range of migration patterns, including journeys to a single [4] or multiple [5, 6] areas, sometimes using various routes to get there [7]. Studies examining species' migration patterns across multiple populations have increased, but few are sufficiently large scale to reveal the migration landscape of entire species, and those that are remain largely descriptive [2, 8]. Therefore, our understanding of which factors shape species' migration movements, how different migration strategies emerge between populations, and whether

these affect population dynamics remains poor [1]. Potential drivers of migration include competition, leading to density-dependent migratory distance (animals from large populations migrating further [9]) or quality-dependent migratory distance (sub-dominant, low-quality individuals migrating further [10]), and winter resource availability close to the breeding grounds (animals in low-quality habitat are more likely to migrate [11]). Differences could have a genetic basis, resulting in closely related colonies following similar migration patterns [12]. Whether such mechanisms drive intraspecific differential migratory strategies across large scales and whether these may affect populations' fitness is unknown. These questions are particularly important for species with high migratory connectivity, where different populations migrate to distinct areas [13], as they could help understand how different populations may be under different selective pressures due to migratory differences, as shown in invertebrates [14], fish [15], and birds [16]. This could also have important implications for conservation by making specific species or populations more vulnerable to changes in their winter habitat [17, 18]. Breeding and migration are linked throughout annual cycles [19], and fitness differences between populations or individuals migrating to different destinations have been found in multiple species [20–22]. Determining how differences in migration strategies can shape fitness landscapes across multiple populations and perhaps even across an entire species' range is therefore paramount to understanding migratory species' population dynamics.

We address these questions in an unprecedented large-scale and in-depth study of the migration strategies of a long-distance migrant, the Atlantic puffin *Fratercula arctica*, across its entire range. Puffins around the British Isles show considerable variation in migration strategy [23–25], and there is evidence from a single-colony study that breeding success varies among migratory routes [26]. Whether this diversity of migration strategies exists across the species' range and whether it has fitness consequences are particularly important questions to answer, because some puffin populations (but not all) have dramatically declined in the last few decades [27–29], and the species is now endangered in Europe [30]. This apparent variability in migratory strategies and population trends among populations makes puffins an ideal species to investigate species-wide drivers of migration and the potential fitness consequences of different migration strategies. We track the migration of 270 adult puffins from 13 populations covering all major breeding grounds across the North Atlantic, including novel data from 12 populations in Canada, Iceland, Ireland, Norway, the UK, and the US. We combine spatial, behavioral, and environmental data to (1) determine puffins' full non-breeding distribution, determine their migratory connectivity between colonies, and assess spatial and behavioral differences between colonies; (2) investigate ocean-wide migration strategies and the role of geographical, environmental, and demographic variables on shaping these spatial and behavioral patterns; and (3) test the potential consequences of different migration strategies on colony productivity.

Distributions differed substantially between colonies (Figure 1, Figure S1). No colony was totally spatially segregated; all 90% occupancy kernels overlapped with two to four other colonies (Table S2), but the overlap decreased with distance between colonies (linear model [LM], $n = 28$, $F_{1,26} = 11.45$, $p = 0.002$).

Wintering hotspots were found around and south of Ireland, southwest of Iceland, at the entrance of the Labrador Sea, and near the Charlie-Gibbs Fracture Zone in the mid-North Atlantic (Figure 1C). Segregation was high between core utilization areas (50% kernels), with most colonies overlapping by <3% (Table S2). Most birds wintered in multiple locations, and so distributions varied throughout the winter (Figure S1). Colonies differed in the total distance covered overwinter, with birds from some colonies covering thousands of kilometers more than others (linear mixed-effects model [LMM], $n = 215$, $\chi_7^2 = 80.5$, $p < 0.001$; Table 1; Table S3), and in the birds' average distance from the colony, ranging from <250 km to >1,700 km ($n = 215$, $\chi_7^2 = 261.8$, $p < 0.001$; Table 1; Table S4). These spatial differences led birds from different colonies to experience different environmental conditions overwinter (Table 1), both in terms of temperature and water productivity ($n = 190$; sea-surface temperature [SST]: $\chi_7^2 = 301.3$, $p < 0.001$; chlorophyll-a: $\chi_7^2 = 118.6$, $p < 0.001$). The SST experienced by puffins was bimodal, with peaks around 6°C and 11°C (Figure S2).

Colonies also differed behaviorally (Table 1), with different flight and foraging effort ($n = 162$; flight: $\chi_7^2 = 72.8$, $p < 0.001$; foraging: $\chi_7^2 = 49.7$, $p < 0.001$). Exposure to different day lengths at different latitudes (Table 1; $n = 190$, $\chi_7^2 = 70.2$, $p < 0.001$) presumably affected the opportunity to engage in flight and foraging (puffins do not dive at night [31]) and their intensity. To account for this, we compared the proportion of daylight hours spent flying and foraging between colonies ("intensity"). Flight and foraging intensity differed between colonies ($n = 190$; sustained flight: $\chi_7^2 = 95.5$, $p < 0.001$; foraging: $\chi_7^2 = 69.0$, $p < 0.001$). Sustained flight was the least frequent behavior (0.6%–4.9% of daylight hours) but varied greatly between colonies, with birds spending 17–102 hr in flight (5–29 min/day). Puffins spent 15%–35% of daylight hours foraging, or 385–753 hr in total (1.8–3.5 hr/day). Therefore, all birds spent the majority of daylight hours sitting on the water. Daily and total energy expenditure varied significantly among colonies (daily energy expenditure [DEE]: $n = 190$, $\chi_7^2 = 367.4$, $p < 0.001$; total energy expenditure [EE]: $n = 168$, $\chi_7^2 = 252.5$, $p < 0.001$).

We tested whether geographical (latitude), environmental (SST and chlorophyll-a), and demographic (population size) variables drive migratory behavior. We found ocean-wide migration patterns, mainly driven by colony size and wintering latitude and mediated by environmental factors (Figure 2a). A first key finding is that puffins from larger colonies, and where local winter conditions were poorer, migrated further (LM, $n = 12$, $R^2 = 0.63$; colony size: parameter estimate [p.e.] = 0.15 ± 0.08 , $F_{1,9} = 14.7$, $p = 0.004$; chlorophyll-a: p.e. = -0.53 ± 0.22 , $F_{1,9} = 6.1$, $p = 0.036$; Figure S3), which supports competition as a driver of migration. These birds spent more 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 (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 (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, also drove ocean-wide migration patterns. Puffins wintering at higher latitudes spent more time foraging (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 , $F_{1,10} = 13.7$, $R^2 = 0.53$, $p = 0.004$), and had higher DEE (p.e. = -32.9 ± 6.9 , $F_{1,9} = 22.9$, $R^2 = 0.69$,

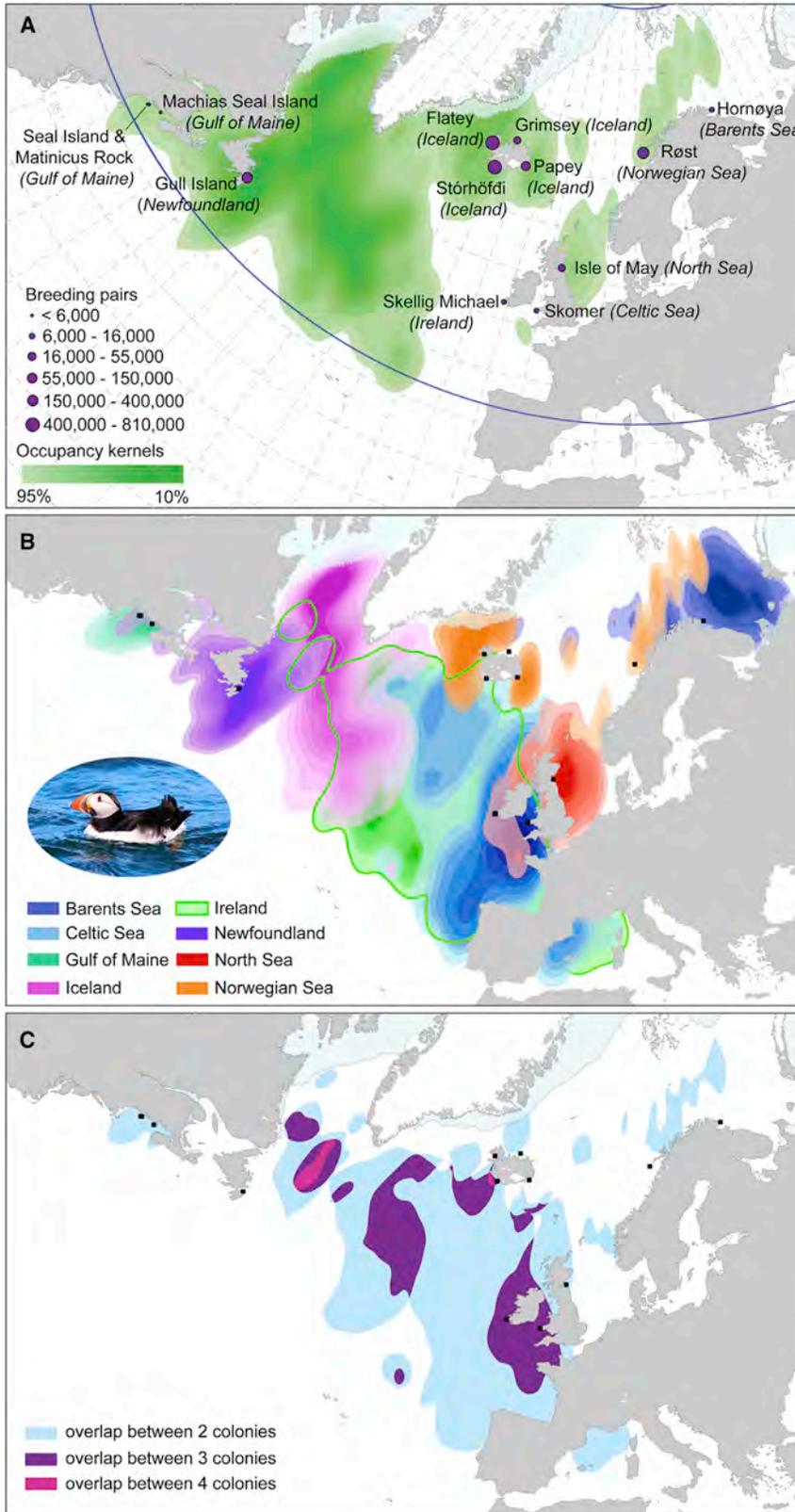


Figure 1. Winter Distribution of Atlantic Puffins across Their Range

(A) Density distribution of puffins from all study colonies across the non-breeding season, obtained by weighting occupancy kernels by colony size (colony or archipelago sizes are indicated with circles of different size). Italic names after each colony's name represent the name used to describe the colony in the main text. The unit of the gray parallels and meridians is 5° . The blue parallels indicate the approximate latitudinal breeding range of puffins.

(B) Occupancy kernels for each colony across the non-breeding season, with each colony in a different color (the kernel for the Irish colony is contoured in green for clarity). Photo: A. Fayet.

(C) Overlap between the 90% occupancy kernels of two to four different colonies. On the lower panels, colonies are indicated with black squares. The light-blue shade represents the approximate ice edge at its mid-winter level.

See also [Figure S1](#) and [Table S2](#).

Table 1. Spatial, Behavioral and Environmental Characteristics of Puffin Migratory Routes from Different Colonies

| | Newfoundland | Barents Sea | Iceland | Ireland | North Sea | Norwegian Sea | Celtic Sea | Gulf of Maine |
|------------------------------------|--------------|-------------|-------------|-------------|-------------|---------------|-------------|---------------|
| Total distance covered (km) | 3,656 ± 242 | 2,375 ± 147 | 3,960 ± 276 | 4,736 ± 238 | 2,874 ± 166 | 4,465 ± 357 | 4,268 ± 195 | 2,804 ± 248 |
| Average distance from colony (km) | 527 ± 50 | 527 ± 35 | 1782 ± 45 | 1,161 ± 74 | 441 ± 35 | 1,358 ± 96 | 878 ± 73 | 238 ± 23 |
| Day length (hr) | 10.7 ± 0.03 | 7.4 ± 0.06 | 10.0 ± 0.03 | 10.3 ± 0.03 | 10.7 ± 0.02 | 8.2 ± 0.1 | 10.6 ± 0.02 | 11.6 ± 0.04 |
| (mean and range) | [4.2–15.3] | [0.0–22.0] | [3.2–18.5] | [3.0–17.0] | [3.8–18.5] | [0.0–22.0] | [4.5–17.5] | [8.5–15.3] |
| Flight intensity (%) | 2.5 ± 0.4 | 3.1 ± 0.3 | 3.8 ± 0.3 | 4.9 ± 0.5 | 2.0 ± 0.2 | 3.5 ± 0.2 | 1.3 ± 0.1 | 0.6 ± 0.2 |
| Total flight effort (hr) | 57 ± 9 | 71 ± 9 | 86 ± 7 | 102 ± 12 | 50 ± 6 | 73 ± 5 | 28 ± 3 | 17 ± 4 |
| Foraging intensity (%) | 21.7 ± 2.9 | 27.4 ± 1.2 | 18.6 ± 1.2 | 29.3 ± 1.3 | 22.8 ± 1.3 | 34.5 ± 1.9 | 16.0 ± 0.9 | 14.5 ± 1.4 |
| Total foraging effort (hr) | 497 ± 80 | 617 ± 37 | 411 ± 24 | 561 ± 19 | 541 ± 31 | 753 ± 41 | 370 ± 22 | 385 ± 31 |
| Winter DEE (kJ/day) | 1,244 ± 9 | 1,356 ± 10 | 1,341 ± 11 | 1,149 ± 13 | 1,100 ± 6 | 1,213 ± 9 | 1,067 ± 4 | 1,147 ± 4 |
| Winter total EE (kJ) | 265 ± 2 | 288 ± 2 | 287 ± 2 | 244 ± 3 | 236 ± 1 | 260 ± 2 | 228 ± 0.8 | 245 ± 0.9 |
| SST (°C) | 9.6 ± 0.6 | 6.1 ± 0.1 | 6.5 ± 0.4 | 10.6 ± 0.3 | 10.7 ± 0.09 | 6.9 ± 0.4 | 11.4 ± 0.2 | 13.8 ± 0.5 |
| Chlorophyll-a (mg/m ³) | 1.13 ± 0.13 | 1.17 ± 0.10 | 0.73 ± 0.06 | 0.77 ± 0.06 | 1.53 ± 0.07 | 0.70 ± 0.07 | 0.81 ± 0.06 | 2.1 ± 0.14 |

The “intensity” values of time represents the percentage of daylight hours spent engaged in a particular behavior, and the total time represents the number of hours spent in this behavior over the whole non-breeding season (mean ± SE). DEE, daily energy expenditure; EE, energy expenditure; SST, sea-surface temperature. See also [Figure S2](#) and [Tables S3](#) and [S4](#).

$p < 0.001$) than birds wintering further south ([Figure 2C](#)). How far from the colony birds migrated was unrelated to latitude (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.

A second key finding is that these ocean-wide patterns were related to colony productivity. More specifically, colony productivity was best predicted by a combination of winter latitude, colony size, average distance from the colony, and winter chlorophyll-a levels (overall additive model compared to the null model: LM, $n = 11$, $F_{4,6} = 13.6$, $R^2 = 0.84$, $p = 0.004$, ΔAIC [Akaike information criterion] = -17.4 ; [Figure 3](#)). In this model, all explanatory variables were negatively correlated with colony productivity but with only marginal significance for 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. = $-5.8e-7 \pm 1.6e-7$, $t_9 = -3.6$, $p = 0.011$; distance from colony: residual p.e. = $-2.8e-4 \pm 1.1e-4$, $t_9 = -2.6$, $p = 0.039$; chlorophyll-a: residual p.e. = -0.3 ± 0.1 , $t_9 = -2.3$, $p = 0.061$; where residual p.e. represents the effect of a single predictor on the residual variation in productivity after taking into account the other three predictors). These relationships occurred together and not separately; therefore, latitude, colony size, and migration distance all explained a significant amount of variation in colony productivity not explained by the other three (see [STAR Methods](#) for details). In other words, high winter latitude, large colony size, and long migration distance (and, to a marginal extent, low ocean productivity at the wintering grounds) were all associated with low colony productivity.

DISCUSSION

We investigated the role of environmental, geographical, and demographic factors as large-scale drivers of migration strategies across a species’ range. We found that colony size, local winter resource availability, and latitude drive large-scale spatial and

behavioral migratory patterns and that these patterns are ultimately linked with colony breeding productivity.

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

Migration routes varied strikingly between colonies, with some birds migrating >1,700 km away and others staying within <250 km of their colony. These complex patterns do not fit the well-known “leap-frog” or “chain” migration patterns often observed in species breeding across a wide latitudinal range [3, 38] and are unusual. Species often share one wintering site (European rollers *Coracias garrulus* [8]) or a few (black-legged kittiwakes *Rissa tridactyla* [2], Monarch butterflies *Danaus plexipus* [5], bobolinks *Dolichonyx oryzivorus* [39]), with the exception of a few (mostly marine) species such as Atlantic cod *Gadus morhua* [40] and leatherback turtles *Dermochelys coriacea* [6]. The drivers of such complex migratory patterns are unclear. In cod, there is evidence for the role of quality-dependent competition, with only large, strong individuals going on long migrations; however, industrial fishing seems to have changed the selection pressures on migratory distance [41]. There is evidence in puffins from the Celtic Sea that individuals taking the longest migration route to the Mediterranean Sea breed more successfully [26]. This, however, remains to be shown for other colonies.

Distance from the colony was unrelated to colony latitude, suggesting that all birds did not search for the same

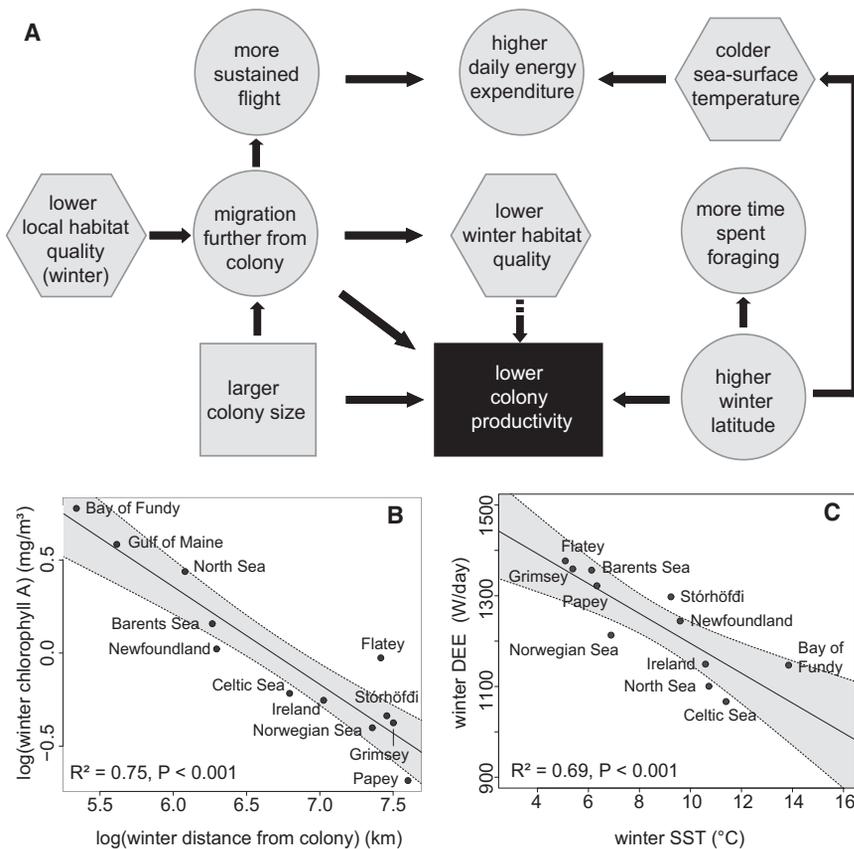


Figure 2. Ocean-wide Patterns of Puffins' Migratory Strategies

(A) Summary of the ocean-wide patterns of migratory strategies driven by colony size, winter latitude, and environmental variables at the whole population level. Arrows indicate significant relationships between variables (see the main text for statistics).

(B and C) Graphical representations of some of the relationships from (A), more specifically the association between (B) winter chlorophyll-a and distance from the colony and between (C) winter DEE and winter SST. Regression lines, 95% confidence intervals (gray areas), R^2 values, and p values were obtained from linear models.

See also Figure S3.

shorter days, spent more time foraging, which also resulted in higher DEE. Higher foraging effort at high latitudes may reflect not lower resource availability (we found no correlation between chlorophyll-a and SST) but increased calorific requirements, due to the larger mass of birds further north and lower temperatures requiring additional thermoregulation [49]. Therefore, we show that geographical and environmental parameters and demographics shape the wintering behavior and energy expenditure of a migratory species at a population

environmental conditions. In fact, puffins from different colonies experienced different day length, temperature, and water productivity, which led to different behavioral patterns and energy expenditures. This may result different populations being under different selective pressures, as occurs in thrushes [16] or salmon [15]. We identified multiple ocean-wide patterns in migratory strategies, driven by three main variables. One was colony size, a good predictor of migration distance. Density-dependent competition is therefore likely to be an important driver of migration. Larger populations may deplete resources near colonies and lead birds to exploit more distant areas and spread more [42]. This is an adaptation of Ashmole's hypothesis for migratory behavior [9, 43]. Supporting theoretical predictions, local winter resource availability also plays a role. Models of partial migration predict increasing migrants-to-residents ratios when the relative difference in habitat quality between breeding and wintering site increases [11, 44]. Support for this hypothesis has been found in multiple taxa, including birds [45], mammals [46], and amphibians [47]. Although most puffin populations seem to be fully migratory, our finding that individuals from colonies with poorer local winter water productivity migrate further implies a similar process. In other words, birds migrate further from the colony both when local habitat quality is poor and intra-specific competition (mediated by colony size) is high.

Birds migrating further spent more time in flight, leading to higher DEE (flight is costly in auks [48]). Puffins migrating to higher latitudes visited colder waters and, despite experiencing

level across its entire range. A key result is that these ocean-wide patterns are linked with population productivity across the species' range. Although qualitative, the first link between wintering area and breeding success at a similar scale was found in thick-billed murres *Uria lomvia*, with stable populations mostly wintering near Canada and declining populations mostly wintering east of Greenland [33]. Here we found three predictors of colony productivity: colony size, wintering latitude, and migratory distance (and, to a lesser extent, water productivity at the wintering grounds). Larger colonies in which birds migrated further, to higher latitudes and poorer waters, had lower productivity, which demonstrates a cost of migration at a species' range level. These birds spent more time engaged in energy-demanding activities such as flight and foraging, experienced colder temperatures, and consequently had higher winter energy expenditure. Although only experimental studies can definitively identify causal processes, one consistent mechanism could be that because of increased energy expenditure overwinter, birds may return to the colony in poorer condition, which is known to delay breeding and reduce breeding success in many species. Winter habitat quality affects arrival time at the breeding grounds, body condition, and subsequent breeding performance in many migratory terrestrial species [50]. In marine species, SST can affect subsequent breeding success in a colony [51, 52]. We show that this is true across a much larger scale. Spring or summer environmental conditions have been linked to breeding performance in several seabirds, probably by affecting prey availability during chick provisioning [27, 53, 54].

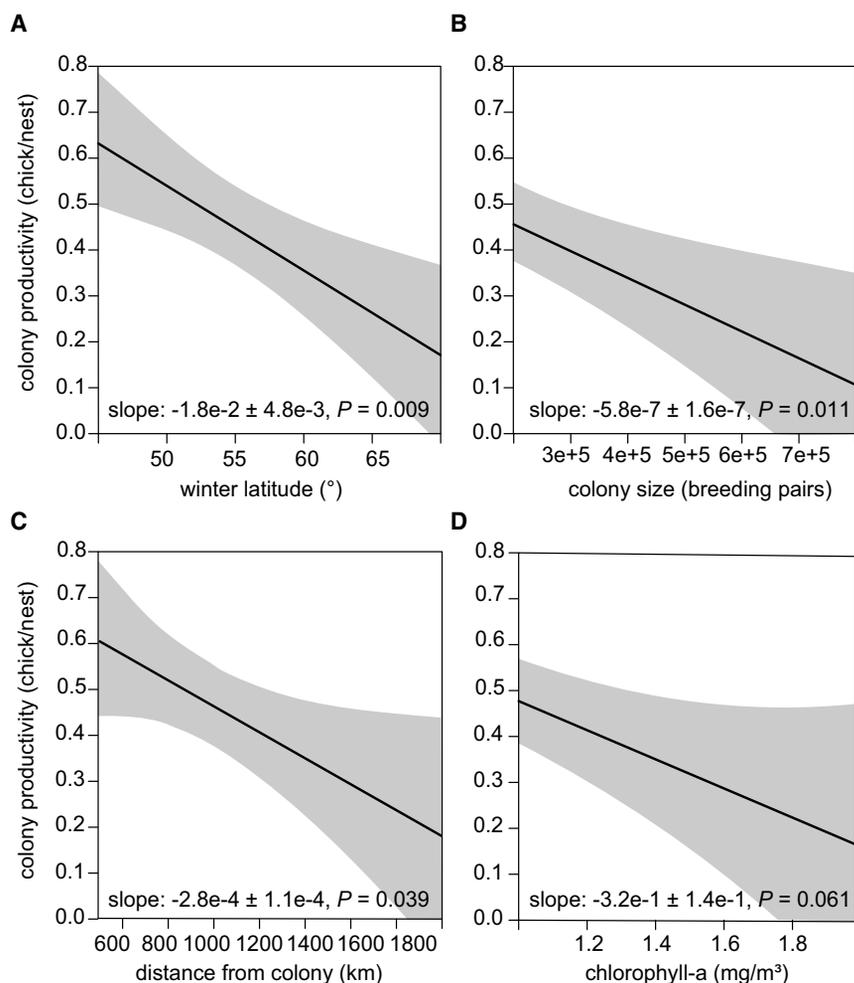


Figure 3. Relationship between Ocean-wide Patterns and Colony Productivity

Effect size plots for the model of colony productivity as a function of winter latitude (A), colony size (B), distance from colony (C), and chlorophyll-a (D), obtained from the best model of colony productivity. Each plot represents the effect of a single predictor on the residual variation in colony productivity after the variation explained by the other three variables was taken into account. The slope of the relationship is represented by a black line, with the 95% confidence intervals in gray. All values are obtained from the LM of colony productivity. See also [Figure S4](#).

Reproductive performance is therefore likely to be affected by a combination of prey availability during breeding (itself affected by colony size through density-dependent competition) and adult body condition related to previous winter conditions. The negative relationship between colony size and productivity raises questions about the origin and maintenance of large colonies. The answer presumably relates to food availability near the colony during breeding [27]. Although we cannot investigate changes in migratory paths, environmental conditions, and breeding productivity over time with our current dataset, our findings suggest that large puffin colonies may not be sustainable anymore, perhaps because of long-term changes in environmental conditions near the breeding [55] or wintering [56] grounds, affecting the birds' ability to both refuel in winter and feed their offspring in summer. This is also likely to be the case for other species that have undergone similar declines in large northern colonies [57].

Our study provides unprecedented insight into the spatial and behavioral migration patterns of an avian species. It reveals how competition and geographical and environmental parameters drive a species' migratory strategies across its range and how migration patterns are reflected in population-level breeding performance. This study starts to uncover these important relationships and warrants further research into the species-wide drivers

and fitness consequences of migration, with important points such as the effect of migration strategies on survival and the consistency of these patterns over time waiting to be explored. Our findings highlight the need for, and benefits of, large-scale collaborative studies to help understand the mechanisms behind the development of animals' migratory routes and determine which factors most influence breeding performance and population dynamics. Such knowledge is also invaluable to understand and tackle widespread population declines in migratory species, with marine species especially under threat by fisheries, pollution, and climate change.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
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 - Activity budgets and energy expenditure

- Environmental data
- Colony productivity
- **QUANTIFICATION AND STATISTICAL ANALYSIS**
- Model of colony productivity

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures and four tables and can be found with this article online at <https://doi.org/10.1016/j.cub.2017.11.009>.

AUTHOR CONTRIBUTIONS

A.L.F. and T.G. conceived the study, all authors collected data, and A.L.F., R.F., and G.J.R. analyzed the data. All authors critically discussed the results. A.L.F. wrote the manuscript with the help of all authors.

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REFERENCES

1. Shaw, A.K. (2016). Drivers of animal migration and implications in changing environments. *Evol. Ecol.* **30**, 991–1007.
2. Frederiksen, M., Moe, B., Daunt, F., Phillips, R.A., Barrett, R.T., Bogdanova, M.I., Boulinier, T., Chardine, J.W., Chastel, O., Chivers, L.S., et al. (2011). Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. *Divers. Distrib.* **18**, 530–542.
3. Newton, I. (2008). *Migration Ecology of Birds* (Academic Press).
4. McGrady, M.J., Maechtle, T.L., Vargas, J.J., Seegar, W.S., and Porras Peña, M.C. (2002). Migration and ranging of peregrine falcons wintering on the Gulf of Mexico coast, Tamaulipas, Mexico. *Condor* **104**, 39–48.
5. Brower, L.P. (1995). Understanding and misunderstanding the migration of the monarch butterfly (*Nymphalidae*) in North America: 1857–1995. *J. Lepid. Soc.* **49**, 304–385.
6. Godley, B.J., Blumenthal, J.M., Broderick, A.C., Coyne, M.S., Godfrey, M.H., Hawkes, L.A., and Witt, M.J. (2008). Satellite tracking of sea turtles: where have we been and where do we go next? *Endanger. Species Res.* **4**, 3–22.
7. Hake, M., Kjellén, N., and Alerstam, T. (2003). Age-dependent migration strategy in honey buzzards *Pernis apivorus* tracked by satellite. *Oikos* **103**, 385–396.
8. Finch, T., Saunders, P., Avilés, J.M., Bermejo, A., Catry, I., de la Puente, J., Emmenegger, T., Mardega, I., Mayet, P., Parejo, D., et al. (2015). A pan-European, multipopulation assessment of migratory connectivity in a near-threatened migrant bird. *Divers. Distrib.* **21**, 1051–1062.
9. Ashmole, N.P. (1963). The regulation of numbers of tropical oceanic birds. *Ibis* **103b**, 458–473.
10. Cristol, D., Baker, M., and Carbone, C. (1999). Differential migration revisited: latitudinal segregation by age and sex class. *Curr. Ornithol.* **15**, 33–88.
11. Taylor, C.M., and Norris, D.R. (2007). Predicting conditions for migration: effects of density dependence and habitat quality. *Biol. Lett.* **3**, 280–283.
12. Berthold, P. (1996). *Control of Bird Migration* (Chapmann & Hall).
13. Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S., and Holmes, R.T. (2002). Links between worlds: unraveling migratory connectivity. *Trends Ecol. Evol.* **17**, 76–83.
14. Gatehouse, A.G. (1997). Behavior and ecological genetics of wind-borne migration by insects. *Annu. Rev. Entomol.* **42**, 475–502.
15. Dodson, J.J., Aubin-Horth, N., Thériault, V., and Páez, D.J. (2013). The evolutionary ecology of alternative migratory tactics in salmonid fishes. *Biol. Rev. Camb. Philos. Soc.* **88**, 602–625.
16. Delmore, K.E., and Irwin, D.E. (2014). Hybrid songbirds employ intermediate routes in a migratory divide. *Ecol. Lett.* **17**, 1211–1218.
17. Sutherland, W.J. (1996). Predicting the consequences of habitat loss for migratory populations. *Proc. Biol. Sci.* **263**, 1325–1327.
18. Betini, G.S., Fitzpatrick, M.J., and Norris, D.R. (2015). Experimental evidence for the effect of habitat loss on the dynamics of migratory networks. *Ecol. Lett.* **18**, 526–534.
19. Marra, P.P., Hobson, K.A., and Holmes, R.T. (1998). Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* **282**, 1884–1886.
20. Gunnarsson, T.G., Gill, J.A., Newton, J., Potts, P.M., and Sutherland, W.J. (2005). Seasonal matching of habitat quality and fitness in a migratory bird. *Proc. Biol. Sci.* **272**, 2319–2323.
21. Alves, J.A., Gunnarsson, T.G., Hayhow, D.B., Appleton, G.F., Potts, P.M., Sutherland, W.J., and Gill, J.A. (2013). Costs, benefits, and fitness consequences of different migratory strategies. *Ecology* **94**, 11–17.
22. Weimerskirch, H., Delord, K., Guitteaud, A., Phillips, R.A., and Pinet, P. (2015). Extreme variation in migration strategies between and within wandering albatross populations during their sabbatical year, and their fitness consequences. *Sci. Rep.* **5**, 8853.
23. Harris, M.P., Daunt, F., Newell, M., Phillips, R.A., and Wanless, S. (2010). Wintering areas of adult Atlantic puffins *Fratercula arctica* from a North Sea colony as revealed by geolocation technology. *Mar. Biol.* **157**, 827–836.
24. Guilford, T., Freeman, R., Boyle, D., Dean, B., Kirk, H., Phillips, R., and Perrins, C. (2011). A dispersive migration in the Atlantic Puffin and its implications for migratory navigation. *PLoS ONE* **6**, e21336.
25. Jessopp, M.J., Cronin, M., Doyle, T.K., Wilson, M., McQuatters-Gollop, A., Newton, S., and Phillips, R.A. (2013). Transatlantic migration by post-breeding puffins: a strategy to exploit a temporarily abundant food resource? *Mar. Biol.* **160**, 2755–2762.
26. Fayet, A.L., Freeman, R., Shoji, A., Boyle, D., Kirk, H.L., Dean, B.J., Perrins, C.M., and Guilford, T. (2016). Drivers and fitness consequences of dispersive migration in a pelagic seabird. *Behav. Ecol.* **27**, 1061–1072.
27. Sandvik, H., Coulson, T., and Sæther, B.-E. (2008). A latitudinal gradient in climate effects on seabird demography: results from interspecific analyses. *Glob. Change Biol.* **14**, 703–713.
28. Burfield, J., and van Bommel, F. (2004). *Birds in Europe. Population Estimates, Trends and Conservation Status* (BirdLife International).
29. Anker-Nilssen, T., and Røstad, O.W. (1993). Census and monitoring of puffins *Fratercula arctica* on Røst, N Norway, 1979–1988. *Ornis Scand. Scand. J. Ornithol.* **24**, 1–9.
30. IUCN 2017. The IUCN Red List of Threatened Species. Version 2017-2. <http://www.iucnredlist.org> Downloaded on 26 October 2017.

31. Shoji, A., Elliott, K., Fayet, A.L., Boyle, D., Perrins, C., and Guilford, T. (2015). Foraging behaviour of sympatric razorbills and puffins. *Mar. Ecol. Prog. Ser.* *520*, 257–267.
32. Harris, M.P., and Wanless, S. (2011). *The Puffin* (T. & A.D. Poyser).
33. Gardarsson, A. (1999). The density of seabirds west of Iceland. *Rit Fiskid.* *16*, 155–169.
34. Boertmann, D. (2011). Seabirds in the central North Atlantic, September 2006: further evidence for an oceanic seabird aggregation area. *Mar. Ornithol.* *39*, 183–188.
35. Frederiksen, M., Descamps, S., Erikstad, K.E., Gaston, A.J., Gilchrist, H.G., Grémillet, D., Johansen, K.L., Kolbeinsson, Y., Linnebjerg, J.F., Mallory, M.L., et al. (2016). Migration and wintering of a declining seabird, the thick-billed murre *Uria lomvia*, on an ocean basin scale: Conservation implications. *Biol. Conserv.* *200*, 26–35.
36. Montevecchi, W.A., Hedd, A., Tranquilla, L.M., Fifield, D.A., Burke, C.M., Regular, P.M., Davoren, G.K., Garthe, S., Robertson, G.J., and Phillips, R.A. (2012). Tracking seabirds to identify ecologically important and high risk marine areas in the western North Atlantic. *Biol. Conserv.* *156*, 62–71.
37. Bennison, A., and Jessopp, M. (2015). At-sea surveys confirm a North Atlantic biodiversity hotspot. *Bird Study* *62*, 262–266.
38. Berthold, P. (2001). *Bird Migration: A General Survey*, Second Edition (Oxford University Press).
39. Renfrew, R.B., Kim, D., Perlut, N., Smith, J., Fox, J., and Marra, P.P. (2013). Phenological matching across hemispheres in a long-distance migratory bird. *Divers. Distrib.* *19*, 1008–1019.
40. Robichaud, D., and Rose, G.A. (2004). Migratory behaviour and range in Atlantic cod: inference from a century of tagging. *Fish Fish.* *5*, 185–214.
41. Jorgensen, C., Dunlop, E.S., Opdal, A.F., and Fiksen, O. (2008). The evolution of spawning migrations: state dependence and fishing-induced changes. *Ecology* *89*, 3436–3448.
42. Alerstam, T., Hedenström, A., and Åkesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos* *103*, 247–260.
43. Diamond, A.W. (1978). Feeding strategies and population size in tropical seabirds. *Am. Nat.* *112*, 215–223.
44. Cohen, D. (1967). Optimization of seasonal migratory behavior. *Am. Nat.* *101*, 5–17.
45. Boyle, W.A. (2011). Short-distance partial migration of Neotropical birds: a community-level test of the foraging limitation hypothesis. *Oikos* *120*, 1803–1816.
46. Eggeman, S.L., Hebblewhite, M., Bohm, H., Whittington, J., and Merrill, E.H. (2016). Behavioural flexibility in migratory behaviour in a long-lived large herbivore. *J. Anim. Ecol.* *85*, 785–797.
47. Grayson, K.L., and Wilbur, H.M. (2009). Sex- and context-dependent migration in a pond-breeding amphibian. *Ecology* *90*, 306–312.
48. Elliott, K.H., Ricklefs, R.E., Gaston, A.J., Hatch, S.A., Speakman, J.R., and Davoren, G.K. (2013). High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. *Proc. Natl. Acad. Sci. USA* *110*, 9380–9384.
49. Whittow, G.C., and Rahn, H. (1984). *Seabird Energetics* (Plenum Press).
50. Norris, D.R., and Marra, P.P. (2007). Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor* *109*, 535–547.
51. Veit, R., McGowan, J., Ainley, D., Wahl, T., and Pyle, P. (1997). Apex marine predator declines ninety percent in association with changing oceanic climate. *Glob. Change Biol.* *3*, 23–28.
52. Bertram, D.F., Mackas, D.L., and McKinnell, S.M. (2001). The seasonal cycle revisited: interannual variation and ecosystem consequences. *Prog. Oceanogr.* *49*, 283–307.
53. Durant, J.M., Anker-Nilssen, T., and Stenseth, N.C. (2003). Trophic interactions under climate fluctuations: the Atlantic puffin as an example. *Proc. Biol. Sci.* *270*, 1461–1466.
54. Durant, J.M., Anker-Nilssen, T., and Stenseth, N.C. (2006). Ocean climate prior to breeding affects the duration of the nestling period in the Atlantic puffin. *Biol. Lett.* *2*, 628–631.
55. Barrett, R.T., Nilsen, E.B., and Anker-Nilssen, T. (2012). Long-term decline in egg size of Atlantic puffins *Fratercula arctica* is related to changes in forage fish stocks and climate conditions. *Mar. Ecol. Prog. Ser.* *457*, 1–10.
56. Rose, G.A. (2005). On distributional responses of North Atlantic fish to climate change. *ICES J. Mar. Sci.* *62*, 1360–1374.
57. Sandvik, H., Reiertsen, T.K., Erikstad, K.E., Anker-Nilssen, T., Barrett, R.T., Lorentsen, S.-H., Systad, G.H., and Myksvoll, M.S. (2014). The decline of Norwegian kittiwake populations: modelling the role of ocean warming. *Clim. Res.* *60*, 91–102.
58. Dean, B., Freeman, R., Kirk, H., Leonard, K., Phillips, R.A., Perrins, C., and Guilford, T. (2013). Behavioural mapping of a pelagic seabird: combining multiple sensors and a hidden Markov model reveals the distribution of at-sea behaviour. *J. R. Soc. Interface* *10*, 20120570.
59. Fayet, A.L., Freeman, R., Shoji, A., Kirk, H.L., Padget, O., Perrins, C.M., and Guilford, T. (2016). Carry-over effects on the annual cycle of a migratory seabird: an experimental study. *J. Anim. Ecol.* *85*, 1516–1527.
60. Shaffer, S.A. (2011). A review of seabird energetics using the doubly labeled water method. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* *158*, 315–322.
61. Harris, M.P., Wanless, S., Murray, S., and Mackley, E. (2005). Isle of May seabird studies in 2004. Report 375 of the JNCC, November 2005. <http://jncc.defra.gov.uk/page-3629>.

STAR★METHODS

KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|----------|------------|
| Experimental Models: Organisms/Strains | | |
| Atlantic puffin <i>Fratercula arctica</i> | Table S1 | N/A |

CONTACT FOR REAGENT AND RESOURCE SHARING

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

EXPERIMENTAL MODEL AND SUBJECT DETAILS

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

METHOD DETAILS

Study sites

Puffins breed across the North Atlantic, approximately between 42° and 80° latitudes and –70° and 65° longitudes. Our study colonies include all major breeding areas across this range (Figure 1A), except Svalbard (< 10,000 pairs, often inaccessible) and the Faroe Islands (~400,000 pairs). While colonies vary in size from a few hundred to several hundred thousand pairs, most are part of archipelagos and we used the total population of the archipelago as a measure of population size. Because the definition of archipelago can vary among archipelagos and sometime includes extremely distant islands, we only included population estimates from islands located within 100km of each study colony, well over the distance where puffins from distinct colonies would be expected to overlap during breeding, as they are thought to forage within ~30km of the colony during breeding. A list of the archipelagos used is available in Table S1.

Spatial data

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

Activity budgets and energy expenditure

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

Environmental data

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

Colony productivity

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

QUANTIFICATION AND STATISTICAL ANALYSIS

Some colonies were pooled for the spatial analyses because of small sample sizes, their proximity to others, and the lack of major differences between tracks. The 4 Icelandic colonies (~300 km apart) were pooled as one “Iceland” group, the two colonies from Maine and the colony from the Bay of Fundy (< 150 km apart) were pooled as one “Gulf of Maine” group, resulting in 8 principal colonies. For readability, all colonies or groups of colonies in the main text are called by the name of the body of water they represent (or, when not possible, their country). The 8 principal colonies are therefore hereafter referred to as Barents Sea, Celtic Sea, Gulf of Maine,

Iceland, Ireland, Newfoundland, North Sea and Norwegian Sea (Figure 1A). When investigating potential relationships between behavior, latitude and environmental conditions, all colonies were counted separately ($n = 12$, with the two very close Maine colonies remaining pooled together) but sample sizes vary depending on the variables included in the model (colony productivity is only available for 11 colonies, and immersion data for 10).

Linear Mixed-Effects Models (LMMs) including year as a random effect (*lme4* package in R) were used to test for among-colony differences in spatial characteristics (total distance covered, average distance from the colony), activity budgets (proportion of time and total amount of time spent in different behavioral states), energy expenditure, and environmental conditions. For analyses including population size, the population size of the entire archipelago was taken for colonies within an archipelago (Table S1). Although study year varied between colonies, we did not include it in the models for lack of degrees of freedom and because evidence suggests puffins are repeatable in their migration route [26] and large scale environmental changes usually take place over longer periods, hence our metrics are unlikely to vary significantly over the duration of our study. Posthoc pairwise comparisons between colonies were realized with *lsmeans* in R (with adjustment for multiple comparisons). Relationships between at-sea behavior and environmental factors were tested with LMMs with year and colony as random effects. Linear models (LM) were used in R to test for relationships between behavior, latitude and environmental conditions across colonies. To determine whether ocean-wide patterns could help predict colony productivity, we used Akaike Information Criteria and R^2 to select the best model predicting colony productivity (using additive models without interaction between variables given our limited degrees of freedom). Data were log-, arcsin- or sqrt-transformed to meet parametric assumptions when necessary (residuals were checked for normality). Means expressed in the text are \pm SE unless stated otherwise. Significance was defined at the 5% level. All statistical details for each test (e.g., sample size, parameter estimates, degrees of freedom, test statistics, P value) can be found in the Results section. Note that in the first part of the Results the sample size n refers to the number of birds (or migration tracks), while in the second part, when we investigate ocean-wide patterns, it refers to the number of populations.

Model of colony productivity

Colony productivity was best predicted by four variables, and covariance analyses were run on these variables. Out of the four predictors of colony productivity (winter latitude, colony size, distance from colony and chlorophyll-a), chlorophyll-a decreased with distance from the colony (p.e. = $-5.9e^{-4} \pm 9.9e^{-5}$, $F_{1,10} = 34.5$, $R^2 = 0.75$, $p < 0.001$) which itself increased with colony size (p.e. = 0.26 ± 0.08 , $F_{1,10} = 9.8$, $R^2 = 0.44$, $p = 0.011$). All other predictors were not correlated with each other. Chlorophyll-a was not correlated with 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. = $-7.3e^{-7} \pm 5.5e^{-7}$, $F_{1,10} = 1.7$, $R^2 = 0.06$, $p = 0.216$). Colony size was not correlated with winter latitude (p.e. = 4295 ± 10128 , $F_{1,1} = 0.2$, $R^2 = 0.08$, $p = 0.681$), and distance from the colony was not correlated with winter latitude (p.e. = 0.03 ± 0.03 , $F_{1,10} = 2.2$, $R^2 = 0.09$, $p = 0.171$). Despite the covariance between chlorophyll-a and migration distance, and migration distance and colony size, the relationships between these variables and colony productivity still held after the variation explained by their covariates was taken into account (as illustrated on Figure 3). In other words, the effect of each of the four predictors on colony productivity remains significant (or marginally significant, for chlorophyll-a), even after the variation explained by the other three variables has been taken into account. Therefore, these relationships are not artifacts of the covariance between explanatory variables. For example, this means that migration distance explains a significant amount of variation in colony productivity once the variation caused by colony size has been removed. Therefore at least some variation in productivity must be controlled by migration distance independently of a direct effect of colony size. Our findings suggest that long migration movements arise from both higher density-dependent competition (driven by larger colony size) and from poor local conditions. These long movements, which we show result in higher energy expenditure, combined with the relatively lower resource availability at the wintering grounds, may lead birds to return to the colony in reduced body condition, which may affect their chance to breed early or rear a chick successfully. These processes do not exclude additional effects on productivity related to colony size during breeding.