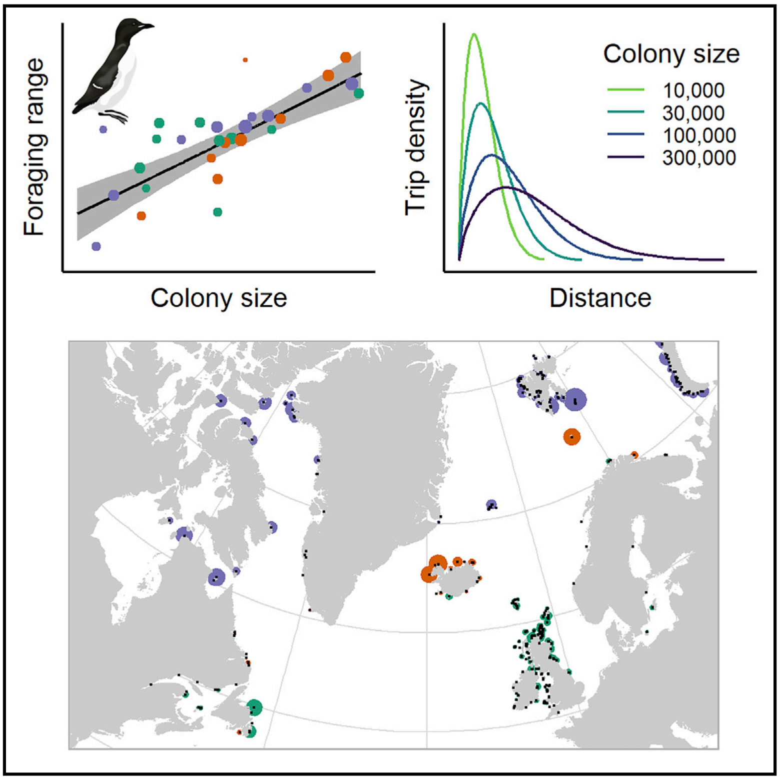
Current Biology

Report

# Foraging range scales with colony size in high-latitude seabirds

## Graphical abstract



## Authors

Allison Patterson, H. Grant Gilchrist,
Sigurd Benjaminsen, ...,
Hallvard Strøm,
Thorkell Lindberg Thórarinsson,
Kyle H. Elliott

## Correspondence

allison.patterson@mail.mcgill.ca

## In brief

Seabird colony size can vary over several orders of magnitude. Colony size likely plays an important role in determining individual behavior. Using tracking data from murres, the world's most densely breeding seabirds, Patterson et al. show how the distribution of foraging-trip distances scales to colony size, consistent with Ashmole's halo theory.

## Highlights

- The distribution of foraging trips around murre colonies scaled to colony size$^{0.33}$
- Colony size can be used to predict foraging areass over a large geographic scale
- Foraging areas of most North Atlantic murre breeding populations are not within protected areas

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Report

# Foraging range scales with colony size in high-latitude seabirds

Allison Patterson,[1,20,21,*] H. Grant Gilchrist,[2] Sigurd Benjaminsen,[3] Mark Bolton,[4] Anne Sophie Bonnet-Lebrun,[5] Gail K. Davoren,[6] Sébastien Descamps,[7] Kjell Einar Erikstad,[3,8] Morten Frederiksen,[9] Anthony J. Gaston,[10] Julia Gulka,[6] Jonas Hentati-Sundberg,[11] Nicholas Per Huffeldt,[9,12] Kasper Lambert Johansen,[9] Aili Lage Labansen,[12] Jannie Fries Linnebjerg,[9] Oliver P. Love,[13] Mark L. Mallory,[14] Flemming Ravn Merkel,[9,11] William A. Montevecchi,[15] Anders Mosbech,[8] Olof Olsson,[16] Ellie Owen,[4] Norman Ratcliffe,[5] Paul M. Regular,[17] Tone Kristin Reiertsen,[3] Yan Ropert-Coudert,[18] Hallvard Strøm,[7] Thorkell Lindberg Thórarinsson,[19] and Kyle H. Elliott[1]

[1]Department of Natural Resource Sciences, McGill University, 21111 Lakeshore Boulevard, Sainte-Anne-de-Bellevue, QC H9X 3V9, Canada
[2]National Wildlife Research Centre, Environment and Climate Change Canada, Ottawa, ON, Canada
[3]Norwegian Institute for Nature Research, Fram Centre, 9296 Tromsø, Norway
[4]RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, Sandy, UK
[5]British Antarctic Survey, High Cross, Madingley Road, Cambridge, UK
[6]Department of Biological Sciences, University of Manitoba, Winnipeg, MB R3T 2N2, Canada
[7]Norwegian Polar Institute, Fram Centre, PO Box 6606 Langnes, 9296 Tromsø, Norway
[8]Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, Trondheim, Norway
[9]Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark
[10]Laskeek Bay Conservation Society, Queen Charlotte, PO Box 867, Queen Charlotte, BC V0T 1S0, Canada
[11]Department of Aquatic Resources, Institute of Marine Research, Swedish University of Agricultural Sciences, Lysekil, Sweden
[12]Greenland Institute of Natural Resources, Kivioq 2, 3900 Nuuk, Greenland
[13]Department of Integrative Biology, University of Windsor, 401 Sunset Avenue, Windsor, ON N9B 3P4, Canada
[14]Biology, Acadia University, 15 University Avenue, Wolfville, NS B4P 2R6, Canada
[15]Psychology and Biology Departments, Memorial University of Newfoundland, St. John's, NL A1C 5S7, Canada
[16]Stockholm Resilience Centre, Stockholm University, Stockholm, Sweden
[17]Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, St. John's, NL, Canada
[18]Centre d'Etudes Biologiques de Chizé, CNRS - La Rochelle Université, Villiers-en-Bois, France
[19]Northeast Iceland Nature Research Centre, Hafnarstétt 3, 640 Húsavík, Iceland
[20]Twitter: @allisonglider
[21]Lead contact
*Correspondence: allison.patterson@mail.mcgill.ca
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## SUMMARY

Density-dependent prey depletion around breeding colonies has long been considered an important factor controlling the population dynamics of colonial animals.[1–4] Ashmole proposed that as seabird colony size increases, intraspecific competition leads to declines in reproductive success, as breeding adults must spend more time and energy to find prey farther from the colony.[1] Seabird colony size often varies over several orders of magnitude within the same species and can include millions of individuals per colony.[5,6] As such, colony size likely plays an important role in determining the individual behavior of its members and how the colony interacts with the surrounding environment.[6] Using tracking data from murres (*Uria* spp.), the world's most densely breeding seabirds, we show that the distribution of foraging-trip distances scales to colony size$^{0.33}$ during the chick-rearing stage, consistent with Ashmole's halo theory.[1,2] This pattern occurred across colonies varying in size over three orders of magnitude and distributed throughout the North Atlantic region. The strong relationship between colony size and foraging range means that the foraging areas of some colonial species can be estimated from colony sizes, which is more practical to measure over a large geographic scale. Two-thirds of the North Atlantic murre population breed at the 16 largest colonies; by extrapolating the predicted foraging ranges to sites without tracking data, we show that only two of these large colonies have significant coverage as marine protected areas. Our results are an important example of how theoretical models, in this case, Ashmole's version of central-place-foraging theory, can be applied to inform conservation and management in colonial breeding species.

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## RESULTS AND DISCUSSION

### Colony size-foraging range relationship

Colonial breeding is pervasive among seabirds, occurring in 95% of species,[7] and density-dependent prey depletion around breeding colonies has long been proposed as an important factor controlling population dynamics. Ashmole's halo theory predicts that, assuming equal distribution and abundance of food, individuals at larger colonies should forage farther than those from small colonies during the same breeding stage. Foraging range should increase with colony size to the 0.5 power because the area available for foraging is proportional to the square of distance from the colony.[8,9] Although prey depletion is widely assumed to limit colony size in seabirds, based on geographical distributions of colonies and variation in trip durations or daily energy expenditure with colony size,[8,10–12] direct measurements of the relationship between colony size and foraging range are scarce.[13,14] Although several studies have shown that prey is less abundant near colonies,[15–17] a link with colony size is necessary to provide support for Ashmole's theory.

We used GPS tracking data collected from common murre (COMU) (*Uria aalge*) and thick-billed murre (TBMU) (*Uria lomvia*) at 29 colonies, ranging in size from 900 to 470,000 breeding pairs, within the North Atlantic region (Figures 1, S1, and S2; Table S1). COMU and TBMU are congeneric species with similar morphology, behavior, energetics, and diet;[18,19] therefore, we expected them to exhibit a similar relationship between foraging range and colony size. Globally, murre colonies range in size over five orders of magnitude, from hundreds to millions of pairs.[18,19] High flight costs, delivery of single prey items to chicks, and open breeding sites that necessitate continuous nest attendance to protect offspring make murres particularly sensitive to increases in foraging range that reduce parental provisioning rates.[20–22] Only data from birds in the chick-rearing stage of breeding at the colony were included in the analysis, as this is the breeding stage when feeding rates are highest and competition should have the greatest effect on foraging range.[20,23] Our analysis included tracking from 973 individual birds (per site median = 16, range = 3–194), collected between 2009 and 2020, with 5,283 foraging trips (per site median = 81, range = 7–1,536; Table S1). We calculated the maximum overwater distance from the colony for each foraging trip (hereafter, trip distance) because murres avoid flying over land.

We developed a foraging-range model to describe how the distribution of maximum foraging-trip distances (foraging range) changes as a function of colony size.[24–26] We used Bayesian distributional regression[27] to model foraging as a function of colony size and other environmental predictors. This approach allowed for modeling of fixed and random effects for all parameters (not just the mean) of the distributions considered and enabled us to derive estimates for the entire conditional distribution of foraging trips.[28,29] The distribution of foraging-trip distances around each colony conformed most closely to a Weibull distribution (STAR Methods). The scale parameter ($\lambda$) of the Weibull distribution increased to the exponent 0.33 (95% CI = 0.22–0.44) of the combined population size of both murre species at each colony (Figure 2; Table S3); the 95% credible interval for the exponent did not overlap with the expected value of 0.5. The foraging-range model predicted that 50% of foraging trips occur within 11.2 km (95% CI = 9.5–13.7) and 34.7 km (95% CI = 24.5–50.5) and 95% of foraging trips occur within 27.5 km (95% CI = 22.3–33.7) and 85.3 km (95% CI = 59.5–122.0) for colonies of 10,000 and 300,000 pairs, respectively (Figure 2). Models using the combined populations of both COMU and TBMU at mixed colonies performed better than models using only the species-specific colony size or models using colony size that accounted for the inverse-distance weighted size of neighboring murre colonies (Table S3). In addition, there was no support for a difference in the scaling parameter between COMU and TBMU (Table S3). Finally, we examined whether broad-scale environmental factors were related to foraging range. Models including colony latitude (increasing day length could influence trip duration and distance), mean July sea surface temperature, maximum primary productivity, and proportion of water available within 30 km of the colony (relative amount of ocean habitat could influence competition) were not competitive with a model based only on colony size (Table S4). Figure S3 shows a comparison of observed and predicted trip distance density distributions for each site.

We extrapolated predicted foraging areas (FAs) within which 95% of trips should occur ($FA_{95}$) based on posterior probability distributions of foraging-trip distances for a given colony size and the overwater distances from the colony. This geographic extrapolation of the foraging-range model assumes that birds use the whole area within their colony's foraging radius. However, as prey are likely to be unevenly distributed, we could expect birds to make repeated, directed trips to highly profitable prey patches within that radius, potentially resulting in different foraging distributions and total exploited areas than predicted. The 95% utilization distribution ($UD_{95}$) is a common metric calculated to represent the FAs used by breeding seabirds. The $UD_{95}$ represents the area in which the population is expected to occur 95% of the time based on the distribution of all locations within trips and, as such, is not directly comparable with the $FA_{95}$. Nevertheless, this comparison is useful to demonstrate that the $FA_{95}$ can provide similar information about the distribution of foraging effort around a colony. For 17 colonies with sufficient tracking data to estimate a representative FA using $UD_{95}$, the mean overlap between the observed $UD_{95}$ and predicted $FA_{95}$ was 61.9% (mean Dice's similarity: 0.619, SD = 0.107; Figure 3; STAR Methods). If a consistent foraging hotspot, such as a fish spawning site, is available, then, many individuals may travel to that hotspot, regardless of the distance. For example, COMUs in Atlantic Canada exploit dense concentrations of spawning capelin (*Mallotus villosus*) during chick-rearing, making directed trips during active spawning. When these prey are not available, however, murres respond by foraging over a wider area.[30,31] Under this scenario, the directionality of foraging trips should be highly concentrated, with less of a relationship to colony size. There was no evidence of a correlation between Dice's similarity and the circular variance in trip bearings ($r = -0.33$, $p = 0.188$), which does not support the hypothesis that colonies where individuals make more directed foraging trips have a foraging distribution less accurately predicted by the foraging-range model (Figure S4). However, Dice's similarity had a strong positive correlation to the total number of individuals tracked ($r = 0.61$, $p = 0.01$) and a modest correlation with the number of years of tracking ($r = 0.49$, $p = 0.046$, Figure S4), suggesting that FAs

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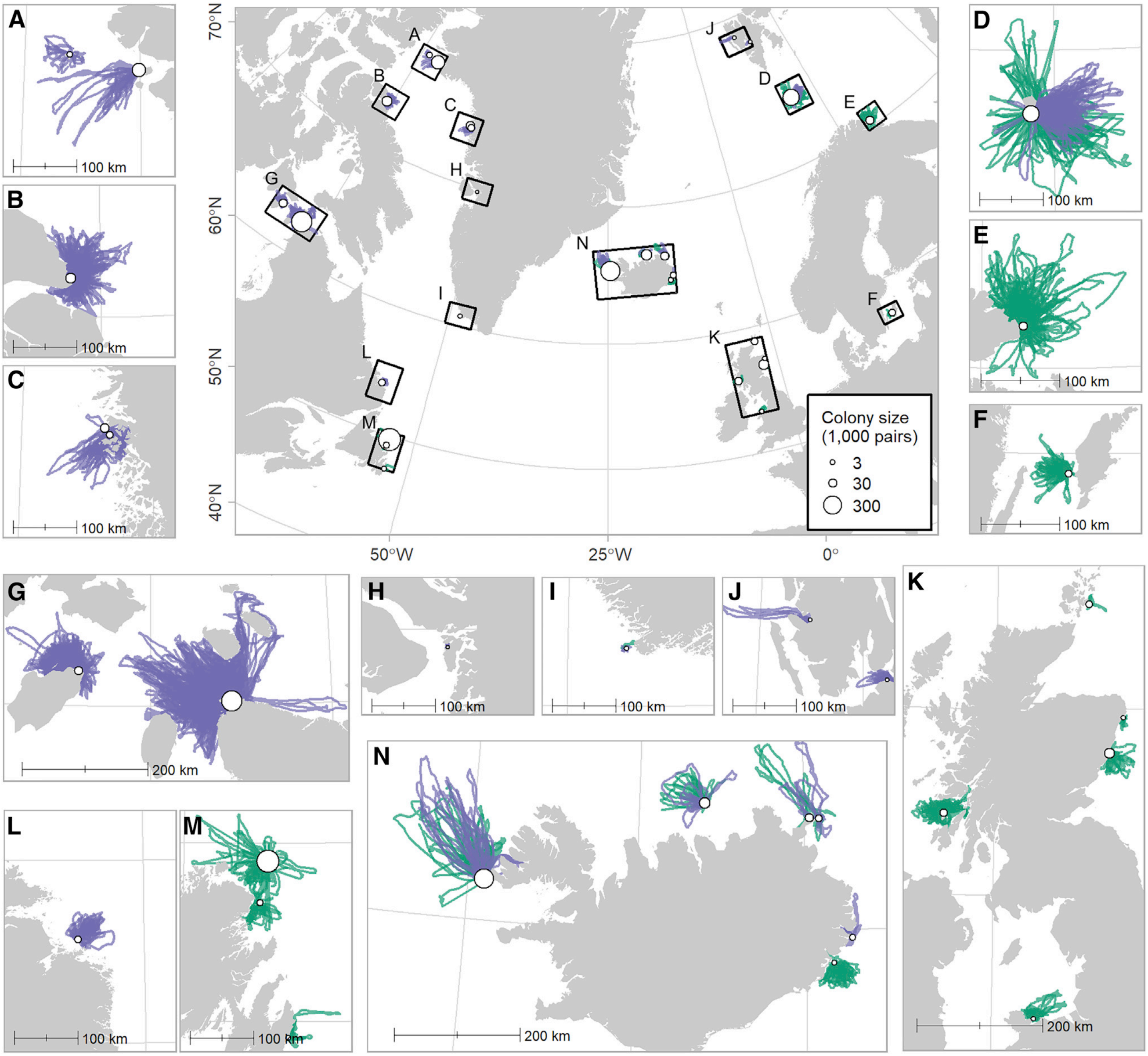

**Figure 1. The distribution of murre colonies with GPS tracking data used in this study**

Point sizes indicate the estimates of combined colony size of both murre species at a site. Inset maps provide detailed views of GPS tracking data for common (green) and thick-billed (purple) murres. All maps use Lambert conformal conical projection, and inset maps are plotted on the same scale. Individual site maps are provided in Figures S1 and S2, and detailed site-level data are provided in Table S1.

were predicted better for sites that were sampled more extensively. Tracking studies tend to have small sample sizes and short duration; individuals tracked may not visit all the areas used by the wider population during that period or even by the tracked individuals over a longer timescale. Increasing variance in trip direction with number of trips and years of tracking indicates that over time, observed distributions will occupy more of the potential foraging range predicted by colony size.

The strength of the relationship between foraging range and colony size, spanning an entire ocean basin, provides convincing evidence for Ashmole's halo theory that intraspecific competition for food is an important factor contributing to negative density dependence in colonial seabirds. Previous multi-colony studies generally tracked birds from colonies over a much smaller geographical range and a smaller range of colony sizes (<75,000 pairs).[8,11–13,32] The cost of commuting between FAs and breeding sites increases with distance for breeding adults, which can constrain chick growth at larger colonies,[33] because the time between feedings increases.[22] Multiple studies have proposed that foraging range should scale with the 0.5 exponent of colony size[8,9,32,34] because FA scales with the square root of foraging range. The scaling factor in our study was lower, at 0.33

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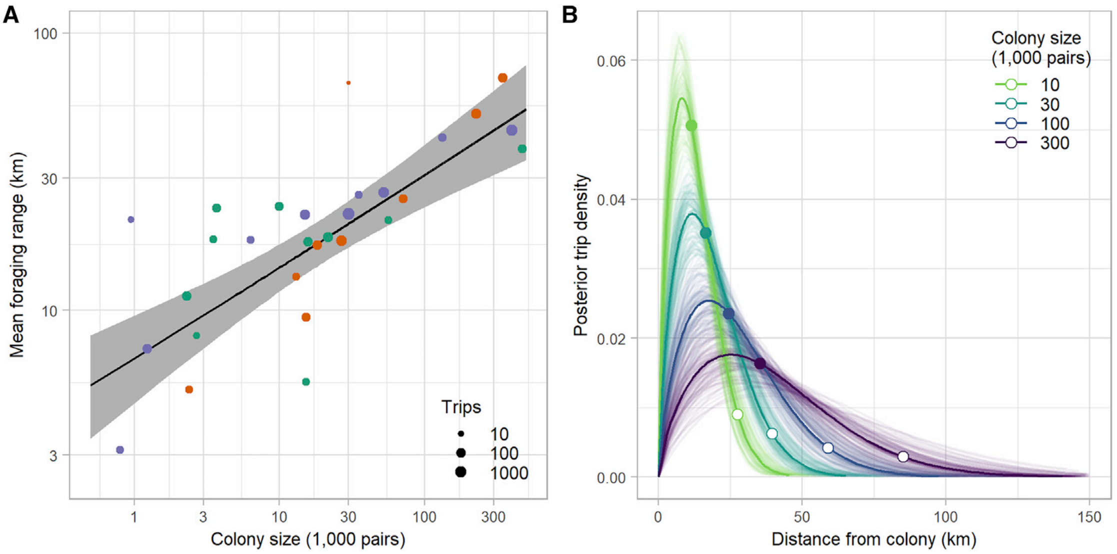

**Figure 2. Relationship between colony size and mean foraging range modeled using a Weibull distribution**

(A) Predicted mean foraging distance as a function of colony size. Points show observed mean foraging range for individual colonies, with point size scaled to the number of trips recorded at each site. Colonies of common murre, thick-billed murre, and mixed species are indicated by green, purple, and orange colors, respectively. The solid line shows the predicted relationship between foraging range and colony size, and the shaded area shows the 95% credible region for this relationship.

(B) Spaghetti plot showing the predicted foraging-trip density distributions for a range of colony sizes. Bold colored lines show the mean predicted density of the foraging-trip distances for a given colony size, and light lines show 500 posterior draws at each level of colony size. Closed points and open points, respectively, show the distance at which 50% and 95% of foraging trips would occur for each colony size. Figure S3 shows observed and predicted trip densities for each site.

(95% CI = 0.22–0.44). This could result from systematic differences in habitat quality that also correlate with colony size, namely that colony size is likely positively correlated with foraging conditions. Alternatively, the lower exponent may arise from predation pressure exerted in three dimensions. Murres are pursuit divers that can forage at depths over 200 m;[18] therefore, foragers may trade-off costs of flying farther to locate prey by making more, deeper dives while remaining closer to the colony.[35,36] Similar scaling is likely to exist among other species, but values will depend on their foraging ecology and environment. Further studies across different taxa of central-place foragers may reveal more general patterns. For example, species that are more constrained in their foraging habitat—like true guillemots (*Cepphus* spp.) foraging in coastal zones and tropical terns foraging along reefs—may show different scaling with colony size.[2] The recent proliferation of tracking studies provides the opportunity for large-scale multi-colony and multi-species studies to better understand this fundamental ecological relationship.

## Predicting murre foraging ranges throughout the North Atlantic

There are an estimated 7,582,000 pairs of murres (3,099,000 COMU and 4,484,000 TBMU) breeding at 384 colonies (larger than 500 pairs) within the North Atlantic region (Table S2). With so many colonies, it is clearly not feasible to directly measure colony-specific foraging radii using GPS tracking. Estimating foraging ranges from colony size data, which are easier to collect and more widely available, offers a pragmatic alternative to infer potential UDs during chick-rearing. Using the foraging-range model described above, we estimate that the predicted 95% FA ($FA_{95}$) for all murre colonies in the North Atlantic is 495,000 $km^2$, with $FA_{95}$ of individual colonies ranging in size from 45 to 29,600 $km^2$ (Figure 4; STAR Methods). Sixteen colonies (4% of all colonies) with at least 100,000 breeding pairs account for 54% of the total North Atlantic murre population and have a combined $FA_{95}$ of 238,000 $km^2$. Because the foraging radii of some larger colonies encompasses smaller neighboring colonies, the areas within these foraging radii would be used by 58% of breeding murres in the North Atlantic, demonstrating that protecting even a relatively small proportion of colonies could protect much of the regional population.

We compared predicted FAs ($FA_{95}$) with the World Database of Protected Areas (WDPA)[37] to evaluate the level of protection for FAs of the North Atlantic murre population. The WDPA may not include all protected areas and does not reflec2t other effective management actions that may be in place within different jurisdictions. Nevertheless, it provides a useful starting point for evaluating the level of potentially effective species protection in place. Forty-eight percent of all colonies, representing 61% of the North Atlantic murre population, have less than 10% of their $FA_{95}$ within protected areas and 18% of colonies (22% of the population) have no overlap with protected areas. Only 17% of colonies, accounting for 6.0% of the population, have at least 90% of their $FA_{95}$ within protected areas. Among the 16 largest colonies, only two have more than 50% of their $FA_{95}$ within protected areas and 9 colonies have less than 10% of their $FA_{95}$ within protected areas. If these 16 colonies with at least 100,000 pairs had protection of $FA_{95}$, this would help safeguard FAs for nearly two-thirds of the North Atlantic population of

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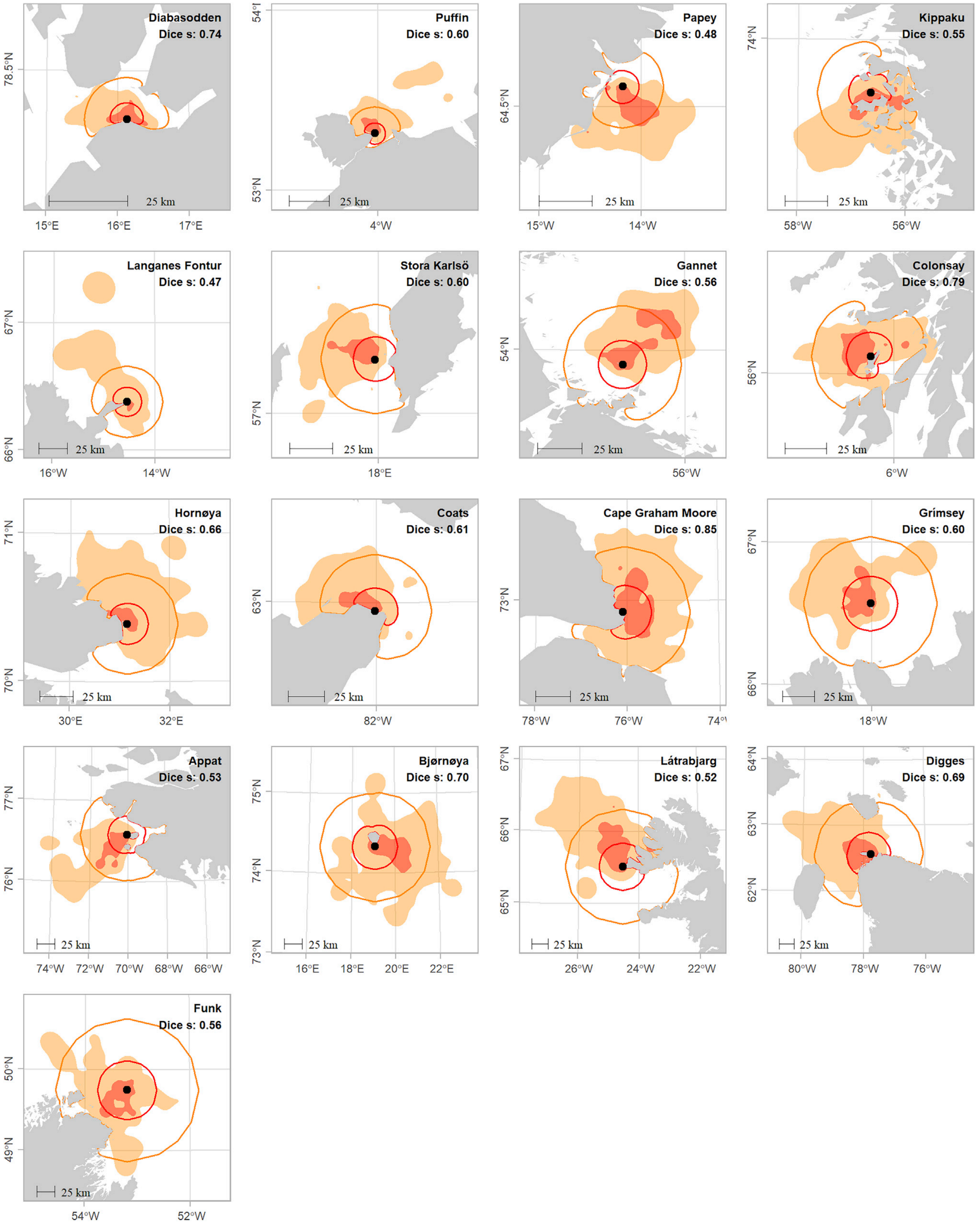

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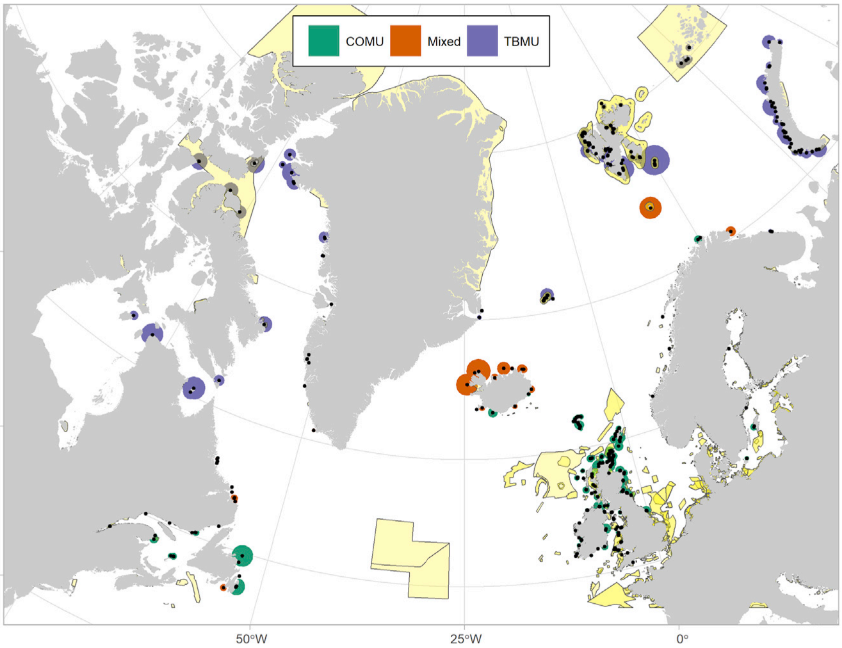

**Figure 4. Predicted 95% foraging area ($FA_{95}$), within which 95% of foraging trips are expected to occur based on colony size, for common murre (COMU) and thick-billed murre (TBMU) colonies (black points) throughout the North Atlantic region**

Colonies were considered mixed if both species accounted for at least 1% of the breeding population. Marine protected areas from the World Database of Protected Areas[37] are shown in yellow.

murres (44% of COMU and 62% of TBMU) during the breeding season. Of course, the effectiveness of a marine protected area for any seabird species depends on the management prescriptions related to specific activities including hunting, fisheries, hydrocarbon exploration and extraction, tourism, and shipping.[38,39] This analysis illustrates the utility of the foraging-range model for informing any area-based conservation measures.

Foraging range is a widely used tool for identifying important areas around seabird colonies.[34,40,41] Thaxter et al.[41] proposed using species-specific foraging ranges to inform Marine Protected Areas around seabird colonies. Our study shows that colony size can be used to further inform estimates of foraging range for species that occur in colonies that range in size over multiple orders of magnitude. Modeling foraging distributions based on colony size has the advantage of being generalizable over a broad geographical and ecological scale, as represented in this study. Despite the many other factors that contribute to the at-sea foraging distribution of seabirds on a local scale, we have demonstrated that colony size alone explained substantial variance in foraging range at a range-wide level. The fundamental constraints imposed by colony size and the energetic costs associated with commuting trips are high; therefore, we would expect the relationship between colony size and foraging range to persist in spite of differences in local environmental conditions. Marine spatial planning should, of course, primarily consider local foraging distributions where these data are available; we would expect observed distributions to deviate from model predictions at sites where environmental conditions are poor, leading to declining reproductive success and colony size.[13,42] However, our study also demonstrates that the interaction between colony size and foraging range should not be ignored in any model that aims to extrapolate habitat use across colonies of different sizes.[13] Generalizable models, informed by ecological theory, are an important contribution to informing conservation for such species on a large spatial scale. Our analysis provides an example of how behavioral theory, in this case Ashmole's halo, a special case of central-place-foraging theory, can be applied to inform conservation and management.[43] Although our dataset is noteworthy in its size, it still represents direct tracking at only 7.5% of the murre colonies within the North Atlantic, which highlights the limitations of predicting foraging habitat through direct tracking of such a widely distributed species.

## STAR★METHODS

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

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - ○ Lead contact
  - ○ Materials availability
  - ○ Data and code availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
- METHOD DETAILS
  - ○ Foraging Trips
  - ○ Colony sizes
  - ○ Environmental variables
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - ○ Foraging range model
  - ○ Comparing foraging range model to utilization distributions
  - ○ Predicting foraging ranges within the North Atlantic murre population

**Figure 3. Overlap between the predicted foraging areas ($FA_{95}$, open polygons), the area within which 50% and 95% of foraging trips are expected to occur based on the foraging-range model, and observed 95% utilization distribution ($UD_{95}$, filled polygons) based on the mean utilization distribution of all GPS tracks from each site**

The 50% (red) and 95% (orange) areas are shown. Dice's similarity for each colony is given in the top-right corner. Figure S4 shows scatterplots comparing Dice's S with variance in trip bearings, number of individuals tracked, and years of tracking for each site.

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## SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.06.084.

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## AUTHOR CONTRIBUTIONS

All authors contributed data. A.P. and K.E.E. conceived of and led the project. A.P. conducted the analysis with support from S.D. Writing was done by A.P., and editing was done by all authors.

## DECLARATION OF INTERESTS

The authors declare no competing interests.

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## REFERENCES

1. Ashmole, N.P. (1963). The regulation of numbers of tropical oceanic birds. Ibis *103b*, 458–473.
2. Storer, R.W. (1952). A Comparison of Variation, Behavior and Evolution in the Sea Bird Genera Uria and Cepphus (University of California Press).
3. Vance, H.M., Hooker, S.K., Mikkelsen, L., van Neer, A., Teilmann, J., Siebert, U., and Johnson, M. (2021). Drivers and constraints on offshore foraging in harbour seals. Sci. Rep. *11*, 6514.
4. Bernstein, R.A., and Gobbel, M. (1979). Partitioning of space in communities of ants. J. Anim. Ecol. *48*, 931–942.
5. Borowicz, A., McDowall, P., Youngflesh, C., Sayre-McCord, T., Clucas, G., Herman, R., Forrest, S., Rider, M., Schwaller, M., Hart, T., et al. (2018). Multi-modal survey of Adélie penguin mega-colonies reveals the Danger Islands as a seabird hotspot. Sci. Rep. *8*, 3926.
6. Brown, C.R. (2016). The ecology and evolution of colony-size variation. Behav. Ecol. Sociobiol. *70*, 1613–1632.
7. Coulson, J.C. (2001). Colonial breeding in seabirds. In Biology of Marine Birds, (CRC Press), pp. 100–127.
8. Lewis, S., Sherratt, T.N., Hamer, K.C., and Wanless, S. (2001). Evidence of intra-specific competition for food in a pelagic seabird. Nature *412*, 816–819.
9. Gaston, A.J., Ydenberg, R.C., and Smith, G.J. (2007). Ashmole's halo and population regulation in seabirds. Mar. Ornithol. *35*, 119–126.
10. Ballance, L.T., Ainley, D.G., Ballard, G., and Barton, K. (2009). An energetic correlate between colony size and foraging effort in seabirds, an example of the Adélie penguin *Pygoscelis adeliae*. J. Avian Biol. *40*, 279–288.
11. Furness, R.W., and Birkhead, T.R. (1984). Seabird colony distributions suggest competition for food supplies during the breeding season. Nature *311*, 655–656.
12. Ainley, D.G., Ribic, C.A., Ballard, G., Heath, S., Gaffney, I., Karl, B.J., Barton, K.J., Wilson, P.R., and Webb, S. (2004). Geographic structure of Adélie penguin populations: overlap in colony-specific foraging areas. Ecol. Monogr. *74*, 159–178.
13. Wakefield, E.D., Owen, E., Baer, J., Carroll, M.J., Daunt, F., Dodd, S.G., Green, J.A., Guilford, T., Mavor, R.A., Miller, P.I., et al. (2017). Breeding density, fine-scale tracking, and large-scale modeling reveal the regional distribution of four seabird species. Ecol. Appl. *27*, 2074–2091.
14. Santora, J.A., Schroeder, I.D., Field, J.C., Wells, B.K., and Sydeman, W.J. (2014). Spatio-temporal dynamics of ocean conditions and forage taxa reveal regional structuring of seabird–prey relationships. Ecol. Appl. *24*, 1730–1747.
15. Birt, V.L., Birt, T.P., Goulet, D., Cairns, D.K., and Montevecchi, W.A. (1987). Ashmole's halo: direct evidence for prey depletion by a seabird. Mar. Ecol. Prog. Ser. *40*, 205–208.
16. Ainley, D.G., Ford, R.G., Brown, E.D., Suryan, R.M., and Irons, D.B. (2003). Prey resources, competition, and geographic structure of kittiwake colonies in Prince William Sound. Ecology *84*, 709–723.
17. Weber, S.B., Richardson, A.J., Brown, J., Bolton, M., Clark, B.L., Godley, B.J., Leat, E., Oppel, S., Shearer, L., Soetaert, K.E.R., et al. (2021). Direct evidence of a prey depletion "halo" surrounding a pelagic predator colony. Proc. Natl. Acad. Sci. USA *118*. e2101325118.
18. Gaston, A.J., and Hipfner, J.M. (2000). Thick-billed murre (*Uria lomvia*), version 2.0. In The Birds of North America (Cornell Lab of Ornithology).
19. Ainley, D.G., Nettleship, D.N., Carter, H.R., and Storey, A.E. (2020). Common murre (*Uria aalge*). In Birds of the World (Cornell Laboratory of Ornithology).
20. Elliott, K.H., Le Vaillant, M., Kato, A., Gaston, A.J., Ropert-Coudert, Y., Hare, J.F., Speakman, J.R., and Croll, D. (2014). Age-related variation in energy expenditure in a long-lived bird within the envelope of an energy ceiling. J. Anim. Ecol. *83*, 136–146.
21. Hentati-Sundberg, J., Olin, A.B., Evans, T.J., Isaksson, N., Berglund, P.-A., and Olsson, O. (2021). A mechanistic framework to inform the spatial management of conflicting fisheries and top predators. J. Appl. Ecol. *58*, 125–134.
22. Houston, A.I., Thompson, W.A., and Gaston, A.J. (1996). The use of a time and energy budget model of a parent bird to investigate limits to fledging mass in the thick-billed murre. Funct. Ecol. *10*, 432–439.
23. Dunn, R.E., Wanless, S., Daunt, F., Harris, M.P., and Green, J.A. (2020). A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle. Sci. Rep. *10*, 5993.
24. Nathan, R., Klein, E., Robledo-Anuncio, J.J., and Revilla, E. (2012). Dispersal kernels: review. In Dispersal Ecology and Evolution (Oxford University Press).
25. Fagan, W.F., Lutscher, F., and Schneider, K. (2007). Population and community consequences of spatial subsidies derived from central-place foraging. Am. Nat. *170*, 902–915.
26. Bullock, J.M., Mallada González, L.M., Tamme, R., Götzenberger, L., White, S.M., Pärtel, M., and Hooftman, D.A.P. (2017). A synthesis of empirical plant dispersal kernels. J. Ecol. *105*, 6–19.
27. Bürkner, P.-C. (2017). brms: an R package for Bayesian multilevel models using Stan. J. Stat. Software *80*, 1–28.

28. Bürkner, P.-C. (2018). Advanced Bayesian multilevel modeling with the R package brms. R J. *10*, 395.
29. Kneib, T., Silbersdorff, A., and Säfken, B. (2021). Rage against the mean—a review of distributional regression approaches. In Econometrics and Statistics (Elsevier).
30. Montevecchi, W., Gerrow, K., Buren, A., Davoren, G., Lewis, K., Montevecchi, M., and Regular, P. (2019). Pursuit-diving seabird endures regime shift involving a three-decade decline in forage fish mass and abundance. Mar. Ecol. Prog. Ser. *627*, 171–178.
31. Gulka, J., and Davoren, G.K. (2019). High individual flexibility in the foraging behavior of a marine predator, the common murre. Mar. Biol. *166*, 83.
32. Wakefield, E.D., Bodey, T.W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R.G., Green, J.A., Grémillet, D., Jackson, A.L., et al. (2013). Space partitioning without territoriality in gannets. Science *341*, 68–70.
33. Gaston, A.J., Chapdelaine, G., and Noble, D.G. (1983). The growth of Thick-billed Murre chicks at colonies in Hudson Strait: inter- and intra-colony variation. Can. J. Zool. *61*, 2465–2475.
34. Jovani, R., Lascelles, B., Garamszegi, L.Z., Mavor, R., Thaxter, C.B., and Oro, D. (2016). Colony size and foraging range in seabirds. Oikos *125*, 968–974.
35. Elliott, K.H., Woo, K.J., Gaston, A.J., Benvenuti, S., Dall'Antonia, L., and Davoren, G.K. (2009). Central-place foraging in an Arctic seabird provides evidence for Storer-Ashmole's Halo. Auk *126*, 613–625.
36. Cairns, D.K., Montevecchi, W., Birt-Friesen, V.L., and Macko, S.A. (1990). Energy expenditures, activity budgets, and prey harvest of breeding common murres. Stud. Avian Biol. *14*, 84–92.
37. UNEP-WCMC; IUCN (2020). Marine protected planet. https://www.protectedplanet.net/marine.
38. Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Yates, O., Lascelles, B., Borboroglu, P.G., and Croxall, J.P. (2019). Threats to seabirds: a global assessment. Biol. Conserv. *237*, 525–537.
39. Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A., and Taylor, P. (2012). Seabird conservation status, threats and priority actions: a global assessment. Bird Conserv. Int. *22*, 1–34.
40. Soanes, L.M., Bright, J.A., Angel, L.P., Arnould, J.P.Y., Bolton, M., Berlincourt, M., Lascelles, B., Owen, E., Simon-Bouhet, B., and Green, J.A. (2016). Defining marine important bird areas: testing the foraging radius approach. Biol. Conserv. *196*, 69–79.
41. Thaxter, C.B., Lascelles, B., Sugar, K., Cook, A.S.C.P., Roos, S., Bolton, M., Langston, R.H.W., and Burton, N.H.K. (2012). Seabird foraging ranges as a preliminary tool for identifying candidate marine protected areas. Biol. Conserv. *156*, 53–61.
42. Cook, A.S.C.P., Dadam, D., Mitchell, I., Ross-Smith, V.H., and Robinson, R.A. (2014). Indicators of seabird reproductive performance demonstrate the impact of commercial fisheries on seabird populations in the North Sea. Ecol. Indic. *38*, 1–11.
43. Berger-Tal, O., Blumstein, D.T., Carroll, S., Fisher, R.N., Mesnick, S.L., Owen, M.A., Saltz, D., St Claire, C.C.S., and Swaisgood, R.R. (2016). A systematic survey of the integration of animal behavior into conservation. Conserv. Biol. *30*, 744–753.
44. R Core Team (2021). R: a language and environment for statistical computing (R Foundation for Statistical Computing).
45. Beal, M., Oppel, S., Handley, J., Pearmain, E.J., Morera-Pujol, V., Carneiro, A.P.B., Davies, T.E., Phillips, R.A., Taylor, P.R., Miller, M.G.R., et al. (2021). track2KBA: an R package for identifying important sites for biodiversity from tracking data. Methods Ecol. Evol. *12*, 2372–2378.
46. Wessel, P., and Smith, W.H.F. (1996). A global, self-consistent, hierarchical, high-resolution shoreline database. J. Geophys. Res. *101*, 8741–8743.
47. Bosch, S., and Fernandez, S. (2022). sdmpredictors: species distribution modelling predictor datasets. R package version 0.2.12 (R Development Team). https://CRAN.R-project.org/package=sdmpredictors.
48. van Etten, J. (2017). R package gdistance: distances and routes on geographical grids. J. Stat. Software *76*, 1–21.
49. Hahsler, M., Piekenbrock, M., and Doran, D. (2019). dbscan: fast density-based clustering with R. J. Stat. Soft. *91*, 1–30.
50. Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., and De Clerck, O.D. (2012). Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Glob. Ecol. Biogeogr. *21*, 272–281.
51. Sbrocco, E.J., and Barber, P.H. (2013). MARSPEC: ocean climate layers for marine spatial ecology. Ecology *94*, 979.
52. Bosch, S., Tyberghein, L., and De Clerck, O. (2018). Sdmpredictors: species distribution modelling predictor datasets. R Package Version 0.2.8.
53. Vehtari, A., Gelman, A., and Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat. Comput. *27*, 1413–1432.
54. Paradis, E., and Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics *35*, 526–528.
55. Calenge, C. (2006). The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Modell. *197*, 516–519.
56. Hijmans, R.J. (2019). Geosphere: spherical trigonometry. R Package Version 1.5-10. https://CRAN.R-project.org/package=geosphere.
57. Lund, U., and Agostinelli, C. (2017). R Package "circular": circular statistics. R Package Version 0.4-93. https://r-forge.r-project.org/projects/circular/2.

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## STAR★METHODS

### KEY RESOURCES TABLE

| REAGENT or RESOURCE | SOURCE | IDENTIFIER |
|---|---|---|
| Deposited data | | |
| Raw GPS tracks | This paper | https://doi.org/10.17632/nhbzwwbymj.1 |
| Foraging trips | This paper | https://doi.org/10.17632/nhbzwwbymj.1 |
| Colony sizes | This paper | https://doi.org/10.17632/nhbzwwbymj.1 |
| Software and algorithms | | |
| R, version 4.1.3 | R Core Team[44] | https://www.R-project.org/ |
| brms, version 2.17.0 | Bürkner[27] | https://cran.r-project.org/web/packages/brms/index.html |
| track2KBA, version 1.0.2 | Beal et al.[45] | https://cran.r-project.org/web/packages/track2KBA/index.html |
| Code used in analysis | This paper | https://doi.org/10.17632/nhbzwwbymj.1 |
| Other | | |
| Coastline | Wessel and Smith[46] | https://www.soest.hawaii.edu/pwessel/gshhg/ |
| Mean July SST | Bosch and Fernandez[47] | https://www.lifewatch.be/sdmpredictors/MS_sst07_5m_lonlat.tif |
| Maximum primary productivity | Bosch and Fernandez[47] | https://bio-oracle.org/data/2.2/Present.Surface.Primary.productivity.Lt.max.BOv2_2.tif.zip |
| Marine protected areas | UNEP-WCMC and IUCM[37] | https://www.protectedplanet.net/marine |

### RESOURCE AVAILABILITY

#### Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Allison Patterson (allison.patterson@mail.mcgill.ca).

#### Materials availability

This study did not generate new unique reagents.

#### Data and code availability

- GPS tracking and colony size data were deposited on Mendeley and are publicly available as of the date of publication. DOIs are listed in the key resources table. Colony size data for colonies in Russia are available on request through the Barent's Portal (http://www.barentsportal.com).
- All original data and code has been deposited at Mendeley and is publicly available as of the date of publication. Deposited data includes raw GPS tracks, trip summaries, and colony size estimates. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

### EXPERIMENTAL MODEL AND SUBJECT DETAILS

Our study focused on adult common (*Uria aalge*) and thick-billed murres (*Uria lomvia*) during the chick-rearing stage of breeding. We collected GPS tracking data at 29 colonies within the North Atlantic region (Figures 1, S1, and S2). A detailed summary of sample sizes at each colony is provided in Table S1. Birds were caught at the nest according to ethical approval from each country's appropriate organization.

### METHOD DETAILS

#### Foraging Trips

Foraging trips were defined as any continuous period of movement more than 1 km from the colony that lasted at least 20 minutes. For each foraging trip, we calculated the maximum overwater distance from the colony (hereafter, trip distance). Overwater distances were calculated on a 0.25 x 0.25 km raster grid using an Albers equal area projection centered on each colony using the 'gdistance'

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package.[48] Details on study site locations and tracking sample sizes are provided in Table S1 and maps of all tracks are shown in Figures S1 and S2.

### Colony sizes

We used existing data sources and consultation with regional experts to compile colony size data for murre colonies in the North Atlantic between 75°W and 75°E (Table S2). Different jurisdictions define the boundaries of adjacent colonies using different criteria. To reduce inconsistencies in how colonies are defined, we used a density-based spatial clustering algorithm to identify colonies that were spatially aggregated (R package 'dbscan', version 1.1-10).[49] Colonies identified as clusters were grouped and assigned the coordinates of the largest colony in the cluster.

To identify the level where competition is occurring for murres we considered three measures of colony size. Species-specific colony size (SSC), defined as the number of pairs of each species breeding at each colony. Combined colony size (CCS), defined as the number of pairs of the two species combined breeding at each colony. Finally, distance weighted colony size (DCS) that incorporates competition with murres from neighboring colonies, calculated as:

$$DCS_i = \sum \frac{CCS_j}{d_j + 1}$$

Where, $i$ is the focal colony, $j$ is an index for all colonies within the maximum recorded foraging range of murres in this study (200 km), $d$ is the distance between colony $i$ and colony $j$.

### Environmental variables

Colony latitude (LAT) was included as a potential predictor of foraging range, because latitude influences the daylight time available for foraging during summer and may also serve as a proxy for marine productivity. Mean July sea surface temperature (SST)[50] at the colony and maximum primary productivity (MPP)[51] were considered as potential predictors of marine conditions. These raster data were obtained from the 'sdmpredictors' package[52] (layer codes: 'MS_sst07_5m' and 'BO22_ppltmax_ss'). We calculated the relative potential foraging area based on the proportion of ocean area within a 30 km area around each colony (WAT), using a global high-resolution shoreline (https://www.soest.hawaii.edu/pwessel/gshhg/).[46] Colonies surrounded by water would have more potential foraging habitat within the same distance as coastal or fjord colonies.[13]

## QUANTIFICATION AND STATISTICAL ANALYSIS

No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment. All analyses were conducted using R version 4.1.3.[44]

### Foraging range model

We used hierarchical Bayesian distributional regression models[27,28] to estimate the effect of colony size and other potential predictors on the response distribution of foraging trip distances around a colony. First, we considered four possible distributions (exponential, lognormal, Gamma, and Weibull distributions) in a fully parameterized model where all distributional parameters depended on fixed effects of site identity and random effects for individual identity. All distributions were fit with a log-link function. Model comparison was performed using leave-one-out cross-validation and ΔELPD (expected log predictive density) to compare among models.[53] ELPD measures the expected predictive accuracy of a Bayesian model when predicting to new datasets, higher values of ELPD indicate better predictive performance.[53] The model fit using the Weibull distribution was 83.6 ΔELPD higher than the next best distribution. All subsequent analyses used the Weibull distribution.

Next, we considered models with three formulations of colony size (SSC, CCS, and DCS) as covariates for the Weibull scale parameter ($\lambda$). Colony size values were log-transformed for all analyses, because we expected foraging range to have a linear relationship with colony size on a log-log scale. We also considered combinations of models allowing for differences in slope or intercepts related to species (SPP). All models included random intercepts for individual identity nested within sites for both the scale and shape parameters. Models were compared using 7-fold leave-one-out cross validation with folds grouped by sites located within the same large marine ecosystem (LME, https://www.lmehub.net/), the same folds were applied to all models. Colonies within the Baltic Sea and North Sea LMEs were grouped to ensure at least three colonies within each fold. The model using CCS and no effects related to species had the best performance (Table S3). Finally, we considered additional effects of environmental variables on foraging range independently and in combination with the best colony size predictor. Model formulation and comparison followed the methods described above for determining the best measure of colony size. Only models including a single environmental and colony size predictor were considered. Models including environmental predictors did not perform better than the model with only CCS as a fixed effect (Table S4).

We used a linear hypothesis test to determine if the coefficient for colony size was different from the expected value of 0.5. We tested for spatial autocorrelation in the residuals from the best model using Moran's I with the 'ape' package.[54] Using the foraging range model identified above, we predicted the conditional distribution of foraging trip distances as a function of colony size by sampling shape and scale values from the posterior distribution and calculating the probability density function for the Weibull distribution (Figure 2). Predicted foraging ranges ($FR_{95}$), the distance from colony within which 95% of trips should occur, were calculated based

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on the quantile function of 500 posterior predictions of the shape and scale parameters. Estimates of $FR_{95}$ are reported as medians with 95% credible intervals.

### Comparing foraging range model to utilization distributions

GPS tracks were linearly interpolated to 5 min intervals, so that each location would be given the same weight in kernel density estimates. Only deployments with a minimum of 5 off colony locations (> 1 km) were included in the analysis. We calculated utilization distributions with the adehabitatHR package[55] using a 300 x 300 km area centered on the colony with a 500 x 500 m grid resolution, in the Albers Equal Area projection. Kernel smoothing parameters were calculated separately for each individual using the *ad hoc* method and utilization distributions (UD) were averaged across all individuals within each colony. We defined the *observed 95% foraging area* as the 95% volume contour of the kernel density estimate, after excluding any areas that overlap with land.

We used the track2KBA R package[45] to assess which sites had enough tracking data to adequately estimate a consistent *observed 95% foraging area* ($UD_{95}$) from the mean utilization distribution. We used 50 iterative resamples to calculate a mean foraging area for a colony from increasing subsamples of all individual tracks. The mean $UD_{95}$ was calculated for each iteration and sample size, and an inclusion rate was calculated for the proportion of out-of-sample locations that overlapped this area. A non-linear generalized least squares regression was fit to estimate the sample size where the inclusion rate reaches an asymptote. Representativeness (*R*) was calculated as:

$$R = \frac{y_n}{A} * 100$$

Where $A$ is the asymptote, $y$ is the inclusion rate achieved at the maximum sample size $n$.[45] Data for a site was considered representative if there were tracking data from at least 10 individuals, representativeness was at least 95%, and the estimated asymptote for inclusion rate was within 10% of the target of 95%. Based on the non-linear generalized least squares regression fits, tracks from 9 individuals (SD = 3.6) were required to obtain an estimated representativeness of 95%. However, a minimum of 10 independent tracks is recommended for inferring population UDs.[45]

The predicted density of foraging trips as a function of colony size and distance was calculated on the same grid used in estimating UDs by calculating the probability density function from posterior samples for a colony of the same size from the foraging range model. We calculated the *predicted 95% foraging area* ($FA_{95}$) based on all cells with a probability of use of at least 0.05. Predicted foraging areas were compared to observed foraging areas using Dice's Similarity Coefficient[32] s:

$$s = \frac{2A(UD_O \cap UD_P)}{A(UD_O) + A(UD_P)}$$

where, $A(UD_O)$ and $A(UD_P)$ are the observed and predicted foraging areas.

We calculated the bearing between the colony and the farthest foraging location within each trip using the 'geosphere' package.[56] For each colony, we calculated the circular variance in bearings using the 'circular' package.[57] We used Spearman's correlation to test if there was a relationship between Dice's Similarity Coefficients and variance in trip bearings, the number of trips measured per site, and the number of years of tracking data per site (Figure S4).

### Predicting foraging ranges within the North Atlantic murre population

We used the foraging range model described above to estimate the 95% foraging range of all colonies with at least 500 breeding pairs. We mapped the 95% foraging area ($FA_{95}$) for each colony as described above and subtracting any areas that intersected land.[46] We then calculated the area within the $FA_{95}$ buffer zone of all colonies and determined their percent overlap with marine protected areas in the World Database of Protected Areas.[37] All overlap analysis was performed using an Albers Equal Area Projection.