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Article:

Title: Space partitioning without territoriality in gannets

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Abstract: Colonial breeding is widespread among animals. Some, such as eusocial insects, may use agonistic behavior to partition available foraging habitat into mutually exclusive territories; others, such as breeding seabirds, do not. We found that northern gannets, satellite-tracked from twelve neighboring colonies, nonetheless forage in largely mutually

exclusive areas and that these colony-specific home ranges are determined by density-dependent competition. This segregation may be enhanced by individual-level public information transfer, leading to cultural evolution and divergence among colonies.

Main Text: Colonial animals are constrained by their colony locations, which are ultimately limited by resource availability (1). However, within species, potential colony home ranges often overlap, implying competition among colonies may also be limiting (2). In eusocial central-place foragers the spatial effects of direct competition among colonies are well understood (2). In contrast, the spatial influences of indirect competition and information transfer on non-territorial species (e.g. seals, swallows and seabirds), where levels of relatedness are much lower, remain conjectural. For example, the hinterland model (3) predicts that breeding seabirds segregate along colonial lines, because of inequalities in travel costs from each colony. Predicted home ranges therefore comprise Voronoi polygons (Fig. 1A), as seen in some territorial animals (2). Food availability is assumed to be proportional to polygon area, limiting colony size. An alternative model proposes that density-dependent competition among colony members is limiting (4). As colonies grow, local prey depletion or disturbance requires birds to travel further to provision their young. However, this model ('Ashmole's halo') does not consider interactions among colonies and tacitly assumes that adjacent colonies' home ranges overlap (5).

Indirect evidence exists to support both models (3, 6, 7) and recent tracking studies suggest that seabirds and pinnipeds segregate along colonial lines (8-12). However, these studies proved inconclusive on the causes and ubiquity of segregation, largely because few colonies were sampled or tracking resolution was low. Here we use high resolution satellite-tracks of the foraging movements of 184 chick-rearing northern gannets Morus bassanus (hereafter gannets) from 12 of the 26 colonies fringing the British Isles (median 17 birds/colony), representing ~80% of the area's breeding population (Fig. 1A, Table S1), to test whether among-colony segregation occurs in a model colonial non-territorial central-place forager. We then use population- and individual-level models to explore potential mechanisms underlying spatial segregation.

Gannets are wide-ranging (max. foraging range ~700 km) pelagic seabirds that forage in patches of enhanced production, primarily on shoaling, mesotrophic fish and to a lesser extent fisheries discards (13-15). In almost all cases we tracked birds from adjacent colonies simultaneously (16). Individual gannet tracks (Figs. 1B and S1) and percentage Utilization Distributions (UDs, Figs. 2A and S2) showed a striking pattern of between-colony variation and spatial segregation, within and across years (Fig. S3). The size of 95% foraging UDs was strongly dependent ($F_{1,8} = 149.7$, $p < 0.001$, $R2 = 0.94$, Fig. S4) on square-root colony size (N). Likewise, maximum foraging range and trip duration were dependent on $N^{0.5}$ (Linear Mixed-Effects (LME) models, $p = 0.002$ and < 0.001, Tables S2 and S3). Birds from colonies of all sizes divided their time equally between foraging and chick attendance (LME, $p = 0.191$, Table S4) and the number of foraging trips/day was negatively dependent on $N^{0.5}$ (LME, $p = 0.024$, Table S5). Prey delivery rate, for which we assume trips/day is a proxy, is therefore negatively dependent on $N^{0.5}$, supporting the prediction that colony size is limited by density-dependent competition (4, 6). Contrary to the hinterland model (3), we found no relationship between colony Voronoi polygon area and colony size ($F_{1,35} < 0.01$, $p = 0.699$, $R^2 < 0.01$, Fig. S5).

Using empirical relationships between colony size and foraging area, we devised a population-level null model of the distribution of foraging gannets, assuming negligible competition between birds from neighboring colonies (16). This successfully explains among-colony segregation when colonies are far apart but predicts extensive overlap between

several study colonies, particularly in the Celtic Sea (Fig. 2A). However, observed UDs were largely mutually exclusive (Fig S2), overlapping markedly less than predicted (Fig. S6). For example, the null Population Overlap Index (POI, the number of potential pairwise interactions between birds from adjacent colonies(16)) for Little Skellig and Bull Rock (populations ~29,700 and 3700 pairs; separation distance 27 km) was 105,000, whereas the empirical estimate was 6000, largely because foraging trips were directed away from closely neighboring colonies (Fig. 1B). This pattern differs from the hinterland model in two key respects: segregation was not absolute and divisions between the UDs of unequally sized colonies were not equidistant between the two (Figs. 1B and S2) but typically occurred closer to the smaller colony, a phenomenon also observed in penguins (9). Hence the predictive performance of the hinterland model (log-likelihood, L = -0.54, AIC 3691, Table S6) was poor in comparison to the null model (L = -0.30, AIC = 2231).

Given the inability of existing models to explain gannet distribution when colonies are close together, we propose a multi-colony extension of Ashmole's halo (4), which we term the density-dependent hinterland (DDH) model. As adjacent colonies grow, foraging ranges increase due to prey depletion or disturbance (6) until their home ranges overlap. At low densities, birds from different colonies may forage together but as prey availability decreases populations respond by spreading down conspecific density gradients to the nearest areas subject to a lower rate of exploitation (6). As a first approximation, we assume a simple inverse relationship between the exploitation by conspecifics from adjacent colonies and the likelihood of new birds foraging in an area (16). However, the trade-off between transport and competition costs means birds favor areas close to their own colonies, so density declines with colony distance d (10). Hence, when colonies are large or close together segregation between home ranges may become absolute. Using these assumptions, we modeled the development of spatial segregation as colonies grow (16). We aim to replicate colony growth at the onset of the breeding season (9) but note that historical colony growth patterns may also influence spatial segregation (6), and that colony sizes are unlikely to be in equilibrium (6, 14). Initial comparisons with our tracking data showed that weighting the relative rate of exploitation by the $d^{-0.5}$ improved this model, implying a decline in competitive fitness with distance. The DDH model proved a better fit to the tracking data (L = -0.58, AIC = 25440) than the null (L = -0.61, AIC = 27015, Table S7, c.f. Figs 2A and B). Furthermore, unlike the null, the DDH model successfully predicted the POI (Fig. 6) and the angular displacement of the centre of gravity of the 75% UDs from their colonies (circular correlation, observed vs. predicted directions, null model, r = 0.214, p = 0.463, n = 12; DDH model, r = 0.761, p = 0.020, n = 12).The shapes of the UDs predicted by the DDH model were closer to those observed (Dice's Similarity Coefficient s = 0.57, Table S8) than the null model's predictions (s = 0.45) (16). The DDH model's greater predictive strength was most marked for colonies with close neighbors (Fig.2, Table S8). Notably, the DDH model predicts greater foraging ranges than the null model (paired t-test, square-root mean distance $t_{24} = 4.542$, p < 0.001), implying that indirect competition from neighboring colonies diminishes chick provisioning rates, limiting colony size (5).

Like Ashmole's halo and the hinterland model, the DDH model assumes gannets are ideal free foragers. However, seabird prey occurs in widely dispersed, partially predictable patches (17). Thus seabirds may not base foraging decisions on personal information (memory) alone but may also exploit public information (8, 18), gained by observing conspecifics at the colony (19-21) or at sea (22, 23), although empirical evidence remains limited (24). To examine these hypotheses, we developed a range of 2D individual-based models of gannets foraging from two colonies (30 and 300 individuals), constrained by energy reserves (Table 1), to determine whether segregation emerges through information sharing (16). Only one

model, incorporating memory and public information transfer at sea and at the colony, produced a significant reduction in overlap between colony UDs (Figs. 3 and S7). Between-colony segregation rapidly became established and then persisted (Fig. S8), a pattern consistent at multiple food patch densities and most marked when colonies were close (Figs S9 and S10).

Public information is probably transmitted unintentionally, as in other colonial species (18, 21, 23, 25, 26). Several traits make this likely: Specifically, on arrival and departure from the nest, gannets signal visually and audibly. Prior to beginning foraging trips they land on the sea, near the colony, frequently departing in groups (14). These behaviors may allow conspecifics to follow or copy successful birds (20, 21), channeling information from the population to the individual, allowing birds to efficiently select foraging locations where they are competitively advantaged over conspecifics from other colonies. While these mechanisms are likely to operate over temporal scales of minutes to weeks, gannets have overlapping generations and a long pre-breeding period ($\geq$ 4 years), during which they attend colonies with increasingly regularity (14, 27). This is thought to allow young birds to learn about prey distribution. If this involves public information acquisition, the preconditions exist for cultural evolution of foraging behavior over much longer time scales (8, 28).

Our results suggest that density-dependent competition, rather than territoriality, causes spatial segregation in a model colonial central-place forager. Although the mechanisms remain unclear, there is increasing recognition that non-territorial colonial central-place foragers utilize public information to inform decisions (18, 21, 23, 25, 26, 28). Contrary to the prevailing view, we predict that between-colony segregation is the norm when aggregations of animals such as bats, seals, bumblebees and birds occur at high densities (i.e. when colonies are clustered or large), forcing a re-examination of our understating of their foraging ecology.

References and Notes:

1. J. F. Wittenberger, G. L. J. Hunt, The adaptive significance of coloniality in birds. Farner, D. S., J. R. King and K. C. Parkes (1985), pp. 1-78.

2. E. S. Adams, Annu. Rev. Ecol. Syst. **32**, 277 (2001).

3. D. K. Cairns, Am. Nat. **134**, 141 (1989).

4. N. P. Ashmole, Ibis **103**, 458 (1963).

5. R. W. Furness, T. R. Birkhead, Nature **311**, 655 (1984).

6. S. Lewis, T. N. Sherratt, K. C. Hamer, S. Wanless, Nature **412**, 816 (2001).

7. K. H. Elliott et al., Auk **126**, 613 (2009).

8. D. Grémillet et al., Mar. Ecol.-Prog. Ser. **268**, 265 (2004).

9. D. G. Ainley et al., Ecol. Monogr.**74**, 159 (2004).

10. E. D. Wakefield et al., Ecol. Monogr.**81**, 141 (2011).

11. S. Wanless, M. P. Harris, Colon. Waterbirds **16**, 176 (1993).

12. A. M. M. Baylis, B. Page, S. D. Goldsworthy, Mar. Ecol.-Prog. Ser. **361**, 279 (2008).

13. K. C. Hamer et al., Mar. Ecol.-Prog. Ser. **338**, 295 (2007).

14. B. Nelson, The Atlantic gannet. (Fenix Books Ltd., Great Yarmouth, UK, ed. 2nd, 2001).

15. S. C. Votier et al., J. Appl. Ecol.**47**, 487 (2010).

16. Information on materials and methods is available on Science Online.

17. P. Fauchald, Mar. Ecol.-Prog. Ser. **391**, 139 (2009).

18. T. J. Valone, Behavioral Ecology and Sociobiology **62**, 1 (2007).

19. P. Ward, A. Zahavi, Ibis **115**, 517 (1973).

20. A. E. Burger, Colon. Waterbirds **20**, 55 (1997).

21. H. Weimerskirch, S. Bertrand, J. Silva, J. C. Marques, E. Goya, Plos One **5**, 8 (2010).

22. N. J. Buckley, Am. Nat. **149**, 1091 (1997).

23. E. D. Silverman, R. R. Veit, G. A. Nevitt, Mar. Ecol.-Prog. Ser. **277**, 25 (2004).

24. H. Richner, P. Heeb, Advances in the Study of Behavior, Vol 24 **24**, 1 (1995).

25. M. Baude, E. Danchin, M. Mugabo, I. Dajoz, Proc. R. Soc. London Ser. B **278**, 2806 (2011).

26. D. K. N. Dechmann et al., Proc. R. Soc. London Ser. B **276**, 2721 (2009).

27. S. C. Votier, W. J. Grecian, S. Patrick, J. Newton, Mar. Biol.**158**, 355 (2011).

28. E. Danchin, L. A. Giraldeau, T. J. Valone, R. H. Wagner, Science **305**, 487 (2004).

29. M. S. Coyne, B. J. Godley, Mar. Ecol.-Prog. Ser. **301**, 1 (2005).

30. R. A. Phillips, J. C. Xavier, J. P. Croxall, Auk **120**, 1082 (2003).

31. D. Nicholls, C. J. R. Robertson, M. D. Murray, Notornis **54**, 137 (2007).

32. B. J. McConnell, C. Chambers, M. A. Fedak, Antarctic Science **4**, 393 (1992).

33. M. D. Sumner. (2011). trip: Spatial analysis of animal track data. R package version 1.1-10.

34. Y. Ropert-Coudert et al., J. Avian Biol. **40**, 380 (2009).

35. K. C. Hamer et al., J. Anim. Ecol. **78**, 880 (2009).

36. S. Garthe, S. Benvenuti, W. A. Montevecchi, Can. J. Zool.-Rev. Can. Zool. **81**, 453 (2003).

37. C. Calenge, Ecol. Model.**197**, 516 (2006).

38. J. Fieberg, C. O. Kochanny, J. Wildl. Manage. **69**, 1346 (2005).

39. J. van Etten. (2012). gdistance: distances and routes on geographical grids. R package version 1.1-2.

40. M. Hasegawa, M. Tanemura, Ann Inst Stat Math **28**, 509 (1976).

41. D. Bates, M. Maechler, B. Bolker. (2011). lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-42.

42. G. Aarts, M. MacKenzie, B. McConnell, M. Fedak, J. Matthiopoulos, Ecography **31**, 140 (2008).

43. J. Pinheiro, D. Bates, S. DebRoy, D. Sarkar. (2012). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-103.

44. U. Wilensky, in http://ccl.northwestern.edu/netlogo/. (Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL., 1999).

45. E. D. Wakefield, R. A. Phillips, J. Matthiopoulos, Mar. Ecol.-Prog. Ser. **391**, 165 (2009).

46. S. Wanless, S. Murray, M. P. Harris, British Birds **98**, 280 (2005).

47. S. Murray, Scottish Birds **31**, 220 (2011).

48. K. C. Hamer, R. A. Phillips, J. K. Hill, S. Wanless, A. G. Wood, Mar. Ecol.-Prog. Ser. **224**, 283 (2001).

49. W. J. Grecian et al., Biol. Conserv.**156**, 43 (2012).

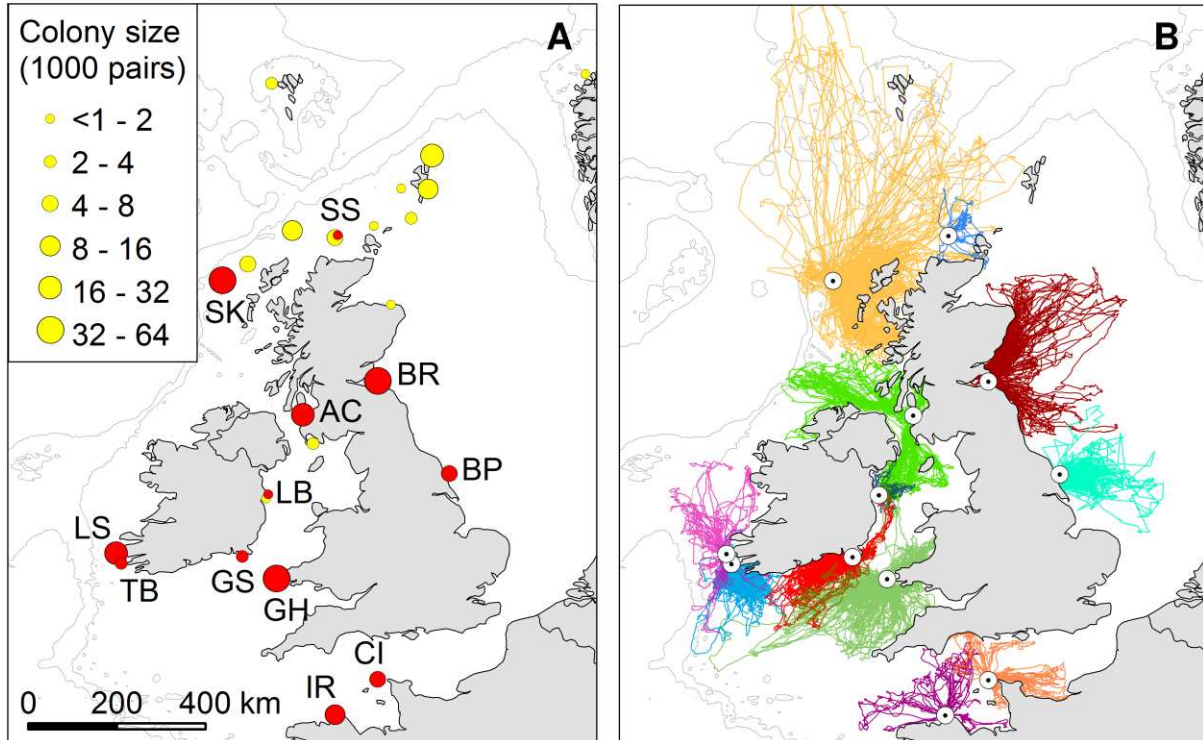50. J. C. Haney, K. M. Fristrup, D. S. Lee, Ornis Scandinavica **23**, 49 (1992).

Fig. 1. Gannets tracked from colonies (**A**) around the British Isles forage in largely mutually-exclusive areas, despite their potential home ranges overlapping (red - study colonies, yellow - others). Home ranges predicted by the hinterland model (3) form Voronoi polygons, bounded by lines of equidistance between colonies (black lines). Satellite tracks from184 individuals (**B**) show that foraging birds direct their movements away from neighboring colonies. Data collected 2011, except St Kilda (SK) collected 2010. Grey lines -200 and 1000 m isobaths; LS - Little Skellig; TB - Bull Rock (mentioned in the text, Table S1 for colony details).
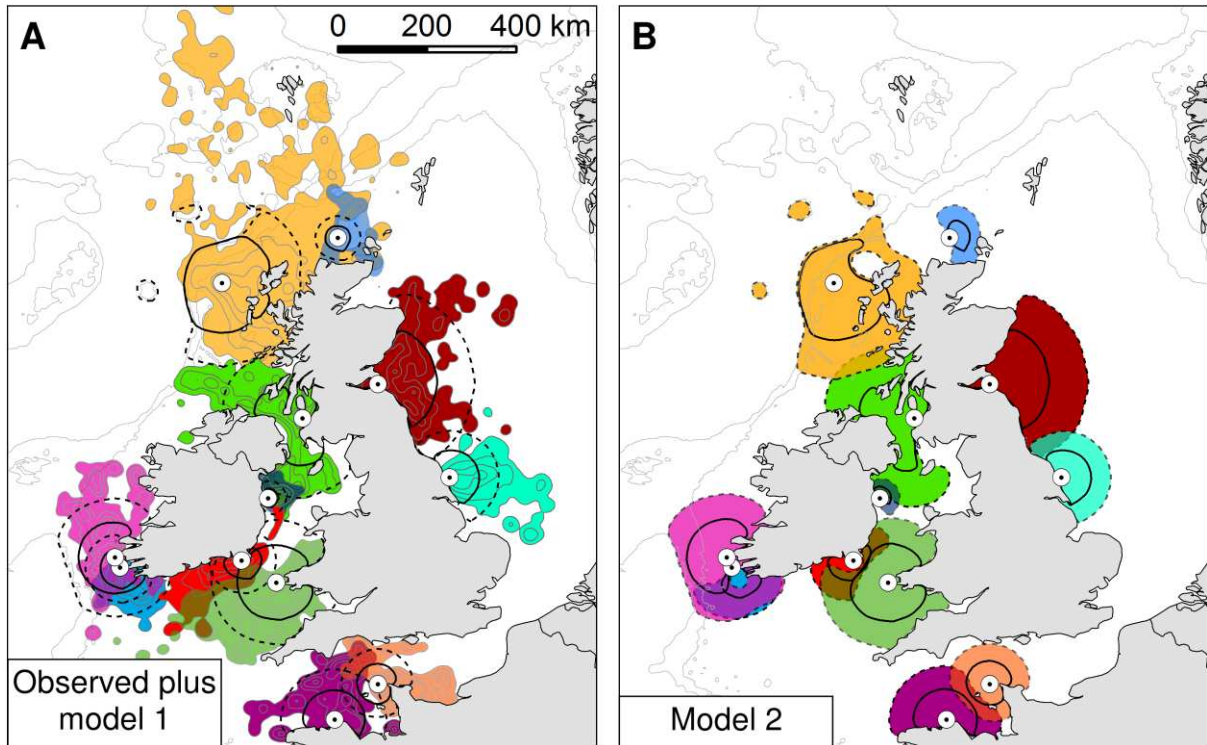
Fig. 2. Density-dependent competition within and between colonies explains large-scale among-colony segregation. Observed colony Utilization Distributions (**A**, colored polygons plus 95, 75, 50 and 25% UD contours) are largely mutually exclusive. This is at odds with the null model (predicted 75 and 95% UDs solid and dashed lines), which assumes density-dependent competition only within colonies, predicting broad overlap between some UDs. The Density-Dependent Hinterland (DDH) model (**B**) additionally assumes competition between colonies, providing a better fit to the tracking data.
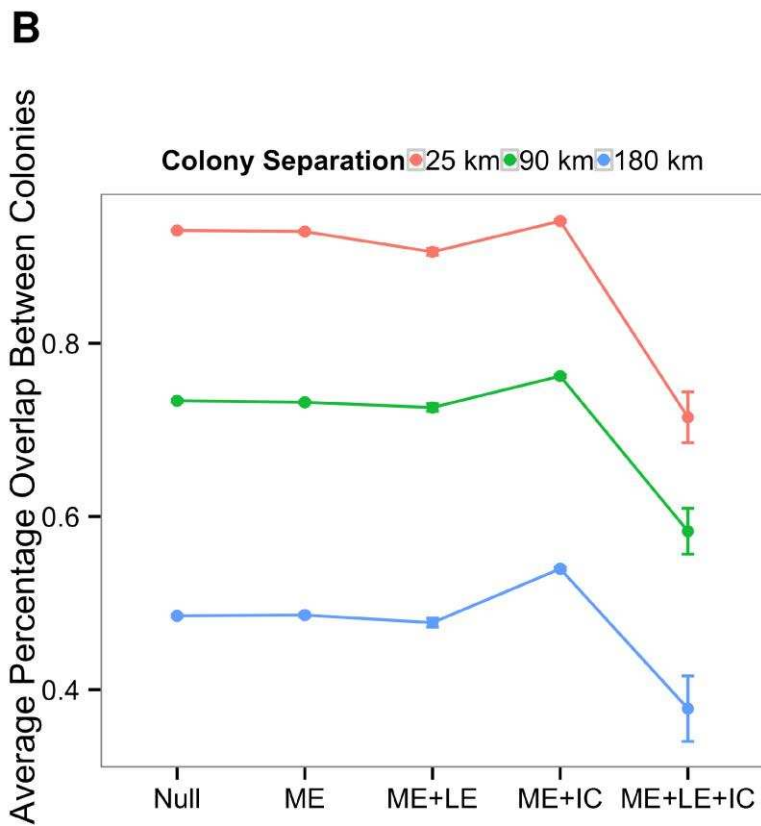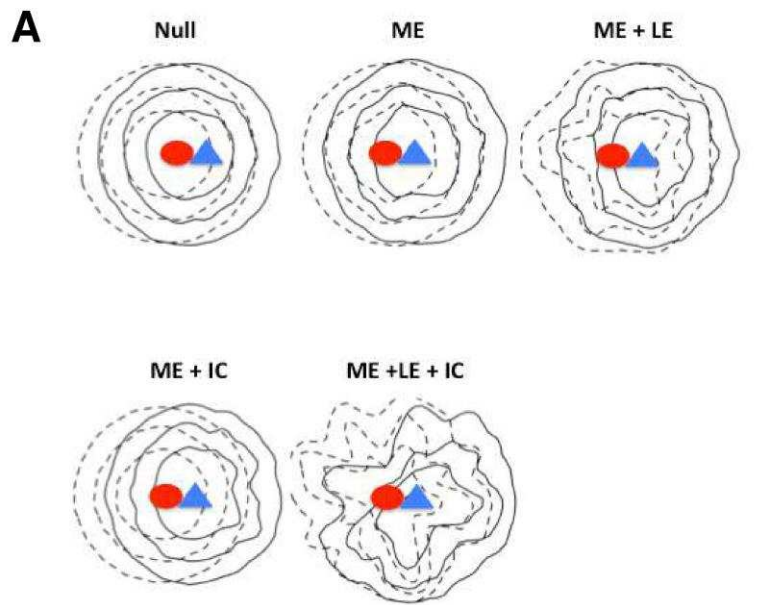
Fig. 3. Individual-based simulations show that overlap between the Utilization Distributions (UDs) of two hypothetical colonies (**A**, solid lines/blue circle - large colony ; dashed lines/red circle - small colony) reduces (**B**) only when birds use private information and gain public information prior to departure and during foraging trips (see Table 1 for model rules). Isopleths - 50, 75 and 95% UDs. Results shown for 25 prey patches. Error bars show 95% CIs.

Table 1. Rules governing information use in individual-based models of foraging gannets (see Table S10 for details).

Foraging rules	Description
Null	Birds forage randomly during each trip
Memory (ME)	Birds return to previously successful locations (private information)
Local Enhancement (ME+LE)	ME + uninformed birds may follow informed birds at sea (private and public information)
Information Centre (ME+IC)	ME + uninformed birds may follow informed birds from their colony (private and public information)
All Sources Combined (ME+LE+IC)	ME + Uninformed birds may follow informed birds from the colony and at sea (public and private information)

Supplementary Materials:

Materials and Methods

Supplementary Text

Figures S1-S13

Tables S1-S10

R model algorithm and supporting data (see additional file R_script_and_data.zip)

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