Space Partitioning Without Territoriality in Gannets

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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 12 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.

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 that 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). By contrast, the spatial influences of indirect competition and information transfer on nonterritorial 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 used 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 and table S1), to test whether among-colony segregation occurs in a model colonial nonterritorial central-place forager. We then used population- and individual-level models to explore potential mechanisms underlying spatial segregation.

Gannets are wide-ranging (maximum 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 (Fig. 1B and fig. S1) and percentage utilization distributions (UDs) (Fig. 2A and fig. S2) showed a distinctive pattern of between-colony variation and spatial segregation, within and across years (fig. S3). The size of 95% foraging UDIs was strongly dependent (F1,6 = 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 N0.5 [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 per day was negatively dependent on N0.5 (LME, P = 0.024; table S5). Prey delivery rate, for which we assume trips per day is a proxy, is therefore negatively dependent on N0.5, 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 (F1,35 < 0.01, P = 0.699, R2 < 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 UDIs 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 UDIs of unequally sized colonies were not equivalent between the two (Fig. 1B and fig. 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 that of the null model (L = −0.30, Akaike information criterion (AIC) = 2231).

Given the inability of existing models to explain gannet distribution when colonies are close together, we propose a multicounty extension of Ashmole’s halo (4), which we term the density-dependent hinterland (DDH) model. As adjacent colonies grow, foraging ranges increase as a result of 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 that birds favor areas closer 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. We aim to replicate colony growth at the onset of the breeding season but note that historical colony growth patterns may also influence spatial segregation and that colony sizes are unlikely to be in equilibrium.

Initial comparisons with our tracking data showed that weighting the relative rate of exploitation by $d^{-0.5}$ 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; compare Fig. 2, A and B). Furthermore, unlike the null, the DDH model successfully predicted the POI (fig. S6) and the angular displacement of the center of gravity of the 75% UDs from their colonies (circular correlation, observed versus 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 ($s = 0.45$). The DDH model’s greater predictive strength was most marked for colonies with close neighbors (Fig. 2 and table S8). Notably, the DDH model predicts greater foraging ranges than the null model (paired $t$ test, square-root mean distance $t_{24} = 4.542, P < 0.001$), which implies that indirect competition from neighboring colonies diminishes chick provisioning rates, limiting colony size.

Like Ashmole’s halo and the hinterland model, the DDH model assumes that gannets are ideal free foragers. However, seabird prey occurs in widely dispersed, partially predictable

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**Fig. 1. Gannet colony foraging ranges.** (A) Gannets tracked from colonies 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). (B) Satellite tracks from 184 individuals show that foraging birds direct their movements away from neighboring colonies (colors correspond to different colonies). Data were collected in 2011, except for St Kilda (SK), which were collected in 2010. Gray lines, 200- and 1000-m isobaths; LS, Little Skellig; TB, Bull Rock (mentioned in the text; see table S1 for colony details).

**Fig. 2. Density-dependent competition and colony segregation.** Density-dependent competition within and between colonies explains large-scale among-colony segregation. (A) Observed colony utilization distributions (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. (B) The density-dependent hinterland (DDH) model additionally assumes competition between colonies, providing a better fit to the tracking data.
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 two-dimensional 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 UDVs (Fig. 3 and fig. 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. Before 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, thereby allowing birds to efficiently select foraging locations where they are competitively advantaged over conspecifics from other colonies. Although these mechanisms are likely to operate over temporal scales of minutes to weeks, gannets have overlapping generations and a long prebreeding period (4–4 years), during which they attend colonies with increasing 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 nonterritorial 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 reexamination of our understating of their foraging ecology.

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

<table>
<thead>
<tr>
<th>Foraging rules</th>
<th>Description</th>
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<tr>
<td>Null</td>
<td>Birds forage randomly during each trip</td>
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<tr>
<td>Memory (ME)</td>
<td>ME or ME + uninformed birds follow successful birds at sea (private information)</td>
</tr>
<tr>
<td>Local enhancement (ME + LE)</td>
<td>ME or ME + uninformed birds follow successful birds at sea (private and public information)</td>
</tr>
<tr>
<td>Information centre (ME + IC)</td>
<td>ME or ME + uninformed birds follow successful birds from the colony (private and public information)</td>
</tr>
<tr>
<td>All sources combined (ME + LE + IC)</td>
<td>ME or ME + uninformed birds follow successful birds from the colony and at sea (public and private information)</td>
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Fig. 3. Utilization distribution overlaps. Individual-based simulations show that overlap between the utilization distributions (UDs) of two hypothetical colonies (á) (solid lines/blue circle, large colony; dashed lines/red circle, small colony) reduces (B) only when birds use private information and gain public information before departure and during foraging trips (see Table 1 for model rules). Isolines: 50, 75, and 95% UDVs. Results shown for 25 prey patches. Error bars show 95% confidence intervals.
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Editor's Summary

This Is the Place
Bats, bees, seals, and many seabirds practice central-place foraging, leaving a central home site, such as a hive or a rookery, to forage in a specific territory. Such species also share the challenge of competing for local resources with individuals from separate colonies. Using satellite tags, Wakefield et al. (p. 68, published online 6 June; see the Perspective by Weimerskirch) followed over 180 northern gannets to determine potential drivers of foraging territory division. Boundaries among colonial territories arose as a result of competition with individuals from other territories. Individuals from the same colony appeared to share information about foraging sites, presumably contributing to the establishment and maintenance of specific, long-term colonial territories.