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A review of the occurrence of inter-colony segregation of seabird foraging areas and the implications for marine environmental impact assessment

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Understanding the determinants of species' distributions is a fundamental aim in ecology and a prerequisite for conservation, but is particularly challenging in the marine environment. Advances in bio-logging technology have resulted in a rapid increase in studies of seabird movement and distribution in recent years. Multi-colony studies examining effects of intra- and inter-colony competition on distribution have found that several species exhibit inter-colony segregation of foraging areas, rather than overlapping distributions. These findings are timely given the increasing rate of human exploitation of marine resources and the need to make robust assessments of likely impacts of proposed marine developments on biodiversity. Here we review the occurrence of foraging area segregation reported by published tracking studies in relation to the Density-Dependent Hinterland (DDH) model, which predicts that segregation occurs in response to inter-colony competition, itself a function of colony size, distance from the colony and prey distribution. We found that inter-colony foraging area segregation occurred in 79% of 39 studies. The frequency of occurrence was similar across the four seabird orders for which data were available, and included species with both smaller (10 – 100 km) and larger (100 – 1000 km) foraging ranges. Many predictions of the DDH model were met, with examples of segregation in response to high levels of inter-colony competition related to colony size and proximity, and enclosed landform restricting the extent of available habitat. Moreover, as predicted by the DDH model, inter-colony overlap tended to occur where birds aggregated in highly productive areas, often remote from all colonies. The apparent prevalence of inter-colony foraging segregation has important implications for assessment of impacts of marine development on protected seabird colonies. If a development area is accessible from multiple colonies, it may impact those colonies much more asymmetrically than previously supposed. Current impact assessment approaches that do not consider spatial inter-colony segregation will therefore be subject to error. We recommend the collection of tracking data from multiple colonies and modelling of inter-colony interactions to predict colony-specific distributions.

Keywords: central-place foraging, space partition, overlap, aggregation, competition

A fundamental goal in ecology and conservation is to understand the factors that drive patterns of avian distribution and abundance (Sutherland *et al.* 2009, Sutherland *et al.* 2013). Seabirds are more threatened, and their conservation status has deteriorated faster over recent decades, than any other comparable avian group (Croxall *et al.* 2012). During the breeding season, seabirds are central-place foragers, returning periodically to the nest site in order to provision and care for their offspring (Orians and Pearson 1979). In common with other central-place foragers (social insects, bats, pinnipeds, etc.), this constraint radically affects their spatial ecology (Bernstein & Gobbel 1979, Kacelnik 1984). Optimal foraging models commonly assume that animals are adapted to maximise the rate of net energy gain per unit time (Stephens & Krebs 1986). For a central-place forager, the costs of foraging measured in terms of either time or energy, increase with increasing distance from the colony. If prey are uniformly distributed and superabundant (i.e. there is no competition for prey) within the area surrounding the colony, the rate of energy gain and foraging efficiency will be highest close to the colony, where travel costs are lowest. However, if the number of foragers close to the colony is sufficient to reduce the per capita rate of prey capture through local prey depletion (Ashmole 1963), or through interference competition (Lewis *et al.* 2001), the rate and efficiency of energy gains close to the colony will diminish relative to unexploited areas that are more distant. Foraging seabirds do not exhibit territorial defence of areas of sea and may be assumed to follow an ideal free-distribution (Fretwell 1972), whereby the net energy gain is equalised across all individuals. The resulting distribution will represent a gradient of decreasing density of foragers with increasing distance from the colony, reflecting the increasing travel costs associated with foraging at more remote locations. The precise relationship between seabird density and distance from the colony will depend on surrounding coastal morphology, which will determine the extent of marine habitat (and hence competitor dilution) at increasing distance from the colony (Wakefield *et al.* 2017). However, in many situations prey are aggregated in patches rather than being uniformly distributed (Wakefield *et al.* 2009), modifying these theoretical distributions radically.

Ashmole (1963) hypothesised that central place foraging constraints impose an upper limit on colony size through the following mechanism: As a colony grows, increasing intra-specific competition close to the colony forces the use of more distant foraging areas. Mean travel costs will therefore increase, reducing net gains from foraging, until eventually a point is reached where breeding success is so low that colony growth falls to zero. This hypothesis led to the notion of colonies exploiting a “halo” of prey resources in the surrounding waters. Cairns’ (1989) hinterland model of colony foraging areas approached foraging optimality from a different perspective. It suggests that seabirds should only exploit areas of sea that lie closer to their home colony than to any other colony. He reasoned that seabirds should not regularly forage in waters which are closer to another colony, since it would be more efficient to exploit such areas from the closer colony. This would result in adjacent colonies having non-overlapping foraging ranges, bounded by lines of equidistance. Cairns (1989) suggested that in regions of uniform ocean productivity, the size of these hinterlands would determine the size of the associated colony. He found a positive correlation between theoretical hinterland size and colony size for European Shags *Phalacrocorax aristotelis* and Black-legged Kittiwakes *Rissa tridactyla*, but not for Northern Gannets *Morus bassanus* or Atlantic Puffins *Fratercula* *arctica*. There are several potential reasons for the lack of correlation in the latter species, principal of which is that their prey may be more patchily distributed (Weimerskirch 2007, Haury *et al.* 1977). Other reasons could be that some colonies are limited by nest site availability, or they may not be at equilibrium with food availability due to past persecution or unnaturally inflated food resources e.g. from fisheries' discards.

Where neighbouring colonies are separated by less than the combined foraging radius of each, foraging areas can potentially overlap. Although Ashmole (1963) did not explicitly consider how seabirds from neighbouring colonies might interact in areas of potential foraging overlap, his "halo" hypothesis suggests a circular region of seabird usage and prey depletion around each colony. More recent suggestions of seabird foraging distribution have tended to draw upon this image, assuming overlap of circular foraging areas accessible to multiple colonies (e.g. Grecian *et al.* 2012, Thaxter *et al.* 2012). Recent data obtained by tracking seabirds simultaneously from neighbouring colonies reveals that segregation of foraging areas does occur, and may be widespread. For example, a study of Northern Gannets from 12 colonies around Britain and Ireland (Wakefield *et al.* 2013) found that birds from different colonies occupied almost exclusive foraging areas, despite their potential foraging ranges overlapping. However, contrary to Cairns' (1989) hinterland model, boundaries between these areas were not equidistant from adjacent colonies. An alternative model was therefore proposed, termed the Density-Dependent Hinterland (DDH) model (Wakefield *et al*. 2013), which combines elements of both Ashmole's halo model and Cairns' hinterland model. In the DDH model, competition is assumed to be a function of both colony size and distance from the colony. Segregation of foraging areas of two neighbouring colonies will occur if potential competition is high. This is likely to be the case where colonies are close (due both to the imperative for central place foragers to minimise travel costs and the effect of radiative spreading from the colony) and when colonies are relatively large. Conversely, the DDH model predicts that hinterlands may overlap in areas where inter-colony competition is low. For example, this could occur in areas where prey are superabundant, where colonies are small or where they are distant from one another.

Segregated foraging grounds have been demonstrated for a diverse range of other colonial central-place foragers, including not only territorial groups such as ants (Brown & Gordon 2000, Adler & Gordon 2003, Schilder *et al.* 2004), but also species that, like seabirds, are non-territorial away from the colony, such as bats (Dawo *et al.* 2013, August *et al.* 2014, Christie and O'Donnell 2014), seals (Curtice *et al.* 2011, Kirkwood & Arnould 2012, Nordstrom *et al.* 2013, Kuhn *et al.* 2014) and corvids (Griffin & Thomas 2000). However, it is still unclear how widespread the phenomenon is in seabirds and whether the DDH model holds across divergent evolutionary lineages within this group. In part, this reflects the practical difficulties associated with establishing the patterns of space use by seabirds at sea. However, recent reductions in the weight and cost of tracking devices have led to a rapid increase in the number of tracking studies of breeding seabirds. It is therefore opportune to review the occurrence of inter-colony foraging segregation in seabirds. Here we: (i) review the peer-reviewed literature for examples of both the occurrence and absence of intra-specific inter-colony segregation of seabird foraging areas; (ii) assess the frequency of segregation across seabird taxonomic orders; (iii) examine suggested causes of segregation in the light of the DDH model and (iv) consider the implications of the phenomenon for seabird conservation.

OCCURRENCE OF INTRA-SPECIFIC INTER-COLONY SEGREGATION OF SEABIRD FORAGING AREAS

Literature search

Structured, systematic searches of the peer-reviewed scientific literature were carried out to identify publications reporting inter-colony spatial segregation or overlap. To reduce negative reporting bias, searches were also conducted for the absence of segregation. The literature search was focussed on publications documenting multiple colony tracking or colour marking studies, where colonies were separated by less than the combined maximum foraging ranges observed. Keywords were used to search Google Scholar and Web of Science for relevant publications. Combinations of the following keyword search terms were used: “spatial”, “space”, “segregate”, “partition”, “aggregate”, “mix”, “overlap”, “feed”, “forage”, “colony”, “seabird”, “area”, “location”, “inter-colony”, “multiple”, “tracking”, “territory”, “competition”, “bird”, “colour”, “mark” and “home range”. The ‘wildcard’ character (*) was used where appropriate to broaden search results. Web of Science results were filtered using different combinations of keywords until <100 results were returned; the number of results was recorded and results were searched for relevant studies. The number of Google Scholar results for each keyword combination was recorded, as was the number of pages searched. The first 10 pages of results were searched for relevant studies. The literature search was conducted in December 2017.

Multiple publications from the same dataset were considered as a single study. For publications that reported studies of multiple species, the presence or absence of segregation was recorded for each species separately. Study species were classified according to taxonomic order and family, following del Hoyo *et al.* (2014), and species nomenclature follows IOC World Bird Names (Gill & Donsker 2018). Where reported, the breeding stage(s) of the foraging individuals was also recorded. For several species, foraging ranges varied very considerably according to breeding stage. In such cases, we only considered breeding stages during which foraging range exceeded inter-colony spacing. The majority of studies identified involved simultaneous (same year and breeding stage) multi-colony tracking. However, we also included studies were the occurrence or absence of segregation was determined by inclusion of a measure of inter-colony competition (such as distance to neighbouring colonies) in a model of space-use. Such an approach does not require simultaneous (Wakefield *et al.* 2011) or multi-colony (Cecere *et al.* 2015) tracking.

Evidence of foraging area segregation

Many of the studies we reviewed present no formal statistical analysis to determine whether the observed pattern of distribution deviated significantly from a null distribution in which colony distributions overlapped without interaction. Rather, inferences and conclusions about segregation were often drawn from the percentage overlap in areas of distribution, or from visual inspections of tracks or kernel density distributions, but without explicit reference to any expected value. In cases where two colonies were separated by a distance substantially less than the sum of the maximum foraging range of both colonies and no, or negligible, overlap in distributions occurred, conclusions regarding segregation could still be drawn in the absence of any formal statistical analysis.

Some studies reported considerable overlap of foraging areas of birds from multiple colonies (often in locations of high biological productivity, at considerable distance from the breeding locations) which could be regarded as instances of “aggregation”, defined as a higher coincident density of birds from multiple colonies than would be expected from their null distributions. However, it was seldom possible to determine from published information whether the proportions of individuals from different colonies in such areas differed substantially from those predicted by the null distributions. We have therefore not attempted to differentiate instances of aggregation from overlapping null distributions, and distributions were classified as “segregated” or “overlapping” only. However, we recognise that there is considerable potential for the proportion of birds originating from contributing colonies to deviate substantially from those predicted by the null distributions in such cases.

We identified 40 papers that presented information on foraging areas of seabird colonies where ranges of neighbouring colonies could potentially overlap. We did not consider studies that examined foraging areas at sub-colony level only, such as Waggitt *et al.* (2014) and Bogdanova *et al.* (2014). One study used plumage dye marking to determine colony foraging grounds; the remainder used bird-borne tracking devices – either global positioning system (GPS), light-based geolocation (GLS), satellite (PTT), compass loggers or Very High Frequency radio (VHF) tags (Table 1). Some studies considered multiple species and some datasets were covered by several papers. Together they comprised 41 unique studies covering 30 seabird species (Table 1). Foraging area segregation was not a primary focus of all the studies reviewed, and the strength of evidence for conclusions regarding the occurrence or absence of segregation varied. We therefore adopted a tiered approach to the classification of foraging distribution in the studies reviewed (Table 2). The strongest evidence was provided by nine studies that conducted a formal statistical assessment of the occurrence of interactions in space-use by neighbouring colonies. Of these, none found evidence of a positive interaction (i.e. birds from neighbouring colonies aggregating at higher densities that expected); two studies found evidence that distributions overlapped as expected if no inter-colony interaction occurred, and the remaining seven found evidence of negative interactions (segregation). In two (Wakefield *et al.* 2011, Catry *et al.* 2013), segregation was temporally and/or spatially variable, occurring for some colonies and/or breeding stages only.

In a further 30 studies, the authors’ assessment of segregation was based on the extent of overlap calculated as percentage, or by visual inspection of distributions (the latter typically in cases were overlap was entirely absent or extremely low). Inter-colony segregation of foraging areas was judged to occur in 24 studies (temporally and/or spatially variable in eight cases), with overlap occurring in the remaining six studies. In two studies no assessment of the occurrence or absence of segregation was made by the authors. Taken together, 31 (79%)

of the 39 studies where inter-colony segregation was assessed, reported segregated foraging areas, of which 10 related to temporally and/or spatially variable segregation. The proportion of studies reporting segregation was similar for both evidence classes (78% for studies where colony interactions were statistically modelled and 80% for studies based on distribution overlap), which suggests the assessment of segregation is not strongly biased by the methods used.

Occurrence of foraging segregation across species, families and orders.

The occurrence of foraging segregation was reported for 24 of 29 species assessed. There were insufficient data to compare the frequency of occurrence of segregation across families and orders using models that account for phylogenetic non-independence (Grafen 1989, Martins & Hansen 1997). Nonetheless, we found that foraging segregation was widespread and occurred to a similar extent in all four orders, and across the eight families represented. Fig. 1 illustrates the number of studies reporting segregation by seabird order and family. There was evidence of segregation for all five species of Sphenisciforme, for nine of 12 Procellariiforme species, seven of eight Suliforme species (all four sulids studied and three of four phalacrocoracids), and three of four Charadriiforme species (two larids and one of two alcids). The foraging ranges of these species vary from a few tens of km in the cases of shags and cormorants (Sapoznikow & Quintana 2003, Evans *et al.* 2015) to several thousands of km in the case of the albatrosses (Wakefield *et al.* 2011). The distance between colonies for which foraging area segregation has been documented range from as little as 2 km for various species of shag and cormorant (Wanless & Harris 1993, Sapoznikow & Quintana 2003), to several hundred km for Black-browed Albatross *Thalassarche melanophris* (Wakefield *et al.* 2011).

Colony-level foraging distributions which rely on an insufficient sample of tracked individuals will tend to underestimate the extent of the foraging areas (Soanes *et al.* 2013) and hence the extent of overlap between neighbouring colonies, leading in turn to over-estimation of the occurrence and strength of segregation. Few studies have formally tested the sufficiency of their sample to describe colony-level distributions, but those which have, tended to conclude that the level of effort required is greater than that which is commonly achieved (Soanes *et al.* 2013, 2015, but see Lascelles *et al.* 2016). We examined whether differences in sampling effort (individuals tracked per colony) could bias the reported or inferred occurrence of segregation. We found no difference in the mean ($\pm$ sd) number of individuals tracked per colony among studies that showed foraging area segregation (28.0 $\pm$ 35.4 $n = 31$) compared with the remaining studies were no segregation was apparent (20.4 $\pm$ 17.2 $n = 8$, pooled variance t-test on $\log_e$ transformed data $t_{37} = 0.61$, $P = 0.54$). Hence the high occurrence of segregation does not appear to be driven by under-sampling of colony-level distributions and it is unlikely therefore that our review and its conclusions are significantly biased by insufficient tracking effort in the studies considered.

The majority (79%) of studies reviewed provided some evidence of inter-colony segregation of seabird foraging areas, at least at some breeding stages and/or locations, indicating that segregation is a widespread phenomenon. However, non-reporting of studies that fail to demonstrate segregation could lead to publication bias and consequent over-estimation of the frequency of segregation. We attempted to minimise such potential bias by including literature search terms relating to the absence of segregation. Further, the assessment of inter-colony segregation was not a primary objective of many of the studies identified, such that the reported occurrence of segregation is unlikely to have been the primary reason for their publication. Finally, we relied on the analysis and judgement of the authors of the reviewed papers to assess the extent of inter-colony segregation of each study, which was therefore blind to the aims of our review.

This review indicates that inter-colony foraging segregation may be common among seabirds and occurs with similar frequency in all orders for which data are available, and across all scales of foraging movement from tens to thousands of kilometres. This finding might be expected since foraging area segregation has a strong theoretical basis and is predicted to result wherever density dependent inter-colony competition for prey occurs (Wakefield *et al.* 2013).

Drivers of inter-colony foraging area segregation

Optimal foraging theory and the DDH model provide a useful framework for understanding the drivers of seabird foraging distribution and inter-colony segregation.

1. Colony size and location

According to the DDH model, segregation will develop through density-dependent competition-avoidance behaviour. One of the principal drivers of inter-colony competition for prey resources, and hence segregation, is colony size. Several authors have made the link between colony size and foraging range, due to intraspecific competition among colony members (Ashmole 1963, Cairns 1989, Lewis *et al.* 2001, Wakefield *et al.* 2017). However, optimal foraging theory suggests that the density of central place foragers is also a function of distance from the colony, because this determines foraging costs. Hence, both the size and proximity of neighbouring colonies will be important in determining the intensity of potential intra-specific inter-colony competition and therefore segregation.

A number of hypothetical examples illustrate this point: consider two neighbouring colonies that are sufficiently close to have overlapping foraging ranges, surrounded by prey that is uniformly or unpredictably distributed. If colony sizes differ greatly, the DDH model predicts that segregation is likely since foraging profitability of birds from the smaller colony will be higher if they avoid areas with higher numbers of conspecifics from the larger colony. In the vicinity of the larger colony, forager density will be high, leading to higher levels of competition and lower profitability, compared with alternative foraging locations within range of the smaller colony but distant from the larger colony (Fig. 2a). An example comes from Ainley *et al.* (2004), who argued that colony size strongly influenced the foraging distribution of Adélie Penguins *Pygoscelis adeliae* from one large and three small colonies in the Ross Sea, Antarctica. The authors found that foraging grounds of the three small colonies overlapped extensively, but that birds from the small colonies almost never overlapped with the larger colony's foraging area, despite it being within their potential range. As the breeding season progressed, foraging distance and area increased noticeably, possibly as parents were able to spend longer at sea after the brood-guard stage and/or as a result of shifts in prey distribution or depletion of prey resources close to the colony. As the foraging area of the larger colony increased, the smaller colonies' foraging ranges shifted to avoid the area newly exploited by the larger colony. It is likely that birds from the three small colonies were able to forage communally, but once birds from the large colony intruded, competition was too high and they foraged elsewhere.

Segregation is also likely to occur between two similarly sized neighbouring colonies, if the colonies are sufficiently large: individuals from either colony would achieve higher average profitability by avoiding areas of potential overlap, as competition would be elevated in such areas (Fig. 2b). However, in a final example, if colonies are small, overlap may occur if competition in the shared area is not sufficiently intense to markedly reduce profitability to birds from either colony (Fig. 2c). Evans *et al.* 2015 provide an example from the European Shag, where two colonies of 35 and 96 pairs located c. 4 km apart showed strongly overlapping foraging areas, indicating an absence of inter-colony competition. Note though, that Wanless and Harris (1993) found strong segregation between two colonies of South Georgia Shags *Leucocarbo georgianus* (formerly Blue-eyed Shag *Phalacrocorax atriceps*) 2.5 km apart, numbering just 11 and 32 nesting pairs, showing that colonies perceived to be small may still segregate strongly.

The distances between colonies and their foraging ranges will modify the relationships described above. Where colonies are widely separated relative to their potential foraging ranges, overlap of foraging areas is more likely to occur in areas distant from both colonies. The null density of foragers will be lower further from the colony (due to both the positive relationship between foraging costs and distance, and also radiative spreading with distance) so that net gains are similar to those of more intensely exploited areas. Hence intra-specific competition for prey will be low, and profitability may be affected only marginally by overlap of usage by multiple, distantly located colonies.

2. Coastal morphology and habitat availability

Coastal morphology in the vicinity of breeding colonies may play a large role in determining the extent of marine habitat available and hence levels of competition for resources in those areas (Wakefield *et al.* 2017). Colonies situated on or close to the mainland, or within inlets or bays, have less potential foraging area available to them than those on remote islands surrounded by open sea. Intra-specific competition, and hence the likelihood of segregation, may be greater for colonies with restricted habitat availability. For example, Sapoznikow and Quintana (2003) studied breeding Imperial Cormorants *Phalacrocorax atriceps* and Rock Shags *Phalacrocorax magellanicus* at two neighbouring colonies in the mouth of a bay in Patagonia. They found no overlap between foraging areas used by Imperial Cormorants from the two colonies, despite being separated by just 2.2 km. Imperial Cormorants from the outer colony exclusively exploited open sea areas whilst individuals from the inner colony foraged entirely within the inlet. Rock Shags breeding in the outer colony similarly showed minimal use of the bay, whilst those breeding on the inner islet showed limited use of the outer area (less than expected under a null model of no segregation) and virtually no overlap with the area used by birds from the outer colony.

3. Prey distribution and abundance

Much of the foregoing discussion has assumed a uniform distribution of prey in the waters surrounding breeding colonies. However, the fish, cephalopods, crustaceans, etc. upon which seabirds prey, are patchily distributed. Understanding of the spatial and temporal scales of prey aggregation has important consequences for consideration of inter-colony foraging area segregation. Aggregation is most likely to occur where prey is both superabundant (i.e. is not depleted by foragers to the extent that competition occurs), and temporally persistent (i.e. predictable). Spatio-temporal variation in prey abundance may interact with the distance-dependent foraging costs of central-place foragers. The distance at which prey patches are located from multiple colonies may be an important factor in determining the extent of shared usage. Whilst foraging grounds close to a colony are more likely to be exclusive, at greater distances where competition is generally lower due to higher foraging costs, foraging areas may overlap (Fig. 3). Ramos *et al.* (2013) found that Cory's Shearwaters *Calonectris borealis* from six colonies were substantially segregated throughout most of their foraging areas, but consistently overlapped in high productivity areas along the Canary Current. Similarly, Paredes *et al.* (2014) found that foraging areas of adjacent Black-legged Kittiwake colonies were highly segregated in neritic waters close to the colonies, but overlapped at more remote oceanic locations. These studies suggest that density-dependant competition drives segregation locally, but that temporally stable areas of high productivity located further away are able to support a greater number of predators, causing segregation to break down.

4. Breeding stage

Several studies, all concerning Procellariiformes, reported variation in the extent of foraging area segregation in relation to breeding stage. Segregation was more pronounced during the breeding stage associated with shorter foraging trips: for example, chick-rearing for Black-browed Albatross (Wakefield *et al.* 2011) and incubation for Laysan Albatross *Phoebastria immutabilis* (Young *et al.* 2009). This accords with the prediction from the DDH model that segregation is less likely to occur at the limit of species' foraging ranges where competition is lowest. In addition, intra-specific competition may be higher (i) during the chick-rearing period, because birds must feed not only themselves but also their offspring, (ii) in the post-brood stage, when both adults forage simultaneously (rather than alternately, as during incubation and brooding), resulting in a higher density of foragers, and greater competition.

Segregation at other levels

This review has focussed on segregation among seabird colonies. However, within-colony segregation has also been documented. It is common for sexual segregation to occur among seabirds, often linked to size dimorphism (Catry *et al.* 2006, Phillips *et al.* 2011, Hedd *et al.* 2014, Cleasby *et al.* 2015). For example, Streaked Shearwaters breeding at two colonies in Japan segregate not only by colony but also by sex (Yamamoto *et al.* 2011). Seabirds have also been observed to segregate by age: Fayet *et al.* (2015) found substantial spatial segregation between immature and adult Manx Shearwaters *Puffinus puffinus*, which the authors attributed to differences in experience. Finally, several studies have examined the foraging distribution of birds nesting in different areas of the same colony. Whilst Waggitt *et al.* (2014) found no differences in foraging areas of Northern Gannets nesting in sub-colonies separated by distances of up to several hundred metres, Bogdanova et al. (2014) and Ceia et al. (2015) both found foraging area segregation of European Shag and Cory's Shearwater, respectively, nesting < 2km apart on opposite sides of their breeding islands. In the case of Cory's Shearwater, Ceia *et al.* (2015) reported partially segregated foraging grounds at ranges of up to 200 km. The authors suggested that such segregation could be mediated by directional bias, whereby individuals initiated trips on a bearing consistent with their colony aspect, reinforced by public information transfer between neighbours. These studies raise the question of what constitutes a seabird "colony" and reveal that foraging area segregation can occur at fine spatial scales, and among age classes and genders.

Development of foraging area segregation - information transfer and sociality

Several studies have demonstrated temporally stable individual specialisation in diet and foraging behaviour (see Ceia and Ramos 2015 and Phillips *et al.* 2017 for reviews), which can have fitness consequences (Quinn 2014) and may be spread by information transfer at the colony. It has been hypothesised that information sharing is a benefit of colonial breeding. Ward and Zahavi (1973) suggested that aggregations of birds (breeding colonies and roosts) act as information centres, where individuals gain knowledge about the location of prey. Weimerskirch *et al.* (2010) found that Guanay Cormorants *Phalacrocorax bougainvillii* use social information to select their bearing when departing the colony to forage. Before departure on a foraging trip, the cormorants briefly congregate on the sea to form a raft whose position is continuously adjusted to the bearing of the largest returning columns of cormorants. The departure bearing of birds leaving the raft to forage corresponds to the bearing of the largest groups of returning birds. Grémillet *et al.* (2004) suggested that group foraging behaviour observed in Cape Gannets *Morus capensis* evolved through the benefits of signalling behaviour and increased flight efficiency. They hypothesised that foraging area asymmetry combined with group foraging behaviour foster the development of 'cultural foraging patterns', which are instilled at the colony level through extensive natal colony fidelity (Klages 1994, Votier *et al.* 2011). This may enhance existing competition-avoidance behaviour, thus leading to segregated foraging grounds. On the basis of individual-based models, Wakefield *et al.* (2013) developed this hypothesis, showing how information sharing among birds from the same colony can initiate and maintain segregation of colony-specific foraging areas. They envisaged that unsuccessful or naive birds follow more successful individuals from the colony to prey patches. This allows information on areas that are less profitable, due to the presence of conspecifics from other colonies, to spread through the population. If this occurs across generations, i.e. young birds follow older birds, colony-specific foraging traditions may arise, leading to cultural divergence.

Despite evidence to suggest that sociality may be an important factor contributing to segregated foraging grounds, segregation has also been observed in nocturnal burrowing species such as Leach's Storm-petrel *Oceanodroma leucorhoa*, where visual signalling of foraging success and information transfer is less likely to occur. Pollet *et al.* (2014) found that Leach's Storm-petrels from two colonies in Nova Scotia situated 380 km apart travelled approximately 1 000 km from their colonies to forage and occupied distinctly separate foraging grounds, despite being within range of each other. This suggests that either information sharing and cultural learning of foraging patterns are not required for the development of foraging area segregation, or that information transfer is possible even in nocturnally active burrow nesting species.

IMPLICATIONS FOR ENVIRONMENTAL IMPACT ASSESSMENT

Improved understanding of the extent and causes of seabird foraging segregation is important for marine ecologists who seek to understand the processes responsible for shaping distributions and interactions of marine biota. However, it is also of applied relevance for marine planning and conservation. Globally, the marine environment is subject to increasing anthropogenic demands and developments such as renewable energy generation schemes frequently cover extremely large areas (1000 – 10000 km^2). In many countries, the statutory consent process requires environmental impact assessments (EIA) that quantify likely impacts on marine biodiversity, including mobile species such as seabirds. Since impacts on legally protected breeding colonies are of particular concern, such EIAs must consider the extent of seabird usage, and consequent impacts, of offshore development sites, especially for seabirds from protected breeding colonies. However, because at-sea surveys can rarely assign colony provenance of seabirds surveyed in development areas, and tracking multiple species from all protected colonies within foraging range may be both costly and logistically challenging, evidence regarding the degrees of connectivity of multiple colonies to a given development site is often lacking. Accordingly, in Europe current EIA practice often relies on simplifying assumptions regarding the distribution of foraging seabirds, such as species-level generic foraging ranges, assuming non-interacting spatial overlap of birds from adjacent colonies (Douse & Tyler 2014). However, if space use of a proposed development area is exclusive to a single colony, impacts will also fall exclusively, exerting a larger impact on the affected colony, whilst excluded colonies will bear no impact. Current EIA practice of apportioning impacts assuming overlapping foraging distributions will therefore be subject to errors of unquantified magnitude (of both over- and under-estimation) in cases where segregation occurs. The apparently high prevalence of inter-colony foraging segregation indicated by this review suggests that such errors may be widespread.

The DDH model allows us to consider which colonies may be most affected by error in EIAs that are introduced by the assumption of shared space use. Perhaps most notably, larger colonies are predicted to competitively exclude smaller neighbouring colonies, thus making larger colonies more likely to show sole use of a foraging area. Since statutory protection is usually afforded to larger colonies, there is a risk that current EIA practice will tend to under-estimate impacts on protected colonies, whilst over-estimating impacts on smaller, unprotected colonies. Conversely, seabirds are most likely to show overlapping foraging areas at the limit of the foraging range where forager densities and competition are lowest. Current EIA practice may therefore be least prone to error in situations where developments occur toward the limit of species' foraging ranges, and also where prey is abundant. However, the studies reviewed here and elsewhere (e.g. Thaxter *et al.* 2010) show that there is often considerable intra-specific inter-colony variation in foraging range such that, in the absence of empirical, site-specific data, the application of generic species-level foraging radii is prone to considerable error.

The studies reviewed here deal solely with the central-place foraging behaviour of breeding seabirds. It is not known to what extent foraging area segregation also applies to non-breeding adults and immatures during the breeding season. Many non-breeding adults and immatures attend the nesting colonies during the breeding season, and although they have greater flexibility regarding the timing of commuting, they nonetheless behave as central place foragers, so will be subject to similar, though not identical, costs and benefits as breeding adults. Due to the difficulty of tracking non-breeding adults and immatures there are currently extremely few empirical data on the marine distribution of these groups (though see Votier *et al.* (2017) for a recent example).

The DDH model predicts that in areas of high prey abundance, such as upwelling or frontal zones, seabirds from multiple colonies may aggregate. If a marine development is situated in such an area, the usage by birds from multiple colonies might lead to impacts on birds from numerous colonies, even at considerable distance from the development. Engineering considerations may favour location of offshore structures, such as windfarms, in shallow waters overlying banks, which are generally productive areas and likely to be a focus of seabird aggregation. Douse and Tyler (2014) recognised that the use of generic foraging ranges may underestimate the geographic extent of impacts, since birds may travel exceptionally long distances to forage in highly productive areas (Dean *et al.* 2015). Therefore, even in cases where impacts are shared among multiple colonies, the simple distance-decay relationships used in EIAs may underestimate the impacts on colonies using highly profitable, if distant, foraging areas. Such considerations may be particularly important for species that show a dual foraging strategy, alternating short trips that permit frequent chick provisioning, with longer trips to more productive areas for self-maintenance (e.g. Shoji *et al.* 2015).

The findings of this review indicate that over- or under-estimation of impacts on individual colonies when using approaches based on simplifying assumptions typically employed in EIAs will be the rule rather than the exception. Furthermore, offshore developments such as arrays of wind turbines, typically cover very considerable areas. If such developments lead to avoidance of such areas by seabirds (Desholm & Kahlert 2005) this indirect form of habitat loss may result in increased competition, and hence segregation, in the surrounding areas used by displaced birds. Under such circumstances, the cumulative effects of multiple adjacent developments will be extremely difficult to predict.

CONCLUSIONS AND FUTURE RESEARCH

This review has examined spatial segregation in seabirds and discussed potential implications of the phenomenon when apportioning impacts of marine developments to particular seabird colonies, particularly those protected by legal designations. The studies reviewed suggest that inter-colony segregation of foraging areas may be widespread across seabird taxa and spatial scales and will arise wherever intra-specific inter-colony competition for prey is sufficiently intense. The spatial and temporal extent of segregation is somewhat variable, even within species. Such variability is likely driven by variation in both the distribution of prey, the size of neighbouring colonies and the distances between colonies. Competition may be absent or of minor importance in circumstances where colony sizes are well below their natural carrying capacity due to anthropogenic impacts (bycatch, predation by invasive species, harvest for human consumption, pollution, etc.). However, seabird declines of recent decades in areas of northwest Europe are generally considered to result from food limitation (Frederiksen *et al.* 2006, Frederiksen *et al*. 2007, 2013, Louzao *et al.* 2015), so prey are unlikely to be superabundant, suggesting that segregation should occur in this region. Historically, harvesting of seabirds for human consumption and lower human exploitation of seabird prey, may have resulted in seabird population sizes falling below prey carrying capacity, leading to lower inter-colony competition and segregation than currently. However, if segregation is mediated by cultural processes (Wakefield *et al*. 2013), there may be some lag in the onset of segregation in response to environmental change as populations become food-limited. It is unclear how long such a lag might continue, but it is unlikely that many seabird populations in this region are in equilibrium with prey availability.

Little information is currently available regarding the incidence of segregation among non-breeding and immature birds associated with different colonies, as tracking studies are usually carried out on breeding adults (but see Camphuysen 2011, Votier *et al.* 2011, Sherley *et al.* 2017). Nor is it clear the extent to which breeding adults from a given colony may segregate at sea from other groups of conspecifics that may be associated with the same colony during the breeding season (e.g. failed breeders, immature birds, etc.), though see Votier *et al.* (2017). This is potentially an important aspect to understand as impacts of marine developments on future breeders may have substantial consequences for population dynamics and, ultimately, colony fate (Sherley *et al.* 2017). Though not a focus of this review, there is a strong suggestion that segregation at the sub-colony level also occurs, but it is not clear what factors cause some sub-colonies to show segregation in some cases (Ceia *et al.* 2015) but not others (Waggitt *et al.* 2014). This review has shown that the strength of segregation may change during the course of the breeding season (e.g. Ainley *et al.* 2004, Yamamoto *et al.* 2011) and there is also a suggestion that segregation can occur outside the breeding season (e.g. Thiebot *et al.* 2011, Fort *et al.* 2012, Ratcliffe *et al.* 2014). Greater understanding of foraging area segregation outside the breeding season will require the development of safe, low cost, long term attachment methods for high precision tags.

The assumption of non-interacting, overlapping colony foraging distributions that underpins the current, widely-used approaches to apportionment of the potential impacts of marine developments to seabird colonies in the UK, appears unrealistic in many situations. Segregation of seabird foraging areas appears commonplace and consequently the distribution of impacts among colonies will differ from the predictions of existing models: fewer colonies are likely to be impacted, but to a higher degree. Whilst we have discussed a variety of such factors that may influence the extent of foraging segregation, with reference to examples from the literature, given the current state of knowledge it is it not possible to reliably determine the extent of colony segregation, or the absence of segregation, for any particular marine location.

For most of the studies reviewed here, the authors' assessment of inter-colony foraging area interactions was not based on inclusion of a measure of inter-colony competition in a space-use model, but rather on a somewhat subjective judgement based on the percentage overlap, or by visual inspection of colony distributions, but without reference to a defined null (i.e. overlapping) distribution. In cases where segregation was complete, statistical analysis may be redundant, but in order to identify effects of inter-colony competition on space use in an unbiased manner, a modelling approach incorporating a measure of inter-colony competition is required. Whilst we recognise that identification of inter-colony interactions was not a primary focus of many of the studies we reviewed here, we would urge authors of future multi-colony seabird foraging distribution studies to include a statistically robust assessment of the extent and direction of potential inter-colony interactions, which account for accessibility and prey availability wherever possible. In addition, we strongly suggest that the assessment of future offshore developments should require the simultaneous collection of tracking data from a representative sample of birds from colonies likely to be affected. The collection and analysis of such data will represent a valuable contribution to improving our understanding of the factors that shape colony foraging distribution and segregation.

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Table 1. Occurrence of inter-colony segregation of foraging areas of seabirds. Breeding stage: PL = pre-laying, incubation = Inc, chick-rearing = CR; Evidence: S = statistical test, O = assessment of overlap, N = No assessment.

Species	Common name	Order	Area	Breeding stage	Method	Evidence	Distribution	Reference
Pygoscelis papua	Gentoo Penguin	Sphenisciformes	Falkland Islands	CR	GPS	O	Segregation	(Masello *et al.* 2010)
Pygoscelis adeliae	Adelie Penguin	Sphenisciformes	Ross Sea, Antarctica	CR	VHF	O	Variable segregation	(Ainley *et al.* 2004)
Eudyptes chrysocome	Southern Rockhopper Penguin	Sphenisciformes	Falkland Islands	CR	GPS	O	Segregation	(Masello *et al.* 2010)
Eudyptes chrysolophus	Macaroni Penguin	Sphenisciformes	South Georgia	CR	PTT	O	Variable segregation	Trathan *et al.* (2006)
Spheniscus magellanicus	Magellanic Penguin	Sphenisciformes	Patagonia, Argentina	CR	PTT	N	Not assessed	(Boersma *et al.* 2009, Wilson *et al.* 2005)
Spheniscus magellanicus	Magellanic Penguin	Sphenisciformes	Falkland Islands	CR	GPS	O	Segregation	(Masello *et al.* 2010)
Oceanodroma leucorhoa	Leach's Storm-petrel	Procellariiformes	Nova Scotia, Canada	IN	GLS	O	Segregation	(Pollet *et al.* 2014)
Phoebastria immutabilis	Laysan albatross	Procellariiformes	Pacific Ocean, Hawaii	IN, CR	GLS	O	Variable segregation	(Young *et al.* 2009)
Phoebastria irrorata	Waved Albatross	Procellariiformes	Galapagos, Ecuador	IN, CR	GPS	O	Variable segregation	(Awkerman *et al.* 2014)
Phoebetria fusca	Sooty Albatross	Procellariiformes	South Atlantic, SW Indian Ocean	IN, CR	GPS & PTT	O	Overlap	(Schoombie *et al.* 2017)
Thalassarche melanophris	Black-browed Albatross	Procellariiformes	Kerguelen	CR	Colour mark	O	Variable segregation	(Weimerskirch *et al.* 1988)
Thalassarche melanophris	Black-browed Albatross	Procellariiformes	Falkland Islands	CR	PTT	O	Segregation	(Huin 2002)
Thalassarche melanophris	Black-browed Albatross	Procellariiformes	Southern Ocean	IN, CR	PTT	S	Variable segregation	(Wakefield *et al.* 2011)
Thalassarche melanophris	Black-browed Albatross	Procellariiformes	Falkland Islands	CR	GPS & GLS	S	Variable segregation	(Catry *et al.* 2013)
Macronectes giganteus	Southern Giant Petrel	Procellariiformes	South Atlantic	IN, CR	GPS	O	Segregation	(Quintana *et al.* 2010)
Pterodroma cookii	Cook's petrel	Procellariiformes	New Zealand	CR	GLS	O	Segregation	(Rayner *et al.* 2008)
Puffinus tenuirostris	Short-tailed Shearwater	Procellariiformes	Tasmania/SE Australia	CR	PTT & GLS	O	Overlap	(Raymond *et al.* 2010)

Puffinus tenuirostris	Short-tailed Shearwater	Procellariiformes	Bass Strait, SE Australia	CR	GPS & GLS	O	Overlap	(Berlincourt and Arnould 2015)
Calonectris leucomelas	Streaked Shearwater	Procellariiformes	Japan	PL, IN	GLS	O	Variable segregation	(Yamamoto *et al.* 2011)
Calonectris diomedea	Scopoli's Shearwater	Procellariiformes	Tunisia and Italy	IN, CR	GPS	S	Segregation	(Cecere *et al.* 2015)
Calonectris diomedea	Scopoli's Shearwater	Procellariiformes	Mallorca, Menorca, Collumbretes	IN, CR	GPS	O	Segregation	(Genovart *et al.* 2018)
Calonectris borealis	Cory's Shearwater	Procellariiformes	North Atlantic Ocean	IN, CR	GPS & compass loggers	O	Variable segregation	(Paiva *et al.* 2010)
Calonectris borealis	Cory's Shearwater	Procellariiformes	North Atlantic Ocean	CR	GPS & PTT	O	Variable segregation	(Ramos *et al.* 2013)
Puffinus puffinus	Manx Shearwater	Procellariiformes	Britain and Ireland	IN, CR	GPS	O	Overlap[1]	(Dean *et al.* 2012, Dean *et al.* 2015)
Morus bassanus	Northern Gannet	Suliformes	Britain and Ireland	CR	GPS & PTT	S	Segregation	(Wakefield *et al.* 2013)
Morus capensis	Cape Gannet	Suliformes	South Africa	CR	GPS	S	Segregation[2]	(Grémillet *et al.* 2004, Grémillet *et al.* 2008)
Morus serrator	Australasian Gannet	Suliformes	Bass Strait, SE Australia	IN	GPS	O	Segregation	(Angel *et al.* 2016)
Sula variegata	Peruvian Booby	Suliformes	Northern Peru	CR	GPS	O	Segregation	(Zavalaga *et al.* 2010a, Zavalaga *et al.* 2010b)
Phalacrocorax magellanicus	Rock Shag	Suliformes	Patagonia, Argentina	IN, CR	VHF	O	Segregation	(Sapoznikow and Quintana 2003)
Leucocarbo atriceps	Imperial Cormorant	Suliformes	Patagonia, Argentina	IN, CR	VHF	O	Segregation	(Sapoznikow and Quintana 2003)
Phalacrocorax aristotelis	European Shag	Suliformes	Isles of Scilly, United Kingdom	IN, CR	GPS	O	Overlap	(Evans *et al.* 2015)
Phalacrocorax aristotelis	European Shag	Suliformes	Britain and Ireland	IN, CR	GPS	S	Overlap	(Wakefield *et al.* 2017)
Leucocarbo georgianus[3]	South Georgia Shag[3]	Suliformes	South Georgia	CR	VHF	O	Segregation	(Wanless and Harris 1993)
Rissa tridactyla	Black-legged Kittiwake	Charadriiformes	Prince William Sound, Alaska	CR	VHF	O	Segregation	(Ainley *et al.* 2003)
Rissa tridactyla	Black-legged Kittiwake	Charadriiformes	Pribilof Islands, Bering Sea	CR	GPS	O	Segregation	(Paredes *et al.* 2012, Paredes *et al.* 2014)
Rissa tridactyla	Black-legged Kittiwake	Charadriiformes	North Sea, NE England	CR	GPS	O	Overlap	(Redfern and Bevan 2014)
Rissa tridactyla	Black-legged Kittiwake	Charadriiformes	Britain and Ireland	IN, CR	GPS	S	Segregation	(Wakefield *et al.* 2017)

Larus fuscus	Lesser Black-backed Gull	Charadriiformes	German coast	IN	GPS	O	Segregation	(Corman *et al.* 2016)
Ptychoramphus aleuticus	Cassin's Auklet	Charadriiformes	Channel Islands, California	IN, CR	VHF	N	Not assessed	(Adams *et al.* 2004)
Alca torda	Razorbill	Charadriiformes	Britain and Ireland	IN, CR	GPS	S	Overlap	(Wakefield *et al.* 2017)
Uria algae	Common Guillemot	Charadriiformes	Britain and Ireland	IN, CR	GPS	S	Segregation	(Wakefield *et al.* 2017)

[1] On short trips (most frequent during chick-rearing) little overlap occurred as foraging ranges were generally less than inter-colony distance for most colonies

[2]Segregation not assessed in Grémillet *et al*. 2008 who studied colonies in South Africa and Namibia, but reported for same South African colonies studied by Grémillet *et al*. 2004.

[3] Formerly known as Blue-eyed Shag *Phalacrocorax atriceps*

Table 2. Number of studies where seabird inter-colony distributions were assessed as overlapping, segregated, or variably segregated, according to the strength of evidence used for the assessment.

Evidence type	**Inter-colony distribution**	**Number of studies**
Formal statistical assessment of inter-colony effect (9 studies)	Overlap	2
	Segregation	5
	Variable segregation	2
Author judgement, based on percentage overlap or visual inspection of colony-level distributions (30 studies)	Overlap	6
	Segregation	16
	Variable segregation	8
No assessment made (2 studies)	No assessment	2

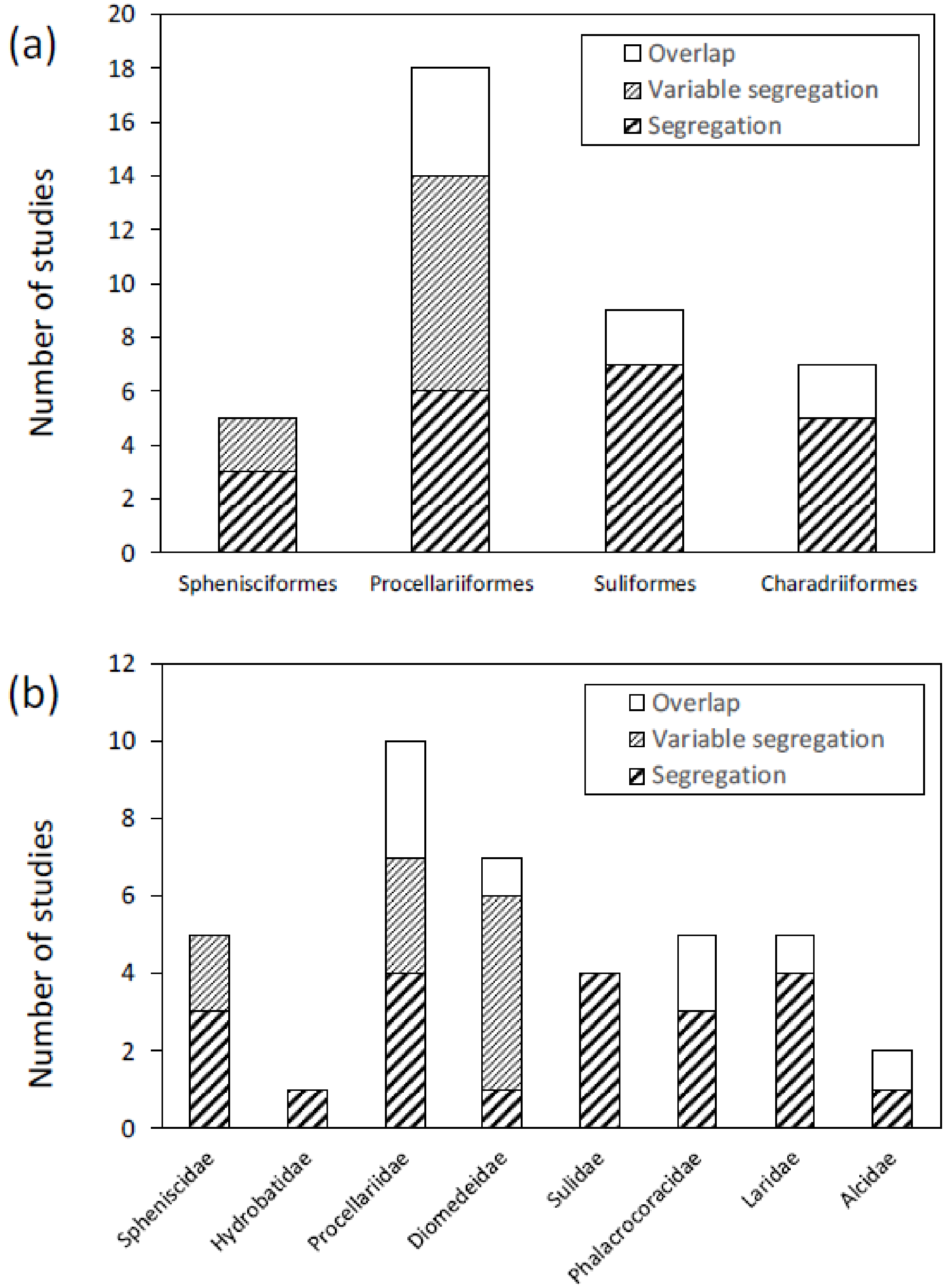

Figure 1. Occurrence of inter-colony foraging area segregation in seabirds by order (a) and family (b).

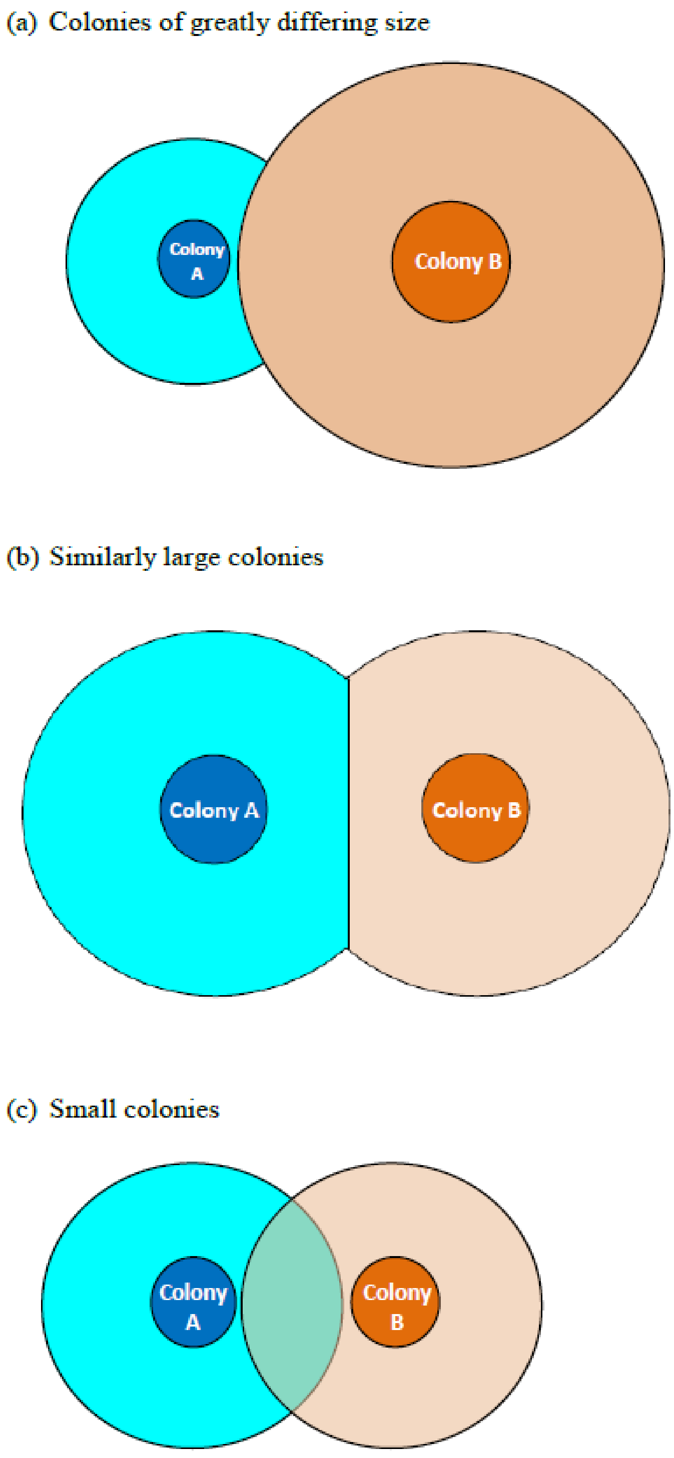

Figure 2. Colony-specific distribution patterns as a function of colony size. Segregation is likely to occur in the vicinity of large colonies where forager density is high (a and b), but least likely where colonies are small and prey availability less likely to be affected by density-dependent competition (c).

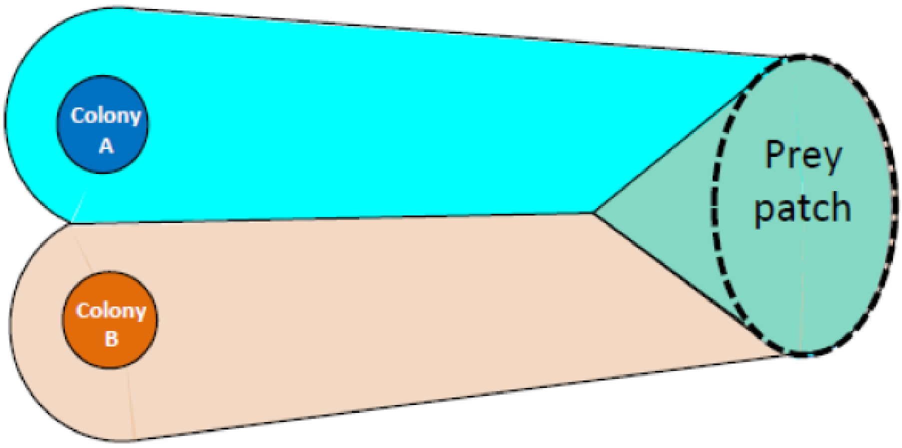

Figure 3. Close to the adjacent colonies, foraging grounds are segregated due to density-dependent competition. However, at greater distances foraging grounds may overlap, especially in areas of predictably high prey density, where effective competition is lower.