Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations

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INTRODUCTION

Foraging seabirds use behavioral strategies specifically adapted to the dynamic prey distribution in the marine environment. When prey are benthic and relatively stationary, being associated to seafloor characteristics, seabirds might develop repetitive individual routines likely adapted to specific areas, thus using memory to increase foraging efficiency (Cook et al. 2006). However, when prey are aggregated in patches that move constantly in space and time (Russell et al. 1992; Fauchald et al. 2000) and are difficult to locate from the sea surface, seabirds might not directly look for prey but instead they may use various mechanisms to detect cues for prey availability such as observing conspecifics (Nevitt and Veit 1999; Silverman et al. 2004; Thiebault et al. forthcoming), prior experience (Davoren et al. 2003a), oceanographic features (Schneider 1982), or odor cues (Nevitt 2008). Among these mechanisms, the interactions with conspecifics might play a major role, especially where animals are congregated in high densities (Buckley 1997; Tremblay et al. 2014). Seabirds aggregate rapidly at fish schools once these are detected (O’Donoghue et al. 2010), which suggests a rapid transfer of information across a particular range surrounding the patch. Potential cooperation between foraging seabirds to detect food has been suggested by means of network foraging (Wittenberger 2004).
and Hunt 1985; Thiebault et al. forthcoming) that enables a rapid transfer of information among connected individuals. In addition, the aggregation of predators itself on a patch of food is assumed to be cued on by foraging seabirds as they are regularly attracted to flocks of conspecifics (Hoffman et al. 1981; Harrison et al. 1991; Buckley 1997), a mechanism known as local enhancement. Foraging aggregations of seabirds on fish schools are common, as suggested by various observations in the Atlantic Ocean (Harrison et al. 1991; Camphuysen and Webb 1999), in the Pacific Ocean (Porter and Sealy 1982; Chilton and Sealy 1987; Mills 1996), and in the Indian Ocean (Hodges and Wochler 1993). These aggregations are most often multispecific and include aquatic predators, such as cetaceans and tuna (Au and Pitman 1986; Oro 1995; Chia and Grosvalet 2001; Tremblay et al. 2014), in addition to various species of seabirds. Seabirds can easily detect flocks of conspecifics (Hoffman et al. 1981; Harrison et al. 1991), and so this kind of aggregation, especially when foraging activity can also be detected, can be used as an indirect cue of the presence of inconspicuous prey (Camphuysen and Webb 1999).

The improvement in foraging success due to local enhancement has been demonstrated in modeling studies (Grunbaum and Veit 2003; Deygout et al. 2010), but in situ observations of the foraging behavior of seabirds and their social interactions at sea are challenging (Galef and Giraldeau 2001; Racine et al. 2012). Pioneering studies on the local enhancement hypothesis include studies that reported the formation of feeding flocks of seabirds (Hoffman et al. 1981; Harrison et al. 1991), which showed that these foragers were attracted to groups of feeding conspecifics. Furthermore, the distance at which flocks of seabirds are detectable can vary with the size of the flocks, as larger flocks are visible from larger distances (Vine 1973). The detectability of a patch of prey could hence not only be improved by the presence of predators but could also vary with the size of the aggregation. Haney et al. (1992) inferred the distance from which seabirds reacted to simulated prey from ship-based chumming experiments and recorded birds being recruited from distances between 4.9 and 11.3 km. To our knowledge, the distance at which predator aggregations can be detected by foraging seabirds, and the related improvement of food detectability of such predator aggregations, has not yet been quantified.

Our study is based on data obtained from the deployment of GPS loggers and camcorders on foraging Cape gannets (Morus capensis) Lichtenstein 1823. This species naturally feeds on pelagic fish schools, mainly sardines (Sardinops sagax) and anchovies (Engraulis encrasicolus) (Batchelor and Ross 1984), and capture prey by plunge diving (Ropert-Coudert, Grémillet, Ryan, et al. 2004). Cape gannets are active only during daytime (Ropert-Coudert, Grémillet, Kato, et al. 2004), indicating the importance of vision for foraging. The concomitant deployment of both GPS loggers and video cameras provides new insights into the interactions within the predatory guild at sea and its influence on seabirds’ movements patterns (Tremblay et al. 2014). The video cameras provided direct observations of the aggregation of predators at food patches, whereas the GPS data allowed us to identify points in the track where seabirds reacted to these aggregation of predators by changing their movement. We studied the mechanism of local enhancement in these foraging seabirds in 2 steps. We first assessed the detection distances in relation to predator aggregations of different sizes by measuring the variation in reaction distances. Secondly, we studied the foraging consequences of joining such patches that are already exploited by other predators by associating the number and frequency of dives with the sizes and types of these predator aggregations.

**MATERIALS AND METHODS**

**Maximum theoretical distance of visibility**

Although vision is generally not obscured over the ocean, the distance at which objects can be visually detected is limited because of the curvature of the earth (distance to the horizon). The maximum distance of visibility then depends on the height of the target as well as that of the observer (see Fig. 2 in Haney et al. 1992 for a schematic description). We calculated the maximum distance at which seabirds could be visibly detectable according to Haney et al. (1992). The atmospheric refraction is not considered in this calculus, assuming that it is negligible for relatively small heights (Haney et al. 1992) such as those from which gannets forage.

\[
\text{distance}_\text{max} = [3.838 \times (\text{height}_\text{target}^{0.65}) \\
+ 3.838 \times (\text{height}_\text{observer}^{0.65})] 
\]

The observer is the study bird, whereas the target corresponds to the aggregation that is joined. The height of birds varies with their activity. The study bird can react to an aggregation while sitting on the water or flying. Equally, the aggregation to which the bird reacts could consist of seabirds either sitting on the water or flying and diving (see Definition of predator aggregations). We assumed that seabirds sitting on the water can be situated at a height from 0 (we used 0.1 m for calculations) to 2 m, due to dwell height, whereas gannets can initiate a dive from up to 30 to 40 m (Nelson 2005). We hence assumed flying gannets to be situated between 2 and 40 m above sea level.

**Data collection**

Thirty-six Cape Gannets were fitted with GPS units and microvideo recorders at Bird Island (33°50’26.6”S, 26°17’14.5”E, Algoa Bay, South Africa) during the breeding season of 2010–2011 between December 8 and January 22. The birds were captured near their nest, when departing to sea after a changeover with their partners. Only 1 adult per nest was equipped during one foraging trip while the partner stayed at the nest guarding the chick. We deployed 2 types of devices that were attached together as 1 unit: a GPS logger (i-GotU GT-600, Mobile Action Technology Inc., Taipei, Taiwan, 43 × 40 × 12 mm, 36 g) to record the movement path and a microvideo camera (Camsports nano, Camsports™, Estrablin, France, 68 × 19 mm, 22 g) to observe the surroundings of the animal. The GPS loggers were set to record a geographical position every 5 s when the animal moved at a speed above 10 km/h and every 10 or 30 s otherwise. The video cameras recorded 736 × 480 pixels images at 25 frames per second with a 74° lens angle, for a maximum of 90 min due to limited battery capacity. The handling process lasted less than 8 min and consisted of taking standard bio-metric measurements of the bird (data not used in this study, except for body mass [to closest 50 g] measured using a spring balance, pesola™, Baar, Switzerland) in addition to fastening the devices with adhesive waterproof tape (Tesa™, Hamburg, Germany). Before the bird was released, a handheld GPS was placed in front of the camera lens so that the Greenwich Mean Time was recorded. The later video observations were hence accurately synchronized to movement data using the satellite derived time. The total mass attached to a bird, so both devices and tape, was 70–75 g, which corresponded to 2.3–3.0% of the birds’ body mass (2400–3100 g). The loggers were attached on the lower back of the bird, in such a way that potential drag due to modification of the birds’ body shape was minimized. The nests were then monitored
regularly, so the study birds were recaptured soon after their return to the colony and the devices were then retrieved.

**Video data analysis**

Video footages were observed frame by frame using a video reader in Matlab (R2010a, The MathWorks, Natick, MA) and the events of interest were visually flagged using a purpose-built video event recorder (Tremblay Y, unpublished software). Video data provided information on the behavior of equipped birds, including taking off, sea landing, and diving, from which we defined flights and foraging events. The surroundings of the study bird were also directly observed, as were interactions with conspecifics and other predators (other seabird species, dolphins, and boats). In this study, we focus on the aggregations of predators joined by the study birds.

**Definition of predator aggregations**

The types of aggregations were characterized based on observations of surrounding conspecifics as well as the behavior of the equipped birds. A “raft” is an aggregation of conspecifics sitting on the water that the study bird either flew past or joined. A “flock” is an aggregation of conspecifics that were flying around in various directions, with some of these observations including dives (either performed by the study bird or by the surroundings birds). Within a “flock,” seabirds sitting on the water could also be observed, but the aggregation was characterized as a flock because flying birds are higher than birds on the water resulting in increased detectability (see Maximum theoretical distance of visibility). A “foraging event” was defined as a spatiotemporal cluster of dives by the study birds. Two successive dives were considered to belong to the same foraging event if they occurred within 1 km or within a 6-min interval time period. These thresholds are based on the observation of the distribution of these parameters (see Supplementary Figures S1–S3).

**Description of predator aggregations**

Predator aggregations were described based on the species present and the number of gannets in the aggregation. The number of gannets in the respective aggregations were counted visually from the video footage, integrating the observations from successive frames. A single frame is a snapshot of the occurring event and, due to the limited field of vision of the camera, this snapshot most often does not include the entire scene. The analysis of successive frames is hence crucial to estimate the whole aggregation, as the equipped bird moves and rotates. The number of conspecifics in an aggregation was then counted over successive frames that were assumed to represent the whole aggregation. Due to inherent constraints in this approach, estimates of numbers are crude, especially for large aggregations. We are nonetheless confident in the order of magnitude as well as in the relative differences between observed aggregations. Seabirds aggregate rapidly on a patch of food once detected, so the number of gannets aggregated could increase during the time the study bird was associated with the aggregation.

We, therefore, differentiated between the number of conspecifics present when the study bird reached the aggregation (used in the analysis of reaction distances) and the total number of conspecifics aggregated at the end of the foraging event (used in the analysis of the foraging activity).

In addition to gannets, we observed the presence of other predator species during foraging events. These observations included dolphins and various species of seabirds. We therefore differentiated among 4 types of aggregations: only gannets, gannets and other seabird species, gannets and dolphins, or gannets, other seabird species, and dolphins.

**Description of the foraging activity at the aggregation**

The foraging activity was assessed from video data for every foraging event by counting the number of dives performed by the study bird. In order to compare between individuals, we also calculated the number of dives per minute. In this case, we excluded the foraging events observed during less than 2 min and the ones where only one dive was observed. The number of dives and the frequency of dives were then related to the observation of surrounding predators (number of gannets and presence of other predators) to estimate their relative influence.

The foraging activity as measured here informs about feeding attempts, but not necessarily successful prey captures (observation not available from our video data). However, a larger number of dives relates to longer exploitation of the patch of food. Because gannets feed on ephemeral food patches (pelagic fish schools), longer exploitation time most probably indicates better foraging conditions.

**GPS data analysis**

The raw tracking data were interpolated using a Bézier curve (Tremblay et al. 2006) to obtain a track with a regular step duration at 5 s. Regular step is a prerequisite for applying the method we used to identify reaction points (see Identification of reaction points for details). These tracking data were used to determine the location of observations from video data, by assigning each of them to the closest point in time. The identification of behavioral reactions of the birds toward predator aggregations resulted from an analysis on the movement patterns (see Identification of reaction points for details). Due to the limited field of view and the relative low resolution of the microcorders, we assumed that the study birds could detect the aggregations well before we could see them in the video records. The detection distance was then calculated as the straight line distance between the identified reaction point and the point where the study bird reached the aggregation.

**Identification of reaction points**

The reaction of birds toward predator aggregations was identified based on the analysis of the trajectories of equipped birds. We assumed that a clear change in movement pattern (change in direction and/or speed) corresponded to the reaction of the study bird following detection of a place of interest toward which the bird moved. To identify changes in movement patterns, we used an adapted version of the segmentation methodology developed by Thiebault and Tremblay (2013). Considering both speed and direction simultaneously, this methodology identifies breaking points along a trajectory that represent decisions by the study animal for a change in its movement pattern. The method was applied on selected portions of a trajectory, corresponding to the flying phase preceding the joining of an aggregation. The start point of such a portion was either a takeoff or the departure from a previous aggregation, and the end point was situated where the equipped bird reached the aggregation. On this portion, the trajectory was analyzed backward, from the aggregation to the starting point of the flying phase. The method detects changes of various intensities in the trajectory, depending on a parameter that defines the scale of segmentation, the tolerance...
parameter (Thiebault and Tremblay 2013). In each portion of interest, we looked for the most noticeable change in behavior, that is, the change that most likely resulted from a sudden reaction of the birds within the portion that precedes the joining of an aggregation. To do so, we implemented a growing tolerance parameter (thus identifying increasingly large changes), until only the largest change was left (either in the track portion of interest or at the beginning of it). If the reaction point was identified in the portion of interest, the study bird must have been flying. Alternately, if the point identified was the first one of the portion of interest, the study bird could either be sitting on the water or flying (depending on the behavior of the bird at the starting point of the portion). An example of the outcome of this process is shown in Figure 1.

Concurrent analysis of video and GPS data
In order to concurrently analyze the video observations and the tracking data, we used a purpose-built interface (Tremblay Y, unpublished software) aimed at allowing rapid visualization of the observed video events located on the trajectory of the animal. The interface dynamically displays video with tracking information, which facilitates the observations of combined data. An illustration of the combined observation from tracking and video data (adapted from the interface) is shown in Figure 1.

RESULTS
We collected concomitant video and GPS data from one foraging trip of 35 different individuals. We observed 36 aggregations, of which 19 were rafts and 17 were flocks, in the video footages of 19 study individuals. Fifteen of the 17 flocks were identified as foraging events (at least one dive performed by the study bird). Besides these observations, one study bird was observed diving behind a fishing boat, in association with a group of conspecifics and other seabird species, and was not included in the analysis because of expected distortion of the detection distance. The remaining 15 study individuals did not join conspecific aggregations within the observation time (~1h30min of video recording) although we observed them interacting with conspecifics in different ways (flying in groups for example).

Maximum theoretical distances of visibility
Independent from the birds’ eye acuity, the maximum theoretical distance at which a gannet can visually detect conspecifics at sea varies from 2.4 to 48.5 km depending on the height of the birds, and thus on their activity (Figure 2). We distinguished between birds on the water or in flight, 2 activities that concern both the study bird and the target aggregation, resulting in 4 scenarios. Birds forming a raft on the water can be detected from a maximum distance that varies between 2.4 and 10.9 km if the observer is also on the water (considering both at 0.1 and 2 m height, respectively, accounting for ocean waves). However, if the observer is flying 20 m high, the raft is potentially detectable from 18.4 to 22.6 km (the raft situated at 0.1 and 2 m high, respectively). A flock of gannets engaged in plunge diving from a height of 30 m can be visible at 24.9 km for a gannet on the water (considering it at 1 m high) or at 38.2 km if the gannet is flying (at 20 m high). Assuming a flying height of 40 m, the maximum theoretical distance at which gannets could visibly detect a flock of diving conspecifics, when flying from between 30 and 40 m above sea level, would be between 45.3 and 48.5 km.

Reaction distances of the study birds
We measured reaction distances of Cape gannets toward conspecific aggregations between 0.2 and 37.6 km (Figure 3). These

![Figure 1](https://academic.oup.com/beheco/article-abstract/25/6/1302/273062/1305)
Illustration of the concurrent analysis of video observations and tracking data, from a portion of a trajectory recorded on a Cape gannet. From the video data, we observed other predators in the surroundings of the study birds, as well as the dives they performed. The predator aggregations were described in terms of number of gannets present and whether dolphins were also present. The foraging activity of the bird was described in terms of the number of dives performed by the study bird. From the GPS data, we identified reaction points (as a major change in movement) and measured reaction distances. The wind blew from 90° at 8.6 m/s, which could explain the very high speed of the bird during the first part of its trip (before the reaction point). Interestingly, we can see the flying speed of the bird increasing progressively as it comes closer to aggregation.

![Figure 2](https://academic.oup.com/beheco/article-abstract/25/6/1302/273062/1306)
Maximum theoretical distance of visibility, due to the curvature of the earth. The distance of visibility varies with the height of objects (here applied to gannets of which the height depends on the activity).
reaction distances were all under or within the ranges of the maximum theoretical distances of visibility, calculated for the different above-mentioned scenarios (4 scenarios differentiated from the birds’ activity). For any of the 4 scenarios, the reaction distances tended to increase with the number of gannets aggregated and the largest reaction distances were measured for larger aggregations. The increase was more clearly defined when the birds reacted to flocks (Figure 3a,b) than when they reacted to rafts (Figure 3c,d).

Rafts that had formed with 1–10 gannets prompted reactions from similar distances if the study bird was sitting on the water or flying (0.2–8.1 and 0.2–6.2 km, respectively, Figure 3c,d). The reaction distance increased to 21.1 km for a study bird in flight responding to a raft formed by 150 gannets (Figure 3d). When sitting on the water, the study birds reacted to flocks of conspecifics from relatively small distances, that is, between 2.2 and 10.1 km, even if the flock consisted of a large number of gannets, of up to 200 (Figure 3a). However, when in flight, they reacted from up to 37.6 km to a flock of 150 gannets (Figure 3b). In this configuration, that is, the study bird in flight responding to a flock of conspecifics, the reaction distance noticeably increased with the number of gannets in the aggregation. However, for one study bird, we measured a short reaction distance to a large flock (Figure 3b). This outlines that even if a large aggregation is detectable from a large distance, the bird does not necessarily react from this distance.

At the aggregation sites: species associations and foraging activity

Gannets were the main observed species, with an estimate of 1025 individuals observed over the 15 foraging events. Aggregations that were larger than 50 gannets also included dolphins (36 individuals observed over 6 foraging events, Figure 4). Observations of other seabird species were less frequent and included 8 cormorants (during 5 foraging events), 3 penguins (during 1 foraging event), 3 petrels (during 1 foraging event), and 1 gull (at 1 foraging event). We observed study birds performing 1–19 dives during a foraging event. Except for one instance, more dives occurred when the aggregation was multispecific (including dolphins and/or other seabird species) than when it was monospecific (gannets only). The number of dives increased with the number of gannets aggregated during a foraging event (Figure 4a). The increase appeared not to be linear but rather at a decreasing rate, potentially reaching an asymptote (13–16 dives when aggregated with 80–200 gannets). One bird was observed associated with a larger aggregation of
about 300 gannets and performed only 5 dives, which drives the regression to decrease for larger aggregations (≥200 gannets). The gannets performed 0.49 dives per minute on average (standard deviation: 0.11). The frequency of dives showed a pattern similar to the number of dives when related to the number of gannets aggregated in a foraging event (Figure 4b). A peak appears when 50–150 gannets were present with ~0.5–~0.7 dives per minute, and the frequency of dives decreases down to ~0.3 dives per minute when more than 200 gannets were present.

**DISCUSSION**

Local enhancement has been proposed as a mechanism of prey detection for foraging seabirds (Hoffman et al. 1981; Harrison et al. 1991), but studying such a mechanism is challenging (Racine et al. 2012). To our knowledge, our study is the first to directly measure distances from which foraging seabirds react to conspecific aggregations, as well as their response to varying sized aggregations. In doing so, our study provides direct support and quantification of the local-enhancement theory from a predator’s perspective.

**The detection capabilities of Cape gannets**

The mechanism of local enhancement suggests that seabirds can detect feeding aggregations at a larger distance than the prey themselves (Buckley 1997). Foraging seabirds may use odor cues or vision to directly or indirectly detect food, depending on the spatial scale (Nevitt and Veit 1999). In the case of foragers such as gannets with an exclusive daytime activity (Robert-Coudert, Grémillet, Kato, et al. 2004) and without external nostrils, vision is probably the main sense involved in the detection of prey. The sense of smell is known to be used by some Procellariiforms and penguins (Verheyden and Jouventin 1994; Nevitt et al. 1995; Wright et al. 2011; Amo et al. 2013), but its importance is yet to be demonstrated in sulids. Although olfactory senses may assist in detection of foraging zones at a large scale, it appears unlikely to be used for the detection of aggregations as they include moving and dynamic individuals with contrasted colors. This is supported by the example given in Figure 1 where the feeding flock could not have been detected through smell as the bird orientated with rather than against the wind.

The reaction distances we measured were all within the possible visual limits according to the earth curvature limitations (Figure 5). The proximity of several reaction distances to the maximum theoretical distance of visibility suggests that gannets have visual abilities close to the physical possible limits based on the earth’s curvature. From an evolutionary perspective, such high visual abilities would have been selected for in these wide open range foragers.

**Detection versus reaction**

We identified the reaction of seabirds toward predator aggregations as a clear change in behavior (in speed and/or direction). The method identified behaviorally consistent breaking points in trajectories, so the reaction points were determined objectively. The derived results were all visually convincing (Figure 1). These points relate to the decision making of birds to react by changing their movements, but they do not necessarily correspond to the point where the bird detected the aggregation. Indeed, a bird that detected a predator aggregation can decide to go straight toward it and join it, to come closer before deciding to go or not, or to not go at all to join the aggregation. First of all, the internal state of an individual (such as hunger) necessarily influences its decision making, but because we studied birds that were leaving the colony after spending some time on the nest and feeding their chicks, we assume them all to be highly motivated to find food. Other processes of decision making that might have influenced our study birds include the search for complementary information (e.g., whether predators in the aggregation were feeding or whether dolphins were present) or the choice between various detected zones. As a consequence, a lag time could exist between the detection of an aggregation and the decision made by the bird to go toward it. The reaction distances we measured could, therefore, be shorter than the detection distance, as it is most probably the case for the distance of less than 1 km that we measured as a reaction to an aggregation with 300 gannets (Figure 3b). In the particular scenario of gannets sitting on
the sea surface and responding to flocks of conspecifics, we measured reaction distances largely smaller than the theoretical distance of visibility (Figure 3a). Assuming that the detection abilities of Cape gannets would be high (see The detection capabilities of Cape gannets), these measures might reflect the behavior of birds that detected an aggregation, approached it, and landed on the water closer to it before actually joining it. In addition, the reaction distances were spread toward lower values when the birds reacted to rafts (Figure 3c,d) than when they reacted to flocks (Figure 3a,b). This suggests that a lag in time between reaction and detection is more common in the first case: as rafts would not necessarily constitute a foraging cue, the decision making to go and join them can be more flexible. However, flocks might constitute a better cue and thus be more attractive to foragers, so that once a flock is detected, it would more readily prompt an immediate reaction of the bird that will directly go toward it. As a consequence, the actual detection capabilities of Cape gannets are probably better estimated on the panel (b) of the Figure 3. Besides, it is also possible that some study birds neglected to react to some aggregations they had detected.

Looking for prey, a forager must first locate prey, then it can decide to go toward the identified location, and only once the location is reached, it can start to forage. The whole process thus comprises several steps, from detection to movement reaction, to eventually foraging. Considering the large areas over which seabirds forage, the steps involved are probably initiated at different spatial and temporal scales. As a consequence, the reaction related to the decision of a forager to orientate toward a detected patch of prey (as defined in our study) most probably occur before (and from a larger distance) than the reaction related to the start of foraging (as defined in Bodey et al. 2014). By not considering the processes in decision making (involved between detection and reaction), but measuring the reaction distances from which foragers decide to move toward predator aggregations, our study provides information on the implementation and the use of local enhancement in foraging seabirds. Further studies could consider seabirds’ visibility in different weather conditions or the use of calls to maintain the cohesion between individuals at sea.

**Reaction distances and their variation with the size of an aggregation**

We measured reaction distances that increased with the size of predator aggregations, which supports the hypothesis that larger aggregations can be detected from a larger distance (Vine 1973; Haney et al. 1992). For small aggregations (<50 gannets), distances were mostly less than 10 km, which corresponds to the recruitment distance estimated empirically by Haney et al. (1992). However, we measured reaction distances of 20 to almost 40 km for larger aggregations (100–150 gannets). These distances correspond to the distance at which albatrosses could respond to olfactory cues (Nevitt et al. 2008), which are not limited by the curvature of the earth and can thus potentially be detected over larger distances. We suggest that gannets would use their vision and benefit from gaining height to detect predator aggregations from such a large distance. Detection would in all likelihood be enhanced by the contrasting plumage of gannets on the seascape.

Theoretical studies based on visual acuity suggested that detection abilities would increase and reach an asymptote with the size of an aggregation (Vine 1973). Although our results show an increase in reaction distances with the size of predator aggregations, they do not show an asymptotic relationship. This could be induced by the small number of observations with large aggregations that we collected, or it could reflect the variation in empirical observations compared with theoretical models. Several processes, such as decision making preceding the reaction distances that we measured or variations in visibility due to weather, could distort the relationship calculated from theoretical detection abilities.

**The use of predators to locate prey**

Our results show that the use of predator aggregations to locate inconspicuous prey results in a major increase of the detection distances. Assuming that a patch of prey would be detectable from 2 km, the presence of a group of gannets feeding on such a patch of prey results in an increase of its detection distance ranging from +200% up to +1650% (considering 20 gannets detectable from 6 km and 150 gannets detectable from 35 km, respectively). Another study based on the same data set and with similar methodology showed that the time to find food was reduced by 50% when the foragers used flying conspecifics (single or in small group) to orientate toward a patch of food (Thiebault et al. forthcoming). All of the 15 individuals that managed to feed on natural prey within the observation time (~1h30min of video record from the beginning of the foraging trip) used one or both of the mechanisms described in these 2 papers to locate prey. In addition, we observed 11 of the remaining 17 individuals modifying their movement pattern to join a raft or a flock as defined in this article or using flying conspecifics as a cue (Thiebault et al. forthcoming) during their search for prey. The prevalence of interactions with conspecifics, together with the resulting significant improvement in foraging efficiency, suggests that using conspecifics as cues to locate prey is an important mechanism in Cape gannets. As a consequence, congregating in high densities might be crucial for seabird foraging efficiency. Breeding in colonies might not only result in a local prey depletion due to competition (Lewis et al. 2001) but could also constitute a requirement for breeders to maintain high foraging efficiency throughout the whole season.

Furthermore, other predator species feeding on the same prey could contribute to an increased detection distance through similar mechanisms. Underwater predators such as marine mammals could potentially locate prey more easily (being in the same environment than the prey) and thus play a specific role in instigating feeding events. A study in the Azores Islands showed that short-beaked Common dolphins *Delphinus delphis* initiated the formation of multispecies aggregations feeding on fish schools (Chua and Grosvalet 2001). Similarly in South Africa, long-beaked Common dolphins *Delphinus capensis* are often observed to initiate foraging events during the sardine run, suggesting that they are responsible for driving the prey from deep to shallow waters, making them accessible to other predator species (Sarano F, personal communication). Cape gannets are distributed in close association with dolphins along the east coast of South Africa and have been observed following them while foraging (O’Donoghue et al. 2010). In another system, northern gannets developed a tight association with whales, suggesting that they use whales as a cue for prey availability (Davoren et al. 2010). The predatory guild might, therefore, constitute a system as a whole that is essential to ensure effective foraging in gannets.

**Foraging activity in relation to aggregation size**

Our data showed that the number of predators aggregated on a patch would not only influence the detection distance of the patch but would also influence the foraging activity of the birds once they have joined the aggregation. We showed that the foraging activity...
(measured both as the number and frequency of dives) increased with the number of conspecifics aggregated up to a threshold and then decreased for very large aggregations. It is, however, difficult to know if diving more was beneficial (more dives = more prey caught) or whether more dives were associated with difficulty in capturing prey. Because foraging gannets are attracted to predator aggregations (Tremblay et al. 2014), and according to in situ video observations of gannets showing that foraging in groups enhances prey capture rates (Thiebault A, Tremblay Y, personal communication), we suspect that these aggregations are largely beneficial. Furthermore, a higher frequency of dives probably means better foraging condition, which corroborates the notion that a medium to large aggregation (~50–200 gannets) would be beneficial for foraging gannets. However, very large predator aggregations may not relate to good foraging conditions. We observed one bird joining a very large aggregation (the largest we observed, ~300 gannets) but performing few dives (5 within 17 min) while at the foraging site. Seabirds feeding on ephemeral patchy resources, such as gannets on pelagic schooling fish, may form ephemeral feeding flocks (Porter and Sealy 1981, 1982; Haney et al. 1992). We, therefore, suspect that this study bird reached an aggregation that was about to vanish, having already attracted many birds. This gannet might have just arrived too late to take advantage of the school of prey. We recorded the behavior of another bird that might also be explained by the ephemeral nature of predator aggregations on patches of prey. This study bird reacted to a large aggregation of conspecifics (~150 gannets) that were all sitting on the water when the bird reached it. The study bird did not join this raft of conspecifics but went to join a smaller aggregation (10 gannets) on another foraging site where it actually dived. Although the first aggregation might have been about to vanish, the study bird decided to join another detected aggregation that was smaller and then potentially at the beginning of the exploitation of the patch. Because the number of foragers on a patch of food progressively increases in time, small aggregations might be more attractive to individual foragers as large aggregations could be aggregations about to vanish. Processes responsible for vanishing aggregations are unclear but could result from the patch of prey being depleted or escaping to depth that render them difficult to catch for aerial predators such as gannets.

Except for one instance, the presence of other predator species, primarily dolphins but also other seabird species, was associated with increased diving activity. Multispecies feeding associations have been suggested to facilitate the foraging ability of seabirds (Chilton and Sealy 1987; Hodges and Woehler 1993; Camphuysen and Webb 1999; Chia and Grosvalet 2001). In contrast, foraging flocks can also generate competition and interferences between foragers (Maniscalco et al. 2001; Davoren et al. 2003b). Consequently, foraging associations at sea produce nonrandom associations between individuals and species (O’Driscoll et al. 1998). The foraging flocks in this study consisted almost exclusively of conspecifics, with larger flocks systematically including dolphins as well, which is consistent with previous findings (Au and Pitman 1986). The systematic presence of dolphins with larger flocks supports the hypothesis that underwater predators allow feeding aggregations to last longer (Harrison et al. 1991; Oro 1995; Bräger 1998). By keeping prey accessible to gannets, dolphins allow for a longer recruitment time and the formation of larger aggregations of gannets. Whether or not these aggregations exacerbate competition remains to be demonstrated, but the frequent observation of multispecies feeding groups suggests such associations to be beneficial (Quéroil et al. 2008). Cape gannets (O’Donoghue et al. 2010), northern gannets (Camphuysen and Webb 1999), and Australasian gannets (Vaughan et al. 2007; Machovsky-Capuška et al. 2011) are commonly observed foraging with dolphins. In addition, a recent modeling study showed that multispecies associations allow for a better disruption of the schools of fish through high-frequency attacks (Leti et al. 2014). We, therefore, suggest that foraging aggregations of gannets and dolphins are likely beneficial to foraging individuals.

CONCLUSION

Our study shows that larger predator aggregations trigger larger reaction distances than smaller ones, supporting the hypothesis that they enhance food detectability (Haney et al. 1992; Buckley 1997; Camphuysen and Webb 1999). In addition, we showed that predator aggregations on a patch of food not only inform about the presence of prey, but the size of the aggregation entails some information about feeding opportunities with large ones being associated with increased foraging activity. Overall, our study supports the use and advantages of local enhancement in foraging seabirds, suggesting that it constitutes a crucial aspect of their foraging behavior. As such, future analysis and modeling of seabird movements might need to account for social aspects. In addition, the classic view that foraging seabirds negatively impact on each other through competition needs to be revised or at least interpreted with caution, as local enhancement requires the presence of a large number of other predators to be effective. The balance between the benefits from local enhancement and the costs from competition needs further investigation, as this has profound consequences in terms of conservation. Indeed, extrapolating from our results, a diverse guild of numerically abundant marine predators in an ecosystem could be instrumental in ensuring resilience against fluctuating and unpredictable prey resources.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.behavco. oxfordjournals.org/

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