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RESEARCH ARTICLE

From colony to first patch: Processes of prey searching and social information in Cape Gannets

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ABSTRACT

Seabirds forage in a highly dynamic environment and prey on fish schools that are patchily distributed. Colonially breeding seabirds regularly commute back and forth from their colony to foraging areas and need to acquire information on the location of food before and/or during each foraging trip. The use of conspecifics as cues to locate prey has long been debated, and although the hypothesis was backed up by modeling studies, observations have been contradictory. We deployed GPS devices coupled with micro video cameras on Cape Gannets to observe the social context of foraging seabirds and the influence of conspecifics on the movement of individuals. The Cape Gannets reached their first patch using a succession of flights interrupted by stops on the water, during which the birds were mainly preening. During flight, the birds reacted to conspecifics by changing direction, either flying in the opposite direction of conspecifics that were flying toward the colony or following conspecifics outward. The time to reach the first patch was significantly reduced (by half) when the birds reacted to conspecifics in these different ways, compared with the birds that did not react. The use of conspecifics flying toward the colony to find food is consistent with the hypothesis that colonies can act as a focal place for information transfer, with foragers updating their flying direction when they detect conspecifics flying toward the colony. The fine-scale reaction of seabirds toward each other at sea, and the associated improved foraging efficiency, as well as the division of trips into a succession of flights, constitute elements that indicate the existence and the use of a structured network among foraging Cape Gannets.

Keywords: biologging, camera, central place forager, GPS, information center, network foraging, seabirds, tracking

De la colonie au premier banc de poissons: Les processus de recherche de proies et d'information sociale chez *Morus capensis*

RÉSUMÉ

Les oiseaux marins se nourrissent dans un environnement fortement dynamique et sur des proies agrégées en bancs. Les oiseaux coloniaux font régulièrement des aller-retours entre la colonie et les zones d'alimentation, et doivent alors acquérir de l'information sur la localisation de leurs proies avant et pendant chaque voyage en mer. L'utilisation de congénères comme source d'information pour localiser des proies a longtemps été débattue, et bien que cette hypothèse soit soutenue par des modèles théoriques, les observations empiriques restent contradictoires. Nous avons déployé des GPS et micro-caméras sur des individus de Morus capensis afin d'observer le contexte social de ces oiseaux au cours de leur recherche alimentaire et l'influence de congénères sur le déplacement des individus. Ceux-ci ont rejoint leur première zone d'alimentation par une succession de vols, interrompus par des arrêts sur l'eau durant lesquels ils faisaient principalement leur toilette. En vol, les oiseaux ont réagi à leurs congénères en modifiant leur direction, soit pour aller en direction opposée de congénères qui volaient vers la colonie, soit pour suivre des congénères au large. Le temps pour rejoindre la première zone d'alimentation était significativement réduit (de moitié) pour les oiseaux ayant réagi à leurs congénères de ces différentes manières, comparé aux oiseaux n'ayant pas réagi. L'utilisation de congénères volant vers la colonie pour trouver de la nourriture est en accord avec l'hypothèse de l'utilisation de la colonie comme point central pour l'échange d'information, à partir duquel les individus en recherche de nourriture pourraient ajuster leur direction de vol au fur et à mesure qu'ils rencontrent des congénères de retour vers la colonie. Les réactions à fine échelle entre oiseaux en mer, associées à l'amélioration de leur efficacité pour trouver de la nourriture, ainsi que le découpage du trajet en vols successifs, constituent des éléments en faveur de

l'existence et de l'utilisation d'un réseau structuré de recherche alimentaire chez M. capensis.

Mots-clés: biologging, caméra, centre d'information, GPS, oiseaux marins, prédateur à place centrale, recherche alimentaire en réseau, suivi

INTRODUCTION

Colonial breeding is particularly common in seabirds (Danchin and Wagner 1997), which often prey on schooling fish that are aggregated in patches that move constantly in space (Russell et al. 1992, Fauchald et al. 2000) and are difficult to locate from the air. In this environment, central-place foragers such as colonial breeders cope with specific constraints. The distance between their breeding location and foraging areas forces them to regularly lose contact with prey in order to return to the colony to feed their offspring. Hence, colonial seabirds need to acquire information on the location of food before and/or during each foraging trip. The use of other predators by means of information transfer on the location of food has been proposed as a way to deal with this challenge (Valone 1989, Pöysä 1992, Barta and Szép 1994, Nevitt and Veit 1999). The importance of such information transfer for the foraging efficiency of individuals may constitute a mechanism to explain the establishment and maintenance of colonial breeding (Ward and Zahavi 1973, Buckley 1997).

In a dynamic environment, animals' constant gathering of information is crucial for reducing uncertainty and for optimizing behavioral decisions such as choice of habitat or mate, avoidance of danger, and individual foraging choices (Danchin et al. 2004, Dall et al. 2005). An animal can acquire information about its environment either by directly interacting with it ("personal information") or by monitoring the behavior of other individuals ("social information") (Danchin et al. 2004). Social information has been defined as "information extracted from interactions with, or observations of, other organisms" (Wagner and Danchin 2010). The information can be deliberately transmitted as a signal or inadvertently produced and used as a cue by surrounding individuals (Danchin et al. 2004, Wagner and Danchin 2010). In a foraging context, the information acquired reduces uncertainties about environmental or social conditions and should thus increase the animal's foraging efficiency and, in turn, its fitness (Goodale et al. 2010).

Several mechanisms for tranferring information on the location of food around a colony have been proposed in the literature. Karl von Frisch (1950) was the first to describe a direct transfer of information between foraging bees by means of a dancing language at the hive. For seabirds, the "information center hypothesis" (Ward and Zahavi 1973) stipulates that colonies serve as information centers where unsuccessful individuals learn from successful ones and follow them to productive areas. Greene (1987) described a more indirect transfer of information whereby foragers track the direction from which successful individuals return. Alternatively, the colony might serve as a recruitment center to which individuals that have found food return in order to inform conspecifics and recruit them to forage as a group (Richner and Heeb 1995). Individuals would thereby benefit from the group—by means of group foraging strategies or antipredation mechanisms, for example. For this to occur, the forager has to return to the colony, which makes the theory unconvincing for gannets that forage on multiple patches over an extensive area during a single foraging trip. More recent studies have questioned the function of a colony as an information center, given that numerous individuals are often coming and going in many directions, thus drowning the potential information (Burger 1997). Besides, Burger (1997) observed that many successful foragers began their foraging trip with a stopover in close proximity to the colony and proposed that foragers could track returning individuals more effectively within this "information halo." It is common to see colonially breeding birds sitting on the water near their colony (Burger 1997, Davoren et al. 2003, Racine et al. 2012, Machovsky-Capuska et al. 2014). In Guanay Cormorants (*Phalacrocorax bougainvillii*), these rafts of individuals have been shown to directly indicate the direction to take from the colony to find a patch of food (Weimerskirch et al. 2010). Recently, Machovsky-Capuska et al. (2014) showed that Australasian Gannets (*Morus serrator*) used these rafts to track the direction from which conspecifics returned when leaving the colony to forage, suggesting that information transfer occurs at these rafts.

Farther from land, seabirds may use various mechanisms to detect prey at sea. At a large scale, they can use prior experience (Davoren et al. 2003), oceanographic features (Schneider 1982), or odor cues (Nevitt 2008) to orient themselves toward a productive area. At a smaller scale, seabirds can observe and use conspecifics as cues to detect inconspicuous prey (Nevitt and Veit 1999, Silverman et al. 2004). The establishment of a foraging network (Wittenberger and Hunt 1985) could enable a rapid transfer of information between connected individuals. As soon as an individual of the network detects prey, it might prompt a chain reaction of surrounding individuals within an increasing range, leading to a rapid aggregation. Then, the aggregation of feeding predators on a patch of food can constitute a cue to the presence of inconspicuous prey, a mechanism known as "local enhancement" (Hoff-

FIGURE 1. Changeover in a Cape Gannet breeding pair. While its partner is settling on the nest, the bird in sky-pointing position is about to leave on a foraging trip. Photo credit: Andréa Thiebault

man et al. 1981, Harrison et al. 1991, Camphuysen and Webb 1999). Among these mechanisms, the ones involving the use of conspecifics might play a major role, especially where animals are congregated in high densities, such as around colonies.

The use of social information for locating food around a colony is highly controversial (Mock et al. 1988, Richner and Heeb 1995, Bijleveld et al. 2010) but is supported by theoretical and modeling studies (Waltz 1982, Valone 1989, Deygout et al. 2010). In particular, game-theory models predict that using social information to find food is an evolutionarily stable strategy for colonial foragers (Barta and Szép 1994, Barta and Giraldeau 2001). Nonetheless, empirical observations that tested the hypothesis are contradictory. Some studies found proof for social information through a range of mechanisms (von Frisch 1950, Brown 1986, Waltz 1987, Burger 1997, Prevot-Julliard and Lebreton 1999, Weimerskirch et al. 2010, Machovsky-Capuska et al. 2014) whereas others rejected it (Mock et al. 1988, Davoren et al. 2003, Mariette and Griffith 2013). Above all, these controversies highlight the difficulties associated with accurately observing and measuring the interactions between individuals and the consequences on their foraging efficiencies (Burger 1984, Galef and Giraldeau 2001, Racine et al. 2012).

To observe seabirds in the vast marine environment and study their at-sea behavior is challenging. Although it is now possible, and relatively easy, to measure seabirds' displacement using global positioning system (GPS) devices (Wilson et al. 2007), it remains difficult to relate their movements to their ecological context. For example, what happens between the departure from the colony and the arrival at the first foraging zone has never been described in detail for any seabird species. We studied Cape Gannets (*Morus capensis* Lichtenstein, 1823; Figure 1), seabirds that breed in large colonies (Crawford et al. 2007) and naturally feed on pelagic fish schools, mainly sardines (*Sardinops sagax*) and anchovies (*Engraulis encrasicolus*) (Batchelor and Ross 1984). Like other gannet species, they capture prey by plunge-diving, visually targeting their prey from the air (Lee and Reddish 1981, Ropert-Coudert et al. 2004b, Machovsky-Capuska et al. 2012). Cape Gannets are active only during daytime (Ropert-Coudert et al. 2004a), and because they do not have external nostrils (necessary for olfaction), vision is probably the main sense involved in detection of prey. We deployed animal-borne video cameras on foraging Cape Gannets in order to directly observe the behavior of these birds at sea and their interactions with conspecifics (Tremblay et al. 2014). We hypothesized that if information transfer occurred, significant behavioral responses to conspecifics would be observed through a concurrent analysis of video images and GPS records. Our objectives here are to (1) describe the first prey-searching phase of a foraging trip, when the animal leaves the colony until it reaches a foraging zone; and (2) assess the prevalence of information transfer between individuals and evaluate its importance.

METHODS

Data Collection

Thirty-six Cape Gannets were fitted with GPS units and micro video recorders at Bird Island (Algoa Bay, South Africa; 33°50′26.6′′S, 26°17′14.5′′E) between December 8 and January 22 during the breeding season of 2010–2011. The birds were captured near their nest when about to depart to sea after a changeover with their partners (Figure 1). Only 1 adult per nest was equipped for 1 foraging trip, while the partner stayed at the nest with the chick. We deployed 2 types of devices that were attached together as 1 unit (Figure 2): a GPS logger (i-GotU GT-600, Mobile Action Technology, Taipei, Taiwan; 43 × 40 × 12 mm, 36 g) to record the movement path, and a micro video camera (Camsports Nano; Camsports, Estrablin, France; 68 × 19 mm, 22 g) to observe the surroundings of the animal. The

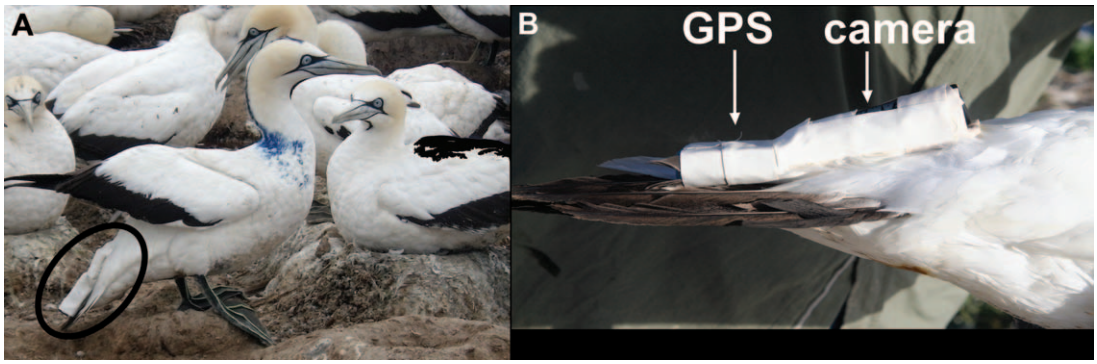

FIGURE 2. Photographs of the devices attached to Cape Gannets. (**A**) The devices are located on the lower-back and tail feathers of the bird. (**B**) A closer view, showing both the GPS device and the micro video camera.

GPS loggers were set to record a geographic position every 5 s when the animal moved faster than 10 km h^{-1}, and every 10 s otherwise. The video cameras recorded at a resolution of 736 × 480 pixels, at 25 frames s^{-1}, with a 74° lens angle, for a maximum of 90 min (due to limited battery capacity). Microphones in the video camera loggers also recorded sound. The handling process lasted <8 min and consisted of taking standard biometric measurements of the bird (these data were not used in the present study, except for body mass, which was measured using a spring balance [Pesola, Baar, Switzerland; precision 50 g]) and attaching the devices with adhesive tape (Tesa, Hamburg, Germany) to the lower back and tail feathers (Figure 2). Just before the bird was released, a handheld GPS was placed in front of the camera lens so that Greenwich Mean Time was recorded. The videos could thus be accurately synchronized to movement data using the satellite-derived time. The total mass attached to a bird, including both devices and tape, was 70–75 g, corresponding to 2.3–3.0% of the bird's body mass (2,400–3,100 g), which is within acceptable limits (Phillips et al. 2003). The loggers were attached to the birds' lower backs in such a way that potential drag due to modification of the birds' body shape was minimized (Culik et al. 1994, Vandenabeele et al. 2012). After release, the nests were monitored regularly (every hour from sunrise to sunset), the study birds were recaptured soon after their return to the colony, and the devices were then retrieved.

Instrument Effects

The potential effects of loggers on the behavior of study birds were minimized by keeping the mass as low as possible and optimizing their shape (Culik et al. 1994, Phillips et al. 2003, Vandenabeele et al. 2012). Nonetheless, we tested for a possible effect of the devices on several aspects of the behavior of the study birds. First of all, we checked that the birds were able to get food during their foraging trips by comparing their mass before and after a trip at sea. Second, on the basis of video footage, we compared the behavior of study birds in groups with their surrounding nonequipped conspecifics. Lastly, we compared the foraging-trip duration of equipped birds with that of nonequipped ones. Foraging-trip duration has been shown to be a reliable proxy for foraging effort in Cape Gannets (Pichegru et al. 2007, Mullers et al. 2009) and is regularly used to assess the effects of tagging on seabirds (Wilson et al. 1986, Phillips et al. 2003, Kidawa et al. 2012). To do so, we monitored the attendance of both partners (every hour from sunrise to sunset) on 14 independent nests where chicks were reared during 10 days. We then compared the pooled foraging-trip duration of the study birds when equipped with the pooled foraging-trip duration of nonequipped birds on control nests.

Data Processing

Video data. Data were treated in MATLAB (R2010a; MathWorks, Natick, Massachusetts, USA). The video footage was analyzed frame-by-frame, and the events of interest were visually flagged using a purpose-built video event recorder. We then located each event by assigning it to the closest point in time on the tracking data (interpolated at 5-s intervals using a Bézier curve with $\mu = 0.1$; Tremblay et al. 2006). Figure 3 illustrates the behavioral events and observations analyzed in the present study.

Behavioral events of the equipped animals included taking off, sea-landing, and diving, from which we inferred 3 activities: flying, sitting on water, and diving. We defined a "stop" as a phase of sitting on the water during which we observed 2 types of comfort behaviors (Ainley 1974). A "washing" behavior was identified by vigorous movements supplemented with typical "splash" sounds, and "preening" was the use of the beak to quietly clean and rearrange feathers. The birds typically landed on the water soon after leaving the breeding colony, so we defined this first stop as a "near-colony raft" (NC-raft). We called "flight" a flying phase, either between 2 stops or between a stop and the first dive. At a larger scale, the "NC-raft-to-patch phase" is

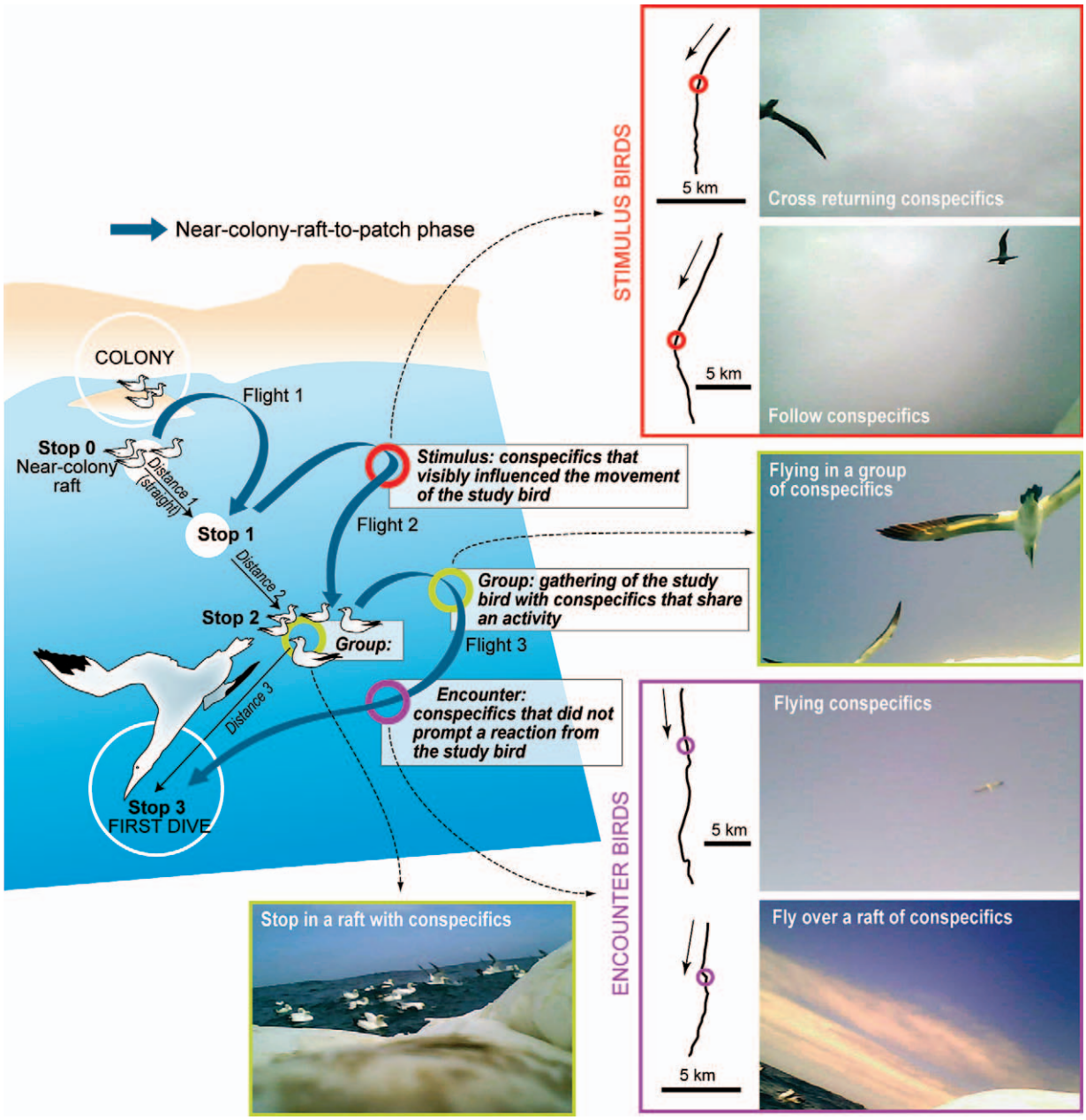

FIGURE 3. Illustration of the near-colony-raft-to-patch phase with stops and flights, as well as the various types of observations of conspecifics in the surroundings of focal Cape Gannets. Color circles correspond to the localization on the trajectory of the video observations.

defined as between the NC-raft and the first dive. Because Cape Gannets are plunge-diving seabirds, we assumed that the first dives corresponded to the first prey-capture attempt.

The video data provided information on the surroundings of the study bird, including conspecifics, other seabird species, dolphins, and boats. For the present study, we focused only on the presence of conspecifics (which featured in 92% of all frames containing surrounding events), from which we defined different types of observations (Figure 3). We use the term "stimulus bird" to refer to a conspecific that visibly influenced the movement of the study bird. A stimulus bird could be observed flying toward the colony, whereupon the study bird flew in the opposite direction (first case), or flying in any given direction, whereupon the study bird immediately followed suit (second case). In the first case, the observation could be connected to the hypothesized

transfer of information at or around a colony (e.g., the information center hypothesis); in the second case, the observation could be connected to the hypothesis of a foraging network among seabirds. In both cases, the stimulus birds prompted a reaction by the study birds, so we studied them as a potential source of information used by foraging seabirds. The flying direction of conspecifics was assessed using both video and GPS data recorded simultaneously (details are given below). We use the term "encounter bird" to refer to a conspecific that did not appear to prompt an immediate reaction from the study bird, as inferred from their trajectory. Examples include the study bird flying over a raft of conspecifics but not joining them, or flying conspecifics not altering the trajectory of the study bird. We call a gathering of the study bird with conspecifics that share an activity (resting, preening, flying, or foraging) a "group." To avoid a potential overestimation in conspecific-driven responses in the close surroundings of the colony (where numerous birds are coming and going in every direction), we considered these observations of conspecifics only when they occurred >2 km from the colony (similar results were obtained with a threshold of 1 or 3 km). This threshold is arbitrary and the results are not sensitive to it (at least between 1 and 3 km), but it is important because we believe that observations close to the colony could be misinterpreted.

To assess the foraging efficiency of birds, we measured the time they spent to find their first patch of food (from the NC-raft). This time is commonly used as a referential variable for studying predation, such as for studies on the optimal foraging theory (MacArthur and Pianka 1966, Charnov 1976) or on the functional response (Holling 1959). We assume the measure of time to be inversely related to the foraging efficiency of these birds.

GPS data. Trajectories were considered as a succession of various portions, such as flights between 2 stops or between the NC-raft and the first dive (the near-colony-raft-to-patch phase). For each portion, we calculated the duration, the straight-line distance, the total distance traveled (cumulated distance calculated between all successive points in the track), and the straightness index (the straight-line distance divided by the total distance traveled; Batschelet 1981).

In addition, we identified the first large turn in the NC-raft-to-patch portion of the trajectories. To do so, the trajectories were split into fine-scale segments of uniform characteristics so that the switch from one segment to another represented the decision by the study animal to change its displacement pattern (Thiebault and Tremblay 2013). The azimuths of all segments were calculated, as well as their minimum successive differences (0–180°), and marked changes in azimuth (changes >45°) were flagged (similar results were found using a threshold of 35°, 40°, or 50°). The first marked change identified from the colony was referred to as the "first large turn."

For each trajectory, we measured the straight-line azimuth from the colony to the NC-raft, then from the NC-raft to the first large turn and to the first dive. All azimuths were computed in the great-circle sense, as a horizontal angle (0–360°) measured clockwise from north.

Concurrent analysis of video and GPS data. GPS data were used to locate events observed from the video record as well as to detect behavioral reactions of the study birds to the observed events in the video. After time synchronization, video images and GPS trajectories were visualized simultaneously using a purpose-built interface in MATLAB. The synchronized observation of both study-bird trajectory and images of the surroundings allowed detection of whether conspecifics influenced the movement of the study bird (as illustrated in Figure 3). The flying direction of the study bird, observed from its trajectory, in addition to the movement of conspecifics on the video (e.g., flying from the left to the right of the field of vision) allowed us to assess the flying direction of conspecifics, in particular when conspecifics were flying toward the colony (Supplemental Material Video 1 and Supplemental Material Video 2).

Statistics

All statistics were considered significant at the 5% level. Means are given ± SD. Circular data were statistically analyzed in MATLAB using the CircStat toolbox (Berens 2009). Statistical tests were used to compare the values of variables in different groups. After testing and rejecting the hypothesis that the distribution of variables was normal (Jarque-Bera test), we compared the distribution in different groups with the nonparametric Wilcoxon rank-sum test.

In order to compare the duration of flights when the birds were flying alone or with a group of conspecifics, we needed to account for pseudoreplication due to repeated observations by the same individuals. We performed two-sample *t*-tests to compare the distribution of flights with or without conspecifics, using only 1 randomly selected flight per bird in each category (alone or in a group), and the process was bootstrapped 500 times. We then calculated the percentage of tests resulting in a significant difference in the mean and variance of the distributions.

RESULTS

We successfully collected concurrent video and GPS data on 35 birds. We recorded 47 hr 46 min 40 s of footage, corresponding to 172,000 frames. Six of the 35 birds were not used in the analysis because the video recordings stopped prior to completion of a flight portion (subsequent to NC-raft) or because the lens was obstructed by feathers.

TABLE 1. Summary statistics for Cape Gannets at the first stop ("near-colony raft"; observations from 35 birds) compared with the following stops along the way (observations from 29 birds) (n = number of observations).

	Near-colony raft			Stops along the way		
	n	Mean ± SD	Minimum–maximum	n	Mean ± SD	Minimum–maximum
Distance from colony (km)	35	0.6 ± 0.2	0.4–1.4	43	10.3 ± 6.1	0.8–23.9
Duration (min)	34	10.9 ± 11.4	0.4–59	43	7.3 ± 5.0	0.6–21
Duration of washing (%)	34	65 ± 24	11–99	19	45 ± 30	9–95
Duration of preening (%)	23	35 ± 18	8–77	36	72 ± 26	11–99
Number of associated conspecifics (when seen)	18	27 ± 17	3–60	13	4 ± 3	1–10

Thus, 29 study birds provided observations for ≥1 flight (subsequent to NC-raft), and the NC-raft-to-patch phase was recorded completely for 12 birds.

Instrument Effects

Equipped birds gained, on average, 156 ± 181 g (n = 33) during their foraging trip. All equipped birds joined groups of conspecifics and engaged in the same activity as surrounding nonequipped birds, either sitting on the water, flying, or foraging. For the period during which we monitored control nests, the foraging-trip duration averaged 19 ± 8 hr (median = 23, range: 6–26, n = 12) and 18 ± 12 hr (median = 17, range: 3–76, n = 156) in equipped and nonequipped birds, respectively. The distributions of trip duration in these 2 groups were not significantly different (Wilcoxon rank-sum test, $P = 0.26$).

The near-colony raft. The summary statistics for the NC-rafts (n = 35; 1 for each bird) are shown in Table 1. Between 30 s and 2.8 min (1 ± 0.5 min) after leaving the colony, all deployed birds landed on the water at an average distance of 0.6 km from the colony. The time spent in the NC-rafts lasted, on average, 11 min and was exclusively devoted to comfort behavior: All study birds started by washing themselves, after which some commenced preening. In addition, 49% of the birds took off within a short time to land again after a few seconds and repeated this procedure 4 ± 3 times (range: 2–14 times). In 51% of the cases, the study birds were seen associated with a group of 3 to 60 conspecifics (27, on average). When the study bird was in a group, comfort behavior was also observed in surrounding conspecifics. Neither the presence of conspecifics nor the size of the group was correlated with the time spent by the study birds in these rafts (respectively: two-sample Kolmogorov-Smirnoff test, $k = 0.26$, $P = 0.56$ and test for linear correlation, $r = 0.19$, $P = 0.27$).

From the Near-colony Raft to the First Dive

After leaving the NC-raft, the birds initiated varying numbers of flights and stops on the water before reaching a foraging area where the first dive occurred (Figure 3). Ninety percent of study birds (26 of 29) landed on the water at least once before reaching a foraging area. Table 2 shows trajectory characteristics as well as video observations for the complete near-colony-raft-to-patch phase (n = 12) and for the flights (n = 73 flights from 29 birds). Table 1 shows summary statistics at the stops (n = 51 stops from 29 birds).

The flights lasted 1 to 35 min, during which the birds covered a distance of 1–28 km. Most of the flights were straight (the average straightness index value was close to 1). During >60% of the flights (45 of 73), conspecifics were

TABLE 2. Trajectory characteristics and video observations for the colony-to-patch phase (n = 12 observations from 12 birds) and for the flights (n = 73 observations from 29 birds) of Cape Gannets.

	Near-colony-raft-to-patch phase			Flights		
	n	Mean ± SD	Minimum–maximum	n	Mean ± SD	Minimum–maximum
Trajectory characteristics						
Duration (min)	12	29 ± 14	9–59	73	9 ± 7	1–35
Straight-line distance (km)	12	15 ± 9	3–38	73	6 ± 5	1–28
Distance traveled (km)	12	18 ± 10	5–42	73	7 ± 6	1–31
Straightness index	12	0.8 ± 0.1	0.6–1	73	0.9 ± 0.1	0.6–1
Observations of conspecifics						
Number of interactions (when seen)	9	–	1–4	20	–	1–4
Number of encounters (when seen)	6	–	1–9	15	–	1–7
Number of individuals in a flying group (when seen)	8	–	1–3	27	–	1–6

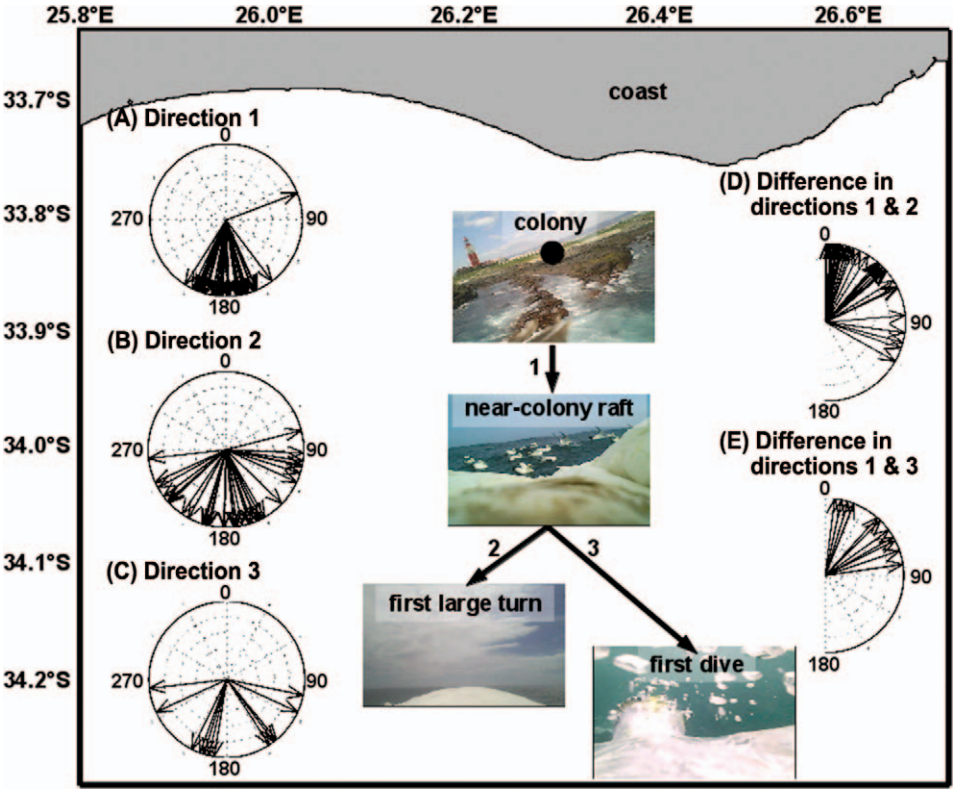

FIGURE 4. Comparison of the azimuth of the near-colony raft (NC-raft) with the following starting direction and the first dive in Cape Gannets' foraging trip. (**A**) Direction from the colony to the NC-raft ($n = 35$). (**B**) Direction from the NC-raft to the first large turn ($n = 35$). (**C**) Direction from the NC-raft to the first dive ($n = 12$). (**D**) Change in direction from the NC-raft to the first large turn ($n = 35$). (**E**) Change in direction from the NC-raft to the first dive ($n = 12$).

observed (Figure 3): 1–4 stimulus birds were observed during 20 flights, group flying (with 1–6 birds) was observed during 27 flights, and 1–7 encounter birds were observed in 15 flights.

The stops on the water lasted 0.6–21 min, during which the birds were mainly preening. For 30% of the stops (13 of 43), we observed 1–10 conspecifics in the surroundings of the bird, and neither the presence of conspecifics nor the size of the group was correlated with the time spent by the study birds in these rafts (respectively: Wilcoxon rank-sum test, $P = 0.16$ and test for linear correlation, $r = 0.04$, $P = 0.78$). However, the distance from the colony of the stops with a group of conspecifics was significantly shorter than that of the stops without conspecifics (8 and 12 km, on average, respectively; Wilcoxon rank-sum test, $P = 0.04$).

On average, the first dive occurred after 29 ± 14 min (ranging from 9 min to 1 hr), at a distance of about 15 ± 9 km from the NC-raft (3–38 km). The trajectories from the NC-raft to the first dive were generally straight, as suggested by the small difference in the straight-line distance and the distance traveled, which resulted in a straightness index value close to 1.

Directions Taken by the Birds

The azimuths taken by Cape Gannets from the colony were always oriented to the south (with average directions of 180°, 174°, and 178°, respectively; Figure 4A, 4B, 4C). From the NC-raft, the distribution of directions taken by the birds to search for prey (to the first large turn) was larger than the distribution of directions from the colony to the NC-raft (Figure 4B and 4A, respectively); the standard deviation of distributions doubled (45° and 23°, respectively). Similarly, the distribution of straight-line azimuths from the NC-raft to the first dives was larger than from the colony to the NC-raft (Figure 4C and 4A, respectively), with a doubling of the standard deviation (45° and 23°, respectively). As a consequence, the differences in azimuths between the NC-raft and the following directions were large (Figure 4D, 4E), and no correlation could be found between the direction of the NC-raft and the directions taken by the birds for their foraging trip (i.e. to the first large turn: circular correlation coefficient, $r = 0.16$, $P = 0.43$, $n = 35$; or to the first dive: circular correlation coefficient, $r = 0.45$, $P = 0.12$, $n = 12$).

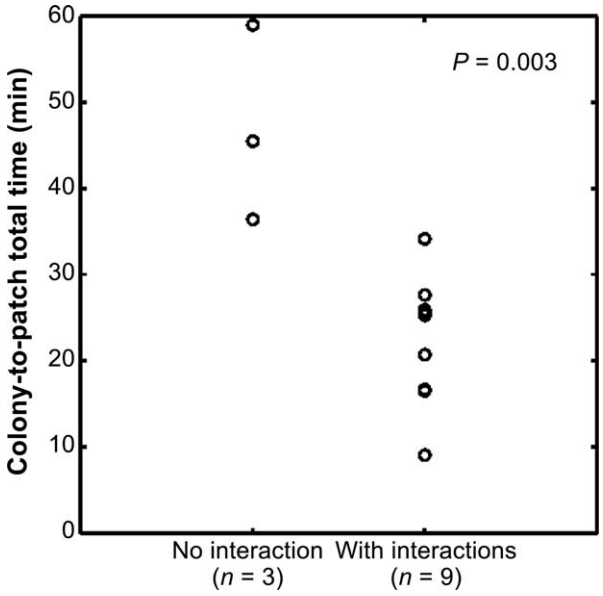

FIGURE 5. Comparison of the colony-to-patch duration between Cape Gannets that had interactions with conspecifics at sea and those that did not. Difference in distributions was tested with a one-sided Kolmogorov-Smirnoff test.

Group Foraging and Information Transfer

We observed 8 of 12 birds (for which the whole NC-raft-to-patch phase was recorded) flying within a group of conspecifics for a part of their way from the NC-raft to the first dive (complete near-colony-raft-to-patch phase recorded). Group flying (with 1 to 6 conspecifics) was observed in 37% of all the flights recorded (27 of 73; Table 2). Flights alone lasted, on average, 7 ± 5 min (range: 1–21 min), whereas flights with a group of conspecifics lasted, on average, 14 ± 8 min (range: 3–35 min). The bootstrapped *t*-test showed that the distributions of the flights' duration with or without conspecifics were significantly different in 98% of the iterations. On average, the flights that were associated with a group of conspecifics were 96% longer in time (range: 36–157%).

In 11 of the 12 birds for which the whole near-colony-raft-to-patch phase was recorded, we observed conspecifics during the recording time. Nine birds reacted to stimulus birds, 1–4 times in a single phase; and for 6 birds, we observed the presence of encounter birds, 1–9 times in a single phase (Table 2). The frequency of reaction to stimulus birds ranged between zero (for birds that did not react to any stimulus birds) to 14 times hr^{-1}, with a mean value of 5 times hr^{-1}. The time spent from the NC-raft to the first dive ranged from 9 to 34 min (22 min, on average) for the birds that reacted to stimulus birds ($n = 9$), whereas it ranged from 36 to 59 min (46 min, on average) for the birds that did not ($n = 3$). When the study birds reacted to stimulus birds along their way, the range of the duration to reach the first foraging patch was significantly smaller (one-sided Kolmogorov-Smirnoff test, $k = 1$, $P = 0.003$), reduced by an average of 50% (Figure 5).

DISCUSSION

Studying the role of conspecifics in the foraging behavior of seabirds is not new (Richner and Heeb 1995, Racine et al. 2012), but individual-level responses have not, to our knowledge, been demonstrated previously. The use of micro video recorders allowed us to observe the presence of conspecifics in a foraging context and to quantify their relative influence on the movement patterns of individuals.

Instrument Effects

The durations of foraging trips of the equipped birds did not differ significantly from those of nonequipped birds, even if the distribution of trip duration in equipped birds showed higher median values. The potential effect of the devices on the foraging behavior of the study birds is unlikely to have influenced our results, at least qualitatively. The mass gain of the birds indicated that they were able to capture prey. In addition, the result showing that the time to find a patch of prey was reduced when birds reacted to stimulus birds was obtained from a comparison between 2 groups of equipped birds. From the video footage, it was clear that equipped birds showed the same behaviors as nonequipped birds. The stops on the water (NC-raft and successive ones) were clearly devoted to washing and preening behavior. Our study birds spent ~30% of their time during the first ~1 hr 30 min of their foraging trip sitting on the water, which is similar to previous observations on the same species (Ropert-Coudert et al. 2004a).

The Use of Stopovers on the Water

When seabirds leave the colony after an extended period on the nest, they need to wash their plumage to remove dirt and potential parasites (Ainley 1974, Clayton 1991). The use of vigorous movements during this behavior also suggests the preparation of muscles and an increase of peripheral circulation before leaving on a foraging trip (Ainley 1974, Viblanc et al. 2011). Stopovers on the water at the onset of a foraging trip have been observed in other seabirds, for example in Common Murres (*Uria aalge*; Burger 1997, Davoren et al. 2003), Ring-billed Gulls (*Larus delawarensis*; Racine et al. 2012), Guanay Cormorants, and Peruvian Boobies (*Sula variegata*; Weimerskirch et al. 2010), and Australasian Gannets (Machovsky-Capuska et al. 2014). We did not find a good match between the colony-to-NC-raft and NC-raft-to-first-dive bearings, nor between the colony-to-NC-raft and NC-raft-to-first-large-turn bearings. We therefore found no support for the "compass-raft hypothesis" previously proposed in Guanay Cormorants (Weimerskirch et al. 2010). Our observations

show that all stops on the water (the NC-raft and the following ones) were devoted to comfort behaviors. In addition to their use for comfort behaviors, the stops on the water could be used to wait for information and look for incoming conspecifics in order to choose a direction to take to forage, as shown in Australasian Gannets (Machovsky-Capuska et al. 2014).

The Prevalence of the Use of Conspecifics

Foraging Cape Gannets reached their foraging sites using a succession of flights and stops on the water, sometimes in small groups and sometimes following or moving in directions opposite those of Cape Gannets flying toward the colony. The reaction of the study birds to the stimulus birds was obvious when both video records and GPS tracks were observed simultaneously (Supplemental Material Video 1 and Supplemental Material Video 2). We observed that study birds reacted, on average, 5 times hr^{-1} to stimulus birds during the searching phase from the colony to the first dive. Given that the camera lens had a limited field of view and a limited resolution, it is likely that our results are an underestimation. Consequently, our results suggest that observing and reacting to conspecifics when searching for food at sea is very common in Cape Gannets, and we suspect that the information acquired is of great importance for their foraging efficiency. Indeed, we also showed that the colony-to-patch time was significantly reduced (by half) when social interactions occurred. Given that the time needed to find the first feeding patch is considered to be inversely correlated with the foraging efficiency, this result suggests that foraging efficiency is increased considerably in a forager-interacting animal compared with a solitary animal. This confirms results obtained theoretically using modeling approaches (Barta and Szép 1994, Barta and Giraldeau 2001, Deygout et al. 2010).

The Colony as a Focal Place for Information Transfer

We observed 2 types of stimulus birds that influenced the foraging behavior of Cape Gannets. The use of conspecifics flying back to the colony to head toward a patch of food is consistent with the hypothesis that colonies can serve as a focal place for information transfer, although we did not study information transfer at the colony per se. The information center hypothesis stipulates that individuals can obtain information at the colony by awaiting the return of successful conspecifics in order to follow them to productive areas (Ward and Zahavi 1973) or by tracking the direction from which successful conspecifics return (Greene 1987). A recent study on the Australasian Gannet, a species closely related to the Cape Gannet, did not find support for a transfer of foraging information between partners at the colony, but they did find support for a transfer of information near the colony, with ~70% of their study birds leaving the NC-raft toward the direction from which conspecifics had just arrived (Machovsky-Capuska et al. 2014). We observed a similar transfer of information farther out at sea, with foraging Cape Gannets adjusting their trajectory to fly in the opposite direction of conspecifics flying toward the colony.

Large numbers of predators aggregate rapidly on a fish shoal (O'Donoghue et al. 2010) and can thus deplete the shoal (or lead to diminished concentrations) in up to 1–2 hr. The short lifespan of a fish shoal once it has been detected by predators requires a quick transfer of information between colonial foragers for it to be reliable. Breeding Cape Gannets are known to perform direct and straight flights on their way back to the colony (Mullers et al. 2009), using tail wind (Adams and Navarro 2005). A sufficiently large food patch, in relation to its distance from the colony (considering the relation between its lifespan and the time required for a forager to reach it), would therefore produce satiated breeding birds that return to the colony and that can be used by foragers leaving the colony to orient themselves toward the given patch of food. Furthermore, assuming that food resources are distributed in hierarchical patches in the marine environment (Russell et al. 1992), birds coming back to the colony might inform conspecifics about the direction of a productive area where several fish shoals could successively surface. Such information transfer is most likely facilitated by the colony that acts as a focal place. This mechanism could be valid within a large range surrounding the colony, with foragers updating their flying direction when they detect conspecifics flying toward the colony.

Arguments in Favor of the Use of a Foraging Network

We observed Cape Gannets reacting to flying conspecifics by following them (the second type of stimulus birds), which supports the hypothesis of a foraging network (Wittenberger and Hunt 1985). Feeding aggregations are assumed to result from an independent accumulation of foragers (Hoffman et al. 1981). The rapid aggregation of seabirds on a patch of food once it has been detected (Haney et al. 1992, O'Donoghue et al. 2010) suggests a rapid transfer of information over an increasing range surrounding the patch. Foragers may cooperate to detect food by means of network foraging (Wittenberger and Hunt 1985) that enables the information to transfer quickly among individuals. Although the benefits of such a network for foragers are shown in theoretical studies (Mock et al. 1988, Barta and Szép 1994, Deygout et al. 2010), observing small groups of seabirds and quantifying their interactions over long distances is challenging. Nonetheless, Silverman et al. (2004) observed nonrandom associations between foragers in small groups prior to the detection of prey, which suggests the existence of cooperation between foragers searching for prey. Although

we could not observe a network among foragers, we did observe Cape Gannets adjusting their flying direction to that of conspecifics encountered at sea and finding a patch of food more quickly when they did so. The fine-scale reactions of seabirds toward each other at sea, in addition to the foraging efficiency of using conspecifics as cues and dividing trips into short-distance flights, constitute elements that could indicate the existence and use of a structured network among foraging Cape Gannets. Moreover, our data show that group formation often occurs before feeding zones are reached. Flights were longer when made in association with conspecifics, as in juvenile Brown Boobies (*S. leucogaster*; Yoda et al. 2011), but feeding areas were reached in a shorter time span. In the context of a social network, flying groups of birds might result in a more visible source of information for conspecifics than flying individuals. In this respect, the prevalence of seabird associations at sea could be a way to improve the efficiency of their foraging strategies, in addition to potentially saving energy during flight (Weimerskirch et al. 2001, Lebar Bajec and Heppner 2009). While the elements that favor the establishment and use of a foraging network are evident, various mechanisms could be operating (Machovsky-Capuska et al. 2014). At a medium to large scale, where the location of food is steady, birds might remain consistent in their foraging locations (Garthe et al. 2007, Soanes et al. 2013, Wakefield et al. 2013) and, potentially, rely on memory (Lewis et al. 2006). However, at smaller scales, or if food location is not stable, social information processes might be a key to detecting inconspicuous prey (Nevitt and Veit 1999).

The Role of Colonial Breeding in Social Information

The use of conspecifics as a cue to locate prey suggests that the colony may act as a concentration mechanism, enabling many individuals to share a common foraging area in which a locally increased bird density might allow foragers to efficiently take cues from each other. The functioning of such a foraging network implies that an optimum ratio of interindividual (or intergroup) distances to interpatch distances exists. Therefore, the efficiency and interest of the network might strongly depend on the food distribution (Barta and Szép 1992, Grünbaum and Veit 2003). Because the marine environment is dynamic and variable (Russell et al. 1992, Weimerskirch 2007), the prey distribution of Cape Gannets varies and the efficiency of their foraging network is probably closely associated with changes in food availability (Deygout et al. 2010).

The efficiency of individual Cape Gannets in finding food probably depends on both the density and distribution of prey and the number of predators in their foraging area. For instance, a decrease in food availability could be compensated by the increased efficiency of foragers that use conspecifics as cues to locate food, whereas a decrease in predator density would limit the capacity of individuals to locate food, even if food is sufficiently available. During the breeding season, the efficiency of the foraging strategies developed by breeders is crucial for their reproductive success, especially during the brooding period, because chicks need regular feeding for their growth and survival (Mullers and Tinbergen 2009). Gannets regroup in colonies during their whole breeding season (Nelson 2005), whereas they can spread over larger areas and migrate during the rest of the year (Ismar et al. 2011, Fifield et al. 2014). The grouping of breeders in colonies probably enhances their foraging efficiency in spite of the potential variations in food availability and, in turn, increases their reproductive success. The importance of using conspecifics for foraging could therefore constitute a condition for the establishment and maintenance of colonial breeding in Cape Gannets. If such use of conspecifics to locate food in the ocean, as demonstrated here in Cape Gannets, is also used by other seabird species that deal with similar challenges (breeding on land and foraging at sea), this could contribute to explain the fact that >95% of the observed colonial species are seabirds (Danchin and Wagner 1997).

The Benefits of Sharing Information

In our study, information was shared inadvertently by the simple presence and behavior (direction of flight) of seabirds, as opposed to deliberate transfer of social information through signals (Danchin et al. 2004). While the individuals that cued on conspecifics probably gained a benefit from acquiring information, the producer of the information might be disadvantaged by having to share the resource (because of increased competition or kleptoparasitism). This depicts the "producer–scrounger" game (Barnard and Sibly 1981), in which producer and scrounger are in competition. Barta and Szép (1994) proposed that the strategy of sharing information can also be beneficial when both types of actors (producers and scroungers) benefit from the transfer of information, by means of group foraging strategies or antipredation mechanisms, for example. Group foraging in the marine environment is common, and it has been suggested that seabirds benefit from multispecies feeding associations for their foraging efficiency (Hoffman et al. 1981, Harrison et al. 1991, Camphuysen and Webb 1999, Clua and Grosvalet 2001, O'Donoghue et al. 2010, Machovsky-Capuska et al. 2011). More specifically, successive predator attacks disturb the cohesiveness of a prey aggregation, such that group foraging on a fish school enhances prey capture (Lett et al. 2014, A. Thiebault et al. personal observation). This suggests that producers in the marine environment would benefit from recruiting conspecifics for capturing prey. Interestingly, our data showed that the stimulus birds, or producers, changed the study bird's behavior

without themselves actively foraging. Therefore, stimulus birds may have already been feeding, may be on their way to feeding sites, or may represent "wrong cues" that could potentially lead to "informational cascades" (Giraldeau et al. 2002). Cape Gannets that have been feeding are recognizable in flight by a bulge on the lower belly (A. Thiebault et al. personal observation). It is therefore likely that Cape Gannets are able, in some cases, to detect whether other birds have been feeding recently or not, and this might serve as a way to discriminate between potential cues.

Conclusions

Four factors would allow and/or favor the use of conspecifics as cues to locate prey: sufficient visibility of the environment (Haney et al. 1992); good detectability of individuals (Bretagnolle 1993, McNaught and Owens 2002); adequate density of individuals (Grünbaum and Veit 2003); and inconspicuous prey that are difficult to locate (Deygout et al. 2010), patchily distributed (Barta and Szép 1992), or both (Weimerskirch 2007). If any of these factors are missing, the process of using cues from other individuals would be difficult and/or the potential benefits associated with using conspecifics as a source of information would be considerably reduced. In preying on shoaling epipelagic prey, Cape Gannets must deal with all these factors. They forage in an open space that allows long-distance visibility; their white plumage with black wing tips increases visibility on the seascape, and this is enhanced by the formation of groups; the relative proximity of the breeding colony guarantees a large number of conspecifics in the area; and underwater prey cannot be visible at large distances for aerial predators. We speculate that the high color contrast of Cape Gannets has an adaptive significance in that it enhances the emergence and maintenance of an efficient foraging network at sea. This is in accordance with similar suggestions made in a study of coloration patterns and lifestyles in Procellariiformes (Bretagnolle 1993) and with the signaling importance of plumage color in passerines (McNaught and Owens 2002). Therefore, a foraging community might be necessary for Cape Gannets, and given that using cues from conspecifics reduces the time to get to foraging patches, we suspect that the large-scale density of potential cues is fundamental in determining the foraging efficiency of individuals. Individual fitness would partly depend on the community of predators, such that a large colony would allow for better foraging efficiency of its members, as has been found recently in honeybees (*Apis mellifera*; Donaldson-Matasci et al. 2013). Consequently, a tradeoff can be expected between intraspecific competition (Ashmole 1963, Furness and Birkhead 1984, Lewis et al. 2001) and foraging facilitation in colonial seabirds.

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