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ORIGINAL PAPER

The contribution of private and public information in foraging by Australasian gannets

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Abstract Predators that forage on foods with temporally and spatially patchy distributions may rely on private or public sources of information to enhance their chances of foraging success. Using GPS tracking, field observations, and videography, we examined potential sites and mechanisms of information acquisition in departures for foraging trips by colonially breeding Australasian gannets (*Morus serrator*). Analyses of the bill-fencing ceremony between mated pairs of breeding gannets did not detect correlations between parameters of this reciprocal behavior and foraging trips, as would have been predicted if gannets used this behavior as a source of private information. Instead, 60 % of the departing birds flew directly to join water rafts of other conspecific en route to the feeding grounds. The departure of solitary birds from the water rafts was synchronized (within 60 s) with the arrival of incoming foragers and also among departing birds. Furthermore, solitary departing birds from the rafts left in the same directional quadrant (90° slices) as the prior arriving (67 %) and also prior departing forager (79 %). When associated plunge dives of conspecific were visible from the colony, providing a public source of information, gannets more often departed from the water rafts in groups. Our study thus provides evidence for the use of water rafts, but not the nest site, as locations of information transfer, and also confirms the use of local enhancement as a strategy for foraging flights by Australasian gannets.

Keywords Decision making · Information-centre hypothesis · Local enhancement · *Morus serrator* · Seabirds · Water rafts

Introduction

Patchily distributed marine pelagic resources can present considerable challenges to predatory seabirds. For a predator to be successful, a long-range foraging strategy can contribute to decisions about when to depart, whether to forage solitarily or in groups, and how to acquire information about the locality and quality of food resources. Among seabirds, several hypotheses of the sources and mechanisms of information acquisition about food sources have been suggested and tested (Richner and Heeb 1995; Wakefield et al. 2013). Colonies may serve as centers for information transfer of feeding sources (ICH: information-center hypothesis) in which nesting birds gain information from successfully returning birds on the nature and

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whereabouts of resources (Horn 1968; Ward and Zahavi 1973; Krebs 1974; Brown 1986; Waltz 1987). More recently, Weimerskirch et al. (2010) suggested that information transfer occurs through compass water rafts near the colony in which social aggregations of rafting birds acquire information on the direction of food sources from the angle of bearing of arriving birds. Finally, another form of cueing, called local enhancement (LE), describes how a foraging group ("flock") attracts individuals to the feeding patch by its visual conspicuousness (Pöysä 1992; Buckley 1997; Grünbaum and Veit 2003; Weimerskirch 2007) and also by vocalizations and other acoustic cues associated with prey capture (Valone 1993).

Predictions in regard to information sources and exchanges of the whereabouts of food in a closely related group of seabirds, the gannets (*Morus* spp.), are also diverse. Based on the gregariousness of gannets, some authors suggested that the transfer of information may occur in gannet colonies (called "gannetries"), as per the ICH (Mock et al. 1988; Richner and Heeb 1995). Others highlight social flock formations and the conspicuous white plumage coloration to indicate the use of LE (McGillivray 1842; Nelson 1978; Hamer et al. 2001; Tickell 2003; Davoren et al. 2003; Adams and Navarro 2005; Bellier et al. 2005). Both of these processes are considered as public sources of information, available to all members of the colony without restriction.

However, as previously shown in honeybees (*Apis mellifera*; Zhang et al. 2005; Zeil 2008), memory could also serve as a private source of information for orientation in patch detection, a mechanism that has been proposed to be important to Atlantic gannets (*M. bassanus*; Drury 1959; Garthe et al. 2007; Hamer et al. 2007; Pettex et al. 2010) and Cape gannets (*M. capensis*; Grémillet et al. 2004; Lewis et al. 2006). Less is known about the at-sea foraging strategies and the factors driving departures from the colony of Australasian gannets (*M. serrator*). However, considering that these gannets have a high divorce rate (43 %; Ismar et al. 2010a), and that they forage under the risk of predation (Stephenson 2005) and injury due to accidental collisions (Machovsky-Capuska et al. 2011a), there is a strong potential benefit to breeding pairs to engage in cooperation to maximize foraging efficiency for the current breeding attempt. An effective way of doing so would be for the returning bird to privately transfer to its mate current information on the nature and whereabouts of resources during changes of guard at the nest.

An example of a species that transfers private information about foraging in this way are honeybees whose workers only signal to nest mates the direction, distance, and quality of foods in a ritual known as the "waggle dance" (von Frisch 1967). Three socioecological factors may help to explain the evolution of this unusual form of signaling: (1) the highly colonial conditions in which honeybees can readily and efficiently exchange information between genetically closely related colony members (King and Cowlishaw 2007); (2) the honeybees within a colony have a close genetic relatedness, and therefore the evolutionary interests of signaler and receiver are tightly aligned (Hamilton 1963); and (3) the foods for which honeybees forage are typically patchily distributed and quickly exhausted, and in these conditions the timely sharing of information increases foraging efficiency (Beekman and Lew 2008).

Fig. 1 Australasian gannets bill fencing. Photo by David Raubenheimer

Gannets have a characteristic pair-greeting ceremony behavior as part of changing guard at the nest, known as "bill fencing" (BF; Fig. 1); this is a sustained bout of bill clashing and facial contact that almost invariably takes place in the critical period separating the return of one parent to the nest and the departure of the other (Nelson 1978; Machovsky-Capuska 2012; Fig. 1). Although bill fencing has been suggested to serve as a courtship display (Cunningham 1866; Townsend 1920), mate recognition (Meseth 1975), and a form of pair bond consolidation (Nelson 1978), its functional roles remain unclear. Based on socioecological similarities with the "waggle dance" in honeybees (criteria 1–3 above), we considered that bill fencing could potentially serve in the private exchange of foraging information.

Australasian gannets are the second rarest member of the seabird group Sulidae and breed exclusively in south-eastern Australia and New Zealand (Nelson 2005). Gannets feed mainly on pelagic fish and squid (Robertson 1992; Schuckard et al. 2012). These highly successful marine predators have been reported to travel for food as far as 388.5 km (Machovsky-Capuska et al. 2013a) with a highly effective foraging technique (72 % feeding success per attempt, Machovsky-Capuska et al. 2011b; Machovsky-Capuska 2012).

Here we use GPS data loggers, behavioral observations, and videography to examine possible mechanisms of information acquisition and the use of navigational cues in Australasian gannets while departing for foraging. In particular, we addressed three questions to test the prediction that gannets use conspecific as well as abiotic factors as navigational cues while departing for foraging: (a) Do Australasian gannets privately transfer information about food sources between members of the same couple using bill-fencing ceremonies? (b) Are the bearings of the departing birds influenced by the arrivals of conspecific at the water rafts? and (c) Do wind speed and duration influence the direction of arrivals and departures for foraging? We predict that if food sources are not visible from the colony, gannets will obtain information from their partners during bill-fencing ceremonies and also cue the whereabouts of food sources from the bearing of incoming birds at the water rafts. Alternatively, if associated conspecific foraging activities (e.g., plunge diving: Machovsky-Capuska et al. 2011a) are visible near the colony, then gannets will rely on the information gained in seeing conspecific foraging. Furthermore, we predict that wind direction will serve as an important navigational cue to the departure bearing of gannets embarking on foraging trips and also facilitates flight when the birds return with heavy prey loads. These analyses allow for a better understanding of the sources of information and decision-making process in Australasian gannets while foraging in a complex marine environment.

Materials and methods

Study area

The study was conducted during chick-rearing periods in December and January 2009–2010 and 2010–2011 on the Beach Colony of Cape Kidnappers gannetry, New Zealand (39°38′48″S, 177°05′36″E). The Beach Colony is one of the four gannetries at Cape Kidnappers and is located at sea level with around 1,000 breeding pairs (Machovsky-Capuska 2012).

GPS deployment and video footage collection

Both members of a breeding pair of adult Australasian gannets rearing 2- to 5-week-old chicks were captured at the same nest located at the periphery of the colony and equipped with GPS data loggers manufactured by e-obs digital telemetry, Germany (http://www.e-obs.de, more details in Machovsky-Capuska et al. 2013a). The devices weighed 45 g, which represents 2 % of the adult body weight (Nelson 1978). Data on position (latitude, longitude, and altitude), speed, and time were recorded at 1 s intervals. The data loggers were attached using Tesa tape to the four central tail feathers as recommended by Ismar et al. (2010b). The first bird in a pair observed to be departing from the nest was captured immediately after adopting the sky-pointing posture (Nelson 1978), then released after the data logger was fitted [approximately 10 min as defined by Machovsky-Capuska et al. (2013a)]. The second bird in the pair was captured the following day while nesting, at a time predicted to be within a range of 1–5 h prior to the arrival of its partner. This estimate was based on Machovsky-Capuska et al. (2013a) suggesting that in this colony, the average duration of foraging trips was approximately 24 h. In all cases, human interference during nest changeover was avoided.

Upon arrival of the first gannet tracked with the GPS data logger, high-resolution video footage of the BF ceremony during nest changeover was recorded using a Canon XH A1S handycam with 20 mm zoom. After observing the adults feeding their chicks, the recently arrived bird was captured, the data logger and tape strips completely removed, and birds were thereafter released at the edge of the colony. Following Machovsky-Capuska (2012), behavioral components of BF ceremonies were analyzed frame by frame using Adobe Premiere Pro CS4. Considering the problems of accurately extracting angles from 2D video footage, we decided to use the number of bill touches during bill-fencing ceremonies for behavioral comparisons. Following Grémillet et al. (2004), the recorded GPS trips were analyzed to determine distance travelled, speed, and time away from the colony. To conduct comparisons with the dance of the honeybees, following von Frisch (1967), relationships between bill touches during BF ceremonies and data collected from GPS data loggers were tested using Pearson's correlations. Bonferroni's correction (Curtin and Schulz 1998) was used to correct for multiple comparisons, based on which we adopted a threshold probability level of $P = 0.005$. Since the flight paths of Australasian gannets were not direct and involved a combination of foraging sites, we calculated the average bearing location of the dives from the colony to represent the intended destination (Pettex et al. 2010; Machovsky-Capuska et al. 2013a). For each gannet pair from which BF was recorded, we computed the average bearing location to quantify the difference in their bearing angle from the colony. Following Machovsky-Capuska et al. (2013a), we randomly permuted these angles between pairs 100,000 times to evaluate the probability that the observed distribution of vectors would occur randomly and thus corrected for biases due to geographic constraint. Data from the GPS units were analyzed using MATLAB 2009 and *PASW Statistics* version 18. Data were initially tested using Levene's test for homoscedasticity and Shapiro–Wilk's test for normality, and two tailed *t*-tests were used for seasonal comparisons.

Departures and behaviors of gannets from the colony

During December and January 2009–2011 austral breeding seasons, population-level departures were observed every hours from dawn to dusk. A single observer conducted scans at a constant focal duration that covered 180° view at 30 s intervals. Scans aimed to record the departure time from the colony and behavior of breeding adult gannets, systematically conducted from the same site on a cliff 40 m above the breeding colony using a 10 × 50 reticulated binoculars and compass (Waltz 1982). Considering that the colony is located at the base of a 60-m flat cliff, scans allowed a complete 180° view subdivided for the purposes of initial data collection into four sectors of 45° within a 1 km range from the colony. Following Burger (1997), departure behaviors were recorded as follows: (1) direct departure (DD, when birds departed from the colony to foraging), (2) landing near conspecific (LC, when birds departed from the colony and landed near another conspecific), and (3) splashdown (S, when birds bathe, preen and head dip while floating on the water alone). In addition, departing behaviors were also related to the presence of associated plunge-diving foraging activity of other gannets visible from the colony (Machovsky-Capuska et al. 2011a). Frequencies of departure behaviors were compared using χ^2 and *Z*-tests, and an increase in direct departures from the colony with associated plunge-diving foraging activity was considered to reflect the use of local enhancement by the departing bird (Buckley 1997; Grünbaum and Veit 2003; Bellier et al. 2005).

Water raft analysis

We defined a water raft as an aggregation of Australasian gannets floating in the water with a spacing of less than 3 m between conspecifics, which had either arrived directly from the colony en-route to foraging or had returned from a foraging trip (Burger 1997). Following Weimerskirch et al. (2010), a second observer recorded the angle of bearing of gannet water rafts every hour from dawn to dusk in paralell to the departures from the colony. For our observations, only the most populated water raft was followed. Thus, rafts were subdivided into sectors of 90° from which flock size and behavior of arriving and departing birds were coded as in Davoren et al. (2003) and Montevecchi et al. (2009). In this procedure, departure behaviors were recorded as follows: (1) indirect departure (ID, when birds departed from the raft to foraging), (2) landing near conspecific (LC, when birds departed from the raft and landed near another conspecific), and (3) colony (C, when birds departed from the raft and landed at the colony). The arrival and departure bearings of Australasian gannets from the water rafts were calculated and corrected to 90° of the observer following Batschelet (1981).

We conducted circular correlations between arrival and subsequent departures (60 s—follower) bearings to test whether departing birds follow the same bearing of the previous arrival bird using correlation coefficient for angular variables and Watson two-sample tests of uniformity (Package circular version 0.4-3 of the software R). In parallel with behavioral observations, a third observer collected a total of 50 h of high-resolution video footage of Australasian gannets rafting using a Canon XH A1S handycam with 20 mm zoom from the same area and altitude of the cliff as previously described. For time-of-the-day comparisons, we separated the day into three segments—early morning, midday, and afternoon—and compared frequencies using the χ^2 test. In addition, hourly measurements of wind direction and speed were downloaded from the National Climate Database from New Zealand's National Institute of Water and Atmospheric Research (NIWA) http://cliflo.niwa.co.nz, with the station selected as Cape Kidnappers WxT Aws (D97601; 39°38′42″S, 177°05′31.2″E). Correlation coefficient for angular variables and Watson's two-sample test of uniformity (Package circular version 0.4-3 of the software R) were also used to test the influence of wind direction and the angle of bearing of the arriving and departing birds. Data were initially tested using Levene's tests for homoscedasticity and Shapiro–Wilk for normality. For statistical comparisons, data were analyzed using *PAWS Statistics*, version 18. We report data as mean ± SE.

Results

Exchange of foraging information at the colony

We succeeded in deploying GPS data loggers on both partners of a nesting pair and filming BF during the nest changeover for the same pairs in 6 couples out of 35 (17 %) attempts, this amounting to approximately 600 h of effort. The major challenge was to capture in our observations the arrival time of foraging Australasian gannets at the colony, which was highly unpredictable, in order to film the BF at changeover and relate it to the foraging trips of both putative signaler and receiver.

A total of 12 individual foraging trips ($n = 2$ in 2010 and $n = 10$ in 2011) from chick-rearing gannets were

Table 1 Bill-fencing ceremony characteristics and foraging parameters for six breeding couples of Australasian gannets fitted with GPS data loggers

Code	Year	Bird A					Bill fencing				Bird B				
		Sex	Maximum distance from colony (km)	Foraging path length (km)	Foraging trip duration (h)	Speed (km h^{-1})	Duration (s)	Couple time (s)	Duration (s)/couple time (s)	Bill touches (s^{-1})	Sex	Maximum distance from colony (km)	Foraging path length (km)	Foraging trip duration (h)	Speed (km h^{-1})
1	2010	F	45.45	267.02	23.40	11.41	15.64	156.36	0.10	1.92	M	94.21	530.90	37.73	14.07
2	2011	M	63.46	389.16	34.73	11.21	31.92	760.80	0.04	0.31	F	76.09	177.83	25.84	6.88
3	2011	M	76.64	301.03	46.24	6.51	15.14	466.68	0.03	0.46	F	68.13	393.28	27.16	14.48
4	2011	M	19.80	220.54	24.99	8.82	14.52	55.00	0.26	0.48	F	69.68	553.09	25.61	21.59
5	2011	F	63.44	239.75	23.08	10.39	56.24	277.80	0.20	0.39	M	44.53	192.65	16.58	11.62
6	2011	F	27.58	152.02	13.35	11.39	39.90	60.68	0.66	0.80	M	109.88	314.00	29.53	10.63

Bird A = first arriving adult, Bird B = second arriving adult

recorded. Gannets foraged over average distances of 63.2 km (±25.9 km), with a mean foraging path length of 310.9 km (±132.2 km) and a mean foraging trip duration of 27.3 h (±8.9 h). During foraging trips, gannets travelled an average speed of 11.6 km h^{-1} (±3.9 km h^{-1}, Table 1). Foraging trip performance was highly consistent between the two consecutive breeding seasons studied, with no significant differences in any of the variables analyzed (maximum distance from colony, *t*-test, $t = 0.38$, $df = 10$, $P = 0.71$, two-tailed; foraging path length *t*-test, $t = 1.03$, $df = 10$, $P = 0.32$, two-tailed; foraging trip duration *t*-test, $t = 0.54$, $df = 10$, $P = 0.60$, two-tailed; and speed *t*-test, $t = 0.43$, $df = 10$, $P = 0.67$, two-tailed).

The analysis of foraging trips ($n = 12$) collected from GPS data loggers, after Bonferroni correction for multiple comparisons, showed no significant correlations between distance travelled, time away from the colony, travel speed, BF duration, bill touches, and the length of time the couple spent together during nest changeovers (Table 2). Furthermore, the distribution of the bearing of foraging trips in the GPS deployments assembled from 100,000 permutations (see "Methods") revealed that the average angular difference between directions of Australasian gannets in BF pairs was not significantly less than expected by chance ($P > 0.05$).

Departures and behaviors of gannets from the colony

When no plunge-diving foraging activity was visible from the colony, 60 % ($n = 1{,}230$) of breeding Australasian gannets departing from CK colony landed in water rafts between 50 and 70 m from the colony, whereas 21 % ($n = 430$) landed alone in a splashdown and 19 % ($n = 390$) departed directly for foraging sites ($\chi^2 = 721.3$; $df = 2$; $P < 0.0001$, Fig. 2a). The majority of the colony departures were made by solitary gannets ($\chi^2 = 57.0$; $df = 3$; $P < 0.0001$, Fig. 2a). However, when plunge-diving conspecific foraging activity was observed within 500 m of the colony (Fig. 2b), DD (60 %, $n = 191$) was higher than LC (30 %, $n = 95$, Fig. 2b). This frequency of DD is significantly higher than when plunge-diving conspecific foraging activity or food sources were not seen near the colony (19 %, $n = 361$, $Z = 15.4$, $P < 0.0001$), suggesting the use of local enhancement by foraging gannets. Thus, the number of departed birds was also larger when associated plunge-diving conspecific foraging activity was observed near to the colony ($\chi^2 = 135.4$, $df = 3$, $P < 0.0001$, Fig. 2b).

Water raft analysis

During our behavioral and video footage analysis, we observed that Australasian gannets formed water rafts near

Table 2 Correlation coefficients for relationships between times of absence from the nest, speed during the trip, flight distance, bill-fencing duration, bill touches, and couple duration for different breeding adults of Australasian gannets fitted with GPS data loggers ($n = 12$)

	Bill-fencing duration (s)		Couple time (s)		Bill touches (s^{-1})		Bird B					
							Maximum distance from colony (km)		Foraging path length (km)		Speed (km h^{-1})	
	C	*P*	*C*	*P*	*C*	*P*	*C*	*P*	*C*	*P*	*C*	*P*
Bird A												
Maximum distance from colony (km)	0.60	0.21	0.32	0.83	−0.30	0.57	−0.37	0.47	0.10	0.85	−0.71	0.12
Foraging path length (km)	−0.46	0.36	0.16	0.76	−0.39	0.45	−0.10	0.85	0.45	0.37	−0.73	0.10
Foraging trip duration (h)	−0.40	0.43	0.57	0.23	−0.76	0.08	0.19	0.72	0.64	0.17	−0.90	0.01
Speed (km h^{-1})	−0.25	0.64	−0.25	0.63	0.14	0.79	−0.27	0.60	0.05	0.93	−0.18	0.73
Bird B												
Maximum distance from colony (km)	−0.28	0.59	−0.31	0.55	0.55	0.25						
Foraging path length (km)	−0.77	0.07	−0.28	0.60	−0.12	0.82						
Foraging trip duration (h)	−0.91	0.01	0.24	0.64	−0.43	0.40						
Speed (km h^{-1})	0.54	0.27	−0.65	0.16	0.62	0.19						
Couple time (s)	0.06	0.92										
Bill-fencing duration (s)	0.40	0.44										

Bird A = first arriving adult, Bird B = second arriving adult. *C* Pearson correlation coefficient, *P* Significance level, with Bonferroni correction $\alpha < 0.005$

the colony, varying in the number of birds and also in location with respect to the colony. We recorded a total of 248 water rafts with a mean of 35.4 ± 15.5 gannets (range 15–71 birds). For the time-of-the-day comparisons (see methods), the largest number of gannets observed rafting at any one time (956 birds) was in the early morning period ($\chi^2 = 9.7$, $df = 2$, $P < 0.05$). Upon arrival at a raft, gannets began to preen, bathe and head dip, and lounged on the water for statistically similar periods in the middle of the day with a mean of 5.0 ± 0.4 min (range 0.1–14.3 min), in early morning (3.5 ± 0.3 min, range 0.06–10.1 min), and in the afternoon periods (4.2 ± 0.4 min, range 0.3–14.6 min; $\chi^2 = 9.9$, $df = 2$, $P = 0.06$). The mean duration of time gannets spent in the raft was 4.4 ± 0.20 min (range 0.06–14.6 min), based on a total of 225 rafting birds recorded.

The frequency of gannets arriving at the water raft directly from foraging (58 %) was similar to that of the colony (42 %), as this difference was not significant ($\chi^2 = 3.4$; $df = 2$; $P = 0.16$). Individual gannets accounted for a significantly greater proportion of raft arrivals (68 %) and departures (55 %) than did groups of two or more birds ($\chi^2 = 27.3$, $df = 3$, $P < 0.0001$). There were significantly more departures from the rafts toward the foraging sites than directly to the colony ($\chi^2 = 882.1$, $df = 2$, $P < 0.0001$).

We found evidence of an association between birds departing indirectly to the foraging sites and others arriving at the water raft from foraging. Seventy percent of departures toward the foraging sites from the raft took place within 60 s of an arrival ($\chi^2 = 103.2$, $df = 2$, $P = 0.001$), and the majority of the departing birds (67 %) departed within the same directional quadrant from which the previous bird had arrived ($\chi^2 = 67.6$, $df = 1$, $P < 0.0001$). Sixty nine percent of departures toward the foraging sites from the raft took place within 60 s of a departure ($\chi^2 = 83.7$; $df = 2$; $P < 0.0001$), and the majority of the birds (79 %) departed within the same directional quadrant from which the previous bird had departed ($\chi^2 = 71.2$; $df = 1$; $P < 0.0001$).

Arrivals at the water rafts from foraging were positively correlated with wind bearing (Table 3). However, there were no significant correlations for either arrival or departure bearings and wind speed <20 and >20 km h^{-1} (Table 3).

Discussion

The use of sensory information by animals is critical in locating and exploiting food resources (Stevens 2013). Birds have evolved complex visual systems that play an important role in orientation and foraging (Aidala et al. 2012). Although gannets are visual predators (Cunningham 1866; Machovsky-Capuska et al. 2011c, 2012, 2013b), very little is known about the source of the sensory cues involved in their foraging habitat recognition (Greif and Siemers 2010). Information on the location of food can be acquired privately (from memory and environmental cues)

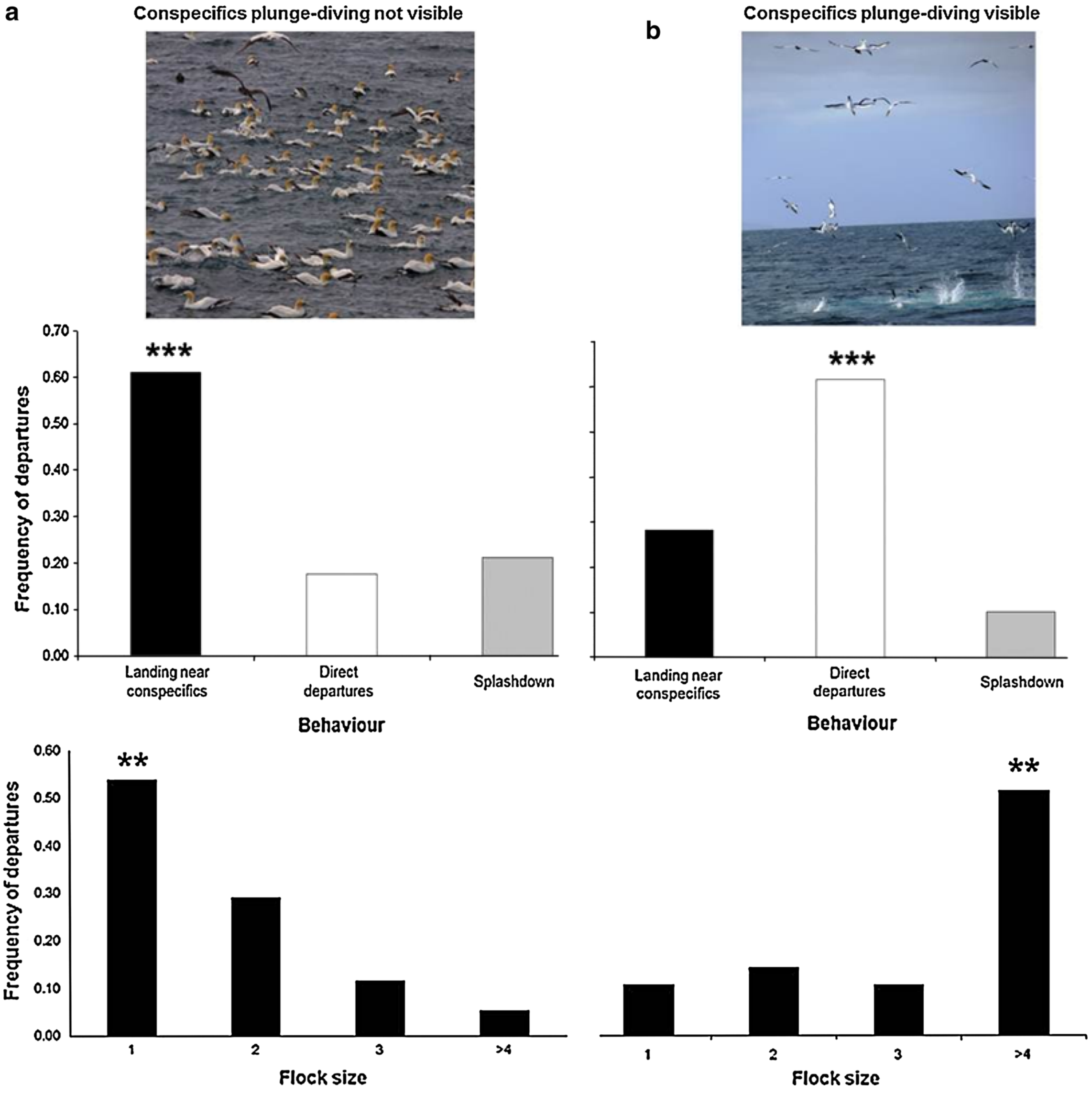

Fig. 2 Frequency of departures and flock size of breeding Australasian gannets. Departure behaviors from the colony, when associated plunge-diving conspecific foraging activity was not visible, and when associated plunge-diving conspecific foraging activity was visible nearby. ** and *** represent statistically significant results ($P < 0.0001$). Photos by Gabriel Machovsky-Capuska

or publically (from the behavior of conspecific; Danchin et al. 2004; Hauber and Zuk 2010). Our study provides evidence of the use of public rather than private information during foraging in Australasian gannets.

Private information

How do gannet partners know how much to invest in parental care? Results about the duration of bill-fencing ceremonies and number of bill touches in relation to distance, duration, and angle of bearing of foraging trips did not provide evidence for the exchange of foraging information between partners.

Instead, individual ecological and social context may have an effect through exposure to wind speed and direction, as has been shown to have a strong effect on the flight behavior of other seabirds and their energy investment while searching for food (Birt-Friesen et al. 1989; Pennycuick 1989). Our analysis of the relationship between arrival and departure bearing with wind direction revealed that the majority of Australasian gannets used tail winds while arriving from foraging, as previously shown in Atlantic and Cape gannets (Grémillet et al. 2004; Garthe et al. 2007).

Public information

It has been suggested that colonies may act as centers for transfer of information (ICH; Ward and Zahavi 1973), and gannet colonies of other species in particular have been

Table 3 Circular correlation coefficients for relationships between arrival and departure angles from e water rafts by Australasian gannets

Wind	Coefficient	Statistic	*P*
Bearing			
Arrival	0.22	1.85	**0.05**
Indirect departure	0.26	1.22	0.08
Speed			
Arrival (km/h)			
<20	0.20	1.64	0.10
>20	−0.001	−0.005	0.99
Indirect departure (km/h)			
<20	0.23	1.79	0.07
>20	−0.11	−0.32	0.74

Bold statistically significant

identified as candidates to test this hypothesis (Mock et al. 1988; Richner and Heeb 1995). The ICH predicts that birds would leave directly for foraging, to maximize the probability that information about food sources is current. We found that 80 % of the birds did not head directly to the feeding grounds when food sources were not visible from the colony, but stopped near the colony in a water raft or by itself before departing for foraging. Our results found that gannets formed water rafts with the highest concentration of birds early in the morning when most started their foraging trips. This is similar to previous findings on common murres (*Uria aalge*) gathering near the colony prior to departing for foraging (Burger 1997).

The evidence for the use of water rafts during both the initiation and completion of foraging trips, in addition to the synchrony between the directional bearing of incoming and subsequent outgoing gannets and also between departing foragers, suggests that water rafts play an important role in updating social information concerning food resources in gannets. These results are consistent with the formation of water rafts to detect conspecifics returning from foraging (Burger 1997) and the use of these rafts as arenas for social information exchange in Guanay cormorants (*Phalacrocorax bougainvillii*) (Weimerskirch et al. 2010). The variation in the bearing location of these water aggregations of gannets with respect to the colony was continuously adjusted to the bearing of the arrival foragers as previously observed in cormorants by Weimerskirch et al. (2010).

Acquiring information from cues and signals of foraging conspecifics, a process called local enhancement (Thorpe 1963), is widespread among seabirds. When plunge-diving foraging activity was observed from the colony within a range of 200–700 m, direct departures (DD) were significantly increased relative to when plunge-diving activity was not visible nearby, supporting the claim that the gannets we observed used local enhancement while foraging, as previously suggested for other gannet species (Nelson 1978; Grémillet et al. 2004). Foraging in this way, gannets have access to more accurate information and can make better-informed decisions by observing and following the behavior of foraging conspecifics (King and Cowlishaw 2007; Conradt 2011). During these events, we have also observed an increase in the number of birds departing from the rafts and the colony. This is likely related to the opportunity to capture food near the colony and possibly also increased feeding success with larger flock size (Fernández-Juricic et al. 2004), something which remains unstested for gannets.

The present study highlights the importance of water rafts as arenas for information exchange for foraging gannets. The results have also provided evidence of the use of a combination of several strategies, including synchronization between arriving and departing birds and among departing foragers, the use of local enhancement and an influence of the wind on foraging by Australasian gannets. Further studies are needed to gain a better understanding of the use of navigational and sensory cues in these marine predators, and its role in generating colony level coordination of foraging departures and paths, while searching and capturing food in complex marine environments.

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Conflict of interest The authors declare that they have no conflict of interest.

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