RAFTING BEHAVIOUR IN THE NORTHERN GANNET *MORUS BASSANUS*: EVIDENCE FOR SOCIAL INFORMATION TRANSFER

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ABSTRACT

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When departing from or returning to their breeding colonies, many seabirds land on the water adjacent to the colony, often forming large aggregations numbering many hundreds of birds. This behaviour is known as 'rafting.' Despite its prevalence, rafting remains poorly understood for most species. One general hypothesis is that rafting allows birds to avoid predators or preen away from the colony and is therefore influenced by environmental or abiotic factors. However, some studies have suggested that rafting facilitates the transfer of social information about foraging locations by allowing birds to orientate to the bearings of conspecifics returning from prey patches at sea. We investigated rafting in a large pelagic seabird, the Northern Gannet *Morus bassanus*, to address two hypotheses: (1) that rafts are a source of social information on the direction of recent foraging grounds and (2) that rafting is influenced by local abiotic conditions. At a large colony in Newfoundland, Canada, we recorded the return and departure directions of gannets, as well as raft size and orientation throughout the day. We also recorded wind strength and precipitation. Consistent with the social information hypothesis, we found that gannets departing from the raft tended to depart in the direction of returning foragers, whereas those departing from the colony did not. We found no correlation between the orientation of the raft and the bearings of returning foragers but did find that rafts were largest in the mornings when, we suggest, the need for social information might be greatest. Raft size, however, was not influenced by the abiotic factors we measured. We therefore conclude that, while abiotic influences do not significantly affect the rafting behaviour of gannets (at least within the range of abiotic conditions for which observations were possible), rafting may serve a social information gathering purpose for gannets.

Key words: gannets, seabirds, foraging, rafting, social information, Newfoundland

INTRODUCTION

Many species of seabirds form dense aggregations on waters adjacent to breeding colonies as they depart from or return to the colony (McSorley et al., 2003; Richards et al., 2019). This behaviour is known as rafting. Despite its prevalence, relatively little research has investigated rafting (other than in penguins [Ainley & Wilson, 2023]) and its purpose therefore remains poorly understood (Richards et al., 2019; Warwick et al., 2016; Wilson et al., 2008).

It is generally accepted that most seabirds use rafts to rest or preen away from the guano of the colony (Carter et al., 2016; Granadeiro et al, 2018), a function that is certainly true in penguins, which actually wash themselves upon departing the colony (Ainley & Wilson, 2023). In some species, rafting may also serve as a predator-avoidance strategy (Fox et al., 1997; Richards et al., 2019). Several studies have suggested that rafting may be driven by temporal variations in weather conditions or other abiotic factors (Carter et al., 2016; Kowalska O'Neil et al., 2023; McSorely, 2003; Sánchez-Román et al., 2018; Warwick et al., 2016; Wilson, 2008). Such suggestions appear to be based on the corollary that, because weather influences the foraging behaviour and time budgets of volant seabirds (Amélineau et al., 2014; De Pascalis et al., 2021; Finney et al., 1999; Lane et al., 2019; Pistorius et al., 2015), it will also drive rafting behaviour. The relationship between abiotic factors and rafting is likely to be complex, however, and few studies have tested this relationship directly. Manx Shearwater *Puffinus puffinus*, for example, form rafts as they return to the colony, and the size of these rafts increases on windier days (Richards et al., 2019). Richards et al. (2019) speculate that stronger winds reduce flight times back to the colony, resulting in the accumulation of birds and, consequently, more rafting birds on windier days. Conversely, several species of albatross, who rely on strong winds for flight, are more likely to raft when wind speeds are lower, presumably while they wait for more favourable conditions before continuing their journey to or from the colony (Kowalska O'Neil et al., 2023).

Whilst rafting may be influenced by abiotic factors, another perhaps more intriguing idea is that rafting may facilitate the transfer of social information—information gained through observation of others (Schmidt et al., 2010)—in this case, the nature and locations of foraging grounds (Burger, 1997; Racine et al., 2012). This notion has its roots in the Information Centre Hypothesis (ICH), which asserts that colonies of birds serve as 'information centres' (Ward & Zahavi, 1973). That is, individuals lacking knowledge of recent food patches can gain information on the location of food patches by observing successful foragers as they return to the colony and then following them as they depart on their next foraging trip. The ICH seeks, in part, to explain the association between group-living and patchily distributed food sources across animal taxa (Davies, Krebs & West, 2012; Gori, 1988): social information, which is more up-to-date than private information (e.g., memory), is likely to be of greater value to animals with harder-to-find food, and living in large groups increases the opportunity to acquire this type of information (Barta & Giraldeau, 2001; Boyd et al., 2016; Davoren et al., 2003; Richner & Heeb, 1995; Sassi et al., 2024).

Most seabirds are colonial breeders (Danchin & Wagner, 1997) that generally feed on widely distributed and often unpredictable prey (Hamer et al., 2000; Weimerskirch et al., 2007). As such, seabirds have been considered good candidates for the ICH (Mock et al., 1988; Richner & Heeb, 1995). However, some species are not well positioned at nesting sites within the colony to observe departing and returning conspecifics (Burger, 1997; Racine et al., 2012). Instead, rafts may provide a better vantage point for such observations, leading to suggestions that rafts act as an 'information halo' around island colonies (Burger, 1997; Evans et al., 2015).

The use of rafting to facilitate social information transfer has been demonstrated in Guanay Cormorants *Leucocarbo bougainvilliorum* who were found to orientate their rafts along the bearings of flocks of conspecifics returning from foraging trips (Weimerskirch et al., 2010). These 'compass rafts' appear to indicate the direction of recent prey patches to cormorants departing the colony to forage. Similarly, Australasian Gannets *Morus serrator* were found to depart the raft shortly after the arrival of returning foragers and in the same direction (Machovsky-Capuksa et al., 2014).

This mechanism of social information transfer, whereby birds cue to the direction of returning foragers, has been termed 'orientation' (Boyd et al., 2016) or, more specifically, 'visual trail following' (Urmy, 2021). Visual trail following can be beneficial, even if only by preventing birds from departing in directions where prey is scarce (Boyd et al., 2016). For central-place foragers such as seabirds, which return to the colony after foraging to provision young, the raft is likely to be the location where birds have the greatest opportunity to encounter and observe returning foragers.

In this study, we investigate rafting in the Northern Gannet *Morus bassanus*, the largest pelagic seabird in the North Atlantic, and consider two hypotheses: (1) that rafts are a source of social information on the direction of recent foraging locations; (2) that rafting is influenced by local abiotic factors.

Northern Gannets (hereafter, *gannets*) breed in large colonies known as 'gannetries' (Nelson, 2003) and are long distance foragers, feeding on lipid-rich fish such as Mackerel *Scomber scombrus* and Capelin *Mallotus villosus* (Garthe et al., 2007; Hamer et al., 2000). Gannets engage extensively in rafting, yet the reasons for this are unclear. A 2016 study by Carter et al. (2016), which used bird-borne global positioning system (GPS) loggers, found that gannets rafted primarily on outbound journeys from the colony, prior to the start of foraging trips. Although this could indicate that rafting serves a bathing or preening function following nest attendance, as those authors suggest, evidence indicates that gannets use social information at colonies (Wakefield et al., 2013) and that information transfer occurs among rafting gannets as they wait to depart to forage (Waggitt et al., 2014).

Gannets tend to take direct routes when returning from foraging grounds, and returning birds form large flocks that converge on the colony (Montevecchi et al., 2009; Pettex et al., 2010; Wakefield et al., 2019). Inbound flocks are, therefore, a conspicuous indication of the direction of recent food patches and, for rafting gannets departing to forage, present an opportunity for visual trail following (Boyd et al., 2016; Weimerskirch et al., 2010).

Although Carter et al. (2016) found no correlation between rafting and foraging distance or duration, visual colony observation, as employed by the present study, may be more useful than bird-borne GPS logging data for determining whether gannets use visual trail following when departing the raft to forage.

If gannets do use the raft to facilitate visual trail following (our first hypothesis), then gannets departing from rafts should do so in the same direction as recently returned conspecifics (prediction 1; Table 1). Additionally, in Guanay Cormorants, the use of rafts as vantage points for visual trail following resulted in rafts orientating towards the bearing of returning flocks. If gannets use rafts for the same reason, we expect their rafts to align with the bearing of returning birds (prediction 2).

Our second hypothesis considers the effects of three different abiotic factors on gannet rafting behaviour. First, we investigate the influence of wind strength. Unlike Manx Shearwater, strong winds do not reduce foraging trip durations in gannets, with birds compensating for unfavourable conditions by spending less time on the water (Lane et al., 2019). If gannets compensate for strong winds by spending less time on the water, it follows that they might do so when encountering strong winds at the colony before departing to forage. We therefore predict that raft size in Northern Gannets will be negatively correlated with windspeed (prediction 3).

Second, we consider the influence of precipitation on rafting. The use of the rafts as locations for bathing has been observed in several species, including the gannet (Carter et al., 2016; Davoren et al., 2003; Granadeiro et al., 2018). Carter et al. (2016) hypothesised that local weather conditions, such as rain, could increase the need for bathing and thus the propensity of gannets to raft. We therefore predict that rafts will be larger when it is raining (prediction 4).

Finally, we consider whether raft size varies throughout the day. Gannets forage throughout the day but are inactive at night, only leaving the colony if disturbed by predators (d'Entremont & Montevecchi, 2022; Garthe et al., 1999). In Australasian Gannets,

TABLE 1
Hypotheses and predictions relating to the drivers of rafting in Northern Gannets *Morus bassanus*

Hypotheses (H) and predictions (P)
H1: Rafts serve as a location for social information transfer on the direction of prey patches
P1. Gannets departing the raft will leave in the same direction as returning birds
P2. The raft will orientate to the bearing of returning flocks
H2: Raft size is influenced by local abiotic factors
P3. Stronger winds will result in smaller rafts
P4. Rafts will be larger when it is raining
P5. Rafts will be largest in the mornings

this pattern appears to result in rafts being largest in the morning as birds depart the colony to begin foraging trips (Machovsky-Capuksa et al., 2014). We suggest the same pattern will be seen in Northern Gannets and, therefore, predict that rafts will be largest in the morning (prediction 5).

MATERIALS AND METHODS

Data Collection

This study was carried out during the breeding season from 02–28 August 2022 at Cape St Mary's Ecological Reserve (46°50′N, 061°09′W) on the southwest coast of the Avalon Peninsula, Newfoundland, Canada. Cape St Mary's is usually inhabited by approximately 15,000 breeding pairs of gannets nesting on the reserve's cliffs (Chardine et al., 2013). At the time of the study, however, the colony had been affected by the 2021/22 avian flu epidemic (European Food Safety Authority et al., 2022), resulting in considerable mortality among the breeding population.

Observations were made during daylight hours (06h00–21h00) and lasted 2–12 h each day depending on weather. Regular breaks were taken to mitigate observer fatigue (Evans et al., 1985). On some days (n = 4), dense fog, which is common in this part of Newfoundland, meant that observations were not possible. Observations also ceased when wind speeds exceeded 50 km/h, when gannets could be seen plunge-diving from the colony, or when cetaceans could be seen feeding. The latter two conditions were excluded to account for the potential effect of local enhancement, whereby birds cue to the feeding activity of conspecifics or heterospecifics (Fisher & Lockler, 1954; Machovsky-Capuksa et al., 2014). All observations were made by a single observer (the author EJP-T), who was situated at a high point of land almost directly above Bird Rock, the most densely populated part of the colony. This position provided a 180° view of the sea in front of the colony, from 150° (SE) to 330° (NW). The same observation position was used throughout the study to ensure consistency of bearing measurements. All data relating to directional bearings were collected using 7×42 compass-equipped, reticulated binoculars. All other observations were made with a pair of 10×42 binoculars and a spotting scope with 20–60× magnification. Wind speed was measured in km/h with a handheld, digital anemometer.

Return/Departure Directions

To determine whether gannets departing the raft did so in the same direction as returning flocks, the sea extending out from the colony was divided into four equal sectors, each encompassing 45° of a compass (Fig. 1; Davoren et al., 2003; Evans et al., 1985; Machovsky-Capuksa et al., 2014). Following Davoren et al. (2003), each 45° sector was scanned for 3 min, and the number of gannets returning in each sector was recorded; flock size was also recorded. This constituted a *return scan* and lasted ~12 min.

Immediately following a return scan, 10 gannets departing directly from the colony and 10 gannets departing from the raft were selected using a continuous scan technique (Altmann, 1974). Data on gannets departing directly from the colony were collected for comparison with those from gannets departing the raft. For the purposes of the present study, we defined a raft as birds sitting on the water within 2 km of the colony (Carter et al., 2016; Weimerskirch et al., 2010); however, field observations showed that visible rafting gannets were generally much closer to the colony than this.

In the case of gannets departing from the colony, their departure behaviour (i.e., whether they departed to sea or rafted on the water) was recorded and coded as in Burger (1997). Focal birds departing the raft or colony to forage were visually tracked as they flew out to sea and until they reached their vanishing point (focal birds could be tracked for up to three minutes in good visibility). The midpoint of the 45° sector in which a gannet reached its vanishing point was taken as the departure direction for that bird (Evans et al., 1985). This process constituted a *departure scan*. A return scan followed by a departure scan constituted a sample period and lasted ~1 h. If the desired number of departing gannets were not identified within ~1 h, the sample period was ended as the quality of information from returning birds was deemed to have diminished considerably by that point.

Because it was not possible to individually identify gannets, some pseudoreplication within the collected data is theoretically possible. However, given the very large number of gannets present at the colony and the fact that departing birds would likely not be expected to return to the colony until several hours after completing a foraging trip, the risk of pseudoreplication was considered negligible.

Compass Rafting/Raft Size

Using the *return scan* method described above, the number of gannets returning in each 45° sector was recorded. Following a return scan, the number of gannets rafting in each sector was recorded (Richards et al., 2019; Sutherland, 2002; Weimerskirch et al., 2010). At the beginning of each raft count, wind speed, time of day, and whether it was raining or not was recorded. Additional raft counts, without return scans, were also performed to capture additional raft size data for predictions 3–5 (Table 1).

Data Analysis

Return/Departure Directions and Compass Rafting

All data analyses were carried out in R (version 4.3.2). Statistical significance was interpreted based on p values, treating p as a continuous measure. For each sample period, mean angles of

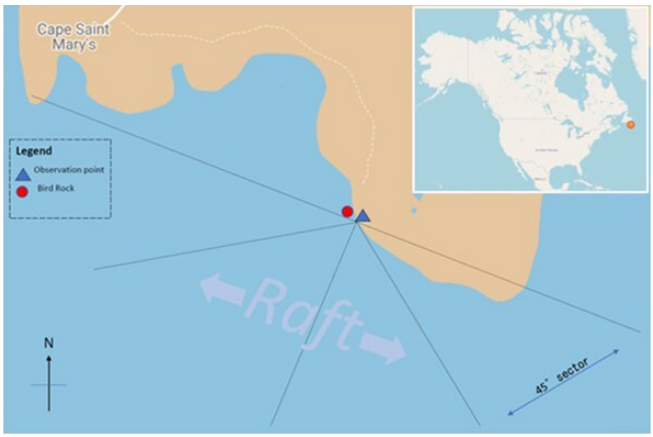

Fig. 1. Cape St Mary's Ecological Reserve, Newfoundland, Canada, showing the observation point (blue triangle) and the position of Bird Rock (red circle). The approximate 45° sectors and general position of the rafting area adjacent to the colony are also shown.

returning gannets were calculated along with the mean directions of gannets departing from the colony and gannets departing from the raft. To test whether departing birds (from either the colony or the raft) followed the same bearings as returning birds, and whether the bearings of rafts oriented to the bearings of returning birds, we conducted circular correlations for angular variables (a circular version of a Pearson's correlation) on the mean bearings (Davoren et al., 2003; Machovsky-Capuksa et al., 2014; "circular" package version 0.4–4; 95% confidence intervals [CI] on bearings were calculated from non-parametric bootstrapping with the "boot" package in R based on 1,000 resamples). Additionally, we conducted a Wilcoxon test to evaluate whether absolute bearing differences (relative to the bearing of returning birds) differed significantly between birds departing from the colony and birds departing from the raft.

Raft Size and Abiotic Variables

To determine the influence of local abiotic factors on raft size, we fitted a generalised linear mixed model (GLMM) to the data using the "lme4" package. The "MuMIn" and "lmerTest" packages were used to generate a general linear model that included R^2 and p values in the output summary, respectively. We included time of day (categorical: morning [06h00–11h59]/afternoon [12h00–16h59]/evening [17h00–21h00]), wind speed (continuous: km/h; normally distributed) and precipitation (categorical: raining/not raining) as explanatory variables in the model. Date was included as a random intercept to account for non-independence of data within each day. The model was assessed for dispersion, and residuals were checked for normal distribution and constant variance.

RESULTS

Return/Departure Directions

Although return scans were easy to perform (i.e., gannets returning to the colony could be observed in each sample period), during departure scans it was sometimes difficult to identify the desired number of gannets departing from the raft or colony. A total of 23 complete sampling periods were conducted over 7 d.

Gannets returned and departed in all 45° sectors. The circular mean bearing of returning gannets during the sampling periods was 234.4° (95% CI [224.4–243.7]), while the circular mean bearings of gannets departing from the raft and from the colony were 225.9° (95% CI [217.5–234.3]) and 224.2° (95% CI [203.2–249.6]), respectively.

TABLE 2
Circular correlation coefficients for angular variables for the mean angle of returns, departures, and raft orientation of Northern Gannets *Morus bassanus* at Cape St Mary's, Newfoundland, Canada

	Correlation coefficient (r)[a]	p	Number of sample periods
Returns vs. departures from rafts	**0.53**	.01	23
Returns vs. departures from colony	0.08	.70	23
Returns vs. raft orientation	−0.25	.06	50

[a] Bold indicates statistically significant correlation coefficients

When no plunge-diving or feeding activity could be seen from the colony, 73.5% of gannets departing from the colony landed at the raft, while the remaining 26.5% flew directly out to sea (total sample size n = 230). Gannets returning from foraging trips returned directly to the colony and were almost never observed joining the raft (97.67%, total sample size n = 301). Gannets generally returned in flocks of two or more birds (70.41%, total sample size n = 1,639). The largest recorded flock was 27 birds, and the median flock size was four (interquartile range [IQR] = 2–6, n = 233).

During the sampling periods, there was a moderate positive circular correlation between the mean bearings of gannets departing from the raft and those of returning gannets, and this finding was significant (r = 0.53, p = .01, n = 23; Table 2; prediction 1; Fig. 2). There was no evidence of a circular correlation between the mean bearings of gannets departing from the colony and those of returning gannets (r = 0.08, p = .70, n = 23).

The absolute bearing differences relative to the bearing of returning birds differed significantly between colony departures and raft departures, with smaller bearing differences for raft departures (two-tailed Wilcoxon test, V = 244.5, p = .001; prediction 1; Fig.3).

Compass Rafting

A total of 50 observations of raft counts with return scans were conducted over 13 d. The circular mean of the bearing of returning gannets for these observations was 235.0°, whereas the circular mean orientation of the raft was 246.2°. Although these numbers indicate that the raft was broadly oriented towards the bearing directions of returning birds, there was no evidence that the mean orientation of the raft tracked the mean bearings of returning birds within individual observation periods (circular correlation coefficient, r = −0.25; p = .06, n = 50; prediction 2; Fig.3).

Raft Size and Abiotic Factors

A total of 64 raft counts were conducted over 16 d. The mean ± standard deviation (SD) raft size was 197.6 ± 129.5 (n = 64). The

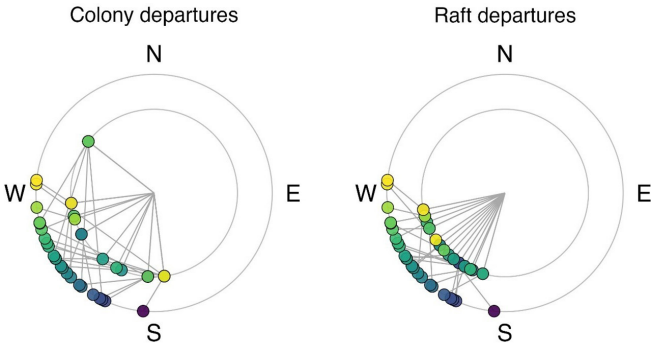

Fig. 2. Average bearing directions of Northern Gannets *Morus bassanus* departing from the colony (left panel) or from the raft (right panel) at Cape St Mary's, Newfoundland, Canada. Inner circles represent departing directions; outer circles represent return directions. Lines connect departures and return bearings recorded during the same observation period. Each marker represents the mean bearing for an observation period, and markers corresponding to the same observation period are plotted in the same colour. Colours indicate the bearing of returning birds.

largest raft recorded was in the morning and numbered 499 birds, whereas the smallest raft, comprising two birds, was recorded in the afternoon. A GLMM that included time of day, wind speed, and precipitation as fixed effects and date as a random effect predicted that rafts were larger in the morning than in the afternoon (effect ± standard error (SE) = 117.76 ± 33.27, t = 58.71, p = .001; prediction 5; Table 3).

There was little evidence that wind strength and precipitation influenced raft size (wind strength: SE = 1.69, t = −0.64, p = .53; precipitation: SE = 39.15, t = 10.15, p = .88; predictions 3 and 4). The marginal R^2 (proportion of total variance explained by fixed effects) and conditional R^2 (proportion of variance explained by both fixed and random effects) for the GLMM were 0.27 and 0.44, respectively (Nakagawa et al., 2017). To test for possible serial autocorrelation, we assessed the residuals by visually interpreting an autocorrelation function (ACF) plot followed by a Ljung–Box test. The majority of spikes in the ACF plot were within the 95% confidence bounds, with no systematic patterns or clear decay. Moreover, the p value from the Ljung-Box test was 0.178, also suggesting a lack of evidence for autocorrelation.

DISCUSSION

We found evidence that when gannets departed the colony we were monitoring, those that left from the nearby raft did so on the same bearing as gannets returning at that time (prediction 1; Table 1). In contrast, we did not find evidence that gannets departing directly from the colony travelled on the same bearing as returning birds. Contrary to prediction 2, we found no evidence that gannets orientated the raft to the direction of returning birds. These findings provide some support for our hypothesis that gannets use rafting to gain social information on the direction of recent prey patches. We also found that the size of the raft was influenced by time of day (prediction 5) but not by wind strength or rain (predictions 3 and 4), providing some evidence to support our second hypothesis, that abiotic factors influence rafting in gannets. Below, we discuss the use of the raft as an information centre and consider why gannet rafts are largest in the morning. Finally, we suggest that our two hypotheses may not be mutually exclusive.

The Raft as an Information Centre

Our study found a correlation between the bearings of gannets returning to the colony from foraging grounds and the bearings of birds departing from the raft to begin foraging trips. We also found that when gannets departed from the raft, their bearings were more aligned with the bearings of returning birds than the bearings of gannets departing directly from the colony. This suggests that the departure directions of rafting gannets are informed, at least in part, by the observations of returning conspecifics and that, in this sense, the raft serves as an information centre where rafting gannets engage in visual trail following. This is consistent with behaviour demonstrated by rafting Australasian Gannets (Machovsky-Capuksa et al., 2014) and rafting Guanay Cormorants (Weimerskirch et al., 2010), along with at-sea behaviour observed in Cape Gannets *Morus capensis* and Common Terns *Sternus hirundo* (Thiebault et al., 2014; Urmy, 2021).

Social information may be particularly important for birds whose prey is widely distributed and occurs in all directions, and information centres are therefore more likely to exist in species that exploit this type of prey (Mock et al., 1988; Richner & Heeb, 1995). During our observations, gannets returned to the colony from all directions, suggesting that prey patches were not concentrated in a single area. Gannets were also observed returning to the colony at all times of the day (06h00–21h00), and thus rafting gannets waiting to depart to forage would have access to a near-continuous stream of information from returning foragers.

However, there are other possible explanations for the correlation in bearings between returning birds and birds departing the raft. For example, gannets might rely on private but widely available information to locate prey patches throughout the day, such that what appears to be visual trail following is simply the result of gannets re-visiting known prey patches from which conspecifics are returning (Montevecchi et al., 2009). Alternatively, wind direction, which we did not record, could also influence departure directions (Waggitt et al., 2014). If wind direction was influencing departure direction, however, we would expect the bearings of gannets departing from the colony also to correlate with those of recently returned birds, yet we found no such correlation.

One question remains: why do gannets departing from the colony not also respond to the bearing of returning birds? It may be that rafts provide a better vantage point than the colony from which to observe returning conspecifics (Burger, 1997; Racine et al., 2012). Throughout our observations at Cape St Mary's, the gannet colony

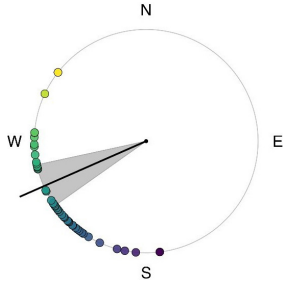

Fig. 3. Orientation of the raft in relation to the bearing of returning Northern Gannets *Morus bassanus* at Cape St Mary's, Newfoundland, Canada. The markers indicate the bearing of birds returning to the colony over 50 observation periods. The black line indicates the average orientation of the raft, with the grey shaded area representing ± 1 standard deviation.

TABLE 3
Generalised linear mixed model predicting Northern Gannet *Morus bassanus* raft size at Cape St Mary's, Newfoundland, Canada. Model conditional theoretical R^2 = 0.44

Explanatory variable	Coefficient[c]	Standard error	t value	p
Intercept	187.08	41.51		
Time (evening)[a]	−53.75	34.55	−1.56	0.13
Time (morning)[a]	**117.76**	33.27	58.71	0.001
Wind strength	−1.07	1.69	−0.64	0.53
Precipitation (rain)[b]	−5.76	39.15	10.15	0.88

[a] Reference category = afternoon
[b] Reference category = no rain
[c] Bold indicates statistically significant coefficient

was almost always shrouded in a gyre of circling gannets. These gyres comprised returning foragers, as well as birds that had returned from the raft and birds that had left nest sites. Birds departing from the colony would likely have their view of returning conspecifics significantly obstructed by these gyres. Similar gyres form at other seabird colonies and were part of the evidence leading Burger et al. (1997) to conclude that rafts are more likely than colonies to serve as information centres. It follows that rafts may also provide a better vantage point for observing departing conspecifics, helping departing gannets to reduce the risk of navigational error by leaving with other gannets departing from the raft (Simons, 2004).

Finally, we found no evidence of a correlation between the mean bearings of returning birds and the mean orientation of the raft (Fig. 3) and, therefore, no support for the use of compass rafting by gannets (prediction 2), as has been observed when Guanay Cormorants engage in visual trail following (Weimerskirch et al., 2010). In Weimerskirch et al.'s (2010) study, in which strong evidence of compass rafting was found, the cormorants occupied a small island where birds could return from foraging grounds across 360° of direction. At Cape St Mary's, however—which is a cliff-based colony on the very large island of Newfoundland—birds foraging at sea can return only within a 180° arc of the colony, as gannets do not typically fly over landmasses. Raft orientation would be less apparent across a 180° range versus a 360° range, which may account for the lack of correlation between the mean bearings of returning birds and the mean orientation of the raft at this study site. Of note, the mean bearing of the largest section of the raft was adjacent to the most populated part of the colony, suggesting that, like Manx Shearwater, gannets may also raft approximately in front of their nest site (Wilson et al., 2008).

Abiotic Influences on Rafting

The abiotic variables included in our GLMM (time of day, windspeed, and precipitation) accounted for 27% of the variation in the raft size in our data. Of the three variables included in the model, raft size was best predicted by time of day and, consistent with our prediction, the largest rafts occurred in the morning (prediction 5). Contrary to our predictions, however, wind strength and rain did not influence raft size (predictions 3 and 4), although

TABLE 4
Overview of known relevant studies into near-colony rafting, with proposed function and findings

Citation	Species	Proposed rafting function and/or findings
Burger, 1997	Common Guillemot *Uria aalge*	Social information: Most birds rafted after departure; raft suggested to be 'information halo'
Fox et al., 1997	Steller's Eider *Polysticta stelleri*	Predator avoidance: Birds rafted in reaction to overflying predators
Wilson et al., 2008	Manx Shearwater *Puffinus puffinus*	No purpose proposed: Rafts formed adjacent to nest sites and moved closer to land in the evenings
Weimerskirch et al., 2010	Guanay Cormorant *Phalacrocorax bougainvillii*	Social information: Rafts orientated to bearings of returning foragers, indicating direction of foraging grounds to departing birds
Machovksy-Capuksa et al., 2014	Australasian Gannet *Morus serrator*	Social information: Birds departing shortly after arrival of returning foragers and in same direction
Carter et al., 2016	Northern Gannet *Morus bassanus*	Rafting not correlated with nest duration attendance or with foraging trip duration or distance (but suggests bathing need, and thus rafting, may be influenced by local weather)
Granadeiro et al., 2018	Black-browed Albatross *Thalassarche melanophris*	Bathing: All birds bathed in rafting area before departing to forage
Richards et al., 2019	Manx Shearwater *Puffinus puffinus*	Predator avoidance (and influenced by wind): Birds raft closer to colony in evenings, forming 'halo' around colony, possibly to assess predation risk before returning to nests. Rafts also larger on windier days.
Kowalska O'Neil, et al., 2023	Wandering Albatross *Diomedea exulans*, Black-browed Albatross *Thalassarche melanophris*, Grey-headed Albatross *T. chrysostoma*, Light-mantled Sooty Albatross *Phoebetria palpebrata*, White-chinned Petrel *Procellaria aequinoctialis*	Environmental influences: Rafting behaviour differed considerably between study species; all study species more likely to raft in stronger winds. All study species more likely to raft on outgoing trips from colony, suggesting rafting related to plumage maintenance.
Ainley & Wilson, 2023	Penguins	Bathing and predator avoidance: Penguins typically bathe after departing the colony and before going out to sea; distance from the beach depends on whether predator is present. Additionally, on returning to the beach, if a predator is sensed, numbers accumulate well off the beach before it is safe to proceed ashore.
Present study, 2026	Northern Gannet *Morus bassanus*	Social information (and diel pattern influence): Rafting birds depart in same direction as recently returned foragers. Rafts are also largest in mornings when, possibly, need for social information is greatest.

the low prevalence of rain (n = 13) during the 64 observation periods may explain the lack of effect of rain within our GLMM. It therefore appears that these environmental factors did not influence gannet foraging behaviour at Cape St Mary's.

Gannets exhibit an obvious diel pattern to foraging activities, foraging throughout daylight hours and generally remaining inactive at night (d'Entremont & Montevecchi, 2022; Garthe et al., 1999; Hamer et al., 2000). The first opportunity that gannets have to leave the colony to forage is therefore in the morning and, because most gannets rafted after leaving the colony (73.5%; n = 230 in this study—remarkably similar to findings from both Machovsky-Capuksa et al. [2014] and Carter et al. [2016]), rafts would necessarily be largest in the morning. We also found that birds returning to the colony almost never rafted (97.67%, n = 301). Instead, returning flocks dissipated into the gyre around the colony before, presumably, returning to their nest site to provision young (of course, it is not possible to determine if some returning foragers joined the raft after joining the gyre). We can therefore assume that rafts at Cape St Mary's are composed primarily of birds that have recently left nest sites, supporting our supposition that large morning rafts are made up of birds waiting to depart to forage. Additionally, we recorded birds returning to the colony from foraging as early as 06h00. Gannets leaving to forage in the afternoon tend to remain at sea overnight, returning the following morning (Montevecchi et al., 2009). These returning gannets will relieve their waiting partners at the nest, further increasing the number of birds rafting in the morning.

Social Information and Morning Rafts

Although rafts may be largest in the morning because most birds are departing the colony to forage at that time and because most birds raft after departing the colony, this does not explain why gannets are driven to raft. Clearly, bathing is an important function of rafting. However, because gannets do not spend all their time in rafts engaged in bathing behaviour, rafting likely provides a secondary benefit. One possibility is that rafting also provides a location for birds to rest following nest attendance and before departing to forage. We suggest that there may be a connection between our social information hypothesis for rafting behaviour and the fact that rafts are largest in the morning.

Gannets have been shown to return to foraging areas where they were recently successful, demonstrating high foraging site fidelity and indicating the use of memory-based foraging tactics (i.e., private information; Montevecchi et al., 2009; Wakefield et al., 2015). However, prey fields may shift or become depleted over time. The value of private information on known foraging grounds may, therefore, be enhanced by the use of social information, helping individuals to 'fine tune' their departure directions or preventing them from leaving in directions where prey is scarce (Boyd et al., 2016; Thiebault et al., 2014). Gannets that have spent the night at the colony, away from foraging grounds, may, we suggest, be most in need of this social information. If rafting facilitates the transfer of social information on recent foraging locations, as our findings may demonstrate, it might be expected that the propensity to raft is greatest in the morning when social information is likely to be of greatest value.

It is likely that rafting serves more than one function for gannets and that, for example, the use of rafts to gain social information may have evolved from the necessity to bathe or rest on the water (Weimerskirch et al., 2010). Observations of gannets rafting, and the time spent engaged in various activities, could help to better understand the hierarchy of these functions and would be a useful area of future study.

ETHICS STATEMENT

A research permit for this study was granted by the Newfoundland Department for Environment and Climate Change. This was an observational study at a popular reserve; no disturbance was caused to the gannets or any of the nesting seabirds present at the reserve.

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AUTHOR CONTRIBUTIONS

Conceptualisation: EPT, LH. Investigation: EPT. Methodology: EPT. Project Administration: EPT. Formal analysis: EPT. Supervision: LH, AP. Writing—original draft: EPT. Writing—review & editing: all coauthors.

REFERENCES

Ainley, D. G., & Wilson, R. P. (2023). *The aquatic world of penguins: Biology of fish-birds.* Springer Nature. https://doi.org/10.1007/978-3-031-33990-5

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3–4), 227–266. https://doi.org/10.1163/156853974X00534

Amélineau, F., Péron, C., Lescroël, A., Authier, M., Provost, P., & Grémillet, D. (2014). Windscape and tortuosity shape the flight costs of northern gannets. *Journal of Experimental Biology*, *217*(Pt 6), 876–885. https://doi.org/10.1242/jeb.097915

Barta, Z., & Giraldeau, L. (2001). Breeding colonies as information centers: A reappraisal of information-based hypotheses using the producer—scrounger game. *Behavioral Ecology*, *12*(2), 121–127. https://doi.org/10.1093/beheco/12.2.121

Boyd, C., Grünbaum, D., Hunt, G. L., Punt, A. E., Weimerskirch, H. & Bertrand, S. (2016). Effectiveness of social information used by seabirds searching for unpredictable and ephemeral prey. *Behavioral Ecology*, *27*(4), 1223–1234. https://doi.org/10.1093/beheco/arw039

Burger, A. E. (1997). Arrival and departure behavior of Common Murres at colonies: Evidence for an information halo? *Colonial Waterbirds*, *20*(1), 55–65. https://doi.org/10.2307/1521764

Carter, M. I. D., Cox, S. L., Scales, K. L., Bicknell, A. W. J., Nicholson, M. D., Atkins, K. M., Morgan, G., Morgan, L., Grecian, W. J., Patrick, S. C., & Votier, S. C. (2016). GPS tracking reveals rafting behaviour of Northern Gannets (*Morus bassanus*): Implications for foraging ecology and conservation. *Bird Study*, *63*(1), 83–95. https://doi.org/10.1080/00063657.2015.1134441

Chardine, J. W., Rail, J.-F. & Wilhelm, S. (2013). Population dynamics of Northern Gannets in North America, 1984–2009. *Journal of Field Ornithology*, *84*(2), 187–192. https://doi.org/10.1111/jofo.12017

Danchin, E., & Wagner, R. H. (1997). The evolution of coloniality: The emergence of new perspectives. *Trends in Ecology and Evolution*, *12*(9), 342–347. https://doi.org/10.1016/S0169-5347(97)01124-5

Davies, N. B., Krebs, J. R., & West, S. A. (2012). *An introduction to behavioural ecology* (4th ed.). Wiley-Blackwell.

Davoren, G., Montevecchi, W., & Anderson, T. (2003). Search strategies of a pursuit-diving seabird and the persistence of prey patches. *Ecological Monographs*, *73*(3), 463–481. http://dx.doi.org/10.1890/02-0208

d'Entremont, K. J. N., & Montevecchi, W. A. (2022). Nocturnal flight activity by Northern Gannets *Morus bassanus* in response to predator disturbance. *Marine Ornithology*, *50*(2), 159–163. http://doi.org/10.5038/2074-1235.50.2.1485

d'Entremont, K., Davoren, G., Walsh, C., Wilhelm, S., & Montevecchi, W. (2022) Intra- and inter-annual shifts in foraging tactics by parental northern gannets *Morus bassanus* indicate changing prey fields. *Marine Ecology Progress Series*, *698*, 155–170. https://doi.org/10.3354/meps14164

De Pascalis, F., Austin, R. E., Green, A., Arnould, J. P. Y., Imperio, S., Maugeri, M., Haakonsson, J., Cecere, J. G., & Rubolini, D. (2021). Influence of rainfall on foraging behaviour of a tropical seabird. *Behavioural Ecology*, *33*(2), 343–351. https://doi.org/10.1093/beheco/arab134

European Food Safety Authority, European Centre for Disease Prevention and Control, European Reference Laboratory for Avian Influenza, Adlhoch, C., Fusaro, A., Gonzales, J. L., Kuiken, T., Marangon, S., Niqueux, É, Staubach, C., Terregino, C., Aznar, I., Muñoz Guajardo, I., & Baldinelli, F. (2022). Avian influenza overview March–June 2022. *EFSA Journal, 20*(8), Article e07415. https://doi.org/10.2903/j.efsa.2022.7415

Evans, R. M., & Welham, C. V. J. (1985). Aggregative mechanisms and behavior in ring-billed gulls departing from a colony. *Canadian Journal of Zoology*, *63*(12), 2767–2774. https://doi.org/10.1139/z85-412

Evans, J. C., Votier, S. C., Dall, S. R. X. (2015). Information use in colonial living. *Biological Reviews*, *91*(3), 658–672. https://doi.org/10.1111/brv.12188

Finney, S. K., Wanless, S., & Harris, M. P. (1999). The effect of weather conditions on the feeding behaviour of a diving bird, the Common Guillemot *Uria aalge*. *Journal of Avian Biology*, *30*(1), 23–30. https://doi.org/10.2307/3677239

Fisher, J., & Lockler, R. M. (1954). *Sea-birds*. Collins.

Fox, A. D., & Mitchell, C. (1997). Rafting behaviour and predator disturbance to Steller's Eiders *Polysticta stelleri* in northern Norway. *Journal für Ornithologie*, *138*(1), 103–109. https://doi.org/10.1007/BF01651656

Garthe, S., Grémillet, D., & Furness, R. W. (1999). At-sea-activity and foraging efficiency in chick-rearing northern gannets *Sula bassana*: A case study in Shetland. *Marine Ecology Progress Series*, *185*, 93–99. https://doi.org/10.3354/meps185093

Garthe, S., Montevecchi, W. A., & Davoren, G. K. (2007). Flight destinations and foraging behaviour of northern gannets (*Sula bassana*) preying on a small forage fish in a low-Arctic ecosystem. *Deep-Sea Research II*, *54*(3–4), 311–320. https://doi.org/10.1016/j.dsr2.2006.11.008

Gori, D. F. (1988). Colony-facilitated foraging in Yellow-Headed Blackbirds: Experimental evidence for information transfer. *Ornis Scandinavica*, *19*(3), 224–230. https://doi.org/10.2307/3676563

Granadeiro, J. P., Campioni, L., & Catry, P. (2018). Albatrosses bathe before departing on a foraging trip: Implications for risk assessments and marine spatial planning. *Bird Conservation International*, *28*(2), 208–215. https://doi.org/10.1017/S0959270916000459

Hamer, K. C., Phillips, R. A., Wanless, S., Harris, M. P., & Wood, A. G. (2000). Foraging ranges, diets and feeding locations of gannets *Morus Bassanus* in the North Sea: Evidence from satellite telemetry. *Marine Ecology Progress Series*, *200*, 257–264. https://doi.org/10.3354/meps200257

Kowalska O'Neil, E. W. M, Frankish, C. K, & Phillips, R. A. (2023). Rafting behaviour of albatrosses and petrels at South Georgia. *Polar Biology*, *46*, 597–610. https://doi.org/10.1007/s00300-023-03146-4

Lane, J., Spracklen, D., & Hamer, K. (2019). Effects of windscape on three-dimensional foraging behaviour in a wide-ranging marine predator, the Northern Gannet. *Marine Ecology Progress Series*, *628*, 183–193. https://doi.org/10.3354/meps13089

Machovsky-Capuska, G. E., Hauber, M. E., Libby, E., Amiot, C., & Raubenheimer, D. (2014). The contribution of private and public information in foraging by Australasian gannets. *Animal Cognition*, *17*(4), 849–858. https://doi.org/10.1007/s10071-013-0716-x

McSorley, C. A., Dean, B. J., Webb, A., & Reid, J. B. (2003). *Seabird use of waters adjacent to colonies: Implications for seaward extensions to existing breeding seabird colony Special Protection Areas* (JNCC Report No. 329). Joint Nature Conservation Committee.

Mock, D. W., Lamey, T. C., & Thompson, D. B. A. (1988). Falsifiability and the information centre hypothesis. *Ornis Scandinavica*, *19*(3), 231–248. https://doi.org/10.2307/3676564

Montevecchi, W., Benvenuti, S., Garthe, S., Davoren, G., & Fifield, D. (2009). Flexible foraging tactics by a large opportunistic seabird preying on forage- and large pelagic fishes. *Marine Ecology Progress Series*, *385*, 295–306. https://doi.org/10.3354/meps08006

Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of the Royal Society Interface*, *14*(134), Article 20170213. https://doi.org/10.1098/rsif.2017.0213

Nelson, B. (2002). *The Atlantic gannet* (2nd ed.). Fenix Books.

Pettex, E., Bonadonna, F., Enstipp, M. R., Siorat, F., & Grémillet, D. (2010). Northern gannets anticipate the spatio–temporal occurrence of their prey. *Journal of Experimental Biology*, *213*(14), 2365–2371. https://doi.org/10.1242/jeb.042267

Pistorius, P. A., Hindell, M. A., Tremblay, Y., & Rishworth, G. M. (2015). Weathering a dynamic seascape: Influences of wind and rain on a seabird's year-round activity budgets. *PLOS One*, *10*(11), Article 0142523. https://doi.org/10.1371/journal.pone.0142623

Racine, F., Giraldeau, L., Patenaude-Monette, M., & Giroux, J. (2012). Evidence of social information on food location in a ring-billed gull colony, but the birds do not use it. *Animal Behaviour*, *84*(1), 175–182. https://doi.org/10.1016/j.anbehav.2012.04.028

Richards, C., Padget, O., Guilford, T., & Bates, A. E. (2019). Manx shearwater (*Puffinus puffinus*) rafting behaviour revealed by GPS tracking and behavioural observations. *PeerJ*, *7*, Article e7863. https://doi.org/10.7717/peerj.7863

Richner, H., & Heeb, P. (1995). Is the information center hypothesis a flop? *Advances in the Study of Behaviour*, *24*, 1–45. https://doi.org/10.1016/S0065-3454(08)60391-5

Sassi, Y., Nouziéres, B., Scacco, M., Tremblay, Y., Duriez, O., & Robira, B. (2024). The use of social information in vulture flight decisions. *Royal Society Proceedings B*, *291*(2018), Article 202311729. https://doi.org/10.1098/rspb.2023.1729

Sánchez-Román, A., Gómez-Navarro, L., Fablet, R., Oro, D., Mason, E., Arcos, J. M., Ruiz, S., & Pascual, A. A. (2019). Rafting behaviour of seabirds as a proxy to describe surface ocean currents in the Balearic Sea. *Nature, Scientific Reports*, *9*, Article 177775. https://doi.org/10.1038/s41598-018-36819-w

Schmidt, K. A., Dall, S. R. X., & Van Gils, J. A. (2010). The ecology of information: An overview on the ecological significance of making informed decisions. *Oikos*, *119*(2), 304–316. https://doi.org/10.1111/j.1600-0706.2009.17573.x

Simons, A. M. (2009). Many wrongs: The advantage of group navigation. *Trends in Ecology and Evolution*, *19*(9), 453–455. https://doi.org/10.1016/j.tree.2004.07.001

Sutherland, W. J. (2002). *Ecological census techniques: A handbook* (2nd ed.). Cambridge University Press.

Thiebault, A., Mullers, R., Pistorius, P., Meza-Torres, M. A., Dubroca, L., Green, D., & Tremblay, Y. (2014). From colony to first patch: Processes of prey searching and social information in Cape Gannets. *The Auk*, *131*(4), 595–609. https://doi.org/10.1642/AUK-13-209.1

Urmy, S. S. (2021). Visual trail following in colonial seabirds: Theory, simulation, and remote observations. *Ecological Monographs*, *91*(1), Article 01429. https://doi.org/10.1002/ecm.1429

Waggitt, J. J., Briffa, M., Grecian, W. J., Newton, J., Patrick, S. C., Stauss, C., & Votier, S. C. (2014). Testing for sub-colony variation in seabird foraging behaviour: Ecological and methodological consequences for understanding colonial living. *Marine Ecology Progress Series*, *498*, 275–285. https://doi.org/10.3354/meps10628

Wakefield, E. D., Bodey, T. W., & Bearhop, S. (2013). Space partitioning without territoriality in gannets. *Science*, *341*(6141), 68–70. https://doi.org/10.1126/science.1236077

Wakefield, E. D., Cleasby, I. R., Bearhop, S., Bodey, T. W., Davies, R. D., Miller, P. I., Newton, J., Votier, S., & Hamer, K. C. (2015). Long-term individual foraging site fidelity—Why some gannets don't change their spots. *Ecology*, *96*(11), 3058–3074. https://doi.org/10.1890/14-1300.1

Wakefield, E. D., Furness, R. W., Lane, J. V, Jeglinski, J. W. E, & Pinder, S. (2019). Immature gannets follow adults in commuting flocks providing a potential mechanism for social learning. *Journal of Avian Biology*, *50*(10), Article e02164. https://doi.org/10.1111/jav.02164

Ward, P., & Zahavi, A. (1973). The importance of certain assemblages of birds as "information-centres" for food-finding. *Ibis*, *115*(4), 517–534. https://doi.org/10.1111/j.1474-919X.1973.tb01990.x

Warwick-Evans, V. C., Atkinson, P. W., Robinson, L. A., & Green, J. A. (2016). Predictive modelling to identify near-shore, fine-scale seabird distributions during the breeding season. *PLOS One*, *11*(3), Article e0150592. https://doi.org/10.1371/journal.pone.0150592

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep-Sea Research II*, *54*(3-4), 211–223. https://doi.org/10.1016/j.dsr2.2006.11.013

Weimerskirch, H., Bertrand, S., Silva, J., Marques, J. C., & Goya, E. (2010). Use of social information in seabirds: Compass rafts indicate the heading of food patches. *PLOS One*, *5*(3), Article e9928. https://doi.org/10.1371/journal.pone.0009928

Wilson, L. J., McSorely, C. A., Gray, C. M., Dean, B. J., Dunn, T. E., Webb, A., & Reid, J. B. (2008). Rafting behaviour of Manx Shearwaters *Puffinus puffinus*. *Seabird*, *21*, 85–92. https://doi.org/10.61350/sbj.21.85

Wilson, L. J., McSorely, C. A., Gray, C. M., Dean, B. J., Dunn, T. E., Webb, A., & Reid, J. B. (2009) Radio-telemetry as a tool to define protected areas for seabirds in the marine environment. *Biological Conservation*, *142*(8), 1808–1817. https://doi.org/10.1016/j.biocon.2009.03.019