

Use of Social Information in Seabirds: Compass Rafts Indicate the Heading of Food Patches

Henri Weimerskirch^{1*}, Sophie Bertrand^{2,3}, Jaime Silva³, Jose Carlos Marques³, Elisa Goya³

1 Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, Villiers en Bois, France, **2** Centre de Recherche Halieuthique, Institut de Recherche pour le Développement, Sète, France, **3** Dirección de Recursos Pelagicos, Instituto del Mar del Perú, Callao, Peru

Abstract

Ward and Zahavi suggested in 1973 that colonies could serve as information centres, through a transfer of information on the location of food resources between unrelated individuals (Information Centre Hypothesis). Using GPS tracking and observations on group movements, we studied the search strategy and information transfer in two of the most colonial seabirds, Guanay cormorants (*Phalacrocorax bougainvillii*) and Peruvian boobies (*Sula variegata*). Both species breed together and feed on the same prey. They do return to the same feeding zone from one trip to the next indicating high unpredictability in the location of food resources. We found that the Guanay cormorants use social information to select their bearing when departing the colony. They form a raft at the sea surface whose position is continuously adjusted to the bearing of the largest returning columns of cormorants. As such, the raft serves as a compass signal that gives an indication on the location of the food patches. Conversely, Peruvian boobies rely mainly on personal information based on memory to take heading at departure. They search for food patches solitarily or in small groups through network foraging by detecting the white plumage of congeners visible at long distance. Our results show that information transfer does occur and we propose a new mechanism of information transfer based on the use of rafts off colonies. The use of rafts for information transfer may be common in central place foraging colonial seabirds that exploit short lasting and/or unpredictably distributed food patches. Over the past decades Guanay cormorants have declined ten times whereas Peruvian boobies have remained relatively stable. We suggest that the decline of the cormorants could be related to reduced social information opportunities and that social behaviour and search strategies have the potential to play an important role in the population dynamics of colonial animals.

Citation: Weimerskirch H, Bertrand S, Silva J, Marques JC, Goya E (2010) Use of Social Information in Seabirds: Compass Rafts Indicate the Heading of Food Patches. PLoS ONE 5(3): e9928. doi:10.1371/journal.pone.0009928

Editor: Brian Gratwicke, Smithsonian's National Zoological Park, United States of America

Received: December 21, 2009; **Accepted:** March 9, 2010; **Published:** March 29, 2010

Copyright: © 2010 Weimerskirch et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Funding: This study was funded by CNRS-INEE (Centre National de la Recherche Scientifique - Institut National Ecologie et Environnement), IRD (Institut de Recherche pour le Développement) and IMARPE (Institut del Mar del Peru). The funders had no role in study design, data collection and analysis, decision to publish or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

* E-mail: henriw@cebc.cnrs.fr

Introduction

Animal living together in a group is a certain period of their life can use personal information obtained from experience and social information from the behaviour of conspecifics to make decisions [1,2]. The balance between personal and social information in decision making is likely to affect the optimal adjustment of behaviour to the most reliable information. Today evidence indicates that social information is common in nature [3,4] and the large group has led to the use of social information and improve the ability to make collective decisions compared to individuals [5].

The high density of individuals and millions of seabirds gather together in a single colony has a large impact on the behaviour, and in the decision about the intensity of individual concentration in the same place. Apart from a decrease in the concentration of food resources, colonies are considered as an efficient way to limit predation [6], reduce the energy cost (diets, etc.), reduce the infection, competition for food resources [7]. Before the concept of social information was developed [4], Ward and Zahavi [8] suggested that colonies may be a source of

information exchange about the location of food, although not a true information centre hypothesis (ICH). Because seabirds often feed in a place and time [6,9], breeding in colonies could provide the opportunity for individuals to obtain information about the location of favourable food patches by watching the behaviour of other individuals when returning from, or leaving feeding grounds. The empirical studies have evidenced that the hypothesis came to mind conclusion (see also in Richner and Heeb (1995) [10]). However, most empirical studies have focused on the demonstration of individual information from the colony to the individual foraging heading of feeding grounds, but the information exchange may also include the colony and be based on the observation of the returning individuals [11,12].

Several alternative hypotheses, related to the ICH, have been proposed to explain the high density of breeding in large groups, based on the individual decision. The local enhancement hypothesis [13,14] suggests that the increase in density of birds foraging from a colony improve the probability of discovering unpredictable food patches. The decision centre hypothesis [10,15] predicts that communal feeding is important for collective foraging at a feeding patch, the effect of individual

congenere a colonie. O he i e indi id al ma impl e
pe onal info ma ion ba ed on pa fo aging e pe ience and
memo [16] o e n o fo aging g and. Thi a e g i
ela i el common hen eabi d ea ch fo e a ce pa iall
agg ega ed in a p edic able a [9].

Mo e ecen modelling die ha e a gge ed ha he differen
h po he e ela ed o ICH a e p obabl no e e i e, and ha ld
be on ide ed in a common fame o k [17], and ha eabi d
ma e a mi e of ea ching a egie [18]. The efo e he ma
e ocial info ma ion a ell a pe onal info ma ion o a o
ma ihi e food ba gh o he off ping and minimi e ime pen
comm ing and ea ching [19,20]. Ho e e , he e i a need fo
mo e mpi cal die , in pa id la ho e ba ed on he d of
indi id al beh i d om he coln o food pa che . The e
die a e diffic l on de ak in nat al condi ion , h i h he
ad ance in eleme minia i a ion ha e opened a p ne
me hod o mpi cally add e he e e ion [21].

C ana co mo an and Pe ian boobie a e he main g ano
p oace b eeding along he Pe ian coa . The concen a e in
e ge colonie ha hi o icall cal d g a p d ed of ha and
of indi id al in a ngle colon , epe en ing one of he old
mo pec ad la aggega ion of eabi d [22]. The el mainl
on Pe ian ancho ([23,24] ha ha ained, n il econ l , he
old la ge ngle-pecie fi he [25]. The black p maged
co mo an , ne in e emel den e colonie and a e ocial
fo age fo ming endle col n mo ing fom colonie o feeding
g and he ea he hi e p maged boobie b eed in la ge, l
le den e colonie [22,26]. O e he pa 50 ea , C ana
co mo an ha e d ama icall dec ea ed fom c.21 million bi d

a statistical analysis using the *Package circular* version 0.3.8 (Correlation Coefficient for Angular Variable, Watson's sample Test of Uniformity) in R.

Results

When leaving chick gano bird a typical central place foraging, making foraging trip from the nest to a rich food area. When one parent forages a sea, the parent guards the chick until it is relieved by the evening member of the pair. Both species foraged individually during the daytime. Individual tracking shows that both booby and cormorant use a 'looping' or 'return' type of foraging, leaving the colony on a path that bears a heading that is kept until each feeding one and then return to the colony, making heading a distance and then a parallel, with an angle <10° (Fig. 1). The 'looping' or 'return' type of foraging is the 'Looping Trip' where the bird changes direction several times before feeding (often) and then returns to the colony from a bearing different from that taken during the approach, with an angle >10° (Fig. 1). Feeding one is clearly visible, as indicated by a change in bearing and a change in bearing (Fig. 1). Feeding one is found in all Return Trip one and in 81.19% of Looping Trip ($\chi^2_1 = 3.3, P = 0.0211$) indicating that in most birds have encountered a prey patch. In the morning, all birds captured were returning from the sea edge, as indicated by the main (mostly) confirming that birds return only after a successful foraging. Return Trip represent 62% of trips for Galapagos cormorant and only 39.8% for booby.

($\chi^2_1 = 5.8, P = 0.0163$). The duration of foraging trip is longer for cormorant than for booby (Mixed ANOVA, 2.0 ± 0.8 h vs 1.2 ± 0.5 h, $F_{1,39} = 32.9, P < 0.001$) and a longer Looping Trip than for Return Trip (1.3 ± 0.8 h vs 1.7 ± 0.6 h for cormorant and 1.4 ± 0.6 h vs 0.9 ± 0.3 h for booby). The maximum range is similar for both species (20.2 ± 11.5 km for booby vs 18.9 ± 6.1 km for cormorant, $F_{1,9} = 0.5, P = 0.480$), but Looping Trip had longer range than Return Trip (21.1 ± 9.7 km vs 16.6 ± 5.8 , $F_{1,39} = 10.4, P = 0.004$). In both species, feeding one is seen at the same location from one trip to the next in one case for each species, with a long distance between successive feeding one (distance between successive feeding one = 19.9 ± 11 km for cormorant and 16.9 ± 12.2 km for booby, $F_{1,29} = 0.5, P = 0.461$). There is no difference in the feeding one distance between successive feeding one during the same day, or from one day to the next.

The bearing taken by individual tracked birds departing from the colony or returning from the feeding one is of great interest. Birds observed to be mainly directed towards the sea and then, with a few exceptions, heading towards the sea (Fig. 2), and do not differ between species (Watson's sample Test, $U = 0.922, P = 0.187$). Individual birds do not change their direction from one trip to the next (Fig. 1). For GPS tracked Galapagos cormorant, the correlation between the bearing when leaving the island and the bearing of the next day's trip (Table 1) confirms that birds do not return to the same feeding one from one trip to the next. For booby, there is a tendency for birds to take the same direction than that of the previous day's trip, only when successive trips are carried out the same day (Table 1).

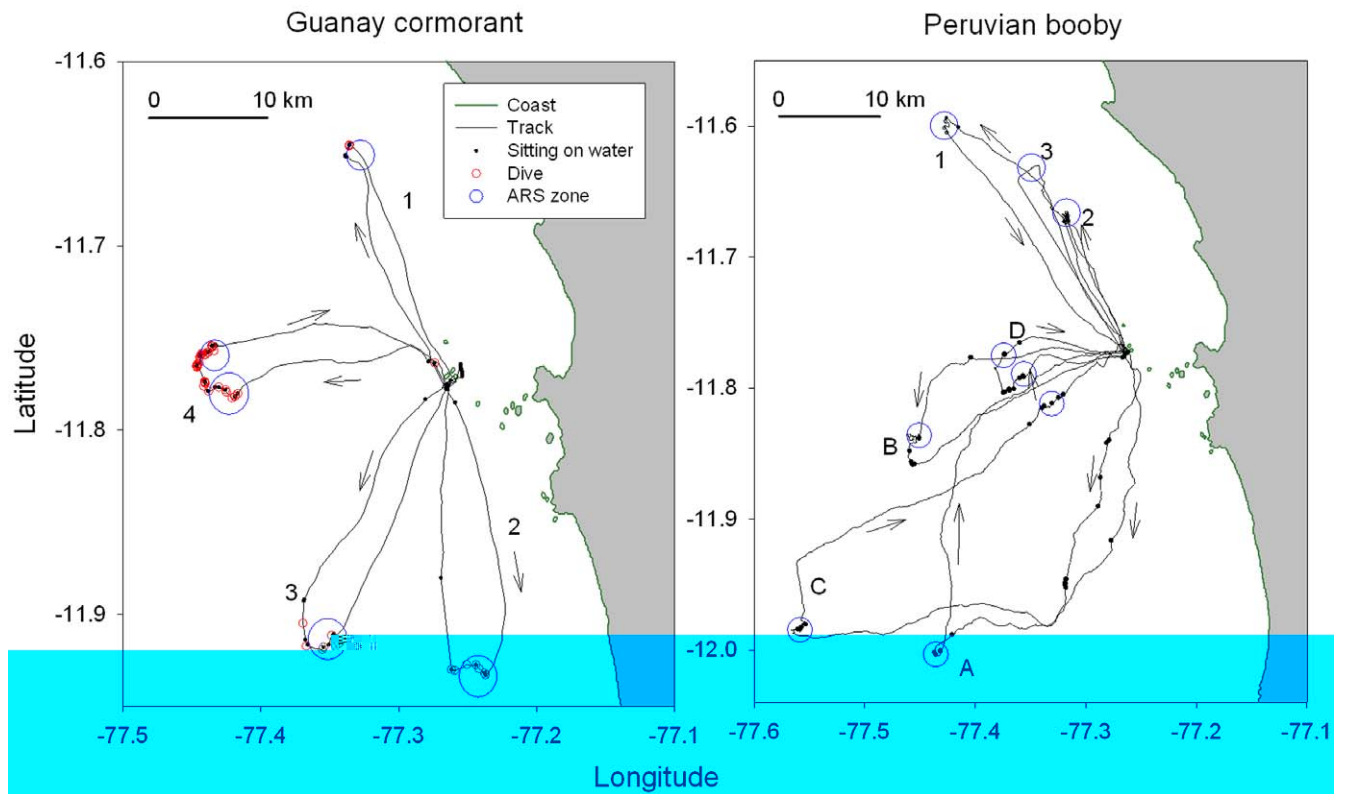
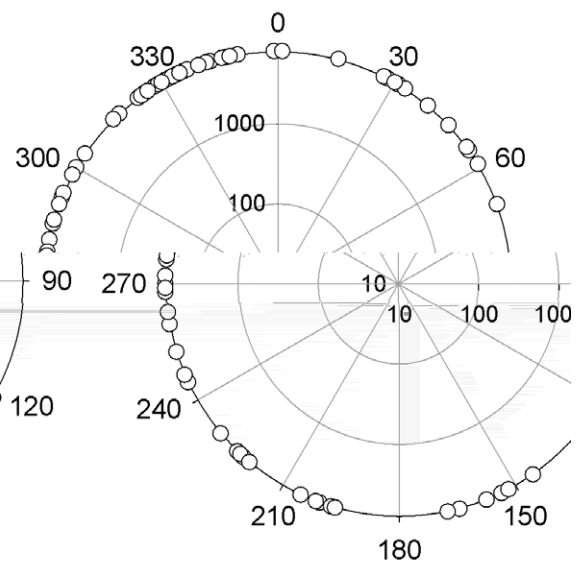
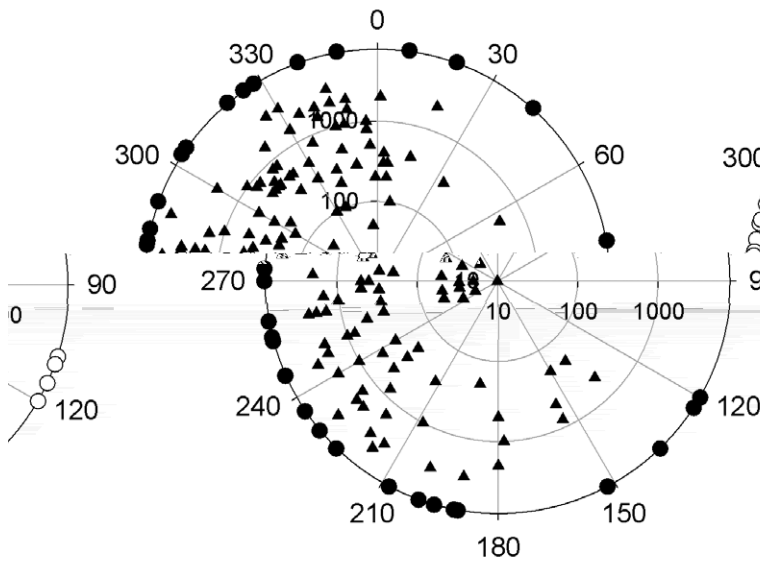


Figure 1. Foraging trips of Guanay cormorants (left) and Peruvian boobies (right) tracked with GPS. Left: four successive return trips of a Guanay cormorant (1–4). Right: three successive return trips of a Peruvian booby (1–3) and four successive tracks (A–D) of a second individual Peruvian booby (looping course A and C, return trip B and D). Arrows indicate the flight direction; dots indicate sitting on the water, small red circles indicate the deep diving events, blue circles indicate zones of area restricted search (ARS). doi:10.1371/journal.pone.0009928.g001

Departure guanay cormorants

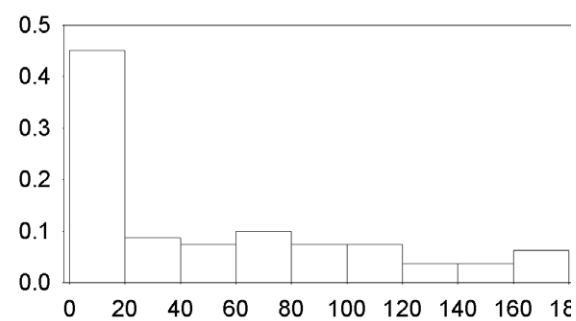
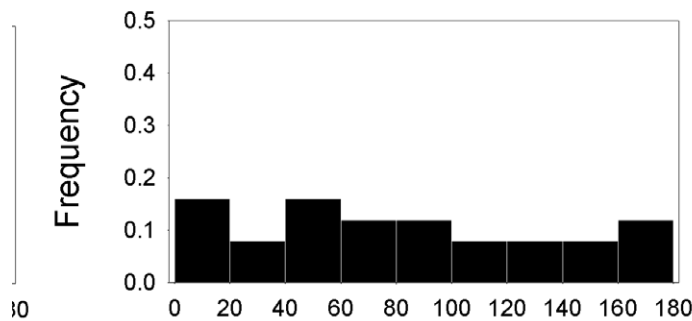
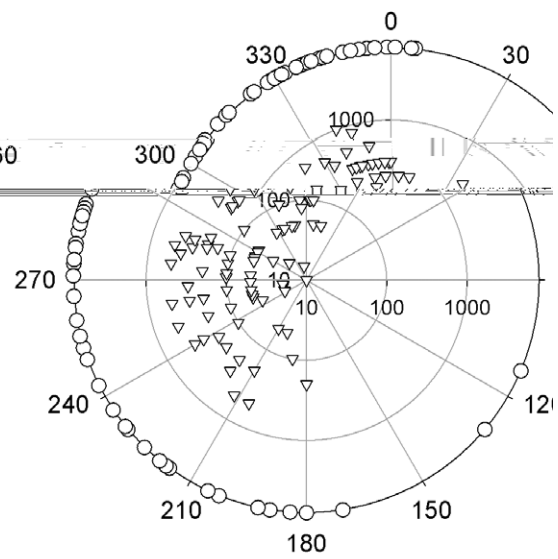
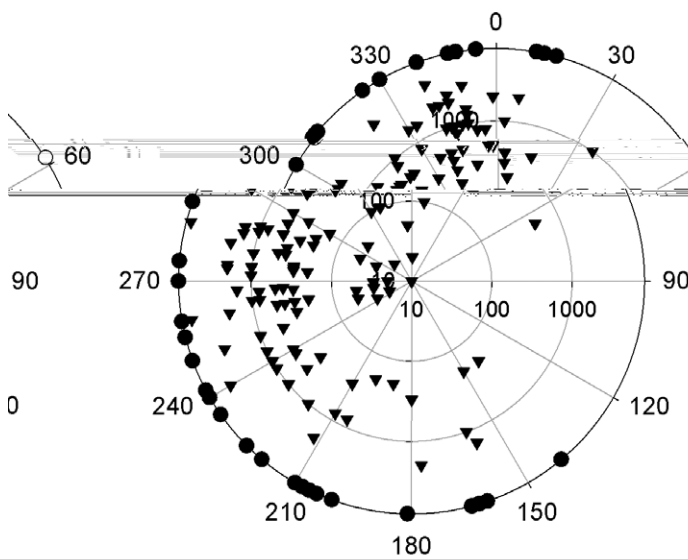
Departure Peruvian Boobies



s

Return Guanay cormorants

Return Peruvian boobie



Difference in angle (°) between return bearing and next departure bearing of the same individual

Figure 2. Bearings taken by groups according to the centre of the island and difference in angle between the return bearing and the departure bearing of Guanay cormorants and Peruvian boobies. Upper four figures: Bearing (in°) taken by groups according to the centre of the island and size of groups (from 10 to 10,000) of Guanay cormorants (black) and Peruvian boobies (white) leaving the island (▲) and returning to the island (▼). The circles indicate the bearings at departure and when returning taken with GPS. Lower two figures: difference in angle between the return bearing and the departure bearing during the next foraging trip of individuals tracked with GPS. doi:10.1371/journal.pone.0009928.g002

Individual tracking of *Guana comoman* has affected departing colonies, birds circle the island and then land on a 300 m, 2 km off the island for a few seconds before heading for a parallel direction (Fig. 3a). This coordinated behaviour has been observed in all tracked birds. Objections from the angle point confirm birds circled and the island in small gaps, and then joined the air. At an intermediate stage 305±163 individuals on the air (range 50-1000). Remarkably, the aerial angle of a bird and the island once, the time interval position continually changed (Fig. 4). The affected one-hour after sunrise, remained open through the day and a few minutes later, before noon, when no more birds were leaving (Fig. 4). Since birds are continuous landing, haking and taking off, the air can be seen from a long distance from the colony at a point of foaming sea (Fig. 3, 5). Individual birds are seen in the air for 5-30 seconds and then look off in the gaps, during one of the other, all in the same direction, forming long columns of birds in gaps, especially in the parallel to the horizon. In the interval, departing gaps in columns flew above the sea surface, the aerial bearing gaps in columns flew at an altitude of 10-30 m above sea surface. The air aligned with the column of birds during flight from the sea, specifically in the large bearing gaps (Circulation coefficient, $r = 0.610$, $F = 4.6$, $P < 0.001$, Fig. 3). Raising off the colony a departure does not occur in Peruvian boobies: they departed only in small gaps of a few birds, and then landed alone or in small or medium sized gaps (Fig. 2), of an included in the large formation of *Guana comoman*. The bearing of the large gaps of *comoman* and booby were strongly correlated (Circulation coefficient, $r = 0.981$, $F = 6.6$, $P < 0.001$).

Discussion

The first, and most important, result of this study indicates clearly that Information Transfer occurs in a colonial seabird through a specific signalling behaviour, before forming a column. The function of this behaviour appears to be a signal that is visible from the colony or from birds that are circling in flight the island (Fig. 3b), pointing the heading to be taken by birds leaving the colony. During this process, *Guana comoman* relies on the information obtained from returning conspecifics. The effect of the platform of a signal on the conspecific

[15]. It is remarkable to note that *Guana comoman* leaving the colony join the column before heading for feeding gaps and before landing and from the air the aerial probability of departure bearing of the incoming column has a high value. The *Guana comoman* aerial information made available from the large column during formation of a parallel path. This is possible only because the majority of the birds have been collected in a parallel path that has been reached either directly by a Return Trip, or after a long time of circling through a Looping Trip. Before noon the birds had found a food patch, they entered in a straight line of the colony making the heading of the incoming column a reliable social information. The social information is an effect of the communication and departed continuously through the alignment of the column after the ending large column (i.e. probability of the movement collected gaps).

After a landing the chick at the colony, birds are alerted by the parents and then a few birds joining the column. The effect of the aerial departure of the most recent information available from conspecifics during formation of a feeding patch. Completion of the had observed on the information memo of the parents, the information would be departed, because of the time spent ending the chick. This makes the effect of information centre has predicted that the location of a food patch would allow a leader to enter in [8]. For *Guana comoman*, the basic condition required for a colony to operate as an information centre is a well filled, i.e. food patches are ephemeral and a leader is available. Colony members can easily detect a departure, no direct from the colony but from the nearby column [7,8,10]. This foraging strategy has probably been selected for the exploitation of food resources through the direction and availability according to the central place colony may change rapidly over time. The characteristics apply to the main part of the seabird, the Peruvian anchovy, an emblematic and an epipelagic fish, particularly in pace and in time [32]. The location of patches available for gaps and birds probably changed continuously as gaps were continuously change in flight direction from one trip to the next in the case of *Guana comoman*, but it also applies to booby. When birds following columns are on a parallel path that has been depleted, they depart from the end of each foraging parallel path and then probably enter in Looping Trip. Birds enter the colony from

Table 1. Circular correlation coefficients between angles for Guanay cormorants and Peruvian boobies fitted with GPS.

Test for:	Foraging flight bearings	Guanay cormorant			Peruvian boobies		
		Coeff	Stat	P	Coeff	Stat	P
Parallelism	Departure trip 1 vs Return trip 1	0.90	4.8	<0.001	0.781	6.6	<0.001
Persistence	Departure trip 1 vs Departure trip 2	0.178	0.9	0.362	0.02	0.2	0.862
Predictability (all days combined)	Return trip 1 vs Next Departure trip 2	0.202	1.0	0.311	0.189	1.4	0.147
Predictability (same day only)	Return trip 1 vs Next Departure trip 2	0.296	1.1	0.265	0.305	2	0.052

doi:10.1371/journal.pone.0009928.t001



Figure 3. Movements of a Guanay cormorant in the vicinity of the colony and view from the sea of a compass raft. (Left) Fine scale movements of a Guanay cormorant tracked by GPS at 1 sec interval in the vicinity of Isla Pescadores (in grey). Two successive foraging trips (1 and 2) from the nest (black circle). The location of the compass raft visited after departure from the colony is indicated by a circle (circle) and the arrows indicate flight direction. (Right) Photograph taken from the sea of a compass raft, with the colonies of seabirds on Isla Pescadores in the back ground. doi:10.1371/journal.pone.0009928.g003

...the next patch, i.e. from a different bearing, has indeed been the compass bearing which then changes direction to adjust to the new bearing of incoming column.

The behaviour of coming before heading to feeding ground and acting as a decision point, unlike of the completely signalling performed by Raven to a conspecific [33]. In seabird, the signalling through arriving could have evolved from the necessity

for birds to drink and a high probability of a high the colony bearing of brooding chick. In Canada, common high function is a high marginal since a minority of the birds joining the compass raft all the time to drink before taking off. The use of arriving information can be probably occur in the seabird species. Indeed many species of colonial seabirds such as albatross, alcid or gannet form a raft off the colony before



Figure 4. Changes in the bearings according to the centre of the island of the compass raft (circle) and of the departing (▲) and returning (▼) groups of Guanay cormorants during two consecutive days. In some cases, when opposing arrows overlay, they appear as a star. doi:10.1371/journal.pone.0009928.g004



Figure 5. View from the summit of the island showing part of a large aggregation of nesting guano birds on Isla Pescadores, with compass raft at sea. The photograph shows part of the seabird aggregations dominated by Guanay cormorants (black plumage), with Peruvian boobies (white plumage) on the edge of the main groups of cormorants. The black arrow indicates the location of the compass raft at sea. doi:10.1371/journal.pone.0009928.g005

heading for the sea, but the arrival of information through which has been overlooked of fact. In Montealegre [12], aggregated information can be passed in the colony itself. He noted that 69% of the arriving birds probably come from the colony before heading to the sea and he suggested that birds flying over the ocean in the vicinity of the colony might be well positioned to gain information on the location of pre-emption [12,34]. Observation on albatrosses also indicates that before departing for the sea, birds fly in a compass raft off the colony before taking off in small groups, often following a leading individual (H.W. Perrin observation). Sea-chasing albatrosses may also be different from the same species according to the species. For example, in Montealegre, compass rafts are probably used when patches are unpredictable [12] but memory and local enhancement are used when pre-emption is predictable and reliable over long periods of time [18]. Theoretically, the coincidence of different sea-chasing albatrosses in the same patch would be a valuable egg [17].

A second important aspect of this study has been the high colonial species, breeding on the same site and feeding on the same prey, can have different sea-chasing strategies. When leaving the colony, individuals of each species based their decision to take a patch based on being different, either by being a conspecific conspecific and the compass raft, or by being memory personal observation. The evidence of different sea-chasing strategies is probably related to the fact that each species has a different prey. A conspecific may have a different prey that makes them a different species and form a different feeding group. The social feeding has a different foraging in immediate groups for a different prey. The different large numbers of fish shoals depend on 10.5 m (H.W. Perrin observed [35]) of different species [26]. The different main social information and the colony are different, including conspecific through the compass raft. We did not find evidence of information transfer between conspecific in boobies which did not form a raft off the colony. Peruvian booby has a different prey, compared to a

long distance when in flight or plunging, which probably favors local enhancement [36,37]. The large colonies of albatrosses in small groups and the main social information when making a decision about heading. The only feed on prey available close to the surface (average 2 m, maximum 6 m H.W. Perrin observed) and can fly in small groups (Perrin observation, [26]). While off shore they can congregate in large numbers through the conspecific of the individual has probably been observed foraging [7,37]. The observation has Peruvian booby tend to head off the decision taken when they entered the colony and the albatrosses, aggregated through personal information, which is a memory-based decision [31]. However, they almost never enter the same feeding site from one individual to the next, and could take their heading and each neighboring patch because the original one is depleted or no longer available.

We found no evidence that information on decision being of food patches may be obtained from the conspecific at sea and the colony. Since booby leave the colony of albatrosses is a possibility of the conspecific of the compass raft of the column of conspecific, but the albatrosses booby tend to form the same decision than conspecific, often in small groups included in the large column of conspecific. However, off shore they are a different piece of evidence that aggregated through conspecific, which a booby join feeding group of conspecific and the plunging booby conspecific are an alternative signal for the albatross conspecific [26].

Historically, Conspecific conspecific tend to be in immediate abundance than Peruvian booby but no data about conspecific have similar population size, with 2 million birds of each species [27]. In the early 1970s, the conspecific of albatrosses were impacted by the unbroken column of Conspecific conspecific heading from the colony to the feeding ground [22]. The decision of albatrosses to work in the 1970s probably led to the crash of the conspecific population at this time [27], which has coincided with the decline of the conspecific, the sea Peruvian booby, which feed on the same prey, has a

