



**HAL**  
open science

# Raking the ocean surface: new patterns of coordinated motion in seabirds

Camille Assali, Nicolas Bez, Yann Tremblay

► **To cite this version:**

Camille Assali, Nicolas Bez, Yann Tremblay. Raking the ocean surface: new patterns of coordinated motion in seabirds. *Journal of Avian Biology*, 2020, 51 (6), 10.1111/jav.02258 . hal-03405001

**HAL Id: hal-03405001**

**<https://hal.umontpellier.fr/hal-03405001>**

Submitted on 27 Mar 2023

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

# Raking the ocean surface: new patterns of coordinated motion in seabirds

Camille Assali, Nicolas Bez and Yann Tremblay

*C. Assali* (<https://orcid.org/0000-0003-2957-2910>) ✉ ([camille.assali@gmail.com](mailto:camille.assali@gmail.com)), *N. Bez and Y. Tremblay*, MARBEC, IRD, Univ. Montpellier, Ifremer, CNRS, Sète, France.

Coordinated movements of seabirds exploiting a prey patch are known to increase prey encounter and capture rates of individuals. These behaviours, based on effective cooperation between seabirds, have only been reported at small scale, i.e. the scale of the prey patch. However, the efficient prey exploitation by seabirds in vast oceans require larger scale processes such as information transfers between individuals. Indeed, information transfers between foraging seabirds (e.g. changes in behaviour) reduce their search cost while increasing their prey encounter rate. Whether or not these information transfer processes imply active cooperation is unknown. Using images from fishing boat radars in the eastern tropical Atlantic, we show the existence of frequent medium-scale patterns of coordinated flights of seabird groups, consisting in seabird fronts ('rake' patterns) of 0.3–4.4 km width, displacing cohesively over 1.2–10.6 km and lasting between 2 and 19 min. For these rakes to be maintained, seabird groups have to adjust their flight speeds and directions, while they are on average distant of 500 m from each other, what cannot occur by chance. These findings suggest the existence of collective and coordinated movements in seabirds during prey searching at several kilometres' scale. This potential cooperation between foraging seabird groups brings new insight in the evolutionary trajectories of seabirds life-style.

Keywords: foraging strategy, group behaviour, radar, rakes, synchronised flight

## Introduction

Various seabird species are known to forage in groups (Takahashi et al. 2004, Weimerskirch et al. 2010, Thiebault et al. 2014b, Sutton et al. 2015, Cook et al. 2017) or to temporarily associate in multi-specific assemblages of predators jointly exploiting resource patches (Au and Pitman 1986, Harrison et al. 1991, Clua and Grosvalet 2001, Hebshi et al. 2008, Veit and Harrison 2017). In addition to shortening foraging search time (Pitcher et al. 1982), group foraging has been suggested to enhance feeding rate and decrease its variance (Clark and Mangel 1984, 1986), as well as to improve patch quality assessment (Brown 1988) by the means of information sharing between individuals. This process consists in inadvertent (passive) or deliberate (active) transfers of social information. Inadvertent transfers of information may rely on social cues that convey discrete information about the presence/absence of some feature

(Danchin et al. 2004) or on public information (i.e. graded information about the quality of the feature; Valone 1989). Information sharing between foragers has been considered as an energetically beneficial factor because 1) it allows for the transmission of food location information among individuals, 2) when a resource location is known, it provides better or faster patch quality estimates (Valone 1989).

However, it is largely unknown whether group formation has to be interpreted either within an individual-oriented producer–scrounger game (Vickery et al. 1991, Ranta et al. 1993) or within a more group-oriented social foraging game (Sih et al. 2009). In the first case, an individual benefit personally from social information (‘scrounger’) by maintaining an appropriate distance to other individuals (‘producers’). Therefore, coordination between foraging individuals is weak. In the second case, groups are actively maintained by individuals by the means of collective decisions and therefore, coordination between individuals is high. These different contexts are not fully exclusive within a species. For example, fresh-water American white pelicans (*Pelecanus erythrorhynchos*) may forage solitary, within uncoordinated groups, or within coordinated groups allowing for herding prey (Anderson 1991, McMahon and Evans 1992).

In seabirds, synchronous diving between individuals have been described in several penguin species (Tremblay and Cherel 1999, Takahashi et al. 2004). Besides, high fish-school attack rates between individuals allow Cape gannets (*Morus capensis*) to increase their prey capture rates (Thiebault et al. 2016a). So far, coordinated movements in seabirds have thus appeared to be restricted to small-scales, i.e. the scales at which preys are herded and/or captured. However, given that 1) cooperation can be beneficial during foraging (Torney et al. 2011), and 2) seabirds can react to each other at scales of about 10 km at least (Haney et al. 1992, Thiebault et al. 2014b), cooperation at those larger scales would exist. In this context, the lack of description of this process is likely due to the observational difficulties at these scales and in such remote and wide places as the high seas.

Recently, radar images obtained from seabird-dedicated radars on board tuna purse seiners provided instantaneous observations of the in-flight seabird community (Assali et al. 2017), showing that seabird groups might frequently distribute themselves within temporary and large clusters of around 5–6 km of diameter, possibly as a way to maintain visual contact during foraging. The size of these clusters suggests that they are associated with medium-scale prey searching, but it remains unclear whether they emerge from simple attraction–repulsion rules at the individual level or from more cognitively complex strategies. Using the same radar-based methodology, the goal of this work was to look for the existence of medium-scale patterns of coordinated flights as a way to question seabird cooperation at that scale. In relation with previous considerations on information transfers between foragers, we evaluated these patterns’ compatibility with a collective motion of foraging seabird groups, allowed by the use of social information. The patterns found were discussed

with respect to prey detectability (potentially altered by sea-state or sun glare), and their evolutionary significance.

## Methods

### Data collection

Tuna purse seiners navigating in tropical areas are equipped with a radar exclusively dedicated to the observation of seabirds, which behaviour and density indicate the potential presence of exploitable tuna schools (e.g. close to the surface and feeding). Radar screen captures were collected on-board a tuna purse seiner by the means of an external video-card (DVI2USB frame-grabber, Epiphan System Inc., Ottawa, Canada) and saved onto a laptop computer, every 15 s. This radar (marine surveillance radar FAR-2137, S-Band, 30 kW, Furuno) scanned a circular area of 11.1–14.8 km radius around the boat. Images were saved as \*.png files (Portable Network Graphic, i.e. lossless compression format) and analysed after the survey. The vessel was part of the French organisation of frozen tropical tuna producers (ORTHONGEL). It operated from 150 to 900 km to the closest coasts, i.e. in the open ocean, off the continental shelf of the Gulf of Guinea.

### Selection of data

Radar images recorded over a whole year were scanned visually to detect patterns of clear and obvious coordination in the movement of seabird echoes. This process was facilitated by the use of a 15 min ‘trail’ in the radar settings, allowing for a good visualization of seabirds traces in time. Seabird traces are very well visible under calm weather conditions, and less so when sea state is such that it introduces wave echoes in the images. Data from May, July and from October to December were either not available, or not exploitable because of bad weather conditions. For the other months, each day of exploitable data was visualised and occurrences of coordinated flights were counted. For the detailed description of these flights, only the days of best data quality were chosen in each month. Since all months were not represented by the same number of exploitable days, this selection allowed for avoiding biases associated with spatial and temporal redundancy (migration period, weather, etc.). In the end, the description of coordinated patterns spread over year 2016 (2 January; 8 February; 2 March; 17 April; 2 June; 30 August; 17 September).

### Data processing

Data processing is similar to the methodology described in Assali et al. (2017). Radar images contain both contextual information (navigation parameters, radar settings, display settings) and signal reflection visualisation (‘radar disk’). Contextual data, such as location of the boat and radar settings (e.g. radius of the radar disk), were converted in

numerical format by an optical character recognition algorithm adapted from Saroch (2011).

Signal saturation in the very first kilometres from the boat ( $2.6 \pm 1.0$  km over an observation range of 11.1–14.8 km) precluded seabird observations around it. This central saturated zone was filtered out by an image closing procedure (dilatation/erosion). In the remaining radar disk, echoes were distinctly identified by a watershed transform algorithm Meyer (1994), allowing for partially lumped echoes to be separated. False echoes resulting from background (white) noise were filtered out considering intensity (less than 10 over 30 levels) and area thresholds (10 pixels) empirically determined, as suggested in Stepanian et al. (2014). Apart from background noise that was deleted, echoes could then stand for seabirds, other boats, sea clutter in the vicinity of the boat, rain clutter or dense rainfalls, and were identified and separated by a procedure further described. All remaining echoes' locations in the image were converted into latitudes and longitudes, knowing the location of the boat both in the image (in the centre of the radar disk) and in space (latitude and longitude coordinates), and the observation range (radius of the radar disk in nautical miles). Echoes' intensity, area and location were saved.

The observation of flying seabirds groups by radar can be biased as the signal is attenuated when the distance to the boat increases. This is automatically corrected by signal processing inside the radar box before visualisation on the screen, but some seabirds might be missed when they are close to the radar disk edge. Furthermore, seabird echoes might either stand for one group of several seabirds, or for one large individual, but as echoes were very often seen merging or splitting, there is a great probability than seabird-echoes rather stand for groups of individuals.

In order to select echoes that had temporal and spatial consistency in subsequent images (i.e. to favour iterative detections of a coherent object, like seabirds or boats), we conducted a tracking procedure of echoes, adapted from Tinevez (2011), constrained by 1) a maximum linking speed of  $80 \text{ km h}^{-1}$  between echoes' centroids of successive images, 2) a maximum gap closing (maximum number of images in which an echo might temporarily disappear) of 3, which corresponds to 30 s, 3) a maximum azimuth difference of  $90^\circ$  between tracks of two successive images, 4) a maximum azimuth difference of  $30^\circ$  between tracks of two images separated by 1–3 images. All echoes that were not members of tracks of at least 5 points (i.e. appearing during 5 images or 1 min), were considered too inconsistent and classified as noisy echoes. Because sea clutter and rain clutter echoes were very densely distributed, some consistency could be randomly obtained. To distinguish tracks of seabird-echoes, boats, sea clutter, rain clutter and rainfalls, we conducted a supervised classification of tracks (see following paragraph 'Classification of tracks'). Track properties were obtained either from echo position over time (averaged speed, difference of azimuth, averaged distance to the central saturated zone edge), or from echoes' properties along tracks (area, intensity).

## Classification of tracks

16 926 tracks were constructed from three days of data (representative of echoes encountered in the dataset). All those tracks were superimposed on radar images, visualised, and manually attributed to one of the following five categories : «seabird» (3767 tracks), «boats» (83 tracks), «sea clutter» (6513 tracks), «rain clutter» (6461 tracks), «dense rainfalls» (102 tracks). A classification procedure was trained with 22 track properties, including their duration, the proportion of missing points (gap closing), the ratio of cumulative distance over absolute distance between starting and ending points of the track, and the mean, the standard deviation and the coefficient of variation of: track ground-speed, difference of azimuth between starting and ending points, averaged echo area, averaged distance to the central saturated zone edge, and mean, median and maximal intensity of the tracked echo. Training was operated by random forest procedure (Breiman 2001) over two thirds of 16 926 echoes tracks (training set).

1. The training set was randomly chosen (11 284 tracks).
2. The number of grown trees was set to 500.
3. The classification was conducted with 1–22 predictors.
4. Each classification model obtained was applied on the validation set (the remaining 5642 tracks) and the confusion matrix was computed. The percentage of correct classification was saved.

This procedure was operated 500 times. The model allowing for the best classification on the validation set was selected (97% of good classification). Classification outputs were approved by visualisation of tracks superimposed on radar images. All the 279 842 tracks (from the seven days used in this study) were classified according to this model, and only the 44 940 tracks associated to seabird-echoes were finally kept for analysis.

## Selection of coordinated movement patterns

Patterns of interest were visually detected as evident organised movements of several seabird-echoes, which tracks were temporary parallel (Fig. 1d). Those cohesive flights, or 'rakes', were selected visually, as they were 1) clearly observable on more than 10 successive images ( $\geq 150$  s) and 2) distinctly differing from movements of other seabird groups observed in the radar disk. When clearly mobile, seabird group could either show transit behaviours (Fig. 1a), movements of grouping (merging of seabird-echoes, Fig. 1b) or splitting (division of seabird-echoes, Fig. 1c), but were not systematically involved in organised and coordinated displacements of several seabird groups such as what we refer to as 'rakes' (Fig. 1d).

Radar images were visualised and tracks of seabird-echoes forming rakes were selected manually and saved for each rake. Rakes that were not clearly formed or occurring in confusing high densities of seabird-echoes in the image were not selected even if suspected. Consequently, the 60 selected rakes do not stand for the exhaustive census of such patterns, but rather

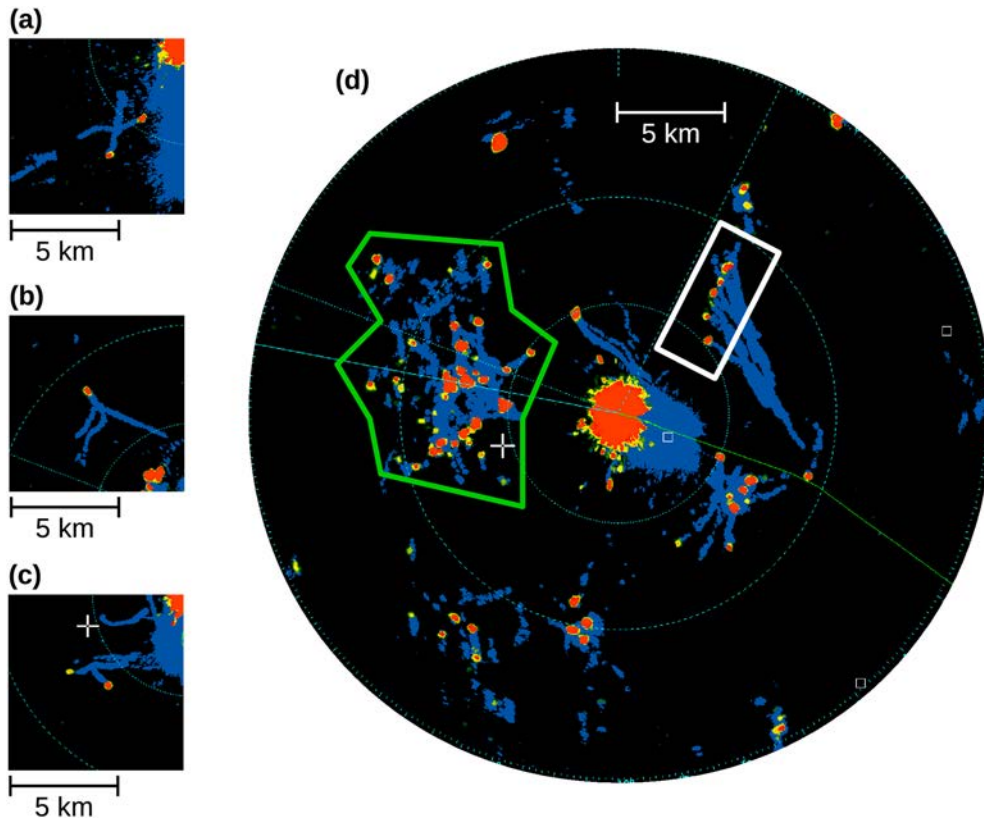


Figure 1. Different seabird flights observed in radar images. Orange dots correspond to seabird-echoes. The large orange area in the upper right corner of (a) and (c), and in the centre of (d), corresponds to the saturated area circling the boat. Blue trails reflect echoes' locations over the last 15 min. The panels show (a) two seabird-echoes transiting independently from each other; (b) three seabird-echoes merging in a single group; (c) two seabird-echoes diverging from a single split echo; (d) a whole radar disk with six seabird-echoes transiting in parallel to each other, forming a rake (white rectangle). Rakes are distinguishable from other seabird movements within the same radar image, because they are formed by coordinated flights of seabirds. The green polygon shows a cluster as defined in Assali et al. 2017.

for the less noisy observations. Similarly, we selected and saved apart all seabird tracks ( $n = 910$ ) that were concomitant with rake patterns but were clearly not part of them. Apart from the parallel and organised aspect of developed rakes, the latter could show different appearances in the radar image during their observation, such as a clear initiation by groups of seabirds starting to fly synchronously and then spreading regularly in space up to forming parallel lines (i.e. in 'rakes'; Fig. 2b<sub>1-2</sub>, c<sub>1-2</sub>, d<sub>1-2</sub>), or seabird groups forming parallel lines and then converging so as to finally disappear in one or several points (Fig. 2d<sub>4</sub>). Conversely, the observation of rakes could be limited because of coordinated seabird-echoes flying out of the radar circle or approaching its edge (Fig. 2a<sub>4</sub>, b<sub>4</sub>), or already deployed when they got detected by the radar (Fig. 2a<sub>1</sub>). As a consequence, reported rakes might not be observed during their entire 'lifetime'.

### Calculation of rake properties

Once a rake and its participating tracks were selected, corresponding images were visualised again to detect the exact time  $t$  when the rake seemed fully and steadily developed. For each rake, the number of involved seabird-echoes, the

distances between nearest neighbours in the rake (mean and standard deviation), as well as the lateral extent (maximum distance between echoes within the rake) were calculated and saved at time  $t$ . As we knew the value of the radar disk radius (two units: number of pixels and nautical miles) those distances were converted from the pixel space (image) to the geographic space, thus finally reported in km. The proportion of seabird-echoes of the image involved in the rake was deduced from the number of involved seabird-echoes at time  $t$ , knowing the total number of tracked seabird-echoes in the image at time  $t$ .

As durations of seabird tracks were known, durations of rakes could be estimated. Some tracks could continue even if not taking part to the rake any more (e.g. all other seabirds of the rake sat on water). As a consequence, we defined the duration of rakes as being the time sequence during which two tracks or more were participating to the coordinated, parallel flight. The travelled distance by individuals participating to a rake was calculated for this time sequence, and corresponds to the distance between the locations of rakes centroids at the beginning and the end of the sequence.

The duration of tracks within a rake could be shorter than the whole duration of the rake because of 1) the recruitment of

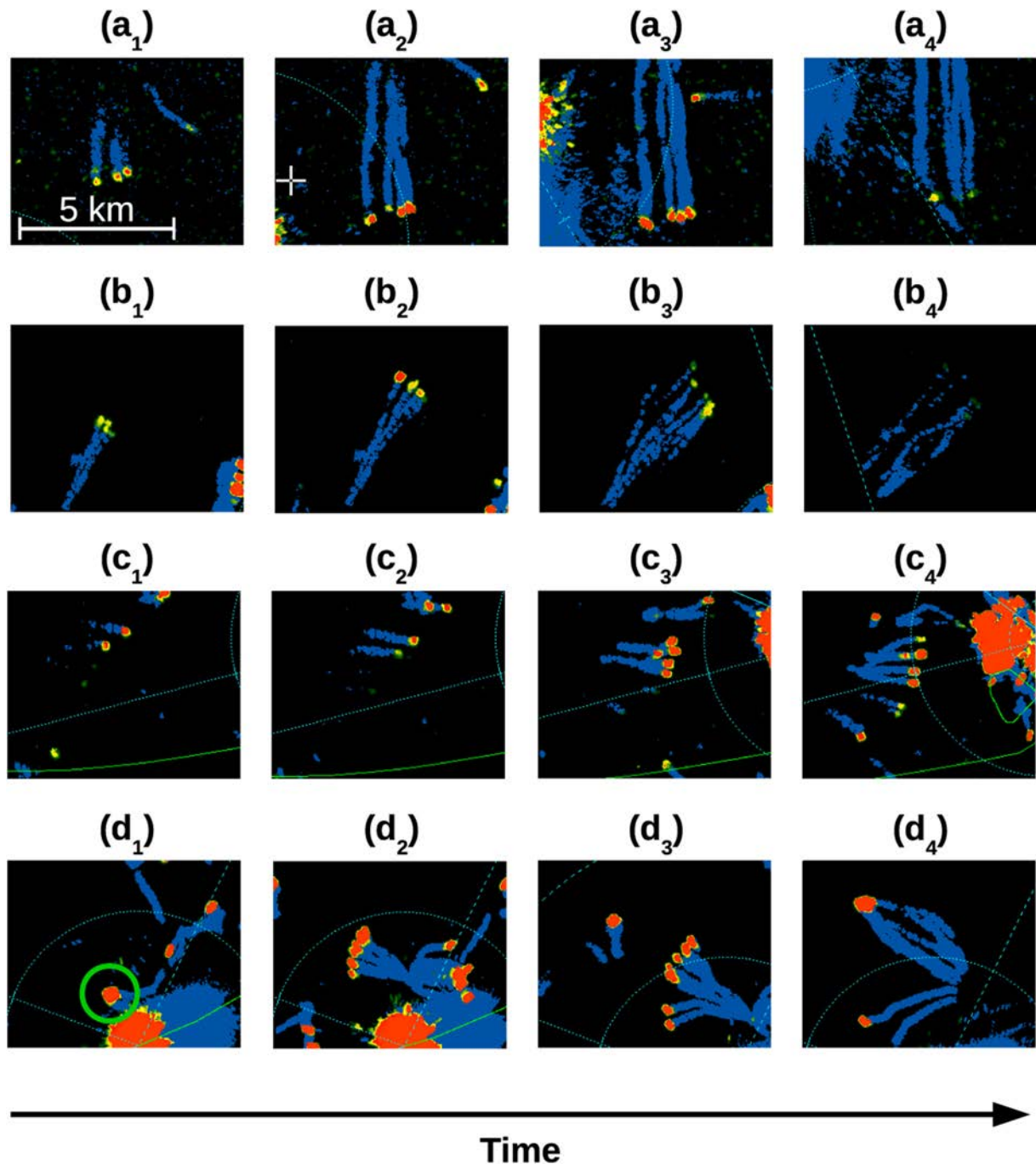


Figure 2. Four examples of seabird flights in rakes, observed in radar images. Orange dots correspond to seabird-echoes. The line (a) shows a rake deployed during all its recording time by the radar, from one of its first occurrences ( $a_1$ ) to its last ( $a_4$ ). The panels  $b_{1-3}$  and  $c_{1-3}$  represent rake initiation by splitting echoes. In ( $b_4$ ), echoes' detection is lost while they approach the radar disk edge. In ( $c_4$ ), other seabirds get in flight over time and participate to the rake. The line (d) documents the entire lifetime of a rake. In ( $d_1$ ), seabirds form a single large echo (green circle). In ( $d_2$ ), they spread regularly in space, forming a rake. In ( $d_3$ ), some seabird groups leave the rake while others maintain their direction to another flying seabird group. In ( $d_4$ ), the rake disappears because seabird groups converged and merged into one single echo. The scale indicated in ( $a_1$ ) is the same for all panels.

birds that were not present since the rake initiation (Fig. 2c<sub>4</sub> and 2) the loss of participants along the rake lifetime.

When it is not specified, results are presented as: (mean  $\pm$  SD).

#### Wind and sun data

The wind speeds and directions were calculated from wind surface velocities ( $x$ ,  $y$ ) available in the section 'Blended

Sea Winds' of the National Centers for Environmental Information (National Oceanic and Atmospheric Administration), on a  $0.25^\circ$  grid, at a time resolution of six hours (NOAA 2017).

Sun elevation and azimuth were calculated from the location of rakes initiation point (latitude, longitude) and time, with the function `sun_position.m` written and corrected by Roy (2004). The latter adapted the algorithm developed by Reda and Andreas (2004).

## Results

Exploitable radar images were exhaustively inspected and patterns of coordinated and parallel flights of seabird groups were visually detected, referred to as 'rakes' in following paragraphs (Fig. 1d). In the 52 days of exploitable data, the number of rakes per day ( $6.3 \pm 5.2$ ) ranged from 0 (five days) to 19 (one day). 60 rakes were selected from seven days (from 5 to 17 rakes per day;  $8.6 \pm 4.2$ ) spread over one year (Methods).

### Description of rakes dynamics

While rakes could appear steadily developed during their entire recording time (Fig. 2a<sub>1-4</sub>), some initiations and endings have been observed too. Initiations were characterized by seabird groups getting simultaneously in flight, spreading regularly over space and adopting the same direction so as to form a pseudo-linear front (Fig. 2b<sub>1-3</sub>, c<sub>1-3</sub>, d<sub>1-3</sub>). When rakes were neither disappearing in the central saturated zone circling the boat, or in the last kilometres close to the radar disk edge, they collapsed because of seabird groups converging and merging (Fig. 2d<sub>4</sub>). This convergence could involve all participants or only a part of them. Finally, rakes did not systematically involve the same seabird groups during their entire lifetime, since some seabirds could be recruited in the rake (Fig. 2c<sub>4</sub>), or leave it independently from other participants (Fig. 2d<sub>3</sub>).

### Number of involved echoes

The number of seabird-echoes within radar images ranged from 0 to 127 ( $24.6 \pm 22.7$ ). When rakes were fully deployed, they involved from 2 to 11 seabird-echoes ( $4.4 \pm 1.8$ ), corresponding to 4–3% of seabird-echoes tracked at the same time ( $29 \pm 19.6\%$ ; Table 1).

### Duration of rakes and travelled distance

The duration of sequences of partly or fully deployed rakes (i.e. two synchronous echoes at least, see methods) lasted from 2 to 19 min ( $8 \pm 4$  min; Table 1).

The distribution of durations of tracks within rakes was significantly different from the distribution of other seabird-echoes tracks' durations (Kolmogorov–Smirnov test,  $p$ -value  $< 0.01$ ). Seabird-echoes tracks involved in those rakes lasted 5 min in average (SD: 3 min), which is longer than other seabird-echoes tracks ( $3 \pm 2$  min).

Sequences during which rakes were involving two seabird-echoes or more consisted in displacements of 1.2–10.6 km ( $4.4 \pm 2.0$  km; Table 1).

### Speed of seabird-echoes

Seabird-echoes within rakes had a mean ground-speed of  $33 \text{ km h}^{-1}$  (min:  $4 \text{ km h}^{-1}$ , max:  $55 \text{ km h}^{-1}$ , SD:  $7 \text{ km h}^{-1}$ ; Table 1). 90% of tracks participating to rakes showed speeds between 19 and  $42 \text{ km h}^{-1}$ .

Concomitant non-raking seabird-echoes that were either joining static seabird groups (probably feeding) or transiting, showed a mean speed of  $25 \text{ km h}^{-1}$  (min:  $0.4 \text{ km h}^{-1}$ , max:  $58 \text{ km h}^{-1}$ , SD:  $12 \text{ km h}^{-1}$ ), with 90% of speed values between 5 and  $44 \text{ km h}^{-1}$ .

### Spatial dimensions of rakes

The mean distance between nearest neighbours at the time of fully developed rakes varied from 200 m to 1.5 km ( $500 \pm 200$  m), with 75% of them lesser or equal to 500 m (Table 1, Fig. 3a). 38% of mean distances between nearest neighbours were in  $[300 \pm 400]$  m and 22% in  $[400 \pm 500]$  m. The lateral extent of rakes varied from 300 m to 4.4 km ( $1.6 \pm 0.89$  km; Table 1, Fig. 3b).

The coefficient of variation (CV) of distances between nearest neighbours at time of fully developed rakes equalled 0.3 in average (min 0.0, max 0.9).

### Influence of wind speeds and directions

The distribution of differences between the mean directions of rakes and wind directions differed from a uniform distribution (Kolmogorov–Smirnov test;  $p$ -value  $< 0.01$ ), as well as the distribution of differences between non-raking seabird tracks directions and wind directions (Kolmogorov–Smirnov test;  $p$ -value  $< 0.01$ ). Differences between wind direction and 1) rakes or 2) non-raking seabird directions averaged to i)  $82^\circ (\pm 39^\circ)$ , and ii)  $80^\circ (\pm 48^\circ)$  respectively. 58% of rakes were directed from  $60^\circ$  to  $120^\circ$  with respect to the wind (Fig. 4a). Only 13% of rakes were against the wind ( $> 120^\circ$ ) whereas 27% differed of less than  $60^\circ$  in direction. Comparatively, 37% of non-raking seabird tracks differed of  $60$ – $120^\circ$  from wind direction, 24% of more than  $120^\circ$ , and 39% of less than  $60^\circ$  (Fig. 4c).

The mean ground-speeds of non-raking seabird tracks had a tendency to increase with decreasing differences between tracks and wind directions (regression slope as significantly different from zero,  $p$ -value  $< 0.01$ ), whereas they were not affected by wind speeds (regression slope was not significantly different from zero,  $p$ -value = 0.08).

Wind speeds ranged from 1.2 to  $25.5 \text{ km h}^{-1}$  ( $11.0 \pm 7.5 \text{ km h}^{-1}$ ). The mean distance between nearest neighbours within rakes was not influenced by wind speeds (regression slope was not significantly different from zero,  $p$ -value = 0.20; Fig. 5a), whereas the lateral extent showed a tendency to decrease with higher wind speeds

Table 1. Descriptive statistics of rakes.

Variable	Minimum	Quantile 0.025	Quantile 0.25	Median	Quantile 0.75	Quantile 0.975	Maximum	Mean	Standard deviation
Number of echoes	2.0	2.0	3.0	4.0	5.0	10.0	11.0	4.4	1.8
Proportion of seabird-echoes involved	0.04	0.04	0.13	0.24	0.44	0.67	0.83	0.29	0.20
Duration (min)	4	4	7	11	14	27	30	11	5
Duration of sub-sequences with multiple ( $\geq 2$ ) tracks (min)	2	2	5	8	10	17	19	8	4
Duration of tracks involved (min)	1	1	2	4	6	14	21	5	3
Distance travelled when multiple ( $\geq 2$ ) tracks (km)	1.2	1.2	2.7	4.3	6.0	10.1	10.6	4.4	2.0
Mean speed of seabird-echoes within tracks ( $\text{km h}^{-1}$ )	4	7	29	33	37	45	55	33	7
Distance to the nearest neighbour (km)	0.2	0.2	0.3	0.4	0.5	1.1	1.5	0.5	0.2
Coefficient of variation of the distance to the nearest neighbour	0.0	0.0	0.1	0.3	0.5	0.9	0.9	0.3	0.3
Lateral extent (km)	0.3	0.5	0.9	1.4	2.0	3.4	4.4	1.6	0.9
Difference between the mean directions of rakes and wind directions ( $^{\circ}$ )	0	0	55	84	104	164	179	82	39
Difference between mean directions of rakes and sun azimuth ( $^{\circ}$ )	5	5	32	84	137	170	171	86	57

(regression slope was significantly different from zero,  $p$ -value  $< 0.01$ ; Fig. 5b).

### Influence of sun azimuth and elevation

The difference between the mean directions of rakes and the sun azimuth varied from 5 to 171 $^{\circ}$  (mean:  $86 \pm 57^{\circ}$ ) and was uniformly distributed within this range (Kolmogorov–Smirnov test;  $p$ -value=0.48; Table 1, Fig. 4b). Moreover, there was no linear tendency for azimuth differences to be related to sun elevation ( $p$ -value=0.80).

The difference between the mean directions of non-raking seabird tracks and the sun azimuth ( $103^{\circ} \pm 53^{\circ}$ ) differed from

a uniform distribution (Kolmogorov–Smirnov test;  $p$ -value  $< 0.01$ ), with 62% of values in  $[90^{\circ}; 180^{\circ}]$  and 35% of values in  $[135^{\circ}; 180^{\circ}]$  (Fig. 4d).

### Discussion

To our knowledge, this is the first observation and description of clearly coordinated movements of seabirds at a medium scale (several kilometres), i.e. a scale not associated with prey capture but rather with prey searching.

Such coordinated flights cannot be randomly obtained. Seabird movements' cohesiveness lasted generally about 8 min,

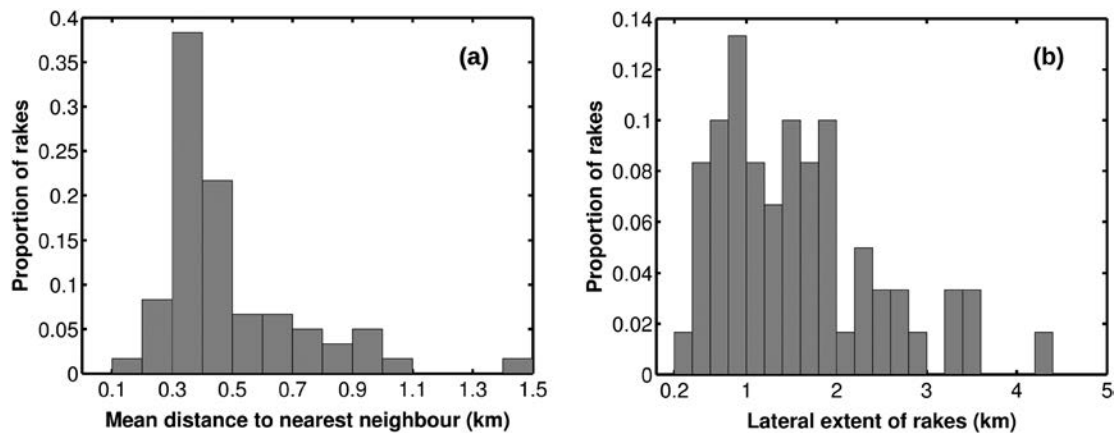


Figure 3. Distribution of spatial dimensions of rakes when they are fully deployed. (a) Mean distance to nearest neighbour within each rake (km); (b) lateral extent of rakes (km).



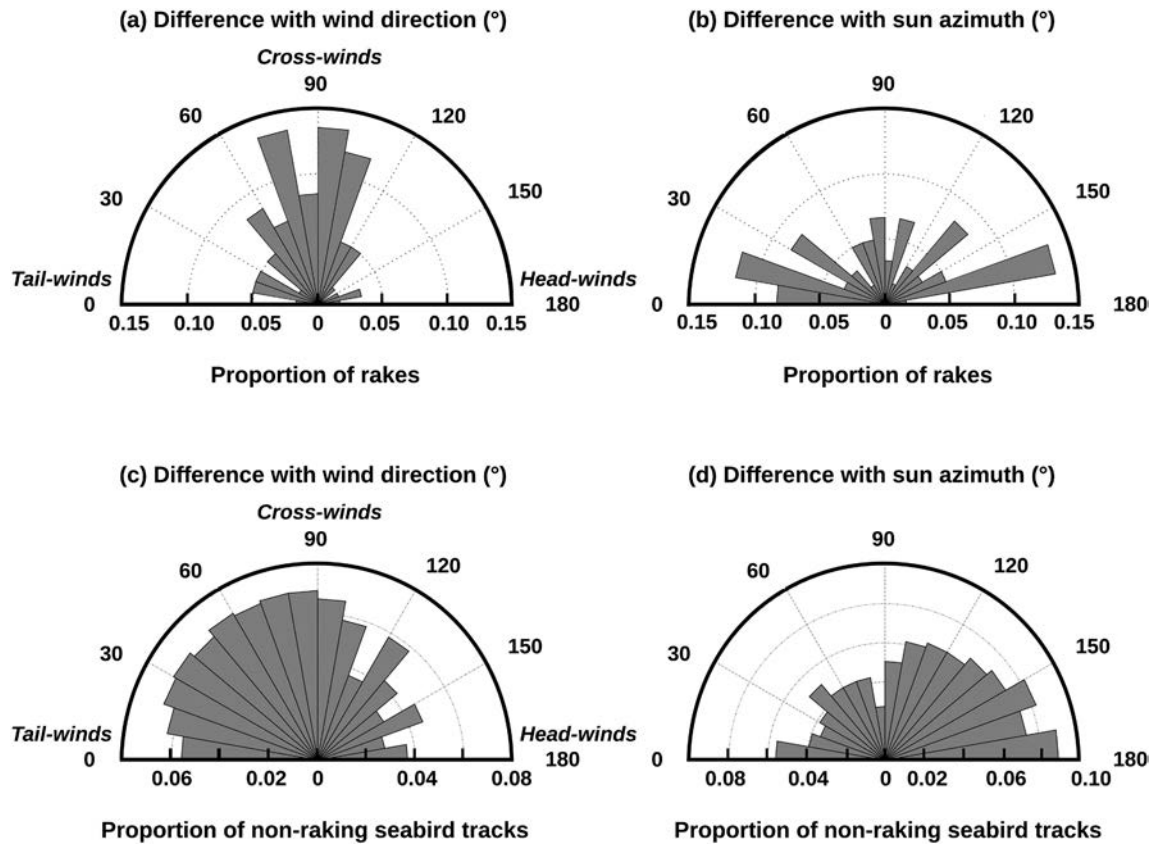


Figure 4. Distributions of the difference between the mean directions of rakes and non-raking seabird tracks and two environmental factors. (a) Distribution of the difference between the mean directions of rakes and wind directions; (b) distribution of the difference between the mean directions of rakes and sun azimuth; (c) distribution of the difference between the mean directions of non-raking seabird tracks and wind directions; (d) distribution of the difference between the mean directions of non-raking seabird tracks and sun azimuth, in degrees.

involved about four echoes (seabirds or seabird groups) and covered distances of about 4 km, ruling out the possibility of random events. Furthermore, radar observations covered at most 10 000 km<sup>2</sup> each day, and were collected from 150 km to 900 km off the coast of the Gulf of Guinea. Given that the Gulf of Guinea's area is about 2 300 000 km<sup>2</sup>, one day

of radar observation documented less than 1% of the area. Given that between 5 and 17 rakes were analysed per day (but more were observed, see Methods) and that the explored area was negligible compared to the entire zone, rakes are not anecdotal features and are likely frequent within the seabird community in the open tropical seas.

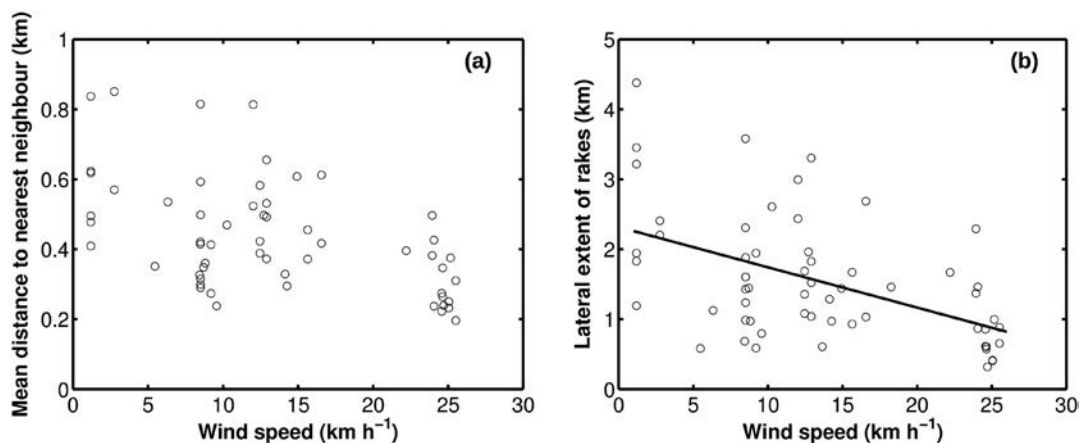


Figure 5. Spatial dimensions of rakes relative to wind speeds. (a) Mean distance between neighbours within rakes (km), and (b) lateral extent of rakes (km), relatively to wind speeds (km h<sup>-1</sup>). Black line results from linear regression ( $p$ -value < 0.01).

Rake patterns require high coordination levels to maintain consistency in speed, bearing and distances between members. Since flight speed is strongly dependent on body size and morphology of seabirds (Pennycuik 1997, Alerstam et al. 2007), efficient rake formation might be limited to similar seabirds species, if not to the same species. Since rakes only involved a limited proportion of seabird-echoes observed in surrounding areas (29% in average), we suggest that 1) all seabirds would not have the same ability to form or join a rake, 2) maintaining collective and aligned flights may become difficult when the number of participants increases.

Despite no observer was on board to confirm that raking birds were actually foraging, the context of radar data acquisition, as well as the behaviours of recorded seabird-echoes, indicate a great probability that rake patterns are conducted by foraging groups of pelagic seabirds.

Firstly, captains of tuna purse seiners (our observation platforms) adapt their searching strategy to the oceanographic context (e.g. targeting thermal fronts) so as to increase their fishing success (Torres-Irineo et al. 2014). With the bird-dedicated radar, they especially focus on foraging seabirds so as to deduce the presence of surface-feeding tuna schools. Consequently, we know that seabirds recorded in radar images are experiencing particularly favorable foraging conditions, because 1) tunas are very likely to be surface-feeding in these zones and seabird may join them in multi-specific feeding assemblages (Au and Pitman 1988, Veit and Harrison 2017); 2) seabirds have a greater chance to encounter prey patches in this oceanographic context.

Furthermore, because of the spatio-temporal distribution of these radar observations, echoes mostly correspond to pelagic seabirds, and might occasionally correspond to migrating birds.

Indeed, Cory's *Calonectris diomedea borealis*, Scopoli's *Calonectris diomedea diomedea*, sooty *Puffinus griseus* and manx *Puffinus puffinus* shearwaters have been reported in inshore waters of the Gulf of Guinea during their autumnal migration, or are known to winter partly in this region despite its eccentricity from the major migratory paths of these species (González-Solís et al. 2007, Passavy 2011, Hedd et al. 2012, Péron and Grémillet 2013, de Boer and Saulino 2017). In addition, migrating long-tailed skuas can stage in the Gulf of Guinea, especially in October and November (Gilg et al. 2013). However, no radar data was exploitable in October, November and December, thus excluding the period during which migrating individuals could have been most probably recorded. Still, Arctic terns may have been recorded during their postbreeding migration, as some individuals follow the west African coast to reach their wintering area in the southern Atlantic (Egevang et al. 2010). Nonetheless, we confirm the presence of raking birds almost all year long, as rake patterns have been observed every month when data was available and exploitable (Methods). This temporal distribution suggests that rakes are rather conducted by annually resident species, such as brown booby (*Sula leucogaster*), brown (*Anous stolidus*) and black (*Anous minutus*) noddy, bridled (*Sterna anaethetus*), sooty (*Sterna fuscata*) and damara tern (*Sterna*

*balaenarum*), or white-tailed tropicbird (*Phaethon lepturus*) that all breed in Tinhosas islands, São Tomé and Príncipe (Bollen et al. 2018).

Among these, pelagic species such as tropicbirds, noddies and terns display different foraging modes. White-tailed tropicbirds mainly forage solitary (Jaquemet et al. 2004, Campos et al. 2017), and occasionally associate with feeding dolphins (Jaquemet et al. 2004, Spear and Ainley 2005). Comparatively, sooty terns, brown and black noddies are highly gregarious and are often found in multi-specific feeding assemblages (Evans 1982, Au and Pitman 1986, Jaquemet et al. 2004, Hebshi et al. 2008, Goyert et al. 2014). Among the numerous species associated with tropical Atlantic tuna fisheries (Reynaud 1994), sooty terns, brown and black noddies may thus be the most probable species involved in raking patterns.

To our knowledge, many bird species form organised group flights (Bajec and Heppner 2009), but only few observations document coordination of foraging seabirds in flight. Underwater movements of penguins revealed synchronised foraging trips and dives (Tremblay and Cherel 1999, Takahashi et al. 2004), presumably allowed by constant visual contact. Synchronisation was also observed in departure times of foraging Australasian gannets (*Morus serrator*) from the near-colony raft (Machovsky-Capuska et al. 2014), in sooty shearwaters (*Puffinus griseus*) flights to join feeding heterospecifics (Hoffman et al. 1981), and in Socotra cormorants (*Phalacrocorax nigrogularis*) foraging trips (Cook et al. 2017). However, rakes involved both synchronisation and coordination, and such patterns have never been observed at scales reaching several kilometres. Thus, collective movements in foraging seabirds might also include the prey-searching phase/scale, and not only the prey-capture phase/scale as previously found (Thiebault et al. 2016a).

Accordingly, one striking characteristic of rakes was the narrow distribution of the mean distance between echoes, peaking markedly between 300 and 500 m. Seabirds have been observed to react to each other at around 10 km (Haney et al. 1992, Thiebault et al. 2014b). In addition, tern commonly fly from 1 to 20 m above sea surface, and more usually at 5–10 m (Cook et al. 2012, Johnston et al. 2014). According to Haney et al. (1992), and considering that atmospheric refraction is negligible for these relatively small heights, the theoretical maximum distance at which a seabird could be visibly detectable by a flying individual would thus range from 7.7 km (if both the target and the observer fly at 1 m above sea surface) to 34.3 km (if the target and the observer fly at 20 m above sea level). Consequently, all seabirds within rakes are undoubtedly within sight of one another even in the largest observed rake (4.4 km long). The functional significance of the inter-seabird distance within rakes is therefore not related to a need for maintaining visual contact. Instead, we suggest that this distance might be related to prey detection. Assuming that rakes were formed for searching prey (we see no other explanation), seabirds may distribute themselves in lines to scan the ocean surface optimally, i.e. avoiding to miss some areas in the scanned space and avoiding duplicate

scanning of the same area. Hence, for their common flight altitude (Cook et al. 2012, Johnston et al. 2014), seabirds may detect a prey patch at half the distance between them: between 150 and 250 m most of the time (possibly depending on the weather conditions, the sea state and prey crypticity). In a foraging context, individuals taking part to rakes could benefit from an extended search effort proportional to the number of participating seabird groups.

As seabird-echoes likely represent small groups of seabirds, this could be seen as a loss of «foraging eyes» since they could spread much more in space and scan a larger surface. However, remaining in small groups is likely to allow aerodynamic advantages of group flight formation (Cutts and Speakman 1994, Weimerskirch et al. 2001). On the contrary, even though the distances between echoes were short, they were not short enough to provide aerodynamic advantage in terms of flight cost. Indeed, echoes distribution within rakes occurs at a much larger scale (order of magnitude:  $10^2$  m) than bird distribution within grouped flight formations (order of magnitude:  $10^0$  m).

Since seabirds forming clusters are also likely to be in visual contact between each other (Assali et al. 2017), they may also benefit from the scanned area of other seabirds in the same way as forming rakes. However, the recruitment of seabirds while rakes looked already fully developed (Fig. 2c<sub>3-4</sub>) and the spontaneous initiation of a rake (Fig. 2b<sub>1-3</sub>, d<sub>1-3</sub>) suggest that individuals may get extra benefit from joining or forming rakes rather than independently cue on feeding opportunities, even within a cluster. Furthermore, the relatively shorter distance between echoes in rakes compared to clusters may allow participants to communicate faster any prey encounter to the others, directly (vocalising; Thiebault et al. 2016b) or indirectly (changing flight behaviour), so as to initiate a convergent movement to the point of interest (Fig. 2d<sub>4</sub>). This would quickly lead to a collective flock feeding event where prey intake rate may increase (Götmark et al. 1986, Thiebault et al. 2016a).

For flying seabirds, direct prey detectability can be affected by sea state (partly induced by wind speeds) and sun glare. Assuming that rakes are composed of individuals looking for prey, we could expect the sun azimuth and elevation and the wind directions to induce preferences in the orientation of rakes, or the wind speeds to constrain seabirds spacing. Seabirds in rakes showed a clear preference for using cross-winds, whereas non-raking birds equally used cross- and tail-winds. Seabirds typically fly slower in head-winds and faster in tail-winds (Spear and Ainley 1997, Weimerskirch et al. 2000, Zavalaga et al. 2010). However, some procellariiforms tend to make extensive use of cross-tail winds (Adams and Flora 2010). For species relying partly on olfactory cues to find prey (Nevitt 2008) the use of cross-winds could allow foraging individuals to optimize their exposure to odours. Still, in this context, the occurrence of raking patterns hints at an additional benefit of the raking strategy compared to solitary foraging.

Cross-winds also allow for increasing the optimal speed, i.e. the speed with the less cost of transport, but not necessarily

the fastest ground speed (Liechti et al. 1994). Seabirds in rakes flew on average at  $33 \text{ km h}^{-1}$ , a ground-speed similar to terns and small gulls flying across-winds under an average wind speed of  $27.4 \text{ km}^{-1}$  (Spear and Ainley 1997). Except for small 'oceanites' species and a few terns or prions (i.e. small seabirds), seabirds in rakes flew slower than the average recorded in most seabirds (Spear and Ainley 1997), even under variable wind speeds and directions (Alerstam et al. 1993). Consequently, the tendency to use cross-winds is probably not aimed at increasing flying speed. The ground-speeds of concomitant non-raking seabird tracks were on average smaller ( $25 \text{ km h}^{-1}$ ) but more variable than the ground-speeds of raking seabirds, which can be explained by the diversity of behaviours of non-raking birds (e.g. transiting or joining feeding groups). Moreover, seabird ground-speeds had a tendency to increase when differences with wind directions decreased (i.e. with tail-winds oriented flights), while wind speeds had no significant influence on seabird speeds. This indicates that transiting or solitary foraging birds, that probably show the highest ground-speed values that have been recorded in this study, had a tendency to use tail-winds. Since 1) rakes were not exclusively developed under cross-winds conditions, 2) birds were seen to be recruited in or to leave a rake, 3) rakes only involved a fraction of the bird community at sea while other seabird-echoes behave differently (e.g. flying but not in a rake), 4) concomitant non-raking birds substantially used both cross- and tail-winds, we reject the hypothesis that rake formation is solely a consequence of environmental constraints such as wind speeds and directions. Rather, as it is certainly more difficult to accelerate against the wind or to decelerate with the wind, we propose that cross-winds is the best (most neutral) wind orientation facilitating speed adjustments. Then, rakes would be easier to maintain and preferentially conducted in cross-winds, especially if different species are involved.

Besides, the range of possible ground-speeds of seabirds widens with increasing wind speeds, even in cross-winds where speed increment caused by the wind is not null (Liechti et al. 1994). Hypothetically, slowest wind speeds may thus allow lesser ground-speeds variability among seabirds, easier ground-speeds adjustment for those forming rakes, then easier alignment over larger distances and easier recruitment of seabirds in rakes. Accordingly, the lateral extent of rakes tended to decrease when the wind speeds increased. On the contrary, the directions of rakes did not seem to be influenced by sun azimuth or elevation, and the distance between nearest neighbours within rakes was not clearly influenced by wind speeds. The sea surface appearance (calm, with ripples, with foam, etc.) and resulting prey detectability may not drive different raking strategies, in terms of spacing between participants or mean direction of rakes. Raking strategy may allow prey detection under a range of sea states.

Interestingly, rakes may imply that all individuals participate with the same effort to the maintenance of the 'searching front', by adjusting speed, direction and distance with others. In this context, individuals may be considered as equally producing information on potential feeding opportunities.

Foraging zones at large scale might be found using olfactory cues (Nevitt 2008) or knowledge (continental shelves (Yen et al. 2004), seamounts (Haney et al. 1995), etc.), then, clusters (Assali et al. 2017) or rakes (this study) might help finding prey patches at medium scales. Once a prey patch is found, the benefits of jointly exploiting it might induce a cooperation between individuals (Thiebault et al. 2016a). Cooperation is more likely to occur when individuals provide inadvertent information when they feed, and have thus been predisposed to signalling and forming cooperative groups (Torney et al. 2011). Contrary to the producer–scrounger game suggesting that scroungers do not engage into producing information while producers suffer the competition with scroungers (Barnard and Sibly 1981), the rake strategy implies that seabirds voluntarily engage themselves into a producer-only game, i.e. based on information sharing (Valone 1989), and which implies obligate collective prey exploitation. Indeed, any prey-finding within a rake formation cannot be hidden to the partners. By participating to coordinated flights, seabirds are likely to optimise their individual prey encounter rate, and could also increase their prey capture rate. Testing this hypothesis would require to combine complementary data such as telemetry, bird-borne video and radar observations, which could allow for assessing the foraging success of raking versus non-raking birds and highlight potential costs and benefits of these different foraging strategies.

As reported in this study, rake patterns have also been observed as transitory flights between two aggregative patterns, with seabird groups expanding, raking, then converging. We suggest that rakes can collapse once a feeding opportunity is found (seabird groups converge and merge). However, we still have no clue about the rake initiation process. In a foraging context, rafts of seabirds could act as information centres (Weimerskirch et al. 2010, Machovsky-Capuska et al. 2014, Thiebault et al. 2014a), conveying information on the presence of prey, allowing unsuccessful or poorly informed individuals to join informed birds, or ensuring a collective initiation of raking patterns.

The ability to associate echoes with a given species will be a key advance for future studies. Furthermore, extending radar studies to other marine ecosystems might provide new opportunities for understanding these phenomena.

### Data availability statement

Data available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.8sf7m0cj8>> (Assali et al. 2020).

*Acknowledgements* – The authors are grateful to Orthongel for allowing the recording of purse-seiner radar images. The authors are thankful to P. Dewals and A. Damiano, who collected the data and supervised their transfer, as well as P. Bach, P. Kouadio, J. Lebranchu, P. Taconet, N. Billet, P. Cauquil and P. Sabarros for their help in logistics for data acquisition and transfer.

### References

- Adams, J. and Flora, S. 2010. Correlating seabird movements with ocean winds: Linking satellite telemetry with ocean scatterometry. – *Mar. Biol.* 157: 915–929.
- Alerstam, T., Gudmundsson, G. A. and Larsson, B. 1993. Flight tracks and speeds of Antarctic and Atlantic seabirds: radar and optical measurements. – *Phil. Trans. R. Soc. B* 340: 55–67.
- Alerstam, T., Rosén, M., Bäckman, J., Ericson, P. G. P. and Hellgren, O. 2007. Flight speeds among bird species: allometric and phylogenetic effects. – *PLoS Biol.* 5: 1656–1662.
- Anderson, J. G. T. 1991. Foraging behavior of the American white pelican (*Pelecanus erythrorhynchos*) in western Nevada. – *Colon. Waterbirds* 14: 166–172.
- Assali, C., Bez, N. and Tremblay, Y. 2017. Seabird distribution patterns observed with fishing vessel's radar reveal previously undescribed sub-meso-scale clusters. – *Sci. Rep.* 7: 1–10.
- Assali, C., Bez, N. and Tremblay, Y. 2020. Data from: Raking the ocean surface: new patterns of coordinated motion in seabirds. – Dryad Digital Repository, <<https://doi.org/10.5061/dryad.8sf7m0cj8>>.
- Au, D. W. K. and Pitman, R. L. 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. – *Condor* 88: 304–317.
- Au, D. W. and Pitman, R. L. 1988. Seabird relationships with tropical tunas and dolphins. – Columbia Univ. Press, pp. 174–212.
- Bajec, I. L. and Heppner, F. H. 2009. Organized flight in birds. – *Anim. Behav.* 78: 777–789.
- Barnard, C. J. and Sibly, R. M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. – *Anim. Behav.* 29: 543–550.
- Bollen, A., Matilde, E. and Barros, N. 2018. An updated assessment of the seabird populations breeding at Príncipe and Tinhosas. – *Ostrich* 89: 47–58.
- Breiman, L. 2001. Random forests. – *Mach. Learn.* 45: 5–32.
- Brown, C. R. 1988. Social foraging in cliff swallows: local enhancement, risk sensitivity, competition and the avoidance of predators. – *Anim. Behav.* 36: 780–792.
- Campos, L. F. A. S., Andrade, A. B., Bertrand, S. and Efe, M. A. 2017. Foraging behavior and at-sea distribution of white-tailed tropic birds in tropical ocean. – *Braz. J. Biol.* 78: 556–563.
- Clark, C. W. and Mangel, M. 1984. Foraging and flocking strategies: information in an uncertain environment. – *Am. Nat.* 123: 626–641.
- Clark, C. W. and Mangel, M. 1986. The evolutionary advantages of group foraging. – *Theor. Popul. Biol.* 30: 45–75.
- Clua, É. and Grosvalet, F. 2001. Mixed-species feeding aggregation of dolphins, large tunas and seabirds in the Azores. – *Aquat. Living Resour.* 14: 11–18.
- Cook, A. S. C. P., Johnston, A., Wright, L. J. and Burton, N. H. K. 2012. A review of flight heights and avoidance rates of birds in relation to offshore wind farms. – *Rep. Prep. behalf Crown Estate*: 618: 1–61.
- Cook, T. R., Gubiani, R., Ryan, P. G. and Muzaffar, S. B. 2017. Group foraging in Socotra cormorants: a biologging approach to the study of a complex behavior. – *Ecol. Evol.* 7: 2025–2038.
- Cutts, C. J. and Speakman, J. R. 1994. Energy savings in formation flight of pink-footed geese. – *J. Exp. Biol.* 189: 251–261.
- Danchin, É., Giraldeau, L.-A., Valone, T. J. and Wagner, R. H. 2004. Public information: from nosy neighbors to cultural evolution. – *Science* 305: 487–491.

- de Boer, M. N. and Saulino, J. T. 2017. Birds recorded off Ghana and Côte d'Ivoire, April–May 2013 and March–May 2014, including species new to each country. – *Bull. ABC* 24: 192–203.
- Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W. and Silk, J. R. D. 2010. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. – *Proc. Natl Acad. Sci. USA* 107: 2078–2081.
- Evans, P. G. H. 1982. Associations between seabirds and cetaceans: a review. – *Mamm. Rev.* 12: 187–206.
- Gilg, O., Moe, B., Hanssen, S. A., Schmidt, N. M., Sittler, B., Hansen, J., Reneerkens, J., Sabard, B., Chastel, O., Moreau, J., Phillips, R. A., Oudman, T., Biersma, E. M., Fenstad, A. A., Lang, J. and Bollache, L. 2013. Trans-equatorial migration routes, staging sites and wintering areas of a high-arctic avian predator: the long-tailed skua (*Stercorarius longicaudus*). – *PLoS One* 8: e64614.
- González-Solís, J., Croxall, J. P., Oro, D. and Ruiz, X. 2007. Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. – *Front. Ecol. Environ.* 5: 297–301.
- Götmark, F., Winkler, D. W. and Andersson, M. 1986. Flock-feeding on fish schools increases individual success in gulls. – *Nature* 319: 589–591.
- Goyert, H. F., Manne, L. L. and Veit, R. R. 2014. Facilitative interactions among the pelagic community of temperate migratory terns, tunas and dolphins. – *Oikos* 123: 1400–1408.
- Haney, J. C., Frstrup, K. M. and Lee, D. S. 1992. Geometry of visual recruitment by seabirds to ephemeral foraging flocks. – *Ornis Scand.* 23: 49–62.
- Haney, J. C., Haury, L. R., Mullineaux, L. S. and Fey, C. L. 1995. Sea-bird aggregation at a deep North Pacific seamount. – *Mar. Biol.* 123: 1–9.
- Harrison, N. M., Whitehouse, M. J., Heinemann, D., Prince, P. A., Hunt Jr., G. L. and Veit, R. R. 1991. Observations of multispecies seabird flocks around south Georgia. – *Auk* 108: 801–810.
- Hebshi, A. J., Duffy, D. C. and Hyrenbach, K. D. 2008. Associations between seabirds and subsurface predators around Oahu, Hawaii. – *Aquat. Biol.* 4: 89–98.
- Hedd, A., Montevicchi, W., Otley, H., Phillips, R. and Fifield, D. 2012. Trans-equatorial migration and habitat use by sooty shearwaters *Puffinus griseus* from the south Atlantic during the nonbreeding season. – *Mar. Ecol. Prog. Ser.* 449: 277–290.
- Hoffman, W., Heinemann, D. and Wiens, J. A. 1981. The ecology of seabird feeding flocks in Alaska. – *Auk* 98: 437–456.
- Jaquemet, S., Le Corre, M. and Weimerskirch, H. 2004. Seabird community structure in a coastal tropical environment: importance of natural factors and fish aggregating devices (FADs). – *Mar. Ecol. Prog. Ser.* 268: 281–292.
- Johnston, A., Cook, A. S. C. P., Wright, L. J., Humphreys, E. M. and Burton, N. H. K. 2014. Modelling flight heights of marine birds to more accurately assess collision risk with offshore wind turbines. – *J. Appl. Ecol.* 51: 31–41.
- Liechti, F., Hedenström, A. and Alerstam, T. 1994. Effects of side-winds on optimal flight speed of birds. – *J. Theor. Biol.* 170: 219–225.
- Machovsky-Capuska, G. E., Hauber, M. E., Libby, E., Amiot, C. and Raubenheimer, D. 2014. The contribution of private and public information in foraging by Australasian gannets. – *Anim. Cogn.* 17: 849–858.
- McMahon, B. F. and Evans, R. M. 1992. Foraging strategies of American white pelicans. – *Behaviour* 120: 69–891.
- Meyer, F. 1994. Topographic distance and watershed lines. – *Signal Process.* 38: 113–125.
- Nevitt, G. A. 2008. Sensory ecology on the high seas: the odor world of the procellariiform seabirds. – *J. Exp. Biol.* 211: 1706–1713.
- NOAA. 2017. Blended sea winds. – National Oceanic and Atmospheric Administration.
- Passavy, G. 2011. Migration of the Sooty shearwater *Puffinus griseus* off Gabon. – *Mar. Ornithol.* 39: 147–150.
- Pennycuik, C. 1997. Actual and 'optimum' flight speeds: field data reassessed. – *J. Exp. Biol.* 200: 2355–2361.
- Péron, C. and Grémillet, D. 2013. Tracking through life stages: adult, immature and juvenile autumn migration in a long-lived seabird. – *PLoS One* 8: e72713.
- Pitcher, T. J., Magurran, A. E. and Winfield, I. J. 1982. Fish in larger shoals find food faster. – *Behav. Ecol. Sociobiol.* 10: 149–151.
- Ranta, E., Rita, H. and Lindstrom, K. 1993. Competition versus cooperation: success of individuals foraging alone and in groups. – *Am. Nat.* 142: 42–58.
- Reda, I. and Andreas, A. 2004. Solar position algorithm for solar radiation applications. – *Sol. Energy* 76: 577–589.
- Reynaud, P.-A. 1994. Manuel d'observation et d'identification des oiseaux pélagiques de l'Atlantique orientale et de l'océan Indien.
- Roy, V. 2004. Sun azimuth and elevation, MATLAB Central File Exchange.
- Saroch, A. 2011. Optical character recognition (lower case and space included), MATLAB Central File Exchange.
- Sih, A., Hanser, S. F. and McHugh, K. A. 2009. Social network theory: new insights and issues for behavioral ecologists. – *Behav. Ecol. Sociobiol.* 63: 975–988.
- Spear, L. B. and Ainley, D. G. 1997. Flight speed of seabirds in relation to wind speed and direction. – *Ibis* 139: 234–251.
- Spear, L. B. and Ainley, D. G. 2005. At-sea distributions and abundance of tropicbirds in the eastern Pacific. – *Ibis* 147: 353–366.
- Stepanian, P. M., Chilson, P. B. and Kelly, J. F. 2014. An introduction to radar image processing in ecology. – *Methods Ecol. Evol.* 5: 730–738.
- Sutton, G. J., Hoskins, A. J. and Arnould, J. P. Y. 2015. Benefits of group foraging depend on prey type in a small marine predator, the little penguin. – *PLoS One* 10: e0144297.
- Takahashi, A., Sato, K., Nishikawa, J., Watanuki, Y. and Naito, Y. 2004. Synchronous diving behavior of Adélie penguins. – *J. Ethol.* 22: 5–11.
- Thiebault, A., Mullers, R., Pistorius, P., Meza-Torres, M. A., Dubroca, L., Green, D. and Tremblay, Y. 2014a. From colony to first patch: processes of prey searching and social information in Cape gannets. – *Auk* 131: 595–609.
- Thiebault, A., Mullers, R. H. E., Pistorius, P. A. and Tremblay, Y. 2014b. Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. – *Behav. Ecol.* 25: 1302–1310.
- Thiebault, A., Semeria, M., Lett, C. and Tremblay, Y. 2016a. How to capture fish in a school? Effect of successive predator attacks on seabird feeding success. – *J. Anim. Ecol.* 85: 157–167.
- Thiebault, A., Pistorius, P., Mullers, R. and Tremblay, Y. 2016b. Seabird acoustic communication at sea: a new perspective using bio-logging devices. – *Sci. Rep.* 6: 30972.
- Tinevez, J.-Y. 2011. Simple tracker – file exchange – Matlab central.
- Torney, C. J., Berdahl, A. and Couzin, I. D. 2011. Signalling and the evolution of cooperative foraging in dynamic environments. – *PLoS Comput. Biol.* 7: e1002194.
- Torres-Irineo, E., Gaertner, D., Chassot, E. and Dreyfus-León, M. 2014. Changes in fishing power and fishing strategies driven by

- new technologies: the case of tropical tuna purse seiners in the eastern Atlantic Ocean. – *Fish. Res.* 155: 10–19.
- Tremblay, Y. and Cherel, Y. 1999. Synchronous underwater foraging behavior in penguins. – *Condor* 101: 179–185.
- Valone, T. J. 1989. Group foraging, public information, and patch estimation. – *Oikos* 56: 357–363.
- Veit, R. R. and Harrison, N. M. 2017. Positive interactions among foraging seabirds, marine mammals and fishes and implications for their conservation. – *Front. Ecol. Evol.* 5: 121.
- Vickery, W. L., Giraldeau, L.-A., Templeton, J. J., Kramer, D. L. and Chapman, C. A. 1991. Producers, scroungers and group foraging. – *Am. Nat.* 137: 847–863.
- Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S. A. and Costa, D. P. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. – *Proc. Biol. Sci.* 267: 1869–1874.
- Weimerskirch, H., Martin, J., Clerquin, Y., Alexandre, P. and Jiraskova, S. 2001. Energy saving in flight formation. – *Nature* 413: 697–698.
- Weimerskirch, H., Bertrand, S., Silva, J., Marques, J. C. and Goya, E. 2010. Use of social information in seabirds: compass rafts indicate the heading of food patches. – *PLoS One* 5: e9928.
- Yen, P. P. W., Sydeman, W. J. and Hyrenbach, K. D. 2004. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. – *J. Mar. Syst.* 50: 79–99.
- Zavalaga, C. B., Halls, J. and Dell’Omo, G. 2010. Marine habitat use of Peruvian boobies: a geographic and oceanographic comparison between inshore and offshore islands. – *ICES J. Mar. Sci.* 67: 940–951.