Variability in foraging behaviour of red-footed boobies nesting on Europa Island

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Seabirds are considered to be good indicators of the marine environment. However, little is known about the effects of environmental variability on the foraging behaviour of tropical seabirds. Red-footed boobies (RFB) nesting on Europa Island (Mozambique Channel) were fitted with GPS devices over four years and different breeding stages. We first show that the durations of foraging trips vary extensively according to the stage of the breeding, being short during brooding, intermediate during incubation and long during fledging. This result highlights the importance of considering breeding stage when conducting comparisons of foraging between sites or years. In addition, we show that RFB adjusted their foraging behaviour between years (2003, 2011, 2012 and 2013) according to the prevailing environmental conditions. During 2011, RFB made longer foraging trips with larger area-restricted search (ARS) zones over a larger total surface area, suggesting that the foraging conditions were probably poor. This year was characterized by a decrease of the major environmental drivers of the Mozambique Channel system, i.e. particularly low chlorophyll concentrations in the northern part of the Mozambique Channel, as well as a weak eddy activity. This observation suggests that environmental conditions may have altered the southward transport and concentration processes structuring the trophic chain, leading to adverse conditions for a central-place forager like the RFB. Our results emphasize that environmental and breeding stage variation should be taken into account to better understand the distribution of these predators in marine tropical ecosystems.

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1. Introduction

As top marine predators, seabirds are generally considered as good indicators of marine environment, reflecting the availability, variability and distribution of lower trophic levels (Furness and Camphuysen, 1997). They can concentrate in large numbers at specific breeding sites on land, and are thus relatively easy to study compared to other marine predators. Breeding seabirds have to make continuous round-trips between the breeding site and foraging zones at sea, and are thus referred as ‘central-place foragers’ (Orians and Pearson, 1979). According to the ‘optimal foraging theory’ (Charnov, 1976), foraging behaviour is adjusted to gain the most benefit for the lowest cost, so that fitness is maximised. When foraging at sea, individuals are expected to spend more time in more profitable areas with a higher prey concentration. This behaviour can be detected by a decrease in the flight speed and an increase in the sinuosity and is generally referred as ‘area-restricted search’ (ARS) behaviour (Kareiva and Odell, 1987). In contrast, a higher flight speed and a lower sinuosity would reduce the time spent within a high-density patch of prey, and thus indicate that the individual is not foraging but rather travelling. When food is less available, individuals may spend more time foraging, or at extended distances from colonies compared to when food is abundant (e.g. Burke and Montevecchi, 2009) and have a lower body condition (e.g. Harding et al., 2011). Individuals may also increase time foraging within ARS (Fauchoir and Tveraa, 2003).
Tropical waters are characterised by an overall lower productivity compared to temperate or polar waters (Longhurst and Pauly, 1987). The distribution and abundance of prey is believed to be more unpredictable than in colder waters (Ashmole, 1971). Foraging strategies must be particularly adapted to these constraints and are expected to be based on reduced flight costs (Ballance, 1995). Relatively fewer studies on seabirds have been carried out in tropical waters compared to other areas, but different foraging strategies to cope with the specific environmental conditions have already been described, such as the association with subsurface predators that make prey available for birds at the surface (Au and Pitman, 1986) or bimodal foraging to optimise self-feeding and the delivery of food to chicks (Sommerfeld and Hennicke, 2010; Sommerfeld et al., 2015; Young et al., 2010; Weimerskirch et al., 2008). However, little is known about the effects of environmental variability on the foraging behaviour of tropical seabirds.

Seabirds tend to forage in zones where primary productivity is high such as upwellings over shelves or fronts and eddies (e.g. Croxall and Wood, 2002; Weichler et al., 2004; Louzao et al., 2006; Vlichis et al., 2006). The Mozambique channel is characterized by intense mesoscale dynamics with large eddies (diameters of 100–300 km) that are generated in the north and leads to a strong transport of water throughout the channel, resulting in a strong spatio-temporal heterogeneity of productivity (De Roij et al., 2002; De Roij et al., 2004; Schouwen et al., 2003).

The Red-footed booby Sula sula (RFB) is a pan-tropical oceanic species that feeds mainly on flying-fish and squid that are caught by plunge-diving or in flight, often in association with subsurface predators like tuna and dolphins that make these preys available at the surface (Au and Pitman, 1986). As in all members of Sulidae, except gannets, the male is smaller and lighter than the female (Nelson, 1978). During the breeding season, the female lays only one egg and both partners of a pair take turns at sea to forage and to feed the chick after hatching. The foraging behaviour of the RFB has been studied previously during the incubation and/or brooding stage, but only during one specific year (Kappes et al., 2011; Lewis et al., 2004, 2005; Lormee et al., 2005; Weimerskirch et al., 2005a, 2005b, 2006) or two years pooled together (Young et al., 2010). Therefore, the variability in their foraging behaviour when conditions at sea vary is yet unknown.

Individuals nesting on Europa Island (Mozambique Channel) were fitted with GPS loggers to collect their positions during foraging trips at sea during different breeding stages over 4 separate years. The aim of the study is to better understand in the RFB: i) the impact of the breeding stage on foraging behaviour, and ii) the interannual variability of foraging behaviour in connection to environmental conditions.

2. Material and methods

2.1. Field work

Field studies were carried out on Europa Island (22°3′S, 40°3′E; Local Time = GMT+3) in the Mozambique Channel, 300 km from the coasts of Madagascar and 500 km from the mainland coast of Africa. Europa hosts 2800–3800 pairs of RFB during the breeding season, all located in the dry Euphoriba stenoclada forest of the northern part of the island (LeCorre and Jouveintin, 1997). The breeding season starts with the laying/incubation stage in late August and September each year. This is followed by the brooding stage that occurs after egg hatching. The breeding season ends the following year in February–April with the fledging stage, when chicks learn how to fly and thus can leave the nest. Birds were tracked between September and November during incubation and/or brooding in 2003 (n = 17), 2011 (n = 33), 2012 (n = 31) and 2013 (n = 41). In 2014, they were studied in January–February during fledging (n = 8, the end of the 2013 breeding season). To study the movements of birds at sea, adults were selected randomly and fitted with GPS loggers: 30 g Technosmart GPS (40 × 30 mm) in 2003 and 20 g iGotU GPS (32 × 22 mm) during the other years. GPS were attached under the three central tail feathers using Tesa tape. Depending on the year and the GPS type, locations were recorded every 10 s, 30 s, 60 s, 120 s or 300 s. Birds were captured on the nests, previously identified with a plastic tag and mapped. One bird per nest was marked on the tail or the breast with a spray paint in order to identify bird rapidly and from a distance. The colony was monitored several times per day to infer the duration of foraging trips and departure and return times of the birds. On several occasions during the field missions, different individuals were captured by hand or with a 6 m telescopic fishing pole fitted with a nylon noose for the birds nesting higher in the trees. They were measured (culmen height and length, wing length) and weighed in a bag with a spring balance. When recaptured for logger recovery, they were weighed again to estimate the gain or loss of weight. In a few cases, both partners at the same nest were fitted with GPS. Boobies were sexed by voices when possible (males have a higher pitched voice than females; Nelson, 1978) or by measurements (females are larger than males; Nelson, 1978; Weimerskirch et al., 2006). Blood samples were also collected in some cases to confirm by molecular sexing the inferred sex in the field (Weimerskirch et al., 2006).

2.2. Analysis of foraging trips

A total of 321 tracks were collected from the four different breeding seasons (n = 17 in 2003, n = 34 in 2011, n = 39 in 2012, n = 165 and 69 in 2013 and 2014 respectively). These tracks represented 1 to 17 successive foraging trips of 112 birds. Complete tracks, starting from the departure of the bird from the nest and ending to his return to the starting point, represented 88% of the total number of tracks. Incomplete tracks were due to battery failure of the GPS devices. Duration of foraging trip (h), total distance covered (km), maximum range from the colony (km) and proportion of time sitting on the water (%) with speeds lower than 10 km h⁻¹ corresponding to birds on the water or diving (Weimerskirch et al., 2005b), were calculated for each track. All analyses were conducted in R 3.1.2 (R Development Core Team, 2014).

2.3. ARS behaviour

First-passage time (FPT) analysis was used in order to detect ARS behaviour. FPT is defined as the time required to cross a circle with a given radius (Faucauld and Tveraa, 2003). First, the track was redischcretized every 50 m through a linear interpolation to obtain movement representations based on a constant step length. FPT was calculated at each location with radii ranging from 0.1 km to 0.9 km, 1 km–10 km, 12 km–20 km and 25–100 km, with an increment of 0.1 km, 0.5 km, 2 km and 5 km, respectively. Peaks in log-transformed variance of the FPT as a function of the radius size were identified, indicating the ARS scale at which the individual increased its search effort. In order to study the behaviour at different scales, one main peak per range of radii was kept, such that the same trip may contain ARS up to 4 different scales. Each foraging trip was then split into homogenous segments using Lavielle’s method (R package adehabitatLT; Calenge, 2006). Segments with a mean FPT value higher than the mean FPT value of the track were considered as ARS behaviour. The analysis was conducted in R following Pinaud (2008). Trip parameters related to ARS were then estimated: number of ARS per trip, total distance...
covered in ARS (km), maximum distance from the colony (km) and proportion of time spent sitting on the water within ARS (%).

2.4. Spatial distribution

Kernel estimation (Worton, 1989) was used to determine the utilization distribution (UD) probability based on the locations of individuals. Kernel density approaches offer the advantages of being widely used, and capable of identifying population-level core habitat areas. Geographic coordinates from GPS tracks were transformed using the projected CRD Moznet/UTM zone 37S. We used the function kernelUD implemented in the R package adehabitatHR (Calenge, 2006). The average scale of area-restricted search (Pinaud and Weimerskirch, 2005) was used as smoothing parameter (h values). We used the function getverticesHR to estimate the size of general (95%) and core (50%) foraging areas.

2.5. Environmental drivers

Depth was delineated using bathymetry data of one minute resolution from The National Oceanic and Atmospheric Administration (NOAA) using the R package marmap (Pante and Simon-Bouhet, 2013). Sea surface temperature (SST) and chlorophyll concentration (Chl a) were both obtained from the MODIS-Aqua satellite (http://disc.sci.gsfc.nasa.gov/giovanni). Monthly composite of SST (in °C) and Chl a (in mg m⁻²) were obtained at a spatial resolution of 4 km. Since the Mozambique Channel is characterised by a strong eddy activity that influences top predators distribution (Weimerskirch et al., 2004; Tew Kai and Marsac, 2010), we used an indicator of mesoscale physical activity, the eddy kinetic energy (EKE) calculated as EKE = 1/2*(U² + V²) where U and V are zonal and meridional geostrophic currents components, respectively, derived from altimetry. In brief, the EKE is the energy associated with the turbulent part of the flow of a fluid and is calculated from sea-level anomaly (SLA).

The Mozambique channel hosts a biological contrast between inshore (highly productive areas along Mozambique and Madagascar coasts) and offshore areas (less productive areas) (Machu and Garçon, 2001; Tew Kai and Marsac, 2009). Thereby, we chose to exclude the inshore waters, as Europa was located in the middle of the Channel in the pelagic domain. Since calculating time series over a wide area along the canal could hide fine variations, we considered the SST and Chl a in two distinct areas: the northern part (12°–15°S, 42°–46°E) where eddy activity forms and the southern part where eddies rapidly move south (18°–21°S, 38°–42°E). For the EKE, the southern part was extended over a larger area around Europa (17°–25°S).

2.6. Statistical analysis

Two different main comparisons of trip parameters were made: i) between breeding stages, using data from the 2013–2014 breeding season, ii) between years during brooding, where tracks from the 4 breeding seasons of this study were available. Whereas sex-specific differences are found in the 2003 data set (Weimerskirch et al., 2006), we found no sex-specific difference in foraging parameters using the entire data set (including additional new tracks from 2011, 2012, 2013 and 2014). Therefore males and females were pooled together for all analyses, except for the weight-analysis due to the strong sexual dimorphism of the species (Nelson, 1978; Weimerskirch et al., 2006). Absence of sex-specific differences were similarly found in other sites for this species (Kappes et al., 2011; Lewis et al., 2005; Young et al., 2010). Because each year some individuals were tracked for several trips, mixed model ANOVA were applied to test for differences in trip parameters between breeding stages and between years, using the function lm in the R package nlme (Pinheiro et al., 2015). Variables were transformed to improve the normality. Duration, total distance covered, maximum range and ARS scales were previously square-root transformed. Proportion of time sitting on the water was arcsine transformed. ‘Duration’, ‘distance covered’ etc. were the dependant variables, ‘year’ or ‘breeding stage’ were fixed factors and ‘individual’ was a random factor. For the analysis of parameters within ARS, ‘trip ID’ nested into ‘individual’ was set as a random effect. Tukey HSD test were used to calculate post hoc comparisons on each factor in the model using the function glht from the R package multcomp (Hothorn et al., 2008). Pearson’s r was used to look for correlation between trip parameters. Values are given as average ± standard deviation (SD).

3. Results

3.1. General foraging behaviour

Almost all trips were performed during the day and lasted on average 6.4 ± 4.4 h. Only 5 trips lasted more than 24 h, including 3 outliers where birds spent several days at sea during the tropical storm Guito (19–20 February 2014). These trips were excluded from the analysis. Trip duration ranged between 0.27 and 14.9 h, (Fig. 1). Trips were oriented in all directions (Fig. 2a), covering a general foraging area (95% of locations) of 33 580 km² and a core foraging area (50% of locations) of 4360 km² (Fig. 2b). The range from the colony was on average 47 ± 37 km, with a maximum of 166 km. The total distance covered was on average 141 ± 101 km. The duration of trips was significantly related to the total distance covered (r = 0.94, n = 259, p < 0.001) and the maximum range (r = 0.95, n = 259, p < 0.001) (Fig. 3). ARS behaviour was detected in 298 out of the 315 tracks (95%). Most ARS zones were located near the maximum foraging range (Fig. 4), at a mean distance from the colony of 47 ± 36 km (range 2.8–176 km). Each track included on average 2.1 ± 1.2 ARS (range 1–7 ARS).

3.2. Comparison between breeding stages

Trip parameters of 208 tracks of 44 individuals were compared during the same breeding season that started in 2013 and finished in 2014 (Fig. 5). Three parameters were significantly different depending on breeding stage: the duration of trips (mixed ANOVA, F2,41 = 6.6, p = 0.003), the total distance covered (mixed ANOVA, F2,41 = 3.9, p = 0.029) and the maximum range (F2,41 = 4.6, p = 0.016). Post hoc comparisons (see Appendix 1) indicate that

![Fig. 1. Distribution of trip durations according to the breeding stage.](image-url)
these parameters were shorter during brooding (respectively $5.0 \pm 3.9$ h, $107 \pm 85$ km, $35 \pm 29$ km; $n = 126$) than during fledging ($8.9 \pm 4.1$ h, $178 \pm 86$ km, $65 \pm 34$ km; $n = 50$). Intermediate values were observed during incubation ($6.8 \pm 4.4$ h, $138 \pm 95$ km, $50 \pm 37$ km; $n = 32$). The proportion of time when birds were sitting on the water did not differ significantly between breeding stages (mixed ANOVA, $F_{2,41} = 1.3$, $p = 0.278$). The foraging area (Table 2), represented by the 95% estimation of the utilization distribution with the kernel method, was much larger during fledging ($32,933$ km$^2$) than brooding ($14,890$ km$^2$) and incubation ($12,539$ km$^2$).

The foraging behaviour within ARS was compared between the three breeding stages (Table 1 & Appendix 1). The mean numbers of ARS were similar (mixed ANOVA, $F_{2,41} = 1.5$, $p = 0.31$). As for the full trips, duration of ARS and maximum distance between ARS and the colony were smaller during brooding than during the other breeding stages (mixed ANOVA, $F_{2,41} = 6.4$, $p = 0.004$). However, the distance covered within ARS did not differ significantly depending on the breeding stage (mixed ANOVA, $F_{2,41} = 2.8$, $p = 0.07$). The mean proportion of time sitting on the water within ARS was higher than during complete trips ($49–61\%$ vs $34–38\%$ respectively; Welch’s t-test, $t = -12.1$, df $= 598.2$, $p < 0.0001$) and differed between stages (mixed ANOVA, $F_{2,41} = 4.3$, $p = 0.02$), with higher values during fledging than during brooding.

### 3.3. Interannual comparison

A strong sexual dimorphism was observed (Fig. 6), with females being significantly heavier than males (ANOVA, $F_{1,151} = 172.1$,
Body weights were significantly different between years (ANOVA, $F_{3,151} = 3.5, p = 0.02$). Birds were on average lighter in 2011 than during the other years, but only the differences between 2011 and 2012 were significant according to post-hoc comparisons.

During brooding, the duration of the trips (mixed ANOVA, $F_{3,58} = 7.8, p < 0.001$), the total distance covered (mixed ANOVA, $F_{3,58} = 9.9, p < 0.001$) and the maximum range from the colony (mixed ANOVA, $F_{3,58} = 6.7, p < 0.001$) were significantly different between years (Fig. 7). Post hoc comparisons (see Appendix 2) showed longer trips in 2011 ($9.5 \pm 4.3$ h, $244 \pm 122$ km and $78 \pm 50$ km; $n = 28$) than in 2012 ($4.3 \pm 2.8$ h, $118 \pm 78$ km and $34 \pm 27$ km; $n = 16$) and 2013 ($5.0 \pm 3.9$ h, $107 \pm 85$ km and $35 \pm 29$ km; $n = 126$) at the 0.05 level of significance. Trips were also shorter in 2003 compared to 2011 ($4.6 \pm 2.6$ h, $119 \pm 59$ km and $30 \pm 14$ km; $n = 4$) but the difference was not significant, probably because of the small sample size. The proportion of time spent on the water differed significantly between years (mixed ANOVA, $F_{3,58} = 31.6, p < 0.001$), with significantly higher values in 2013 ($34 \pm 14$%) than in 2003 ($9 \pm 3$%), 2011 ($17 \pm 5$%) and 2012 ($13 \pm 6$%).

The distribution of the duration and maximum range of foraging trips (Fig. 8) shows that the increase in these parameters in 2011 is due to birds making a larger proportion of long trips (in duration and range), leading to a tendency for a bimodal distribution of trips in 2011 compared to the other years.
Foraging parameters within the ARS zones identified were compared between years (Table 3 & Appendix 2). The number of ARS per trip did not vary significantly between years (mixed ANOVA, $F_{3,58} = 1.84, p = 0.15$). We observed the same patterns within ARS and for the entire trip. Indeed, duration of ARS (mixed ANOVA, $F_{3,58} = 0.02, p = 0.0001$), distance covered within ARS (mixed ANOVA, $F_{3,58} = 10.9, p < 0.0001$) and maximum range between ARS and the colony (mixed ANOVA, $F_{3,58} = 9.26, p < 0.0001$) were significantly larger in 2011 than during other years. In addition, the proportion of time spent sitting on the water within ARS zones was higher in 2011 than during other years. In addition, the proportion of time spent sitting on the water within ARS zones was higher in 2011 (mixed ANOVA, $F_{3,58} = 10.6, p < 0.0001$). The foraging area was much larger in 2011 ($26\,315\,\text{km}^2$) than during the other years (range $1588\text{–}14\,890\,\text{km}^2$, Table 4).

### 3.4. Variability of environmental drivers

The chlorophyll $a$ concentration in the Mozambique Channel is overall low. The average concentration during the 2003–2013 period was $0.153 \pm 0.021\,\text{mg}\,\text{m}^{-3}$ in the southern zone of the channel and $0.154 \pm 0.023\,\text{mg}\,\text{m}^{-3}$ in the northern zone. In the northern zone (Fig. 9a), the productivity was the highest in 2003 and decreased to a minimum reached in 2011, followed by an increase. In the southern zone (Fig. 9b), a completely different pattern was observed, with more variation over the years. The average value of eddy kinetic energy in the southern part of the Mozambique Channel around Europa between 2003 and 2013 was $1000 \pm 107\,\text{cm}^2\,\text{s}^{-2}$. As observed for the chlorophyll $a$ parameter in the northern sector, a decrease of the mesoscale activity occurred...
compared to 5 h for a range of 35 km during brooding. It is known cubation lasted on average 7 h with a foraging range of 50 km, (Weimerskirch et al., 2005a). Here we found that trips during incubation, versus 5 h and a range of 39 km during brooding according to the stage of the breeding season, being intermediate during incubation, shorter during brooding of the chick and longer fl during incubation, shorter during brooding of the chick and longer.

**Table 3**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>2003 mean ± SD</th>
<th>2011 mean ± SD</th>
<th>2012 mean ± SD</th>
<th>2013 mean ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of ARS per trip</td>
<td>1.3 ± 0.5</td>
<td>2.0 ± 0.8</td>
<td>2.6 ± 1.5</td>
<td>2.2 ± 1.2</td>
</tr>
<tr>
<td>Duration (h)</td>
<td>1.5 ± 1.1</td>
<td>3.3 ± 2.1</td>
<td>0.9 ± 0.9</td>
<td>1.7 ± 1.9</td>
</tr>
<tr>
<td>Total distance covered (km)</td>
<td>28.8 ± 20.6</td>
<td>46.0 ± 32.8</td>
<td>16.7 ± 16</td>
<td>21.6 ± 23.1</td>
</tr>
<tr>
<td>Maximum distance from the colony (km)</td>
<td>26.8 ± 14</td>
<td>77.3 ± 48.1</td>
<td>24.5 ± 16.2</td>
<td>34.2 ± 27.4</td>
</tr>
<tr>
<td>% time sitting on the water</td>
<td>15 ± 6</td>
<td>37 ± 15</td>
<td>28 ± 23</td>
<td>49 ± 22</td>
</tr>
</tbody>
</table>

Table 4

General (95%) and core (50%) foraging area of red-footed boobies nesting on Europa according to years.

<table>
<thead>
<tr>
<th>Year</th>
<th>2003 (n = 4)</th>
<th>2011 (n = 28)</th>
<th>2012 (n = 16)</th>
<th>2013 (n = 126)</th>
</tr>
</thead>
<tbody>
<tr>
<td>95% area (km²)</td>
<td>1588</td>
<td>26 315</td>
<td>7537</td>
<td>14 890</td>
</tr>
<tr>
<td>50% area (km²)</td>
<td>220</td>
<td>3947</td>
<td>1138</td>
<td>1715</td>
</tr>
</tbody>
</table>

with a minimum in 2011 (843 ± 63 mg m⁻³), followed by an increase (Fig. 10).

4. Discussion

In this study we showed that RFB nesting on Europa varied extensively their foraging behaviour in relation to the different stages of the breeding season, but also between years in relation to the prevailing environmental conditions.

4.1. Foraging behaviour during the breeding season

The duration of foraging trips of RFB varied extensively according to the stage of the breeding season, being intermediate during incubation, shorter during brooding of the chick and longer during fledging i.e. the late chick-rearing period. Monitoring of the nest attendance of RFB in Europa has already revealed that trip duration decreased from the incubation to the brooding stage (Lormee et al., 2005). This trend was confirmed later by the use of loggers, with a mean trip duration of 10 h and a range of 67 km during incubation, versus 5 h and a range of 39 km during brooding (Weimerskirch et al., 2005a). Here we found that trips during incubation lasted on average 7 h with a foraging range of 50 km, compared to 5 h for a range of 35 km during brooding. It is known that foraging effort can be higher during brooding than incubation, because birds have to minimize their time at sea to maximize the rate of food delivery to chicks, and at the same time alternate with their partner on the nest to guard the small chick. In contrast, Young et al. (2010) observed that trip distribution during brooding of RFB on Palmyra Atoll in the equatorial Pacific Ocean was bimodal, suggesting important behavioural differences between sites. This strategy is also used in masked boobies Sula dactylatra (Weimerskirch et al., 2008; Sommerfeld et al., 2015) and many Procellariiform species (Shaffer et al., 2003; Weimerskirch et al., 1993). For example, red-tailed tropicbirds Phaethon rubricauda on Christmas Island had a bimodal pattern of foraging during brooding, when the feeding pressure is higher, whereas incubating adults undertook only long trips (Sommerfeld and Hennicke, 2010). The alternation of short and long foraging trips could allow the optimisation of simultaneous food delivery to chicks and self-feeding when local resources are poor (Weimerskirch et al., 1993). The absence of that pattern in Europa during favourable years could thus mean that there are sufficient resources nearby the colony. However during unfavourable years such as in 2011, birds may have to shift to a bimodal strategy as they do at other sites where food availability is lower (Young et al., 2010).

Far less is known about RFB adults’ foraging behaviour when they are provisioning large chicks. In our study we show that the duration of trips, the distance covered and the maximum range from the colony were much longer at this stage than during brooding and, to a lesser extent, than during incubation. This can be explained by the increased chick needs as it grows larger, after the first month of brooding. At the end of the breeding season, when chicks start to forage at sea on their own but are still fed by the parents, their food requirement may be reduced, and adults could progressively supply the chick in a smaller extent. In Dong Island (northern South China Sea), Guo et al. (2010) reported that when

![Fig. 9](image-url)  
**Fig. 9.** Time series of winter (June–August) mean chlorophyll a concentration (±SD) a) in the north and b) in the south of the Mozambique Channel, over the 2003–2013 period.

![Fig. 10](image-url)  
**Fig. 10.** Time series (September–October) of mean eddy kinetic energy (EKE) (±SD) in the south of the Mozambique Channel around Europa over the 2003–2013 period.
parents feed large chicks, they progressively decrease provisioning from the first fledging of the chick until his independence. At the same time, juveniles’ foraging trips lengthened progressively and this period served mainly to juvenile birds to develop foraging skills (Guo et al., 2010). Because the period of fledging occurs 3–4 months after hatching, an alternative explanation could be that the increasing length of the trips is the result of a seasonal displacement of resources farther from the colony.

Most of the previous studies on RFB were carried out during the period pooling incubation and brooding. We saw here that foraging behaviour varies extensively between breeding stages, highlighting the importance to consider the same stage when doing comparisons between sites or years.

4.2. Variability of the foraging range between sites

Traditionally, the RFB has been considered to be the most pelagic of all boobies (Nelson, 1978; Schreiber et al., 1996). At Europa, it was thought that RFB were strictly diurnal forager and that they never spent the night at sea (Weimerskirch et al., 2005a). Here we confirmed that most of the birds left early in the morning and returned to the colony before or just after dusk, but a few individuals spent the night at sea. The tracks of three of these five individuals coincide with the tropical storm Guito (19–20 February 2014). Birds could have been caught in the storm, preventing them from returning to the colony, or could deliberately have avoided the storm. Daylight in Europa during the studied seasons was on average 12.5 h and trips lasted on average 6.4 ± 4.4 h, allowing each partner of a pair to make a foraging trip during the same day. If the limited-time of daylight represents a constraint to foraging, it is less apparent in Europa than for example in Johnston Atoll (central Pacific Ocean), where average trip duration of RFB was 14 h (Lewis et al., 2004), i.e. slightly longer than the local daylight duration.

Foraging trips at Europa were longer than at Tromelin Island where mean duration was 4 h and maximum range was 31 km (Kappes et al., 2011). In a study of two nearby islands in the oligotrophic central Pacific, Young et al. (2015) observed that RFB foraged farther, faster, and for longer durations around Tern Island (average duration of 8 h, maximum range of 61 km and absolute area of polygon of 37 789 km²) than at Palmyra Atoll (respectively 13 h, 105 km and 52 089 km²). These differences between sites can be explained by the size of populations and associated intra-specific competition (Grémillet et al., 2004; Wakefield et al., 2013). However, maximum ranges of brooding birds were greater at Palmyra than at Europa, despite larger numbers of RFB nesting at Europa. Europa has nonetheless a relatively small population that may explain the relatively short duration and short range of foraging trips of RFB compared to other sites. However, observed variability in foraging range can also be influenced by environmental factors like the presence of oceanographic features (Harding et al., 2013) or the variation in oceanic productivity around the colony (Ballance et al., 1997; Paiva et al., 2010). Indeed, overall RFB appear to have a very variable duration of foraging trips according to the sites that lie in contrasted environmental conditions. Although the trip duration is influenced by a variety of factors, the primary factor influencing duration may be the availability of prey, the lower the availability of prey, the longer the foraging trips to find and catch sufficient amounts of prey or to reach distant more productive areas (e.g. Suryan et al., 2000). A comparison of the oceanographic conditions around the different breeding sites would be necessary to test these hypotheses.

4.3. Optimisation of the foraging behaviour

When seabirds reach a patch of prey, they are supposed to reduce their speed and increase their sinuosity to remain in the zone of interest and maximize their probability of prey acquisition (Weimerskirch et al., 2007). This behaviour was clearly detectable on GPS tracks of RFB. The strategy of the RFB was to rapidly leave the colony with a nearly linear path until reaching a zone where an ARS (Area-Restricted Search) was performed and then rapidly return to the colony. ARS were almost systematically located at the maximum range of the trip, similar to other Sulid species such as Peruvian boobies (Weimerskirch et al., 2012) or northern and Cape gannets (Garthe et al., 1999; Grémillet et al., 2004). RFB nesting on Europa seemed to have smaller ARS nested into larger ones, as is the case for yellow-nosed albatross Thalassarche cartari for example (Pinaud and Weimerskirch, 2005). That scale-dependent pattern of foraging movement fits well with the heterogeneous and hierarchichal distribution of patchy resources (Fauld, 1999).

RFB spent on average two-thirds of their foraging time in flight, the rest sitting on the water or diving. This proportion is higher than in seabirds from temperate or polar waters such as gannets (Garthe et al., 1999, 2003; Ropert-Coudert et al., 2004), alcids (Kato et al., 2003) or albatrosses (Weimerskirch and Guionnet, 2002). The proportion of time sitting on the water (when speed was lower than 10 km h⁻¹) was the same during incubation, brooding and fledging (34–38% on average). This could mean that RFB did not increase their foraging effort by plunging more often for example during brooding to balance the fact that trips were shorter during this breeding stage. Nevertheless this parameter should be interpreted carefully because we did not distinguish between birds foraging or resting on the surface of the water. This issue was well studied by Sommerfeld et al. (2013), who observed that ARS zones of masked boobies are often falsely detected when birds are resting on the water, mostly during short trips in close proximity to the colony. Nonetheless, the probability of ARS behaviour increased with the number of dives, suggesting that ARS behaviour may anyway be used as a proxy to identify important feeding areas. During brooding, we observed that birds made shorter trips and used larger ARS zones where they concentrated their foraging effort.

4.4. Interannual variation in the foraging behaviour

In 2003, only trips to the east were observed, but sample size was small (Weimerskirch et al., 2005a). However, this result was not observed in the other years, when birds headed in all directions. This pluriannual study confirms that RFB nesting on Europa did not exhibit directional preference nor orient their trip towards well defined foraging areas.

This study shows that foraging parameters of RFB varied extensively between years, and that 2011 was probably unfavourable compared to other years. Indeed, foraging trips were about twice as long in duration and length, with birds using a larger total surface area and larger ARS zones. Although the number of tracks obtained in 2011 was five times less than in 2013, the global foraging surface area was almost twice the size, highlighting an unusual behaviour in 2011. The ARS zones were also longer in duration and length.

The distribution of the duration and range of foraging trips also suggested that RFB may have adopted a bimodal foraging strategy in 2011 when condition were unfavourable, whereas during other years the distribution was more Poisson-shape. RFB may have thus flexible foraging strategy, with short trips when conditions are favourable, and with the alternation of short and long trips when conditions around a site close to productive waters become unfavourable some years, or in sites where waters are unfavourable every season, such as in the North Pacific colonies (Young et al., 2010).
4.5. Influence of environmental parameters

As seabirds tend to forage in zones where primary productivity is high and predictable, they are supposed to search for specific predictable processes where productivity and prey availability are increased such as bathymetric features (e.g. Bograd et al., 1997; Maxwell et al., 2012). However, we saw that RFB nesting on Europa headed in all direction and didn’t target specific topographic structures such as the close Bassas da India seamounts. RFB may rather search for mobile and transient oceanographic features such as eddies that move southward in the Mozambique Channel (Tew Kai and Marsac, 2010). In polar and temperate pelagic waters, it is known that resources are often predictable so that top predators tend to target associated oceanographic features such as fronts or eddy edges (e.g. Cotté et al., 2011). In tropical waters, that are in comparison less productive, several studies on tropical seabirds used chlorophyll and/or SST to explain their use of specific areas (Ballance et al., 1997; Jaquemet et al., 2005). Previous work suggested that RFB generally headed in the direction of zones where productivity was enhanced (Weimerskirch et al., 2005a).

We hypothesize that the foraging conditions were probably poor for RFB in 2011 compared to other years, since trips were significantly longer and birds lighter. Birds may have had to forage further and longer to bring enough food to the chick. Indeed, 2011 was a poor year in terms of chlorophyll concentration in the northern part of the Mozambique Channel, but not in the southern part where Europa is located. This year also presented the weakest mesoscale activity (through EKE) around Europa over the whole 10-years period, suggesting a decline in food supply, since mesoscale activity was reported to affect productivity (Jose et al., 2014; Tew Kai and Marsac, 2009). Considering the lifetime of organisms, a depletion in primary production in the north of the Channel will induce a lower density of zooplankton later southwards, and subsequently less prey available for seabirds. The edge of eddies is known to be beneficial for the concentration of prey due to their structuring effect (Sabarros et al., 2009). For instance, the probability of observing the feeding of great frigatebirds Fregata minor breeding in Europa is positively linked with the development of dynamical fronts at the edge of eddies (Tew Kai et al., 2009; De Monte et al., 2012; Jaquemet et al., 2014). During ship-based survey, Jaquemet et al. (2014) observed that RFB concentrated in divergence zones characterised by low sea level anomalies, low geostrophic currents, and high zooplankton biomass close to the surface. A global reduction of the eddy activity in 2011 could thus have altered the transport and concentration processes structuring the trophic chain, leading to adverse conditions for a central-place forager like the RFB.

5. Conclusion

Thanks to a large data set over different breeding stages and several years, we have shown that RFB nesting on Europa varied extensively their foraging behaviour in poor and heterogeneous waters according to the stage of the breeding cycle and the environmental variability. Since we observed variations between the different stages of the breeding season within a specific year, we strongly encourage future work to consider the same stages when comparing foraging parameters between sites or years. Foraging behaviour also varied extensively between years, probably in relation to the prevailing environmental conditions. In 2011, foraging trips were longer in duration and range, suggesting unfavourable conditions compared to other years. Particularly low productivity and low eddy activity matched this modified foraging behaviour.

Since RFB inhabit all tropical oceans around the world (Schreiber et al., 1996), this species is a good model to study the influence of environmental conditions on habitat and foraging behaviour of a top marine predator in tropical ecosystems. In this study we focused on the colony nesting on Europa, but important differences in foraging behaviour appear to exist between sites. It would be interesting in the future to compare the behaviour of individuals breeding in different sites with sharply contrasted oceanographic conditions. This would help to understand why such differences occur, to predict the favourable oceanic areas for these predators, and overall to learn more about the potential environmental conditions involved in the evolution of foraging behaviours. Besides the fundamental interest to study these questions, a better understanding of the distribution of these marine predators would provide information on high-biodiversity areas in marine pelagic ecosystems.

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