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Original article

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

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ABSTRACT

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.

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 (Fauchald and Tveraa, 2003).

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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; Louzão et al., 2006; Vilchis 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 southward transport of waters throughout the channel, resulting in a strong spatiotemporal heterogeneity of productivity (De Ruijter et al., 2002; De Ruijter et al., 2004; Schouten 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 conducted 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 Jouventin, 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 (Fauchald and Tveraa, 2003). First, the track was rediscretized 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