



Inter-population variation in the behaviour of adult and juvenile Red-footed Boobies *Sula sula*

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Early life is a critical phase of the life cycle of animals and is attracting increased attention because little information is available on the behaviour of young individuals during this period. Behaviour during early life is probably influenced by the environmental conditions encountered by young animals, but data on intraspecific variation between breeding sites during this crucial period of life are limited. Here we study variability in the foraging behaviour of juveniles and adults in three colonies of a pantropical seabird, the Red-footed Booby *Sula sula*. Both adults and juveniles were measured and fitted with GPS loggers in three remote islands: Genovesa (Galapagos, Eastern Pacific Ocean), Europa (Western Indian Ocean) and Surprise (New Caledonia, Western Pacific Ocean). Foraging behaviour was compared between age-classes, sex and colonies by examining trip characteristics, different behaviours at sea, potential associations between individuals and morphological characteristics. Compared with adults, juveniles conducted shorter trips that were restricted to around the colony, especially on Genovesa (max. range: 203.4 ± 125.1 km and 3.6 ± 3.1 km, respectively). Juveniles appeared more constrained by poor flight skills and experience rather than by their morphology. Adults travelled 45% of the time during at-sea trips, whereas juveniles spent a lower proportion of time travelling but foraged more often using an 'area-restricted search' behaviour, potentially training to catch prey. Associations between juveniles were commonly detected in the three colonies and occurred mostly during foraging, suggesting that social learning is an important strategy. Variability of morphometric measurements in both adults and juveniles was high between sites, with larger birds found on Genovesa. These results suggest that adaptations to local environmental conditions are already visible in their early life. Future studies should continue to investigate the behavioural flexibility of juvenile birds to better understand the effect of local environmental conditions during this critical stage of life.

Keywords: age-class, associations, colony, foraging, seabird, tropical.

For most long-lived animal species, the first months of independence are a critical period in their life-history (Gaillard *et al.* 1998). Predation and starvation often lead to a higher mortality in juveniles than in adults (Sullivan 1989). Although the study of juveniles is a growing research field, little information is as yet available on their behaviour. In particular, it is not known how variable their foraging behaviour is in relation to the

environmental conditions they encounter during this critical period.

Multi-site studies are necessary to better understand the behavioural variability at the species level and thus to improve our understanding of population dynamics and the evolution of life-history traits (Dhondt 2001, Frederiksen *et al.* 2005). Such studies have also direct implications for conservation measures (Perrins & Hiron 1993). Seabirds are interesting models to study population differentiation (Friesen *et al.* 2007), as most species show a high degree of natal philopatry

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(Warham 1996) and extensive geographical variation in morphology (del Hoyo *et al.* 1996). However, most demographic and behavioural studies of seabirds focus on variations observed within a particular colony over time and/or individuals, and studies of the same species between several sites have received much less attention (Frederiksen *et al.* 2005, Grémillet & Boulinier 2009). During the breeding season, adult seabirds can adjust their foraging behaviour in relation to intrinsic determinants such as the breeding stage that imply different energetic constraints on the individuals (Ricklefs 1983). For example, adults during brooding have to minimize their time at sea to maximize the rate of food delivery to chicks. In Northern Gannets *Morus bassanus*, individuals can optimize their foraging trips with age (Votier *et al.* 2017, Grecian *et al.* 2018), indicating that the experience of the individual is an important intrinsic determinant of the foraging behaviour. Some species may use social information taken from congeners. For example, Guanay Cormorants *Phalacrocorax bougainvillii* use the flight direction of congeners and the position of rafts off the colony as an indication of the location of food patches (Weimerskirch *et al.* 2010). Cape Gannets *Morus capensis* form frequent associations at sea (Thiebault *et al.* 2014) and Brown Boobies *Sula leucogaster* follow other conspecifics to find food sources (Yoda *et al.* 2011). However, it is not known whether this type of behaviour is specific to certain colonies or generally used at the species level. On the other hand, the foraging behaviour of adults also varies according to extrinsic determinants, such as the marine environment and its fluctuation, affecting prey availability. Differences in behaviour and demographic parameters between colonies, for the same breeding stage, are thus presumably an adaptive response to local environmental variability (Weimerskirch 2001, Rayner *et al.* 2008, Wolf *et al.* 2009, Nevoux *et al.* 2010, Mendez *et al.* 2017a).

Juvenile seabirds often demonstrate a lack of experience in foraging abilities (Daunt *et al.* 2007, Alderman *et al.* 2010, Riotte-Lambert & Weimerskirch 2013) and a high sensitivity to environmental variability (Porter & Coulson 1987), leading to generally higher mortality than adults (Lack 1954). In juveniles, foraging behaviour seems to result from different intrinsic determinants such as morphological parameters and/or the experience of the individual (Weimerskirch *et al.* 2000, Yoda

et al. 2004, Daunt *et al.* 2007). However, the correlation between these two factors is generally unknown and may vary between species. Juveniles are less experienced and are typically smaller than adults, and morphology and inexperience could both independently affect juvenile foraging behaviour. Usually, juvenile oceanic seabirds leave their natal colony quickly for the open ocean during their first flight (Burger 1980). However, some species pass through a transition phase where they leave the colony to forage at sea but return to the nest to be fed by their parents. That post-fledging stage can last several months in Boobies or Frigatebirds (Burger 1980) and presupposes a progressive development of flight capabilities (Yoda *et al.* 2004, Yamamoto *et al.* 2017) and/or hunting techniques (Castillo-Guerrero & Mellink 2006, Yoda *et al.* 2007, Mendez *et al.* 2017b). The specificities of the post-fledging stage, such as the behaviour exhibited by juveniles, should be directly linked to the environmental context, but potential variations between colonies has never been described before.

The Red-footed Booby *Sula sula* is a long-lived seabird widely distributed throughout the pantropical latitudes that exhibits a long transition stage (Nelson 1978). During breeding, both partners take turns caring for the nest and foraging at sea. The duration and the range of the foraging trips have previously been shown to vary strongly between colonies (Mendez *et al.* 2017a). However, trips seem to be structured in a similar way at species level, with birds departing and returning to the colony in a pretty straight trajectory, although varying their foraging activity in the middle sections of the trips (Weimerskirch *et al.* 2005a, 2005b, 2005c, Mendez *et al.* 2016, 2017a). During those sections, birds reduce their speed and increase their sinuosity to adopt an 'area-restricted search' (ARS) behaviour (Kareiva & Odell 1987), suggesting that they found a patch of prey (Weimerskirch *et al.* 2005a). Juveniles leave the nest for the first time about 130 days after hatching (Nelson 1969) and become independent after a post-fledging transition period lasting between 90 and 180 days (Nelson 1969, Diamond 1974, Guo *et al.* 2010, Mendez *et al.* 2017b). A previous study that tracked juvenile Red-footed Boobies showed that the duration and the range of their trips increased over time (Mendez *et al.* 2017b). Moreover, they spent more time intensively foraging compared to adults, which could result from needing more attempts to capture prey, and

they are frequently associated with congeners at sea (Mendez *et al.* 2017b).

Here, we compare for the first time the foraging behaviour of adults and juveniles in three different environments. As the long post-fledging period observed in Boobies is likely to be due to juveniles enhancing their foraging skills (Mendez *et al.* 2017b), we predicted that the foraging behaviour should differ (1) between juveniles and adults in each site and (2) between juveniles from different sites in response to the environmental context, similarly to adults (Mendez *et al.* 2017a). To avoid the effect of individual improvement with experience during early life (Mendez *et al.* 2017b) and make a straightforward comparison between adults and juveniles, all juveniles were studied shortly after fledging when carrying out their earliest flights. By taking into account the age-class, sex and colony, we aimed to better understand the effect of intrinsic (morphometrics, experience) and extrinsic determinants (local environment) on the foraging behaviour in order to identify the relative importance of these different factors. To examine this, morphometric measurements were obtained from both adults and juveniles, whose trips at sea were recorded using GPS loggers. For each trip, we estimated the departure and return time, trip duration, total distance covered, maximum range and different behaviours used (travelling, intensive foraging, resting, extensive foraging). The frequency, duration and size of ARS zones, identified as bouts of intensive foraging, were also calculated. As young birds seem to rely on social enhancement to identify prey patches (Mendez *et al.* 2017b), associations at sea between individuals were investigated in the three colonies.

METHODS

Study sites and data collection

Morphometric and movement data of adult and post-fledging juvenile Red-footed Boobies were collected at three remote sites. Genovesa Island (0.3°N, 89.9°W; area: 14 km²) lies in the Galapagos Archipelago and hosts the largest population of Red-footed Boobies in the world (140 000 breeding pairs; Nelson 1978). Birds were studied in 2014 during a 13-day period (10–22 November). Different breeding stages were observed at the same time in the colony (including adults

taking care of their offspring after fledging), but only incubating adults were tracked. Europa (22.3°S, 40.3°E; area: 28 km²) lies in a French atoll in the Mozambique Channel (Indian Ocean). During the breeding season, Europa hosts about 2800–3800 pairs of Red-footed Boobies (Le Corre & Jouventin 1997). Both adults and juveniles were tracked during the post-fledging period in 2014 for 12 days (27 January–2 February). We also included morphometric measures from adult birds studied at Europa during the same breeding season some months before the post-fledging care period (September–November 2013). The third colony was on Surprise (18.8°S, 164.0°E; area: 0.3 km²), a small island located in the Entrecasteaux reef (north of mainland New Caledonia). Birds were tracked in 2015 during a 6-day period (24–29 November). Although the majority of adults from the colony were taking care of fledging juveniles, adult data were collected from individuals that were still brooding a chick. All juveniles in the study were recently fledged birds, but the precise age was not known.

On the three islands, both adults and juveniles were captured by hand or with a telescopic fishing pole fitted with a nylon noose for those birds nesting higher in the trees. Juveniles are brown with grey legs and feet and adults are clearer with red legs and feet and are thus easy to distinguish. A labile dye was used to mark individuals on the tail or breast to identify them rapidly from a distance. They were measured (culmen height and length, wing length) and weighed in a bag with a spring balance during the study periods indicated above. Adults were sexed by measurements (females are 20% larger than males; Nelson 1978, Weimerskirch *et al.* 2006) and by voice when possible (males have a higher pitched voice than females; Nelson 1978); this method can sex Red-footed Boobies with 100% accuracy (Lormée *et al.* 2000). Only juveniles from Europa could be sexed using molecular markers from blood samples following standard techniques as detailed in Weimerskirch *et al.* (2005b). Birds were fitted with iGotU GPS loggers (Mobile Action Technology, 32 × 22 mm, 20 g) weighing less than 3% of the adult weight and thus not exceeding the generally recommended thresholds (Kenward 2000). The loggers were attached under three central tail feathers using waterproof tape (Tesa 4651; Hamburg, Germany) (Wilson *et al.* 1997). Handling never lasted more than 10 min. Once released, the bird quickly

returned to its nest or perch and resumed natural behaviour. No nest abandonment was observed after handling. After a few days, birds were caught again to retrieve the logger containing all the geographical positions recorded at a predefined frequency. The number of studied individuals and position-recording frequencies of each site are indicated in Table 1.

Track analysis

Each outward/return trip from the nest recorded by GPS loggers was considered as a distinct 'track'. During their first trips, juveniles made the majority of short flights over land and progressively spent more time over the sea. Tracks containing more than 80% of their locations over land were excluded from the dataset to focus only on the foraging behaviour at sea. With this filter, GPS locations on land ($n = 5047$) represented 4.85% of the dataset ($n = 104\,166$) and thus $\approx 95\%$ of the GPS locations were at sea. As the position-recording frequency differed between sites and age-classes (Table 1), only tracks lasting at least 6 min (= two successive positions separated by 180 s) were included in the analyses to homogenize the dataset. The maximum speed was set to 90 km/h (Weimerskirch *et al.* 2005c). The duration of a foraging trip (h), total distance covered (km) and maximum range from the colony (km) were calculated for each track. Departure and return times of each trip were linked to the time of day. Night periods were defined when the sun was more than 6 degrees below the horizon, between the end of the evening civil twilight (dusk) and the beginning of the morning civil twilight (dawn) using the function *getElevation* of the R package *GeoLight*. Base maps were generated using the R package *ggmap*. All analyses were made using R software (R Development Core Team 2014).

Behaviour clustering and ARS identification

The Expectation Maximisation binary Clustering (EMbC) algorithm (Garriga *et al.* 2016) was used to identify the different behaviours of individuals along tracks. To avoid the influence of the position-recording frequency, settled differently according to site and age (Table 1), trips of adults and juveniles of the three study sites were first linearly interpolated (with one location every 2 min). All trips were then treated simultaneously in the analysis conducted with the EMbC R-package in the R software (R Development Core Team 2014). The EMbC algorithm is a robust, non-supervised multi-variate clustering algorithm based on two input variables: speed and turning angle, obtained from successive locations. The output is four clusters, delimited by different intervals of speed and turning angle, which could be biologically interpreted. Each GPS location was labelled with one of these four behaviours: resting (0–4 km/h and 0–0.32 radians), intense foraging (0–9 km/h and 0.32–3.14 radians), travelling (4–90 km/h and 0–0.3 radians) and relocating (9–90 km/h and 0.3–3.14 radians). Relocating reflects important turns with a steady speed and can be interpreted as an overall food search through a displacement between restricted areas of intensive foraging. For each study site and age-class (adults/juveniles), we calculated the average proportions of the four behaviours used. ARS zones were defined when at least three successive locations were labelled as intensive foraging by the EMbC algorithm (Mendez *et al.* 2017a,b). To simplify the description of the different behaviour along the trajectory, we merged ARS zones when fewer than four locations labelled with another behaviour were observed between them (Mendez *et al.* 2017a,b). The frequency (number of ARS zones per hour), the duration and the surface of

Table 1. Data collected on adult and juvenile Red-footed Boobies fitted with GPS loggers. GEN = Genovesa, SUR = Surprise, EU = Europa.

	Number of individuals		Number of tracks collected		GPS frequency (s)	
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
GEN	37	18	44	242	120	60
SUR	6	10	22	78	180	60
EU	7	21	58	124	120	60

ARS (area of the minimum convex polygon including all positions of an ARS zone) were calculated.

Associations between individuals

Pairwise comparisons between all locations from one bird with all the locations from the other birds were generated to study associations between individuals during their foraging trips (Mendez *et al.* 2017b). Locations within 50 m of the nest were ignored to limit the study of associations to those occurring at sea. Association events were identified when the difference in latitude and longitude were both lower than 0.002° (c. 280 m) within a time interval of 30 s (following Mendez *et al.* 2017b). To avoid very short random encounters, tracks containing only one association event were ignored.

Statistical analysis

All morphological parameters were compared between sex, age-class and site using linear models. For mass, we used a linear mixed-effect model and added the variable 'timing' (deployment or recovery of the GPS) with 'individual' as a random factor using the function *lmer* from the R package *lme4* (Bates *et al.* 2015). To test for differences in trip parameters between sites, age-classes and sex, linear mixed-effects models with 'individual' as a random factor were applied to avoid pseudo-replication due to multiple tracks of the same individual. Culmen length was added to these models, assuming that it could be indicative of the age of the juveniles (Yoda *et al.* 2004). Sex did not explain a significant amount of variation in trip duration (LMM: χ^2_1 ($n = 244$) 0.77, $P = 0.38$), total distance covered (LMM: χ^2_1 ($n = 244$) 0.53, $P = 0.47$) or maximum range (LMM: χ^2_1 ($n = 244$) 0.28, $P = 0.60$) of the trips made by individuals whose sex was known. Therefore, we pooled the data regardless of sex ($n = 552$) to include all trips from juveniles whose sex was unknown in the analyses. Distributions of departure from the colony and return times were compared between adults and juveniles using the two-sample Kolmogorov–Smirnov test. Time differences between dawn and departure, and dusk and return, were compared between sites using linear mixed-effects models with 'individual' as a random factor. We used chi-square to test whether

the proportions of each behaviour identified using the EMbC algorithm differed between age-classes or between sites. To test whether associations between juveniles were more likely to occur during ARS behaviour, we compared observed proportions of associations between two birds occurring during ARS behaviour of (1) both birds, (2) one of the two birds and (3) neither of the two birds, with relative expected proportions under the null hypothesis that ARS behaviour and associations between two individuals were independent. All average values are given as mean \pm standard deviation.

RESULTS

Sexual dimorphism was marked in adults and also juveniles (Fig. 1). Females were heavier than males (LMM: χ^2_1 ($n = 229$) 127.26, $P < 0.001$), possessed a longer and thicker culmen (LM: $F_{1,113} = 42.37$, $P < 0.001$ and $F_{1,112} = 8.59$, $P = 0.004$) and longer wings (LM: $F_{1,109} = 39.00$, $P < 0.001$). All morphological measures differed between the three sites: mass (LMM: χ^2_2 ($n = 229$) 9.13, $P = 0.01$), culmen length (LM: $F_{2,113} = 38.11$, $P < 0.001$), culmen height (LM: $F_{2,112} = 16.53$, $P < 0.001$) and wing length (LM: $F_{2,109} = 11.14$, $df = 2$, $P < 0.001$). Higher values for all measurements were observed in Genovesa than in Surprise and Europa. Interestingly, Red-footed Boobies from Europa had the shortest culmen length, whereas birds from Surprise had the shortest wing length. The interaction between the age-class and the timing of weighing (deployment or recovery of the GPS) was significant (LMM: χ^2_1 ($n = 229$) 4.59, $P = 0.032$). Indeed, the mass of the birds differed significantly between adults and juveniles at GPS deployment but not at GPS recovery. Juveniles had significantly smaller culmen (in length and height) than adults (LM: $F_{1,113} = 7.76$, $P = 0.006$ and $F_{1,112} = 29.75$, $P < 0.001$, respectively; Fig. 1), regardless of sex. However, wing length was not statistically different between adults and juveniles (LM: $F_{1,109} = 0.46$, $P = 0.49$).

For the trip parameters (duration, total distance covered, maximum range), we pooled the data regardless of sex (see Methods). Culmen length was not significant in any of the three models (LMM: χ^2_1 ($n = 552$) 0.25, 0.24, 1.28, $P = 0.62$, 0.63, 0.26, respectively). In all sites, adults made longer trips than juveniles (LMM: χ^2_1 ($n = 552$) 54.10, $P < 0.001$) and reached greater distances from the colony (LMM: χ^2_1 ($n = 552$) 82.45,

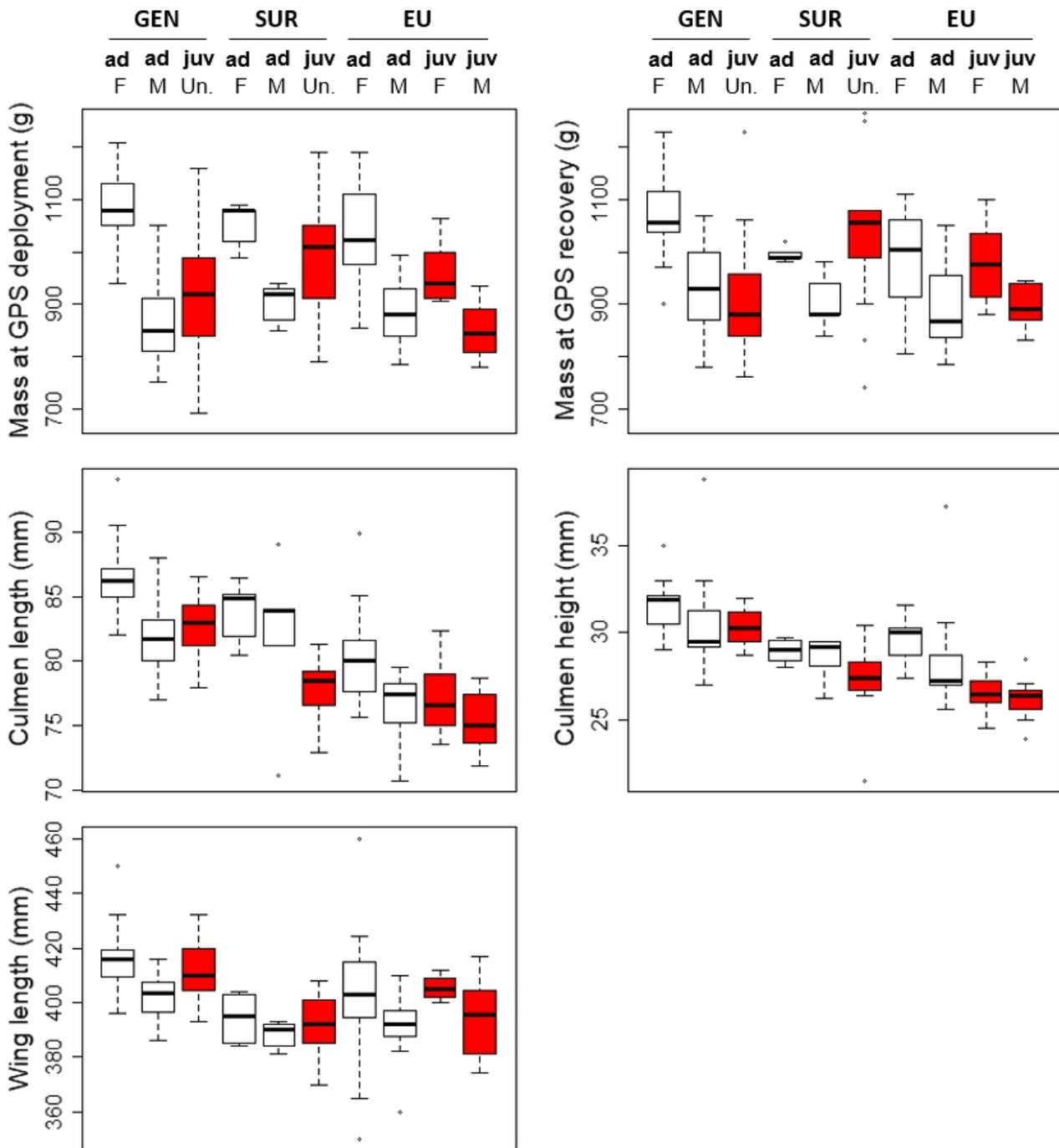


Figure 1. Mass at GPS deployment (g), mass at GPS recovery (g), culmen length (mm), culmen height (mm) and wing length (mm) of juvenile (in red) and adult (in white) Red-footed Boobies from Genovesa, Surprise and Europa. F = females; M = males; Un. = unknown sex. [Colour figure can be viewed at wileyonlinelibrary.com]

$P < 0.001$) (Fig. 2). For all trip parameters, the interaction between age and site was significant (LMM: χ^2_2 ($n = 552$) 20.87, 28.89, 26.38, respectively, $P < 0.001$ for all). The difference between

the duration and maximum range of juveniles and adults (Figs 2, 3 and 4) was particularly marked on Genovesa (1.6 ± 1.0 h vs. 39.3 ± 26.8 h and 3.6 ± 3.1 km vs. 203.4 ± 125.1 km) but less

pronounced in Europa (4.2 ± 2.3 h vs. 9.1 ± 4.0 h and 12.7 ± 8.1 km vs. 64.9 ± 32.8 km) and Surprise (2.7 ± 3.5 h vs. 11.2 ± 10.9 h and 8.5 ± 13.4 km vs. 68.7 ± 54.9 km). Adults in Genovesa made considerably longer trips (in duration and distance) compared with Surprise (Tukey's honest significant difference (HSD) test, $P < 0.001$) and Europa (Tukey's HSD test, $P < 0.001$) (Fig. 3). Regarding juveniles (Fig. 4), Europa birds made longer trips (in duration and distance) than those from Surprise (Tukey's HSD test, $P = 0.04$ for both) and Genovesa (Tukey's HSD test, $P < 0.001$ for both). Juveniles from Surprise made shorter trips on average than birds from Genovesa but showed a greater range of values (Tukey's HSD test, $P = 0.02$ for duration and $P = 0.005$ for maximum range). For all comparisons, the total distance covered followed the same trends as the maximum range.

For the three sites, the distribution of departure times and return times was significantly different between adults and juveniles (Genovesa: $D = 0.82$, $P < 0.001$ and $D = 0.76$, $P < 0.001$; Surprise: $D = 0.48$, $P < 0.001$ and $D = 0.57$, $P < 0.001$; Europa: $D = 0.28$, $P = 0.004$ and

$D = 0.88$, $P < 0.001$, respectively). In adults, the time difference between dawn and departure time, and between dusk and return time, did not differ significantly between sites (LMM: χ^2_2 ($n = 125$) 4.16, $P = 0.12$; χ^2_2 ($n = 125$) 5.28, $P = 0.07$, respectively). Adults from the three colonies tended to leave around sunrise and return around sunset, over a short time range (Fig. 5). Juveniles from the three sites left the colony later in the day than adults and tended to avoid departures and returns during the night. In juveniles, the time difference between dawn and departure time, and between dusk and return time, differed significantly between sites (LMM: χ^2_2 ($n = 454$) 92.55, $P < 0.001$; χ^2_2 ($n = 454$) 30.97, $P < 0.001$, respectively). The time differences did not differ between birds from Europa and Surprise (Tukey's HSD test, $P = 0.69$ for dawn/departure and $P = 0.16$ for dusk/return) but differed from birds from Genovesa (Tukey's HSD test, $P < 0.001$ for both periods of the day). On Genovesa, departures and returns of juveniles took place all day long, with more returns in the middle of the afternoon. Juveniles from Surprise left the colony all day long but more frequently early in the morning, whereas on Europa most departures took place in the

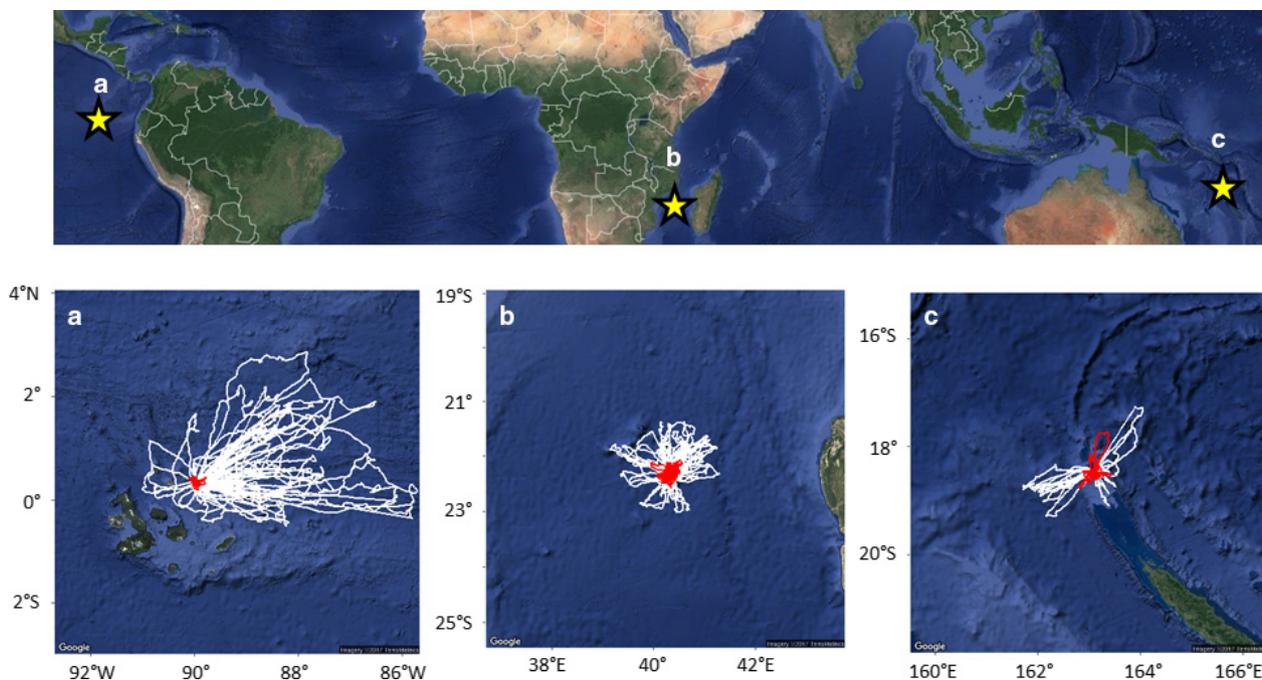


Figure 2. Distribution of the tracks of at-sea adult (in white) and juvenile (in red) Red-footed Boobies from (a) Genovesa, (b) Europa and (c) Surprise. The three zoomed maps are at the same scale. [Colour figure can be viewed at wileyonlinelibrary.com]

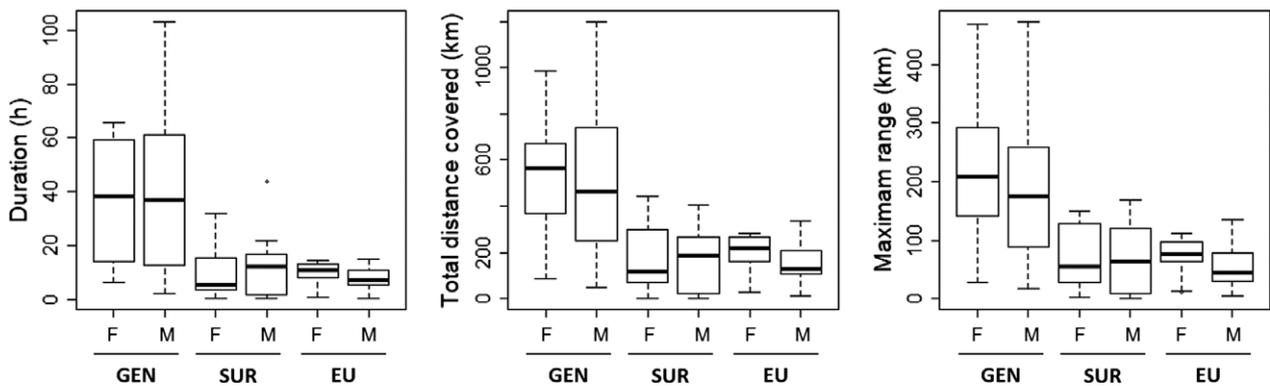


Figure 3. Duration (h), total distance covered (km) and maximum range (km) of the tracks made at sea by adult Red-footed Boobies from Genovesa, Surprise and Europa. F = females; M = males. [Colour figure can be viewed at wileyonlinelibrary.com]

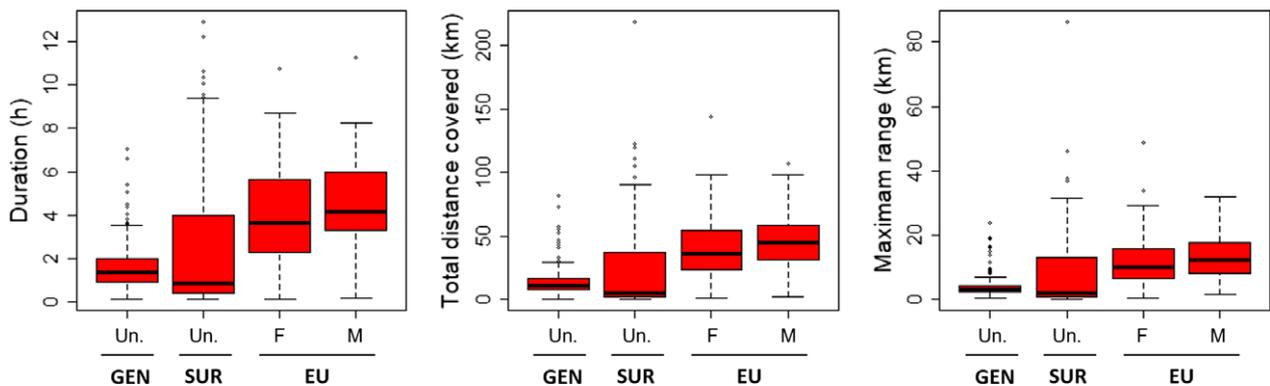


Figure 4. Duration (h), total distance covered (km) and maximum range (km) of the tracks made at sea by juvenile Red-footed Boobies from Genovesa, Surprise and Europa. F = females; M = males; Un. = unknown sex. [Colour figure can be viewed at wileyonlinelibrary.com]

middle of the day. Juveniles from both Surprise and Europa returned most of the time at the end of the afternoon (Fig. 5).

The relative behaviour distribution was significantly different between adults and juveniles (χ^2_3 ($n = 8$) 24.87, $P < 0.001$). However, the relative behaviour distribution was similar between sites for each age-class (Fig. 6), with average proportions of the four behaviours not statistically different between sites for adults (χ^2_6 ($n = 12$) 12.87, $P = 0.05$) and juveniles (χ^2_6 ($n = 12$) 6.25, $P = 0.40$). The main difference between adults and juveniles was that adults were mainly travelling during at-sea trips ($51 \pm 13\%$ of their time), whereas juveniles were more often intensively foraging ($45 \pm 18\%$ of their time) on average for all sites. Adults were then intensively foraging, relocating and resting ($23 \pm 9\%$, $10 \pm 5\%$ and $9 \pm 6\%$ of their time, respectively). Juveniles were

resting as much as travelling and relocating ($18 \pm 12\%$, $16 \pm 10\%$ and $16 \pm 11\%$ of their time, respectively) on average for all sites. The same analysis excluding the small proportions of locations recorded on land gave a similar result. These locations on land were not identified with any particular behaviour and their relative behaviour distribution did not show any pattern.

Successive locations identified as sites of intensive foraging were defined as ARS zones (Fig. S1). All trips made by adult birds contained ARS zones except one short trip (duration = 22 min) made by a bird from Surprise. Trips by juveniles that did not contain ARS zones represented $\approx 12\%$ of the dataset and were mostly of short duration (32 ± 27 min, $n = 53$). Whereas these trips without ARS were rare in juveniles from Genovesa (9.9%) and Europa (4.0%), they represented a larger part of the trips made by juveniles from

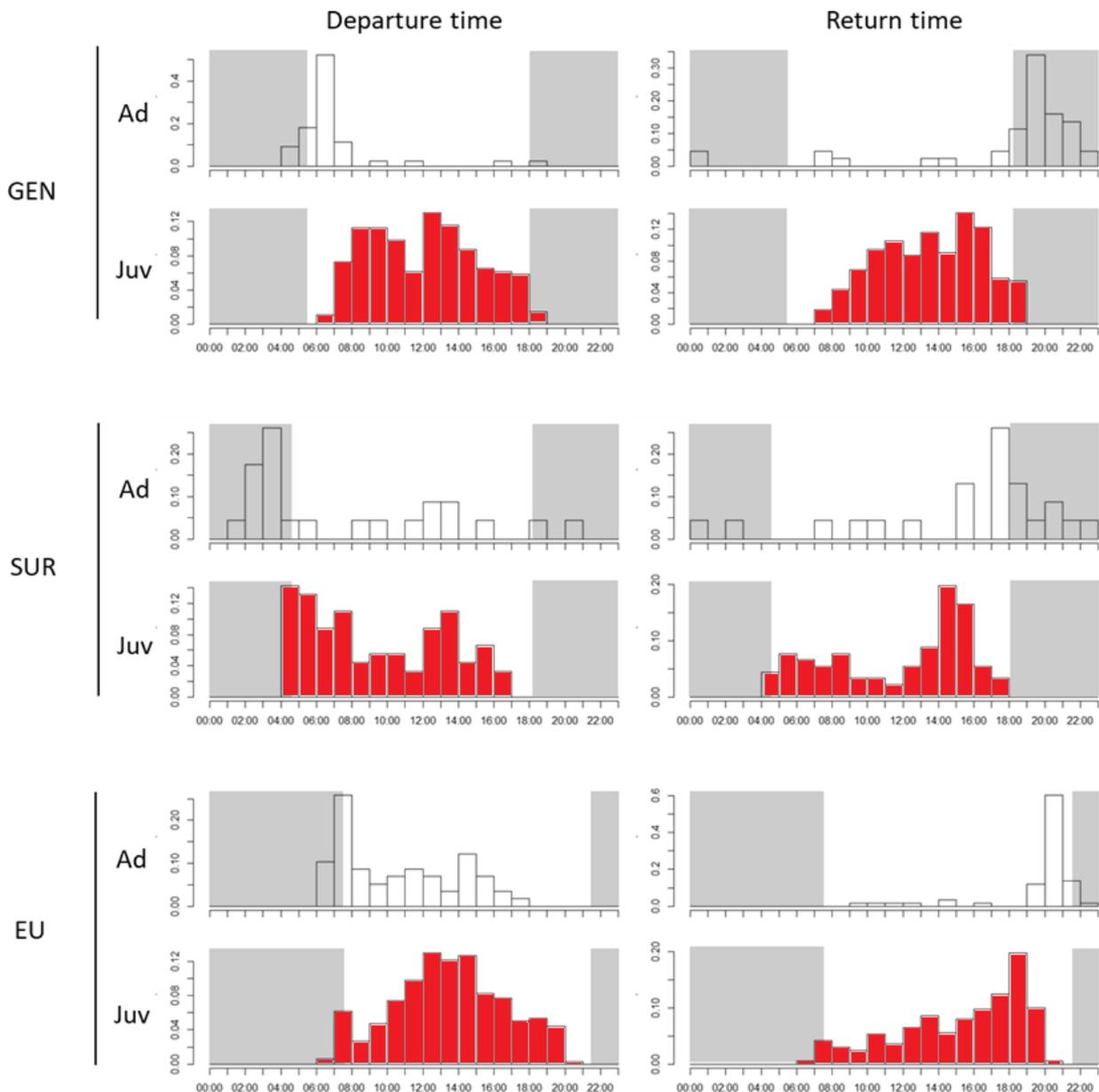


Figure 5. Departure times (left panel) and return times (right panel) of adult and juvenile Red-footed Boobies from Genovesa, Surprise and Europa. The night-time period (between dusk and dawn) is indicated in grey. [Colour figure can be viewed at wileyonlinelibrary.com]

Surprise (30.8%). Regarding the tracks that contained ARS zones, analysis of the frequency (the number of ARS zones per hour; Table 2) showed a significant interaction between age-class and site (LMM: χ^2_2 ($n = 568$) 7.52, $P = 0.02$). ARS frequency was significantly different between adults and juveniles in Genovesa but not in Surprise and Europa. Adults from the three sites visited on average fewer than one ARS zone per hour. In

tracks containing ARS zones, the ARS frequency of juveniles was mainly higher than that of adults, being often greater than one ARS zone per hour.

The time spent in ARS zones was similar for the three sites (LMM: χ^2_2 ($n = 514$) 3.7, $P = 0.16$) but differed between age-classes (LMM: χ^2_2 ($n = 514$) 24.27, $P < 0.001$) with higher values for juveniles (Table 2). Time spent in ARS zones was 15 ± 9 min ($n = 123$) for adults and

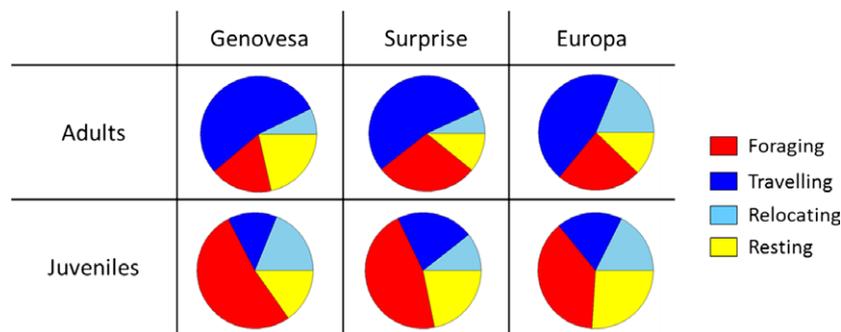


Figure 6. Average proportions of behaviours assigned along tracks of adult and juvenile Red-footed Boobies from Genovesa, Surprise and Europa. [Colour figure can be viewed at wileyonlinelibrary.com]

26 ± 20 min ($n = 440$) for juveniles. Conversely, the surface areas of ARS zones were similar for age-classes (LMM: χ^2_1 ($n = 511$) 2.05, $P = 0.15$) but differed between sites (LMM: χ^2_2 ($n = 511$) 13.50, $P = 0.001$), being larger on Europa (0.56 ± 1 km², $n = 176$) than on Genovesa (0.33 ± 0.5 km², $n = 260$) or Surprise (0.35 ± 0.5 km², $n = 75$).

Associations between tracked juvenile Red-footed Boobies were commonly observed in Europa, Genovesa and, to a lesser extent, Surprise (Table 3; see Fig. S2). On Europa, juveniles

associated more than 60% of the time with one or two other juveniles along the same track, and more than 15% of the time with three other birds. On Genovesa and Surprise, juveniles associated with only one other juvenile more than 70% of the time. Adult Red-footed Boobies rarely associated between themselves in trips on Europa (four of 58 trips) and Surprise (one of 22 trips). Associations between adults were more frequent on Genovesa (nine of 44 trips). On all the datasets, only one association between an adult and a juvenile occurred on Surprise (Fig. S2).

We tested whether the associations between juveniles were more likely to occur while they were in an ARS zone (Table 4). In Genovesa, locations identified inside ARS zones represented 49% of all juvenile GPS locations. Under the null hypothesis that time in ARS zone and time associated with another juvenile were independent, we would expect to find 24% of associations ($p_2 = 0.49 \times 0.49$) between two individuals in the same ARS zone, 26% of the time in ARS zones not associated with another individual ($p_0 = (1 - 0.49) \times (1 - 0.49)$) and 50% of the time with only one other individual being in the ARS zone ($p_1 = 1 - (p_0 + p_2)$). We found that $p_0 = 27\%$, $p_1 = 28\%$ and $p_2 = 45\%$ (Table 4), indicating that

Table 2. Frequency (n/h), time spent in (min) and surface area (km²) of area-restricted search (ARS) zones of juvenile and adult Red-footed Boobies from Genovesa, Surprise and Europa.

	ARS frequency (n/h)	ARS duration (min)	ARS surface (km ²)
Adults			
Genovesa	0.5 ± 0.2	13.1 ± 4.8	0.25 ± 0.16
Surprise	0.9 ± 0.7	15.7 ± 8.6	0.33 ± 0.52
Europa	0.7 ± 0.3	15.9 ± 12	0.46 ± 0.76
Juveniles			
Genovesa	1.0 ± 0.5	28.3 ± 21.8	0.34 ± 0.54
Surprise	1.0 ± 0.9	21.1 ± 15.4	0.36 ± 0.46
Europa	1.0 ± 0.4	23.4 ± 19.2	0.61 ± 1.05

Table 3. Description of the associations occurring between juvenile Red-footed Boobies from Genovesa, Surprise and Europa. n_{ind} = total number of tracked individuals, n_{tracks} = total number of tracks.

	Proportion of tracks including associations	Proportion of associated portion along tracks	Maximum number of individuals associated along a track
Genovesa ($n_{ind} = 18$, $n_{tracks} = 278$)	0.42	0.11 ± 0.09	5
Surprise ($n_{ind} = 10$, $n_{tracks} = 95$)	0.21	0.07 ± 0.05	2
Europa ($n_{ind} = 21$, $n_{tracks} = 134$)	0.57	0.14 ± 0.13	9

associations were more likely to occur while in ARS zones (χ^2_2 ($n = 115$) 277.18, $P < 0.001$). In Europa, the probability that an association occurs when both juveniles were in ARS zones was also significantly higher than expected (χ^2_2 ($n = 75$) 936.25, $P < 0.001$). However, associations between juveniles in Surprise occurred less often in ARS zones than expected (χ^2_2 ($n = 18$) 42.99, $P = 0.001$). Juveniles associated predominantly during intensive foraging behaviour in the three colonies, including Surprise (Table 4). However, the proportions of the different behaviours assigned to associated locations were significantly different from the proportions observed all along the tracks in Europa (χ^2_3 ($n = 8$) 17.47, $P < 0.001$), but not in Surprise (χ^2_3 ($n = 8$) 2.07, $P = 0.56$) and Genovesa (χ^2_3 ($n = 8$) 4.98, $P = 0.17$).

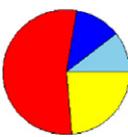
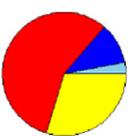
DISCUSSION

In this study, we analysed the foraging behaviour of adult and juvenile Red-footed Boobies breeding in three distant colonies. Juveniles had significantly smaller culmen but similar wing length compared with adults. Morphometric measurements differed between colonies, with larger birds found on

Genovesa for both age-classes. Trips at sea differed between adults and juveniles independent of morphological differences, the latter performing trips closer to the colony. Adults travelled almost half of their time, whereas juveniles most often used a slow and sinuous behaviour that might reflect attempts to catch prey. Frequent associations between tracked juveniles were detected in all colonies. After distinguishing common characteristics observed at the three sites for adults and then juveniles, we discuss the differences and how local environmental conditions can impact both adult and juvenile foraging trips. As adults were tracked during different breeding stages in the different colonies, we could not distinguish extrinsic local adaptations due to the environment from intrinsic constraints due to the breeding stage. Thus, the discussion focuses on colony-specific contrasts in morphology and foraging behaviour between age-classes, with particular attention to interactions between juvenile development and prevailing conditions.

Intraspecies comparisons are important to better understand the effect of intrinsic (morphometrics, experience) and extrinsic determinants (local environmental variability) on foraging behaviour. They also make it possible to distinguish common

Table 4. Probabilities of associations between pairs of juvenile Red-footed Boobies from Genovesa, Surprise and Europa occurring outside ARS zones of both juveniles (p_0), inside ARS zone of one of the two juveniles (p_1) and inside ARS zones of both juveniles.

	No juvenile in ARS (p_0)	One juvenile in ARS (p_1)	Both juveniles in ARS (p_2)	P -value (χ^2 , $df = 2$)	Behaviour during associations
Genovesa ($n_{ind} = 18$, $n_{tracks} = 115$)					
P_{exp}	0.26	0.50	0.24	<0.001 (277.18)	
P_{obs}	0.27	0.28	0.45		
Surprise ($n_{ind} = 9$, $n_{tracks} = 18$)					
P_{exp}	0.31	0.50	0.19	<0.001 (42.99)	
P_{obs}	0.64	0.33	0.03		
Europa ($n_{ind} = 20$, $n_{tracks} = 75$)					
P_{exp}	0.34	0.48	0.18	<0.001 (936.25)	
P_{obs}	0.30	0.27	0.43		

P_{exp} : expected probabilities under the null hypothesis (independent of pair associations and ARS zones). P_{obs} : observed probabilities. The pie charts show the proportions of different behaviours assigned to associated locations. n_{ind} = number of associated individuals, n_{tracks} = number of tracks including associations. ■, Foraging; ■, Travelling; ■, Relocating; ■, Resting.

features at the species level from local adaptations at the level of colonies. Some foraging patterns appeared to be shared by all adult Red-footed Boobies throughout their pantropical range (Weimerskirch *et al.* 2005a, Mendez *et al.* 2017a). In Johnston Atoll (central Pacific Ocean), Red-footed Boobies show a flexible daily foraging strategy linked to the time available to forage, with an increase of the dive rate and the proportion of time spent in flight as the number of hours of daylight available decreases (Lewis *et al.* 2004). In our study, adults from the three sites generally left the colony around sunrise to return around sunset, maximizing the time spent at sea during the daytime period. Despite the sexual dimorphism of this species (Nelson 1978), no evidence for a sex difference in trip duration or maximum range was detected between adult males and females, as also observed in other colonies (Lewis *et al.* 2005, Mendez *et al.* 2017a). Adults travelled fast and in a straight line during about 50% of a foraging trip. In all sites, the clear majority of adult trips included ARS zones, where birds concentrate their foraging effort through a sinuous and slow trajectory. These foraging events could occur all along the foraging trip, but a main foraging activity was often observed at the extremity of the path, surrounded by a relatively straight flight from and to the colony.

Regarding juveniles, common features were also observed and differed from those of adults. Their foraging range was much more restricted around the colony compared with that of adults due to shorter round trips throughout the daytime period. Usually, young birds are limited by their development (Marchetti & Price 1989) and thus do not have the physical ability to perform long trips at sea. Here, sexual dimorphism was already visible at the juvenile stage, with females larger and heavier than males on Europa. Mass was highly variable and juveniles were sometimes heavier or lighter than adults depending on the site and/or breeding stage at which adults were weighed, with trends sometimes reversed between the deployment and the recovery of the GPS. For the three sites, mass was no longer significantly different between adults and juveniles at the recovery of the GPS, compared with deployment. This is likely to be due to the mass gain of juveniles that are still fed by the parents at an unmeasured frequency and quantity. Juveniles were slightly smaller in bill length compared

with adults, indicating that development was not yet fully completed. However, the length of their wings was not different from adults. In species that do not receive post-fledging parental care, failure to reach the ocean on the first flight and/or difficulties in prey capture are the major causes of mortality during the first weeks at sea. Juveniles therefore need to be almost fully developed for their first flights, as in the case of many species such as Marbled Murrelet *Brachyramphus marmoratus* and Wandering Albatrosses *Diomedea exulans*, where development of wings and bill is completed primarily in the nest before fledging (Weimerskirch *et al.* 2000, Janssen *et al.* 2011). Even if the pressure to become independent is lower in juveniles of species that receive a long post-fledging care period, they seem to show a similar pattern. Growth of the culmen and wing length of the Brown Booby, a close relative of the Red-footed Booby, has already stopped by the time the juveniles fledge (Yoda *et al.* 2004). Even if changes in external appearance are not visible, we must keep in mind that physiological changes such as cardiovascular or muscular changes can still occur. However, short trips made by juveniles may instead be the consequences of their poor flight skills and foraging experience (Yoda *et al.* 2004, Daunt *et al.* 2007) rather than their morphology. Here, this possibility is supported by the absence of an effect of morphology on trip characteristics in either adults or juveniles.

Unlike adults that travelled over long distances from the colony during their foraging trips to reach distant foraging grounds, juveniles from the three sites were more often identified in intensive foraging behaviour, characterized by a slow and sinuous trajectory. Juveniles also showed more ARS zones per hour compared with adults and spent a longer time in active foraging within the ARS zone. They may thus compensate for their lack of experience with more attempts to catch prey (Porter & Sealy 1982), which allows them to become progressively as efficient as adults. Boobies feed in oligotrophic tropical waters, where resources are scarcer and more heterogeneously distributed than in temperate or polar waters (Longhurst & Pauly 1987, Ballance *et al.* 1997, Weimerskirch 2007). They mainly catch flying fish and flying squid when those emerge from the surface or just below the surface (Weimerskirch *et al.* 2005a). As with most tropical seabirds, Boobies can associate with sub-surface predators (such as

Yellowfin Tuna *Thunnus albacares*, Skipjack Tuna *Katsuwonus pelamis*, Pantropical Spotted Dolphin *Stenella attenuata* or Spinner Dolphin *Stenella longirostris*) that bring prey close to the surface (Au & Pitman 1986, Weimerskirch *et al.* 2005c, Thiebot & Weimerskirch 2013). The surface area of the ARS zones did not differ between juveniles and adults, suggesting that both foraged on prey patches of similar size that could correspond to these association events with sub-surface predators. Other tropical boobies and frigatebirds feed on the same prey type as the Red-footed Booby (Nelson 1967, Burger 1980, Yoda *et al.* 2004, Castillo-Guerrero & Mellink 2006) and also show a particularly long transition phase. That extensive post-care period could allow time for juveniles to acquire potentially specific complex skills after several weeks or months of practice, including an efficient search for favourable foraging areas. Juvenile Red-footed Boobies seem to be pushed to go further out to sea rapidly, as a previous study of their successive trips during a longer deployment period was able to show an increase in the duration and the range of their trips over time (Mendez *et al.* 2017b).

Potential associations between tracked juveniles along their trips were detected in all three colonies. Considering that the sample size represents a small fraction of each colony, this inter-colony study reveals that these associations, previously described only in Europa (Mendez *et al.* 2017b), seem to be a common strategy used in the early life of Red-footed Boobies. Juveniles could thus rely more on social enhancement to identify prey patches compared with adults. Indeed, social learning can entail a learning process through interactions with congeners (Hatch & Lefebvre 1997, Laland & Williams 1997, Mazur & Seher 2008, Kitowski 2009). In other species, juveniles of Blue-footed Boobies *Sula nebouxii* tended to fly in groups (Castillo-Guerrero & Mellink 2006) and Brown Boobies were shown to follow other conspecifics (Yoda *et al.* 2011). Associations between juveniles occurred more often than by chance inside ARS zones in Europa and Genovesa but not in Surprise. However, juveniles from the three colonies (including Surprise) associated particularly during intensive foraging. The difference between juveniles from Surprise and those from the two other colonies may be due to the smaller sample size at Surprise or could indicate that the method used to detect the ARS is not optimal. Indeed,

short tracks where no ARS zones were detected still contained many locations identified as 'intensive foraging', although no more than two successive locations. As ARS zones were defined with a minimum of three successive locations (Methods), some short ARS behaviour may have been undetected. Juveniles may join other individuals that are already foraging and thus indicating the presence of prey. This strategy may directly enhance the foraging success of the juveniles during their developmental stage. On the other hand, juvenile Red-footed Boobies seem rarely to associate with experienced adults (only one example in our study). If foraging with adults can sometimes be an efficient strategy to learn and find profitable areas (Kitowski 2009), this was not the case here, as adult Red-footed Boobies left the colony earlier in the morning and, above all, focused their foraging effort at distances unreachable for juveniles. In Manx Shearwater *Puffinus puffinus*, a spatial segregation that may result from a lower foraging efficiency that excludes the immature from the more productive foraging areas visited by adults was also observed (Fayet *et al.* 2015) and suggests that this process may last after the juvenile phase during the immature phase. Foraging specializations can be learned through an independent 'exploration-refinement' process, where exploratory behaviours during early life become canalized and refined with age and experience (Votier *et al.* 2017, Grecian *et al.* 2018). For example, in Atlantic Puffin *Fratercula arctica*, juveniles make long exploratory trips to different areas that may help them to acquire the experience needed to navigate their environment and find appropriate foraging zones (Guilford *et al.* 2011). Young Scopoli's Shearwater *Calonectris diomedea* seem also to have reduced navigational ability and progressively learn fine-scale migration routes towards the more profitable travelling and wintering areas (Péron & Grémillet 2013). In a more extreme example, juvenile Wandering Albatrosses do not restrict their movement to specific areas (Riotte-Lambert & Weimerskirch 2013) and can travel across the whole Southern Ocean during their first year at sea, where they may acquire knowledge and progressively reduce their range and adopt a foraging strategy that is consistent from year to year (De Grissac *et al.* 2016). In Northern Gannets, immatures show a larger foraging distribution than adults and a smaller individual foraging site fidelity linked to oceanographic fronts that offer better foraging

conditions (Votier *et al.* 2017, Grecian *et al.* 2018). Here, juvenile Red-footed Boobies showed the opposite pattern, with a smaller foraging distribution than adults. This difference can be explained by the absence of post-fledging parental care in Northern Gannets (Montevecchi *et al.* 1984), which are forced to search actively for prey during their first flights while they do not yet know the most profitable areas.

Variability in foraging behaviour in relation to contrasting environmental conditions between breeding sites has already been documented in adults of several species such as Cape Gannets (Pichegru *et al.* 2007, Moseley *et al.* 2012), Northern Gannets (Hamer *et al.* 2001, Garthe *et al.* 2007, Pettex *et al.* 2012), Gentoo Penguin *Pygoscelis papua* (Lescroel & Bost 2005) and other marine predators, e.g. Northern Fur Seals *Callorhinus ursinus* (Robson *et al.* 2004). Here, despite some common features in the structure of adults' at-sea trips, the foraging range of adult Red-footed Boobies differed extensively between the three colonies and showed great plasticity at the species level. Such variability has been previously interpreted as the result of different local environmental constraints, especially regarding colony size and oceanography (Mendez *et al.* 2017a). Beyond the variability of prey concentration and/or predictability around each colony, the intra- and interspecific competition related to the Red-footed Booby population size and the presence of other Booby species in a colony can push adult birds to forage further, as seems to be the case in Genovesa (Mendez *et al.* 2017a). Here, adults in Genovesa were tracked during incubation, whereas adults in Surprise and Europa were brooding their chick and taking care of their fledging juveniles, respectively. Incubation is known to be the less constraining breeding stage, as adults only need to feed themselves (Weimerskirch *et al.* 2005a, Mendez *et al.* 2016). The tracking of birds during different breeding stages could therefore also explain partly the differences observed between sites, with adults from Genovesa having the possibility to leave the nest for a longer time and to reach further areas.

The foraging range of juveniles differed also in size between colonies but not in the same way as for adults. For example, juveniles from Genovesa showed the smallest foraging range and adults the longest one compared with Europa and Surprise. All studied juveniles had recently fledged but

neither observations in the field nor morphometric measures allowed their precise growth stage to distinguished. The variations of the juveniles' foraging behaviour observed between sites could thus be linked to the habitat or to a potential delay in growth stage, affecting gained experience over time and, to a lesser extent, morphology. During the post-fledging care period, parents progressively increase the quantity of food they bring to their juveniles (Guo *et al.* 2010). As juveniles grow, parents progressively decrease the amount of food, forcing juveniles to extend their foraging trips. This may also change or be modulated by environmental conditions. The duration of the post-fledging care period is generally estimated as between 90 and 180 days (Nelson 1969, Diamond 1974, Guo *et al.* 2010, Mendez *et al.* 2017b). Whereas juveniles appear to be independent after 90 days in the Galapagos (Nelson 1978) and 118 days in the Xisha (China Sea) archipelago (Guo *et al.* 2010), no juveniles in Aldabra appeared to be fed 1 month after their first flight (Diamond 1974). Therefore, the duration of the post-fledging care period seems to differ between breeding sites. This difference could be explained by the need for a longer or shorter learning period depending on the site, probably due to the difficulty in efficiently finding and acquiring resources in different habitats. Lastly, the size of both adults and juveniles varied according to the site, with larger individuals found on Genovesa than on Europa or Surprise. Red-footed Boobies exhibit a strong population genetic isolation, with a particularly high level of differentiation between Genovesa and other colonies (Morris-Pocock *et al.* 2016). Even though the regional variations of the measurements of the Red-footed Booby are not extreme, it has previously been proposed that the relatively large breeding form in the Galapagos may be an adaptation to an impoverished environment, enabling the female to produce large eggs (Nelson 1978). Differences in environmental quality can lead to evolutionary divergence in egg size between populations, with selection favouring larger eggs or hatchlings in poor-quality environments (Fox 2000, Bashey 2006, Rollinson & Hutchings 2013). Even if the average concentration of chlorophyll-*a*, a common proxy of environmental richness, is higher around Genovesa than around Europa, Red-footed Boobies from Galapagos forage in a surface area about six times larger than the

foraging area from Europa, probably to avoid intra- and interspecific competition (Mendez *et al.* 2017a). Reaching such distances is costly for birds and may explain the larger body size observed in Red-footed Boobies from Genovesa as an adaptation to a particularly unfavourable environment. Moreover, juveniles from Europa had a smaller culmen compared with other colonies and juveniles from Surprise had shorter wings, showing that juveniles do not develop in a similar way according to the colony.

To conclude, our study shows that juvenile and adult Red-footed Boobies showed differences in their foraging behaviour, and these differences might be interpreted as corresponding to the learning phase, with birds extending their foraging range progressively and thus using the travelling mode during longer periods. The short foraging range of juveniles seemed to result from poor flight skills and foraging experience rather than constraints due to their morphology. Juveniles intensively foraging in frequent ARS zones suggested that they are often training to catch prey. Associations between juveniles were common in the three remote colonies and occurred mostly during intensive foraging, showing that social learning is an important feature in the early life of the Red-footed Booby. On the other hand, birds showed morphological differences between the site that could reflect constraints due to local environmental conditions, already visible in their early life. In a rapidly changing world, we encourage future inter-population studies to collect and compile data from immature birds to better understand their behavioural flexibility in response to local environmental conditions at this critical stage of life.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Example of a trip made by a juvenile Red-footed Booby from Genovesa.

Figure S2. Example of associations (red dots) between juveniles from (a) Genovesa, (b) Surprise, (c) Europa, and (d) between an adult (in black) and a juvenile (in blue) from Surprise. The yellow star represents the nest.