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, as well as morphological characteristics. Compared to adults, juveniles conducted shorter trips that were restricted 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, while juveniles travelled a lower proportion of time 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:** Seabird, tropical, foraging, age class, colony, associations

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 still 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 & Hirons 1993). Seabirds are interesting models to study population differentiation (Friesen et al. 2007) since most species show a high degree of natal philopatry (Warham 1996) and extensive geographic variation in morphology (del Hoyo et al. 1996). However, while most demographic and behavioural studies of seabirds focus on variations observed within a particular colony over time and/or individuals, 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 the 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
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to adults, which could result from needing more attempts to capture prey, and are frequently associated with congeners at sea (Mendez et al. 2017b).

Here, we compare for the first time the foraging behaviour between adults and juveniles in three different environments. Since 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 i) between juveniles and adults in each site and ii) between juveniles from different sites in response to the environmental context, similarly to adults (Mendez et al. 2017a). All juveniles were studied shortly after fledging when doing among their earliest flights to avoid the effect of individual improvement with experience during the early life (Mendez et al. 2017b) and make straightforward comparison between adults and juveniles. By taking into account the age class, sex and colony, we aimed at better understanding 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. Since 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 (November 10th – November 22nd). 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 2 800-3 800 pairs of Red-footed Boobies (Le Corre & Jouventin 1997). Adults and juveniles were both tracked during the post-fledging period in 2014 for 12 days (January 27th – February 2nd). 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 (November 24th – November 29th). While 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 age was not known precisely.

On the three islands, both adults and juveniles were captured by hand or with a telescopic fishing pole fitted with a nylon noose for the birds nesting higher in the trees. While juveniles are brown with grey legs and feet, adults are clearer with red legs and feet and 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 by 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). The handling never lasted more than 10 minutes. 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 pre-defined 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 a 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 = 5 047) represented 4.85% of the dataset (n = 104 166) and thus = 95 % of the GPS locations were at sea. Since the position-recording frequency differed between sites and age classes (Table 1), only tracks lasting at least six minutes (= two successive positions spaced by 180 sec) were included in the analyses to homogenise the dataset. The maximum speed was set to 90 km h⁻¹ (Weimerskirch et al. 2005c). The duration of foraging trip (h), total distance covered (km) and maximum range from the colony (km) were calculated for each track. Departure and return time of each trip were linked to the time of day. Night periods were defined when the sun was more than six 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 \textit{getElevation} of the R package \textit{GeoLight}. Base maps were generated using the R package \textit{ggmap}. All analyses were made using R software (R Development Core Team 2014).

\textbf{Behaviour clustering and ARS identification}

The Expectation Maximisation binary Clustering (EMbC) algorithm (Garriga \textit{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 from adults and juveniles of the three study sites were first linearly interpolated (with one location every two minutes). 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: the speed and the 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\(^{-1}\) and 0 - 0.32 radians), intense foraging (0 - 9 km h\(^{-1}\) and 0.32 - 3.14 radians), travelling (4 - 90 km h\(^{-1}\) and 0 - 0.3 radians), and relocating (9 - 90 km h\(^{-1}\) 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. Zones of area-restricted search (ARS) were defined when at least three successive locations were labelled as intensive foraging by the EMbC algorithm (Mendez \textit{et al}. 2017a, 2017b). To simplify the description of the different behaviour along the trajectory, we merged ARS when less than four locations labelled with another behaviour were observed between them (Mendez \textit{et al}. 2017a, 2017b). The frequency (number of ARS zones per hour), the duration and the surface of ARS (area of the minimum convex polygon including all positions of an ARS zone) were calculated.

\textbf{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 \textit{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 sec (following Mendez \textit{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). The sex did not explain a significant amount of variation in trip duration (LMM: $\chi^2(1, n = 244) = 0.77, P = 0.38$), total distance covered (LMM: $\chi^2(1, n = 244) = 0.53, P = 0.47$) or maximum range (LMM: $\chi^2(1, n = 244) = 0.28, P = 0.60$) 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 $\chi^2$ to test whether 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 i) both birds, ii) one of the two birds, iii) neither of the two birds, to relative expected proportions under the null hypothesis that ARS behaviour and associations between two individuals were independent. All average values are given as mean ± standard deviation.

RESULTS

Sexual dimorphism was marked in adults and also juveniles (Fig. 1). Females were heavier than males (LMM: $\chi^2(1, n = 229) = 127.26, P < 0.001$), 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: the mass (LMM: $\chi^2(2, n = 229) = 9.13, P = 0.01$), the culmen length (LM: $F_{2,113} = 38.11, P < 0.001$), the culmen height (LM: $F_{2,112} = 16.53, P < 0.001$) and the wing length (LM: $F_{2,109} = 11.14, df = 2, P < 0.001$). Higher values for all measurements were observed in Genovesa compared to Surprise and Europa. Interestingly, Red-footed Boobies from Europa had the shortest culmen length while 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: $\chi^2(1, n = 229) = 4.59, P = 0.032$). 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) compared to 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: $F_{1,109} = 0.46$, $P = 0.49$).

About the trip parameters (duration, total distance covered, maximum range), we pooled the data regardless of sex (see Methods). The culmen length was not significant in any of the three models (LMM: $\chi^2(1, n = 552) = 0.25, 0.24, 1.28$, $P = 0.62, 0.63, 0.26$, respectively). In all sites, adults made longer trips than juveniles (LMM: $\chi^2(1, n = 552) = 54.10$, $P < 0.001$) and reached greater distances from the colony (LMM: $\chi^2(1, n = 552) = 82.45$, $P < 0.001$) (Fig. 2). For all trip parameters, the interaction between age and site was significant (LMM: $\chi^2(2, n = 552) = 20.87, 28.89, 26.38$ respectively, $P < 0.001$ for all). The difference between the duration and maximum range of juveniles and adults (Fig. 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) and Surprise (2.7 ± 3.5 h vs 11.2 ± 10.9 h and 8.5 ± 13.4 vs 68.7 ± 54.9 km). Adults in Genovesa made considerably longer trips (in duration and distance) compared to Surprise (Tukey’s 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 larger 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 were 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 significantly differ between sites (LMM: $\chi^2(2, n = 125) = 4.16$, $P = 0.12$; $\chi^2(2, n = 125) = 5.28$, $P = 0.07$, 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 used to leave 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, significantly differed between sites (LMM: $\chi^2(2, n = 454) = 92.55$, $P < 0.001$; $\chi^2(2, n = 454) = 30.97$, $P < 0.001$, 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 period 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, while on Europa most departures took
place in the middle of the day. Both juveniles from 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 ($\chi^2(3, n = 8) = 24.87, P < 0.001$). 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 ($\chi^2(6, n = 12) = 12.87, P = 0.05$) and juveniles ($\chi^2(6, n = 12) = 6.25, P = 0.40$). The main difference between adults and juveniles was that adults were mainly travelling during at sea-trips (51 ± 13% of their time) whereas juveniles were more often intensively foraging (45 ± 18% of their time) on average for all sites. Adults were then intensively foraging, relocating and resting (23 ± 9%, 10 ± 5% and 9 ± 6% of their time, respectively). Juveniles were resting as much as travelling and relocating (18 ± 12%, 16 ± 10% and 16 ± 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 intensive foraging were defined as area-restricted search (ARS) zones (see Supporting Online Information Fig. S1). All trips made by adult birds did contain 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 ≈ 12% of the dataset and were mostly of short duration (32 ± 27 min, $n = 53$). While 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 Surprise (30.8%). Regarding the tracks that contained ARS zones, the analysis of the frequency (the number of ARS zones per hour; Table 2) showed a significant interaction between age class and site (LMM: $\chi^2(2, n = 568) = 7.52, P = 0.02$). The ARS frequency was significantly different between adults and juveniles in Genovesa, but not in Surprise and Europa. Adults from the three sites made on average less 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: $\chi^2(2, n = 514) = 3.7, P = 0.16$) but differed between age classes (LMM: $\chi^2(2, n = 514) = 24.27, P < 0.001$) with higher values for juveniles (Table 2). Time spent in ARS zones were 15 ± 9 min ($n = 123$) for adults and 26 ± 20 min ($n = 440$) for juveniles. Conversely, the surface areas of ARS zones were similar for age classes (LMM: $\chi^2(1, n = 511) = 2.05, P = 0.15$) but differed between sites (LMM: $\chi^2(2, n = 511) = 13.50, P = 0.001$), being larger on Europa (0.56 ± 1 km$^2$, $n = 176$) compared to Genovesa (0.33 ± 0.5 km$^2$, $n = 260$) and Surprise (0.35 ± 0.5 km$^2$, $n = 75$).

Associations between tracked juvenile Red-footed Boobies were commonly observed in Europa, Genovesa and, to a lesser extent, Surprise (Table 3; see Supporting Online Information Fig. S2). On Europa, juveniles associated in more than 60% of the time with one or two other juveniles along the same track, and more than 15% of the time with 3 other
birds. On Genovesa and Surprise, juveniles associated with only one other juvenile in more than 70% of the time. Adult Red-footed Boobies rarely associated between themselves in trips on Europa (4 of 58 trips) and Surprise (1 of 22 trips). Associations between adults were more frequent on Genovesa (9 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 \( (p_2 = 0.49*0.49) \) between two individuals in the same ARS zone, 26% of time in ARS zones not associated with another individual \( (p_2 = 1 - (1-0.49) * (1-0.49)) \) and 50% of the time with only one of the 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 associations were more likely to occur while in ARS zones \( (\chi^2(2, n = 115) = 277.18, P < 0.001) \). In Europa, the probability that an association occurs when both juveniles were in ARS zones was also significantly higher than expected \( (\chi^2(2, n = 75) = 936.25, P < 0.001) \). However, associations between juveniles in Surprise occurred less often in ARS than expected \( (\chi^2(2, n = 18) = 42.99, P = 0.001) \). 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 \( (\chi^2(3, n = 8) = 17.47, P < 0.001) \), but not in Surprise \( (\chi^2(3, n = 8) = 2.07, P = 0.56) \) and Genovesa \( (\chi^2(3, n = 8) = 4.98, P = 0.17) \).

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 to 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 while 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 will discuss the differences and how local environmental conditions can impact both adult and juvenile foraging trips. Since 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.

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Intra-species 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 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 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 area-restricted search (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 to adults due to shorter round trips throughout the daytime period. Usually, young birds can be limited by their development (Marchetti and Price 1989) and thus not have the physical ability to perform long trips at sea. Here, the sexual dimorphism was already visible at the juvenile stage, with females larger and heavier than males on Europa. The 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, the mass was no longer significantly different between adults and juveniles at the recovery of the GPS, compared to deployment. This is likely 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 to 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 it is the case for many species such as Marbled Murrelet Brachyramphus marmoratus or Wandering Albatrosses Diomedea exulans where development of wings and bill is completed primarily in the nest before fledging (Janssen et al. 2011, Weimerskirch et al. 2000). 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. The growth of the culmen and wing length of the
Brown Booby, a close relative of the Red-footed Booby, is already stopped by the time that the juveniles fledged (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 to adults and spent a longer time in active foraging within the ARS zone. They may thus compensate their lack of experience with more attempts to catch prey (Porter & Sealy 1982) which allow 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 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, Thiebot & Weimerskirch 2013, Weimerskirch et al. 2005c). 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 since 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 than adults. Indeed, social learning can entail a learning process through interactions with congeners (e.g. Hatch & Lefebvre 1997, Laland & Williams 1997, Mazur & Seher 2008, Kitowski 2009). In other species, juveniles of Blue-footed Boobies Sula nebouxii tended to fly

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in groups (Castillo-Guerrero & Mellink, 2006) and Brown Boobies were shown to follow other conspecifics (Yoda et al. 2011). In Europa and Genovesa, associations between juveniles occurred more often than by chance inside ARS zones, 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 to detect the ARS is not optimal. Indeed, short tracks where no ARS were detected still contained a lot of locations identified as ‘intensive foraging’, but no more than two successive locations. Since ARS were defined with a minimum of three successive locations (see 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 to rarely 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), here it was not the case since adult Red-footed Boobies left the colony earlier in the morning but, 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 exclude the immature from the more productive foraging areas visited by adults, was also observed (Fayet et al. 2015) and suggest 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 Puffins 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 learn progressively fine-scale migration routes towards the more profitable travelling and wintering areas (Péron & Grémillet 2013). In a more extreme way, 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), that are forced to actively search for prey during their first flights while they do not yet know the most profitable areas.

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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 like 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 a 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 it seems to be the case in Genovesa (see 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 that could had the possibility to leave the nest during a longer time and reach further areas.

The foraging range of juveniles differed also in size between colonies but not in the same way than for adults. For example, juveniles from Genovesa showed the smallest foraging range while adults showed the longest one compared to Europa and Surprise. All studied juveniles had recently fledged but both observations on the field and morphometric measures could not allow distinguishing their precise growth stage. 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 juvenile (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 with environmental conditions. The duration of the post-fledging care period is generally estimated between 90 and 180 days (Nelson 1969, Diamond 1974, Guo et al. 2010, Mendez et al. 2017b). While 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 one 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 compared to Europa and 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 if the regional variations of the measurements of the Red-footed Booby are not extreme, it was previously 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 the environment 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 of a particularly unfavourable environment. Moreover, juveniles from Europa had a smaller culmen compared to other colonies while 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 from local environmental conditions, already visible in their early life. In a rapidly changing world, we encourage future inter-population studies to collect and/or compile data from immature birds to better understand their behavioural flexibility in response to local environmental conditions at this critical stage of life.

This research was funded by a European Research Council Advanced Grant under the European Community’s Seven Framework Program FP7/2007–2013 (Grant Agreement ERC-2012-ADG_20120314 to Henri Weimerskirch). We thank Terres Australes et Antarctiques Françaises (TAAF) for their logistic support, and the FAZOI for transport to Europa and for support while on Europa island. We thank the Agence des Aires Marines Protégées (AAMP) from New Caledonia and the crew of the mission ‘INTER-CASTEAUX 2015’. We thank the Galapagos National Park Service and the Ministry of the Environment of Ecuador for permission to work in the park, and the Charles Darwin Research Station for logistical support. We thank J.B. Pons and J. Lallemand for the assistance in the field. Lastly, we thank the three anonymous reviewers, the editor and the associate editor of the journal whose suggestions greatly helped to improve the manuscript.
REFERENCES


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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of the article:

**Figure S1.** Example of a trip made by a juvenile Red-footed Booby from Genovesa. The colours of the dots are relative to the behaviour assigned to the location. ARS zones are framed in red. The yellow star represents the nest.

**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.
Figure legends

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.

Figure 2. Distribution of the tracks of at-sea adult (in white) and juvenile (in red) Red-footed Boobies from A) Genovesa, B) Europa, C) Surprise. The three zoomed maps are at the same scale.

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

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.

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.

Figure 6. Average proportions of behaviours assigned along tracks of adult and juvenile Red-footed Boobies from Genovesa, Surprise and Europa.
Tables

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

<table>
<thead>
<tr>
<th></th>
<th>Number of individuals</th>
<th>Number of tracks collected</th>
<th>GPS frequency (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Adults</td>
<td>Juveniles</td>
<td>Adults</td>
</tr>
<tr>
<td>GEN</td>
<td>37</td>
<td>18</td>
<td>44</td>
</tr>
<tr>
<td>SUR</td>
<td>6</td>
<td>10</td>
<td>22</td>
</tr>
<tr>
<td>EU</td>
<td>7</td>
<td>21</td>
<td>58</td>
</tr>
</tbody>
</table>

Table 2. Frequency (number h⁻¹), 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.

<table>
<thead>
<tr>
<th></th>
<th>ARS frequency (nb/h)</th>
<th>ARS duration (min)</th>
<th>ARS surface (km²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td>Genovesa</td>
<td>0.5 ± 0.2</td>
<td>13.1 ± 4.8</td>
</tr>
<tr>
<td></td>
<td>Surprise</td>
<td>0.9 ± 0.7</td>
<td>15.7 ± 8.6</td>
</tr>
<tr>
<td></td>
<td>Europa</td>
<td>0.7 ± 0.3</td>
<td>15.9 ± 12</td>
</tr>
<tr>
<td>Juveniles</td>
<td>Genovesa</td>
<td>1.0 ± 0.5</td>
<td>28.3 ± 21.8</td>
</tr>
<tr>
<td></td>
<td>Surprise</td>
<td>1.0 ± 0.9</td>
<td>21.1 ± 15.4</td>
</tr>
<tr>
<td></td>
<td>Europa</td>
<td>1.0 ± 0.4</td>
<td>23.4 ± 19.2</td>
</tr>
</tbody>
</table>
Table 3. Description of the associations occurring between juvenile Red-footed Boobies from Genovesa, Surprise and Europa. \( n_{\text{ind}} \) = total number of tracked individuals, \( n_{\text{tracks}} \) = total number of tracks.

<table>
<thead>
<tr>
<th>Location</th>
<th>( n_{\text{ind}} )</th>
<th>( n_{\text{tracks}} )</th>
<th>Proportion of tracks including associations</th>
<th>Proportion of associated portion along tracks ( \pm )</th>
<th>Maximum number of individuals associated along a track</th>
</tr>
</thead>
<tbody>
<tr>
<td>Genovesa</td>
<td>18</td>
<td>278</td>
<td>0.42</td>
<td>0.11 ± 0.09</td>
<td>5</td>
</tr>
<tr>
<td>Surprise</td>
<td>10</td>
<td>95</td>
<td>0.21</td>
<td>0.07 ± 0.05</td>
<td>2</td>
</tr>
<tr>
<td>Europa</td>
<td>21</td>
<td>134</td>
<td>0.57</td>
<td>0.14 ± 0.13</td>
<td>9</td>
</tr>
</tbody>
</table>
Table 4. Probabilities of associations between pair of juvenile Red-footed Boobies from Genovesa, Surprise and Europa occurring outside ARS zones of both juveniles (p0), inside ARS zone of one of the two juveniles (p1) and inside ARS zones of both juveniles. $P_{\text{exp}}$: expected probabilities under the null hypothesis (independency of pair associations and ARS zones). $P_{\text{obs}}$: observed probabilities. The pie charts show the proportions of different behaviours assigned to associated locations. $n_{\text{ind}}$ = number of associated individuals, $n_{\text{tracks}}$ = number of tracks including associations.

<table>
<thead>
<tr>
<th>Location</th>
<th>$n_{\text{ind}}$</th>
<th>$n_{\text{tracks}}$</th>
<th>$P_{\text{exp}}$ (No juv in ARS)</th>
<th>$P_{\text{exp}}$ (One juv in ARS)</th>
<th>$P_{\text{exp}}$ (Both juv in ARS)</th>
<th>$P$-value ($\chi^2$, df = 2)</th>
<th>Behaviour during associations</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Genovesa</strong> ($n_{\text{ind}} = 18$, $n_{\text{tracks}} = 115$)</td>
<td></td>
<td></td>
<td>0.26</td>
<td>0.50</td>
<td>0.24</td>
<td>$P &lt; 0.001$ (277.18)</td>
<td>![Pie Chart 1]</td>
</tr>
<tr>
<td><strong>Surprise</strong> ($n_{\text{ind}} = 9$, $n_{\text{tracks}} = 18$)</td>
<td></td>
<td></td>
<td>0.31</td>
<td>0.50</td>
<td>0.19</td>
<td>$P &lt; 0.001$ (42.99)</td>
<td>![Pie Chart 2]</td>
</tr>
<tr>
<td><strong>Europa</strong> ($n_{\text{ind}} = 20$, $n_{\text{tracks}} = 75$)</td>
<td></td>
<td></td>
<td>0.34</td>
<td>0.48</td>
<td>0.18</td>
<td>$P &lt; 0.001$ (936.25)</td>
<td>![Pie Chart 3]</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Behaviour</th>
<th>Foraging</th>
<th>Travelling</th>
<th>Relocating</th>
<th>Resting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pie Chart 1</td>
<td>![Pie Chart 1]</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pie Chart 2</td>
<td>![Pie Chart 2]</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pie Chart 3</td>
<td>![Pie Chart 3]</td>
<td></td>
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</tbody>
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