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Diversity of migration strategies among great frigatebirds populations

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Migratory behavior varies extensively between bird taxa, from long distance migration to purely sedentary behavior. Variability in migratory behavior also occurs within taxa, where individuals within some species, or even populations, show mixed strategies. The same variability occurs in seabird species. We examined the migratory behavior of distinct populations of great frigatebirds *Fregata minor* in three distant oceanographic basins. Great frigatebird populations showed extensive variation in post-breeding migratory behavior. Birds from Europa Island (Mozambique Channel) made long-distance migration to numerous distinct roosting sites in the Indian Ocean, New Caledonia birds made shorter distance migrations to roosting sites in the southwestern Pacific Ocean, and Galapagos birds were resident within the archipelago year round. Juvenile birds from Europa Is. and New Caledonia dispersed widely whereas Galapagos juveniles were resident year round. The migratory behavior of Europa Is. and New Caledonia resulted in complete separation of foraging grounds between breeding adults, non-breeding adults, and juveniles, whereas in the Galapagos the overlap was complete. We suggest that population variability in migratory behavior may have arisen because of different environmental conditions at sea, and also depends on the availability of suitable roosting sites on oceanic islands. The results also highlight the capacity of frigatebirds to remain airborne most of the time even outside the breeding season when they have to molt.

Migration is a crucial response to spatial variations of the environment, allowing individuals to avoid unfavorable conditions during their annual life cycle (Cresswell et al. 2011). Migratory behavior and the routes taken are assumed to be optimal, to minimize travel duration and total energy expenditure (Alerstam and Lindström 1990, Alerstam 2011) so that survival and future reproductive performances are maximized (Drent 2006). However, the annual cycles can differ markedly between populations and among individuals within populations. Whether animals are resident or migratory has major consequences for interactions and processes in local versus distant environments (Bauer and Hoye 2014), and ultimately contrasted consequences for fitness (Newton 2008). Thus, within populations some individuals may migrate between habitats whilst others remain resident in a single habitat (Dingle 1996), a situation that is referred to as partial migration (Chapman et al. 2011). Today there is no clear understanding if migratory behavior is transmitted genetically to offspring, nor the amount of flexibility juvenile birds have to adopt one behavior or the other. Whereas many species are clearly migratory and others sedentary, in many cases the situation is unclear because migratory behavior is difficult to study. Only recently has it become possible to study the detailed migratory movements of individuals, and examine important question such as the ontogeny of migratory behavior (Sergio et al. 2014).

Breeding seabirds are central-place foragers and often move over extensive distances to reach distant feeding grounds (Weimerskirch 2007). By their length, such movements tend to be similar to migratory movements. As the breeding season ends many species remain in the vicinity, or within the range used during breeding, whereas others undertake long migrations (Shaffer et al. 2006, Guilford et al. 2009, Egevang et al. 2010). Migratory seabirds adjust their migration route relative to particular wind regimes (Felicísimo et al. 2008). As in land birds, partial migration occurs in some seabird species. For example, different populations of migrating shearwaters breeding in different marine environment appear to have specific wintering grounds that exhibit similar oceanographic characteristics

(Gonzales-Solis et al. 2007). However, different populations of the same species may winter in different habitats (Weimerskirch et al. 2015a). For example some individuals or populations of south polar skuas *Stercorarius maccormicki* winter in tropical waters while others winter in polar habitats in the northern hemisphere (Weimerskirch et al. 2015b).

Among seabirds, frigatebirds are extreme in many aspects of their life history that put strong constraints on their potential migratory behaviour. They cannot land at the sea surface because their plumage is not waterproof. They feed exclusively at sea, especially on flying fish that they catch on the wing (Weimerskirch et al. 2004). They have the lowest wing loading of any bird, which provides them with a unique capacity for soaring flight using air currents (Pennycuick 1989). This capacity allows them to fly at extremely low costs, without landing or resting on the sea surface (Pennycuick 1989, Weimerskirch et al. 2016) and thus travel over thousands of kilometers when they are central place foragers during the breeding season (Weimerskirch et al. 2004, 2010). The non-breeding life-history of frigatebirds is poorly documented. They are presumed to range over large oceanic distances as suggested by band recoveries (Sibley and Clapp 1967) and from recent satellite telemetry in the Indian Ocean (Weimerskirch et al. 2006, 2016). Whereas breeding sites are relatively rare (Nelson 1976), for example only three significant colonies in the entire Indian Ocean, they use several oceanic islands as roosting sites. However, the status of the birds observed on roosting sites is unknown, they could be either immatures, or post-breeding adults, as is their colony of origin. It is also not documented whether breeding sites are also used as roosting sites by adults, or whether frigatebirds migrate to specific sites outside the breeding season, or disperse widely without a typical migratory behavior.

Here, we investigate the movements outside the breeding season of three distinct great frigatebird *Fregata minor* populations nesting in the Indian Ocean (Europa Island), in the south western Pacific Ocean (New Caledonia) and in the eastern Pacific Ocean (Galapagos Islands, Fig. 1). The nesting grounds of these populations have variable degrees of isolation and are surrounded by different oceanographic contexts. Europa Island is located in the Mozambique Channel, with relatively rich tropical waters and strong eddy activity whereas New Caledonia is surrounded by more oligotrophic waters. The Galapagos Islands are located on the Equator, at the convergence of several currents, with a strong heterogeneity in oceanographic habitats. The aims of the study are to document the post breeding behavior of great frigatebirds; to examine whether each population of the same species has similar migratory behaviors or distinct non-breeding strategies, and to determine the extent of overlap between the distributions of non-breeding and breeding birds. In addition we examine here whether juvenile birds follow the same migratory routes or sedentary behavior as adults, and whether juvenile behavior differs between colonies.

Methods

Field study and equipment

The study was carried out on three sites, Europa Island (40.3°E–22.3°S) in the Mozambique Channel, Isla Genovesa (89.9°E–0.3°N) Galapagos Islands and three islets around New Caledonia, Chesterfields (158.4°E–9.9°S), Surprise (163.1°E–18.5°S) and Walpole (168.9°E–22.6°S) (Fig. 1). Adults brooding small chicks or feeding large chicks, and juvenile birds were captured on or nearby the nests using a long telescopic pole equipped with a noose by day, or by hand using night vision googles at night. Frigatebirds were equipped with Argos PTTs powered with solar panel. All loggers were attached to back feathers with black adhesive Tesa tape, centred between the wings. The mass of loggers (9.5–20 g) was always below 2% of the bird body mass (1.1–1.6 kg).

On Europa Island, an estimated 1500 breeding pairs of great frigatebirds are breeding (Le Corre and Jouventin 1997). Field work was carried out in September–November (period of incubation and small chick brooding) 2003, 2011, 2012 and 2013 and in January–March (period of large chick rearing and fledging) 2014 and 2015. A total of 38 adults and 24 juvenile birds were equipped with PTT 100 (Microwave Telemetry, Columbia, USA) 9.5 g solar powered Argos Transmitters and 20 g Solar GPS/PTTs (6 juveniles).

In the Galapagos, the study was carried out on Isla Genovesa in November 2009 and 2014 when several hundreds of pairs were breeding. The total breeding population for the Galapagos Islands is estimated to several thousand pairs. A total of 8 adults rearing large chicks and 7 juveniles were equipped with Argos PTTs.

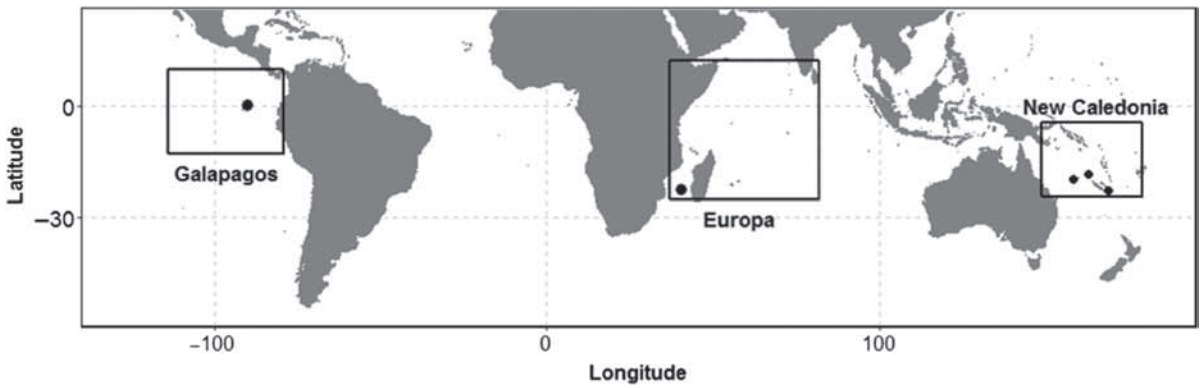

Figure 1. Location of the three sectors (squares) considered in the study. Black dots indicate the location of the breeding sites from where great frigatebirds movements were tracked.

In New Caledonia, the study took place on Ile Longue, Chesterfield Reefs; [with several hundred great frigatebirds breeding pairs (Borsa et al. 2010)] in May–June 2012, on Walpole Island [500–900 pairs (Barré and Dutson 2000)] in September 2014 and on Surprise Island, d'Entrecasteaux Reefs [tens of pairs (Robinet et al. 1997)] in December 2015. Twenty-four Argos tags were deployed on adults (6 on the Chesterfield colony, 10 on Surprise, 8 on Walpole). In addition, 3 juvenile birds were equipped with 9.5 Argos solar PTTs on Walpole Island.

Analyses

Birds were considered to have stopped reproduction when they no longer made central place foraging trips from the breeding colony and left definitively the breeding island for other sites. On islands other than the breeding colony they may either stop for a short period, without returning ('stop-over sites') or stop for a variable duration and adopt a central place foraging behaviour, returning to the same site on successive foraging trips at sea ('roosting sites'). In the analyses, the tracking period was divided into four different behaviours. 1) Reproduction when birds are central place foraging from the breeding colony, 2) roosting, when central foraging from a site other than the breeding colony, 3) migration when moving between breeding and roosting sites, 4) stop-overs occur during migration of adults, and during dispersal movement of juveniles, when birds stopped on a site during migratory or dispersive movements but continue their movements without making central place foraging around the site.

We used Kernel analysis to infer density distributions of breeding adults according to colonies and sexes. The 90 and 50% Kernels were calculated using the kernel UD function in the 'adehabitatHR' package (Calenge 2006). The smoothing parameter was chosen as the minimum value that minimized the number of vertices (1 for Galapagos and New-Caledonia, 0.5 for Europa). We considered 90% instead of 95% density contours as the broad home to compensate for the large smoothing. The 50% density contours indicate the core area range (Gallerani Lawson and Rodgers 1997).

Statistical analyses were done using Statistica 12 and the R Package. All values are given as mean ± 1 SD unless stated otherwise. Individuals were tracked for several successive foraging trips prior and after migration, when they are central place foragers. We analyzed foraging parameters using mixed-model ANOVAs to take possible pseudoreplication problems into account. Foraging parameters (trip duration, range, distance covered, time on land) were taken as dependent variables, colony and sex were entered as fixed factors and individual bird was included as a random factor.

Results

Foraging behaviour during breeding prior to migration

During the month preceding migration, great frigatebirds were central-place foragers from the nesting sites, provisioning chicks (Fig. 2–4). The duration and maximum range of foraging trips from the colony varied between sites (Table 1). New Caledonian birds made the shortest trips in range and duration, Galapagos birds made the longer foraging trips in range and duration, whereas Europa Is. birds made trips of intermediate duration and range (Table 1). For each site, males always made longer foraging trips in range and duration than females ($F_{1,28} = 5.8$, $p = 0.027$ and $F_{1,26} = 4.3$, $p = 0.046$ respectively). During the month of the breeding period prior to migration when foraging from the breeding colony, birds spent 83.2% of their time in flight and the remaining time on land in the colony for stays of 0.6 d on average, with marginal difference between sites (Table 1).

Migration

After they stopped breeding, either at the end of chick rearing, or after a late breeding failure, birds migrated to roosting site. Migratory behaviour differed extensively between sites. Post-breeding birds from Europa Is. (Fig. 2) and New Caledonia (Fig. 3) migrated north-ward to distant roosting sites. Conversely, post-breeding adults from the Galapagos remained within the Galapagos archipelago, moving to

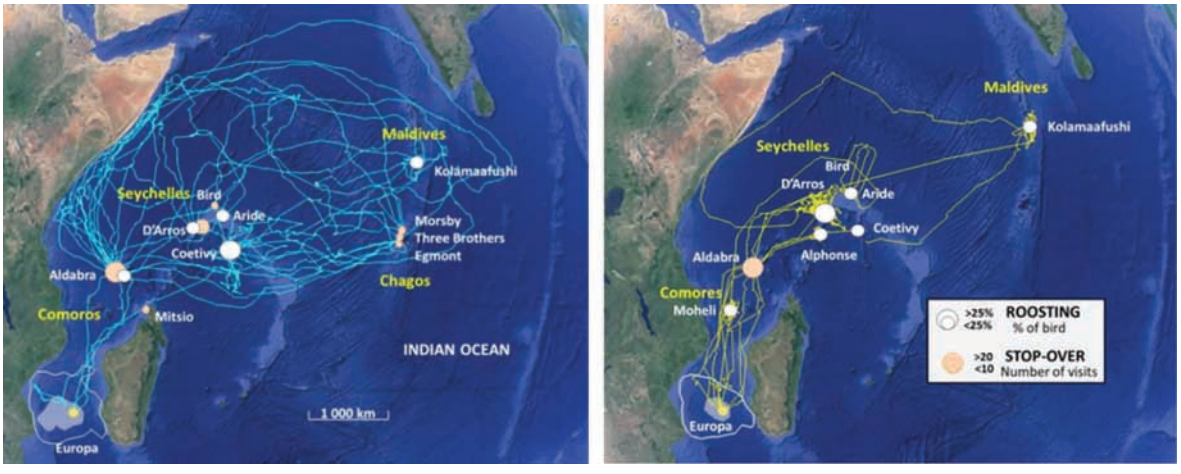

Figure 2. Migratory movements of post-breeding male (left) and post-breeding female (right) adult great frigatebirds from Europa Island, with the roosting sites and stop-overs in the Indian Ocean, and central place foraging movements from roosting sites. 90% kernels of the foraging zones during breeding of birds before migration are indicated.

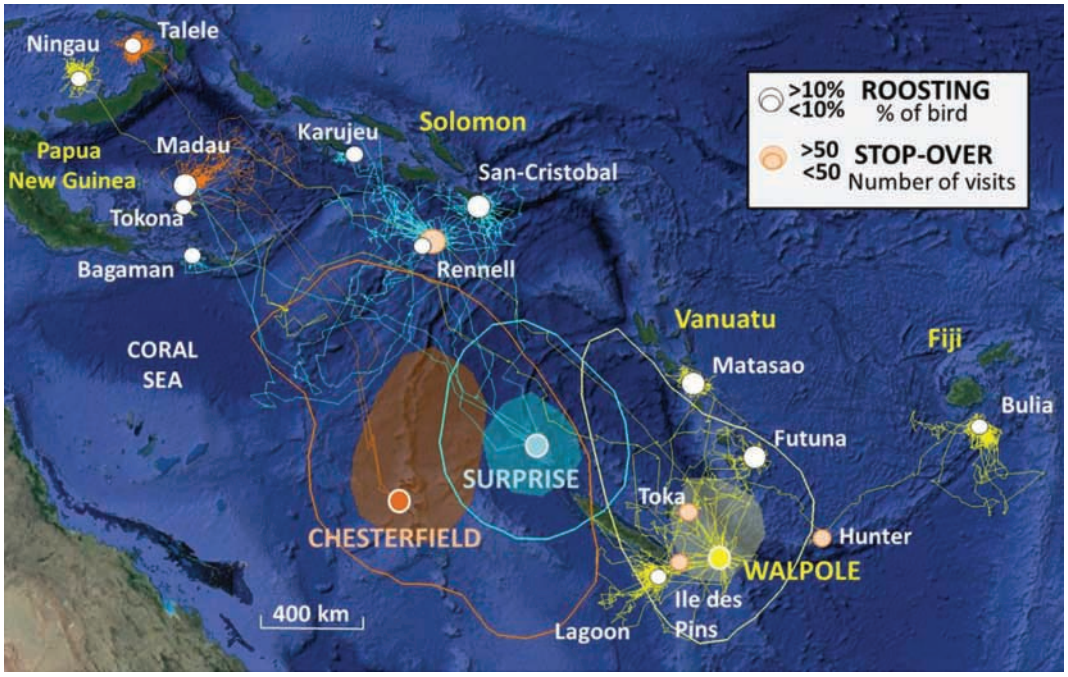

Figure 3. Map of the south-western Pacific Ocean showing the migratory movements and foraging from roosting sites from three colonies around New Caledonia: Chesterfield Islands (orange), Surprise Island (Red) and Walpole Island (yellow). 95% kernels of the foraging zones during breeding of birds before migration are indicated.

roosting sites different from, but close to, the Genovesa nesting colony (Fig. 4).

Adult birds from Europa migrated into the Seychelles archipelago, especially in the Amirantes group (Darros, Coetivy, Alphonse, Table 2), Aldabra and Aride, but also to the Comoros and the Maldives (Fig. 2). The New Caledonia birds moved northward into several islands off Vanuatu Solomon Islands, Papua–New Guinea and Fiji Islands

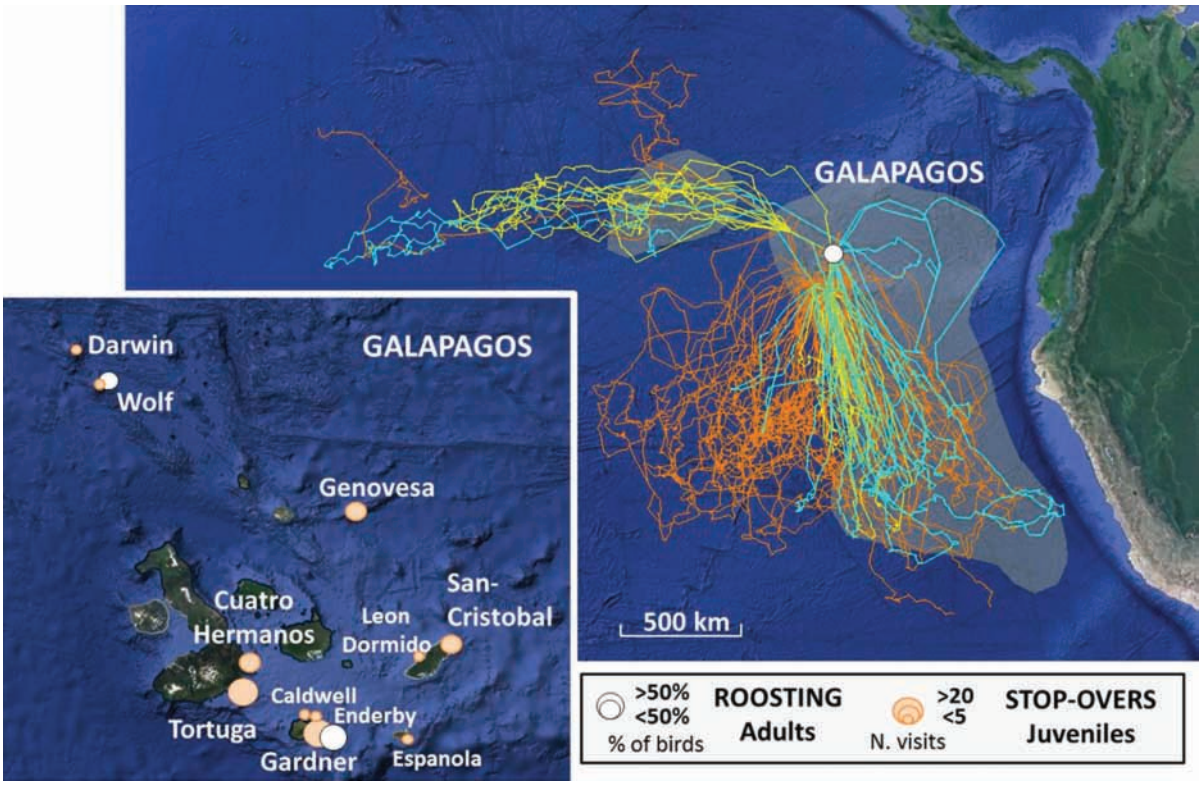

Figure 4. Foraging movements of males (blue) and females (yellow) adult Galapagos great frigatebirds from the roosting sites in the eastern equatorial Pacific, with the movements of juveniles (orange). Insert: (Galapagos archipelago showing the breeding site – Isla Genovesa – and the roosting sites and stop-overs).

Table 1. Comparison of foraging and movement parameters of great frigatebirds between Europa, New Caledonia and Galapagos during breeding, migration and roosting.

	Europa	Galapagos	New Caledonia	Differences between regions
a) Breeding				
Trip duration (d)	3.5 ± 3.1 (177)	5.7 ± 6.1 (57)	2.1 ± 2.5 (291)	$F_{2,29} = 4.6$, $p = 0.02$
Range (km)	280 ± 645	578 ± 632	196 ± 197 (291)	$F_{2,29} = 5.8$, $p < 0.01$
Duration on land (d)	0.9 ± 1.0 (164)	0.6 ± 0.8 (63)	0.4 ± 0.6 (271)	$F_{2,29} = 3.1$, $p = 0.062$
b) Migration				
Duration	17.5 ± 17.7		5.8 ± 4.7	$F_{1,26} = 8.1$, $p = 0.021$
Distance covered (km)	5757 ± 6504		1716 ± 1075	$F_{1,26} = 6.5$, $p = 0.02$
Range (km)	2446 ± 918 (15)	199 ± 122 (6)	1140 ± 723 (15)	$F_{2,31} = 19.3$, $p < 0.001$
c) Roosting				
Trip duration (d)	2.2 ± 2.8 (451)	7.7 ± 8.8 (48)	1.3 ± 1.6 (992)	$F_{2,45} = 10.7$, $p < 0.001$
Range (km)	142 ± 463 (442)	446 ± 519 (48)	68 ± 63 (951)	$F_{2,45} = 2.3$, $p = 0.10$
Duration on land	0.8 ± 1.0 (324)	2.0 ± 1.6 (25)	0.3 ± 0.5 (919)	$F_{2,31} = 6.3$, $p = 0.005$

(Fig. 3). Europa Is. birds made migratory movements longer in duration, range and distance covered than New Caledonian birds (Table 1). Europa Is. birds also used several islands as stop-overs, especially Aldabra that appears as an important hub for great frigatebirds in the western Indian Ocean. This was particularly true for males, since females showed much less stop-overs during their migration. In the New Caledonia area, Rennell Island represented a major stop-over on the migratory route of the birds.

Roosting

Just after they arrived on their roosting sites, birds began to exhibit a central-place foraging behaviour. Most birds had a single roosting site from where they foraged, but some birds moved between two and four roosting sites (Table 2).

The foraging trips from roosting sites differed extensively between colonies (Table 1). Females migrating from Europa Is. remained on the same single roosting site and foraged within short range (average 140 km) from it, whereas males made long oceanic trips up to more than 2000 km from the roosting site, with stop-overs on some islands (Fig. 2). The New Caledonia birds all foraged at short range and for short duration from their roosting sites (Fig. 3, Table 1). In the Galapagos, non-breeding birds foraged in the same areas as those used during breeding (Fig. 4). In the Galapagos, foraging trips from roosting sites were much longer in duration and range than the other sites (Table 1). In all sites, rest periods on roosting sites between two foraging trips were always short, rarely exceeding two days, and differed between sites, Galapagos birds spending longer rests on roosting sites than birds from other colonies (Table 1). In all sites, foraging duration and range tended to be shorter during the roosting period in comparison to the breeding season. During the roosting period birds spent 75.4% of their time in flight.

Return from migration

For most birds, transmitters stopped working during the non-breeding season, possibly when lost during moult. In New Caledonia, one adult male and one adult female bird returned to the breeding sites after 4–6 months spent on the roosting site (Fig. 5). The return journey was similar to the outward journey in duration and distance covered (Fig. 5).

Dispersal of juveniles

Like adults, juveniles showed extreme variation in their dispersive movement after fledging. Juvenile birds from Europa Is. dispersed over the entire Indian Ocean and visited more sites than adults, but mainly as stop-overs and for relatively short periods (Fig. 6, Table 2). Juvenile birds from the Galapagos moved to roosting sites within the Galapagos archipelago, from where they made central-place foraging trips similar to those of adults, although longer in duration (Fig. 4). The two juveniles tracked from Walpole off New Caledonia dispersed north of the Coral Sea and in the Solomon Sea, visiting several islands and islets (Fig. 7). For Europa Is. juveniles, after tracking periods of up to 2 yr, we found no clear settlement to a particular roosting site as in adults.

Discussion

The three great frigatebird populations monitored in this study have different migration strategies. Europa Island birds migrate to distant roosting sites mainly located in the Seychelles archipelago, up to the Maldives. Galapagos birds do not migrate, and they roost within the archipelago, but on islets different from the breeding sites, at distances of 100–190 km from the latter. New Caledonia birds show intermediate patterns, migrating to roosting sites located at distances of ca 1000 km. From the roosting sites birds show a central-place foraging pattern similar to that used during breeding, i.e. foraging continuously at sea with short rests on the roosting sites.

Great frigatebirds have the ability to make extensive movements at the scale of an ocean basin (Dearborn et al. 2003, Weimerskirch et al. 2016). During these large-scale movements outside the breeding season, birds may visit sites other than their breeding colony, and use them for roosting or stop-over. Some of these sites may be breeding colonies, such as Aldabra, with the largest breeding population in the Indian Ocean, and the closest colony from Europa Is. Our tracking data show that Aldabra constitutes a major stop-over site functioning as a hub, but a minor roosting site for Europa Is. birds. Christmas Island, which is the third major breeding site for the species in the entire Indian Ocean, is also visited by juvenile birds from Europa Island. Our

Table 2. Frequentation of roosting and stop-over sites used by adult male, adult female, and juvenile great frigatebirds from Europa, expressed as percentage of the total number of individuals sampled in each category for roosting sites (sample size into parentheses) and as the number of visits for stop-over sites.

	Adult males (n = 6)		Adult females (n = 8)		Juveniles (n = 12)
Country, site	Roosting % (n)	Stop-over V (n)	Roosting % (n)	Stop-over V (n)	Stop-over V (n)
Madagascar					
Nosy Mitsio	–	1	–	–	28 (1)
Moramba bay	–	–	–	–	3 (1)
Nossi Be	–	–	–	–	1
Nisi Hara	–	–	–	–	1
Nosi Lava	–	–	–	–	1
Nosy Iranja	–	–	–	–	1
Comores					
Moheli	–	–	12.5 (1)	–	12 (2)
Seychelles					
Aldabra	16.7 (1)	17 (5)	–	–	–
Cosmoledo	–	–	–	–	1
Aride	16.7 (1)	5 (2)	12.5 (1)	–	–
Bird	–	–	–	1	11 (2)
D'Arros	16.7 (1)	12 (2)	37.5 (3)	–	108 (6)
Eagle	–	–	–	–	10 (3)
Marie-Louis	–	–	–	–	1
Coetivy	33.3 (2)	20 (4)	12.5 (1)	–	–
Alphonse	–	–	12.5 (1)	–	12 (3)
Bijoutier	–	–	–	–	2 (2)
Desroches	–	–	–	1	–
Farquhar	–	–	–	–	2 (1)
Chagos					
Diego Garcia	–	–	–	–	7 (4)
Egmont	–	1	–	–	4 (2)
Danger	–	3 (1)	–	–	1
Est Three Brothers	–	2 (2)	–	–	6 (5)
Nelson	–	–	–	–	3 (3)
Est Morsby	–	9 (2)	–	–	11 (5)
Salomon	–	1	–	–	2 (2)
Maldives					
Kolamaafushi	16.7 (1)	–	12.5 (1)	–	–
Cocos-Christmas					
North Cocos	–	–	–	–	8 (2)
Christmas	–	–	–	–	5 (1)
Indonesia					
P. Breueh, Sumatra	–	–	–	–	1
P. Pini, Sumatra	–	–	–	–	42 (3)
P. Legundi, Sumatra	–	–	–	–	1
Teluk Dalem, Sumatra	–	–	–	–	1
P. Panatian, Java	–	–	–	–	1
Teluk Paraja, Java	–	–	–	–	1
Jakarta, Java	–	–	–	–	16 (1)
P. Tjinjil, Java	–	–	–	–	1
Kuta, Bali	–	–	–	–	4 (1)
P. Belang, Bali	–	–	–	–	1
Teluk Perapat, Timor	–	–	–	–	1
Seringapatam	–	–	–	–	1
Eastern Africa					
Mogadiscio, Somalia	–	–	–	–	1
Mohoro Bay, Tanzania	–	–	–	–	2 (1)
Lindi Bay, Tanzania	–	–	–	–	3 (1)
Mchinga Bay, Tanzania	–	–	–	–	1
Shungu Bay, Tanzania	–	–	–	–	1
Australia					
Ashmore and Cartier	–	–	–	–	2 (1)
Reef north of Australia	–	–	–	–	1

tracking study shows that post breeding adults can move to distant roosting sites that are specific to a population, with possible overlap between different populations on the same roosting sites. Genetic analyses of blood parasites transmitted to seabirds suggest that migrations between the Pacific and the Indian oceans explain the large-scale distribution

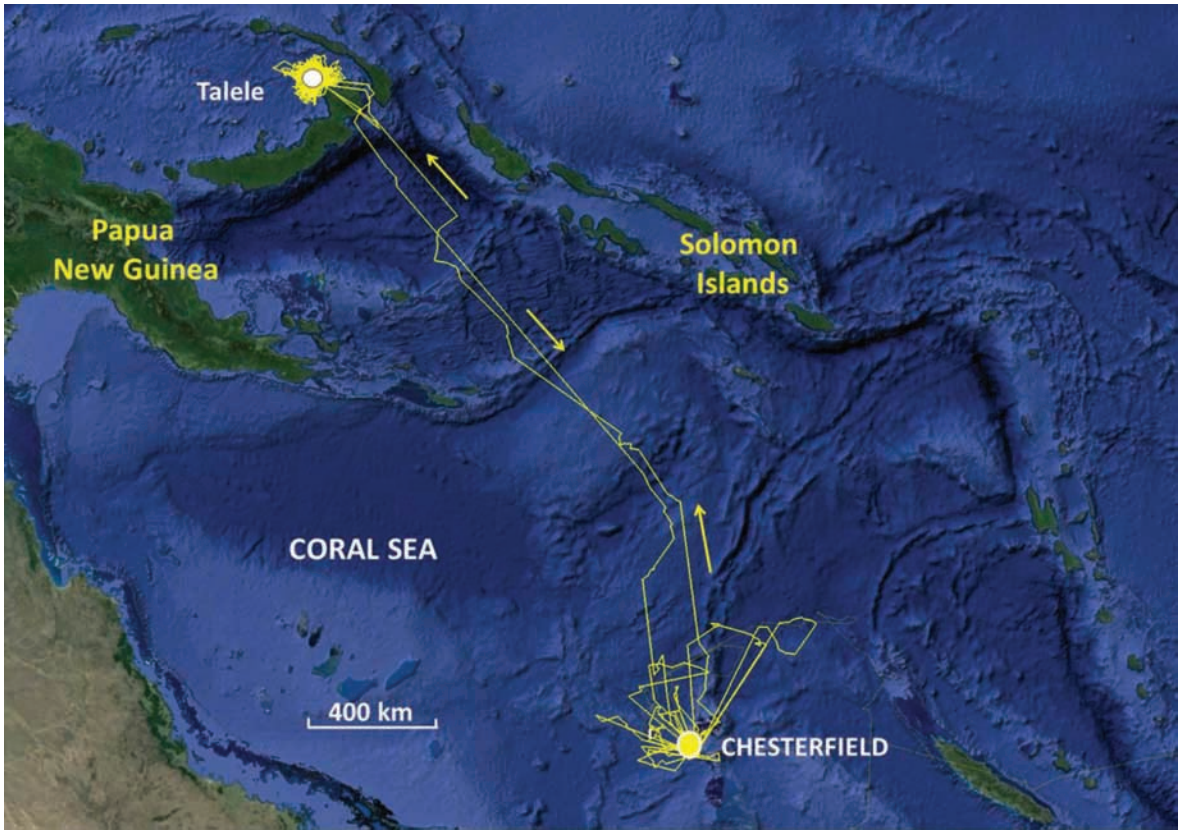

Figure 5. Complete migratory movement (yellow) of a male frigatebirds breeding on Chesterfield island (with movements one month prior to migraton), off New Caledonia to the roosting site on Talele Island, Papua New Guinea, with movements from the roosting site. Arrows indicate outward and return journeys.

of parasites in frigatebird populations (Bastien et al. 2014), lending support to the overlap hypothesis. Although movements between islands regularly occur, significant genetic differences between breeding sites have been reported (Dearborn et al. 2003, Levin and Parker 2012). Therefore, dispersal movements from one breeding site leading to

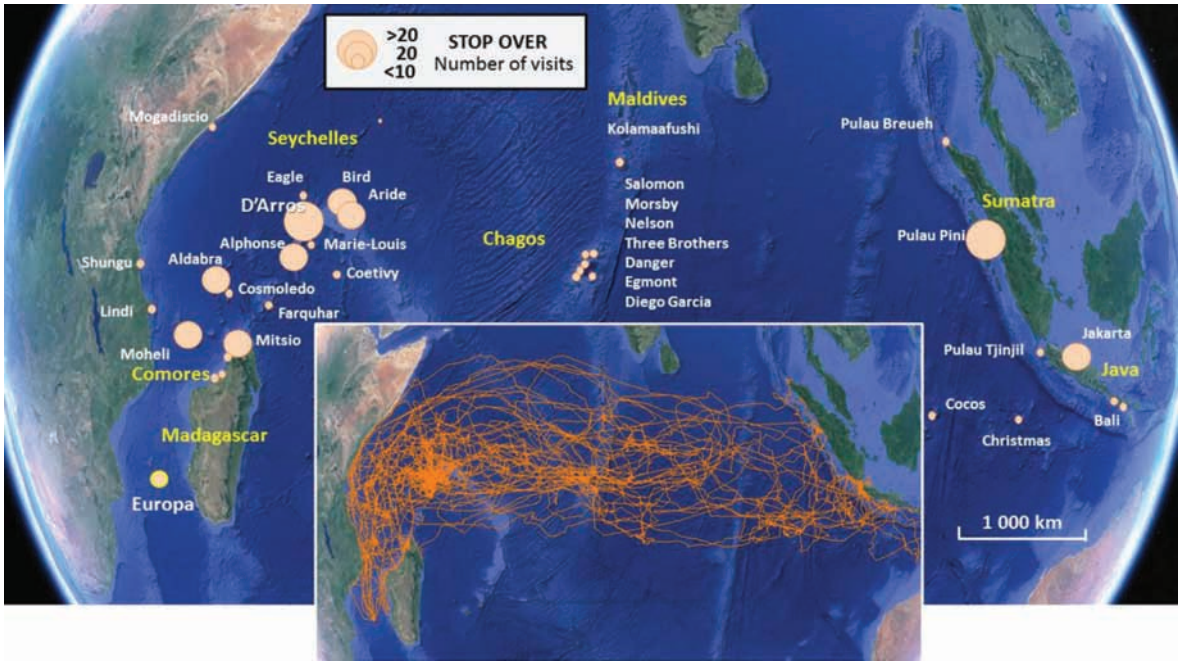

Figure 6. Dispersal movements of juvenile great frigatebirds from Europa in the Indian Ocean, with the stop-over sites used.

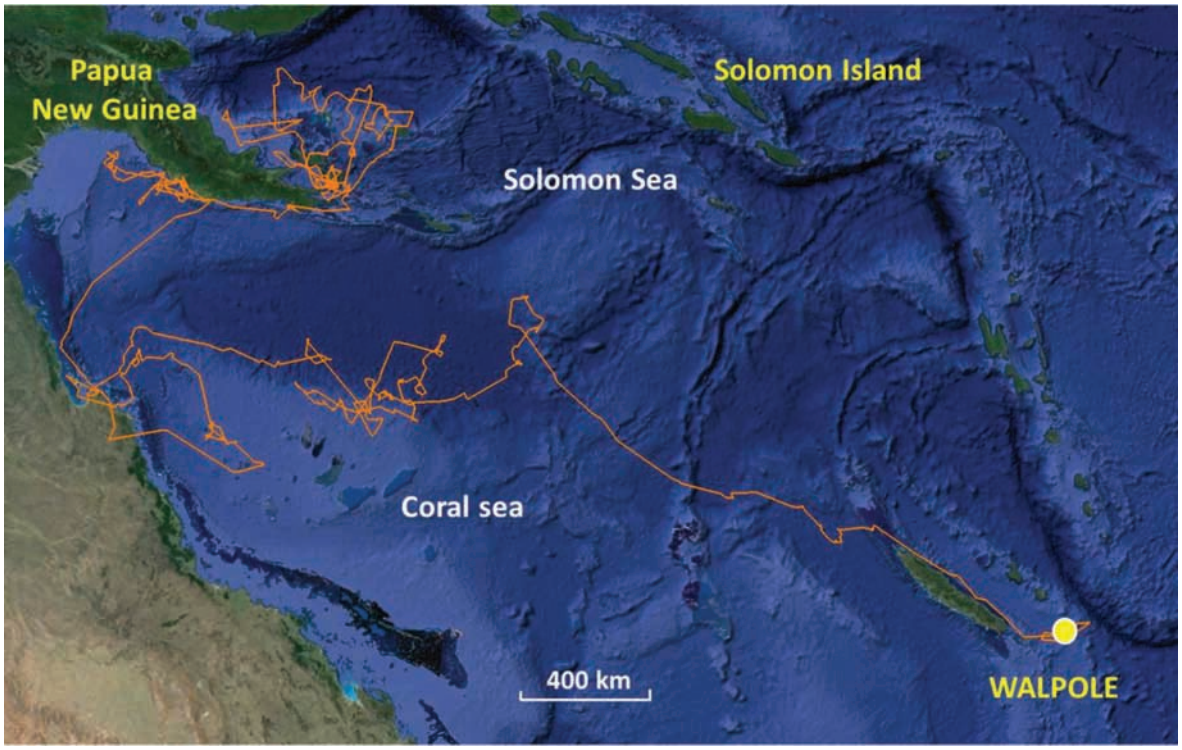

Figure 7. Dispersive movement of a juvenile great frigatebird fledged from Walpole Island off New Caledonia between 29/11/2015 and 20/03/2015.

breeding on another site are likely to be rare in great frigatebirds (Dearborn et al. 2003, Levin and Parker 2012). This result indicates strong philopatry in this wide-ranging species. The different migratory behaviours observed between populations of three distinct oceanic basins may have provided the opportunity for evolutionary divergence between resident and migratory population, as it has been proposed previously for Cook's petrel *Pterodroma cookii* (Rayner et al. 2011). Presently three sub-species are recognised for our three study populations: *F. m. aldabrensis* for Europa Island and other western Indian Ocean colonies, *F. m. minor* for the New Caledonian and other south-west Pacific islands, and *F. m. ridgwayi* for the Cocos and Galapagos Islands (Orta et al. 2016). Future genetic studies comparing the Galapagos population with other migratory populations would allow a test of this hypothesis. Additional information on the potential movements within the three basins is also required to better understand the amount of exchanges between breeding sites.

Although frigatebirds have the ability to visit any island because of their capacity to make long range movements at low cost (Weimerskirch et al. 2016), they appear to select few sites for roosting. Roosting sites may have been selected for their potential to provide food in the surrounding waters, or to be breeding sites of seabird species that great frigatebirds can kleptoparasitize. Roosting sites also appear to have been selected because of their ability to provide a place with no or low human disturbance. Remarkably, stop-over sites of Europa Is. birds are all located on oceanic islands, with the exception of occasional short stops along the coast of Africa or Indonesia. Frigatebirds are sensitive to human disturbance when breeding, but our results suggest that roosting sites may also necessitate quietness. Indeed, all nesting sites, but also the major roosting sites appear to be sites where there is no human presence. The central Seychelles concentrate large numbers of non-breeding frigatebirds, but no breeding individuals (D'Arros, Aride). Aldabra is a major breeding site for great frigatebirds, with breeding birds foraging north of the island (Weimerskirch et al. 2010). The presence of this large population may be the reason why the island is not used as a roosting site by Europa Island birds, although it is an important stop-over site for brief visits. Similarly, the three breeding sites off New Caledonia are remote islands with no human presence: they are the major breeding sites for great frigatebirds in the region (Robinet et al. 1997, Barré and Dutson 2000, Borsa et al. 2010), whereas the roosting sites further north are not breeding sites. Interestingly, these roosting sites are located in very productive waters. However these islands, although remote, are probably susceptible to human disturbances, and this may partly explain why birds are not breeding at these northern sites.

In terms of conservation, our results suggest that while the sustainability of the great frigatebird populations is a local issue in the Galapagos the appropriate management scales for populations from Europa Island and New Caledonia are sub-regional and even international. New Caledonia's remote islets are key places for the reproduction of the species in the south-western Pacific Ocean. Other islands, situated further north in more productive waters, are used as roosting places and may be suitable for reproduction, but are not used as such, while birds coming from all over the region reach New Caledonia waters to breed. Preliminary results from the present study were taken into account in the strategic analysis that was undertaken by the

government of New Caledonia prior to the creation of the Coral Sea Nature Park (Gardes et al. 2014).

During breeding as non-breeding great frigatebirds spend little time ashore, and spend most of their time foraging at sea. During breeding, the time spent resting was 15.7% while the time spent resting on roosting sites reached 24.6%. Through an annual cycle including the breeding and non-breeding season, adult frigatebirds spend an estimated 80.6% of their time in flight (Europa Island: 78.2%; New Caledonia: 80.3%; Galapagos: 85.8%). Juvenile birds spend an estimated 91.5% in flight during their first two years after fledging. This is made possible by the ability of frigatebirds to stay aloft for periods lasting more than two months by taking advantage of atmospheric conditions at small scale (convection under clouds) and at large scale (global circulation) (Weimerskirch et al. 2016), and their ability to sleep while airborne (Rattenborg 2006). However a recent study indicates that sleep periods in flight are extremely short (Rattenborg et al. 2016) . Thus, because of the small proportion of time spent on land, frigatebirds appear to sleep little during their life cycle, and the few opportunities to rest when reaching roosting or stop-over sites may be important to recover from extended flight, and may require quiet sites suitable for restoring from extended awakeness flight periods. Another surprising result of our study, is that frigatebirds never stay for extended periods ashore, either during breeding or non-breeding seasons. While it is not surprising that frigatebirds, like many other seabirds do not spend long periods ashore during the breeding season, because of the need to feed the chick regularly, it is surprising that during the non-breeding season birds similarly spend little time ashore. Indeed, frigatebirds are unable to rest at the sea surface, as all other seabirds do. Since frigatebirds moult their flight feathers outside the breeding season (De Korte and De Vries 1978), it would have been expected that they decrease their activity while moulting like other seabirds do (Weimerskirch et al. 2015b, Cherel et al. 2016), and thus spend extended periods ashore.

The dispersive behaviour of juvenile frigatebirds differed between colonies. Whereas the Galapagos birds roosted in the archipelago in sites similar or different from the roosting sites of adults, juveniles from Europa Island made large scale dispersive movements throughout the Indian Ocean, and after one year, were still not settled in a particular roosting site. Furthermore, when dispersing, most of the stop-over sites were those used as roosting sites by adults from their colony of origin. Europa Island birds appear to have dispersive movements influenced mainly by wind conditions encountered (Weimerskirch et al. 2016) and not by internal programming that would bring them to the same roosting sites as adults. In other seabird species juveniles generally follow similar routes as those taken by adults (Péron and Grémillet 2013, de Grissac et al. 2016). Juvenile frigatebirds from Europa Island and possibly New Caledonia appear to have a wandering period before they settle in a roosting site. Whether the roosting site will be the same as those of their parents is not known yet. In albatrosses where the oceanic grounds used during the non-breeding period differed extensively between and within populations, the wintering grounds are probably not genetically determined but acquired during the first years at sea (Weimerskirch et al. 2015a). The propensity of juvenile frigatebirds from Europa Island (and probably New Caledonia) to wander over vast sectors, visiting many potential future roosting sites, suggests that this first dispersive phase will allow birds to select future roosting sites. Some juveniles from the Galapagos dispersed to the north, but their signal was lost after 2–5 weeks suggesting an early death, whereas those birds roosting in the Galapagos and foraging from there were tracked for more than one year, and thus survived for a much longer period, suggesting that the resident strategy is optimal in the context of this isolated archipelago. The differences between sites also suggest that at Europa Island and in New Caledonia, juveniles have an inherited program to disperse to the north of the breeding site and wander for several years, using this period to select their future roosting sites. Most of the Galapagos juveniles remain around the natal site from where they forage partly in similar zones as adults.

Thus great frigatebirds appear to display a typical partial migratory behaviour between populations, with some showing typical migratory behaviour between nesting grounds and roosting sites, and the Galapagos birds being sedentary. The local environmental conditions on the breeding grounds and feeding grounds could be an important reason for the evolution of distinct behaviours. Our results suggest a clear segregation between the foraging zones of birds from the same population between breeding sites and roosting sites, with no overlap at sea between the two sub-populations of breeding and non-breeding birds. The Galapagos colony, where roosting birds and breeding birds overlap extensively at sea, provides an exception to the pattern described above. The reason for this difference may be the isolation of the Galapagos with respect to other remote islands in the eastern central Pacific. Also the waters around the Galapagos may be rich enough to provide enough resources for the breeding and non-breeding population, as well as the juvenile population. Seabirds are unique in that the breeding grounds are distinct from feeding grounds at sea, and frigatebirds are also unique among seabirds with their inability to rest on the sea-surface as any other seabird do during the entire non-breeding season. Frigatebirds are also exceptional in that they are found breeding throughout the year and have a long breeding season,almost one year (Nelson 1976) and as a consequence the timing of migration is not limited to a short period, but rather flexible; birds migrate when the breeding season is over, and this might occur almost throughout the year. Similarly juvenile leave the natal colony at Europa Island between April and October, when southerly winds favour their dispersal into the central Indian Ocean (Weimerskirch et al. 2016). Thus migration may have evolved in frigatebirds mainly to reduce overlap, and thus competition for food resources, between the breeding population and non-breeding or with juvenile birds. In the Galapagos, birds remain sedentary either because resources, albeit distant, are sufficient to support a large population, or because potential roosting sites are too distant and difficult to reach with regard to wind conditions. These extensive differences between colonies may result in distinct fitness and demographics. Other factors that are generally considered to affect the evolution of migratory behaviour, such as transport costs or mortality (Alerstam et al. 2003) are probably less influential in frigatebirds because they appear

to have extremely low costs of movements over extensive distances (Weimerskirch et al. 2016) and are long-lived.

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