INTRODUCTION

Foraging behaviour is a central life-history trait of animals (Stearns, 1980). Movement and foraging behaviour are assumed to be progressively acquired during the early life of animals to attain adult capacities after a variable time (Rotics et al., 2016). The first year of independence from parents is a critical period with high mortality due to lower physical and foraging capacities compared with adults (Lindström, 1999). Recent studies using telemetry have shown that juvenile long-lived birds have lower foraging capacities than adults (Breed, Bowen, & Leonard, 2011; Daunt, Afanasyev, Adam, Croxall, & Wanless, 2007; Marchetti & Price, 1989; Riotte-Lambert & Weimerskirch, 2013). Attaining the movement and foraging capacities of adults may require several months to several years according to the flight mode and foraging strategies used. However, few studies are available on the early development of these capacities that develop either prior to complete independence from the parents or after leaving the nest independently from parents. In brown boobies (Sula leucogaster), the time spent in sustained flight by juveniles increases before independence (Yoda, Kohno, & Naito, 2004). Juvenile
With high temporal resolution the development of foraging and flight capacities. Some species have very specific flight techniques that are supposed to require a long learning phase. Frigatebirds (Fregata) have extreme adaptations to soaring flight, with the lowest wing loading of any bird (Pennycook, 1983) and the inability to land on water, which force them to stay continuously in flight for months (Weimerskirch, Bishop, Jeannard-du-Dot, Prudor, & Sachs, 2016). Thus similarly to raptors, frigatebirds have to adjust their gliding air-speed according to the risk of touching the sea surface or switching to costly flapping flight (Horvitz et al., 2014). Frigatebirds have the longest chick-rearing period of any flying bird (Nelson, 1975), and an atypical transition phase where the young juvenile is still fed by the female, but has started to practise foraging flights at sea (Nelson, 1975). This transition phase lasts 4–8 months and is supposed to be a period of learning necessary to acquire the extreme and complex flight capacities of adults. This period constitutes a unique opportunity to study the development of flight and foraging capacities of an oceanic seabird.

Using this unique opportunity, we used GPS and accelerometers to study the three-dimensional movements and body acceleration of juvenile great frigatebirds in order to examine the development of flight capacities and foraging tactics and compared them with the adult flight. We examined which flight parameters are developed during this learning period and which ones are already equivalent to those of adults. According to previous studies on other species (Rotics et al., 2016; Yoda et al., 2004; Yoda, Kohno, & Naito, 2007), our first hypothesis is that the capacities of juveniles are lower than those of adults at the beginning of the learning period. Our second prediction is that juvenile frigatebirds’ capacities may attain those of adults before they become independent from parents. This acquisition of adult capacities by juveniles would be the signal for juveniles to leave their breeding site and become independent.

2 | MATERIALS AND METHODS

2.1 | Field procedure

The study was carried out on Europa Island (20°22’S; 40°20’E) in the Mozambique Channel. In September 2013, February 2014 and February 2015, 37 solar-powered GPS-accelerometer (GPS/ACC, e-obs GmbH) were deployed on 19 breeding adults and on 18 fledgling great frigatebirds (Table S1). The device measured 130 × 30 × 12 mm and weighed 30 g, which is 1.88%–3.55% of the frigatebirds’ weight. It was attached to the back feathers with waterproof tape (Tesa, Germany). The devices were set to record the altitude and GPS location every 5 min and tri-axial acceleration for 10 s at 19 or 33 Hz every 1 or 2 min for 24 hr or between 3:00 and 16:00 UTC (sunrise to sunset). Data were transmitted to a base station installed in the colony each time when the bird returned to the colony. Loggers were recovered after 2–5 months or left on the birds where they detached during the moult of feathers.

We also fitted 9.5 g solar-powered PTT devices (Microwave Telemetry) on five juveniles. These PTTs were attached with tape on back feathers and recorded Argos location transmitted by satellite. They dropped off when birds lost feathers during their moult (5–18 months later). Moreover, as we recovered most GPS/ACC only before the migration departure of birds, we used GPS/PTTs information to control whether movement patterns changed during the last trips prior to migration.

During this fieldwork and in 2003 and 2008 (De Monte et al., 2012; Weimerskirch, Chastel, Barbraud, & Tostain, 2003), 86 great frigatebirds were caught for other experiments and their morphological data were used in this study: body mass, wing length (from wrist articulation to the longest primary feathers) and length of culmen length.

2.2 | Data analysis

The acceleration data were analysed using Igor Pro version 6.3 (WaveMetrics Inc.). The raw acceleration data were converted to physical acceleration units in m/s², using the values of gravity (1G = 9.81 m/s²) for each axis. At first, the static acceleration was approximated by applying a smoothing function to the total acceleration recorded for each axis (Gleiss, Wilson, & Shepard, 2011; Shepard et al., 2008). We used the box smooth function of IGOR Pro, which is similar to running means of 1 s, to generate the static component. The dynamic acceleration is then determined by subtracting the static component of the total acceleration. Then, VeDBA was calculated as:

\[ VeDBA = \sqrt{(Ax - \overline{Ax})^2 + (Ay - \overline{Ay})^2 + (Az - \overline{Az})^2} \]

where \( Ax \), \( Ay \), and \( Az \) are the total acceleration in direction n and \( \overline{Ax} \), \( \overline{Ay} \), and \( \overline{Az} \) are the static component of the acceleration. VeDBA is a vectorial sum of the 3-axis of dynamic accelerations and a putative measure of energy expenditure (Elliott, 2016).

The flapping flight was detected by high frequency and high-amplitude fluctuations of the dorso-ventral acceleration using the package ‘Ethographer’ on IGOR PRO (Sakamoto et al., 2009). We generated a spectrum from acceleration signals based on the continuous wavelet transformation and then group each second of the spectrum into two clusters (flapping and non-flapping) by an unsupervised classification algorithm, the k-means clustering method (Sakamoto et al., 2009). Number of wings flapping was calculated as a sum of the reciprocal of the dominant cycle for each second classified as flapping. Then, mean flapping frequency and mean VeDBA were calculated between two GPS locations.

GPS data (WSG84) were converted to UTM, and the distance, mean speed between two locations and distance from the colony were calculated. Ascent rates between two locations were calculated as a difference in altitude divided by the time difference.
2.3 | Dataset

Frigatebirds have a very specific flight pattern, alternating periods of travelling where they climb under (altitudes 0–700 m) or inside (700–4,000 m) cumulus clouds by soaring up to several thousands of metres, and then cover long distances by gliding, and periods of foraging close to the surface (Figure 1). We classified flights into six behaviours according to flapping frequency and the ascent rate following Weimerskirch et al. (2016) (Table S2). For all locations at sea with altitudes lower than 20 m, birds were considered ‘foraging’ and actively flapping (Weimerskirch et al., 2016); otherwise, they were in ‘travelling’ mode when they stayed at altitude between 20 and 4,000 m (Weimerskirch et al., 2016, 2003) (Table S3).

By combining GPS and accelerometer data, we built a data matrix to estimate a series of parameters describing the flight of frigatebirds. A total of 22 parameters were estimated (Table S4). We first checked for correlations between parameters, and after removing 10 parameters with collinearity, we kept 12 parameters describing the flight characteristics of adult and juvenile frigatebirds. Since adults spent most of their time at sea, to compare gliding and soaring between juveniles and adults we used only locations at sea. The parameters examined were as follows:

- Duration of each trip (hr).
- Maximum range from the colony for each trip (km).
- Maximum altitude for each trip (m).
- Mean travel speed between two locations (km/hr).
- Ascent rate, when birds are soaring between two locations (m/s).
- Flapping frequency (flap/min).
- Gliding efficiency: as distance covered between two locations divided by descent rate (\(\text{km/m.s}^{-1}\)) (calculated below 700 m which is the basis of cumulus clouds).
- Proportion of time spent at sea for each trip.
- Soaring and gliding proportion at sea for each trip.
- Average energy expenditure for each trip: average VeDBA (used as a proxy of energy expenditure (Weimerskirch et al., 2016)), calculated during foraging and over the sea during soaring (m/s²).

2.4 | Statistical analysis

We analysed changes in flight and foraging parameters over time using linear mixed models (fit by maximum likelihood) with or without transformations (ln, square roots) and generalized linear mixed models (Poisson’s family) (Table S5). When examining changes over time in parameters, we excluded the first 52 days of recording, since during this period juveniles were flying mainly over ground. For this change over time, we used data only for 2015 (longest monitoring period with most loggers) and examined the slopes in the changes over time of all juveniles combined and of all adults. Sexes were combined because in both adults and juveniles, only a few males were tracked, and in juveniles for some individuals, sex was not known (Table S1). When we performed the same analyses for females only, the results were identical to results with all individuals pooled, suggesting that pooling individuals gave us more statistical power in the analyses without hiding sex effects. To test for differences between adults and juveniles in changes of parameters over time, we first performed the analysis for the entire study period, from 53 days to the end (140 days). To test whether juveniles parameters improve and become similar to adults over time, we also compared slopes over three stages of the study period, the beginning (days 53–70), the middle stage (days 71–119) and the final stage (days 120–140).

For all mixed models, individuals were included as random factors and we checked conformity of residuals and estimated marginal R² and conditional R² following Nakagawa & Schielzeth method (\texttt{mumIn} package (Johnson, 2014)).

For morphological data, we used a nonparametric analysis (Mann & Whitney U test). All statistical analysis was performed in R (R Core Team, 2016).
### RESULTS

#### 3.1 Average parameters of juveniles and adults

Most average flight parameters of juveniles and adults were different (Table 1). On average, adults foraging trips at sea were longer in duration and range than those of juveniles. Adults flew higher and faster, had a higher gliding efficiency than juveniles and flapped their wings less frequently. However, juveniles had a higher ascent rate throughout the study period. VeDBA (when soaring and foraging) was similar between adults and juveniles (Table 1).

#### 3.2 Changes over time in flight and foraging parameters and comparison between juveniles and adults

PTT tracks, where the departure in migration was recorded, showed that the changes in foraging range of juveniles prior to migration were similar to those of juveniles fitted with GPS/Acc (Figure S1). All flight and foraging parameters of juveniles changed over time (Table 1—Juveniles) (Table S6 for $r^2$ estimates).

During the same period of recording of juvenile behaviour, a number of adult flight and foraging parameters changed over time (Table 1—Adults) (Table S7 for $r^2$ estimates). Since these changes suggest the influence of seasonal or environmental conditions (wind, convection, etc.), we compared the changes over time between parameters of juveniles and adults by taking into account the changes in conditions observed in adults. We used adults as reference and tested differences between the two groups: negative slopes of the model indicate juvenile parameters being lower than those of adults (Table 1—Difference juveniles vs. adults) (Table S8 for $r^2$ estimates).

For six flight parameters, those of juveniles improved over time. Two parameters reach values similar to those of adults (Tables 1 and 2, e.g. Figure 2): travel speed (Figure 2) and the proportion of time spent at sea (Figure S5). At the same time, four parameters of juveniles increased to adult values but without reaching them: trip duration (Figure S2), maximum range (Figure S3), maximum altitude (Figure S4) and gliding efficiency between 50 and 700 m (Figure S5). However, gliding efficiency reached adult values if the last 5 days of the period, when a change in behaviour occurred (Figure S5), are excluded (slope of 3.09; $Z$ value = 32.8; $p$ value = .176).

Three flight parameters appear to be higher in juveniles than adult (Tables 1 and 2, e.g. Figure 3): ascent rate (Figure S7), soaring (Figure 3) and gliding proportion (Figure S9). Conversely, juveniles always flapped more frequently their wings than adults (Figure S8), mainly because they spent more time in foraging mode when at sea (1.56% foraging adult ±2.0%; 3.19% foraging juvenile ±5.1%; difference between juveniles and adults: $Z$ value = 3.215; $p$ value = .0013**). Ascent rates were higher in juveniles at the beginning and then reach adult’s value.

#### Table 1

<table>
<thead>
<tr>
<th>Flight parameters per trip</th>
<th>Juveniles</th>
<th>Adults</th>
<th>Difference juveniles vs. adults</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>Slope</td>
</tr>
<tr>
<td>Duration trip (hr)</td>
<td>3.627</td>
<td>4.854</td>
<td>0.244</td>
</tr>
<tr>
<td>Maximum range (km)</td>
<td>12.972</td>
<td>15.431</td>
<td>0.279</td>
</tr>
<tr>
<td>Maximum altitude (m)</td>
<td>606</td>
<td>513.558</td>
<td>0.040</td>
</tr>
<tr>
<td>Travel speed (km/hr)</td>
<td>17.892</td>
<td>11.893</td>
<td>0.119</td>
</tr>
<tr>
<td>Ascent rate (m/s)</td>
<td>0.437</td>
<td>0.495</td>
<td>0.200</td>
</tr>
<tr>
<td>Flapping frequency (flap/min)</td>
<td>71.378</td>
<td>48.221</td>
<td>4.967</td>
</tr>
<tr>
<td>Gliding efficiency between 50 and 700 m (m/s²)</td>
<td>16.718</td>
<td>17.204</td>
<td>-0.054</td>
</tr>
<tr>
<td>Proportion time spend at sea</td>
<td>0.506</td>
<td>0.303</td>
<td>0.087</td>
</tr>
<tr>
<td>VeDBA in foraging (m/s²)</td>
<td>4.689</td>
<td>2.215</td>
<td>-0.130</td>
</tr>
<tr>
<td>At sea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soaring proportion</td>
<td>0.336</td>
<td>0.116</td>
<td>-0.015</td>
</tr>
<tr>
<td>Gliding proportion</td>
<td>-0.017</td>
<td>0.149</td>
<td>-0.017</td>
</tr>
<tr>
<td>VeDBA in soaring (m/s²)</td>
<td>0.336</td>
<td>0.116</td>
<td>0.053</td>
</tr>
</tbody>
</table>

Note: Grey = juvenile parameters significantly higher than adults.
Finally (Tables 1 and 2, e.g. Figure 4), VeDBA during foraging (Figure 4) and during soaring (Figure S10) changed similarly over time between juveniles and adults with no statistically significant differences in average values.

### Table 2

<table>
<thead>
<tr>
<th>Flight parameter per trip</th>
<th>Difference juveniles versus adults (in general)</th>
<th>Difference juveniles versus adults (days 53–70)</th>
<th>Difference juveniles versus adults (days 71–119)</th>
<th>Difference juveniles versus adults (days 120–140)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Slope</td>
<td>Test value</td>
<td>Significant</td>
<td>Slope</td>
</tr>
<tr>
<td>Duration trip (hr)</td>
<td>-1.852</td>
<td>-8.766</td>
<td>&lt;0.001</td>
<td>-2.537</td>
</tr>
<tr>
<td>Maximum range (km)</td>
<td>-2.011</td>
<td>-7.616</td>
<td>&lt;0.001</td>
<td>-2.838</td>
</tr>
<tr>
<td>Maximum altitude (m)</td>
<td>-0.662</td>
<td>-3.710</td>
<td>&lt;0.001</td>
<td>-1.1485</td>
</tr>
<tr>
<td>Travel speed (km/hr)</td>
<td>-0.092</td>
<td>-1.995</td>
<td>0.051</td>
<td>-0.252</td>
</tr>
<tr>
<td>Ascent rate (m/s)</td>
<td>0.295</td>
<td>4.270</td>
<td>&lt;0.001</td>
<td>0.149</td>
</tr>
<tr>
<td>Flapping frequency (flap/min)</td>
<td>0.204</td>
<td>2.512</td>
<td>0.012</td>
<td>-0.134</td>
</tr>
<tr>
<td>Gliding efficiency between 50 and 700 m/m/s</td>
<td>-0.383</td>
<td>-6.160</td>
<td>&lt;0.001</td>
<td>-0.447</td>
</tr>
<tr>
<td>Proportion time spend at sea</td>
<td>-0.437</td>
<td>-5.157</td>
<td>&lt;0.001</td>
<td>-0.62</td>
</tr>
<tr>
<td>VeDBA in foraging (m/s²)</td>
<td>-0.088</td>
<td>-1.256</td>
<td>0.225</td>
<td>0.066</td>
</tr>
<tr>
<td>Soaring proportion</td>
<td>0.083</td>
<td>4.689</td>
<td>&lt;0.001</td>
<td>0.156</td>
</tr>
<tr>
<td>Gliding proportion</td>
<td>0.116</td>
<td>4.718</td>
<td>&lt;0.001</td>
<td>0.157</td>
</tr>
<tr>
<td>VeDBA in soaring (m/s²)</td>
<td>-0.076</td>
<td>-1.105</td>
<td>0.284</td>
<td>-0.023</td>
</tr>
</tbody>
</table>

Note: Grey = juvenile parameters significantly higher than adults.

3.3 | Morphology

Among juveniles and adults, females were heavier than males and have longer culmen and wings (Figure S11, Table S9). Body mass of female juvenile (n = 26) was lower than female adults (n = 34) (Mann–Whitney U test, W = 291, p < .05), with no detectable differences in culmen length (Mann–Whitney U test, W = 331.5, p = .101). Among males, there were no differences between juveniles (n = 14) and adults (n = 14) in body mass (Mann–Whitney U test, W = 102, p = .871) and culmen length (Mann–Whitney U test, W = 102, p = .871) (Figure S11A,B).

However, wings were longer in juveniles than adults for females (n_juv = 26; n_adt = 35) (Mann–Whitney U test, W = 615.5, p < .05), but not for males (n_juv = 14; n_adt = 9) (Mann–Whitney U test, W = 88.5, p = .114) (Figure S11C).

4 | DISCUSSION

This work showed how foraging and flight capacities of a juvenile seabird develop between the early flights and complete independence from the parents. This transition period occurring in frigatebirds and boobies is unique among seabirds and supposed to be necessary for birds to acquire complex flights and foraging skills of adults (Nelson, 1975). Only two studies examined this period on a small number of brown boobies (Yoda et al., 2004, 2007). However, the transition phase is much longer in frigatebirds, suggesting a longer learning period necessary to acquire the extreme flight tactics of this species using soaring flight extensively to stay continuously in flight for months (Weimerskirch et al., 2016). Similar work on the acquisition
Our results confirmed our first hypothesis that flight capacities of juvenile great frigatebirds improve over time. Indeed, most flight parameters improved during this learning period. Juveniles increased the proportion of time spent at sea, travel speed and foraging range during the transition phase. During the first 52 days of the learning period, they spent a significant part of their flight over the ground (58.51%). This period probably corresponds to the first stages of flight training. While they progressively spent more time at sea, VeDBA is similar to adults. Thus, juvenile frigatebirds take several months to acquire the travelling abilities of adults at sea. However, at the same time, when at sea, young frigatebirds spent more time in active foraging behaviour close to the surface compared with adults, probably for training in another complex behaviour of catching prey on the wing. This foraging behaviour may be even more complex to attain than flight, but poor foraging success is compensated by the food brought by parents.

While juvenile flight parameters show important change over time during the transition phase attributable to improvement in flight techniques, some adult flight parameters changed as well. These changes are probably due to seasonal changes in environmental factors. The flight of frigatebirds is heavily dependent on wind and convection, and the presence of cumulus (Weimerskirch et al., 2016). Variations in convection linked to the seasonal increase in temperatures affect flight capacities of sailing birds (Shepard & Lambertucci, 2013). The study period occurred during the summer when temperatures, convection and cloud cover increase, and this seasonal change probably explains the changes in some adult flight parameters. Since juveniles face the same changing seasonal constraints as adults, it is therefore important to compare the changes in adult and juvenile flight parameters over the same period assuming that adults and juveniles are equally impacted by environmental conditions.

Juveniles progressively spent more time at sea, and during trips at sea, some flight parameters did not change over time compared with adults: juveniles have already reached soaring and gliding capacities of adults and expended as much energy in soaring at sea and foraging than adults. These results differ from terrestrial soaring birds such as juvenile storks that expend more energy than adults during the entire migration that occurs just after independence (Rotics et al., 2016).

Although juveniles increased some foraging parameters, such as foraging range, altitude, duration and gliding efficiency, they do not attain those of adults except for gliding efficiency that reached values similar to those of adults when excluding the last 5 days of soaring flight was carried out during the first migration of juvenile white storks (Rotics et al., 2016).

Our results confirmed our first hypothesis that flight capacities of juvenile great frigatebirds improve over time. Indeed, most flight parameters improved during this learning period. Juveniles increased the proportion of time spent at sea, travel speed and foraging range during the transition phase. During the first 52 days of the learning period, they spent a significant part of their flight over the ground (58.51%). This period probably corresponds to the first stages of flight training. While they progressively spent more time at sea, VeDBA is similar to adults. Thus, juvenile frigatebirds take several months to acquire the travelling abilities of adults at sea. However, at the same time, when at sea, young frigatebirds spent more time in active foraging behaviour close to the surface compared with adults, probably for training in another complex behaviour of catching prey on the wing. This foraging behaviour may be even more complex to attain than flight, but poor foraging success is compensated by the food brought by parents.

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where behaviour appeared atypical. During the transition phase, juveniles return to the colony every evening to be eventually fed by their parents that return on the island at this time. These results were also found by Yoda et al. (2004) on brown boobies after a breeding in captivity. It is interesting to note that during this period, juvenile gliding efficiency improved compared with adults, especially for flights above 700 m (juvenile GLMM: slope of 0.063; Z value = 7.670; \(p < .001\)), that is these flights when birds have to enter into cumulus clouds to soar (Weimerskirch et al., 2016). This technique of flights into clouds is probably very complex to acquire (Sachs & Weimerskirch, 2018) and requires longer learning periods, and juveniles, by flying at lower altitudes than adults, probably rarely enter into cumulus clouds whose base is at 700 m of altitude. Conversely, juveniles have developed rapidly their soaring and gliding capacities and had similar energy expenditures than adults for each behaviour type. However, since juveniles spent more time foraging, a more expensive activity than travelling, they probably expend more energy per unit of time during the foraging trips of the training phase. In addition, it is possible that juvenile frigatebirds, similarly to condors, may use social information from congeners using thermals (Williams, King, Duriez, Börger, & Shepard, 2018), but this may occur only close to the colony where bird densities are high. At long distance from the colony, frigatebirds are foraging solitarily.

Some flight parameters appear to increase to reach values higher than those of adults. This is the case for the time spent actively foraging, that is attempting to catch prey close to the surface. This suggests that juveniles probably have to spend more time close to the surface to try to catch prey. In other seabirds, juveniles similarly spend more time foraging than adults (Breed et al., 2011; Daunt et al., 2007; Marchetti & Price, 1989; Riotte-Lambert & Weimerskirch, 2013). Frigatebirds spend most of their time at sea soaring and gliding, with little flapping, except during foraging phases close to the surface, when they are searching and catching prey, and have intensive phases of flapping flight (Weimerskirch et al., 2016).

One unexpected result of this study is that for some flight parameters, juveniles are more efficient than adults, either after a phase of improvement or immediately since the first flights at sea. Juvenile great frigatebirds have higher ascent rate for the first period of flight at sea and especially for the last 5 days when differences between adult and juvenile in ascent rates (Figure S7) and gliding efficiency (Figure S5) increase steeply. We have no explanation for this pattern that could be due to particular environmental conditions occurring at this time and affecting adults and juveniles differently. The overall higher ascent rates of juveniles are very surprising and in contrast with our initial hypothesis and results of other studies (Rotics et al., 2016; Yoda et al., 2004). They suggest that juveniles are more
efficient for some flight aspects than adults. Juveniles appear to outperform adults, in their first flights at sea, when climbing in thermals with their lower wing loading, but it takes more time to learn capacities to climb in cumulus clouds, probably because climbing inside cumulus is challenging (Sachs & Weimerskirch, 2018). As flight efficiency is linked to the morphology (Pennycuick, 1983), we compared morphology of adults and juveniles of great frigatebird from Europa Island. Juveniles are lighter than adults and at the same time have longer wings. Since soaring capacities depend on the wing loading and aspect ratio (Pennycuick, 1983), the lighter mass and longer wings confer to juveniles an advantage for soaring. A lower wing loading and higher aspect ratio in juveniles would allow them to use thermal soaring more efficiently (Weimerskirch et al., 2016) and, furthermore, may compensate their low ability of foraging. Juvenile great frigatebirds, contrary to adults, have extensive dispersal phases when they can stay aloft for months (Weimerskirch et al., 2016). Longer wings and thus lower wing loading could be an advantage for juveniles during their dispersion phase around the equator, where convection is very high.

Our study has shown that the unique long transition period observed in frigatebirds is a period when juvenile birds progressively improve flight parameters. Frigatebirds are among the longest lived birds, with the longest periods of immaturity after the juvenile phase (Weimerskirch, 2001), suggesting that improvement of foraging efficiency still occurs during the years following the first year at sea. The transition period may therefore be a period of learning for movement capacities, with unique morphological adaptations specific to juveniles, followed by a very long period of improvement of foraging skills. Whether these successive stages are specific to extreme birds such as frigatebirds or found in other species would be interesting to investigate in other bird species.

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AUTHORS’ CONTRIBUTIONS

H.W. conceived, A.P. did the field work and prepared the data, A.K. analysed the accelerometer data, A.C. performed all the other analyses, and A.C. and H.W. wrote the paper.

DATA AVAILABILITY STATEMENT

Data are available in Dryad Digital Repository: https://doi.org/10.5061/dryad.wpzgmsbgr (Corbeau, Prudor, Kato, & Weimerskirch, 2019).

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REFERENCES


SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.