INTRODUCTION

According to the optimal foraging theory, individuals implement feeding strategies aimed at maximizing energetic gains while minimizing costs (Stephens & Krebs 1986). Individual specialisations have been suggested to improve feeding efficiency by reducing intra-specific competition or allowing individuals to catch prey they can handle and digest most efficiently (Bolnick et al. 2003, Estes et al. 2003). Food consumption rates and body condition differ among diet specialists, and these differences may reflect differences in an individual's intrinsic quality (dit Durell et al. 2001, Bolnick et al. 2003, Anderson et al. 2009, Svanbäck & Persson 2009, Cucherousset et al. 2011). Specialisations in foraging, involving the repetition of specific behaviours to acquire food or dietary choices over time, have until recently been poorly investigated.
Individual specialists have been defined as ‘individuals whose niche is substantially narrower than their population’s niche for reasons not attributable to their sex, age or discrete morphological group’ (Bolnick et al. 2003, p. 3). Even populations usually thought to be generalists can actually be composed of individual specialists, referred to as Type ‘B’ generalists (individuals each specialising on a different but narrow range of food types) as opposed to Type ‘A’ generalists (individuals all taking a wide range of food types) (Araújo et al. 2011, Loxdale et al. 2011, Layman & Allgeier 2012, Fodrie et al. 2015).

Information on individual specialisations is crucial, as they may have significant ecological consequences at the individual and population levels, and may impact ecological processes and foraging dynamics (Bolnick et al. 2003, Matich et al. 2011, Ceia & Ramos 2015). Thus, it is of importance to identify the mechanisms generating inter-individual variation and study the wider implications of variation in foraging behaviour to understand trophic relationships between the animals and their environment (Bolnick et al. 2003, Baylis et al. 2015, Ceia & Ramos 2015, Kernaléguen et al. 2015). The study of individual specialisations requires longitudinal sampling, in which the same individuals are sampled over time (Bolnick et al. 2003, Araújo et al. 2011). Ideally, the use of complementary techniques that represent different time-scales and resolutions should be implemented to accurately describe individual specialisations and their persistence (Kernaléguen et al. 2016). Seabirds are suitable models to study individual specialisations, as most species nest in large colonies that allow for easy access to individuals that use the same environment, are strongly constrained during breeding as central place foragers and may compete for the same resources (Ratcliffe et al. 2013).

Gentoo penguins Pygoscelis papua are among the most widespread penguin species, distributed from the northern subantarctic islands (Crozet; 46°S) to the Antarctic Peninsula (62 to 69°S; Williams 1995). These birds are considered inshore opportunistic foragers, consuming both benthic and pelagic species, and exhibiting high plasticity in their diet, marine habitat use and dive behaviour (Bost & Jouventin 1990, Woehler 1995, Lescroël & Bost 2005, Miller et al. 2009). They consume patchy prey encompassing a large size range, from small crustaceans to large fish species (Hindell 1989, Robinson & Hindell 1996). Accordingly, their diets vary substantially among breeding locations, within colonies and also within individuals of the same colony (Croxall et al. 1988, Bost & Jouventin 1990, Robinson & Hindell 1996, Lescroël et al. 2004, Polito et al. 2015).

As gentoo penguins are long-lived and sedentary (Williams & Rodwell 1992), individuals are expected to learn to apply efficient foraging tactics throughout their lifetime and, thus, increase their individual efficiency when foraging under situations of competition or food limitation (Estes et al. 2003). Indeed, recent studies suggest that individuals exhibit some degree of prey selection and specialisation, as judged by stomach content analysis and stable isotope values (Polito et al. 2015). However, there is little information on individual consistency in foraging behaviour and on whether such specialisations are linked to diet in this species.

In the present study, we investigated inter- and intra-individual variation in the foraging ecology of gentoo penguins. We used complementary bio-logging and stable isotope analysis, coupled with morphometric measurements to: (1) describe their inter-individual variation in morphology, spatial use and dive behaviour; (2) quantify their intra-individual variation in foraging behaviour; (3) investigate the links between consistency in foraging behaviour, distances travelled and body condition; and (4) describe their inter-individual variation in feeding ecology, and determine if dietary specialisations exist and are maintained outside of the breeding season. We predicted that: (1) individuals would differ greatly in foraging metrics, as gentoo penguin diet and behaviour are known to vary among colonies and between individuals of the same colonies, and that such variation would be attributed to differences in body mass, which influences dive depth (Lescroël et al. 2004, Lescroël & Bost 2005, Cook et al. 2013, Polito et al. 2015, Camprasse et al. 2017); (2) dietary and behavioural consistency would be detected, as populations usually considered generalists are increasingly shown to be composed of individual specialists (Woo et al. 2008, Araújo et al. 2011, Loxdale et al. 2011, Layman & Allgeier 2012, Fodrie et al. 2015); and (3) individuals displaying higher consistency in foraging behaviour would travel shorter distances and have higher body condition, as such consistency is thought to allow individuals to forage more efficiently (Bolnick et al. 2003, Estes et al. 2003).

**MATERIALS AND METHODS**

**Study site and instrumentation**

The study was performed at Kerguelen Island in the southern Indian Ocean, one of the major breed-
ing grounds for gentoo penguins (hereafter referred to as gentoos) with 40,000 pairs (Lescroël et al. 2004, Lynch 2013). Gentoos breed along most of the Kerguelen coastline in many small to medium-sized colonies ranging from 15 to >400 pairs). As the diet and foraging behaviour of this species are known to vary substantially among colonies and within breeding locations, especially on Kerguelen Island (Lescroël et al. 2004, Lescroël & Bost 2005), 2 colonies were selected to ensure that the patterns observed were not solely dependent upon colony location. Accordingly, field work was conducted at the Pointe Suzanne and Estacade colonies (ca. 20 km apart, 49° 26' S, 70° 26' E and 49° 15' S, 70° 33' E, respectively, with ca. 50 and 25 chicks, respectively; Fig. 1). Both colonies face the open ocean. The Pointe Suzanne colony, however, faces a wider range of foraging habitats due to its proximity to a more sheltered bay (Baie Norvégienne). The Estacade colony is localized westward of the Polar Front, a productive frontal zone, on the eastward side of the Kerguelen shelf. Gentoos were in the late chick-rearing (i.e. crèche) stage at both study sites. Logistical constraints prevented sampling other colonies, as well as greater sample sizes, and so our results on site effects must be interpreted with caution.

We deployed data loggers on breeding gentoos during the late chick-rearing period (crèche stage: chicks >4−5 wk old), in the 2014/15 breeding season (Table 1). To determine the at-sea movements and diving behaviour of the penguins, we used Fastloc GPS loggers (F2G 134A; FastLoc®, Sirtrack; 69 × 28 × 21 mm, 39 g in air), alone or in combination with time-depth recorders (TDR, LAT1800S, Lotek Wireless; 36 × 11 × 7.2 mm, 4.8 g in air). GPS loggers were programmed to sample position every 5 min. The TDR units were set to record depth and temperature at 1 s intervals. All attached devices, alone or in combination, weighed <1% body mass.

At Pointe Suzanne, sampling occurred between 24 November and 9 December 2014. In total, 24 birds were instrumented for 4 to 16 d according to the possibilities of recapture. We used either 2 kinds of instruments (GPS+TDR: n = 18), or only 1 instrument (GPS: n = 4, TDR: n = 2). At Estacade, 9 birds were instrumented between 20 December 2014 and 4 January 2015 with GPS+TDR for 4 to 15 d.

All instrumented birds were confirmed breeders, with only birds that were observed feeding chicks being sampled. Individuals were weighed in a cloth bag using a suspension scale (±25 g, Pesola) before data loggers were attached to the dorsal feathers using waterproof tape (Tesa 4651) and cyanoacrylate glue (Loctite 401 Instant Adhesive). Individuals were then released and resumed normal behaviours. With the exception of 3 individuals from Estacade that were recaptured on the beach a few kilometres north or south of the colony, all birds were recaptured at the colony after several foraging trips. The data loggers were removed and individuals were weighed again. Measurements of bill length and depth were taken with Vernier callipers (±0.05 mm) and flipper length with a
metal ruler (±1 mm). In addition, a blood sample (0.5−1.5 ml) was obtained by venipuncture of a tarsal vein for stable isotope analysis and molecular sex determination. Feathers (n = 3–6) were plucked from the thorax region for stable isotope analysis. Handling times ranged from 15 to 20 min, during which the bird’s head was covered with a hood to reduce stress.

Of the 33 birds instrumented at the 2 study sites, 28 birds were recaptured, of which 4 did not go to sea to forage and 2 individuals had TDRs that malfunctioned. Overall, 22 individuals provided data which were analysed (Pointe Suzanne: n = 17, Estacade: n = 5). All 22 individuals conducted more than 1 trip, with 19 providing both TDR and GPS data.

### Isotopic analyses

The δ13C values of seabirds reflect their foraging habitats (Cherel & Hobson 2007, Jaeger et al. 2010), while their δ15N values increase with trophic level (Cherel et al. 2010). Isotopic values were measured on whole blood and feathers. The rationale is that the 2 complementary tissues integrate different periods of information, due to the fact that the keratin in feathers is inert after synthesis (details in Cherel et al. 2008). Blood is a metabolic active tissue that integrates a period of weeks before sampling, whereas feathers reflect the diet at the time they were grown, as feathers are metabolically inert after they are grown (Cherel et al. 2000). In the present study, blood isotopic values integrated a few weeks before sampling, thus corresponding to the breeding period (Bearhop et al. 2006). In contrast, gentoos moult once a year, at the end of the breeding period, after a period of 10 d at sea dedicated to replenishment of body reserves (Croxall & Davis 1999, Polito et al. 2011). They then fast ashore for about 3 wk, using their body reserves to cover the energetic and nutrient needs for moulting and fasting (Croxall & Davis 1999). Hence, the isotopic values of feathers document the foraging ecology of penguins during the pre-moult period of hyperphagia at sea during which they build up energy reserves (Cherel et al. 2008), here almost 1 yr before sampling the instrumented gentoos.

In the laboratory, blood samples were freeze-dried and powdered. Lipid extraction was unnecessary, as the C:N mass ratio was <3.5 for all blood samples (Cherel et al. 2005b); C:N mass ratios ± SD were 3.29 ± 0.06 (whole blood, n = 25) and 3.17 ± 0.05 (feathers, n = 27). A pool of 3 feathers bird−1 was cleaned of surface lipids and contaminants using a 2:1 chloroform:methanol bath, air-dried and cut into small pieces. For each feather, the rachis and the top 5 mm of the feather synthesised at sea were discarded before analysis so that the remaining feather sections were homogeneous and corresponded to the fasting period (Cherel et al. 2005a).

Nitrogen and carbon isotopic ratios were measured on aliquots of 0.2 to 0.4 mg with a continuous-flow isotope-ratio mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyser (Thermo Scientific Flash EA 1112). Results are

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presented in the usual δ notation relative to Vienna PeeDee Belemnite (VPDB) for carbon and atmospheric N₂ (AIR) for nitrogen. Replicate measurements of internal laboratory standards (acetanilide and peptone) indicated measurement errors <0.15‰ for both δ¹³C and δ¹⁵N. Blood and/or feather sampling was not possible on all individuals instrumented, resulting in the collection of either no samples, only feathers, only blood, or both samples for each individual. Stable isotope values were obtained from 25 individuals for blood (11 females, 14 males), and 27 individuals for feathers (11 females, 13 males, 3 unknown). Both tissues were sampled in 24 individuals (11 females, 13 males). Of these 24 individuals, 16 also had both GPS and TDR data, 1 had TDR data only, 3 had GPS data only, and 4 did not have any bio-logging data.

**Data processing**

All data analyses were conducted in the R Statistical Environment in version 3.3 (R Core Team 2015). The GPS records for each bird were visually inspected to identify individual foraging trips. As some birds hauled out in some locations distant from the colony for a few hours to several days, foraging trips were defined as the time between when an individual left a land-based position until it came back ashore. The diveMove package (Luque 2007) was used to apply a speed filter to the GPS data to remove erroneous locations (with a speed threshold of 1.5 m s⁻¹ based on the 95th percentile of swim speeds for all individuals). The GPS records were interpolated to 1 s intervals in the adehabitatLT package (Calenge 2015) to provide spatial information for the dive records. Furthermore, the packages trip (Sumner 2009) and sp (Pevesma & Bivand 2005) were used to obtain summaries of at-sea movements and investigate the consistency in habitat use. Individual tracks were overlaid with a grid comprised of 2 × 2 km cells, where the number of grid cells used were calculated for each trip. Means and coefficients of variation for each individual were calculated for trip duration, maximum range, and horizontal distance travelled per trip and per hour. Bearing for each trip was calculated as the angle between the colony and the most distal point of the tracks, and standard deviation in bearing was calculated for each individual using the circular package (Agostinelli & Lund 2011).

The diveMove package was used to obtain summaries of diving metrics from TDR records (only dives deeper than 2 m were considered to be foraging dives, following Lescroël & Bost 2005). The lubridate package (Grollemund & Wickham 2011) was used to identify night and day dives based on sunset and sunrise times at the relevant sites. Benthic and pelagic dives were determined based on the proportion of dive time that was spent in the bottom phase for each dive (phase detected by the ‘diveStats’ function after descent and before ascent), and the depth achieved on consecutive dives. If the dive depth stayed within 5% of the maximum depth for this dive for more than 15 s, and if the dive was within 5% of the maximum depth achieved during the last 15 min of diving, the dive was labelled as ‘flat-benthic’. If the dive was within 5% of the maximum depth achieved for ‘flat-benthic’ dives during the last 15 min of diving, but the other criterion was not met, the dive was labelled as ‘V-benthic’. If the dive met neither of these criteria, the dive was labelled as ‘pelagic’. The proportion of pelagic dives was then determined. Means and standard deviations per trip were calculated for bottom time and mean bottom depth of each dive, the total vertical distance travelled per trip and per hour, and the proportion of pelagic and night diving. Horizontal and vertical distances travelled were summed to provide an index of foraging energy expenditure per trip and per hour (Wilson et al. 1986).

An index of consistency in habitat use was calculated for each animal. For each trip, the number of grid cells used by the individuals was identified. The number of shared grid cells between each pair of trips (e.g. trip 1 and trip 2, trip 2 and trip 3, trip 1 and trip 3 etc.) was determined and the average of these calculated. This number was then divided by the average number of grid cells used per trip. Different grid cell sizes were tested to calculate the index of consistency in habitat use (from 1 × 1 km to 10 × 10 km) to check the influence of grid cell size on our estimate of spatial consistency. Indices obtained, regardless of cell grid sizes, were highly correlated, and data from the 2 × 2 km grid cell size are presented.

**Statistical analyses**

Body mass and morphometric measurements were correlated (linear regressions: beak depth: \( F \_1,18 = 14.62, R^2 = 0.42, p = 0.001 \); flipper length: \( F \_1,18 = 14.15, R^2 = 0.65, p = 0.001 \)) and therefore, only relationships with body mass were further investigated in models. A principal component analysis was run on flipper and bill length and bill depth with the FactoMineR package (Lê et al. 2008). Residuals from a linear regression of the first principal component against body
mass were then used as an index of body condition (Cuervo et al. 2009). The first principal component of the morphometric measurements explained 72.2% of the total variation and was therefore used as an estimate of structural size. There was no significant difference between the sexes in the slopes or elevations of the linear regressions of body mass on this estimate of structural size. Therefore, data were pooled to estimate individual body condition.

The following spatial metrics were highly correlated: trip duration and maximum range (linear mixed effects models: $F_{1,17} = 61.17$, $R^2 = 0.78$, $p < 0.001$); and maximum range and total distance travelled (linear mixed effects models: $F_{1,17} = 285.7$, $R^2 = 0.94$, $p < 0.001$). Consequently, only maximum range was used in linear mixed effects models. Similarly, the following diving metrics were highly correlated: bottom depth and total vertical distance travelled (linear mixed effects models: $F_{1,17} = 41.41$, $R^2 = 0.69$, $p < 0.001$); and dive time and bottom depth (linear mixed effects models: $F_{1,17} = 91.04$, $R^2 = 0.83$, $p < 0.001$). Thus, only bottom depth was included in further analyses.

Following a preliminary analysis to remove outliers, we used linear regressions, and linear mixed effects models in the package lme4 (Bates et al. 2014) where individuals had repeated samples, to investigate relationships between morphometric measurements, consistency in foraging strategies and stable isotope values. For all models, backward-stepwise model selection was used to select the most parsimonious model (Ratcliffe et al. 2013). First, the most appropriate random effects structure was identified with the restricted maximum likelihood (REML), then the best fixed effects structure was determined using maximum likelihood (ML) after models were compared with the ANOVA function, and the most parsimonious models were found based on their Akaike’s Information Criteria. For models in which 1 observation per trip was used (i.e. for spatial use metrics), individuals were included in the random effects. For models in which multiple observations per trip were used (i.e. for diving behaviour metrics), trip nested within individuals was included in the random effects. The selected models were refitted with REML to estimate the model parameters (Zuur et al. 2009). The residuals of the models were inspected, and whenever there was evidence of heterogeneity in the residuals, a sex- and/or site-specific variance structure was applied (Zuur et al. 2009).

More specifically, in order to describe the inter-individual variation in morphology and foraging behaviour, we investigated the effects of sex and stage on morphometric measurements, and the effects of sex, site and body mass on foraging metrics (interactions between fixed effects could not be investigated due to small sample sizes). A $k$-means clustering analysis was performed to determine whether individuals clustered according to their foraging behaviour. In order to quantify the intra-individual variation in diving behaviour and spatial use, we used the R package ape (Paradis et al. 2004) to perform a variance component analysis. This method calculates the variance, standard deviation and proportion of total variance occurring at the levels of individual, and trip within individual when multiple observations per trip were obtained, as well as the residual variation (Ratcliffe et al. 2013, Harris et al. 2014). An estimate of individual specialisation is given by the proportion of variance explained by the individual variance component (Bolnick et al. 2003, Dingemanse & Dochtermann 2013, Ratcliffe et al. 2013). When models including sex, site or body mass were better than the equivalent models without fixed effects (i.e. null models), the variance component analysis was run on both null and optimal models to quantify the reduction in variance explained by the individual, or the trip effects after the inclusion of the fixed effects (Ratcliffe et al. 2013). In order to investigate the links between consistency in foraging behaviour, vertical and horizontal distances travelled, and body condition, linear regressions were used. In order to quantify the inter-individual variation in trophic niche and foraging behaviour, and determine if dietary specialisations were maintained outside of a single breeding season, relationships between carbon and nitrogen values in blood and feathers, respectively, were investigated. Results presented are means ± SD, unless stated otherwise.

RESULTS

Inter-individual variation in morphometry and at-sea behaviour

Gentoo penguins varied considerably in their body condition, mass and morphometric measurements (Tables 1 & 2). Body condition indices were lower at Pointe Suzanne (linear regression: $F_{1,18} = 14.42$, $R^2 = 0.4$, $p = 0.001$) compared to Estacade but similar between sexes (linear regression: $F_{1,18} = 0.37$, $R^2 = −0.03$, $p = 0.5$). Lastly, females had smaller bill lengths than males (linear regression: $F_{1,18} = 32.68$, $R^2 = 0.63$, $p < 0.001$), as well as flipper lengths (linear regression: $F_{1,18} = 4.96$, $R^2 = 0.2$, $p = 0.04$).
Table 2. Summary of morphometric measurements for gentoo penguins
*Pygoscelis papua* instrumented and retrieved at Pointe Suzanne and Estacade
(Kerguelen Islands, Indian Ocean) during the crèche period in December 2014 to January 2015; F: female, M: male

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<tr>
<th>Measurement</th>
<th>Pointe Suzanne</th>
<th>Estacade</th>
<th>Minimum</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Body condition index</td>
<td></td>
<td></td>
<td>−0.1 ± 0.5</td>
<td>0.4</td>
</tr>
<tr>
<td>Body mass (kg)</td>
<td></td>
<td></td>
<td>1.3 ± 0.2</td>
<td>1.4</td>
</tr>
<tr>
<td>Bill depth (mm)</td>
<td></td>
<td></td>
<td>5.2 ± 0.8</td>
<td>6.8</td>
</tr>
<tr>
<td>Bill length (mm)</td>
<td></td>
<td></td>
<td>16.1 ± 1.5</td>
<td>18.4</td>
</tr>
<tr>
<td>Flipper length (mm)</td>
<td></td>
<td></td>
<td>85.5 ± 6.3</td>
<td>95.0</td>
</tr>
</tbody>
</table>

Table 3. Summary of spatial use metrics for gentoo penguins *Pygoscelis papua*
instrumented and retrieved at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) during the crèche period in December 2014 to January 2015 (values are means ± SD); F: female, M: male

<table>
<thead>
<tr>
<th>Bird Sex</th>
<th>Mean bearing (°)</th>
<th>Trip duration (h)</th>
<th>Maximum range (km)</th>
<th>Total horizontal distance (km)</th>
<th>Horizontal distance h⁻¹ (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pointe Suzanne</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4 F</td>
<td>98.8 ± 0.6</td>
<td>6.6 ± 5.1</td>
<td>3.3 ± 1.7</td>
<td>9.9 ± 5.8</td>
<td>1.8 ± 0.8</td>
</tr>
<tr>
<td>7 F</td>
<td>116.9 ± 0.3</td>
<td>26.4 ± 25.7</td>
<td>17.2 ± 10.8</td>
<td>54.3 ± 43.1</td>
<td>2.9 ± 1.2</td>
</tr>
<tr>
<td>9 F</td>
<td>55.5 ± 1.1</td>
<td>5.1 ± 3.1</td>
<td>4.0 ± 1.0</td>
<td>11.0 ± 6.0</td>
<td>2.3 ± 0.6</td>
</tr>
<tr>
<td>10 F</td>
<td>129.9 ± 0.2</td>
<td>7.9 ± 4.5</td>
<td>5.7 ± 2.1</td>
<td>17.5 ± 8.6</td>
<td>2.4 ± 0.5</td>
</tr>
<tr>
<td>13 F</td>
<td>11.5 ± 1.5</td>
<td>66.0 ± 61.7</td>
<td>39.4 ± 18.7</td>
<td>133.8 ± 98.7</td>
<td>2.3 ± 0.8</td>
</tr>
<tr>
<td>15 F</td>
<td>127.5 ± 0.2</td>
<td>11.5 ± 7.5</td>
<td>13.9 ± 3.4</td>
<td>35.0 ± 16.7</td>
<td>3.3 ± 0.6</td>
</tr>
<tr>
<td>20 F</td>
<td>127.0 ± 0.1</td>
<td>8.2 ± 8.3</td>
<td>10.0 ± 8.9</td>
<td>24.9 ± 25.3</td>
<td>3.0 ± 0.1</td>
</tr>
<tr>
<td>22 F</td>
<td>90.4 ± 0.4</td>
<td>33.8 ± 35.4</td>
<td>17.4 ± 15.4</td>
<td>72.4 ± 70.2</td>
<td>2.2 ± 0.4</td>
</tr>
<tr>
<td>24 F</td>
<td>162.2 ± 0.0</td>
<td>14.6 ± 7.4</td>
<td>9.9 ± 1.5</td>
<td>23.9 ± 8.6</td>
<td>2.3 ± 0.8</td>
</tr>
<tr>
<td>1 M</td>
<td>106.0 ± 0.4</td>
<td>4.8 ± 3.8</td>
<td>4.7 ± 2.8</td>
<td>10.9 ± 6.2</td>
<td>2.6 ± 1.0</td>
</tr>
<tr>
<td>2 M</td>
<td>66.3 ± 0.5</td>
<td>8.5 ± 5.7</td>
<td>7.7 ± 4.6</td>
<td>22.4 ± 15.1</td>
<td>2.9 ± 0.6</td>
</tr>
<tr>
<td>3 M</td>
<td>56.3 ± 0.8</td>
<td>77.6 ± 43.7</td>
<td>78.3 ± 62.8</td>
<td>217.4 ± 187.3</td>
<td>2.5 ± 1.0</td>
</tr>
<tr>
<td>5 M</td>
<td>125.2 ± 0.1</td>
<td>20.2 ± 16.5</td>
<td>25.4 ± 10.8</td>
<td>67.1 ± 41.3</td>
<td>3.7 ± 0.7</td>
</tr>
<tr>
<td>11 M</td>
<td>56.4 ± 0.5</td>
<td>56.0 ± 75.2</td>
<td>59.4 ± 70.2</td>
<td>164.4 ± 211.0</td>
<td>3.2 ± 0.4</td>
</tr>
<tr>
<td>12 M</td>
<td>107.0 ± 0.1</td>
<td>70.0 ± 38.6</td>
<td>32.3 ± 3.8</td>
<td>140.5 ± 60.9</td>
<td>2.1 ± 0.3</td>
</tr>
<tr>
<td>14 M</td>
<td>91.2 ± 0.1</td>
<td>18.8 ± 10.7</td>
<td>21.9 ± 10.2</td>
<td>53.2 ± 28.2</td>
<td>2.9 ± 0.3</td>
</tr>
<tr>
<td>17 M</td>
<td>114.4 ± 0.1</td>
<td>19.8 ± 17.1</td>
<td>17.6 ± 12.2</td>
<td>49.5 ± 38.8</td>
<td>2.5 ± 0.4</td>
</tr>
<tr>
<td>Estacade</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>27 F</td>
<td>127.9 ± 0.2</td>
<td>11.1 ± 12.8</td>
<td>9.5 ± 6.3</td>
<td>23.3 ± 16.8</td>
<td>3.1 ± 1.4</td>
</tr>
<tr>
<td>25 M</td>
<td>79.7 ± 0.2</td>
<td>44.8 ± 5.3</td>
<td>28.7 ± 2.4</td>
<td>89.4 ± 2.4</td>
<td>2.0 ± 0.3</td>
</tr>
<tr>
<td>30 M</td>
<td>77.3 ± 0.3</td>
<td>17.9 ± 1.0</td>
<td>16.9 ± 2.1</td>
<td>48.9 ± 3.4</td>
<td>2.7 ± 0.2</td>
</tr>
<tr>
<td>26 –</td>
<td>137.2 ± 0.1</td>
<td>12.9 ± 7.7</td>
<td>15.4 ± 12.3</td>
<td>35.1 ± 29.0</td>
<td>2.5 ± 0.8</td>
</tr>
<tr>
<td>28 –</td>
<td>86.3 ± 0.8</td>
<td>42.9 ± 61.0</td>
<td>36.9 ± 42.9</td>
<td>120.7 ± 164.5</td>
<td>3.5 ± 1.0</td>
</tr>
</tbody>
</table>
while others dived for much longer and deeper, and travelled much greater vertical distances (Table 5). On average, individuals spent 70.9 ± 20.1 (29.5−106.8) s at the bottom of dives, dived to bottom depths of 26.0 ± 14.7 (5.1−61.6) m, and travelled total vertical distances of 26.6 ± 23.2 (2.1−74.5) km, and hourly vertical distances of 0.8 ± 0.2 (0.4−1.1) km. Accordingly, the distance travelled (both horizontal and vertical) varied between individuals (mean distance per trip: 96.6 ± 81.0 [13.3−279.6] km; mean distance per hour of foraging: 3.5 ± 0.6 [2.3−4.8] km).

Sex and site did not significantly influence dive depth (Table 4). Some individuals performed almost entirely pelagic dives while, for others, benthic dives represented up to 48% of all dives (Table 5). Furthermore, individuals varied in their diving schedule, with some individuals diving half of their time at night, and other individuals diving mostly during the day (Table 5, Fig. 2). Daylight dives were on average 30.3 ± 37.5 m deep and 68.5 ± 53.2 s long (n = 24 336, 75% of dives recorded) while night dives were on average 9.2 ± 10.2 m deep and 52.3 ± 39.9 s long (n = 8298, 25% of dives recorded). Several individuals dived at night during multiple-day trips while other birds performed short trips (ca. 10 km from the colony) and dived predominantly at night. The frequency of night diving increased with the proportion of pelagic diving, which averaged 76.8% during the day and 92.9% at night (Fig. 2).

Table 4. Model ANOVA testing the effect of gentoo penguin *Pygoscelis papua* sex and site on maximum range, bottom depth and repeatability, including bird as a random factor or trip nested within bird (likelihood ratio [LR] for linear mixed effects models and *F* values for simple linear regressions). The last row reports on the linear mixed effects model testing the effect of dive depth on the proportion of pelagic dives. Values in **bold** are significant.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Type of model</th>
<th>Parameters</th>
<th>LR/ <em>F</em> test</th>
<th>df</th>
<th><em>p</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum range</td>
<td>Linear mixed effects</td>
<td><strong>Random effect: bird</strong></td>
<td>33.21</td>
<td>6</td>
<td><strong>&lt;0.0001</strong></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fixed effects</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sex</td>
<td>3.21</td>
<td>8</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Site</td>
<td>0</td>
<td>8</td>
<td>0.98</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Body mass</td>
<td>3.15</td>
<td>8</td>
<td>0.08</td>
</tr>
<tr>
<td>Bottom depth</td>
<td>Linear mixed effects</td>
<td><strong>Random effect: bird/trip</strong></td>
<td>1236.29</td>
<td>9</td>
<td><strong>&lt;0.0001</strong></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fixed effects</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sex</td>
<td>3.2</td>
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<td>0.07</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Site</td>
<td>0.46</td>
<td>8</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Body mass</td>
<td>7.29</td>
<td>8</td>
<td>0.01</td>
</tr>
<tr>
<td>Repeatability indices</td>
<td>Linear model</td>
<td><strong>Fixed effects</strong></td>
<td>84.83</td>
<td>4</td>
<td><strong>&lt;0.0001</strong></td>
</tr>
<tr>
<td>Proportion of pelagic dives</td>
<td>Linear mixed effects</td>
<td>Dive depth</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 5. Summary of dive metrics and distances travelled for gentoo penguins *Pygoscelis papua* instrumented and retrieved at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) during the crèche period in December 2014 to January 2015 (values are means ± SD); F: female, M: male, -: unsexed.
The large differences in standard deviations between individuals indicate a substantial degree of intra-individual variation both in spatial use and dive metrics (Tables 3–5, respectively). At the population level, the variance component analysis showed low to moderate individual specialisations both in dive behaviour and spatial use (Table 6). The indices of consistency in habitat use were not influenced by sex or site (Table 4, mean 0.37 ± 0.20, range: 0.05–0.73, Fig. 3). Some penguins were very consistent in the proportion of pelagic or benthic dives they performed (e.g. individual 14 stayed within 10% of its own values) while others varied greatly (e.g. individual 28 ranged from 47 to 98% of pelagic dives between trips; Fig. 4). The total (horizontal + vertical) distance travelled per hour was not correlated with repeatability indices (linear regression: \( F_{1,17} = 0.97, R^2 = -0.002, p = 0.34 \)). Lastly, body condition did not vary with consistency in habitat use (linear regression: \( F_{1,12} = 0.16, R^2 = -0.07, p = 0.70 \)).
Tissue isotope values varied widely among individuals, with δ\(^{13}\)C and δ\(^{15}\)N ranges of 4.0 and 5.8‰ in blood and 4.2 and 4.4‰ in feathers, respectively (Table 7). Values for δ\(^{13}\)C and δ\(^{15}\)N co-varied positively in both tissues (linear regression: \(F_{1,23} = 31.94, R^2 = -0.56, p < 0.001\) and \(F_{1,22} = 38.72, R^2 = -0.62, p < 0.001\) in blood and feathers, respectively; Fig. 5).

There was no significant difference between the sexes in their δ\(^{13}\)C values, but males had higher δ\(^{15}\)N values in blood and feathers (linear mixed effects models: \(t_{23} = 3.4, p = 0.002\) and \(t_{23} = 0.9, p = 0.4\), for nitrogen and carbon, respectively). Site did not influence δ\(^{15}\)N and δ\(^{13}\)C values (\(t_{23} = -0.6, p = 0.5\), and \(t_{23} = -0.5, p = 0.6\), respectively). Isotopic values in blood and feathers were positively and linearly correlated. Excluding an outlier (that was depicted by a preliminary statistical analysis) increased the strength of the relationships.

Table 6. Variance component analysis of dive depths, total distances travelled and bearings to most distal point for gentoo penguins \textit{Pygoscelis papua} instrumented at Pointe Suzanne and Estacade during the crèche period in December 2014 to January 2015. \(\sigma^2\)% is an estimate of individual specialisation (see ‘Materials and methods’ for details).

<table>
<thead>
<tr>
<th>Variance component</th>
<th>(\sigma^2)</th>
<th>(\Sigma)</th>
<th>(\sigma^2)%</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Maximum range</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>127.6</td>
<td>11.3</td>
<td>13.7</td>
</tr>
<tr>
<td>Residual</td>
<td>802.6</td>
<td>28.3</td>
<td>86.3</td>
</tr>
<tr>
<td><strong>Bearings to most distal point</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>1572.7</td>
<td>39.7</td>
<td>52.9</td>
</tr>
<tr>
<td>Residual</td>
<td>1397.6</td>
<td>37.4</td>
<td>47.1</td>
</tr>
<tr>
<td><strong>Mean bottom depth (null model)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>244.2</td>
<td>15.6</td>
<td>6.2</td>
</tr>
<tr>
<td>Trip</td>
<td>62.6</td>
<td>7.9</td>
<td>1.6</td>
</tr>
<tr>
<td>Residual</td>
<td>3612.8</td>
<td>60.1</td>
<td>92.2</td>
</tr>
<tr>
<td><strong>Mean bottom depth (model with mass)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>150.9</td>
<td>12.3</td>
<td>4.0</td>
</tr>
<tr>
<td>Trip</td>
<td>62.6</td>
<td>7.9</td>
<td>1.6</td>
</tr>
<tr>
<td>Residual</td>
<td>3612.4</td>
<td>60.1</td>
<td>94.4</td>
</tr>
<tr>
<td><strong>Proportion of pelagic diving (null model)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>166.4</td>
<td>12.9</td>
<td>76.7</td>
</tr>
<tr>
<td>Residual</td>
<td>80.1</td>
<td>9.0</td>
<td>32.5</td>
</tr>
<tr>
<td><strong>Proportion of pelagic diving (model with mass)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Individual</td>
<td>33.5</td>
<td>5.8</td>
<td>153.5</td>
</tr>
<tr>
<td>Residual</td>
<td>31.9</td>
<td>5.6</td>
<td>48.7</td>
</tr>
</tbody>
</table>

Table 7. Summary of stable isotope values for gentoo penguins \textit{Pygoscelis papua} sampled at Pointe Suzanne and Estacade (Kerguelen Islands, Indian Ocean) in December 2014 to January 2015; F: female, M: male, –: unsexed, NA: missing data.
Camprasse et al.: Variation in gentoo penguin foraging ecology

that explained 67 and 70% of the inter-individual $\delta^{13}$C and $\delta^{15}$N variations, respectively (Fig. 6).

There was no relationship between maximum distances reached and blood $\delta^{15}$N or $\delta^{13}$C values (linear mixed effects model: $t_{18} = 0.1$, $p = 0.9$, and $t_{18} = -1.1$, $p = 0.3$). This was also the case for stable isotope values and bearings to the most distal point (linear mixed effects model: $t_{18} = -0.2$, $p = 0.9$, and $t_{18} = 0.1$, $p = 0.9$, respectively). Lastly, $\delta^{15}$N or $\delta^{13}$C values were not influenced by repeatability in spatial use (linear mixed effects model: $t_{10} = 1.0$, $p = 0.3$, and $t_{10} = 1.0$, $p = 0.3$, respectively) or body condition (linear mixed effects model: $t_{11} = 1.9$, $p = 0.1$, and $t_{11} = 1.8$, $p = 0.1$, respectively).

**DISCUSSION**

The salient findings of this study concerning an opportunistic coastal forager, the gentoo penguin, can be summarized as follows. (1) Individuals exhibited very large inter- and intra-individual variation in spatial use and diving behaviour. Heavy individuals tended to dive deeper, perform more benthic dives and travel farther. (2) Despite the large intra-individual variation in foraging, some consistency in bearing, proportion of pelagic and night diving, maximum ranges and dive depths was observed in approximately a third of individuals. Foraging behaviour and behavioural consistency were not influ-
enced by sex and site. (3) There were large inter-
individual variations in stable isotope values, and
dietary specialisations were present and maintained
outside of the single breeding season sampled.

As inshore foragers, gentoos are known to strongly
differ in their foraging behaviour according to the
local environment (Lescroël & Bost 2005). Our first
prediction was that instrumented individuals would
differ greatly in foraging metrics among colonies and
among individuals of the same colony. In the present
study, site did not seem to influence foraging metrics.
However, within a single colony, birds exhibited a
large inter-individual variation in foraging behaviour,
with some birds conducting very short trips
within 5 to 10 km of the colony while others travelled
to areas 120 to 140 km away. The more pelagic indi-
viduals performed up to half of their dives at night
during short trips, while more benthic foragers dived
predominantly during the day and reached greater
depths, regardless of colony. This is consistent with
other studies reporting that this species has high
behavioural flexibility over its wide range (Wilson et
Kokubun et al. 2010). Such flexible foraging habits
likely provide a buffer against changes in prey avail-
ability and distribution in a limited, coastal environ-
ment (Lescroël & Bost 2005, Miller et al. 2009), as
shown in other inshore foragers (Hoskins et al. 2008,

In the present study, some of the individuals per-
formed trips longer (up to 5.6 d) than previously
reported during the crèche period in gentoos on Ker-
guelen Island (on average 1.3 d in Estacade, Lescroël
et al. 2009). It is possible that some of these birds
abandoned breeding during the study, as continued
provisioning status could not be determined upon
recapture for all birds. However, a third of birds
known to still be provisioning chicks at the end of the
study conducted such long trips. The large inter-
individual variation in foraging behaviour observed
in instrumented birds could be related to inter-indi-
vidual variation in morphology (Bost & Jouventin
1990, this study). Indeed, individuals with higher
body mass tended to travel farther, dive deeper and
perform more benthic dives, contributing to the ob-
served inter-individual differences in foraging. Dif-
fences in dive patterns, associated with larger oxy-
gen stores in heavier birds, have been reported in
other diving birds (Mori 1998, Cook et al. 2013).

We predicted that behavioural consistency would
be detected in instrumented individuals, as numer-
ous populations considered generalists have actually
be shown to be comprised of individual specialists
(Woo et al. 2008, Araújo et al. 2011, Loxdale et al.
2011, Layman & Allgeier 2012, Fodrie et al. 2015). In
the present study, at the population level, individual
specialisations in foraging metrics were low to mod-
erate, with bearings to most distal locations and the
proportion of pelagic diving exhibiting the highest
repeatability. This suggests that gentoos stay consist-
tent in some aspects of their foraging behaviour,
which may help to reduce intra-specific competition
and/or may allow individuals to catch prey they can
easily handle and digest (Bolnick et al. 2003, Estes et
al. 2003). This seems particularly relevant in inshore
foragers, as they are restricted in their foraging range
(Cook et al. 2006, Ratcliffe et al. 2013, Harris et al.
2014).

However, a significant degree of behavioural consis-
tency at the population level does not mean that all
individuals are consistent (Woo et al. 2008, Ceia et al.
2012). Indeed, we observed a large variation in the
degree of individual consistency in spatial use and
dive behaviour between instrumented individuals.
While some birds exhibited similar foraging strate-
gies over the course of multiple consecutive trips,
others did not. For example, some individuals dis-
played consistency in the proportion of pelagic diving
from one trip to the next while others were able to
switch from being mostly benthic on one trip to being
toos having stable or expanding populations in parts
of their range (e.g. Antarctic Peninsula), where symp-
atriically breeding penguin species, more depend-
ent on specific resources such as Antarctic krill,
experience strong population declines (Miller et al.
2009, Polito et al. 2015).

Our third prediction was that individuals displaying
higher consistency in foraging behaviour would have
reduced horizontal and vertical distances travelled,
and higher body conditions as individual specialisa-
tions are thought to improve foraging efficiency (Wa-
tanuki 1992, Voslamber et al. 1995, Annett & Pierotti
1999, Golet et al. 2000, Votier et al. 2004). Contrary to
this prediction, no difference in distance travelled
(per hour) or body condition was found between con-
sistent and non-consistent individuals in the present
study. Thus, it seems that instrumented individuals
adopted different strategies based on intrinsic factors
(i.e. morphology, prey preferences, etc.), ultimately
resulting in different repeatability indices. Indeed, the heavier, more benthic individuals performed more distant and longer trips, and such trips were less repeatable within the timeframe of the study.

Generally, it is unclear whether specialists perform better than generalists, as contradictory results have been reported in the literature (Golet et al. 2000, Votier et al. 2004, Ceia et al. 2012, Dehnhard et al. 2016). Our findings are in agreement with results on a long-distance forager, the wandering albatross Diomedea exulans, demonstrating that specialist and generalist individuals had similar levels of body condition (Ceia et al. 2012). No effect of specialisation on reproductive outcomes has been detected in other bird species (Votier et al. 2004, Katsner et al. 2005, Dehnhard et al. 2016). Indeed, even though generalists may deliver somewhat less energy per day, specialisation may not have an impact on measures of evolutionary fitness (Woo et al. 2008). In contrast, other studies on gulls, cormorants, guillemots and skuas have shown specialists to have higher reproductive success, food delivery rates, chick condition or adult survival (Watanuki 1992, Voslamber et al. 1995, Annett & Pierotti 1999, Golet et al. 2000, Votier et al. 2004). In gentoos, individual specialisations in foraging behaviour may be linked with intrinsic factors, and may be more or less advantageous depending on prey availability, with generalists performing better when food availability is low.

Lastly, in agreement with our second prediction, long-term dietary consistency was detected in the birds sampled. Stable isotope values in blood and feathers in breeding gentoos were positively correlated, indicating that dietary specialisations are maintained outside of the breeding season. This is consistent with recent stomach contents and stable isotope analysis studies on the diet of gentoos, indicating that they may not be as opportunistic as previously thought (Clausen et al. 2005, Polito et al. 2015). Within generalist populations, 2 types can be found: type ‘A’ generalists, when individuals all take a wide range of food types; and type ‘B’ generalists, when individuals each specialise on a different range of food types (Bearhop et al. 2004). The results from our study, documenting a large inter-individual variation in diet, matching the high inter-individual variation in foraging behaviour, and documenting the fact that instrumented birds tend to display a similar feeding ecology in the breeding and inter-breeding seasons, seem to indicate that gentoos at the studied site are type ‘B’ generalists.

The results of the present study should be interpreted with caution for two main reasons: the large difference in sample sizes between colonies where deployments were performed, and the potentially poor environmental conditions the instrumented birds experienced, seemingly leading to low prey availability as judged by the low number of chicks raised by gentoos and sympatrically breeding shags (E. C. M. Camprasse pers. obs.). More data are needed from Estacade to confirm the lack of a site effect on the gentoos’ foraging behaviour and feeding ecology. Factors including a high incidence of night diving and long trip durations could reflect poor environmental conditions in the 2014/2015 breeding season, forcing penguins to forage in sub-optimal conditions. This is consistent with poor breeding success on Kerguelen Islands during deployments compared with normal years, with brooders losing chicks at the crèche stage (E. C. M. Camprasse pers. obs.). In the present study, shallow nighttime dives were observed in the more pelagic individuals, probably to allow them to take advantage of pelagic prey distributed near the surface at night during their diurnal vertical migration. Night/twilight diving has been recorded in pygoscelid penguins including gentoos (Croxall et al. 1988, Williams & Rodwell 1992, Robinson & Hindell 1996) and other penguin species (Schiavini & Rey 2004, Rey et al. 2012), but was thought to be uncommon in such visual predators (Williams 1995, Bost et al. 2002). Lastly, low prey availability, linked with the seemingly poor environmental conditions experienced by the birds instrumented in the present study, could increase the degree of individual specialisation, as individuals are forced to add different alternative prey not consumed by conspecifics to their diet (Svanbäck & Bolnick 2007, Tinker et al. 2008).

In summary, we showed that gentoo penguins on Kerguelen Island exhibited large inter- and intra-individual variations in foraging behaviour. These may provide gentoos greater resilience to buffer against changes in prey availability and fast changing environmental conditions, especially as their foraging range is usually limited (Lescroël & Bost 2005, Polito et al. 2015). However, within this context, gentoos still exhibit individual specialisation, helping them reduce intra-specific competition and/or increasing their foraging efficiency (dit Durell 2000, Masello et al. 2013). Dietary specialisations outside of a single breeding season were also highlighted, suggesting that gentoo penguins are type ‘B’ generalists. The next step to understand the consequences of individual specialisations would be to look at the link between behavioural consistency and reproductive output, which could not be done in this study due to
logistical constraints. In order to fully understand the effects of individual consistency of parents on their offspring, researchers should also aim at obtaining information on both partners of breeding pairs (Polito et al. 2015). In the future, repetitive sampling of the same individuals across stages of the same breeding season and across years will help to characterize the persistence of dietary specializations at different temporal scales in seabirds.

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