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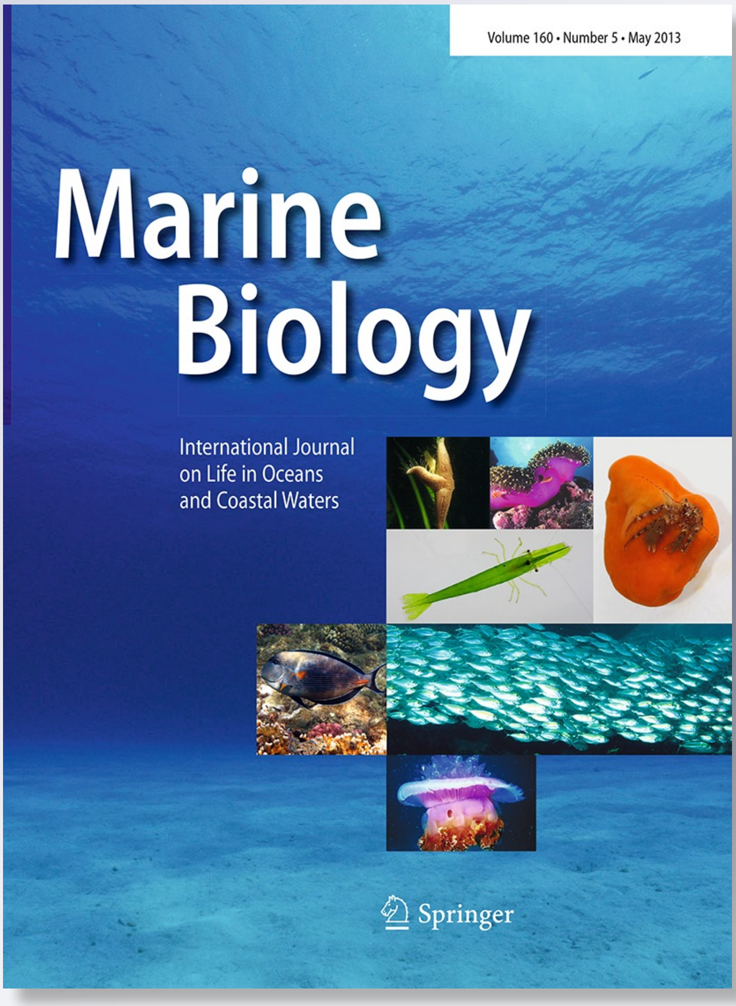

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ORIGINAL PAPER

How age and sex drive the foraging behaviour in the king penguin

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Abstract As predicted by life history theory, once recruited into the breeding population and with increasing age, long-lived animals should be able to manage more efficiently the conflict between self-maintenance and reproduction. Consequently, breeding performances should improve with age before stabilizing at a certain level. Using temperature–depth recorders and isotopic analysis, we tested how age affects the foraging behaviour of king penguin *Aptenodytes patagonicus* during one trip in the chick-rearing phase. Depending on sex and age, king penguins expressed two different foraging strategies. Older birds gained more daily mass per unit body mass than younger ones. Older females conducted shorter trips, dived deeper and performed more prey pursuits. They also had higher blood levels of $\delta^{15}N$ than younger individuals and males indicating sex- and age-specific dietary regimes. However, we found no differences in carbon isotopic signature, suggesting that individuals exploited the same foraging areas independently of sex and age. Our results suggest that king penguins are able to increase the quantity of energy extracted with increasing age and that such a strategy is sex-related. Our study is the first to reveal of an interaction between age and sex in determining foraging efficiency in king penguins.

Introduction

Intrinsic factors, such as age or sex (Daunt et al. 2007; Weimerskirch et al. 1997; Welcker et al. 2009; Pinet et al. 2012), are known to affect an individual's ability to forage, and the subsequent energy allocation to different functions (e.g. reproduction and self-maintenance). For example, sex influences foraging behaviour in species where sex-specific strategies result from sexual dimorphism that causes differences in hunting abilities (Kato et al. 2000), but also in monomorphic species where density-dependent responses may shape foraging strategies to decrease intra-specific competition (Lewis et al. 2005). With age, the individual improves its knowledge of the environment (Pärt 2001), can expand the range of dietary items available (Rütz et al.

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2006) and diversify its panel of hunting tactics (Daunt et al. 2007). So far, most studies examined improvements in foraging abilities from the juveniles to the mature stages of life (Lack 1954; Marchetti and Price 1989), but very few have compared the foraging strategies of first year breeding adults and older ones (but see Brandt 1984).

Seabirds, in which a clear dichotomy between on-land breeding and at-sea foraging is observed, are useful models to examine how age affects foraging behaviour. Seabirds are generally long-lived, abundant and accessible to scientists when on land. The age-related improvement in foraging efficiency becomes even more critical when birds exploit highly stochastic environments because individuals have to adjust their behaviour to the unpredictability of the resources available. Here, we can expect older individuals to be able to better use their environment than younger ones through an enhanced ability in finding prey patch and exploiting them. Among long-lived central-place foraging seabirds, king penguins *Aptenodytes patagonicus* are confronted with harsh conditions during their breeding cycle that extends over a year (Barrat 1976). They often cover large distances to find prey, exploiting oceanic zones as far as 500 km away from their breeding colony during the austral summer (Bost et al. 1997), and can dive as deep as ~340 m, remaining submerged for several minutes (Pütz and Cherel 2005). Thus, the optimisation of the trade-off between energy gain (prey capture) and expenditure/effort (linked to their travel until foraging areas and diving constraints) should be more apparent for this species, especially during the breeding season when the need to come periodically ashore to feed the young adds other constrains to the birds' overall activity.

Using temperature–depth recorders (TDR) and isotope analysis, we investigated the foraging behaviour of both male and female chick-rearing king penguins of known age at Crozet Archipelago, Indian Ocean. We predicted that old birds extract a greater quantity of energy from the environment than young ones. In addition, we also expect males, being larger, to be able to dive deeper and for longer, and perform longer foraging trip than females allowing them to have access to a larger volume of water, hence increasing their probability to encounter prey.

Materials and methods

Study area and individuals

The study was carried out at the king penguin colony of '*La Grande Manchotière*', on Possession Island, Crozet Archipelago (46°25′S, 51°45′E). Following the hatching of their single egg, members of a pair alternate feeding trips at sea and chick rearing on land. During the chick-rearing phase of the 2009–2010 breeding season, a total of 21 known-aged king penguins were equipped with data loggers to monitor their foraging activities at sea. Each of the 21 individuals belonged to different breeding pairs.

Since 1998, a subset of birds from '*La Grande Manchotière*' (100–450 individuals) is implanted each year with subcutaneous passive transponder tags (see Descamps et al. 2002) when they are 10-month-old, that is, just before fledging. No adverse effects of subcutaneous PIT tags (3.85 × 32 mm; 0.8 g) have been observed. They were shown not to affect survival of king penguins (Froget et al. 1998) and Adélie penguins *Pygoscelis adeliae* (Clarke and Kerry 1998). Blood samples are collected from all PIT-tagged birds for subsequent sex determination (methods adapted from Griffiths et al. 1998). According to Weimerskirch et al. (1992), the mean age at first breeding in king penguins is 6 years, ranging from 4 to 7 years, and almost 90 % of birds are breeding at the age of 8 years. Based on these observations, we equipped breeding birds from two age classes: 5-year-old (5 females and 4 males) and 9-year-old birds (7 females and 5 males).

These birds were captured outside of the colony when they departed for and return from a trip to sea. To evaluate the bird's isotopic signature, 1 ml of blood was collected from wing vein into a heparinised syringe after their foraging trip. Blood samples were centrifuged at 6,000 RPM for 5 min to separate red blood cells from plasma and stored at −20 °C. Before the logger deployment, penguins were weighed and measured (flipper and beak lengths) to calculate structural size (SSI) and body condition (BC) indices (Schulte-Hostedde et al. 2005). We used a principal component analysis to established SSI as follows: $SSI = PC1 = 0.25 * \text{Beak length} + 0.75 * \text{Flipper length}$. The first principal component (PC1) between these two parameters explained 71 % of the variation. BC was then defined as the residuals of a regression of body mass on SSI (see values in the Supplementary material). All equipped birds were recaptured after one foraging trip and all data loggers were retrieved. To evaluate the birds' mass gain (kg) during the foraging trip, as well as their mass gained per day ($g\ d^{-1}$) and their mass gained per day per unit mass (relationship between g per day and weight before the trip), they were weighed again upon their return before they entered the colony, except for four birds which came back during the night (these birds were subsequently excluded from the analysis). All individuals bred normally after the experiment. To control for the effect of the equipment on trip duration, we also selected 24 unequipped birds from the database, which were equitably chosen from sex and age groups (5- and 9-year-olds), and that conducted their brooding foraging trips at the same period as the equipped ones. No difference was observed between the equipped and control birds according to age and sex (Wilcoxon rank sum tests;

$W = 758.5$, $p = 0.836$, and $W = 786$, $p = 0.900$, for 9-year-old birds, and $W = 723$, $p = 0.858$, and $W = 796.5$, $p = 0.875$, for 5-year-old birds, and for males and females, respectively; Table 1).

Data loggers

Data loggers (Mk9, Wildlife Computers, US) measured 85 × 17 × 17 mm and weighed <30 g, on average 0.25 % of a king penguin's body mass and 0.35 % of the body mass of the lightest king penguin. The cross-sectional area of the logger represented ≤1 % of the cross-section of the birds (Bannasch et al. 1994). The loggers had a flash memory of 64 Mbit, into which data were stored at 12-bit resolution. Devices were attached to the feathers on the centre of the lower back of the individuals to minimize drag effect (Bannasch et al. 1994) using waterproof Tesa® tape (Wilson and Wilson 1989). Depth (0–1,000 m, resolution of 0.5 m and accuracy of ±1 %) was measured every second.

Data analysis

Data downloaded from the loggers were analysed using IGOR Pro (version 6.04, WaveMetrics, USA). Dives started when the depth reached was >1 m. Dives were divided into three phases: the descent, bottom and ascent phases (Wilson 1995). The beginning and end of the bottom phases were defined as the combination of two conditions: (a) the depth was >85 % of the maximum depth of the dive and (b) the absolute value of the vertical transit rate became <0.25 m/s (see Kato et al. 2006). The duration of each whole dive (1–495 s) and of each dive phase, as well as the maximum dive depth (2–344.5 m), were determined automatically. The bimodal distribution of maximum depth frequencies, classically observed in king penguins, allowed us to separate shallow from deep dives (Kooyman et al. 1992). In the subsequent analysis, we only studied dives >50 m, as we assumed they represented mainly feeding dives (Charrassin et al. 1998). In addition, we analysed only those dives >50 m that belong to a sequence of repeated dives, that is, a dive bout, as they represent the majority of the feeding dives (Charrassin et al. 2002). The bout-ending criteria (BEC, see Gentry and Kooyman 1986) were used to determine the end of a dive bout. BEC values were obtained using a break point analysis ('segmented' package in R) after plotting a log curve of post-dive time for each bird (see values in the Supplementary material). The number of vertical undulations during the bottom phase, that is, brief up-and-down changes in the dive profile (called 'wiggles' thereafter), was calculated and used as a proxy for prey encounters (Wilson et al. 1992; Bost et al. 2007; Hanuise et al. 2010). The minimum change in depth profile during the wiggle was 2 m.

Laboratory analyses

Based on the equipped penguins' mean trip duration ± standard deviation (SD), of 12.2 ± 3.9 days, and on the turnover of plasma, we assumed that the isotopic signature in the plasma should reflect the diet of the birds over the trip duration (Hobson and Clark 1993; Bearhop et al. 2002). Prior to the isotopic analyses, lipids were extracted from the plasma using cyclohexane (Cherel et al. 2010). The plasma was then lyophilized during 48 h and powdered (Hobson et al. 1997). Stable carbon and nitrogen isotope assays were carried out at the laboratory of Littoral, Environnement et Sociétés (LIENSS, La Rochelle, France). Stable nitrogen isotope measurements (^{15}N:^{14}N, $\delta^{15}N$) indicate the trophic position of consumers (Cherel et al. 2010). Alternatively, stable carbon signatures (^{13}C:^{12}C, $\delta^{13}C$), for which the variation along the food chain is relatively low, are mainly used in the marine environment to indicate the foraging habitats of predators, neritic versus pelagic (Cherel et al. 2010).

Statistics

Statistical analyses were conducted using the R 2.12.1 statistical environment (R Development Core Team 2008). Wiggles and maximum dive depth were analysed with linear mixed models (LMMs) fitted by restricted maximum likelihood (REML) using the 'nlme' package (Pinheiro et al. 2010). Bird identity was included as a random term in order to account for repeated measurements on the same individual. Age, sex (but also their interaction), structural size and body condition indices were included as fixed effects. Moreover, trip duration was also included as fixed effect in the maximum dive depth analysis. Normality of residuals was asserted using the Shapiro–Wilk normality test. Whenever necessary, data were transformed prior to analysis using Box-Cox power transformations, that is, $x' = \frac{x^p - 1}{p}$ (where p is the power maximizing normality likelihood, obtained with the 'bcPower' function from the 'car' package in R) to ensure normality of residuals was satisfied. Fixed effects were then removed one by one from the model. The most appropriate model was selected using the Akaike's information criterion (AICc; AIC adjusted for small sample size; Burnham and Anderson 2002). In general, the model with the lowest AICc was selected, except when ΔAICc <2 (Burnham and Anderson 1998). For the latter, models with the smallest number of independent variables were favoured. The threshold for significance was set at 0.05. To compare difference in trip durations, mass gained, time to reach the foraging area (i.e. time from departure from the colony to the beginning of the first deep dives), number of dives and isotopic signature, we used linear models (LMs), with age and sex as fixed effects,

Table 1 Mean foraging trip duration (in days), mean mass gained (in kg) and number of dives (±SD) performed during the foraging trip according to sex and age

	Trip duration (days)		Mass gain (kg)		Number of dives	
5-year-old						
Females ($N = 5$)	13.20 ± 2.28^{a}		2.06 ± 0.81^{a}		1,208.4 ± 214.66^{a}	
Females (unequipped) ($N = 6$)	*14.33 ± 3.98^{a}*	15.10 ± 3.14^{a}		2.78 ± 0.98^{a}		1,332.0 ± 264.5^{a}
Males ($N = 4$)	17.50 ± 2.38^{b}		3.32 ± 0.76^{b}		1,486.5 ± 260.49^{a}	
Males (unequipped) ($N = 6$)	*16.67 ± 3.27^{b}*					
9-year-old						
Females ($N = 7$)	9.29 ± 2.98^{c}		2.09 ± 1.27^{a}		790.86 ± 313.70^{b}	
Females (unequipped) ($N = 6$)	*9.67 ± 3.56^{c}*	10.1 ± 3.03^{b}		2.50 ± 1.19^{a}		920.3 ± 388.0^{b}
Males ($N = 5$)	11.20 ± 2.73^{a}		3.12 ± 0.87^{a}		1,101.6 ± 442.65^{c}	
Males (unequipped) ($N = 6$)	*10.33 ± 3.77^{a}*					

Different letters indicate significant differences ($p < 0.05$)

Table 2 Linear models that best explained (a) the mass gain and (b) the daily mass gain per unit body mass

	Estimate	SE	t value	p value
(a)				
Intercept	2.081	0.315	6.603	<0.001
Sex (males–females)	1.139	0.459	2.479	0.026
(b)				
Intercept	0.005	0.008	0.579	0.571
Age	0.002	0.001	2.156	0.048

after having tested the SSI and BC effects. Trip duration was also included as fixed factor to compare the analyses of the isotopic signature.

Results

Body mass gain

Sex was retained in the best model explaining the total mass gained (AICc = 48.63, ΔAICc = 0.15 with the closest model, that is, model including also the age). Consequently, age had no significant effect on the total mass gained during the feeding trip (2.50 ± 1.19 kg for seven young breeders and 2.78 ± 0.98 kg for 10 old breeders) but males gained significantly more mass than females over the trip (3.10 ± 0.80 kg for eight males and 2.08 ± 1.08 kg for nine females; LM: $t = 2.479$, $p = 0.026$; Tables 1, 2a). Age and sex were not retained in the best model explaining the daily mass gain. However, age was retained in the best model explaining the daily mass gain per unit body mass (AICc = −111.95, ΔAICc = 0.44 with the closest model, that is, model including also the sex). The daily mass gain per unit body mass was positively related to age (LM: $t = 2.156$, $p = 0.048$; Table 2b; Fig. 1). The body condition index (BC) before the foraging trip had a significant negative effect on the total mass gain, the daily mass gain and the daily mass gain per unit body mass (LMs: $t = -2.460$, $p = 0.027$; $t = -2.798$, $p = 0.014$; and $t = -3.351$, $p = 0.004$, respectively). The structural size index (SSI) had a significant positive effect on the total mass gain (LM: $t = 2.393$, $p = 0.030$), but no effect on the daily mass gain and the daily mass gain per unit body mass.

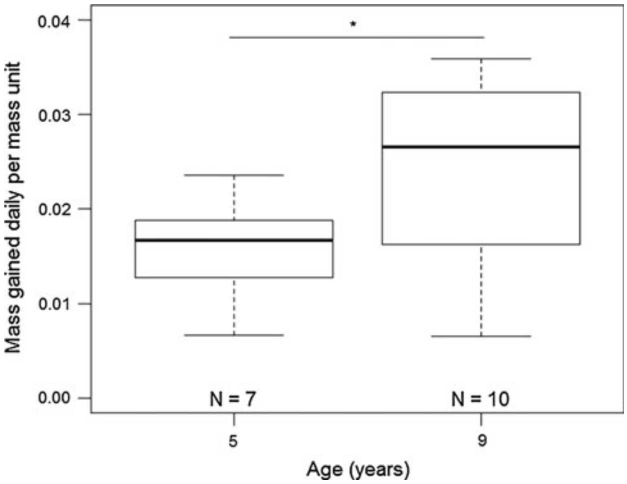

Fig. 1 Mass gained daily per body mass unit during foraging trip according to age. The *asterisk* indicates a significant difference ($p < 0.05$). *Black lines* indicate the mean value ± SD

Foraging behaviour

All data loggers recorded complete trips and collected a total of 23,032 deep dives (>50 m) from 21 individuals.

Age and sex were retained in the best model explaining the trip duration (AICc = 103.18, ΔAICc = 0.99 with the closest model, that is, model including also the interaction between age and sex). Trip duration was significantly related to age and sex (LM: $t = -4.091$, $p < 0.001$ and $t = 2.437$, $p = 0.025$, $N = 21$ individuals, respectively; Tables 1, 3a), with older females performed the shortest trips and young males the longest. Obviously, males did a greater total number of dive over the foraging trip than females (LM: $t = 2.148$, $p = 0.046$). Moreover, younger breeders did a greater total number of dive over the foraging trip than older breeders (LM: $t = -2.922$, $p = 0.009$). Age and sex had no effect on the daily number of dives (LMs: $t = -0.051$, $p = 0.960$ and $t = 0.680$, $p = 0.505$, $N = 21$ individuals, respectively). Age was retained in the best model explaining the time to reach the foraging area (AICc = 150.80, ΔAICc = 0.09 with the closest model, that is, model including also the sex). Time to reach the foraging area was not different between sex and negatively linked to the age (LM: $t = -2.234$, $p = 0.038$; Fig. 2). BC had no effect on trip duration or the time it took the birds to reach the foraging area was observed, while SSI had a significant and positive effect only on foraging trip duration (LM: $t = 4.339$, $p < 0.001$).

Table 3 Linear models that best explained (a) the foraging trip duration and (b) the time to reach foraging area (i.e. execution of the first deep dives of the first diving bout)

	Estimate	SE	*t* value	*p* value
(a)				
Intercept	19.984	2.354	8.491	<0.001
Age	−1.237	0.302	−4.091	<0.001
Sex (males–females)	2.946	1.209	2.437	0.025
(b)				
Intercept	37.021	6.923	5.348	<0.001
Age	−2.049	0.917	−2.234	0.038

Age, sex, their interaction, BC, SSI and the trip duration were retained in the best model explaining the maximum dive depth (AICc = 162,956.80, ΔAICc = 2.30 with the closest model, that is, model without SSI). The maximum dive depths were negatively related to the trip duration as individuals performing short trips (on average 9.0 days) dived deeper than breeders with long foraging trips (on average 15.2 days) (mean ± SD: 169 ± 25 and 145 ± 7 m, respectively; LMM: $t = -3.947$, $p = 0.002$; Table 4a). Although age and sex did not have significant effect on the maximum dive depth, the interaction between age and sex had a significant effect on it (LMM: $t = 2.379$, $p = 0.032$; Fig. 3; Table 4a): the positive effect of age was

Table 4 Linear mixed models that best explained (a) the maximum dive depth and (b) the number of wiggles performed during a dive

	Estimate	SE	*t* value	*p* value
(a)				
Intercept	54.530	2.852	19.121	<0.001
Age	−1.455	1.900	−0.766	0.456
Sex (males–females)	−2.685	1.696	−1.583	0.136
BC	5.822	9.005	0.646	0.528
SSI	0.888	0.906	0.980	0.344
Trip duration	−0.976	0.247	−3.947	0.002
Age × sex	6.298	2.647	2.379	0.032
(b)				
Intercept	7.035	0.128	55.102	<0.001
Maximum dive depth	−0.008	4×10^{-4}	−21.517	<0.001
Age	0.142	0.162	0.880	0.391
Sex (males–females)	0.061	0.160	0.382	0.707
Body condition	1.678	1.075	1.561	0.137
Maximum dive depth × sex	−0.001	4×10^{-4}	−3.028	0.003
Maximum dive depth × age	−0.002	4×10^{-4}	−4.440	<0.001

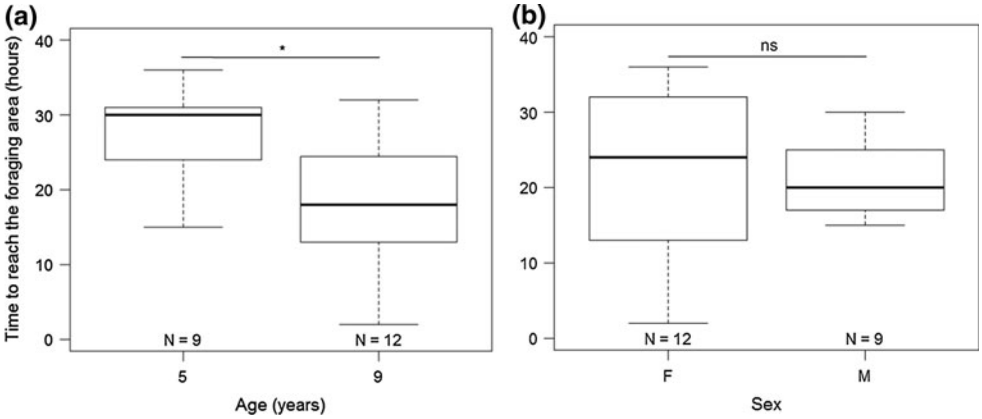

Fig. 2 Time of individuals to reach the foraging area from the departure from the colony to the first deep dive (>50 m) including in the first diving bout (in hours), according to (**a**) age, and (**b**) sex (F represents females and M represents males) The *asterisk* indicates a significant difference ($p < 0.05$). *Black lines* indicate the mean value ± SD

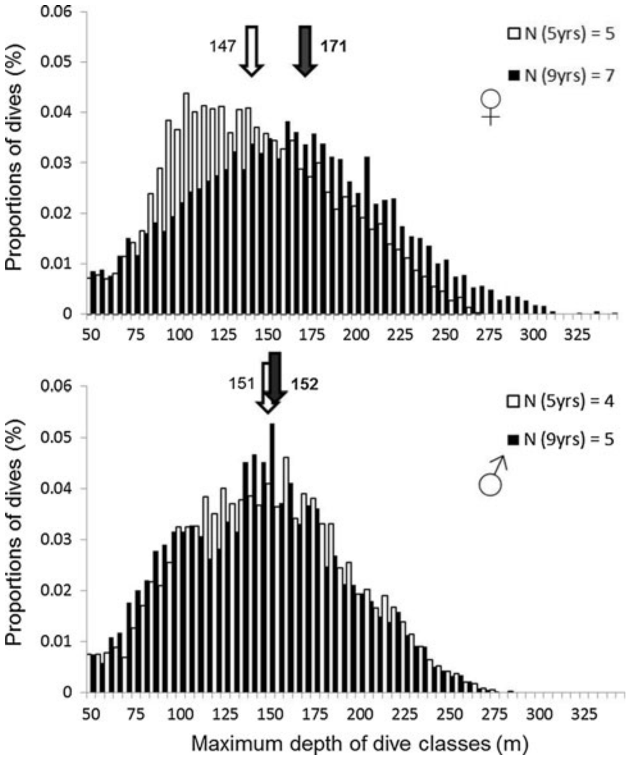

Fig. 3 Dive distribution of the maximum dive depth (dives >50 m and within diving bouts) according to sex (above graph depicts females, bottom graph depicts males) and age (*open bars* depict 5-year-old breeders, *filled bars* depict 9-year-old breeders). *Open* and *closed arrows* indicate mean values for 5- and 9-year-old breeders, respectively

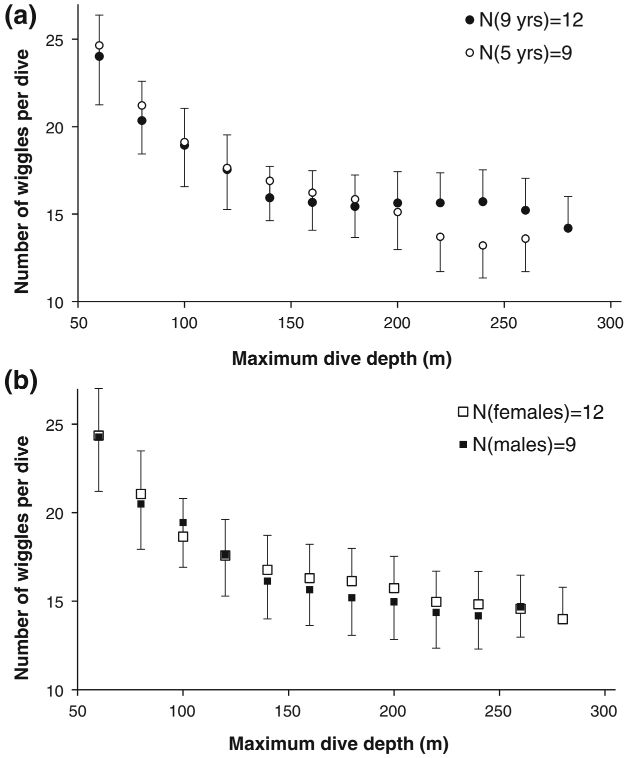

Fig. 4 Relationship between the mean number of wiggles during the bottom phase of deep dives (dives >50 m) and the maximum depth of the dive (in metres) according to **a** the sex (*open symbols* depict to females and *filled symbols* refer to males) and **b** age (*open symbols* depict to 5-year-old breeders, *filled symbols* refer to 9-year-old individuals). Results are presented as mean ± SD

greater in females than in males, meaning that 9-year-old females dived deeper than males of the same age.

The maximum dive depth, age, sex, BC, the interaction between age and sex, and between sex and maximum dive depth were retained in the best model explaining the mean number of wiggles during the bottom phase of a dive (AICc = 82,558.15, ΔAICc = 0.28 with the closest model, that is, model including also the SSI). This model that best explained the mean number of wiggles during the bottom phase of a dive in relation to the maximum dive depth indicated that the number of wiggles per dive decreased with increasing maximum depth (LMM: $t = -21.517$, $p < 0.001$; Table 4b). With increasing maximum depth, 9-year-old breeders performed more wiggles per dive than 5-year-old breeders (LMM: $t = -4.440$, $p < 0.001$; Fig. 4) and females performed more wiggles per dive than males (LMM: $t = -3.028$, $p = 0.003$).

Isotopic signature

We found no effect of age or sex on the mean value of δ^{13}C ($\delta^{13}C = -24.4 \pm 0.3$ ‰).

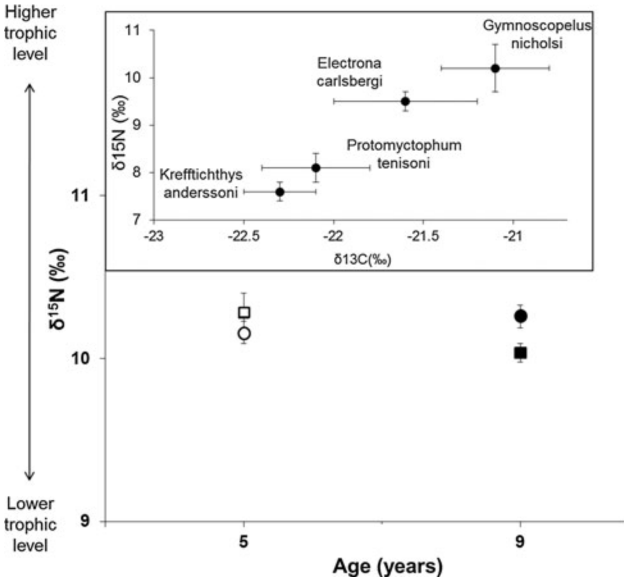

Fig. 5 Mean value of δ^{15}N (±SD) according to age and sex (*circles* refer to females and *squares* refer to males). The *upper box* corresponds to the mean values (±SD) of δ^{15}N and δ^{13}C of the main prey of king penguins (from Ridoux 1994; Cherel et al. 2010)

Table 5 Linear models that best explained the $\delta^{15}N$ value

	Estimate	SE	*t* value	*p* value
Intercept	10.040	0.199	50.552	<0.001
Age	0.025	0.026	0.937	0.362
Sex (males–females)	0.546	0.300	1.820	0.086
Age × Sex	−0.086	0.040	−2.150	0.046

Age, sex and their interaction were retained in the best model explaining the value of $\delta^{15}N$ ($AICc = -14.38$, $\Delta AICc = 1.50$ with the closest model, that is, model including also the trip duration). The mean value of $\delta^{15}N$ did not appear to depend strictly on the age or sex of the individuals (LMs: $t = 0.937$, $p = 0.362$ and $t = 1.820$, $p = 0.086$, respectively; Fig. 5; Table 5). However, the interaction between sex and age had a significant effect on $\delta^{15}N$ values (LM: $t = -2.150$, $p = 0.046$). In other words, older females had a higher mean value of $\delta^{15}N$ than older males.

Discussion

The foraging behaviour of king penguins changed with age and sex. Age affected mainly the diving effort as younger breeders conducted longer trips and they also performed a greater number of dives ones per trip than older. However, this greater overall effort did not translate into a higher gain in total body mass, which suggests that king penguins improve their foraging efficiency with age. Indeed, older birds were able to extract the same amount of food as the younger ones, but over a shorter period which resulted in a larger daily mass gain per unit body mass. A similar situation was found in European shags *Phalacrocorax aristotelis*, in which foraging effort was higher for naive breeders than experienced ones (Daunt et al. 2007).

We observed that the maximum dive depth was negatively correlated with trip duration. This observation is consistent with previous studies. In the vicinity of the Antarctic Polar Frontal Zone, which is an upwelling zone where Antarctic waters sink under sub-Antarctic waters, nutrients are brought closer to the surface. Hence, prey is probably located higher in the water column at the front (Charrassin and Bost 2001). We can thus hypothesize that birds performing longer trips may forage further away from the colony, thus getting closer to the Polar Front, assuming they kept a constant heading during their onward journey. Since the time to reach the foraging area was shorter for old birds than young ones, we suggest that older birds may be more successful in finding feeding areas or in returning to previously found higher quality foraging areas. We can at least suggest that these birds are able to optimise the commuting parts of their trips. These results could be compared to the findings among wandering albatrosses *Diomedea exulans* from Crozet Archipelago. In this species, age and sex of individuals influence their choice of foraging areas. Old wandering albatross males (>30 years) forage in Antarctic waters while younger males and females forage to the north of the Antarctic Polar Frontal Zone (Lecomte et al. 2010). Such a clear spatial segregation seems unlikely for king penguins from Crozet Archipelago, as they feed primarily near the Antarctic Polar Front, where sub-Antarctic waters meet Antarctic ones (Charrassin and Bost 2001) and we found no differences in stable carbon signature.

Age affected the vertical segregation of birds in the water column: females of the two age classes exploited the different depth strata, although they did not target different prey (no change in $\delta^{15}N$ with age). Vertical segregation was noted in other species, such as cormorants (*Phalacrocorax sp.*), but it was related to sex (e.g. Kato et al. 1999), or more explicitly to differences in body size, as larger individuals had enhanced diving capacities (Schreer and Kovacs 1997). Age-specific vertical segregation of the foraging niche may help reduce intra-specific competition (González-Solís et al. 2000). We also found sex- and, for female, age-related differences in the number of prey encountered (i.e. number of wiggles): older females performed more prey pursuits than both younger and older males with increasing maximum depth, especially for very deep dives (>200 m). The number of wiggles is an index that provides an indirect estimate of the prey encounter rate (Bost et al. 2007). Importantly, however, wiggles do not inform whether a prey has been captured or not (Hanuise et al. 2010). A greater number of wiggles can thus be interpreted in two ways: either an individual needs to perform more pursuits to capture the same number of prey, or it captures more prey or different types of prey. Further data are needed to resolve this issue. However, the greater efficiency of experienced, older individuals (Pärt 1995) suggests that a higher manoeuvrability in older females may explain this optimisation in hunting performances. The age-specific trends in prey hunting ability reported here differ from the findings of Zimmer et al. (2011) in little penguins *Eudyptula minor*. These authors compared the diving activity of little penguins, across three age classes (Nisbet and Dann 2009), and did not find difference in foraging efficiency. Nevertheless, middle-aged little penguins expected to be birds with optimum breeding abilities differed in their dive organization compared to young and old breeders (Zimmer et al. 2011). In fact, middle-aged little penguins made shorter dives and they reached the bottom of the dive faster than younger and old birds. However, unlike in king penguins, there was no effect of age on the prey encounter rate of little penguins

(Zimmer et al. 2011). In a very recent study on king penguin, we also found differences in diving capacities between young and older breeders; young breeders (i.e. 5-year-old) might have a higher drag than old birds (8- and 9-year-olds) implying therefore that old birds could travel at lower costs than young ones (Le Vaillant et al. 2012).

An explanation of the differences in the number of prey encountered in king penguins, especially for females, is that they adapted their dietary regimes with age to better fit their energetic requirements, as suggested by the sex proportion of high trophic level prey in older females (higher level of δ^{15}N). During the austral summer, king penguins feed mainly on four myctophid species that are abundant near the Antarctic Polar Front (Koubbi et al. 2001): the comparatively large, *Electrona carlsbergi* (~80 mm) and *Gymnoscopelus nicholsi* (~98 mm), and the smaller *Krefftichtys anderssoni* (~44 mm) and *Potomyctophum tension* (~43 mm) (Cherel and Ridoux 1992; Ridoux 1994; Cherel et al. 2010). The isotopic signature of the main prey of king penguins (see upper box in the Fig. 5 from Cherel et al. 2010) suggests that older females ingested proportionately more large prey, such as *G. nicholsi*, than older males did. Since all myctophid species have about the same calorific value (8 kJ g^{-1} wet mass; Cherel and Ridoux 1992), the strategy of older females may accordingly lead them to gain mass more quickly during their foraging trips. Nevertheless, differences between our groups are very small compared to what was shown in other birds species, including other penguins with sex-specific strategies to optimise energy acquisition (Forero et al. 2002 for Magellanic penguin *Spheniscus magellanicus*), but also in other seabirds (see Forero et al. 2005 for southern giant petrel *Macronectes giganteus*; and Awkerman et al. 2007 for waved albatross *Phoebastria irrorata*). In fact, in king penguins, no differences in δ^{15}N was found among breeders (at incubation or chick-rearing stage), moulting adults and chicks (Cherel et al. 2005).

Here, we demonstrated that king penguins' foraging behaviour is related to age. Indeed, prey pursuit (hunting) abilities improved with age, at least for females, which also affected foraging effort and allowed a reduction in foraging trip duration. This difference in foraging behaviour between first and older breeders could be one explanation of age-dependent reproductive performance. Indeed, as in several long-lived seabird species (DeForest and Gaston 1996; Forslund and Pärt 1995; Nisbet and Dann 2009), the breeding success in king penguin depends on age. Our long-term database showed a lower breeding success in younger individuals compared with penguins more than 6-year-old (unpublished data). The purpose of our investigation here was focused on how age and sex affect the foraging behaviour, not on their effect on breeding success. In our equipped birds, two of the 12 older individuals bred successfully, but we had no information about the mass of chicks during their growth. None of the young breeders were successful. Yet, it would not make a lot of sense to relate breeding success at the end of the season to a single trip made by only one member of a pair. The breeding output of a pair at the end of the season depends on several factors, including the cumulative foraging and breeding efforts by the two members of the pair and eventual compensation processes (Saraux et al. 2011). With this in mind, it would be particularly interesting to conduct long-term studies in the future, in which the foraging activities of the same individuals are monitored during the course of the breeding season and over years. Additional parameters, especially physiological ones like hormone levels (Angelier et al. 2008; Cottin et al. 2011), may also vary with age (Goutte et al. 2010) and studying them might allow a better understanding of the effect of ageing on foraging efficiency.

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Ethical note All procedures employed during animal handling, PIT-tag implantations and data-logger deployments were approved by the Ethical Committee of the French Polar Institute (IPEV Program ECOPHY 137: permits 01/315/AUT issued on the 4 July 2001, 01/322/AUT issued on the 16 August 2001, 2005-191 issued on the 21 November, 2009-57 issued on the 26 August, and 2009-59 issued on the August 29). The handling of individuals was performed without anaesthetic and lasted no longer than 15 min.

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