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Original Article

Individual parameters shape foraging activity in breeding king penguins

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The variability in individual fitness within a population is likely to be mediated through individual foraging ability and tactics, themselves linked to age- or experience-related processes, but also to differences in individual quality. Not only age, experience, and quality but also sex-related foraging strategies should particularly play an important role in long-lived central-place foragers that have to cope with strong environmental constraints. We monitored the foraging effort (foraging trip durations and number of trips) of 262 known-age micro-tagged king penguins, *Aptenodytes patagonicus*, at different breeding stages during one of their breeding cycles. We investigated how their age (4–11 years old), sex, past breeding experience (the number of successful breeding attempts), and breeding quality (the expected breeding success, corresponding to the residual of the linear relationship between the age and on the number of past breeding success divided by the number of breeding attempts) affected foraging over a whole breeding season. During the incubation, younger birds (4 years old) undertook longer foraging trips compared with older ones. During the brooding phase and the second period of the crèching phase, more experienced birds performed shorter foraging trip than those with a low breeding experience, whereas, during the first period of the crèching phase, individuals with better breeding quality performed shorter foraging trips at sea than low breeding quality individuals. Sex-specific foraging patterns were also observed depending on the period of the breeding cycle. Our study shows, for the first time, how foraging effort can be driven by a complex interplay of several individual parameters according to breeding stage and resource availability and abundance.

Key words: **age, breeding quality, experience, seabirds, sex.**

INTRODUCTION

Life-history theory predicts that a trade-off between self-maintenance and reproduction is expressed through different patterns within a population according to the principle that optimal energy allocation is modulated by resource availability (Boggs 1992). However, energy allocation ability is also affected by individuals' intrinsic factors, such as age (Clutton-Brock 1988), sex (Kato et al. 2000), or individual quality. The latter can be assessed through indices, such as expected breeding success or past breeding experience (Lescroël et al. 2009; Moyes et al. 2011), as the more individuals gain in experience, the more they increase their efficiency in those numerous tasks related to reproduction, until performances reach a plateau at a given age before potentially declining under the effects of senescence (Pärt 1995; Daunt et al. 2001; Pärt 2001; Broussard et al. 2008; but see Elliott et al. 2015 for an absence of obvious decline in behavioral performances with age). Lower breeding performance in younger individuals can be the result of individuals breeding later in a season (DeForest and Gaston 1996; Ezard et al. 2007; McCleery et al. 2008), thereby leading to a mismatch with the peak of food availability (Durant et al. 2007). Improvement in breeding performance has been generally considered to be essentially mediated through changes in foraging ability, as it affects the capacity to provision the offspring (Stearns 1992). Age-related improvement in reproductive performance may, therefore, reflect the accumulation of both breeding and foraging experience with each new breeding event (Le Vaillant et al. 2013). As such, the number of previous reproductive attempts, especially the successful ones (Lewis et al. 2006), or simply the presence at the breeding colony as a proxy of knowledge of breeding areas and

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ability to deal with environmental conditions (Harcourt et al. 2007; Lescroël et al. 2009) has been often used to measure the level of breeding experience of an individual.

Nevertheless, the expected correlations between life-history traits and age/experience are not necessarily observed (Clutton-Brock 1985; Yoccoz et al. 2002; Moyes et al. 2006; Elliott et al. 2015), highlighting the presence of variation among individuals in their energy acquisition and in phenotypic traits associated with their survival and reproduction (Wilson and Nussey 2010). The "Selection Hypothesis" can partially explain the larger proportion of high-quality individuals in older age classes compared with younger age classes by a disappearance of individuals of lower phenotypic quality in younger age groups (Curio 1983; Cam and Monnat 2000; Beauplet et al. 2006). This results in the observation of higher survival and reproduction probabilities in the older age classes than expected if all individuals were of identical quality (Cam and Monnat 2000; Barbraud and Weimerskirch 2005; Moyes et al. 2009). The concept of individual quality is however difficult to define (but see Wilson and Nussey 2010). Numerous traits have been used to measure differences in quality between individuals (Moyes et al. 2009): 1) reproductive or parental traits, such as laying and hatching date (Blackmer et al. 2005; Lewis et al. 2006), number of previous successful breeding attempts (Lescroël et al. 2010; Moyes et al. 2011), or age at maturity (Côté and Festa-Bianchet 2001); 2) morphological traits, such as body size and condition indexes (Jensen et al. 2004); 3) behavioral traits, such as social rank (Hamel et al. 2009); and 4) physiological traits, such as hormonal, immunological status, or telomere length (Magee et al. 2006; Angelier et al. 2007; Bauch et al. 2013; Le Vaillant et al. forthcoming).

Differences in survival and reproductive rates between individuals of various quality levels are expected to be even more pronounced during unfavorable environmental conditions. For instance, during years of reduced regional primary productivity and/or access to the colony, higher-quality breeders of Adélie penguins, *Pygoscelis adeliae*, foraged more efficiently, leading to a greater breeding success (Lescroël et al. 2010). Central-place foragers such as seabirds, which feed at sea but breed on land, are very sensitive to changes in their environment (Le Bohec et al. 2008; Wolf et al. 2010; Barbraud et al. 2011). Time spent and energy expended during their foraging trips at sea vary according to resource availability, influence the ability of parents to provision their chicks, and consequently affect their breeding success (Orians and Pearson 1979; Chivers et al. 2012). In this context, it is crucial to understand the ontogeny of behavioral strategies and how changes in resources availability influence these behavioral patterns.

To examine how individual characteristics may affect foraging behavior and strategies over a breeding event, we conducted a study on king penguins, *Aptenodytes patagonicus*. These birds experience harsh and changing environmental conditions during their more-than-a-year breeding cycle (Stonehouse 1960; Barrat 1976; Descamps et al. 2002). This particularly long breeding cycle leads to different foraging strategies in this species according to the breeding phase (incubation, brooding, and crèching periods) and to the season (summer vs. winter). As breeding experience and quality are not linearly linked to age, but present exponential or logarithmic relationships, these variables may have different effect on behavior. Using an automatic identification system installed in 1998 in Crozet Archipelago (see Gendner et al. 2005), we investigated foraging trip duration and/or number of foraging trips in 262 micro-tagged, known-age (from 4 to 11 years old) king penguins during an entire breeding cycle, for which breeding experience (past breeding experience [PBS]) and quality (breeding quality index [BQI]) were evaluated. We predicted a positive effect of age, experience, and quality on foraging effort, effect that might be even more pronounced in critical phases of their breeding cycle, such as during the austral winter when resources availability is low.

MATERIALS AND METHODS

Permits and ethics statement

All animal handling procedures employed during the fieldwork were approved by the Ethical Committee of the French Polar Institute (Institut Polaire Paul-Emile Victor) and conducted in accordance with its guidelines, also complying with French laws including those related to conservation and welfare. Authorizations to enter the breeding site (permit nos. 2005–191 issued on 21 November 2005 and 2006–67 issued on the 6 November 2006) and handle birds (permit nos. 99/346/AUT issued on 30 November 1999, 00/240/AUT issued on 5 September 2000, 01/315/AUT issued on 4 July 2001, 01/322/AUT issued on 16 August 2001, 2003–113 and 2003–114 issued on 7 October 2003, 2004–182 and 2004–183 issued on 14 December 2004, 2005–203 issued on 1 December 2005, and 2006–73 issued on 6 November 2006) were delivered first by the French "Ministère de l'Aménagement du Territoire et de l'Environnement" and then by the "Terres Australes et Antarctiques Françaises" (TAAF).

Study site and monitoring system

Our study was conducted on the king penguin breeding colony of "La Grande Manchotière" in Possession Island, Crozet Archipelago (46°25′S, 51°45′E). Since 1998, cohorts of circa 10-month-old chicks are implanted each year, just before fledging, with subcutaneous passive integrated transponder (PIT of $3.85 \times 32\,\mathrm{mm}^2$ and 0.8 g) without any other external mark (see Supplementary Appendix A1 for more details). While avoiding the impact of flipper bands on penguin life-history traits (Gauthier-Clerc et al. 2004; Saraux, Le Bohec, et al. 2011), no adverse effects on survival of king penguins (Froget et al. 1998) or breeding success, recruitment, or survival of great tits *Parus major* (Nicolaus et al. 2009) have been observed with PIT tags. Furthermore, concerns about infections should be minimal, as PIT tags were kept sealed sterile in iodine capsules (Betadine) and removed from the capsules only by the process of injecting them into the bird. Moreover, Vétédine soap and alcoholic antiseptic solutions were used to disinfect the skin and the injecting needle before each insertion. Flesh wounds did not seem infected thereafter (personal observations on recaptured birds). Morphological traits (bill length, flipper length, and body mass) were measured at tagging to estimate individual structural size and body condition indexes at fledging (Schulte-Hostedde et al. 2005; Saraux, Viblanc, et al. 2011). Blood samples were collected from the birds' flipper vein and used to determine genetically the sex of individuals (adapted from Griffiths et al. 1998). Micro-tagged birds were then monitored from their tagging to the breeding season 2009, that is, the breeding season was studied here, using an automatic monitoring system formed by PIT-reading antennae buried underground at the access pathways used by the birds to leave or enter into the colony (Gendner et al. 2005; Figure 1; more details are given in Supplementary Appendix A1). It enables continuous monitoring whatever the climatic conditions (Gauthier-Clerc et al. 2004; Saraux, Le Bohec, et al. 2011; Le Maho et al. 2011).

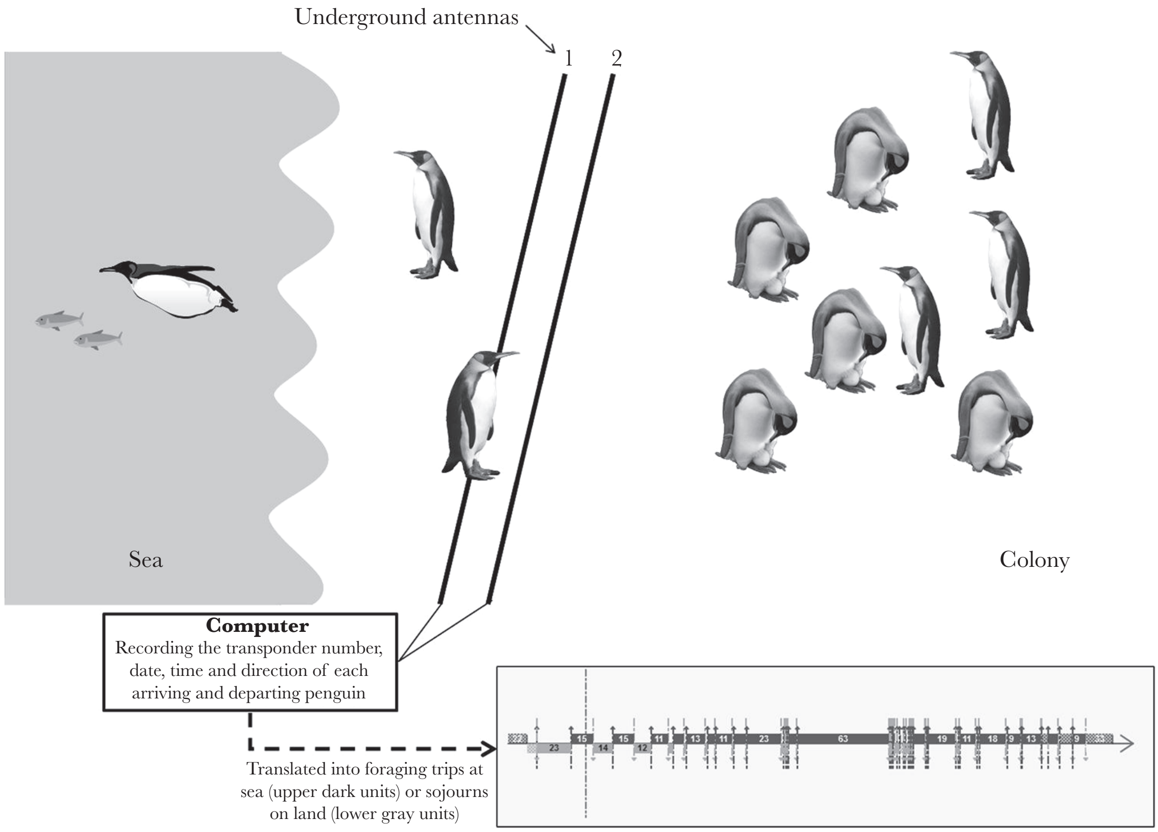

Figure 1
Schematic representation of the automatic monitoring system of the free-living micro-tagged king penguins breeding at La Baie du Marin on the Possession Island, Crozet Archipelago.

We could thus determine the past breeding performances of 262 known-age king penguins (142 females and 120 males, not paired as confirmed by the unmatched patterns between the sojourns on land/at sea of the individuals), as well as their foraging trip durations, breeding cycle length, and breeding success during the 2009 breeding season (see below). In order to use comparable sample sizes in each age class, birds were randomly selected in each cohort among individuals breeding in 2009 (using the *sample()* function in R 2.14.0 statistical environment [R Development Core Team 2012] for each age class): $N_{\text{4-year-old}} = 33$, $N_{\text{5-year-old}} = 44$, $N_{\text{6-year-old}} = 31$, $N_{\text{7-year-old}} = 28$, $N_{\text{8-year-old}} = 30$, $N_{\text{9-year-old}} = 34$, $N_{\text{10-year-old}} = 31$, and $N_{\text{11-year-old}} = 31$ (more details are available in Supplementary Appendix A1). The lifespan of unbanded king penguins is still unknown (estimated to be ca. 20 years according to Gauthier-Clerc et al. 2004); however, the oldest micro-tagged individuals of our long-term monitoring (implanted when they were breeding in 1991) were more than 22 years of age in 2009. Consequently, our studied birds ranging from 4 to 11 years of age were clearly not senescent.

Breeding activities

Breeding activities and outcomes were established by interpreting the movements of the birds between their breeding area and the sea (see Descamps et al. 2002; Figure 1). When there was a doubt concerning the breeding status, interpretations were confirmed by direct observations of body and plumage conditions using continuous video recordings during summer on the main passageway of the birds (see Supplementary Appendix A1 for more details). From the detection data analysis, we thus extracted the timing of breeding (the annual arrival date at the colony and the date of the beginning of the annual breeding cycle, later called breeding initiation date, which allows us to define individuals as early breeders [laying date prior to 1 January] or late breeders [laying date posterior to 1 January]) and the length of the annual breeding cycle. Incubation phase, brooding phase and 3 crèching phases (Crèche 1, Crèche 2, and Crèche 3; i.e., when the chicks are left alone, without parents, being present at the colony, and aggregate in groups of various sizes) were also identified to study foraging trips separately for each of the breeding phases. Breeding output was defined as successful when an individual was resuming a succession of short trips at sea and short sojourns on land after the winter, which is a pattern characteristic of a bird of a pair that laid an egg that succeeded in fledging a chick (i.e., breeding output = 1). A failure was defined when a breeding bird stopped performing regular shift patterns characteristic of the incubation and brooding periods, or demonstrated no feeding activities during Crèche 3 (i.e., breeding output = 0).

Breeding experience and quality

Breeding experience, defined as the past breeding success (PBS) of an individual, represented the number of successful breeding events during the bird's life until 2009. A breeding quality index (BQI) was calculated as the difference between the observed breeding success in 2009 (0 or 1) and the expected breeding success (see methods adapted from Lescroël et al. 2009). Briefly, the expected breeding success of an individual corresponded to the residuals of the linear regression between its PBS (from 0 to 3 successful breeding attempts) according to the total number of breeding attempts over bird's life (from 0 to 8 attempts) and the age of the individual in 2009. The age at which an individual was seen for the first time in the breeding colony after fledging was used in order to assess its knowledge of the breeding area, both the breeding colony and the sea conditions close to the colony (i.e., age at first return to the colony). The age at which an individual did its first breeding attempt and the total number of breeding attempts were also considered, but because both variables had no effect, we do not present the results related to these variables.

Foraging trips

Departure and return dates of each trip at sea were determined for each individual throughout its 2009 breeding cycle. The antennae of the permanent automatic identification system are placed circa 25–30 m from the sea. After exiting the antennae, birds may spend some time on the beach before their departure for a foraging trip (personal observation), so that only trips out of the colony lasting more than 3 days were considered as foraging trips at sea during the crèching periods (see Saraux et al. 2012). Foraging trip durations and number of trips at sea were estimated independently for each breeding stage. Mean trip duration could differ remarkably not only between breeding phases but also between shifts within a phase (Barrat 1976; Descamps et al. 2002). To compare trips between breeding phases in a global model, we standardized foraging trips within breeding phase (stand(x) = x − mean/standard error; more details are given in Supplementary Appendix A1). As duration of incubation and brooding shifts in king penguins might also be sex specific, this parameter was incorporated into our models.

Statistics

All statistics were computed using the R 2.14.0 statistical environment. Trip durations for each breeding stage were analyzed using a maximum of likelihood mixed model approach (linear mixed models [LMMs] using the lme4 package; Bates 2010). Individuals were computed as a random effect, enabling us to account for repeated measures, as birds were tracked over multiple trips. Normality of residuals was asserted using Shapiro–Wilk normality test, and visual inspection of the residuals indicated no violation of assumptions of homoscedasticity. Breeding success and breeding initiation date were analyzed using generalized linear model (GLM) and linear model (LM), respectively. Models were fitted either with binomial or with normal distribution. Explanatory variables were age, sex, PBS, BQI, age at first return to the breeding colony, initiation date of the current breeding, and trip category (i.e., after standardization according to trip length; see more details in Supplementary Appendix A1). As age, PBS, and BQI were correlated, we thus performed separate models for each of these 3 variables. Moreover, as the effect of age, experience, and quality on behavior was not necessarily linear, we also included quadratic terms of these variables in our models. The most appropriate model was selected using the Akaike's information criterion (AIC). The model exhibiting the lowest AIC was selected, except when ΔAIC < 2. In that specific case, AIC weights were examined, as well as the number of parameters (models with smaller number of variables being favored, i.e., the most parsimonious models). Parameters have been tested both as categorical and continuous variables. Only selected models are presented in the Results section: only models that included continuous variables were retained. Data are presented as mean ± standard deviation unless stated otherwise.

In order to compare different groups (e.g., males vs. females or between cohorts), we first checked for normality and homoscedasticity between groups, and pairwise t-tests with Bonferroni correction were used when making multiple comparisons (differences were thus considered significant for $P < 0.05/n$, with n the number of comparisons performed).

RESULTS

Foraging effort

Incubating period

During the incubation, younger individuals performed longer foraging trips than older birds (Figure 2a and Supplementary Appendix A2; LMM: $t = -2.828$, $P = 0.005$ and $t = 2.537$, $P = 0.011$ for linear and quadratic effect, respectively): 4-year-old individuals performing very long foraging trips compared with the other age classes (pairwise t-tests given in Figure 2a; on average 26.4 ± 8.1 days for 4-year-old individuals vs. 19.2 ± 3.1 days, 17.8 ± 4.6 days, 17.9 ± 3.0 days, 19.0 ± 5.9 days, 18.1 ± 4.8 days, 17.6 ± 4.5 days, and 18.3 ± 4.4 days for 5-, 6-, 7-, 8-, 9-, 10- and 11-year-old individuals, respectively). The duration of foraging trips was significantly shorter for females than males (Figure 2a; on average 17.2 ± 5.3 days for females vs. 23.2 ± 8.0 days for males; $t = 4.979$, $P < 0.001$). Finally, the later the birds started to breed, the longer their foraging trip durations (Figure 2b; on average 17.9 ± 3.8 days for early breeders vs. 25.0 ± 7.8 days for late breeders; $t = 7.611$, $P < 0.001$).

Brooding period

Only one 4-year-old individual reached the brooding phase in 2009, but failed its breeding attempt at this stage. This bird was therefore excluded from the following analyses. We found a quadratic effect of PBS on foraging trip durations (Figure 3 and Supplementary Appendix A3; LMM: $t = -2.997$, $P = 0.003$), with individuals that expressed the greatest PBS performing shorter foraging trips compared with other birds (see pairwise t-tests given in Figure 3; on average 9.9 ± 4.3 days for individuals that performed 3 successful breeding events during their life vs. 13.5 ± 5.2 days, 11.8 ± 3.8 days, and 11.6 ± 4.9 days for individuals that performed 0, 1, or 2 successful breeding events during their life, respectively).

Crèching period

Individuals expressing a higher BQI performed shorter foraging trips during Crèche 1 (Figure 4 and Supplementary Appendix A4; LMM: $t = -2.229$, $P = 0.026$). Females performed longer foraging trips than males (Figure 4; on average 11.1 ± 6.9 days for females vs. 9.2 ± 6.3 days for males, LMM: $t = -2.700$, $P = 0.007$).

The foraging trip duration during Crèche 2 was negatively related to PBS (Figure 5 and Supplementary Appendix A5a; $t = -2.491$, $P = 0.013$; see pairwise t-tests given in Figure 4; on average 60.4 ± 24.8 days for individuals that performed 0 successful breeding events during their life vs. 36.2 ± 27.9 days and 37.1 ± 24.8 days for individuals that performed 2 and 3 successful breeding events during their life, respectively). Moreover, females performed fewer foraging trips during Crèche 2 than males (Supplementary Appendix A5b; on average 2.2 ± 1.3 foraging trips for females vs. 3.0 ± 1.2 foraging trips for males; LM: $t = 3.014$,

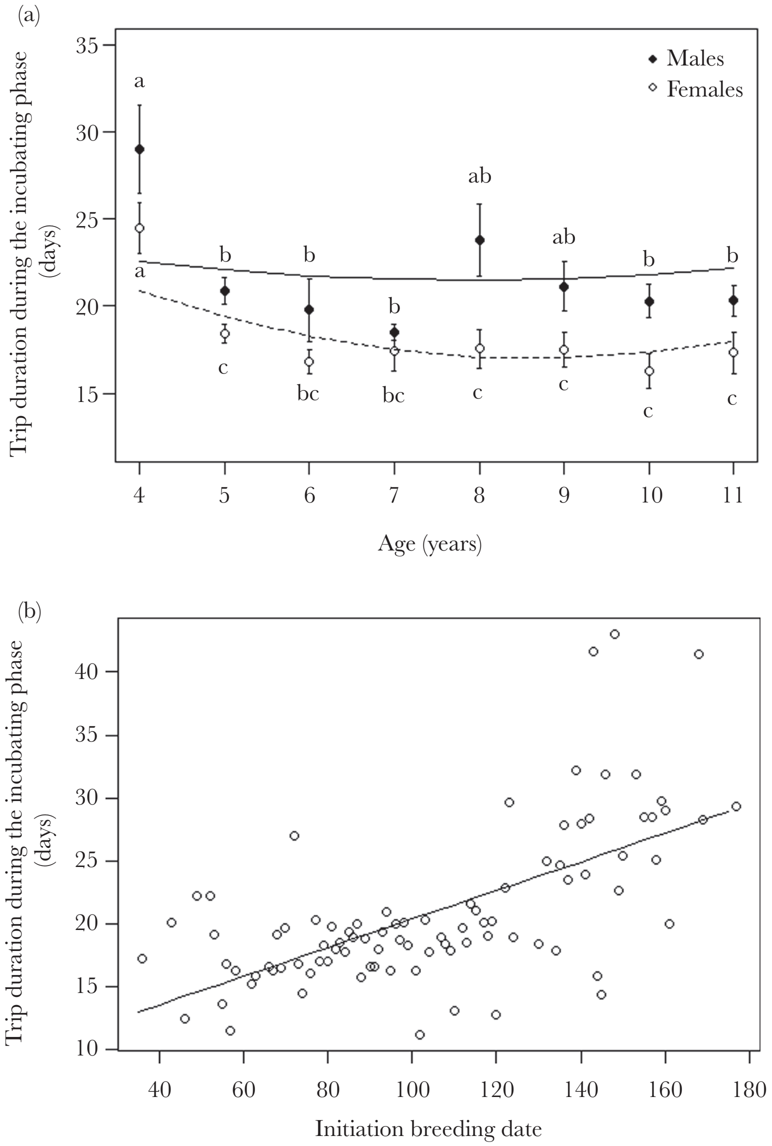

Figure 2
(a) Trip duration during the incubation period (mean ± SE in days) according to the age of the individuals. Filled symbols depict males and opened symbols depict females. Filled and dotted curves correspond to the predictions of the selected models for males and females, respectively. Values not sharing a common letter are significantly different; (b) trip duration during the incubation period (in days) according to the initiation breeding date (1 corresponds to 1 September 2009). The line corresponds to the linear relationship between initiation breeding date and trip duration.

$P = 0.004$). The number of winter foraging trips increased with the BQI ($t = 4.767$, $P = 0.002$).

The foraging trip duration during the last phase of the breeding cycle (Crèche 3) was not explained by any of the individual parameters tested in this study (see Supplementary Appendix A6 for model selection).

Breeding phenology and success

Successful breeders in the previous year started their breeding season later than those that had failed or did not breed (Supplementary Appendix A7; LM: $t = 13.304$, $P < 0.001$): on average successful breeders in the previous year started their breeding season 19 January 2009 ± 15.9 days, whereas failed or nonbreeders in the previous year started their breeding season 2 December 2008 ± 27 days. The breeding initiation date was negatively related to the BQI (Figure 6; LM: $t = -6.489$, $P < 0.001$ and $t = 4.304$, $P < 0.001$ for linear and quadratic effect, respectively).

Older individuals were more successful than younger ones (Figure 7 and Supplementary Appendix A8; GLM: $t = 3.603$, $P < 0.001$). The earlier an individual started to breed, the greater its chance to successfully reproduce ($t = -3.914$, $P < 0.001$).

DISCUSSION

The individual characteristics of king penguins affect their foraging behavior differently depending on the breeding period. The age of an individual affected the duration of its foraging trips only during the incubation period, with longer trips being performed by younger breeders. Foraging behavior during the other breeding periods (brooding and crèching) was mainly driven by individual

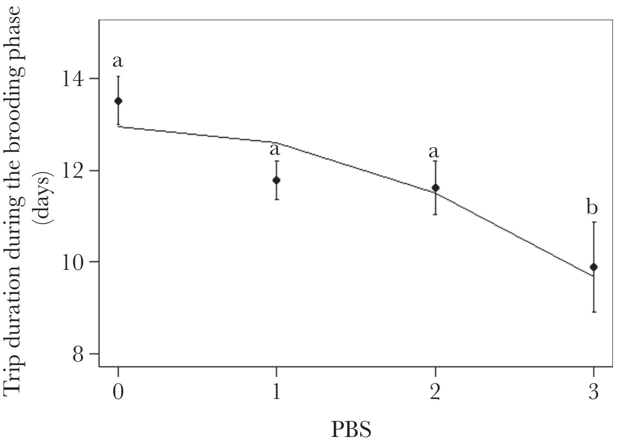

Figure 3
Trip duration during the brooding phase (mean ± SE in days) according to the PBS. The curve corresponds to the prediction of the selected model. Values not sharing a common letter are significantly different.

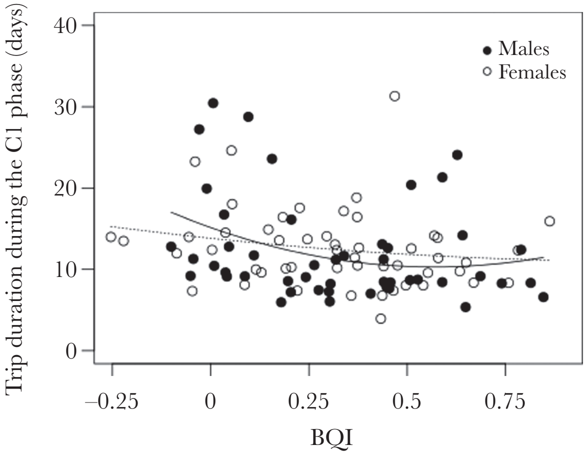

Figure 4
Trip duration during the first phase of the crèching period (mean ± SE in days) according to the BQI. Filled symbols depict males and opened symbols depict females. Filled and dotted curves correspond to the predictions for males and females, respectively.

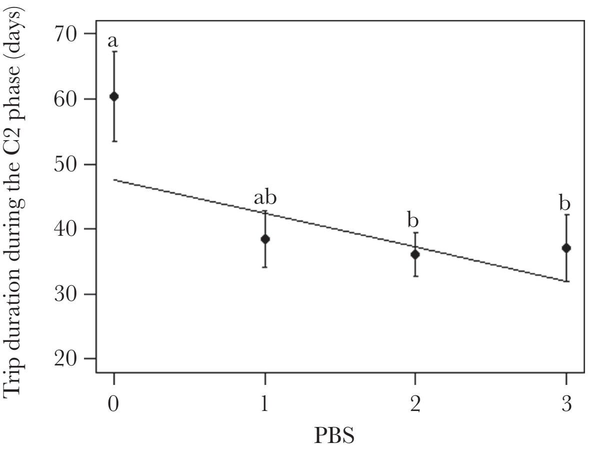

Figure 5
Trip duration during the second phase of the crèching period (mean ± SE in days) according to the PBS. The line corresponds to the prediction of the selected model. Values not sharing a common letter are significantly different.

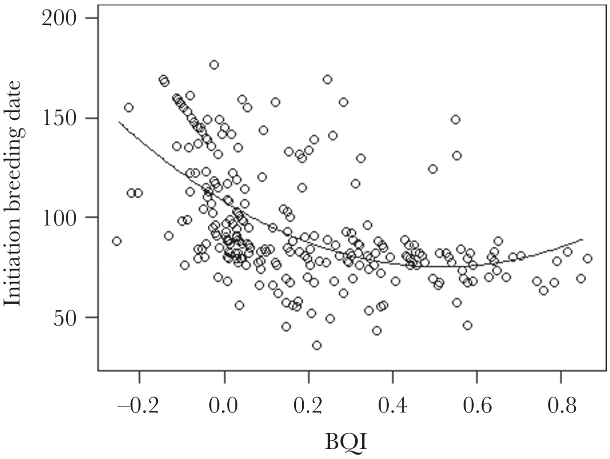

Figure 6
Initiation breeding date (1 corresponds to 1 September 2009) according to BQI. The line corresponds to the prediction of the model selected.

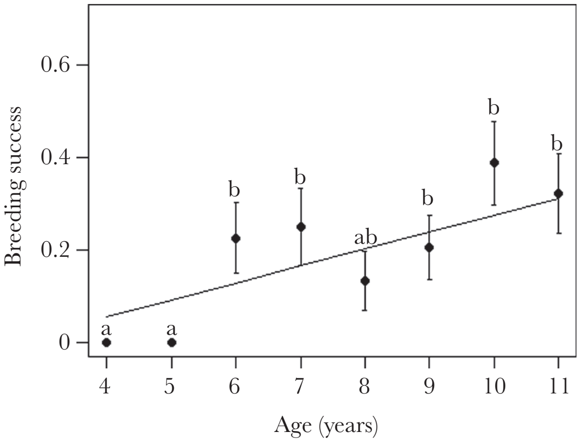

Figure 7
Breeding success in 2009 (mean ± SE) according to the age of the individuals. The line corresponds to the prediction of the model selected. Values not sharing a common letter are significantly different.

breeding experience and quality (see schematic representation of our findings in Figure 8).

The age-related difference in trip durations observed during the incubation period may be explained by the age-related differences in foraging success and diving/swimming (or flying) parameters observed in seabirds (in wandering albatrosses *Diomedea exulans*, Lecomte et al. 2010) and more particularly in penguin species (in little *Eudyptula minor*, Zimmer et al. 2011 and king penguins, Le Vaillant et al. 2012, 2013). Longer foraging trips conducted by younger breeders during the first part of the breeding cycle may be partly explained by the fact that they may not explore the same foraging areas as older birds. Numerous studies showed that foraging areas of birds can differ between age classes (Pärt 2001; Lecomte et al. 2010; Pelletier et al. 2014). Accordingly, the feeding grounds used by young incubating king penguins may potentially be either less productive and/or further from the colony, leading therefore to a higher foraging effort (more time to find and/or catch prey). King penguins feed mainly on myctophid fishes and onychoteuthid squids (Cherel and Ridoux 1993; Olsson and North 1995; Cherel and Weimerskirch 1999; Cherel et al. 2002). During the austral summer their preferred prey are usually available and abundant in

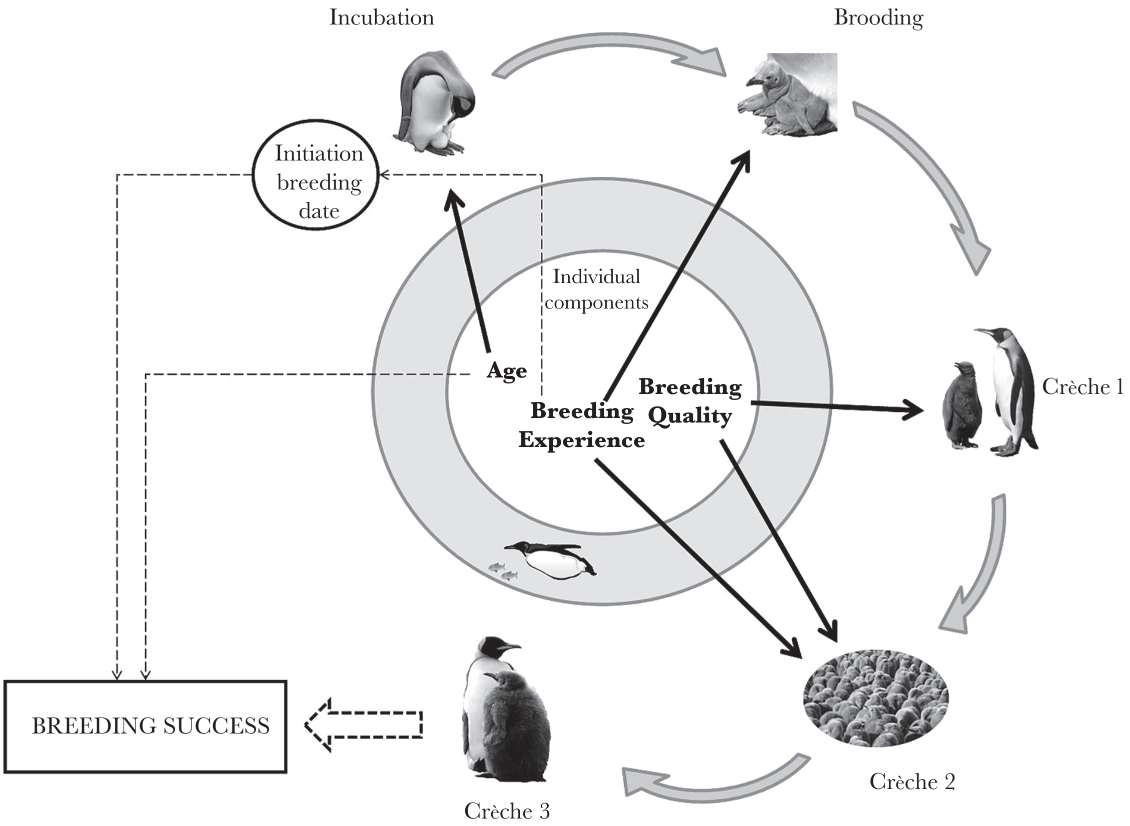

Figure 8
Individual components (i.e., age, breeding experience, and breeding quality) involve in king penguin foraging effort during the different phases of the breeding cycle (bold arrows) and affecting some components of individual fitness (i.e., initiation breeding date and breeding success) (dotted arrows).

areas rich in primary production, that is, around the Polar Front, which are between 300 and 700 km from Crozet Archipelago (Charrassin and Bost 2001), and at depths between 100 and 1000 m, depending on the time of the day (Koslov et al. 1991; Koubbi et al. 2001). Young penguins could have difficulties coping with these constraints and finding these rich areas. In addition, as air-breathing predators, king penguins are subjected to strong constraints linked with deep-diving activity (e.g., pressure, buoyancy, energetic expenditures; see Le Vaillant et al. 2012), especially during the sequences of repeated feeding dives of several minutes up to 350 m (Pütz and Cherel 2005). These constraints are a fortiori greater for younger and less experienced birds that are still likely to improve their diving abilities (e.g. Ponganis et al. 1999). The higher foraging effort and the lower foraging efficiency of young breeders (Le Vaillant et al. 2012, 2013) support the hypothesis of learning process in king penguins. Another hypothesis would be that the age-related differences in foraging trip duration found here result from intraspecific competition. Although it has not been noted in king penguins yet, cooperative foraging strategies with synchronous diving behavior have been observed in several diving birds (Hoffman et al. 1981; Tremblay and Cherel 1999; Takahashi, Sato, Naito, et al. 2004; Takahashi, Sato, Nishikawa, et al. 2004). Similarly, young black-browed albatrosses, *Thalassarche melanophris*, suffer from stronger intraspecific competition for resources than middle-aged individuals during abnormally warm sea surface temperature events (Pardo et al. 2013). Finally, given that, in the present study, 4- and 5-year-old king penguins started to breed 15–60 days later than older ones in 2009, the potential mismatch (Durant et al. 2007) of the younger breeders with the peak of resource availability may have led to greater difficulty in finding prey for these young birds, thereby increasing the duration of their foraging trips.

We found that the breeding quality of an individual affected the duration of its foraging trips during the brooding period and most of the crèching period. Yet, breeding experience and quality had a differential effect according to the period of the breeding cycle. Chick rearing is a costly period for parents that must feed not only for themselves but also for their chicks. During the brooding period and the second crèching period, individuals with a higher breeding experience performed shorter foraging trips than less experienced ones. The influence of breeding quality was also strong during the first crèching period during which parents have to feed their chicks even more frequently than during the brooding because the chick's needs are increasing with time (Barrat 1976). Individuals that reared several chicks successfully in the past might have more experience in dealing with the need to decrease foraging trip duration while increasing the energetic cost of foraging to provision their chicks more frequently. Alternatively, younger individuals potentially have more difficulty coping with winter environmental conditions, which is often seen as the most challenging period of the king penguin breeding cycle (Barrat 1976; Charrassin and Bost 2001). Breeders have to travel longer distances during the winter than during the summer time to find their prey (see the Figure 9 distances traveled by king penguins in summer [Bost et al. 1997] and in winter [Bost et al. 2004]). They also have to dive deeper and spend more time at the bottom phase (i.e., the phase during which penguins are close to their maximum dive depth in order to

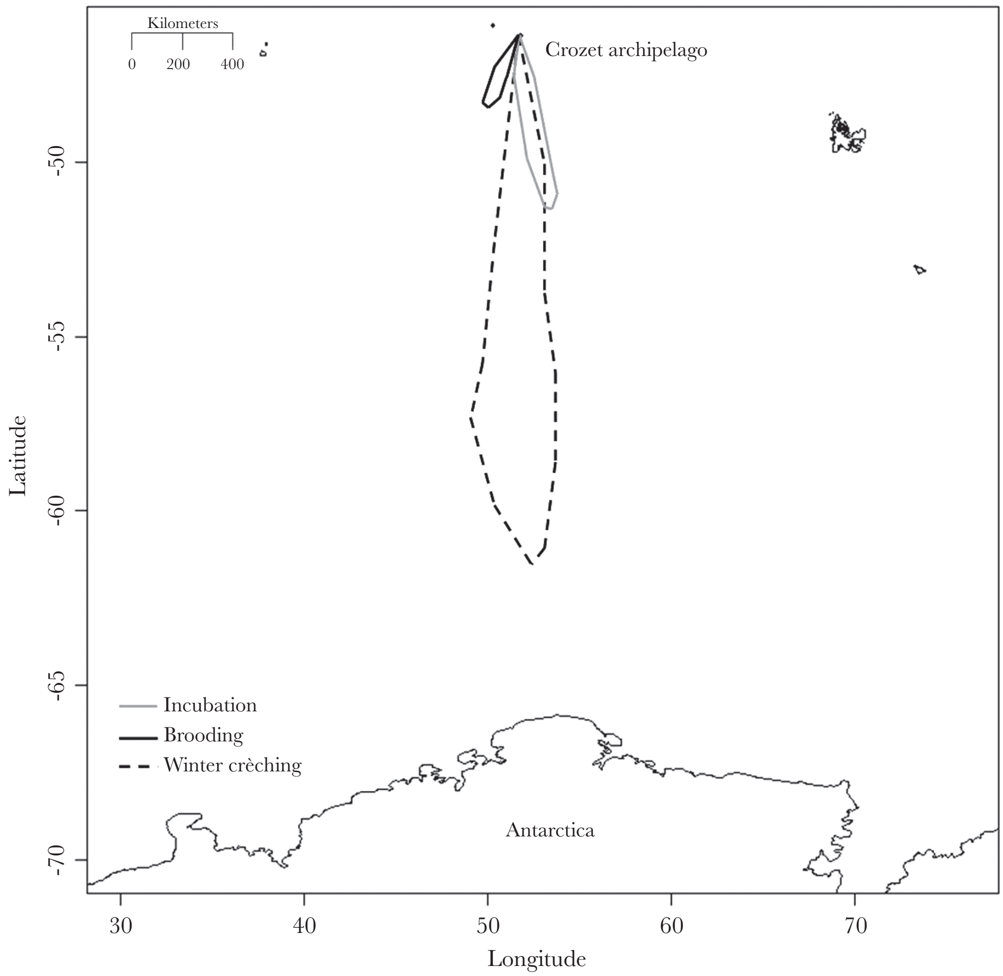

Figure 9

Illustration of the feeding routes taken by king penguins from Crozet archipelago during the austral summer (incubation period in solid dark line and brooding period in solid gray line) and winter (crèching period in dashed black line) (adapted from Charrassin and Bost 2001; Bost et al. 2004).

pursue and catch prey; see Ropert-Coudert et al. 2000; Charrassin et al. 2002), resources therefore being less available, more unpredictable, and/or more distant from the breeding site (Charrassin and Bost 2001; Olsson and van der Jeugd 2002). In this context, the breeding experience and quality of an individual are obviously decisive on the foraging performance. A study in Adélie penguins showed that higher-quality breeders were more efficient (i.e., they conducted shorter foraging trips and needed less recuperation time between 2 consecutive dives) than poor-quality ones during years of very harsh environmental conditions (Lescroël et al. 2010). King penguins with greater breeding experience and of higher breeding quality have already endured the harsh conditions of the austral winter during their past chick rearing events, making them more efficient in managing their foraging effort than younger ones.

Males perform longer foraging trips at sea during the incubation than females, confirming previous observations (Weimerskirch et al. 1992; Descamps et al. 2002). Males combine courtship period and first incubation shift on land (Barrat 1976), resulting in a fasting period that can last for up to 1 month (Cherel et al. 1988) and during which they lose more than 20% of their mass on average (Robin et al. 2001). To compensate for this extended fasting period, they subsequently perform a long foraging trip at sea to rebuild their reserves, longer than any other summer foraging trips and than that of females. During the winter period, females conducted longer trips and consequently achieved fewer foraging trips in the same time window. A slight sexual dimorphism exists in this species (Barrat 1976; Olsson and van der Jeugd 2002). Being smaller than males, females accordingly produce a greater foraging effort to catch and/or find prey, or to reach the remote feeding areas, especially during periods of lower resource availability. This higher effort might partly explain the lower survival probability of king penguin females during years of harsher environmental conditions compared with males (Olsson and van der Jeugd 2002). With the return of spring (i.e., Crèche 3) and the close proximity of resources to the colony, sex-related differences become less evident.

Finally, breeding success was affected by the age of individuals and by the breeding initiation date, which is itself influenced by the individual breeding quality. Our results are consistent with numerous studies on several long-lived species, with younger breeders, and/or individuals of lower breeding quality performing less well in terms of breeding activities than older breeders and/or individuals with greater breeding quality (Forslund and Pärt 1995; DeForest and Gaston 1996; Bowen et al. 2006; Ezard et al. 2007; Nisbet and Dann 2009; Moyes et al. 2011; Froy et al. 2013). As observed in other species, this lower breeding success has also been explained by the late breeding attempts of young birds during the season (DeForest and Gaston 1996; Ezard et al. 2007; McCleery et al. 2008). In our study, king penguins younger than 6-year-old did not rear a chick until fledging, and 66% of these birds failed during incubation. Accumulation of breeding experience with age would increase reproductive performances (Clutton-Brock 1988; Pardo et al. 2013) by improving accomplishment of the tasks linked to reproduction. With age, parents better protect their egg or/and the offspring against predators (Pyle et al. 1991; Bregnballe 2006) or they increase their foraging efficiency due to learning-based improvements in their foraging techniques (Jansen 1990; Bowen et al. 2006; Daunt et al. 2007), as suggested by the "Constraint Hypothesis" (i.e., at a given age, an individual may be constrained by its lake of experience/skills in breeding or foraging duties, for instance; Curio 1983). Nevertheless, our results show that the improvement in foraging performances with age may explain only a small part of the breeding success, age effects being only apparent during the incubation period.

In conclusion, our study on a long-lived seabird with an over-a-year breeding cycle highlights a complex interplay of age, breeding experience, and quality of the individual on the birds' foraging and breeding effort. Nevertheless, we show that breeding experience and quality play a key role during a costly part of the breeding period, that is, when birds are rearing a chick. The monitoring of behavioral and physiological traits in longitudinal foraging studies should allow us to better distinguish intraindividual aging patterns from selection processes and interindividual heterogeneity and would improve our understanding of aging and age-dependent foraging and breeding parameters, and their interactions with environmental variability.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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