

# Inter-individual differences in the foraging behavior of breeding Adélie penguins are driven by individual quality and sex

Amelie Lescroël<sup>1,\*</sup>, Phil O'B. Lyver<sup>2</sup>, Dennis Jongsomjit<sup>1</sup>, Sam Veloz<sup>1</sup>,  
Katie M. Dugger<sup>3</sup>, Peter Kappes<sup>4</sup>, Brian J. Karl<sup>2</sup>, Amy L. Whitehead<sup>5</sup>, Roger Pech<sup>2</sup>,  
Theresa L. Cole<sup>2,6</sup>, Grant Ballard<sup>1</sup>

<sup>1</sup>Point Blue Conservation Science, 3820 Cypress Drive, Suite 11, Petaluma, CA 94954, USA

<sup>2</sup>Manaaki Whenua Landcare Research, PO Box 69040, Lincoln 7640, New Zealand

<sup>3</sup>US Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA

<sup>4</sup>Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331, USA

<sup>5</sup>National Institute for Water and Atmosphere, PO Box 8602, Christchurch 8440, New Zealand

<sup>6</sup>Department of Zoology, University of Otago, PO Box 56, Dunedin 9054, New Zealand

**ABSTRACT:** Inter-individual differences in demographic traits of iteroparous species can arise through learning and maturation, as well as from permanent differences in individual 'quality' and sex-specific constraints. As the ability to acquire energy determines the resources an individual can allocate to reproduction and self-maintenance, foraging behavior is a key trait to study to better understand the mechanisms underlying these differences. So far, most seabird studies have focused on the effect of maturation and learning processes on foraging performance, while only a few have included measures of individual quality. Here, we investigated the effects of age, breeding experience, sex, and individual breeding quality on the foraging behavior and location of 83 known-age Adélie penguins at Cape Bird, Ross Sea, Antarctica. Over a 2 yr period, we showed that (1) high-quality birds dived deeper than lower quality ones, apparently catching a higher number of prey per dive and targeting different foraging locations; (2) females performed longer foraging trips and a higher number of dives compared to males; (3) there were no significant age-related differences in foraging behavior; and (4) breeding experience had a weak influence on foraging behavior. We suggest that high-quality individuals have higher physiological ability, enabling them to dive deeper and forage more effectively. Further inquiry should focus on determining the physiological differences among penguins of different quality.

**KEY WORDS:** Ross Sea · Breeding performance · Satellite telemetry · Foraging locations · Diving behavior · Age variation · Breeding experience · Seabirds

—Resale or republication not permitted without written consent of the publisher—

## 1. INTRODUCTION

Inter-individual differences in demographic traits of iteroparous species have been well demonstrated (e.g. Clutton-Brock 1988, Newton 1989, Massot et al. 2011). Through processes of learning and physio-

logical maturation, reproductive performance and survival tend to increase throughout early life and stabilize during early-to mid-adulthood. In older age classes, these fitness components either decrease (i.e. senescence due to mutation accumulation, Hamilton 1966; antagonistic pleiotropy, Williams 1957; or less

efficient DNA repair maintenance, Kirkwood 1977), remain constant (due to the removal of less proficient individuals, Cam et al. 2002; or high mortality levels before senescence can be detected, Kirkwood & Austad 2000), or increase (reproductive performance only, due to terminal investment, Stearns 1992, Descamps et al. 2007). Beyond true age, breeding experience also influences reproductive performance, with more experienced breeders often achieving higher breeding success (e.g. Sydeman et al. 1991, Daunt et al. 2007, Kappes 2019). It can also affect survival through costs of reproduction (Stearns 1992), with the first reproduction event often acting as a selective filter (Nevoux et al. 2007, Lescroël et al. 2009).

In addition to the learning and maturation processes, permanent differences in individual intrinsic 'quality' (i.e. demographic heterogeneity; Fox et al. 2006, Cam 2009) can also underlie inter-individual differences in demographic traits. While the specific mechanisms involved are still debated, some individuals can reproduce more successfully than others, often without exhibiting increased survival costs (Cam et al. 2002, 2016, Lescroël et al. 2009). As the ability to acquire energy from the surrounding environment determines the resources an individual can allocate to reproduction and self-maintenance, foraging behavior is a key trait to study to better understand the mechanisms underlying inter-individual differences in demographic traits.

Seabirds are a model organism to investigate inter-individual variation in foraging behavior (see review in Clay et al. 2018), due to their relative longevity, size, and accessibility, along with relatively well-known demographic rates for some species. While most studies have focused on the effect of maturation and learning on foraging performance (e.g. Catry et al. 2006, Daunt et al. 2007, Lecomte et al. 2010, Elliott et al. 2015, Froy et al. 2015), only a few studies have included measures of individual heterogeneity (Lewis et al. 2006, Lescroël et al. 2010, 2019), while even fewer have combined both types of data (Lewis et al. 2006, Lescroël et al. 2019). While it has been shown that foraging performance is highest in mature, experienced breeders, evidence for age-related changes in foraging performance of seabirds later in life remains limited and inconsistent across species and geographic locations (e.g. little blue penguins *Eudyptula novaehollandiae*, Zimmer et al. 2011, Pelletier et al. 2014; wandering albatrosses *Diomedea exulans*, Lecomte et al. 2010, Froy et al. 2015). Nevertheless, it remains difficult to couple long-term demographic data and foraging behavior of known individuals.

As seabirds are central-place foragers during the breeding period (Orians & Pearson 1979), they are spatially and temporally constrained in their movements. Moreover, the frequency of feeding can affect chick growth rates and fledging-mass-related prospects for subsequent survival (Salihoglu et al. 2001, Chapman et al. 2011, Ainley et al. 2018). It is therefore important for breeding birds to forage as close and as quickly as possible to their breeding colony. The degree to which breeding seabirds attempt to maximize energy intake per energy spent or unit time may depend on their sex. For example, if one sex invests more in nest defense activities (e.g. males in black-legged kittiwakes *Rissa tridactyla*, Jodice et al. 2002), then that sex is more likely to focus on maximizing energy intake per unit time so as to also maximize time spent at the colony. Sexual differences in foraging behavior are common among seabirds, including within species with little or no sexual dimorphism (e.g. Lewis et al. 2002). These differences have been explained either by a sex-specific allocation of foraging effort between parents and offspring (Thaxter et al. 2009), differences in time spent defending the nest (Wanless & Harris 1986, Creelman & Storey 1991, Fraser et al. 2002), or spatial segregation due to intraspecific competition or habitat selection (Cleasby et al. 2015). It has also been suggested that in dimorphic species, trophic differences could be driven by differences in physiological performance, with the larger sex tending to dive deeper to access higher trophic level prey items (Bearhop et al. 2006). Finally, to fully understand the ecological constraints and performance of diving seabirds, it is important to take into account not only their horizontal movements (i.e. how far away from the colony they travel) but also the vertical component of their foraging behavior (i.e. how deep they dive).

Drawing upon a long-term study of Adélie penguins *Pygoscelis adeliae* in the Ross Sea, Antarctica, Lescroël et al. (2009) found evidence of individual heterogeneity among breeding adults. Other studies also found that the level of intraspecific competition as a function of colony size can lead to differences in foraging behavior (Ainley et al. 2004, Lescroël et al. 2010). At Cape Crozier, the largest colony in this ongoing study (>300 000 breeding pairs), differences in foraging behavior under harsh environmental conditions correlated to differences in intrinsic quality, with high 'quality' breeders foraging more efficiently (Lescroël et al. 2010). Furthermore, under 'normal' environmental conditions, Lescroël et al. (2019) found a positive effect of age, either linear or leveling off at old ages, on the foraging performance of

Adélie penguins breeding at Cape Crozier. The Adélie penguin is a slightly dimorphic species, with adult males on average larger than adult females in mass (~11%) as well as bill (~8%) and flipper length (~3%) (Ainley & Emison 1972). Across all age classes, males were found to be more efficient foragers than females (Lescroël et al. 2019). These previous studies only focused on diving behavior; the spatial (horizontal) aspect of inter-individual differences in foraging behavior is less understood. To generalize and extend these conclusions, we tested the following hypotheses in a medium-size Adélie penguin colony (Cape Bird: ~70 000 breeding pairs) over 2 consecutive breeding seasons (2009–2010 and 2010–2011): (1) among intrinsic factors, age and breeding experience are the main drivers of inter-individual differences in the foraging behavior of seabirds; and (2) other sex-, age-, and experience-independent factors such as superior, genetically determined physiological ability or other inherent individual differences, summarized under the concept of ‘individual quality’ (Wilson & Nussey 2010), are the main drivers of inter-individual differences in the foraging behavior of seabirds.

## 2. MATERIALS AND METHODS

### 2.1. Satellite tag deployment

Our study was conducted at Cape Bird (77° 13' S, 166° 26' E), Ross Island, Antarctica, during the guard (December) and crèche (January) stages of the 2009–2010 (hereafter 2009) and 2010–2011 (hereafter 2010) austral breeding seasons. Between 20 December and 19 January, a total of 83 breeding Adélie penguins (40 in 2009; 43 in 2010) of known ages were equipped with SPLASH tags that weighed 62 g (1.6% of an average adult penguin) and measured  $3.2 \times 10^{-4} \text{ m}^2$  (1.0–1.6% of an adult's total size; Wildlife Computers). Birds were caught by hand on the nest and equipped with a SPLASH tag using black Tesa® tape (see Ballard et al. 2001 for more details). The tags recorded depth, light intensity, and temperature every 1 s, and they uploaded short periodic messages to Argos satellites ([www.argos-system.org/](http://www.argos-system.org/)) for horizontal position calculations. Tags were set to transmit (when dry) to Argos every 45 s for the first 8 successive transmissions and then switch to once every 90 s thereafter, with up to 1440 transmissions allowed per day. Tags were programmed to turn off after being dry for 6 h in order to conserve batteries, but to turn back on as soon as

they were wet. Between 1 and 3 foraging trips, lasting from 0.55–5.92 d, were recorded for each equipped individual; only the first trip of each individual was kept for analysis. Each individual was only sampled once over the 2 seasons.

### 2.2. Data processing and filtering

All satellite transmissions were received and processed within the Argos system (CLS Corporation). Satellite positions were filtered using the ‘argosfilter’ package in R (Freitas 2012), which first removes all locations with location Class Z, which are points for which the location process failed. All locations that required unrealistic swimming speeds ( $>2.3 \text{ m s}^{-1}$ ) were removed unless the point was  $<5 \text{ km}$  from the previous location. Finally all spikes in the animal's path with angles smaller than 15 and 25° were removed if their extension was higher than 2500 and 5000 m, respectively (Freitas et al. 2008). As a result, an average of  $17.6 \pm 16.7$  locations  $\text{ind.}^{-1}$  were kept, for a total of 1409 locations. Out of these, 141 had Class 3 location errors ( $<250 \text{ m}$  estimated error), 266 had Class 2 location errors ( $>250$  and  $<350 \text{ m}$ ), 301 had Class 1 location errors ( $>350$  and  $<1500 \text{ m}$ ), 156 had Class 0 location errors ( $>1500 \text{ m}$ ), and 545 had Class A and B location errors (no accuracy estimation). Because raw Argos positions are biased by satellite orbital parameters and the penguins' latitudinal positions (Georges et al. 1997), we used a linear interpolation algorithm (Tremblay et al. 2006) to create a temporally uniform interpolated distribution of locations every 1 min between known locations. This 1 min interpolation interval was chosen so as to be able to assign a different geographic location to every dive, as Adélie penguins dive continuously throughout their trip (Ford et al. 2015). Because of the differences in temporal resolution between the dive (1 s) and satellite (1 min, after interpolation) data, we used temporal proximity to assign an approximate geographic location to each dive (cf. Ballard et al. 2019). Great circle distance (i.e. the shortest distance between 2 points on the surface of a sphere, measured along the surface of the sphere) for foraging trip locations were calculated in km to a single point representing the center of the North Cape Bird colony location using the ‘argosfilter’ package.

Diving data were processed using the program *divesum v.7.5.5* (G. Ballard unpubl. software; cf. Lescroël et al. 2010, Ballard et al. 2019). This program corrected the record baseline and computed several individual dive parameters, including maxi-

mum dive depth for each dive, post-dive recovery intervals, and the number of undulations (number of changes in underwater swimming direction from ascent to descent  $>1$  m). Considering the SPLASH tag specifications (resolution of depth sensor:  $\pm 0.5$  m) and sample rate (1 Hz), only dives  $\geq 1$  m deep and  $\geq 3$  s long were included. The divesum program classified dives into 3 types: 'foraging', 'exploratory', and 'other' (Chappell et al. 1993, Ropert-Coudert et al. 2001, Schreer et al. 2001, Bost et al. 2007, Lescroël et al. 2010). Foraging and exploratory dives were both at least 10 m. Foraging dives had  $\geq 4$  undulations and either (1)  $\geq 15$  s bottom time, (2) 30% of the dive duration spent in slow depth change rate and 30% with fast depth change rate, or (3)  $\geq 6$  undulations and rapid ( $\geq 1$  m  $s^{-1}$ ) ascent/descent phases. Exploratory dives had  $< 4$  undulations or  $< 15$  s bottom time and fewer than 6 undulations. All other dives were categorized as 'other' and are thought to be primarily commuting dives. The number of undulations performed within each foraging dive is thought to reflect the number of prey caught during that dive (Ropert-Coudert et al. 2001, Bost et al. 2007, Ballard et al. 2019).

### 2.3. Potential intrinsic drivers of foraging behavior

#### 2.3.1. Age

In Adélie penguins, age at first breeding is highly variable and ranges from 3 to 12 yr (mean  $\pm$  SD: females:  $5.5 \pm 1.3$ ,  $n = 584$ ; males:  $5.9 \pm 1.5$ ,  $n = 704$ ; V. Morandini et al. unpubl. data). Banding studies have shown that some individuals reach 20+ yr of age and are still breeding into their late teens (Ainley 2002, K. M. Dugger, D. G. Ainley, & G. Ballard unpubl. data). Equipped birds were banded as chicks on the left flipper with a numbered stainless steel band (see Dugger et al. 2006 for details on band design and effect or lack thereof on foraging behavior) and were aged 3–14 yr old when they were equipped with a SPLASH tag. The oldest age class of banded penguin that was present at Cape Bird was 14 yr. Because our sample was more limited in size and less homogeneously spread across all ages than in previous studies (Grémillet et al. 2018, Lescroël et al. 2019), we chose to divide it into 3 age groups: young (3–6 yr old,  $n = 18$ ), mature (7–10 yr old,  $n = 38$ ), and old (11–14 yr old,  $n = 27$ ) breeders, rather than use age as a continuous variable. Groups were based on these previous studies and our knowledge of Adélie penguin biology (Ainley 2002).

#### 2.3.2. Sex

We genetically determined the sex of each individual by extracting the DNA from feather samples, undertaking PCR using sex-determining primers, and visualizing the amplified DNA under electrophoresis (Zhang et al. 2013). Feather samples were collected from each individual when SPLASH tags were retrieved. A total of 39 females and 44 males was equipped with tags; 15 females, 25 males in 2009 and 24 females, 19 males in 2010. Our samples included a higher proportion of females in the young age class than in the old age class, reflecting the lower age at first breeding for females (Ainley & DeMaster 1980, Ainley et al. 1983, Morandini et al. unpubl. data), but making it more difficult to disentangle the respective effects of sex and age.

#### 2.3.3. Breeding experience

Several seabird studies have shown that experienced breeders are better foragers than naïve breeders (e.g. Daunt et al. 2007, Limmer & Becker 2009). We hypothesized that trying to feed chicks during the first year of breeding was a significant learning event that would improve the foraging performance of birds in subsequent years. Alternatively, the first reproductive event could act as a selective filter, with lower-quality individuals experiencing higher costs and higher mortality (Cam & Monnat 2000, Barbraud & Weimerskirch 2005, Beauplet et al. 2006, Nevoux et al. 2007, Lescroël et al. 2009). Therefore, we divided our samples between 2 groups based on breeding experience: (1) inexperienced birds with no previous breeding experience ( $n = 22$ ) and (2) experienced birds with at least 1 yr of previous breeding experience ( $n = 61$ ).

#### 2.3.4. Individual quality

Based on the assumption that superior, genetically determined physiological ability or other inherent individual differences lead to superior breeding outcomes (supported by Lescroël et al. 2009), we used the Breeding Quality Index (BQI) of each equipped individual as an index of their age-independent 'individual quality' (Grémillet et al. 2018). After being banded as chicks, birds were followed every year to determine whether they survived, attempted to breed, and raised at least 1 chick to the crèche stage. We first calculated a probability of breeding success for each

year and individual using 4 independent variables (age, previous breeding experience, colony of origin, and breeding year). The BQI of each individual was then calculated as the mean per individual of the difference between the actual breeding success and the predicted breeding success for every year during which a given individual had been re-sighted when at least 3 yr old, up to the year when we equipped it with a SPLASH tag. More details about the BQI calculation for known-age birds can be found in Grémillet et al. (2018). Negative BQI values indicate lower than average long-term breeding performance, while positive values indicate above average long-term breeding performance. BQI for the equipped birds in this study ranged from  $-0.26$  to  $0.57$ . Because our sample was limited in size and not homogeneously spread across all BQI values, we decided to use BQI classes rather than BQI as a continuous variable. Based on the BQI frequency distribution in the banded bird population of Cape Bird in 2009 and 2010, we divided our sample into 3 quality classes: (1) low-quality ( $BQI < 0$ ,  $n = 34$ ), (2) medium-quality ( $0 \leq BQI \leq 0.35$ ,  $n = 34$ ), and (3) high-quality ( $BQI > 0.35$ ,  $n = 10$ ) individuals. Out of the 83 equipped birds, 5 were re-sighted for the first time since being banded as chicks and could not be assigned a BQI value.

## 2.4. Foraging behavior variables

### 2.4.1. Predictions

We tested the following 8 predictions (Pred.) derived from our initial hypotheses:

Pred. (1.1) Older, more experienced birds exhibit more dive undulations (1.1a) closer to the colony (i.e. exhibit lower maximum foraging distances), or at (1.1b) greater depths.

Pred. (1.2) Older, more experienced birds exhibit (1.2a) shorter trip durations, (1.2b) a fewer number of foraging dives, or (1.2c) more undulations per foraging dive.

Pred. (1.3) Pred. (1.1) and (1.2) result in niche partitioning among age classes in terms of both (1.3a) foraging distance to the colony (i.e. there is a low 2-dimensional [2D] spatial overlap among age classes), and (1.3b) foraging distance to the sea surface (i.e. there is a low 3-dimensional [3D] spatial overlap among age classes).

Pred. (2.1) High-BQI birds exhibit more dive undulations (2.1a) closer to the colony (i.e. exhibit lower maximum foraging distances), or at (2.1b) greater depths.

Pred. (2.2) High-BQI birds exhibit (2.2a) shorter trip durations, (2.2b) a fewer number of foraging dives, or (2.2c) more undulations per foraging dive.

Pred. (2.3) Pred. (2.1) and (2.2) result in niche partitioning among BQI classes in terms of both (2.3a) foraging distance to the colony (i.e. there is a low 2D spatial overlap among age classes), and (2.3b) foraging distance to the sea surface (i.e. there is a low 3D spatial overlap among BQI classes).

As sex-related differences in foraging behavior have often been found in Adélie penguins (Clarke et al. 1998, Ballard et al. 2001, 2010a, Lescroël et al. 2010), we accounted for sex in testing these predictions (see Section 2.5).

### 2.4.2. Trip duration

We determined trip duration, in days, for each individual bird using the depth and temperature profiles recorded by the SPLASH tags. Trip duration was calculated as time elapsed between first entrance in the water (shown by a drop in temperature to  $-1.8^{\circ}\text{C}$ , followed by a first shallow dive) and exit at the end of the at-sea period (shown by a return to higher temperatures and stable, 0 m depth).

### 2.4.3. Maximum foraging distance

Maximum foraging distance, in km, was calculated based on the Argos location data, as the great circle distance between the most distant foraging trip location and the center of the northern-most portion of the Cape Bird colony.

### 2.4.4. Foraging dives, depth, number of undulations, and post-dive intervals

For each individual trip, we considered the number of dives classified as 'foraging', the maximum depth of each foraging dive, and the number of undulations performed within each foraging dive. Adélie penguins, like many other seabirds and marine mammals, dive in bouts, with most dives occurring in rapid succession with longer temporal gaps between bouts. To separate post-dive recovery intervals (PDIs) from inter-bout duration, we used a maximum likelihood approach (Luque & Guinet 2007) using the 'diveMove' package (Luque 2007) in R, which allowed us to determine a bout-ending-criterion (BEC). In this study,  $BEC = 63.9$  s; we therefore only considered PDIs  $< 64$  s.

#### 2.4.5. Space use overlap

To examine the 2D space use of the different age, sex, experience, and BQI classes, we developed 2D utilization distributions (UD) using foraging locations and a fixed-kernel density estimation (Worton 1989) with the 'adehabitatHR' package in R (Calenge 2006). The UD can be defined as the probability density that an animal is found at a given location. To define this space for the classes varying in numbers of individuals (e.g. age, BQI, etc.), we calculated the UD for each individual in a given class, then calculated the average UD value across all individuals within any given grid cell. To visualize the UD distributions, we created 50% UDs for each class. We considered the 50% probability contour to be the 'core' of an individual's home range (e.g. Simpfendorfer et al. 2012). Individual kernels were estimated with a constant smoothing parameter ( $h = 2000$ ) based on the average Argos type in our data and error estimates provided by Boyd & Brightsmith (2013). The space use overlap between classes was quantified with the 'kerneloverlap' function in 'adehabitatHR' (Calenge 2006), using Bhattacharyya's affinity (BA) and the utilization distribution overlap index (UDOI) as recommended by Fieberg & Kochanny (2005). The BA index is a general measure of similarity between UD estimates and varies between 0 (no overlap) and 1 (complete overlap), whereas the UDOI quantifies space-use sharing where values  $<1$  indicate less overlap and values  $>1$  indicate higher overlap, relative to uniform space use.

While satellite positional data allowed us to track the horizontal movements of the penguins, the addition of dive data gave us the ability to examine their use of 3D space. To do this, we developed 50% distributions using a 3D kernel estimator with the 'ks' package (Duong 2013) in R. Kernels were smoothed using the plug-in bandwidth ( $H$ ) selector (Gitzen et al. 2006, Duong 2007) calculated as the average  $H$ -value across all individuals. Similar to the 2D kernels, we first built UD kernels for each individual in a given class, then averaged across the individuals by cell (in 3D space) to get an average 3D UD for each class. Following Simpfendorfer et al. (2012), we accounted for the uncertainty in the positional data by multiplying the smoothing factor by a value  $>1$ . To determine this multiplier, we calculated the 50% UD for each age and BQI class and multiplied the smoothing factor by values from 1 to 10. We then determined the amount of change in the ratios between the 50% UDs for each multiplier value. We standardized this amount of change by dividing by the aver-

age ratio across all multiplier values. Finally, we calculated the standardized change values for each multiplier and we used the multiplier closest to one with the smallest change. In our case, this multiplier was 3. UDOI was calculated using the 'ks' package in R, as the number of 3D pixels that overlapped between the different classes multiplied by the volume of each 3D pixel, making sure to standardize the pixel size across classes. We also calculated BA values with adaptations for 3D data as defined in Cooper et al. (2014).

## 2.5. Statistical analyses

To investigate the separate effects of sex, season, age, BQI, and breeding experience, we used ANOVAs (followed by Tukey's post hoc tests to detect differences between groups) for the variables calculated at the scale of the trip (trip duration, maximum foraging distance, number of foraging dives), and linear mixed models with bird ID as a random effect for variables calculated at the scale of the dive (maximum foraging depth, number of undulations per dive). As we had an unbalanced number of males and females by age class, with more young females and more old males, we first tested for an effect of sex on our variables of interest and if there was one, we tested for an effect of age or BQI within each sex class. Otherwise, both sexes were pooled. We also separately tested for the effect of the study season, including season as an additive fixed effect together with age or BQI in subsequent models for those variables for which there was an effect of the season, pooling data from different seasons together when there was not. Because breeding experience was correlated with age, with all young birds having no previous breeding experience and old birds all having at least 1 yr of previous breeding experience, we tested for the effect of breeding experience on birds aged 6–8 only. As there was the same number of females ( $n = 14$ ) and males ( $n = 14$ ) in this age class, we were able to explore the effect of breeding experience across sexes.

In an attempt to further understand the effects of individual quality (as proxied by BQI) on diving performances, we also looked at the effects of BQI on the relationship between (1) PDIs and maximum dive depth, and (2) PDIs and maximum dive duration, using linear mixed models with bird ID as a random effect nested within season. Linear mixed models were implemented with the 'nlme' package (Pinheiro et al. 2017) in R and we included an autocorrelation

structure ('corAR1', an autoregressive process of order 1) in order to account for the temporal autocorrelation between dives. All statistics were performed using R v.3.4.2 (R Development Core Team 2017). Means  $\pm$  SE are given unless indicated otherwise.

### 3. RESULTS

#### 3.1. Trip duration

Female Adélie penguins took significantly longer trips ( $1.44 \pm 0.14$  d) than males ( $1.09 \pm 0.04$  d;  $F_{1,87} = 6.35$ ,  $p = 0.014$ ). There were no significant differences between breeding seasons ( $F_{1,87} = 1.58$ ,  $p = 0.212$ ) so we pooled data from both years. Age did not significantly influence trip duration within females ( $F_{2,36} = 0.39$ ,  $p = 0.681$ ) or males ( $F_{2,41} = 0.54$ ,  $p = 0.585$ ), nor did BQI ( $F_{2,31} = 0.76$ ,  $p = 0.474$  for females;  $F_{2,41} = 0.16$ ,  $p = 0.851$  for males). For birds aged 6–8 yr, there were no significant differences in trip duration between inexperienced and experienced individuals ( $F_{1,30} = 1.38$ ,  $p = 0.249$ ).

#### 3.2. Maximum foraging distance

Differences in trip duration between females and males did not translate into significant differences in the maximum foraging distance from the colony ( $34.77 \pm 5.08$  km for females,  $26.36 \pm 1.90$  km for males;  $F_{1,67} = 2.57$ ,  $p = 0.114$ ). We observed a significant difference in maximum foraging distance between seasons, with shorter maximum distance traveled in 2009 compared to 2010 ( $24.59 \pm 1.57$  km in 2009,  $36.69 \pm 5.09$  km in 2010;  $F_{1,67} = 5.55$ ,  $p = 0.022$ ). Thus, season was included in further models. There was no significant difference in foraging distance with age ( $F_{2,65} = 0.75$ ,  $p = 0.476$ ), BQI ( $F_{2,61} = 0.14$ ,  $p = 0.872$ ), or breeding experience ( $F_{1,20} = 1.97$ ,  $p = 0.176$ ).

#### 3.3. Number of foraging dives

Females performed significantly more foraging dives ( $378.10 \pm 29.20$  dives) than males ( $288.07 \pm 16.22$  dives;  $F_{1,81} = 7.71$ ,  $p = 0.007$ ) on a given foraging trip. The number of foraging dives per trip did not vary between seasons ( $F_{1,81} = 0.17$ ,  $p = 0.680$ ). Within each sex, the number of foraging dives did not differ significantly among age classes ( $F_{2,36} = 0.42$ ,  $p = 0.659$  for females;  $F_{2,41} = 0.03$ ,  $p = 0.969$  for males) or BQI classes ( $F_{2,31} = 0.14$ ,  $p = 0.871$  for females;  $F_{2,41}$

$= 0.44$ ,  $p = 0.650$  for males). High-quality individuals, however, exhibited less variability among individuals of the same category (SD = 108.53 for females, 40.88 for males) than medium (SD = 158.42 for females, 118.43 for males) or low-quality birds (SD = 222.40 for females, 110.03 for males). There was no significant effect of breeding experience ( $F_{1,28} = 1.43$ ,  $p = 0.242$ ).

#### 3.4. Average maximum foraging depth

Average maximum foraging depth did not differ between females ( $43.93 \pm 3.02$  m) and males ( $45.36 \pm 4.16$  m;  $t_{81} = 0.34$ ,  $p = 0.731$ ) or between seasons ( $t_{81} = 1.63$ ,  $p = 0.107$ ), age classes ( $t_{80} = 0.80$ ,  $p = 0.428$  for mature breeders compared to young breeders;  $t_{80} = 0.27$ ,  $p = 0.786$  for old breeders compared to young breeders) or breeding experience ( $t_{28} = -0.04$ ,  $p = 0.968$ ). High-quality birds, however, dived significantly deeper ( $57.59 \pm 6.56$  m;  $t_{75} = 2.09$ ,  $p = 0.040$ ) than either low ( $43.85 \pm 3.14$  m) or medium-quality ones ( $44.32 \pm 4.44$  m).

#### 3.5. Number of undulations per dive

The number of undulations per foraging dive did not vary between sexes ( $t_{81} = 0.25$ ,  $p = 0.803$ ) but was higher in 2009 ( $4.28 \pm 0.18$  undulations) than in 2010 ( $3.72 \pm 0.25$  undulations;  $t_{81} = -2.24$ ,  $p = 0.028$ ). Taking into account the effect of season, mature ( $t_{79} = 0.34$ ,  $p = 0.736$ ) and old breeders ( $t_{79} = 0.67$ ,  $p = 0.502$ ) did not perform significantly more undulations than young breeders. High-quality birds, however, performed more undulations per dive ( $4.99 \pm 0.40$  undulations;  $t_{74} = 2.02$ ,  $p = 0.047$ ) than medium ( $4.12 \pm 0.27$  undulations) and low quality ones ( $4.18 \pm 0.24$  undulations). Experienced breeders also tended to perform slightly more undulations per dive ( $4.34 \pm 0.53$  undulations) than inexperienced individuals ( $3.47 \pm 0.53$  undulations), but this difference was not statistically significant ( $t_{27} = 1.63$ ,  $p = 0.114$ ).

#### 3.6. Post-dive intervals

High-BQI birds exhibited shorter PDIs than medium- or low-BQI birds ( $t_{74} = -5.09$ ,  $p < 0.001$ ) after deep dives ( $>85$  m; Fig. 1). When looking at the relationship between PDI and dive duration for dives deeper than 85 m, we found that low-BQI birds showed increasing PDIs for increasing dive durations

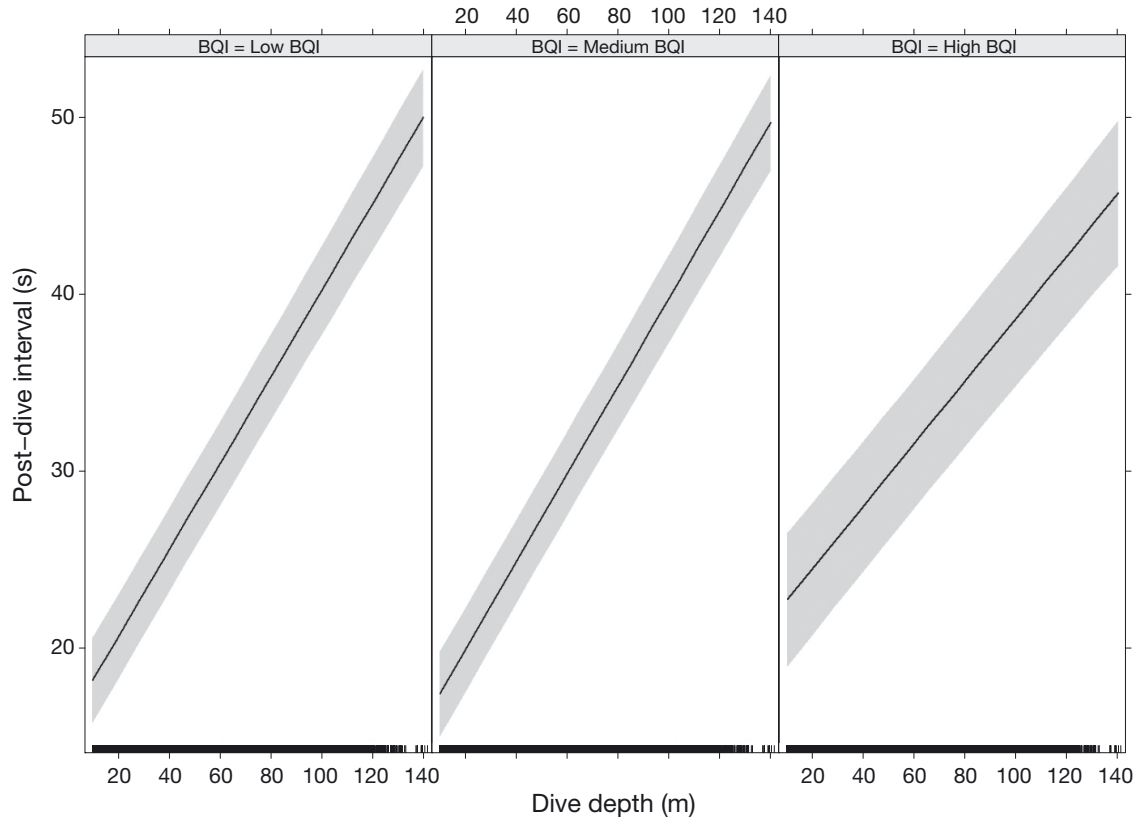


Fig. 1. Post-dive recovery interval duration versus depth of the previous dive depending on the breeding quality index (BQI) class of the foraging individual for Adélie penguins breeding at Cape Bird. Black line: prediction; gray shading: 95% CI

( $t_{25} = -2.43$ ,  $p = 0.015$ ) while medium- and high-BQI birds surprisingly showed decreasing PDIs for increasing dive durations (Fig. 2). Overall, high-BQI birds exhibit shorter PDIs than low-BQI birds when dive duration exceeds 193 s, and shorter PDIs than medium-BQI birds when dive duration exceeds 217 s.

### 3.7. Spatial use overlap

The 2D overlap in 50% core areas was high (>50% overlap) among sexes (Table 1, Fig. 3A), seasons (Table 2, Fig. 3B), and age classes (Table 3, Fig. 3C). Old birds had a more restricted core area (19.98 km<sup>2</sup>) than young (30.76 km<sup>2</sup>) and mature (30.04 km<sup>2</sup>) individuals. The most notable difference in horizontal habitat use was among BQI classes, with low overlap between high-BQI birds and either medium- or low-BQI birds (Table 4, Fig. 3D). All birds foraged west and north of the breeding colony, but high-BQI birds also exhibited concentrated foraging activity to the southwest, within McMurdo Sound. Overlap was also low between breeding experience classes (Table 5, Fig. 3E), with experienced birds (aged 6–8 yr) showing a more extended core area, espe-

cially to the west, compared to inexperienced ones.

The 3D overlap in 50% core volumes tended to be lower than 2D overlap for all groups, showing additional differentiation in vertical habitat use (Tables 1–5). Males seemed to forage deeper than females just north of the colony (Fig. 4A), even though sex differences in diving depth were not significant overall and the 50% core volume of females was larger (Table 1). The 50% core volume exploited by Adélie penguins was larger in 2010 than 2009 (Table 2), with birds foraging in the same 3D space in 2010 as in 2009 but also exploiting deeper areas, farther away (Fig. 4B). In terms of age, young birds showed the most different 50% core volumes (Table 3) compared to the 2 other age classes, tending to exploit shallower depths in areas slightly farther away from the colony (Fig. 4C). High-BQI birds showed very little 3D overlap with either medium- or low-BQI birds (Table 4), concentrating their effort at deeper depths and further to the southwest of the colony (Fig. 4D). Finally, experienced breeders had a much bigger 3D foraging volume than inexperienced birds (Table 5), but there was no other obvious difference in their use of the water column (Fig. 4E).



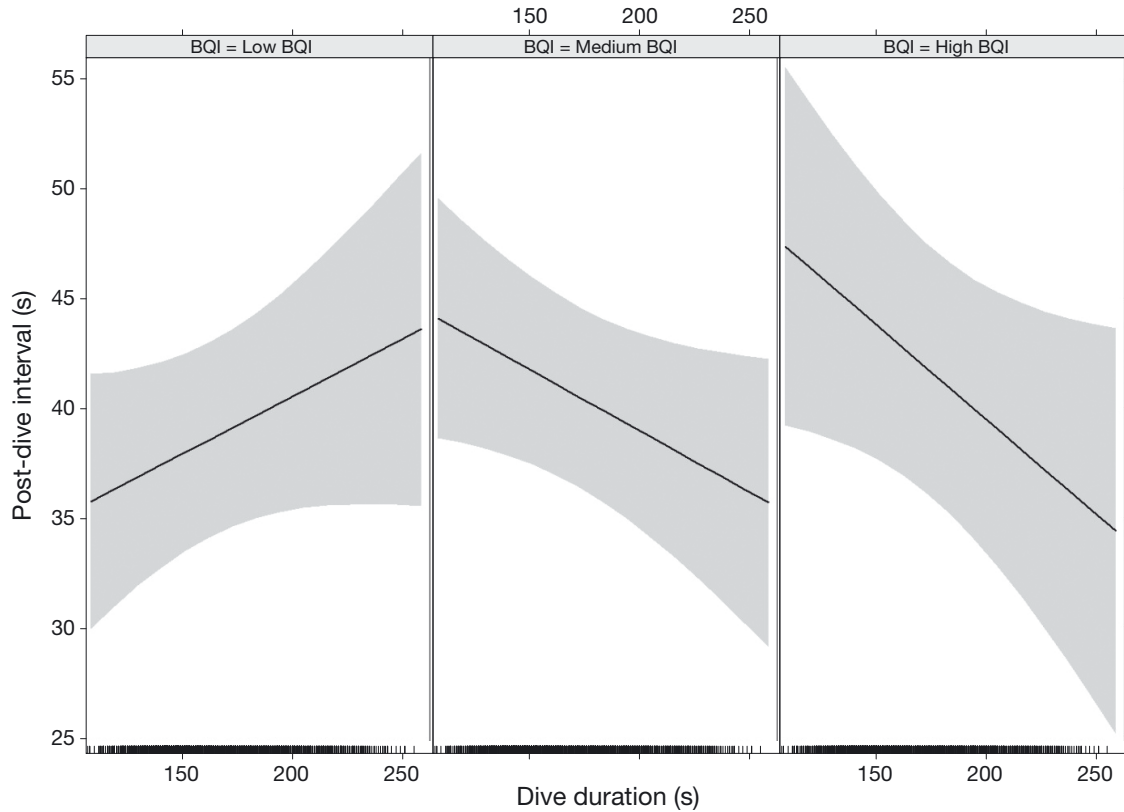


Fig. 2. Post-dive recovery interval duration versus duration of the previous dive (for dives >85 m) depending on the breeding quality index (BQI) class of the foraging individual for Adélie penguins breeding at Cape Bird. Black line: prediction; gray shading: 95% CI

Table 1. Adélie penguin 2D and 3D spatial use depending on sex. The % overlap is presented as the percentage of core area for the group in the row covered by the core area for the group in the column. UD50: the 50% utilization distribution area (in km<sup>2</sup> for 2D) or volume (in km<sup>3</sup> for 3D). Bhattacharyya's affinity (BA) index is also calculated for core areas, where BA = 1.00 indicates exact similarity

Sex	UD50	-% overlap-		-BA index-		
		F	M	F	M	
2D	F	33.23	1	0.60	1.00	-
	M	22.78	0.85	1	0.88	1.00
3D	F	15.63	1	0.47	1.00	-
	M	12.11	0.61	1	0.73	1.00

#### 4. DISCUSSION

Contrary to our first set of predictions, we found no significant differences among age classes in the foraging variables that we examined, and only limited differences among experience categories (Table 6). On the other hand, high-BQI birds dived deeper than medium- or low-BQI birds, exhibited more undulations, and targeted different foraging locations in terms of both horizontal and vertical habitat use. Sex

was also a significant driver of inter-individual variation in foraging behavior, as females performed more foraging dives during longer trips.

##### 4.1. Seasonal variation in foraging behavior

Seasonal foraging pattern differences are well known in seabirds, as they respond to variability in the availability and distribution of food resources (e.g. Suryan et al. 2002, Daunt et al. 2006, Cherel et al. 2007, Ainley et al. 2015). In 2010, Adélie penguins foraged farther away from the colony, although not for significantly longer time periods, to achieve the same number of foraging dives at the same depth. Although we do not know what prey they ingested, the lower number of undulations per dive suggests birds experienced fewer prey items in 2010 compared to 2009, consistent with the supposition that availability of prey, in terms of prey species, habitat, and abundance, differed between the 2 study years. However, there was no major difference in the spatial location of the core foraging areas between seasons; these areas were located to the north and west of the breeding colony, with an additional smaller

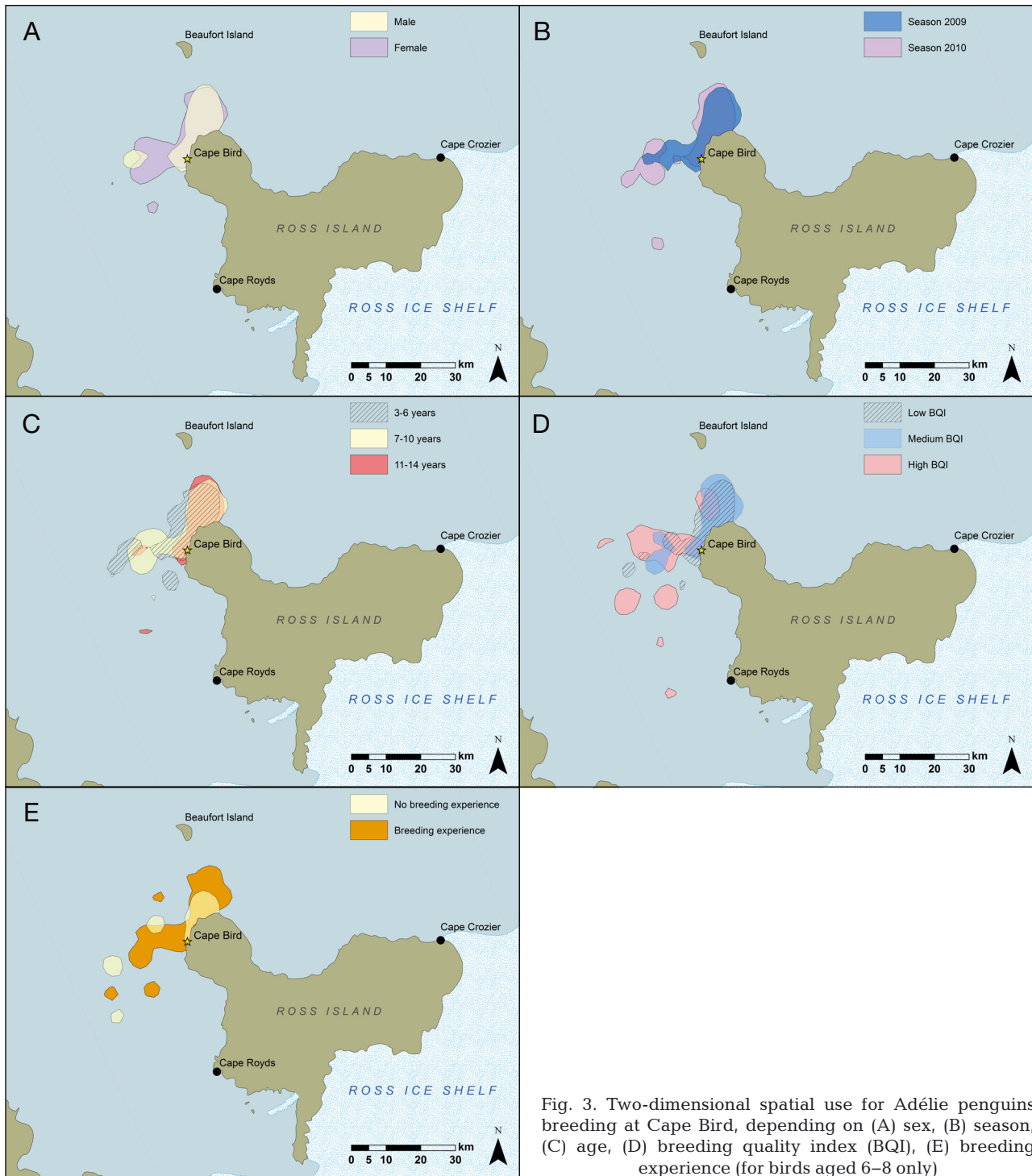


Fig. 3. Two-dimensional spatial use for Adélie penguins breeding at Cape Bird, depending on (A) sex, (B) season, (C) age, (D) breeding quality index (BQI), (E) breeding experience (for birds aged 6–8 only)

area to the southwest in 2010. Despite the suspected lower prey availability in 2010, breeders were still able to provision their chicks regularly, with trips lasting  $1.39 \pm 0.92$  d (mean  $\pm$  SD,  $n = 43$ ), while breeders from the larger Cape Crozier colony, where high levels of intra- and interspecific competition

lead to seasonal prey depletion (Ainley et al. 2004, 2006, 2015), were at sea for  $1.97 \pm 1.64$  d (mean  $\pm$  SD,  $n = 42$ ) in the same year (Lescroël et al. 2019). Thus, while there may have been differences in the preyscape between the 2 years, nothing appeared to be out of the typical range of variation.

Table 2. Adélie penguin 2D and 3D spatial use depending on season. See Table 1 for details

	Season	UD50	% overlap		BA index	
			2009	2010	2009	2010
2D	2009	25.17	1	0.71	1.00	–
	2010	30.91	0.57	1	0.85	1.00
3D	2009	8.78	1	0.62	1.00	–
	2010	18.90	0.29	1	0.64	1.00

#### 4.2. Learning and maturation processes

We were not able to detect any significant differences in foraging behavior among age and breeding experience classes, although experienced breeders showed some signs of performing better and targeting slightly different areas than inexperienced ones. In a previous study at the larger, more competitive Cape Crozier colony, we showed that age accounted for 3–5% of the inter-individual variation in foraging performance (Lescroël et al. 2019). Therefore, it is possible that our relatively small sample size (per age class within each sex) in the present study did not allow us to detect small magnitude differences, and/or differences within one of the defined age classes. Alternatively, the lower intraspecific competition at

Table 3. Adélie penguin 2D and 3D spatial use depending on age class. See Table 1 for details

	Age	UD50	% overlap			BA index		
			Young	Mature	Old	Young	Mature	Old
2D	Young	30.76	1	0.64	0.53	1.00	–	–
	Mature	30.04	0.68	1	0.61	0.83	1.00	–
	Old	19.98	0.75	0.82	1	0.81	0.86	1.00
3D	Young	15.21	1	0.38	0.35	1.00	–	–
	Mature	13.43	0.43	1	0.48	0.55	1.00	–
	Old	10.72	0.50	0.60	1	0.60	0.71	1.00

Table 4. Adélie penguin 2D and 3D spatial use depending on breeding quality index (BQI). See Table 1 for details

	BQI	UD50	% overlap			BA index		
			Low	Medium	High	Low	Medium	High
2D	Low	24.25	1	0.68	0.40	1.00	–	–
	Medium	25.63	0.67	1	0.42	0.85	1.00	–
	High	31.28	0.31	0.33	1	0.75	0.66	1.00
3D	Low	12.17	1	0.55	0.13	1.00	–	–
	Medium	12.90	0.52	1	0.14	0.73	1.00	–
	High	9.37	0.17	0.19	1	0.12	0.13	1.00

Table 5. Adélie penguin 2D and 3D spatial use depending on breeding experience (for birds aged 6–8 only). See Table 1 for details

	Experience	UD50	% overlap		BA index	
			0	1+	0	1+
2D	0	14.03	1	0.48	1.00	–
	1+	33.25	0.23	1	0.72	1.00
3D	0	1.87	1	0.62	1.00	–
	1+	11.90	0.10	1	0.32	1.00

Cape Bird may have allowed most breeders to forage within the same distance to the colony and depth.

In this way, the lack of separation in 2D and 3D foraging ranges of different age classes of Adélie penguins close to the Cape Bird colony conformed with central place foraging theory (Orians & Pearson 1979), but was contrary to our initial hypothesis that the younger birds would be forced to forage further from the colony because they lacked the experience and physical capabilities to acquire prey the older birds possessed. The maximum extent of the ‘foraging halo’ for Adélie penguins is limited by the amount of time and effort required to swim out, catch prey, and return to the colony to provision chicks (Ballance et al. 2009). Indeed, feeding frequency is a major factor behind chick growth (Salihoglu et al. 2001). Adélie penguin

parents on Ross Island during the guard and early crèche stage forage most of the time when at sea (Ford et al. 2015), beginning prey searching immediately upon leaving the colony. The large overlap between foraging volumes of the different age classes does not, however, exclude potential differences in prey types.

Overall, we suggest that the level of inter- and intraspecific competition in the vicinity of the seabird breeding colonies, and the resulting prey availability, can influence the magnitude of inter-individual differences in foraging behavior. Here, the smaller size of the Cape Bird breeding population and the resulting lower level of competition compared to the very large Cape Crozier population (Ballance et al. 2009, Lescroël et al. 2010) could at least partially explain the contrasting results reported on inter-individual variation of foraging behavior among age classes in Adélie penguins between Cape Bird and Cape Crozier.

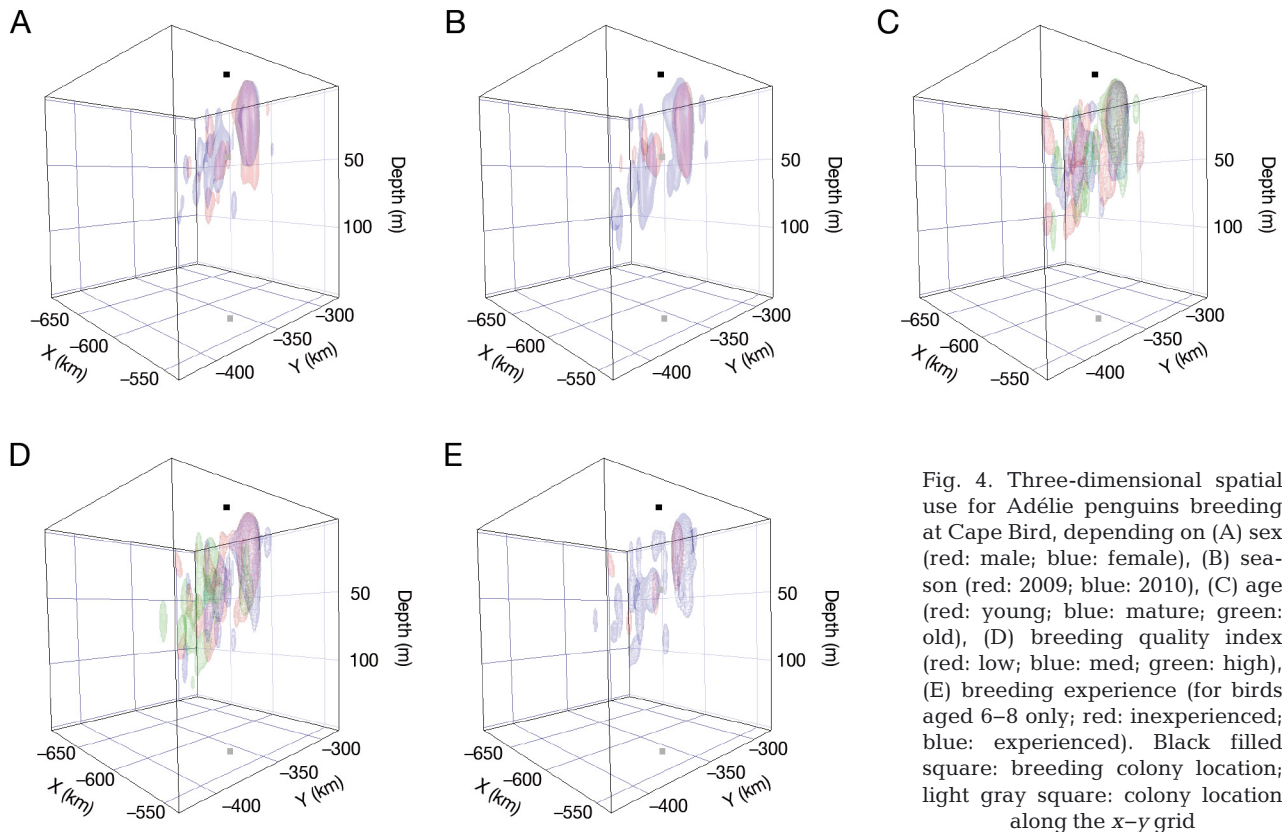


Fig. 4. Three-dimensional spatial use for Adélie penguins breeding at Cape Bird, depending on (A) sex (red: male; blue: female), (B) season (red: 2009; blue: 2010), (C) age (red: young; blue: mature; green: old), (D) breeding quality index (red: low; blue: med; green: high), (E) breeding experience (for birds aged 6–8 only; red: inexperienced; blue: experienced). Black filled square: breeding colony location; light gray square: colony location along the x–y grid

Table 6. Summary of predictions and respective outcomes (*T*: true; *F*: false) for foraging parameters of Adélie penguins breeding at Cape Bird, Ross Island, Antarctica. BQI: breeding quality index

Prediction: some groups exhibit ...	Potential driver of inter-individual differences		
	Age	BQI	Breeding experience
Shorter maximum foraging distances	F	F	F
Deeper dives	F	<i>T</i>	F
Shorter trip durations	F	F	F
Fewer foraging dives	F	F	F
More successful foraging dives	F	<i>T</i>	F
Partitioning in 2D habitat use	F	<i>T</i>	<i>T</i>
Partitioning in 3D habitat use	F	<i>T</i>	<i>T</i>

### 4.3. Sex-specific constraints

At the larger Cape Crozier colony, female Adélie penguins stayed longer at sea for the same amount of food caught or brought back to the colony and dived to shallower depths (Ballard et al. 2010b, Lescoërl et al. 2010). This pattern was also found at Béchervaise Island, where female Adélie penguins made longer foraging trips than males, ranged greater distances

more frequently, and consumed larger quantities of krill as opposed to fish (Clarke et al. 1998). In Adélie Land, however, Angelier et al. (2008) did not find any significant sex difference in foraging success, trip duration, or maximal foraging range; and neither did Cimino et al. (2016) at Arthur Harbor, western Antarctic Peninsula. At Cape Bird, we demonstrated that female Adélie penguins made longer trips and more dives, but did not range greater distances and dived to similar depths as males.

As highlighted by Clarke et al. (1998), sex differences in foraging behavior may become particularly important when food is less available, as a means of both reducing intraspecific competition and maximizing the chances of each member of the pair locating food for the chicks. We also previously suggested that male Adélie penguins tend to maximize net energy gain per unit time, so as to spend more time at the colony defending their territory, while females tend to maximize net energy gain per energy spent (Lescoërl et al. 2019). The lower levels of intraspecific competition at Cape Bird compared to Cape Crozier, due to the smaller breeding population, may explain the smaller magnitude of

sex differences at this colony. Food seems to be available enough in the close vicinity of Cape Bird that males can perform short trips and spend enough time defending their nests without having to dive deeper.

#### 4.4. Other fixed inter-individual differences

Other sex-, age-, and experience-independent factors, such as those reflected by our BQI, were important correlates of inter-individual differences in the foraging behavior of Adélie penguins. In an earlier study of all 3 Adélie penguin colonies on Ross Island (Lescroël et al. 2010), we found that high-quality individuals were diving deeper than lower quality ones and foraged efficiently overall when environmental conditions were more challenging. However, study birds were of unknown age; these high-quality individuals could have been older and/or more experienced. Interestingly, we had also showed that intra-specific competition (based on colony size) did not affect or reveal any relationship between breeding quality and foraging strategy (Lescroël et al. 2010). Here, we showed that, independent of age and experience, high-quality individuals breeding at Cape Bird dive about 30% deeper and perform more undulations per dive than lower quality birds. High-quality individuals are also a more homogeneous group, exhibiting less variability in the number of foraging dives performed per trip. These results suggest that these high-quality individuals could have different, genetically determined physiological capabilities enabling them to reach deeper depths repeatedly at a lower cost, or a cost they can afford. Indeed, we showed that high-quality individuals exhibit shorter recovery intervals (i.e. PDIs) than lower quality individuals after deep dives (>85 m). Within these deep dives, high-quality individuals exhibit shorter PDIs than low-quality individuals when dive duration exceeds 193 s, and shorter PDIs than medium-quality individuals when dive duration exceeds 217 s, while the calculated aerobic dive limit (cADL) for Adélie penguins is 46–68 s (Chappell et al. 1993). As the number of undulations per dive increases with dive duration ( $t = 78.13$ ,  $p < 0.001$ ), it is advantageous for high-quality individuals to be able to remain submerged for longer durations at what seems like a lower physiological cost. The mechanisms underlying this variation in ADL between birds of different BQI remain unknown and could be due to variation in blood oxygen stores, muscle oxygen stores, respiratory oxygen stores, diving metabolic rate, or oxygen management during the dive. Body size could also affect oxygen stores, buoy-

ancy, and mechanical power, but preliminary analyses did not show any significant influence of size measurements on the foraging behavior of Adélie penguins (A. Lescroël unpubl. data). It is possible that these deeper dives are made profitable by gaining access to the more energy-rich Antarctic silverfish *Pleuragramma antarcticum* (Ainley et al. 2015). Acoustic surveys indicated that adult Antarctic silverfish generally formed layers between 150 and 450 m depth; however, juvenile silverfish of 40–80 mm standard length were also present around depths of 80 m (O'Driscoll et al. 2009, B. Saenz et al. unpubl. data). While mean maximum dive depths of all BQI classes were <80 m, high-quality birds regularly dived to depths deeper or equal to 75 m (i.e. for about 20% of their foraging dives), reaching up to 147 m.

By foraging farther west and south, high-quality individuals avoided the higher concentrations of birds feeding nearer to the Cape Bird colony (including those from Cape Crozier and Beaufort Island), thus potentially reducing competition for prey and potentially increasing the efficiency of their provisioning activities (Ainley et al. 2004; see also Ford et al. 2015 for depiction of colony-specific foraging areas). This strategy also took them away from penguins foraging from Cape Crozier, the largest colony on Ross Island (one of the largest in the world; mean colony size of 280 721 breeding pairs during 2009–2011; P. O'B. Lyver & K. Barton unpubl. data), that progressively feed westwards over the season to overlap with the foraging ranges of the Cape Bird penguins (Ainley et al. 2003). Foraging south also took the high-quality individuals towards the highly productive retreating sea-ice edge where opportunities for prey acquisition would likely have been higher (Ballard et al. 2012). While these individuals may have encountered other Adélie penguins foraging from Cape Royds, competition would have been low since this colony is small (Ainley et al. 2004). It is more likely the birds encountered inter-specific competition with other large krill-eating species such as minke whales *Balaenoptera bonaerensis* that have been observed feeding in numbers along the sea-ice edge (Ainley et al. 2006, Ballard et al. 2012).

At the interface of dynamic and fixed characteristics lies cognitive ability (i.e. the ability of animals to perceive, process, and react to stimuli from the environment), which is likely to differ among individuals and to improve with age and experience. Although little is known about the cognitive ability of seabirds in relation to foraging (but see Kitaysky et al. 2006), there is evidence that seabirds can use public information to locate new food patches and memory to

relocate them, giving rise to individual foraging site fidelity (Weimerskirch et al. 2010, Regular et al. 2013, Wakefield et al. 2013, 2015). Among Ross Island penguins in general, they seem to be knowledgeable of the preyscape only within a 2 d period or within 10 km of where they previously foraged (Ford et al. 2015). Testing whether high-quality individuals have higher cognitive abilities than lower quality ones would require carefully controlled experiments, which is challenging in the wild. Inter-individual differences in locomotion ability and reaction speeds, however, could be more easily investigated (e.g. using acceleration data).

#### 4.5. Limitations

It remains extremely challenging to couple individual long-term demographic data and at-sea foraging data. Ideally, we would have been repeatedly attaching tags to the same individuals from age 3–20 yr (i.e. to perform a longitudinal study), while making sure that a large and balanced sample size was maintained among sexes, age, and quality classes. However, many individuals die before they reach old ages, high-quality individuals are a minority in animal populations (Clutton-Brock 1988, Newton 1989, Annett & Pierotti 1999), and small biologging devices have only recently become available. These limitations resulted in small sample sizes for some groups, which constrained the complexity of the analyses we could perform and prevented us from evaluating the potential interaction between age and individual quality. In an attempt to minimize disturbance, we only equipped each individual during a single foraging trip. Thus, due to behavioral plasticity, a single foraging trip from each bird might not always be representative of their behavior across the entire breeding season. However, it must be noted that several studies reported relative individual differences in foraging behavior (foraging efficiency, diving depth) that were maintained over time scales ranging from several weeks (Takahashi et al. 2003 in Adélie penguins) to several years (Woo et al. 2008 in thick-billed murre *Uria lomvia*, Lescroël et al. 2010, 2014 in Adélie penguins). By taking into account both age and individual quality, this cross-sectional study represents an important step forward in identifying the drivers of inter-individual differences in the foraging behavior of seabirds in different contexts.

We were also limited by the lack of information on the type of prey targeted by the equipped individuals (i.e. krill vs. fish) or their availability. Acoustic sur-

veys in the Ross Sea indicate that crystal krill *Euphausia crystallophias* and Antarctic silverfish *Pleuragramma antarctica* are common over the continental shelf region (O'Driscoll et al. 2009, Davis 2016). Both species are important dietary components for top predators in Antarctic waters (Fischer & Hureau 1985), in particular Adélie penguins (Ainley et al. 1998, 2003, 2015, Saenz et al. unpubl. data), but they have very different energy values, with an individual silverfish being about 20 times more energy-rich than an individual crystal krill (Wiebe et al. 1975, Ainley et al. 2003, Ju & Harvey 2004, Mayzaud et al. 2011). However, with silverfish tending to be located deeper (>80 m) than krill in the early season (Ainley et al. 2015), it would be more energetically costly to catch for a penguin. Energy-rich Antarctic silverfish and other cryopelagic species (e.g. *Pagothenia borchgrevinki*, *Trematomus* spp.) are common on the Ross Sea continental shelf (Barrera-Oro 2002, O'Driscoll et al. 2009, Pinkerton et al. 2010, Davis 2016) and are particularly important for Adélie penguin chick development (Ainley et al. 2003, 2015, 2018, Ballance et al. 2009, Whitehead et al. 2015).

#### 5. CONCLUSIONS

Evidence from this study only poorly supported our initial hypotheses that variations in Adélie penguin foraging behavior would be related to age and breeding experience. We recognize that the small sample sizes within some age classes might have limited our ability to detect and interpret differences in foraging parameters. However, we found compelling evidence that individual quality and sex both drive part of the inter-individual differences in the foraging behavior of Adélie penguins, in terms of foraging trip duration, diving depth, and foraging location. Sparse information on the abundance and distribution of prey eaten by Adélie penguins offshore of Cape Bird limited our interpretation of findings. We do not know whether the penguins from Cape Bird in our study were responding to availability of fish or krill. Further inquiry should therefore focus on identifying the range and amounts of different prey taken by Adélie penguins at different times of the breeding season in relation to the availability of this prey within their foraging areas, as has been accomplished somewhat preliminarily (one season) at Cape Crozier (Ainley et al. 2015) and Cape Royds (Saenz et al. unpubl. data), along with evaluating the potential interaction effect of age and individual quality through longitudinal studies.

**Acknowledgements.** Financial support was provided by New Zealand's Ministry of Business, Innovation and Employment grants (C09X0510, C01X1001, and C01X1710) and NSF grants (OPP 9526865, 9814882, 0125608, 0440643, 0944411, and 1543498). Logistic support was provided by the Antarctica New Zealand and the US Antarctic Program. Animal manipulations were conducted under Landcare Research Animal Ethics permits 05/09/01 and 10/09/01. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. This is Point Blue Conservation Science Contribution #2275.

#### LITERATURE CITED

- Ainley DG (2002) The Adélie penguin: bellwether of climate change. Columbia University Press, New York, NY
- ✦ Ainley DG, DeMaster DP (1980) Survival and mortality in a population of Adélie penguins. *Ecology* 61:522–530
- ✦ Ainley DG, Emison WB (1972) Sexual size dimorphism in Adélie penguins. *Ibis* 114:267–271
- Ainley DG, LeResche RE, Sladen WJL (1983) Breeding biology of the Adélie penguin. University of California Press, Berkeley, CA
- ✦ Ainley DG, Wilson PR, Barton KJ, Ballard G, Nur N, Karl B (1998) Diet and foraging effort of Adélie penguins in relation to pack-ice conditions in the southern Ross Sea. *Polar Biol* 20:311–319
- ✦ Ainley DG, Ballard G, Barton KJ, Karl BJ, Rau GH, Ribic CA, Wilson PR (2003) Spatial and temporal variation of diet within a presumed metapopulation of Adélie penguins. *Condor* 105:95–106
- ✦ Ainley DG, Ribic CA, Ballard G, Heath S and others (2004) Geographic structure of Adélie penguin populations: overlap in colony-specific foraging areas. *Ecol Monogr* 74:159–178
- ✦ Ainley DG, Ballard G, Dugger KM (2006) Competition among penguins and cetaceans reveals trophic cascades in the western Ross Sea, Antarctica. *Ecology* 87:2080–2093
- ✦ Ainley DG, Ballard G, Jones RM, Jongsomjit D, Pierce SD, Smith WO Jr, Veloz S (2015) Trophic cascades in the western Ross Sea, Antarctica: revisited. *Mar Ecol Prog Ser* 534:1–16
- ✦ Ainley DG, Dugger KM, La Mesa M, Ballard G and others (2018) Post-fledging survival of Adélie penguins at multiple colonies: chicks raised on fish do well. *Mar Ecol Prog Ser* 601:239–251
- ✦ Angelier F, Bost CA, Giraudeau M, Bouteloup G, Dano S, Chastel O (2008) Corticosterone and foraging behavior in a diving seabird: the Adélie penguin, *Pygoscelis adeliae*. *Gen Comp Endocrinol* 156:134–144
- ✦ Annett CA, Pierotti R (1999) Long-term reproductive output in western gulls: consequences of alternate tactics in diet choice. *Ecology* 80:288–297
- ✦ Ballance LT, Ainley DG, Ballard G, Barton K (2009) An energetic correlate between colony size and foraging effort in seabirds, an example of the Adélie penguin *Pygoscelis adeliae*. *J Avian Biol* 40:279–288
- ✦ Ballard G, Ainley DG, Ribic CA, Barton KR (2001) Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adélie penguins. *Condor* 103:481–490
- ✦ Ballard G, Dugger KM, Nur N, Ainley DG (2010a) Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. *Mar Ecol Prog Ser* 405:287–302
- ✦ Ballard G, Toniolo V, Ainley DG, Parkinson CL, Arrigo KR, Trathan PN (2010b) Responding to climate change: Adélie penguins confront astronomical and ocean boundaries. *Ecology* 91:2056–2069
- ✦ Ballard G, Jongsomjit D, Veloz SD, Ainley DG (2012) Coexistence of mesopredators in an intact polar ocean ecosystem: the basis for defining a Ross Sea marine protected area. *Biol Conserv* 156:72–82
- ✦ Ballard G, Schmidt AE, Toniolo V, Veloz S, Jongsomjit D, Arrigo KR, Ainley DG (2019) Fine-scale oceanographic features characterizing successful Adélie penguin foraging in the SW Ross Sea. *Mar Ecol Prog Ser* 608:263–277
- ✦ Barbraud C, Weimerskirch H (2005) Environmental conditions and breeding experience affect costs of reproduction in blue petrels. *Ecology* 86:682–692
- ✦ Barrera-Oro E (2002) The role of fish in the Antarctic marine food web: differences between inshore and offshore waters in the southern Scotia Arc and West Antarctic Peninsula. *Antarct Sci* 14:293–309
- ✦ Bearhop S, Phillips RA, McGill R, Chérel Y, Dawson DA, Croxall JP (2006) Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Mar Ecol Prog Ser* 311:157–164
- ✦ Beauplet G, Barbraud C, Dabin W, Küssener C, Guinet C (2006) Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. *Oikos* 112:430–441
- ✦ Bost CA, Handrich Y, Butler PJ, Fahlman A, Halsey LG, Woakes AJ, Ropert-Coudert Y (2007) Changes in dive profiles as an indicator of feeding success in king and Adélie penguins. *Deep Sea Res II* 54:248–255
- ✦ Boyd JD, Brightsmith DJ (2013) Error properties of Argos satellite telemetry locations using least squares and Kalman filtering. *PLOS ONE* 8:e63051
- ✦ Calenge C (2006) The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Modell* 197:516–519
- Cam E (2009) Contribution of capture-mark-recapture modeling to studies of evolution by natural selection. In: Thomson DL, Cooch EG, Conroy MJ (eds) *Modeling demographic processes in marked populations*. Springer, New York, NY, p 83–129
- ✦ Cam E, Monnat JY (2000) Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. *J Anim Ecol* 69:380–394
- ✦ Cam E, Link WA, Cooch EG, Monnat JY, Danchin E (2002) Individual covariation in life-history traits: seeing the trees despite the forest. *Am Nat* 159:96–105
- ✦ Cam E, Aubry LM, Authier M (2016) The conundrum of heterogeneities in life history studies. *Trends Ecol Evol* 31: 872–886
- ✦ Catry P, Phillips RA, Phalan B, Croxall JP (2006) Senescence effects in an extremely long-lived bird: the grey-headed albatross *Thalassarche chrysostoma*. *Proc R Soc B* 273: 1625–1630
- ✦ Chapman EW, Hofmann EE, Patterson DL, Ribic CA, Fraser WR (2011) Marine and terrestrial factors affecting Adélie penguin *Pygoscelis adeliae* chick growth and recruitment off the Western Antarctic Peninsula. *Mar Ecol Prog Ser* 436:273–289
- ✦ Chappell MA, Shoemaker VH, Janes DN, Bucher TL, Maloney SK (1993) Diving behavior during foraging in breeding Adélie penguins. *Ecology* 74:1204–1215
- ✦ Chérel Y, Hobson KA, Guinet C, Vanpé C (2007) Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. *J Anim Ecol* 76:826–836

- Cimino MA, Moline MA, Fraser WR, Patterson-Fraser DL, Oliver MJ (2016) Climate-driven sympatry may not lead to foraging competition between congeneric top-predators. *Sci Rep* 6:18820
- Clarke J, Manly B, Kerry K, Gardner H, Franchi E, Corsolini S, Focardi S (1998) Sex differences in Adélie penguin foraging strategies. *Polar Biol* 20:248–258
- Clay TA, Pearmain EJ, McGill RA, Manica A, Phillips RA (2018) Age-related variation in non-breeding foraging behaviour and carry-over effects on fitness in an extremely long-lived bird. *Funct Ecol* 32:1832–1846
- Cleasby IR, Wakefield ED, Bodey TW, Davies RD and others (2015) Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Mar Ecol Prog Ser* 518:1–12
- Clutton-Brock TH (1988) Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, IL
- Cooper NW, Sherry TW, Marra PP (2014) Modeling three-dimensional space use and overlap in birds. *Auk* 131: 681–693
- Creelman E, Storey AE (1991) Sex differences in reproductive behavior of Atlantic puffins. *Condor* 93:390–398
- Daunt F, Afanasyev V, Silk JRD, Wanless S (2006) Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. *Behav Ecol Sociobiol* 59:381–388
- Daunt F, Wanless S, Harris MP, Money L, Monaghan P (2007) Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. *Funct Ecol* 21:561–567
- Davis LB (2016) Distributions of *Euphausia superba*, *Euphausia crystallorophias*, and *Pleuragramma antarcticum* with correlations to environmental variables in the Western Ross Sea, Antarctica. MSc thesis, Old Dominion University, Norfolk, VA
- Descamps S, Boutin S, Berteaux D, Gaillard JM (2007) Female red squirrels fit Williams' hypothesis of increasing reproductive effort with increasing age. *J Anim Ecol* 76:1192–1201
- Dugger KM, Ballard G, Ainley DG, Barton KJ (2006) Effects of flipper bands on foraging behavior and survival of Adélie penguins (*Pygoscelis adeliae*). *Auk* 123:858–869
- Duong T (2007) ks: kernel density estimation and kernel discriminant analysis for multivariate data in R. *J Stat Softw* 21:1–16
- Duong T (2013) ks: kernel smoothing. R package version 1.8.11. <https://cran.r-project.org/web/packages/ks/ks.pdf>
- Elliott KH, Hare JF, Le Vaillant M, Gaston AJ, Ropert-Coudert Y, Anderson WG (2015) Ageing gracefully: physiology but not behaviour declines with age in a diving seabird. *Funct Ecol* 29:219–228
- Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. *J Wildl Manag* 69:1346–1359
- Fischer W, Hureau JC (1985) Southern Ocean: Fishing Areas 48, 58 and 88 (CCAMLR Convention Area). FAO, Rome
- Ford RG, Ainley DG, Lescroël A, Lyver PO, Toniolo V, Ballard G (2015) Testing assumptions of central place foraging theory: a study of Adélie penguins *Pygoscelis adeliae* in the Ross Sea. *J Avian Biol* 46:193–205
- Fox GA, Kendall BE, Fitzpatrick JW, Woolfenden GE (2006) Consequences of heterogeneity in survival probability in a population of Florida scrub-jays. *J Anim Ecol* 75:921–927
- Fraser GS, Jones IL, Hunter FM (2002) Male-female differences in parental care in monogamous crested auklets. *Condor* 104:413–423
- Freitas C (2012) Argos locations filter: package 'argosfilter'. [www.cran.r-project.org/web/packages/argosfilter/argosfilter.pdf](http://www.cran.r-project.org/web/packages/argosfilter/argosfilter.pdf)
- Freitas C, Lydersen C, Fedak MA, Kovacs KM (2008) A simple new algorithm to filter marine mammal Argos locations. *Mar Mamm Sci* 24:315–325
- Froy H, Lewis S, Catry P, Bishop CM and others (2015) Age-related variation in foraging behaviour in the wandering albatross at South Georgia: no evidence for senescence. *PLOS ONE* 10:e0116415
- Georges JY, Guinet C, Jouventin P, Weimerskirch H (1997) Satellite tracking of seabirds: interpretation of activity pattern from the frequency of satellite locations. *Ibis* 139: 403–405
- Gitzen RA, Millsbaugh JJ, Kernohan BJ (2006) Bandwidth selection for fixed-kernel analysis of animal utilization distributions. *J Wildl Manag* 70:1334–1344
- Grémillet D, Lescroël A, Ballard G, Dugger KM, Massaro M, Porzig EL, Ainley DG (2018) Energetic fitness: field metabolic rates assessed via 3D accelerometry complement conventional fitness metrics. *Funct Ecol* 32: 1203–1213
- Hamilton WD (1966) The moulding of senescence by natural selection. *J Theor Biol* 12:12–45
- Jodice PG, Roby DD, Hatch SA, Gill VA, Lanctot RB, Visser GH (2002) Does food availability affect energy expenditure rates of nesting seabirds? A supplemental-feeding experiment with black-legged kittiwakes (*Rissa tridactyla*). *Can J Zool* 80:214–222
- Ju SJ, Harvey HR (2004) Lipids as markers of nutritional condition and diet in the Antarctic krill *Euphausia superba* and *Euphausia crystallorophias* during austral winter. *Deep Sea Res II* 51:2199–2214
- Kappes PJ (2019) The influence of alternate life history strategies and natal conditions on the reproductive performance of Adélie penguins breeding on Ross Island, Antarctica. PhD dissertation, Oregon State University, Corvallis, OR. [https://ir.library.oregonstate.edu/concern/graduate\\_thesis\\_or\\_dissertations/bz60d273w](https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/bz60d273w)
- Kirkwood TB (1977) Evolution of ageing. *Nature* 270:301–304
- Kirkwood TB, Austad SN (2000) Why do we age? *Nature* 408:233–238
- Kitaysky AS, Kitaiskaia EV, Piatt JF, Wingfield JC (2006) A mechanistic link between chick diet and decline in seabirds? *Proc R Soc B* 273:445–450
- Lecomte VJ, Sorci G, Cornet S, Jaeger A and others (2010) Patterns of aging in the long-lived wandering albatross. *Proc Natl Acad Sci USA* 107:6370–6375
- Lescroël A, Dugger KM, Ballard G, Ainley DG (2009) Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. *J Anim Ecol* 78:798–806
- Lescroël A, Ballard G, Toniolo V, Barton KJ, Wilson PR, Lyver PO, Ainley DG (2010) Working less to gain more: when breeding quality relates to foraging efficiency. *Ecology* 91:2044–2055
- Lescroël A, Ballard G, Grémillet D, Authier M, Ainley DG (2014) Antarctic climate change: extreme events disrupt plastic phenotypic response in Adélie penguins. *PLOS ONE* 9:e85291
- Lescroël A, Ballard G, Massaro M, Dugger K and others (2019) Evidence of age-related improvement in the foraging efficiency of Adélie penguins. *Sci Rep* 9:3375
- Lewis S, Benvenuti S, Dall-Antonia L, Griffiths R and others (2002) Sex-specific foraging behaviour in a monomorphic seabird. *Proc R Soc B* 269:1687–1693
- Lewis S, Wanless S, Elston DA, Schultz MD and others



- (2006) Determinants of quality in a long-lived colonial species. *J Anim Ecol* 75:1304–1312
- ✦ Limmer B, Becker PH (2009) Improvement in chick provisioning with parental experience in a seabird. *Anim Behav* 77:1095–1101
- ✦ Luque SP (2007) Diving behaviour analysis in R. *R News* 7: 8–14
- Luque SP, Guinet C (2007) A maximum likelihood approach for identifying dive bouts improve accuracy, precision and objectivity. *Behaviour* 144:1315–1332
- ✦ Massot M, Clobert J, Montes-Poloni L, Haussy C, Cubo J, Meylan S (2011) An integrative study of ageing in a wild population of common lizards. *Funct Ecol* 25:848–858
- ✦ Mayzaud P, Chevallier J, Tavernier E, Moteki M, Koubbi P (2011) Lipid composition of the Antarctic fish *Pleuragramma antarcticum*. Influence of age class. *Polar Sci* 5: 264–271
- ✦ Nevoux M, Weimerskirch H, Barbraud C (2007) Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross. *J Anim Ecol* 76:159–167
- Newton I (ed) (1989) Lifetime reproduction in birds. Academic Press, London
- O'Driscoll R, Macaulay G, Gauthier S, Pinkerton M, Hanchet S (2009) Preliminary acoustic results from the New Zealand IPY-CAML survey of the Ross Sea region in Feb-Mar 2008. CCAMLR document WG-FSA-08/31. Convention for the Conservation of Antarctic Marine Living Resources, Hobart
- Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DH, Mitchell R, Stairs GR (eds) Analysis of ecological systems. Ohio State University Press, Columbus, OH, p 155–177
- ✦ Pelletier L, Chiaradia A, Kato A, Ropert-Coudert Y (2014) Fine-scale spatial age segregation in the limited foraging area of an inshore seabird species, the little penguin. *Oecologia* 176:399–408
- Pinheiro J, Bates D, DebRoy S, Sarkar D, Heisterkamp S, Van Willigen B, Maintainer R (2017) Package 'nlme': linear and nonlinear mixed effects models. R package version 3-1. <https://cran.r-project.org/web/packages/nlme/nlme.pdf>
- Pinkerton MH, Bradford-Grieve JM, Hanchet SM (2010) A balanced model of the food web of the Ross Sea, Antarctica. *CCAMLR Sci* 17:1–31
- R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Regular PM, Hedd A, Montevecchi WA (2013) Must marine predators always follow scaling laws? Memory guides the foraging decisions of a pursuit-diving seabird. *Anim Behav* 86:545–552
- ✦ Ropert-Coudert Y, Kato A, Baudat J, Bost CA, Le Maho Y, Naito Y (2001) Feeding strategies of free-ranging Adélie penguins *Pygoscelis adeliae* analysed by multiple data recording. *Polar Biol* 24:460–466
- ✦ Salihoglu B, Fraser WR, Hofmann EE (2001) Factors affecting fledging weight of Adélie penguin (*Pygoscelis adeliae*) chicks: a modeling study. *Polar Biol* 24: 328–337
- ✦ Schreer JF, Kovacs KM, Hines RO (2001) Comparative diving patterns of pinnipeds and seabirds. *Ecol Monogr* 71: 137–162
- ✦ Simpfendorfer CA, Olsen EM, Heupel MR, Moland E (2012) Three-dimensional kernel utilization distributions improve estimates of space use in aquatic animals. *Can J Fish Aquat Sci* 69:565–572
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- ✦ Suryan RM, Irons DB, Kaufman M, Benson J, Jodice PGR, Roby DD, Brown ED (2002) Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the black-legged kittiwake *Rissa tridactyla*. *Mar Ecol Prog Ser* 236:273–287
- ✦ Sydeman WJ, Penniman JF, Penniman TM, Pyle P, Ainley DG (1991) Breeding performance in the western gull: effects of parental age, timing of breeding and year in relation to food availability. *J Anim Ecol* 60:135–149
- ✦ Takahashi A, Watanuki Y, Sato K, Kato A, Arai N, Nishikawa J, Naito Y (2003) Parental foraging effort and offspring growth in Adélie penguins: Does working hard improve reproductive success? *Funct Ecol* 17:590–597
- ✦ Thaxter CB, Daunt F, Hamer KC, Watanuki Y and others (2009) Sex-specific food provisioning in a monomorphic seabird, the common guillemot *Uria aalge*: Nest defence, foraging efficiency or parental effort? *J Avian Biol* 40: 75–84
- ✦ Tremblay Y, Shaffer SA, Fowler SL, Kuhn CE and others (2006) Interpolation of animal tracking data in a fluid environment. *J Exp Biol* 209:128–140
- ✦ Wakefield ED, Bodey TW, Bearhop S, Blackburn J and others (2013) Space partitioning without territoriality in gannets. *Science* 341:68–70
- ✦ Wakefield ED, Cleasby IR, Bearhop S, Bodey TW and others (2015) Long-term individual foraging site fidelity — why some gannets don't change their spots. *Ecology* 96: 3058–3074
- ✦ Wanless S, Harris MP (1986) Time spent at the colony by male and female guillemots *Uria aalge* and razorbills *Alca torda*. *Bird Study* 33:168–176
- ✦ Weimerskirch H, Bertrand S, Silva J, Marques JC, Goya E (2010) Use of social information in seabirds: compass rafts indicate the heading of food patches. *PLOS ONE* 5: e9928
- ✦ Whitehead AL, Lyver PO'B, Ballard G, Barton K and others (2015) Factors driving Adélie penguin chick size, mass and condition at colonies of different sizes in the Southern Ross Sea. *Mar Ecol Prog Ser* 523:199–213
- Wiebe PH, Boyd S, Cox JL (1975) Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon. *Fish Bull* 73:777–786
- ✦ Williams GC (1957) Pleiotropy, natural selection, and the evolution of senescence. *Evolution* 11:398–411
- ✦ Wilson AJ, Nussey DH (2010) What is individual quality? An evolutionary perspective. *Trends Ecol Evol* 25:207–214
- ✦ Woo KJ, Elliott KH, Davidson M, Gaston AJ, Davoren GK (2008) Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. *J Anim Ecol* 77:1082–1091
- ✦ Worton BJ (1989) Optimal smoothing parameters for multivariate fixed and adaptive kernel methods. *J Stat Comput Simul* 32:45–57
- ✦ Zhang P, Han J, Liu Q, Zhang J, Zhang X (2013) Sex identification of four penguin species using locus-specific PCR. *Zoo Biol* 32:257–261
- ✦ Zimmer I, Ropert-Coudert Y, Kato A, Ancel A, Chiaradia A (2011) Does foraging performance change with age in female little penguins (*Eudyptula minor*)? *PLOS ONE* 6: e16098