


# A novel foraging strategy in gentoo penguins breeding at sub-Antarctic Marion Island

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**Abstract** To help meet the high energy demands of raising the young, some seabirds alternate between short, frequent foraging trips to maximize food delivery to the young, and infrequent, long foraging trips that serve towards self-maintenance. Our study is the first to investigate the foraging behaviour of gentoo penguins at Marion Island, which we did through a combined use of GPS loggers and time-depth recorders. The shallow shelf between Marion and Prince Edward Islands proved to be an important foraging area, and penguins exploited this area using a novel foraging strategy. Penguins undertook alternating trips of relatively short and long durations. Short trips, performed in the afternoon, were likely associated with self-maintenance as they were followed by roosting on the beach overnight and not returning to the colony. They were followed by longer and more distant foraging trips, after which birds returned to the colony to provision chicks.

To our knowledge, this is the first study to demonstrate alternating trip lengths in gentoo penguins and the first to associate short trips with self-maintenance in seabirds. We suggest that due to the close proximity of a predictable foraging area for these penguins at Marion Island, there is minimal energetic cost to return to land after self-provisioning. Hence, unlike other seabirds that feed at greater distances from their breeding colonies, gentoo penguins are afforded the opportunity for short self-maintenance trips. Finally, we argue that these birds may be using this novel strategy due to sub-optimal feeding conditions resulting from environmental change.

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## Introduction

Animals forage to meet the energy requirements needed to maintain vital physiological functions and support physical activities (Spitz et al. 2012). Optimal foraging theory assumes that the foraging behaviour of animals promotes maximum fitness (Emlen 1966; MacArthur and Pianka 1966). Thus, to maximize energy gain per unit time, animals forage selectively and make decisions, such as how far to travel and what to eat (Stephens and Krebs 1986). It is these decisions that shape the foraging behaviours and strategies of animals.

For animals that are central-place foragers, such as breeding seabirds, fitness is, to a large extent, governed by the rate at which resources are delivered to their young (Orians and Pearson 1979; Rishworth et al. 2014). The temporal and spatial separation between foraging and breeding areas imposes an energetic constraint (Pinaud and Weimerskirch 2002; Ropert-Coudert et al. 2004; Miller et al. 2010). In this regard, there is an important trade-off between the time allocated to a foraging trip and the need to provision

offspring. Furthermore, seabirds must allocate resources to both feeding chicks and maintenance of their own body condition to ensure survival (Trivers 1974; Stearns 1976; Ydenberg et al. 1994). To meet the high energetic demands of breeding, some seabird species are known to alternate between frequent, short, chick-provisioning foraging trips punctuated by long self-maintenance trips (Weimerskirch et al. 1994; Ropert-Coudert et al. 2004). During the longer trips, seabirds either target more distant areas of known high productivity, such as marginal sea ice zones (Jakubas et al. 2012) or continental shelf edges (Magalhães et al. 2008), or spend a longer time foraging in the same area used during short trips (Ropert-Coudert et al. 2004; Clarke et al. 2006).

A bimodal foraging trip duration during chick rearing has mostly been reported in the Procellariiformes (e.g. Weimerskirch et al. 1994; Weimerskirch 1998; Magalhães et al. 2008; Shoji et al. 2015) but has also been documented in little auks *Alle alle* (Welcker et al. 2009; Brown et al. 2012; Jakubas et al. 2012) and some penguins (Jansen et al. 1998; Clarke 2001; Taylor et al. 2002; Ropert-Coudert et al. 2004; Saraux et al. 2011). However, bimodal foraging does not appear to be species-specific (Weimerskirch et al. 1994; Angelier et al. 2008; Paiva et al. 2010). Rather, it is more prevalent in seabirds that breed in colonies which have more than one foraging area available to them (Ropert-Coudert et al. 2004) or are located in low-productivity areas (Welcker et al. 2009; Paiva et al. 2010; Brown et al. 2012). While breeding, when the body condition of a parent seabird dips below a threshold, they will make the decision to perform a long self-maintenance trip to restore the body reserves (e.g. Tveraa et al. 1997). For seabirds foraging in low-productivity areas, this threshold may be easier to reach than it is for their counterparts in high-productivity areas.

Due to a 23% increase in their global population (Lynch 2013), the gentoo penguin *Pygoscelis papua* has recently received the status of *Least Concern* from the International Union for Conservation of Nature (IUCN, Birdlife 2016). However, the population of gentoo penguins residing at Marion Island in the Southern Ocean has decreased by more than half over the past two decades (Crawford et al. 2014). This decline has been suggested to be due to declining prey availability (Allan et al. 2013; Crawford et al. 2014) as it coincides with long-term changes in the local marine environment brought about by the southward migration of the sub-Antarctic polar front (Ansorge et al. 2009; Downes et al. 2011). Accordingly, the crustacean component of these birds' diet is significantly different in recent years compared to during the 1980s and mid-1990s (Adams and Klages 1989; Carpenter-Kling 2016). Furthermore, the dominant species of Notothenioid fish in the diet has changed from *Lepidonotothen squamifrons* to *L. larseni*

since the 1980s (Adam and Klages 1989; Carpenter-Kling 2016), a change that is mirrored in the diet of the inshore foraging Crozet shag *Phalacrocorax [atriceps] melanogenis* (Espitalier-Noël et al. 1988; Crawford et al. 2003).

Here, we report, for the first time, the foraging distribution and fine-scale movement of gentoo penguins breeding on Marion Island in the southern Indian Ocean and explore foraging strategies in this population. Elsewhere, gentoo penguins are known to be inshore foragers (Croxall et al. 1988; Lescroël and Bost 2005; Takahashi et al. 2008), typically benthic foragers (e.g. Kokubun et al. 2010), but they are also able to forage pelagically (e.g. Takahashi et al. 2008). Consequently, we expected birds to be foraging both pelagically and benthically over the shelf area close to the island.

## Materials and methods

### Study site

The Prince Edward Archipelago (46.9°, 37.8°E) is located in the southwest Indian sector of the Southern Ocean and consists of Marion Island (240 km<sup>2</sup>) and Prince Edward Island (45 km<sup>2</sup>). Between the two islands is a shallow shelf approximately less than 200 m deep. Beyond this shelf, the seabed drops off steeply to approximately 3000 m (Ansorge and Lutjeharms 2002).

Tracking instruments were deployed on gentoo penguins near Trypot Beach (46°53'14.33"S, 37°52'1.66"E) situated on the northeastern coast of Marion Island. Gentoo penguins leaving from this beach to forage have direct access to the shallow inter-island shelf. The colony consisted of 99 breeding pairs in 2014, of which 74 were brooding chicks and 25 were incubating eggs at the time of deployment.

### Deployment and recovery of devices

Global positioning system (GPS) loggers (CatTraQ™ GPS loggers, Catnip Technologies, USA; 44.5 mm × 35.5 mm × 13 mm, 26.3 g) covered in black heat-shrink tubing for waterproofing, and time-depth recorder (TDR) loggers (G5 long life, CEFAS Technology Limited, England, 35.5 mm × 11.5 mm, 2.7 g) were deployed on ten adult gentoo penguins which were brooding recently hatched chicks from 20 to 30 August 2014. GPS loggers were programmed to log position every two minutes and the TDR loggers were programmed to sample depth every 2 s at 12-bit resolution. The TDR loggers were secured to the bottom of the GPS loggers using strips of TESA® tape (Beiersdorf AG, Germany), so that only one unit was attached to the penguins.

Nests identified as suitable for unit deployment were observed from approximately 14:00 until after sunset. Once

a nesting bird was relieved by its partner and had moved a small distance away from the colony, the bird was captured using a hook on the end of a two-metre pole. The GPS and TDR units were then attached to the feathers along the dorsal midline of the penguin's lower back using TESA<sup>®</sup> tape and secured with cable ties and cyanoacrylate glue (Loctite 401<sup>®</sup>). Instrumented birds were marked on the chest feathers with Porcimar dye (Porcimar, Jørgen Kruuse A/S, Denmark) to facilitate recapture through easy identification of individuals. Gentoo penguins are typically diurnal foragers that return to their nest daily (Adams and Wilson 1987; Lescroël and Bost 2005). To capture multiple trips of individuals, loggers were only retrieved approximately five days after deployment. Disturbance was minimised at the colony by retrieving devices where birds exited the sea.

### TDR analyses

All analyses were conducted in R (version 3.3.1.; R Core Team 2016) and were only performed on complete foraging trips.

TDR data were processed using the package *diveMove* (Luque 2007). A feasible zero offset correction and time budget summaries were selected by visual inspection of each trip (Luque and Fried 2011). Actual time of dive, total dive duration, bottom time (the duration between the end of descent and the beginning of ascent) and maximum depth (calculated as the deepest point reached during a dive) were determined for each foraging trip.

In addition, dive profiles of every dive were visually inspected using Igor Pro version 7.0 (Wave Metrics Inc., Lake Oswego, OR, USA) and classified as either benthic or pelagic. The first criterion to identify benthic dives was if the dive's profile was U- or square-shaped (i.e. there was a steady descent followed by an extended time spent at a horizontal bottom phase with little vertical undulation and a steady ascent; see Tremblay and Chérel 2000). The second criterion used to identify benthic dives was if the maximum depth of a series of dives was uniform with a lack of deeper dives, suggesting that the sea floor was the limit; i.e. if the difference in maximum depth reached during a dive was within  $\pm 10\%$  of the maximum depth reached during the preceding dive.

### GPS analyses

GPS data were processed using the package *trip* (Sumner 2015). Erroneous GPS locations, based on a transit speed of greater than  $10 \text{ km}\cdot\text{h}^{-1}$  (Lescroël and Bost 2005), were filtered from the data using an algorithm formulated by McConnell et al. (1992). On average, the speed filtering removed  $3.67 \pm 1.76$  of recorded locations from each foraging trip. Furthermore, when the birds were submerged,

GPS loggers were interrupted, causing irregular time intervals between positional fixes within the tracks. On average, time interval between positional fixes was  $13 \text{ min} \pm 26 \text{ min} 19 \text{ s}$ . To correct for this, the filtered data were processed using a non-stop, continuous, time-correlated, random walk model to estimate the approximate foraging track, using the package *crawl* (Johnson et al. 2008). Dive locations based on the onset of a dive could then be interpolated onto this track.

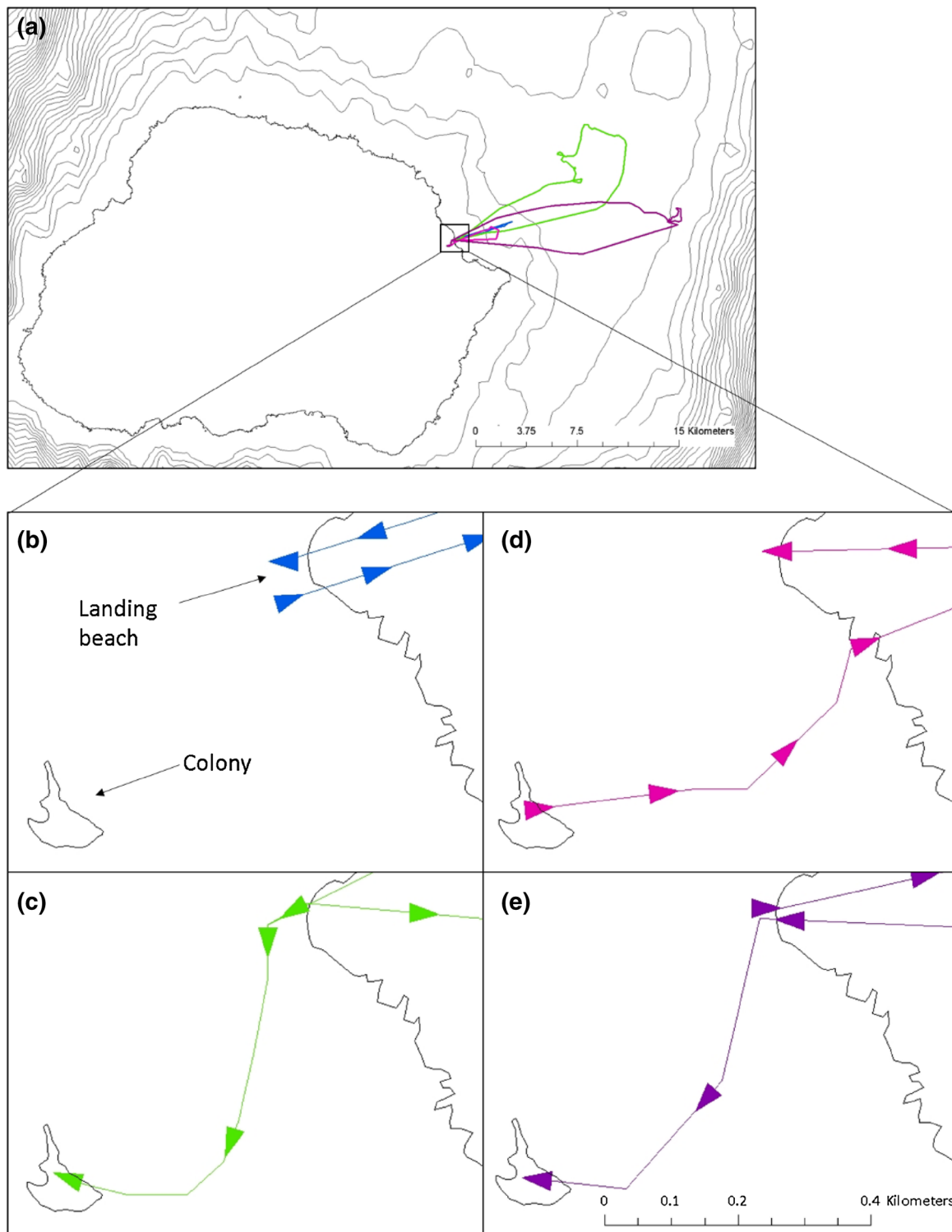
Locations on the approximate foraging tracks were interpolated for one-minute intervals to calculate the total path length (sum of the displacements between all interpolated fixes), maximum distance from the colony (greatest distance reached from the last point on land for that trip), trip duration (time between the last and first points on land before and after a foraging trip) and average travelling speed for each trip, in the package *Move* (Kranstauber and Smolla 2016).

Visualization of the GPS tracks revealed that the birds were alternating between two classes of foraging trips (Fig. 1). The first entailed short afternoon trips, whereafter the birds returned to the shore and remained overnight on the beach and did not return to the colony. The second class involved a long full-day trip whereafter the birds returned directly to the colony after being at sea, where chick provisioning typically occurred (pers. obs). For trips that were only recorded by TDR loggers and not GPS loggers, long trips were defined by whether a foraging trip was followed by a day of non-foraging activity (i.e. no dives were recorded). It was assumed that, during this time, the adult had returned to the nest and was performing nest duties. This division of trips is supported by foraging trips that were recorded concurrently in GPS and TDR data. Furthermore, gentoo penguins are rarely seen on the beach in daylight hours during the breeding season (pers. obs.).

Dive profiles were projected along GPS tracks so that 3D plots could be generated in ArcScene 10.4 (ESRI). This provides a spatiotemporal illustration of the penguin's dive activity and helped in visualizing how the birds are foraging within their environments.

### Statistical analyses

Only dives that were  $>5 \text{ m}$  were considered for analyses as these were assumed to represent active foraging behaviour (Kokubun et al. 2010; Pelletier et al. 2014). Dives shallower than five metres were considered to be travelling dives without active foraging (Miller et al. 2009; Kokubun et al. 2010). Kernel density distributions (Worton 1989) were then calculated using dive locations in the package *adehabitatHR* (Calenge 2006) to delineate the active foraging distribution of birds. The most appropriate smoothing factor was chosen using ad hoc calculations (Worton 1989)



**Fig. 1** **a** Four GPS tracks over four consecutive days of a gentoo penguin (ID: gen02) during 20–30 August 2014 at Marion Island. **b** The bird departs for a short trip and returns to the same beach to roost for the night; **c** on the following day, the bird departs for a long trip and

returns to its colony for the night; **d** on the third day, the bird undertakes a short trip and roosts on the beach overnight; and **e** on the fourth day, it departs for a long trip and returns to its colony overnight

and grid size was set at  $0.02^\circ$  (to match the grid size of the bathymetry data, see below). Foraging distributions representing areas of high prey encounter or the “hot-spot” foraging area, core foraging area and active foraging area were calculated as the areas within the 25, 50 and 90% kernel density contours, respectively (Lyver et al. 2011; Pelletier et al. 2014). Kernel density contours were plotted against the bathymetry contours, which were generated by integrating data from General Bathymetric Charts of the Oceans (GEBCO; <http://www.gebco.net>) and fine-scale in situ data collected by the South African Navy (SAN; <http://www.sanho.co.za>).

Most dive and GPS parameters violated the assumption of normality and homogeneity of variance that are assumed by linear models (Zuur et al. 2009). Distributions assumed by commonly implemented generalized linear models were also not appropriate. To determine whether dive parameters (dive depth, total dive duration and bottom time) differed between the foraging trip types, we, therefore, used Monte Carlo permutation tests. For each of the three dive parameters, we calculated the difference between the median dive parameter value for short trips and that for long trips. We then permuted (randomized) the foraging trip labels 9999 times, calculating the difference between the medians for each permutation. *P* values were calculated as the proportion of times the absolute observed difference was less than the absolute difference from the randomized data.

Similarly, a Kruskal–Wallis test with 9999 Monte Carlo permutations and a stratification defined by bird identity (to control for repeated measure from individuals), implemented in the *coin* package (Hothorn et al. 2006), was used to investigate whether the birds performed significantly more benthic or pelagic dives during short or long trips. The GPS-derived parameters (path length, maximum distance reached and trip duration) were compared in the same way, except for average speed, which was compared using a nested one-way analysis of variance (ANOVA).

Values are given as mean  $\pm$  standard deviation unless otherwise specified.

## Results

### Instrument recovery and classification of foraging trips

Instruments from nine out of the 10 deployments were retrieved within 4–10 days of logger deployment. A total of 59 complete trips were obtained from the TDRs, but only 30 of these were concurrent with complete GPS trips.

Of the 59 trips recorded by TDRs, 42 trips were classified as long and 17 trips were classified as short. Of the 30 concurrent GPS tracks obtained, 19 were defined as long and 11 as short. Seven out of the nine birds undertook short

foraging trips. Four of these alternated between short and long trips, two executed several long trips before performing a short trip and the remaining bird performed only one short trip directly after logger deployment.

### At-sea foraging distribution

Birds departed in a northeasterly direction and remained almost exclusively over the inter-island shelf above the 150-m isobath (Fig. 2 a, b). All birds returned to the same beach from which they departed except one bird which returned to a different beach after one of its short foraging trips. The “hot-spot”, core and active foraging areas were noticeably smaller during short trips (1.19, 2.92 and 14.87 km<sup>2</sup>, respectively) compared to long trips (10.47, 26.18 and 97.35 km<sup>2</sup>, respectively, Fig. 2c, d).

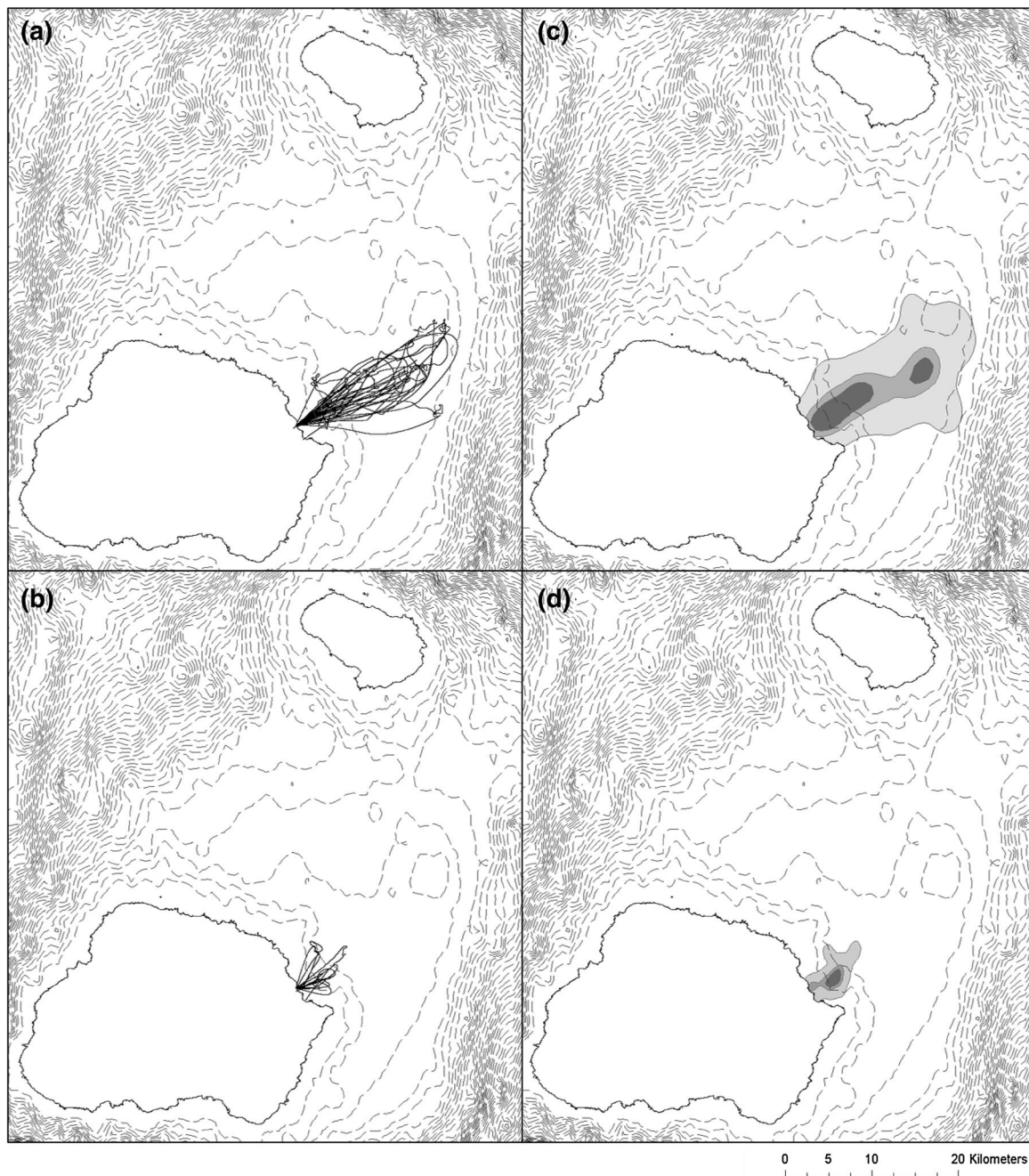
### Foraging trip characteristics

All birds performed foraging trips during the day and returned to land at night. Departure times differed according to the type of foraging trip. In general, birds departing on long trips left between 6 and 7 am, whereas penguins departing on a short trip tended to leave between 3 and 4 pm (Fig. 3). The time that birds returned from a long trip was more variable, between 1 and 7 pm, compared to that of penguins returning from short trips, between 6 and 7 pm (Fig. 3). Shortly after returning from a long trip, the birds returned to the colony (e.g. Fig. 1c, e).

Permutation tests showed that there were significant differences between path length ( $p < 0.01$ ), maximum distance reached ( $p < 0.01$ ) and trip duration ( $p < 0.01$ , Fig. 4). Given as median; inter-quartile range, birds travelled further (long trips: 26.0; 10.0 km and short trips: 6.3; 3.9 km), reached a greater distance from the shore (long trips: 11.0; 5.0 km and short trips: 3.1; 1.2 km) and spent significantly more time at sea (long trips: 10.5; 1.5 h and short trips: 2.5; 0.6 h) during long trips compared to short trips. Mean travelling speed during short ( $2.64 \pm 0.59$  km h<sup>-1</sup>) and long ( $2.24 \pm 0.62$  km h<sup>-1</sup>) trips was, however, similar ( $p = 0.81$ ).

### Dive parameter characteristics

Permutation tests showed that there were significant differences between the maximum dive depths ( $p < 0.01$ ) and dive times ( $p < 0.01$ ) between short and long trips (Fig. 5). There was no difference between bottom time ( $p = 0.87$ ), however. Given as median; inter-quartile range, dives on long trips were deeper (133.2; 75.8 m) and longer (236; 68 s) than dives on short trips (65.7; 96.8 and 180; 148 s, respectively, Fig. 6; Online Appendices 1, 2), whereas bottom time was similar during short (100, 44 s) and long (100, 74 s) trips. The diving depths

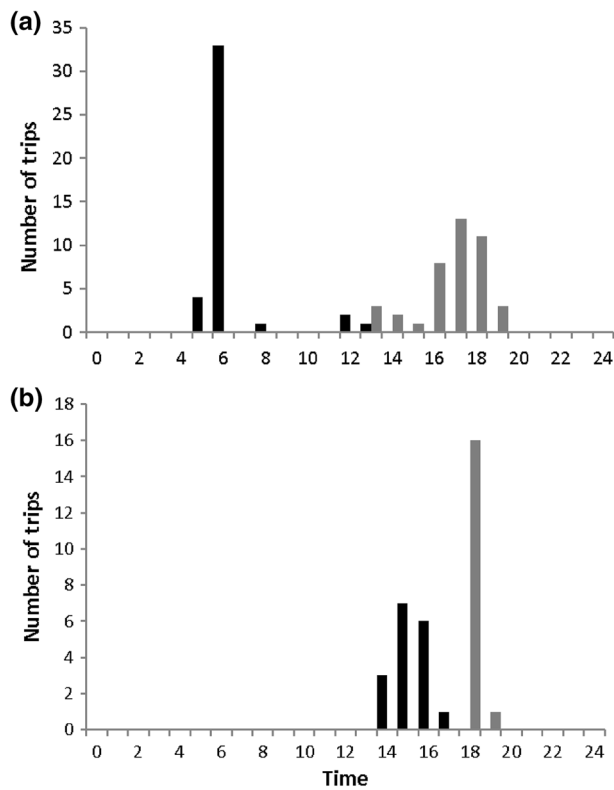


**Fig. 2** Tracks of gentoo penguins during the chick-guarding period at Trypot Beach colony, Marion Island, during 20–30 August 2014, for penguins executing presumed **a** long and **b** short trips and the kernel density distributions of the diving locations for **c** long and **d** short

trips. The “hot spot”, core, and active foraging areas (25, 50 and 90% kernel density contours, respectively) have been indicated (from darkest to lightest grey, respectively). Isobaths (dashed lines) are at 50-m intervals between Marion and Prince Edward Islands

of the birds followed a bimodal distribution for both types of trips (Fig. 4). During short trips, depths between 0 and 40 m (43% of all dives) and 111–130 m (30% of all dives) were most common, whereas depths between 40 and 60 m (10% of all dives) and 130–150 m (55% of all dives) were most common during long trips. Furthermore, birds

performed significantly more benthic dives during long trips compared to short trips ( $p < 0.01$ ). Given as median; inter quartile-range, 83.3, 27.6% of dives were classified as benthic than during long trips; where 61.3, 54.7% of dives were classified as benthic during short trips (e.g. Fig. 5, Online Appendices 1, 2).



**Fig. 3** Departure (*black*) and arrival (*grey*) times for **a** long and **b** short foraging trips for all tracked gentoo penguins during the chick-guarding period at Trypot Beach colony, Marion Island, during 20–30 August 2014

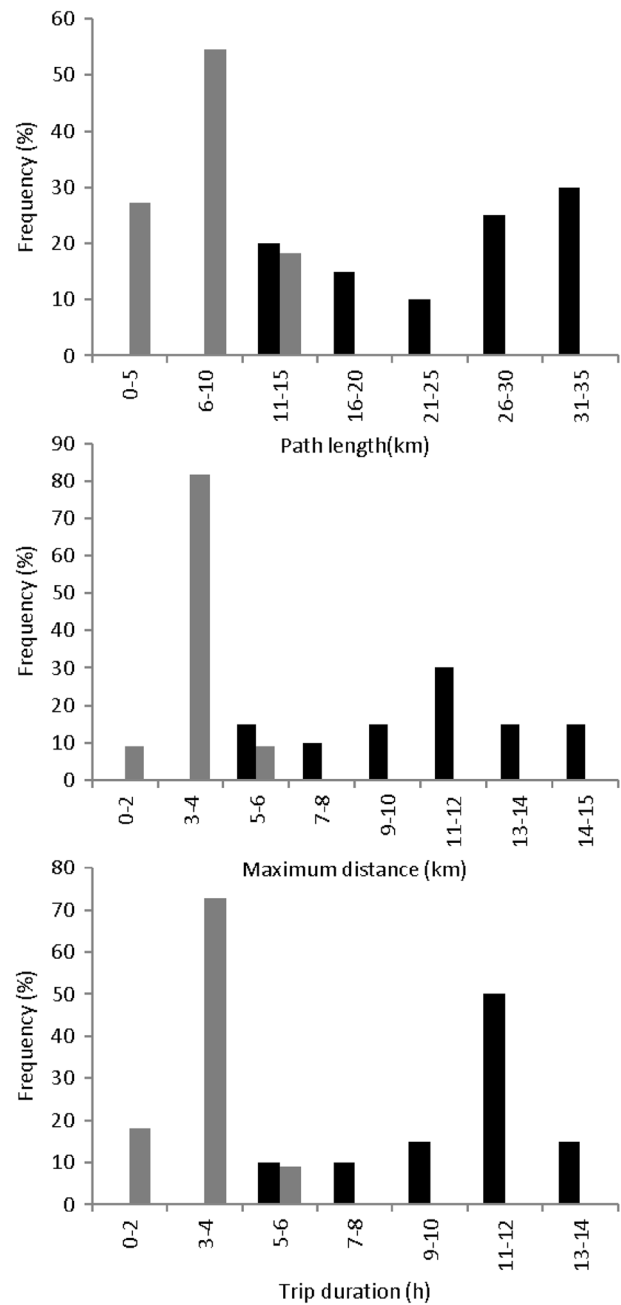
**Discussion**

**Device effects**

Concerns have been raised regarding the consequences of animal-borne instruments on penguin behaviour and foraging efficiency (Wilson et al. 1986). However, Kokubun et al. (2010) found that larger loggers than the ones used in this study did not have any noticeable effect on the foraging efficiency of gentoo penguins at the South Shetland Islands. In our study, devices were placed in a caudal position on the birds, a placement that has been found to minimize the amount of drag caused by a device (Bannasch et al. 1994) and the overall weight of the devices were <1% of the average body mass of the birds. Therefore, it is unlikely that the loggers used in this study would have had a substantial effect on the foraging behaviour of instrumented birds.

**Novel foraging strategy in gentoo penguins**

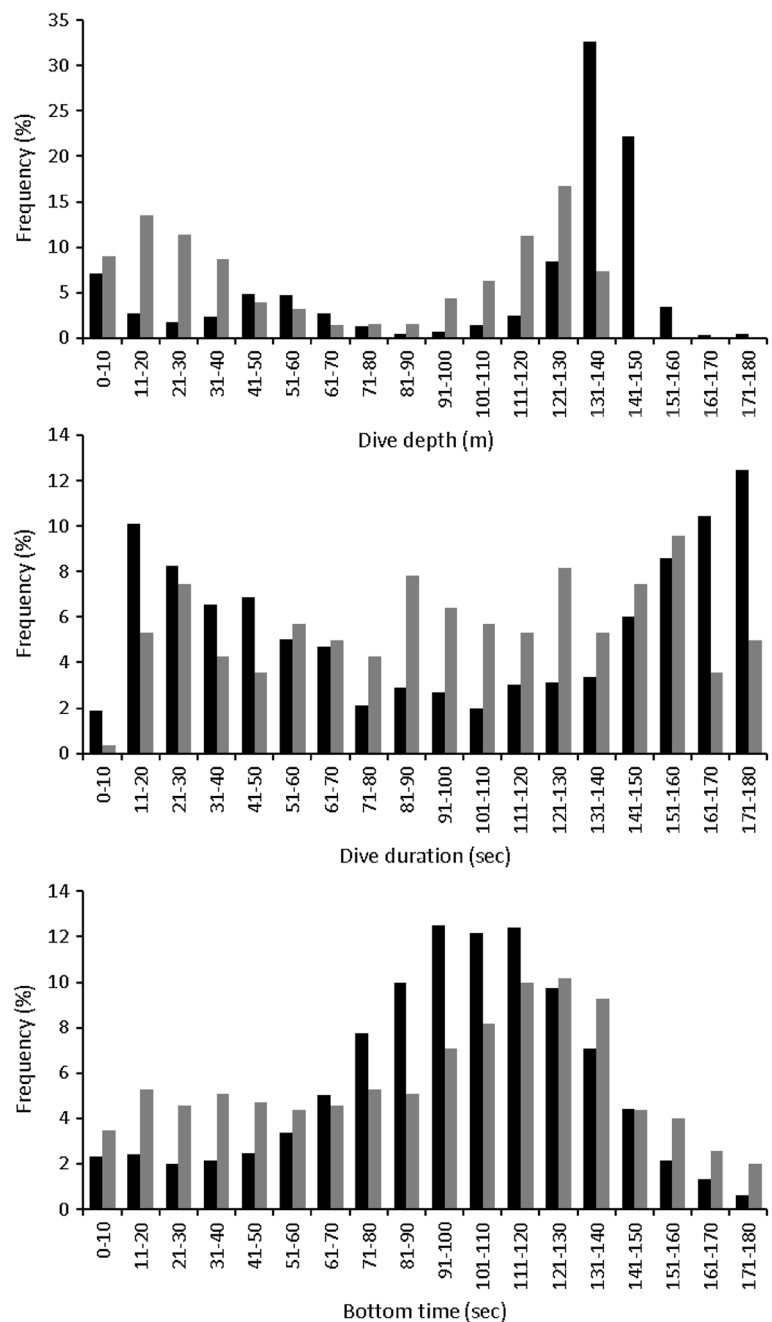
In setting out to understand the foraging distribution and fine-scale movement of gentoo penguins breeding on Marion Island, it was clearly evident that birds were executing



**Fig. 4** Frequency histograms of (from *top to bottom*) path length, maximum distance and trip duration for gentoo penguins guarding chicks at Trypot Beach colony, Marion Island, during 20–30 August 2014, for short (*grey*) and long (*black*) trips

two types of foraging trips during chick rearing. First, short, inshore trips (mean maximum distance of about 3 km from island) which were performed in the afternoon were characterized by short and shallow dives. Second, longer, more distant, day-long trips (mean maximum distance of about 10 km from island) were characterized by deeper, longer and significantly more benthic dives. The short afternoon trips were always followed by the birds roosting on the

**Fig. 5** Frequency histograms of (from *top to bottom*) maximum dive depth, dive duration and *bottom* time for gentoo penguins guarding chicks at Trypot Beach colony, Marion Island, during 20–30 August 2014, for short (*grey*) and long (*black*) trips

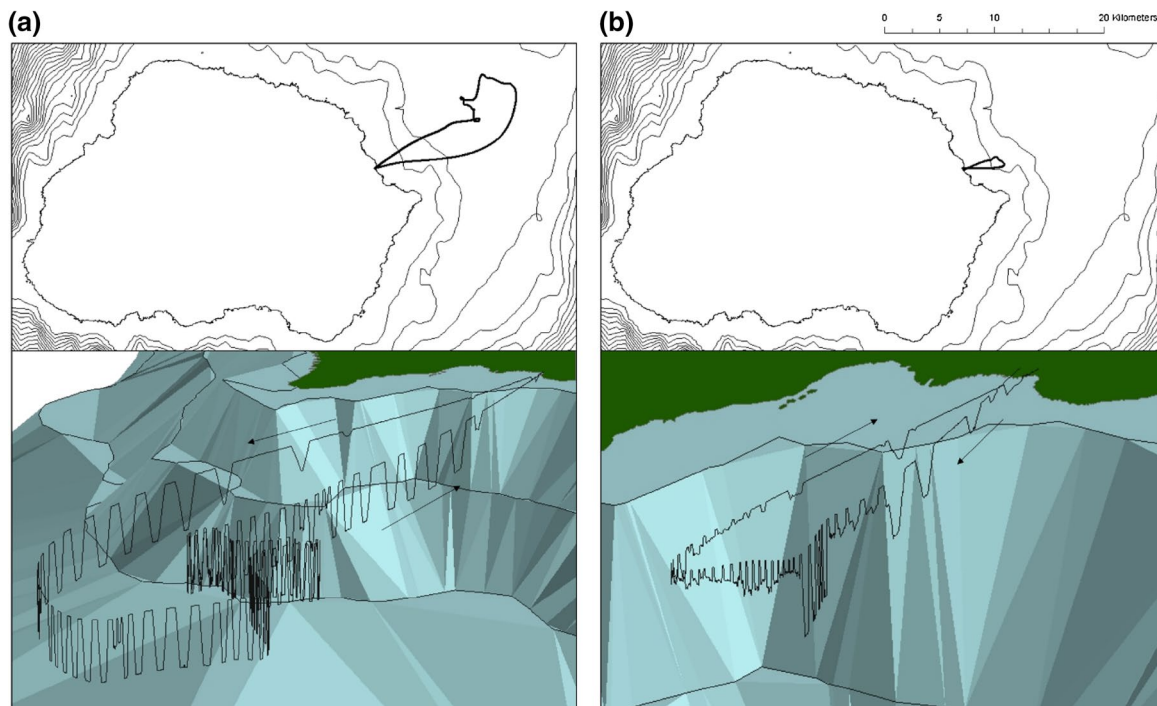


beach overnight, and, the following day, a long trip where-after the birds returned to their colonies to provision their chicks. Gentoo penguins can digest the flesh of fish within 8–16 h (Gales 1985); therefore, all the food consumed during short trips was likely digested by adults and not fed to their chicks. It can, therefore, be hypothesized that the function of these short afternoon trips is self-maintenance, where the adult replenishes body reserves, and the longer full-day trips have the function of, but are not limited to, chick provisioning.

Although bimodal foraging has not been previously described for gentoo penguins, this species is known to

show substantial variation in foraging trip durations; where most birds forage diurnally, some birds extend foraging overnight (Adams and Wilson 1987; Williams and Rothery 1990; Lescroël and Bost 2005). This does not necessarily entail increased foraging at night, as penguins are visual predators and have limited ability to detect prey in low-light conditions (Wilson et al. 1993, 1996; Lescroël and Bost 2005). Furthermore, it is thought that by remaining at sea overnight, the cost of thermoregulation and risk of predation for the Humboldt penguin, *Spheniscus humboldti*, was less than the cost of travelling back to land and returning to the sea the following morning (Taylor et al. 2002). For





**Fig. 6** Three-dimensional representation of **a** a long trip and **b** a short foraging trip of a gentoo penguin (ID:gen02) during 20–30 August 2014 at Marion Island. See Online Appendix 2 for video

gentoo penguins at Marion Island, the close proximity of their foraging area to land means that the cost of remaining at sea overnight might outweigh that of returning to land to rest and thereby promote the short self-maintenance trips that were observed.

Gentoo penguins rarely exceed foraging ranges of 30 km while breeding (Croxall et al. 1988; Robinson and Hindell 1996; Lescroël and Bost 2005; Takahashi et al. 2008), with a maximum distance of 15.5 km from the island recorded in this study. This limited, inshore foraging makes them highly dependent on the local marine environment (Bost and Jouventin 1990; Lescroël et al. 2004). Therefore, to buffer this dependency on local resources, they are opportunistic feeders that exhibit high plasticity in foraging strategies within and between localities across their range (Croxall et al. 1988; Lescroël and Bost 2005; Miller et al. 2009; Handley et al. 2016). This flexibility has been revealed in their response to local habitat features such as bathymetry (Lescroël and Bost 2005), the characteristics of prey which are locally available (Croxall et al. 1988; Lescroël and Bost 2005) and as an adaptation to temporal changes in prey availability (Miller et al. 2009).

Marion Island is believed to be undergoing significant change in prey availability in recent years, which has led to sub-optimal feeding conditions for resident inshore-foraging seabirds—the gentoo penguin and Crozet shag (Allan et al. 2013). This might further validate the need

for additional short, self-maintenance trips. Historically, a smaller percentage of birds appeared to be undertaking these afternoon trips as out of 100 birds monitored at the colony, only 13 departed for the sea in the afternoon (Adam and Wilson 1987). Eleven of these birds returned to the colony the following day (it is unsure whether they remained out at sea or returned to land elsewhere) and two returned the same day after a few hours at sea. Despite our limited sample size, this is in contrast to our observations where nearly all (7 of 9 birds) individuals performed a short afternoon trip. Furthermore, one must consider the reduced population size for gentoo penguins over the last 20 years at Marion Island (Crawford et al. 2014). One might expect that with a smaller contemporary population, there would be reduced intra-specific competition at sea and birds would not need to forage additionally in the afternoons (Fretwell and Calver 1969; Delord et al. 2004). However, this again does not appear to be the case as many birds are performing the short afternoon trips.

Not only is this the first time that a bimodal foraging strategy has been observed for gentoo penguins, it is also the first time that self-maintenance trips in seabirds have been associated with shorter foraging trips. Only yellow-eyed penguins *Megadyptes antipodes* at Oamaru, New Zealand, have been observed to be performing short afternoon trips followed by longer, full-day trips (Mattern et al. 2007). However, the authors do not associate these short

trips with self-maintenance. We argue here that although not all food foraged by a gentoo penguin during a full-day trip is provisioned to the chick and some of this food is retained for self-feeding (Gales 1985), the prey captured during this long trip is not enough to maintain parental body condition and provision for a brood. Therefore, we suggest, due to decreasing prey availability in the inshore environment at the Prince Edward Islands in recent years (Allan et al. 2013; Crawford et al. 2014), and a higher prevalence of short trips in 2014 compared to 1984 (Adams and Wilson 1987), that short afternoon trips performed by resident gentoo penguins at Marion Island are, indeed, for self-maintenance and not just a function of being relieved from nest duties early enough in the day to afford an afternoon foraging trip.

#### *At-sea foraging distribution*

Beyond the novel long and short trips undertaken by the birds at Marion Island, they largely resemble those of other colonies throughout their distribution. For the long trips, birds travelled similar distances compared to gentoo penguins brooding chicks at New Island, Falkland Islands (Masello et al. 2010), King George Island, South Shetland Islands (Kokubun et al. 2010), Admiralty Bay (Miller et al. 2010) and Cape Sherriff, Antarctica (Croxall et al. 1988; Miller et al. 2010). Similarly, where gentoo penguin colonies faced onto shallower shelf waters as opposed to steeply sloping seabeds, so too did the birds from Marion Island utilise a largely benthic foraging strategy, e.g. Kerguelen Archipelago (Lescroël et al. 2005) and King George Island (Kokubun et al. 2010).

The diet of the birds during the study period also fits well with the space-use patterns exhibited. During the chick-rearing period, birds consume more fish than at any other time of their breeding cycle (Adams and Klages 1989; Carpenter-Kling 2016). In particular, their diet is made up of primarily benthic Notothenioid fish, and the remainder consists of the benthic shrimp *Nauticaris marionis* and the pelagic krill *Euphausia vallentini* (Adams and Klages 1989; Carpenter-Kling 2016). The inter-island shelf between Marion and Prince Edward islands provides favourable habitat for Notothenioid fish (Dewitt et al. 1990; Pakhomov et al. 2006) and both species of crustaceans are readily found here (Perissinotto and McQuaid 1992; Hunt and Pakhomov 2003). The fact that the birds foraged exclusively on the inter-island shelf, largely above the 150-m isobath, is probably associated with restricted foraging range while caring for brood and prey availability during this part of the annual cycle.

To optimize its foraging efficiency, a benthic foraging species will aim to maximize the amount of time spent at the sea bottom where prey is encountered (Wilson et al.

1996; Tremblay and Cherel 2000; Zimmer et al. 2010). This approach may be highly beneficial as prey distribution is limited by the sea floor which increases spatial predictability of prey (Kokubun et al. 2010). Therefore, it is not surprising that the bottom time was similar between chick-provisioning and self-maintenance trips as birds may have been foraging at a constant prey search or capture effort per dive during the different types of trips.

Another clear aspect in both trip types, is a bimodal distribution in dive depth. This distribution has also been noted for gentoo penguins elsewhere and it has been suggested that dives to different depths for different functions (Williams and Rothery 1990; Williams et al. 1992; Robinson and Hindell 1996; Lescroël and Bost 2005). For example, dives that were shallower than 10 metres were most likely associated with travelling, exploratory in nature, or targeting pelagic prey (e.g. *E. vallentini*), and deeper dives seeking benthic prey (e.g. Notothenioid fishes and *N. marionis*, Williams et al. 1992; Lescroël and Bost 2005).

## Conclusions and future directions

The inter-island shelf between Marion and Prince Edward Islands was identified as an important foraging area for gentoo penguins. Furthermore, these birds were shown to exhibit a novel foraging strategy among seabirds as they undertook short trips, likely for self-maintenance and longer trips, likely for chick-provisioning. Food limitation, potentially driven by oceanographic changes in these shelf waters (Allan et al. 2013), may have caused the recent decline in gentoo penguin numbers at Marion Island (Crawford et al. 2014). We suspect, therefore, that the short trips undertaken are a response to poor prey availability in the local environment. There is much scope for furthering our understanding of gentoo penguin behaviour and environmental drivers of population changes through inter-colony comparisons of foraging behaviour at this breeding locality. This is particularly relevant when considering the importance of Gentoo penguins as a critical indicator species for the state of the local environment.

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**Conflict of interest** The authors declare that they have no conflict of interest.

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