ORIGINAL PAPER

Plasticity in the foraging behavior of male Southern Rockhopper Penguins (*Eudyptes chrysocome*) during incubation in the Falkland/Malvinas Islands

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Abstract

Environmental changes often affect the persistence of species or populations at different spatial and temporal scales. Thus, species must either adapt to these changes or experience negative impacts at the individual or population levels. Southern Rockhopper Penguins *Eudyptes chrysocome* are distributed throughout the Southern Ocean and have experienced substantial declines in the past which were linked to various anthropogenic and environmental factors. The aim of this study was to investigate the foraging behavior of male Southern Rockhopper Penguins at Berkeley Sound, East Falkland, Falkland/Malvinas Islands, during incubation, a period at-sea which is crucial for replenishing body condition between two extended fasting periods ashore. Thus, birds are forced to forage efficiently during that time to balance their energy demands. We linked their at-sea distribution and foraging behavior to satellite-derived sea surface temperatures and temperature-depth profiles which were recorded by devices attached to the birds. While Southern Rockhopper Penguins usually travel several hundreds of km out into the open sea on multiple-day trips during incubation, we found in our study that most birds foraged close inshore, less than 9 km away from their colony, and regularly returned to their breeding site. We propose that this behavior occurred in response to the close proximity of the 8 °C SST isotherm and the vertical stratification of the waters therein. Also, while usually feeding pelagically in open waters, there are strong indications that Southern Rockhopper Penguins performed benthic or, at least, near-bottom dives to catch their prey during these short trips. The consequences of this behavioral plasticity in response to variations in sea temperatures and inferred prey availability are discussed, especially with regard to predicted global climate change.

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Introduction

Environmental changes often negatively affect the persistence of populations or species (Stenseth et al. 2002; Walther et al. 2002). However, all organisms have developed structural (long-term), physiological (medium-term), and behavioral (short-term) adaptations that may help them to survive in a changing environment. Short-term adjustments to changing environmental conditions can occur predominantly through behavioral plasticity, allowing individuals to react promptly to changes in the environment (e.g., Wcislo 1989; Wong and Candolin 2015). The foraging behavior of central place foragers is strongly influenced by prey availability and distribution, and changes in predator behavior over time may reflect modifications in the abundance and/or the distribution of food (e.g., Cairns 1987). For example, temperature differences of even 2 °C can render the tidal fronts off Patagonia,

Southwest Atlantic Ocean, less prominent and can lead to massive blooms of gelatinous zooplankton and depress populations of copepods (Sabatini and Martos 2002). This influences the plankton community structure by changing the timing of recruitment and the population growth which in turn affects the trophic chain it generates. Even these "slight" temperature modifications have a bottom-up effect on the entire trophic chain, ultimately affecting top predators' foraging areas and diet (e.g., Garcia-Godos and Goya 2006; Grémillet and Boulinier 2009; Masello et al. 2010; Baylis et al. 2012; Lescroël et al. 2014). Moreover, if these predators feed towards the bottom of the trophic chain, their feeding behavior will be more closely linked and vulnerable to oceanographic conditions affecting primary productivity in their feeding area. Therefore, multi-year studies on the behavior of a predator can elucidate alterations in the marine environment utilized.

Southern Rockhopper penguins (*Eudyptes chrysocome*, SRP) are meso-predators and distributed throughout the Southern Ocean in the Atlantic, Pacific, and Indian Oceans (Pütz et al. 2013). SRP are currently classified as Vulnerable to extinction (BirdLife International 2017) due to substantial population declines in recent decades over its entire range. These have been linked to several factors such as habitat degradation, chemical pollution, and algal blooms, among others (see review in Pütz et al. 2013; Trathan et al. 2014). In the Southwest Atlantic, there are two main assemblages: Staten Island (ca. 130,000 pairs, Raya Rey et al. 2014) and the Falklands/Malvinas archipelago (ca. 320,000 pairs, Baylis et al. 2013).

SRP feed mainly on low trophic level prey like pelagic crustaceans and, to a lesser degree, small cephalopods and fish (Pütz et al. 2001, 2013). This makes them susceptible to changes in local primary productivity, because their main prey is highly linked to the oceanographic conditions (sea-surface temperature (SST), Chlorophyll-a concentration). For example, surface water stratification becomes shallower with increasing SST, thereby providing fewer nutrients for primary productivity compared to a deeper mixed layer (Behrenfeld et al. 2006). However, very deep water mixing may also negatively impact on primary productivity (Smetacek and Passow 1990). Furthermore, plankton species composition is also influenced by changes in SST (Hays et al. 2005). Thus, it can be expected that their preferred foraging areas are also influenced by the prevailing oceanographic conditions (Dehnhard et al. 2013). Studies have shown a link between SST and overwintering survival of SRP at both, the Falklands/Malvinas archipelago and Staten Island (Raya Rey et al. 2007; Dehnhard et al. 2013). In particular, extreme shifts in SST had negative effects on the survival of adults at both sites. In times of accelerated climatic change, modifications in SST fluctuations are predicted which would thus directly affect the survival of this species.

Generally, male SRP return from their winter migration several days earlier than females (Pütz et al. 2013). After egg laying, both partners remain at the nest for some days before the male leaves for 2–4 weeks. When he returns, the female departs to the sea for 1–2 weeks to restore body condition (Pütz et al. 2013). After hatching and during the guard stage, which lasts about 3 weeks, the female alone provisions the offspring with food while the male guards the chicks. Males only leave to regain body condition for some days after the chicks have crèched. Thus, in male SRP, the period at-sea during incubation and is crucial for replenishing body condition and balancing energy demands, because it lies between two extended fasting periods of up to 40 days (Strange 1982; Poisbleau et al. 2008; Pütz et al. 2013). The aim of this study was to (a) investigate the foraging behavior of male SRP in the northeast of East Falkland during the incubation period; (b) compare their behavior amongst study years and with data collected from the same colony in 2000, and (c) determine any potential links between the penguins' behavior and local sea-surface temperatures (SST).

Materials and methods

Between 2011 and 2014, a total of 62 male SRP from different colonies in Berkeley Sound (51.5°S, 57.9°W) to the northeast of East Falkland, Falkland/Malvinas Islands (Fig. 1), were externally equipped with either Time-Depth-Recorders (TDR) or Global Positioning System-Loggers (GPS) at the onset of the incubation period (for details see Table 1). In brief, penguins clearly associated with a specific nest containing two eggs were visually checked for bill dimensions. Then, the bird with the larger bill was caught, weighed to the nearest 0.1 kg and bill dimensions measured to verify visual sex determination (Hull 1996; Pütz et al. 2013). Devices were then attached on the mid-line of the back as far distally as possible without impairing the preen gland, using black tape (Tesa, Beiersdorf AG, Hamburg, Germany) according to the method described by Wilson et al. (1997). The whole process took less than 15 min per bird. Recovery of the devices took place during subsequent visits to the colony from 2 weeks after equipment onwards (Table 1). Birds carrying a device were caught and the devices and any remains of the attachment material were removed. To minimize handling times during this critical period, no further body mass weights were taken.

Technical features of the devices used

All devices were hydrodynamically shaped following the recommendations by Bannasch et al. (1994). The Time-Depth-Recorders (MK9, Wildlife Computers, USA) used were embedded in epoxy resin and weighed, including

Fig. 1 Location of Berkeley Sound in the northeast of East Falkland, Falkland/Malvinas Islands. The upper panel provides an overview of the Southwest Atlantic, the middle panel shows the Falkland/Malvinas Islands and the lower panel details bathymetry (modified from British Admiralty Nautical Chart 2550) and study sites within Berkeley Sound. The 30-m depth contours are in red, the 50-m depth contour in dark blue
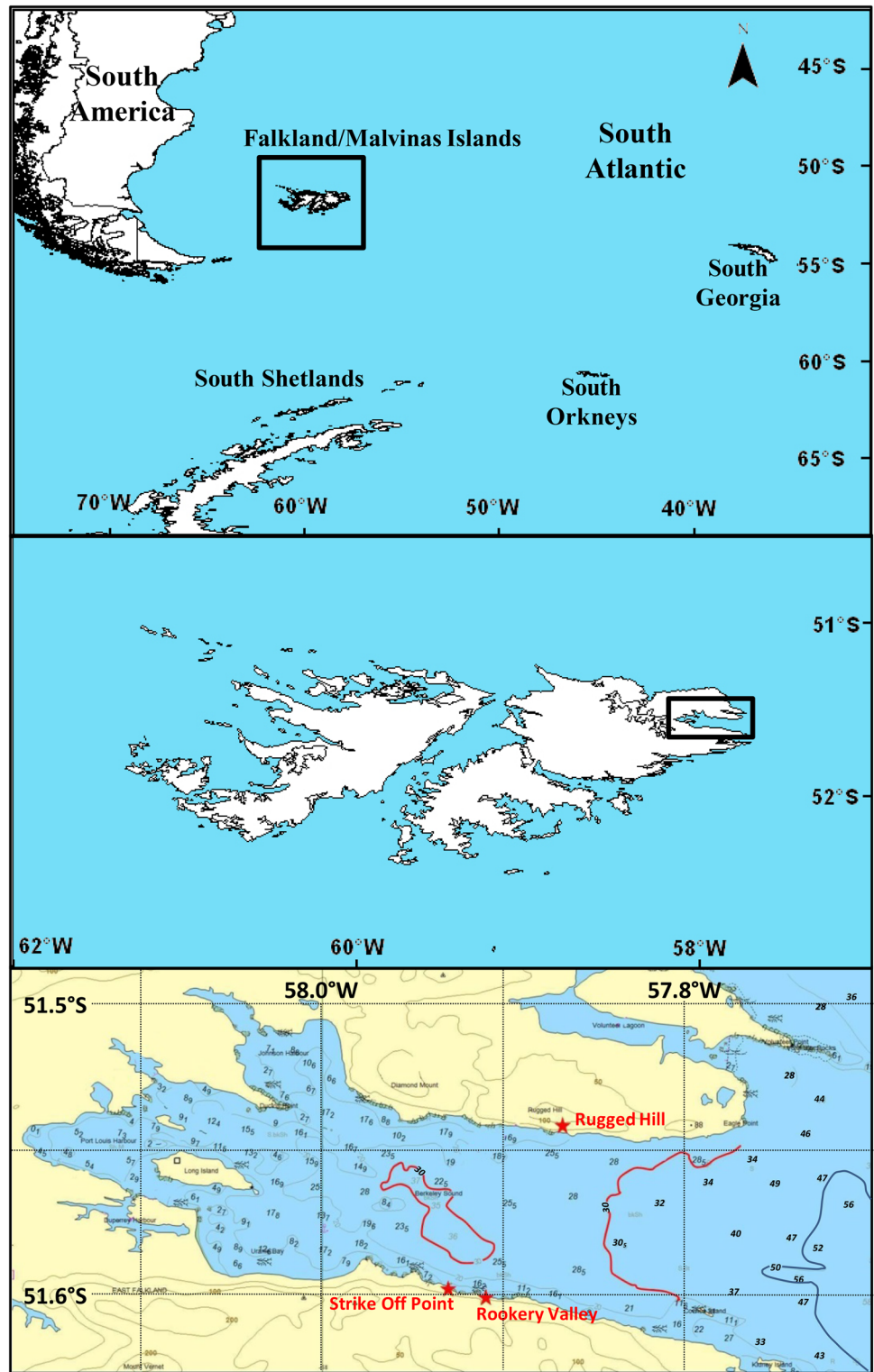
attachment material, less than 50 g, corresponding to ca. 1.3% of the mean SRP weight of 2.64 ± 0.23 kg. They had maximum dimensions of $90 \times 21 \times 21$ mm and were programmed with MK9HOST (Wildlife Computers). The TDRs were each equipped with a pressure sensor, a light sensor, and a temperature sensor, programmed to record every 3 s. To optimize energy consumption, a saltwater switch prevented data being recorded while at the surface. The pressure sensor recorded the dive depth between 0 and 350 m, accurate to within 0.5 m (range 0–20 m), 1 m (range

Table 1 Details on study sites, years studied, and devices used on incubating male Southern Rockhopper Penguins, *Eudyptes chrysocome*, from colonies in Berkeley Sound, East Falkland, Falkland/Malvinas Islands

Location	Latitude	Longitude	Year	Equipment	Recovery of devices	Birds (*n*)	Device
Rookery Valley	51.600°S	57.908°W	2011	20–23 Nov	9–13 Dec	9	TDR
						3	Mini-GPS
			2012	11–13 Nov	25–28 Nov	9	TDR
						9	Mini-GPS
			2013	12–14 Nov	28 Nov–6 Dec	4	TDR
						10	Mini-GPS
Strike Off Point	51.599°S	57.928°W	2013	14–16 Nov	28 Nov–3 Dec	5	TDR
						8	Mini-GPS
Rugged Hill	51.543°S	57.852°W	2014	20 Nov	2 Dec	5	nanoFix Geo

TDR MK9 (Wildlife Computers, USA), *Mini-GPS* GPS-TDRs (Earth & Ocean Technologies, Kiel Germany), *Fix Geo* nanoFix Geo (Pathtrack Ltd, Otley, UK)

20–200 m), and 5 m (range 200–350 m), and the temperature sensor recorded between −40 and 60 °C with an accuracy of ±0.1 °C. The data from the light sensor were not used in this study.

The GPS-TDRs (Mini-GPS, Earth & Ocean Technologies, Kiel, Germany) used in 2011–2013 weighed ca. 40 g including attachment material (corresponding to ca. 1% of the mean SRP weight) and had maximum dimensions of 57 × 34 × 20 mm, excluding a 46-mm-long temperature sensor with a diameter of 4 mm protruding at the rear end of the devices. They were programmed to record geographical position via GPS at varying intervals depending on the activity of the study birds, which was triggered by the pressure sensor. Additionally, temperature and depth were recorded every 3 s with an accuracy of 3.5 cm and 0.005 °C, respectively. The GPS-tags used in 2014 were nanoFix Geo (Pathtrack Ltd, Otley, UK), that measured 55 × 23 × 15 mm, excluding the 3-cm-long whip antenna at the rear, and weighed ca. 30 g (corresponding to ca. 0.8% of the mean SRP weight). The tags recorded only position and were programmed to collect fixes every 5 min. However, they were equipped with saltwater switches to optimize power consumption and maximize fix acquisition by preventing the search for satellites when underwater but initiating searches as soon as the tag was exposed to air. The tags collected snapshots of the satellite constellation and locations were afterwards processed from online ephemeris data, which considerably reduced the time to obtain fixes and saved battery power.

It is well accepted that the external attachment of devices on free-ranging penguins has the potential to impact on their foraging behavior and breeding success (e.g., Taylor et al. 2001; Wilson and McMahon 2006; Ropert-Coudert et al. 2007), with effects increasing under unfavorable environmental conditions (Ballard et al. 2001). Several measures were taken in this study to reduce the impact of the devices on the penguins' behavior (e.g., hydrodynamics, see above). No logger effect on trip duration, diving behavior, hatching and breeding success or in adult survival was observed in a comparable study on SRP from New Island, Falkland/Malvinas Islands (Ludynia et al. 2012, 2013). Accordingly, in our study, no effect on the immediate egg survival and hatching success was apparent, and breeding success was also not affected which was determined by a comparison of chick survival in our study area compared with a control area in the SRP colony at Rookery Valley (chick survival 24 January 2012 was 69% in study area versus 70% in control area). Therefore, we assume that the externally attached devices were not detrimental per se to the penguins and have not essentially altered the birds' behavior. This is further substantiated by studies on the winter dispersal of Magellanic Penguins (*Spheniscus magellanicus*, Pütz et al. 2000) and SRP (Pütz et al. 2002, 2006a), where also no device effects were apparent over much longer attachment periods.

Positional data analysis

The positional data obtained were graphically analyzed showing 50 and 95% kernel distributions of each year combined with the average monthly sea-surface temperatures (SST) at the time (NASA remote sensing MODIS-Aqua SST, 4 km resolution). In addition, the average SST for the area surrounding the colony in December of each year between 2011 and 2014 was obtained from http://indl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/CMB/GLOBAL/.Reyn_SmithOIv2/.monthly/.sst).

Data derived from the integrated temperature sensors of the Mini-GPS in years 2011–2013 were used to create vertical water temperature profiles for selected time periods and locations. Measurements processed derived from the deepest area within Berkeley Sound (c.f. Fig. 1) for all 3 years and from two locations outside Berkeley Sound in 2011. The latter two locations were both situated to the east of the 8 °C isotherm (c.f. Fig. 2), one 200 km and the other one 275 km away from the breeding site, and were chosen because of an accumulation of fixes indicating intense foraging activity. Dive depths associated with a water temperature measurement were averaged over 5-m depth classes to compensate
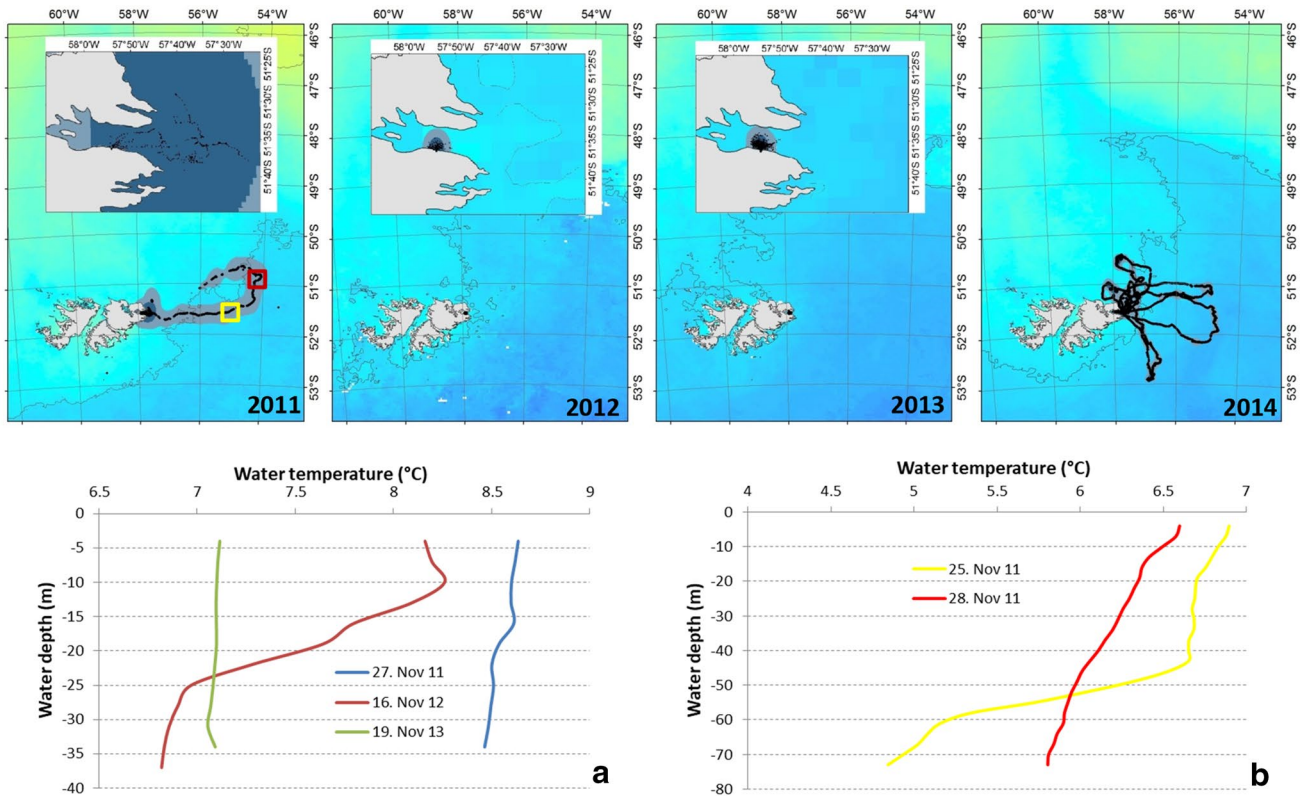
Fig. 2 Foraging tracks of male Southern Rockhopper Penguins, *Eudyptes chrysocome*, from colonies in Berkeley Sound, East Falklands, Falkland/Malvinas Islands, during the incubation period. Insets show 95 and 50% kernels of the foraging ranges. Shaded background colors provide SST from dark blue (colder) to light green (warmer). Also given is the 8 °C SST isotherm in December for the years stud-ied. Vertical temperature profiles for water depths between 30 and 37 m are given for **a** selected positions and dates in 2011–2013 inside Berkeley Sound and **b** for 2011 in areas outside Berkeley Sound, indi-cated by squares in red and yellow. Colors in b mirror the colors of the squares indicating the areas sampled

for any delay in measurement during descent and ascent. The resulting temperature profiles are only based on the birds that remained in the respective areas on the specific dates given.

Dive data analysis

Foraging trips were classified as long if they lasted more than 24 h (= multiple-day trips) and as short (= day trips) if they lasted less than 24 h. Only dives > 5 m were used in the analysis. Dive data from MK9 were analyzed with INSTRUMENT HELPER (Wildlife Computers); dive data recorded by the Mini-GPS were analyzed using MULTI-TRACE (Jensen Software Systems, Kiel, Germany). Forag-ing trip durations were estimated from 2011 to 2013 as the interval between the first and the last dive recorded, and in 2014 as the interval between the first and the last positional fixes at sea. The following parameters were considered in the analysis of the 2011–2013 depth data: Daily foraging time (time difference between the first and the last dive of the day), mean dive depth (m), maximum dive depth (m), dive duration, duration of bottom time (time spent at 80% of the maximum dive depth), number of wiggles (abrupt changes in dive depth during the bottom time), and vertical velocities during descent and ascent. From these data, diving efficiency (time at bottom/(dive + post-dive duration); Ydenberg and Clark 1989) and foraging efficiency (number of wiggles/min bottom time) were calculated.

GLMMs were generated to compare behaviors amongst years and foraging trip types (long vs. short), with individual as a random effect: X-type (long/short = factor) + year, ran-dom = ~ 1|id and the model is based on restricted maximum likelihood (REML). The percentage of variability explained by the random effect was estimated as the proportion of the total variance included in the intercept of the generated model. Models were compared with individual nested within year as a random factor in order to determine the variability due to year, but given that year was not a significant random effect in any model, year was eliminated from the random effects and only included as a fixed effect. Variables were graphically tested for normality by analyzing the linearity of their qq residual plots. Models were compared with versus

without the random effect (id) and then with versus without the fixed effects: foraging trip type (short or long) and year (all years with dive depth measurements for individuals breeding within the Berkley Sound, i.e., 2011–2013) with a χ^2 estimation. Marginal (R^2m) and conditional R^2 (R^2c) of the generated models were also reported to evaluate how well the data adjusted to fixed effects alone (R^2m) or fixed and random effects (R^2c, following Nakagawa and Schielzeth 2013; Nakagawa et al. 2017). All models were generated in R (version 3.4.1) using packages nlme (Pinheiro et al. 2017), lme4 (Bates et al. 2015), and MuMIn (Barton 2018) and significance was set at $p < 0.05$.

Tremblay and Cherel (2000) identified benthic diving in SRP, based on a square-waved shape of the dives, a uniform maximum depth and the lack of deeper dives, all indicators that the sea floor limited the dive depths. In accordance, we visually inspected the foraging trips of all animals equipped with a depth sensor and whose foraging trip positions were located inside Berkeley Sound for indications of a dive depth limitation by the sea floor. However, consistent diving to a certain depth range was rare, which was assumed to be related to the undulating sea bottom ranging in depth from between 0 and 37 m.

Therefore, GLMs were generated with the following structure (X-dive type(benthic/pelagic) as a fixed effect, with two randomly chosen subsamples of 1000 dives to depths between 31 and 37 m (=maximum depth to be reached in Berkeley Sound) and compared by a t test: one subsample contained pelagic dives performed by birds from the colony at Rookery Valley over the continental shelf in 2000 (data taken from Pütz et al. 2006b), the other consisted of presumed benthic dives performed by SRP from Rookery Valley within Berkeley Sound in 2012–2013 (this study).

Results

Foraging areas in relation to water temperature

In 2011, and more noticeably in 2012 and 2013, nearly all individuals performed short daily trips in shallow waters contained within Berkeley Sound (Fig. 2). In 2011, only 2 out of 12 study birds performed exclusively one long trip, six conducted only short trips and the remaining four exhibited a mixture of short and long trips (Table 2). The two exclusive multi-day trips were directed either just beyond the entrance of Berkeley Sound or much further to the east in colder waters well beyond the 8 °C isotherm, more than 300 km away from the colony (Fig. 2, Table 2). In 2012 and 2013, all SRP equipped with GPS-Loggers foraged less than 9 km away from their breeding site within the Berkeley Sound, while the 8 °C isotherm was either further to the west (2012) or very close (2013) to the breeding site. Accordingly, the proportion of individuals performing multiple-day trips was very low (one bird made a 6-day trip in 2012 and two individuals made two longer trips in 2013), and these individuals also made several single-day trips (Table 2). In 2014, SRP performed multi-day trips, up to 230 km away from the colony, although 2 birds made 7-day trips in total

Table 2 Foraging parameters of incubating Southern Rockhopper Penguins, *Eudyptes chrysocome*, from colonies in Berkeley Sound, Falkland/Malvinas Islands: Rookery Valley in 2011–2013, Strike Off Point in 2013 and Rugged Hill in 2014 (*s* short < 24 h, *l* long > 24 h)

	Short trips	Long trips	2011	2012	2013	2014
No. of foraging trips (individuals)	452 (55)	9 (9)	s: 76 (10) l: 6 (6[a])	s: 145 (18) l: 1 (1[b])	s: 231 (27) l: 2 (2[b])	s: 7 (2) l: 5 (5[c])
Foraging trip duration (days)	0.4 ± 0.1	8.1 ± 2.1	s: 0.4 ± 0.1 l: 6.6 ± 2.8	s 0.4 ± 0.1 l: 6.5	s: 0.3 ± 0.1 l: 1.3	s: 0.5 ± 0.1 l: 8.7 ± 1.7
Max distance to colony (km)			s: 40 l: 310	7	9	s: 12 l: 230
Daily foraging duration (h)	7.6 ± 3.1	16.6 ± 3.7	10.7 ± 6.0	7.7 ± 3.3	8.1 ± 3.3	
Mean dive depth (m)	19 ± 5	24 ± 9	19 ± 8	17 ± 5	22 ± 4	
Max dive depth (m)	31 ± 6	51 ± 14	37 ± 16	29 ± 8	34 ± 5	
Diving efficiency	0.38 ± 0.06	0.47 ± 0.14	0.44 ± 0.11	0.40 ± 0.06	0.36 ± 0.05	
Foraging efficiency	3.5 ± 1.1	2.4 ± 0.9	2.9 ± 1.0	4.1 ± 1.2	3.3 ± 1.0	

Calculation of foraging trip duration is based on the time difference between the first and last dive in birds studied between 2011 and 2013 and between the first and last position at sea in birds studied in 2014. Values are given as mean ± SD

[a]Four out of six individuals performed both, short and long trips

[b]These individuals also preformed short trips

[c]Two of these individuals also performed short trips

before starting their multiple-day trip. Also, in 2014 the 8 °C SST isotherm was located further to the east (Fig. 2).

Taking into account the vertical temperature profiles, which are based on recordings of the temperature sensors integrated into the GPS-loggers, there were also pronounced differences between 2011 and 2013 within the deepest foraging area in Berkeley Sound, where water depths exceed 30 m (Fig. 1). In 2011, the water body was well mixed with a temperature of > 8.5 °C (Fig. 2). A well-mixed water body was also apparent in 2013, but the temperature was lower at between 7.1 and 7.2 °C. In contrast, in 2012 the water exhibited a pronounced stratification, with temperatures above 8 °C in the upper 10 m, a temperature decrease between 10 and 25 m down to 6.9 °C, and a mixed water body onwards to the sea floor with temperatures of 6.8–6.9 °C.

For spatial comparison, the two areas sampled in 2011 outside Berkeley Sound, indicated by squares in Fig. 2, were colder but showed the same vertical mixing pattern, at least in the upper 40 m. The area just off the mouth of Berkeley Sound, sampled on 25 November 2011, exhibited a stratified water mass with a water temperature > 6.5 °C down to 40 m, followed by a decrease in temperature to 5 °C over the next 20 m and a further, but less pronounced decrease between 60 and 75 m. In contrast, 3 days later, on 28 November 2011, and further away from Berkeley Sound, water temperature decreased continuously from 6.6 °C near the surface to just above 5.8 °C at a water depth of 70 m.

Diving behavior

For years 2011–2013, the calculation of specific foraging characteristics allowed the comparison of selected dive parameters (Tables 2 and 3). Daily foraging duration was more than twice as high in long compared with short trips. However, daily foraging duration differed only marginally amongst years (trip type: $\chi^2 = 208.3$, $p < 0.01$ and year: $\chi^2 = 3.7$, $p = 0.05$; random effects of individual accounted for 32% of the variability in the data, $R^2m = 0.47$–$R^2c = 0.57$). The mean and maximum dive depths reached by individuals were again higher during long trips, and also differed amongst years (mean depth: trip type: $\chi^2 = 25.7$, $p < 0.01$ and year: $\chi^2 = 27.8$, $p < 0.01$; random effects (37% of variability, $R^2m = 0.12$–$R^2c = 0.38$), and maximum depth: trip type: $\chi^2 = 130.1$, $p < 0.01$ and year: $\chi^2 = 19.4$, $p < 0.01$; random effects (36% of variability, $R^2m = 0.34$–$R^2c = 0.53$). Dive efficiency (time at bottom/[dive + post-dive duration]) differed amongst years but not between foraging trip types (trip type: $\chi^2 = 0.2$, $p = 0.66$ and year: $\chi^2 = 5.5$, $p = 0.02$; identity explained 57% of variability $R^2m = 0.18$–$R^2c = 0.69$). Foraging efficiency (number of wiggles/bottom time) also differed amongst years but also between foraging trip types, being higher in one-day trips than in multi-day trips, particularly in 2012 (trip type: $\chi^2 = 12.0$, $p \leq 0.01$ and year: $\chi^2 = 8.2$, $p < 0.01$; identity explained 53% of the variability, $R^2m = 0.04$–$R^2c = 0.62$, see Table 3).

From 2011 to 2013, many birds engaged in day trips which were directed to shallow waters depths < 37 m within the Sound, with maximum dive depths often coinciding with the maximum water depths (Fig. 1). The subsamples of benthic (years 2012 and 2013) and pelagic (year 2000, data obtained in the colony at Rookery Valley, taken from Pütz et al. 2006b) dives revealed significant differences with regard to the performance of the dives (Fig. 3, Table 4). In comparison, total dive duration and post-dive interval were significantly shorter in benthic dives. When compared to pelagic dives, benthic dives showed similar bottom time, more wiggles and faster descent and ascent speeds. Accordingly, the calculated diving and foraging efficiencies were both higher in benthic foraging SRPs.

Table 3 χ^2 test and statistical significance of fixed (type and year) and random effects (ID and ID nested within year) of GLMMs of foraging parameters of male Southern Rockhopper Penguins, *Eudyptes chryso-come*, from the colony at Rookery Valley, Berkeley Sound, Falkland/Malvinas Islands, in 2011–2013

	Fixed effects		Random effects	
	Type (long vs. short)	Year (2011–2013)	ID vs. ID (year)	ID vs. no random
Daily foraging duration	$\chi^2 = 208.3$ $p < 0.01$	$\chi^2 = 3.7$ $p = 0.05$	$\chi^2 \approx 0$ $p = 1$	$\chi^2 = 34.5$; $p < 0.01$ 32% of variability explained
Mean dive depth	$\chi^2 = 25.7$ $p < 0.01$	$\chi^2 = 27.8$ $p < 0.01$	$\chi^2 \approx 0$ $p = 1$	$\chi^2 = 67.6$; $p < 0.01$ 37% of variability explained
Maximum dive depth	$\chi^2 = 130.1$ $p < 0.01$	$\chi^2 = 19.4$ $p < 0.01$	$\chi^2 \approx 0$ $p = 1$	$\chi^2 = 60.4$; $p < 0.01$ 36% of variability explained
Diving efficiency	$\chi^2 = 0.2$ $p = 0.66$	$\chi^2 = 5.5$ $p = 0.02$	$\chi^2 \approx 0$ $p = 1$	$\chi^2 = 282.8$; $p < 0.01$ 57% of variability explained
Foraging efficiency	$\chi^2 = 12.0$ $p < 0.01$	$\chi^2 = 8.2$ $p < 0.01$	$\chi^2 \approx 0$ $p = 1$	$\chi^2 = 282.8$; $p < 0.01$ 53% of variability explained

Fig. 3 Depth profile of a male Southern Rockhopper Penguin, *Eudyptes chrysocome*, from the colony at Rookery Valley in Berkeley Sound, East Falklands, Falkland/Malvinas Islands, during incubation in 2013. At the top, the whole dive profile is shown; red areas mark daily dive bouts (middle) and further details (bottom). Benthic dives are only identifiable in the right hand graphs. For details see text
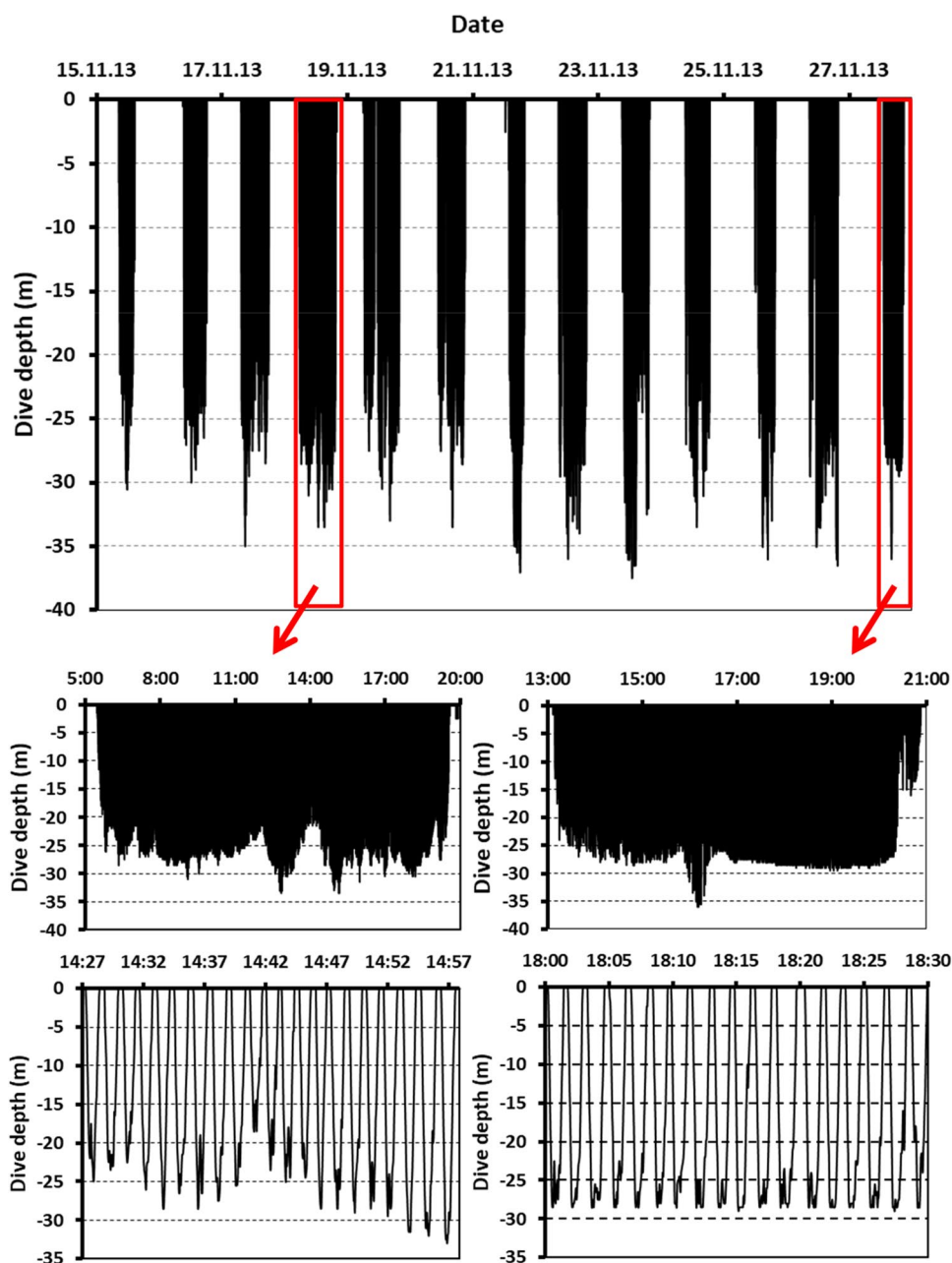
Discussion

Foraging trip duration

The breeding cycle of SRP is well established throughout its distributional range (Williams 1995; Pütz et al. 2013). Generally, after the second (B-) egg has been laid, partners share incubation duties for some days. Then, males depart for a foraging trip lasting between several days up to 3 weeks before returning to the nest to exchange incubation duties, thereby enabling the female to perform a multi-day foraging trip before the chicks hatch after a total incubation period of between 32 and 34 days. However, the exact timings of

the three periods—shared incubation, long male, and long female foraging trip—can vary annually and spatially. For example, on Crozet males depart on average 11.7 days after the B-egg has been laid (Williams 1995) and on Macquarie it takes on average 10 days (Hull et al. 2004). A comparison of the foraging trip durations of SRP from breeding sites in the Southwest Atlantic is shown in Table 5. In the Falkland/Malvinas Islands, eggs are laid in early November and most males leave by mid-November to perform their long incubation trip (Pütz et al. 2003, 2006b; Ludynia et al. 2013). However, in our study, in 2011–2013 SRP from the colonies in Berkeley Sound performed almost exclusively short day trips, during which they foraged close to the breeding site

Table 4 Statistical comparison (*t test* of a GLM) of two randomly selected subsamples of benthic (2012–2013, $n = 1000$) and pelagic dives (2000, $n = 1000$; data from Pütz et al. 2006b) between 30 and 37 m for selected diving parameters of male Southern Rockhopper Penguins, *Eudyptes chrysocome*, from Berkeley Sound, Falkland/Malvinas Islands

Variable	Benthic	Pelagic	t	p
Dive duration (s)	76.7 ± 9.5	91.7 ± 11.7	31.5	< 0.0001
Post-dive interval (s)	20.4 ± 6.0	35.5 ± 15.0	32.2	< 0.0001
Bottom time (s)	35.9 ± 11.3	35.5 ± 12.8	0.8	0.43
No. of wiggles (n)	1.9 ± 1.8	1.0 ± 1.0	13.3	< 0.0001
Descent rate (m/s)	1.36 ± 0.18	1.25 ± 0.26	10.8	< 0.0001
Foraging efficiency	2.86 ± 2.69	1.46 ± 1.41	17.7	< 0.0001

Means are given ± SD

and frequently returned to their partner (452 short versus 9 long trips, c.f. Table 2). This is even more surprising as in 2000 the birds from Rookery Valley still conformed to the established schedule (Pütz et al. 2006b). In 2014, birds from the Rugged Hill again returned to the established behavioral pattern and performed multi-day trips, although they still lasted less long than in conspecifics from other breeding sites before 2011 and were in some birds still preceded by a series of short trips. How can these behavioral changes be explained?

Several studies on seabirds have shown that mass gain at sea is positively related to foraging trip duration (e.g., Weimerskirch 1995; Barlow and Croxall 2002; Emmerson et al. 2011), because foraging trip lengths may vary depending on food availability and foraging success (e.g., Cairns

1987; Williams 1995). The long foraging trip by male SRP during incubation occurs in the middle of two extended fasting periods of up to ca. 40 days (Strange 1982; Poisbleau et al. 2008; Pütz et al. 2013). Birds are thus not only obliged to gain enough food to refill their empty energy stores but also to build up enough energy reserves to sustain them during the following fasting period. It is therefore important for male SRP to have a reliable foraging ground with sufficient food supply during their time at sea (Ludynia et al. 2013) and it appears that usually male SRP perform long trips owing to their need to restore their body mass. For example, during the incubation period, male SRP from Isla de los Estados foraged in deep waters extending south and east from the breeding site for 13–19 days (Pütz et al. 2006b; Raya Rey et al. 2007). Breeding birds from New Island in the southwest of the Falkland/Malvinas Islands foraged to the west, sometimes as far as the eastern entrance of the Magellan Strait (Boersma et al. 2002; Ludynia et al. 2013). Also, male SRP from the Seal Bay colony to the north of East Falkland at a linear distance of 25 km from the study colonies in Berkeley Sound foraged to the north of the colony at the Patagonian Shelf slope (Pütz et al. 2003). In all cases, the foraging ranges exceeded 100 km and included waters deeper than 200 m.

Given this common behavior displayed by birds from various colonies, we suggest that the unusual behavior observed in our study in years 2011–2013 was triggered by favorable food conditions just off the colony, enabling SRP to meet their elevated energy demand while performing day trips and returning to the incubating partner on a daily basis. These short trips have the advantage that no energy is wasted to

Table 5 Comparison of foraging trip durations of incubating male Southern Rockhopper Penguins, *Eudyptes chrysocome*, at various breeding sites in the Southwest Atlantic

Location	Year	Birds (n)	Onset	Duration (days)	End	Range (days)	Source
Staten Island	2001–2002	10	2–6 Nov	22.2		17–33	Pütz et al. (2006a, b)
New Island	1998–1999	12		> 3			Boersma et al. (2002)
Seal Bay	1998	4	8–16 Nov	18.5		11–24	Pütz et al. (2003)
Seal Bay	1999	5	17–26 Nov	20.0		12–27	Pütz et al. (2003)
Rookery Valley	2000	10	21–23 Nov	13.3		9–24	Pütz et al. (2006a, b)
New Island	2009	6[a]	9 Nov (mean)	14.2	25 Nov (mean)	12–18	Ludynia et al. (2013)
New Island	2010	6	20 Nov (mean)	15.5	5 Dec (mean)	10–19	Ludynia et al. (2013)
Rookery Valley	2011	12[b]	20–23 Nov	0.8	29 Nov–12 Dec	1–11	This study
Rookery Valley	2012	18[c]	11–13 Nov	0.3	23–26 Nov	1–6	This study
Rookery Valley	2013	14[c]	10–15 Nov	0.3	28 Nov–3 Dec	1–2	This study
Strike Off Point	2013	13[c]	14–16 Nov	0.4	28 Nov–1 Dec	1–2	This study
Rugged Hill	2014	5[d]	20–24 Nov	4.6	22 Nov–6 Dec	1–12	This study

[a] 4 birds also made 9 short trips

[b] 4 birds also made short trips and 6 birds only made short trips

[c] 1 bird also made a long trip, all the rest were short trips

[d] 2 birds also made 7 short trips but long trips started 22 and 24 Nov, respectively

travel to remote foraging grounds, and to have to rest at sea overnight when light intensity is too low to forage efficiently (Wilson et al. 1993), which is energetically more demanding than resting ashore due to the higher thermal conductivity of water compared to air and the need to maintain body temperature (Froget et al. 2004; Green et al. 2009). Furthermore, the increased presence of two birds at the nest site may result in an enhanced nest defense from predators or conspecifics (Morrison et al. 2017). Thus, these factors may not only considerably reduce the elevated energy demand during that critical period, but may also result in a higher hatching success.

Trip duration and SST

Changes in SST are known to influence food availability by affecting primary productivity, which in turn determines prey abundance (Richardson and Schoeman 2004; Frederiksen et al. 2006) and species composition (Scheffer and Carpenter 2003; Hays et al. 2005). Accordingly, links between oceanographic variability and foraging success have been shown for a number of higher trophic level consumers, in particular seabirds and marine mammals (e.g., Bost et al. 2009; Forcada and Trathan 2009; Thorne et al. 2015). In our study, a decreased SST resulted in a considerably reduced foraging trip duration and foraging range. The same phenomenon, to a lesser extent, has been observed in SRP during the chick-rearing period (Dehnhard et al. 2016). Furthermore, it could be shown that lower SST increased not only the likelihood of SRP individual survival over the winter months (Raya Rey et al. 2007; Dehnhard et al. 2013) but also individual body mass at the onset of the reproduction period (Dehnhard et al. 2015a). In turn, the latter resulted in earlier egg-laying dates with increased clutch masses (Dehnhard et al. 2015b) and an overall higher breeding success (Crawford et al. 2008).

However, over the past decades, the global Rockhopper Penguin population has significantly decreased (Pütz et al. 2013), with declines related to both decreasing (Guinard et al. 1998) or increasing SST (Cunningham and Moors 1994; Thompson and Sagar 2002; Hilton et al. 2006; Raya Rey et al. 2007), indicating that these birds are highly sensitive to changes in SST in either direction. As a specific example, in 2016, a mass mortality occurred in SRP in the Falklands during the molting period, which was attributed to pre-molt starvation following much colder than usual sea temperatures, which in turn was assumed to have resulted in reduced food availability (Crofts and Stanworth 2017; Morgenthaler et al. 2018). Thus, in SRP, environmental differences may be buffered only to a certain extent by behavioral plasticity.

A generally increasing SST in the Southern Ocean, as predicted by climate change scenarios, may therefore have a large influence on the distance to reliable foraging grounds and subsequently impact on the species' persistence. For example, in King Penguins *Aptenodytes patagonicus* climate change was predicted to result in increasing distances to the preferred foraging grounds at the Antarctic Polar Frontal Zone (APFZ), which in turn will have negative consequences on breeding success and recruitment (Péron et al. 2012).

3D temperature profiles

While the SST derived from satellite data may provide a reasonable proxy for differences in the behavior of marine air-breathing vertebrates, further clues can be derived from vertical temperature profiles collected by the study animals in situ (e.g., Boehme et al. 2008; Sala et al. 2017). In our study, pronounced differences could be found with regard to the overall temperature of the whole water body as well as its stratification. This was particularly evident in the inshore waters of Berkeley Sound, where temperature differed by 1.5 °C in a well-mixed water body when comparing 2011 and 2013. On the contrary, in 2012 the water body was highly stratified with a pronounced thermocline. This scenario may have been mirrored in the foraging behavior of the SRP, because in 2011 in relatively warm, well-mixed waters a higher number of multiple-day trips was observed (7.8%) when compared to 2012 (0.7%) and 2013 (0.9%; c.f. Table 3). Also, in 2011 in colder waters to the east of the 8° SST thermocline, differences in the water bodies were apparent, with a stratification in the area visited by the study bird on 25 November, whereas the water to the northeast was colder but less stratified, potentially impacting on prey availability. In addition to the above-mentioned assumption that SRP benefit from slightly colder than usual conditions with regard to SST, the occurrence of a stratified water body may further enhance their foraging success. Thus, vertical temperature profiles can provide further clues, beyond 2D satellite-derived SST data, about specific behaviors displayed by penguins (e.g., Sala et al. 2017), but also other seabirds and marine mammals in general (Boehme et al. 2008; Treasure et al. 2017). In any case, much more research is needed on the relationship between ocean temperatures in three dimensions, food availability, and behavioral plasticity of predators to further elucidate potential climate change scenarios throughout the food web.

Diving behavior

The assumed profitable food availability is also manifested in the diving behavior of SRP in 2011–2013. While the mean dive depth, which in turn determines dive duration and other diving parameters (Wilson 1995), was comparable to conspecifics from the Falkland Islands in 2000 and from

Staten Island in 2001 and 2002 (Pütz et al. 2006b), the diving efficiency was much higher. However, while this could be a consequence of the different thresholds for analysis (5 m in this study compare to 3 m in Pütz et al. 2006b), it may also indicate a substantial amount of beneficial benthic or near-bottom diving, which is further substantiated by the comparatively high diving efficiency.

Benthic or near-bottom diving has already been described for Chinstrap *Pygoscelis antarctica* (Takahashi et al. 2003), Gentoo *P. papua* (Xavier et al. 2017), Yellow-eyed *Megadyptes antipodes* (Mattern et al. 2007), and Northern Rockhopper Penguins *Eudyptes moseleyi* (Tremblay and Cherel 2000). According to Tremblay and Cherel (2000), an indication for benthic diving is a consistent, uniform dive depth over time, with the lack of deeper dives. This was also apparent in SRP from New Island, West Falklands, and the serial dives within a certain depth range were subsequently attributed to benthic diving (Ludynia et al. 2013). However, although this pattern was less obvious in our data set, which is assumed to be due to heterogeneity in the water depths within Berkeley Sound (c.f. Fig. 1), we strongly believe that SRPs in Berkeley Sound foraged frequently at or, at least, near the bottom, because dive depths were often similar to that of the maximum water depth. Furthermore, our sub-samples of randomly selected dives to the same water depth range within and outside Berkeley Sound revealed significant differences in the diving performance. Benthic dives were significantly shorter than pelagic dives, but included a comparable bottom time and a shorter post-dive interval, which consequently resulted in a higher diving efficiency. In contrast, for Northern Rockhopper Penguins, a closely related species, benthic dives lasted longer, included a longer bottom time and had longer post-dive intervals than pelagic dives, but still exhibited a higher diving efficiency (Tremblay and Cherel 2000). One explanation for these differences could be the fact that benthic dives in the study of Tremblay and Cherel (2000) were on average 8.6 m deeper than pelagic dives, whereas in our study benthic and pelagic dives were compared within the same depth range, with subsample means differing by less than 1 m. In both studies, vertical velocities displayed during descent and ascent phases were higher in benthic dives than in pelagic dives, which can be explained by the fact that birds proceed to the sea bottom without searching for prey in the water column, thereby minimizing transit and maximizing bottom times. In penguins, dive duration and vertical velocities, among others, are strongly related to the maximum dive depth achieved (e.g., Wilson 1995). However, these parameters may differ depending on the maximization of bottom time, which is favorable in both, benthic and pelagic dives, when prey is distributed at a certain depth range only. In King Penguins, for example, it could be shown that these parameters differ between different dive shapes, with W-shaped dives,

assumed to be performed when prey is located at a certain depth range only, having higher vertical velocities than U-shaped dives, where prey is supposed to be distributed more evenly in the water column (Pütz and Cherel 2005). All these parameters also influence the calculation of diving efficiency and foraging success, which subsequently were significantly higher in benthic dives. It thus appears that SRP maximized their efficiency in benthic dives by higher descent and ascent rates while bottom times were comparable, resulting in shorter total dive durations. By applying this strategy, about 37% of each dive cycle (=dive duration plus post-dive interval) were spent at the bottom, whereas in pelagic dives the bottom time accounted for only 28% of each dive.

To summarize, male SRP in our study showed significant behavioral plasticity. Despite being previously recognized as multiple-day foragers during incubation, they obviously have the capability to adapt to favorable food conditions under changing marine regimes, resulting not only in shorter foraging trip durations, but also in a complete change of behavior as birds returned regularly to their nest site in the evening. Furthermore, there appeared to be a substantial amount of benthic diving involved in short trips. While less favorable conditions have been reported to increase foraging ranges and success and ultimately negatively influenced chick growth, this is the first time that a substantial behavioral change following environmental changes actually has the potential to improve reproductive conditions. The importance of such behavioral flexibility for the survival of individual species is evident in African Penguin *Spheniscus demersus* fledglings that travel to places where food once has been but is no longer present (Sherley et al. 2017), contributing to an already decreasing population. However, this behavior may be unique to genetically determined juveniles who have not yet built up enough experience to locate sufficient food resources, whereas growing experience in aging birds may fine-tune the genetically predetermined behavior. For example, in King Penguins, it could be shown that fledglings from different breeding sites explored the same food resources, whereas adults showed significant differences in their foraging preferences (Pütz et al. 2014).

Compliance with ethical standards

Conflict of interest The authors declare that no conflict of interest exists.

Ethical approval This study was approved by the Environmental Planning Department of the Falkland Island Government under Section 9 of the Conservation of Wildlife and Nature Ordinance 1999 (FIG Research License R16/2011-13). All applicable international, national, and institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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