ORIGINAL PAPER

Foraging plasticity of breeding Northern Rockhopper Penguins, *Eudyptes moseleyi*, in response to changing energy requirements

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Abstract

During the breeding season, seabirds must balance the changing demands of self- and off-spring provisioning with the constraints imposed by central-place foraging. Recently, it was shown that Northern Rockhopper Penguins at Tristan da Cunha in the South Atlantic Ocean switch diet from lower to higher trophic level prey throughout their breeding cycle. Here, we investigated if this switch is reflected in their foraging behaviour, using time-depth recorders to study the diving behaviour of 27 guard and 10 crèche birds during the breeding season 2010 at Tristan da Cunha and obtaining complementary stomach contents of 20 birds. While no significant effects of breeding stage were detected on any foraging trip or dive parameters, stage/prey had a significant effect on feeding dive parameters, with dive duration, bottom time, and maximum depth explaining the majority of the dissimilarity amongst categories. We verified the previously shown dietary shift from zooplankton and cephalopods during the guard stage to a higher-energy fish-based diet during the crèche stage, which was reflected in a change in dive behaviour from shorter, shallower to longer, deeper dives. This prey switching behaviour may reflect preferential selection to account for the increased physiological needs of chicks or simply mirror changes in local prey abundance. Nonetheless, we show that Northern Rockhopper Penguins demonstrate behavioural plasticity as a response to their changing energy requirements, which is a critical trait when living in a spatio-temporally heterogeneous environment. This ability is likely to be particularly important under extrinsic constraints such as long-term environmental change.

Keywords Northern rockhopper penguin · *Eudyptes moseleyi* · Tristan da Cunha · Dietary shift · Generalist · Foraging plasticity

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Introduction

The foraging behaviour of seabirds is dictated by the dispersion, abundance and availability of prey and, during breeding, also by the rate at which food must be delivered to the nest to provision the brood (Lack 1968; Weimerskirch et al. 1994). While seabirds such as albatrosses and petrels may exploit food resources distant from their breeding sites (Davis and Cuthbert 2001), penguins, being non-volant, are much more limited in their foraging ranges (Wilson 1985), making the proximity of their food crucial. This is particularly important during breeding, when birds are constrained to act as central-place foragers (Orians and Pearson 1979) and obliged to catch enough food to provision both their chicks and themselves (Croxall and Davis 1999; Boersma et al. 2015). The inability of penguins to forage over long distances during this phase of their life cycle can be partially compensated for by their ability to forage at depth (Elliott et al. 2013). The

chick-rearing period in particular is highly demanding due to the increasing energetic requirements of the growing chick and, to meet these changing nutritional demands, penguins must adjust their foraging behaviour by either increasing the amount of food ingested, or their feeding frequency or by targeting higher-energy prey species (e.g. Gentoo Penguins, *Pygoscelis papua*, Williams and Rothery 1990; Chinstrap Penguins, *P. Antarctica*, Jansen et al. 2002; Little Penguins, *Eudyptula minor*, Zimmer et al. 2011 and Magellanic Penguins, *Spheniscus magellanicus*, Sala et al. 2012).

Prey switching linked to changing circumstances has been observed in many penguin species, ranging from some of the largest (King Penguins, *Aptenodytes patagonicus*, Charassin et al. 1998) to the smallest species (Gentoo Penguins, Handley et al. 2016; Southern Rockhopper, *Eudyptes chrysocome*, Schiavini and Raya Rey 2004 and Northern Rockhopper, *E. moseleyi*, Penguins, Tremblay and Cherel 2003; Booth and McQuaid 2013). Understanding how predators modify their diving behaviour with respect to prey type is, however, complex (Ropert-Coudert et al. 2002; Wilson et al. 2002), and given that targeting different prey requires changing dive characteristics, this is particularly true in generalist predators that feed on a variety of prey species and lack a single behavioural search and capture pattern (Davoren et al. 2003; Wilson et al. 2005). The combined use of time-depth recorders (TDRs) with subsequent detailed analysis of dive characteristics and stomach contents has therefore proven to be useful in attempting to disentangle the relationship between dive behaviour and prey selection in penguins (e.g. Ropert-Coudert et al. 2006; Bost et al. 2007; Deagle et al. 2008).

Preying on a mixture of fish, crustaceans and cephalopods (Tremblay and Cherel 2003; Booth and McQuaid 2013), the Northern Rockhopper Penguin appears to be a true generalist. Booth and McQuaid (2013), however, showed that they switch from a zooplankton to fish-dominated diet (i.e. from lower to higher trophic level prey) between the guard and crèche stages of the breeding cycle, making them an ideal species to explore the link between foraging behaviour and dietary shifts in a generalist predator. The species breeds on four islands in the Tristan da Cunha archipelago in the South Atlantic, which, together with Gough Island, supports over 80% of the global population of this species (Cuthbert et al. 2009; Robson et al. 2011). Given the volcanic origin of these breeding sites and the lack of a peri-insular shelf, the Northern Rockhopper Penguin is obliged to be an oceanic forager and can forage in water more than 1000 m deep within approximately 5 km of the island. Here, we test the hypothesis that the dietary shift between the two chick-rearing phases, guard and crèche, will be reflected in the diving characteristics of Northern Rockhopper Penguins, combining diving and stomach content data from breeding birds at Tristan, the main island of Tristan da Cunha.

Materials and methods

Study area and species

Fieldwork was carried out during chick rearing, between November and December 2010, at the Stony Beach colony on Tristan da Cunha, the main island of the archipelago (Fig. 1). The colony is divided into two sub-colonies, approximately 500 m apart: Stony Hill (37°09′54″S, 12°16′18″W) and Stony Beach (37°09′36″S, 12°16′06″W), with an estimated 280 and 260 breeding pairs, respectively, in the year of study (Tristan da Cunha Conservation Department unpubl. data). Birds nest on rocky hillsides at both sites, using a single path to leave and return to the rookery.

Like other *Eudyptes* penguins, Northern Rockhopper Penguins have a synchronised breeding cycle with highly defined parental shifts in nest attendance. Once the eggs hatch, male birds remain at the nest during the guard stage (2–3 weeks), whilst females undertake daily foraging trips to provide food. After this period, chicks form loose crèches (crèche stage), and are provisioned by both parents until they fledge at the age of 63–70 days (Cuthbert 2013). Northern Rockhopper Penguins display brood reduction and usually only a single chick is reared (Cuthbert 2013; Stein and Williams 2013).

TDR deployment and diet sampling

Time-depth recorders (TDR; model G5, Cefas Technology Limited, UK) were attached to 30 guard stage birds (all female) between November 1st and November 9th 2010 at the Stony Beach sub-colony, and to 13 crèche stage birds (sex unconfirmed) between November 22nd and December 3rd 2010 at Stony Hill. Within each breeding stage, data were collected over approximately 10 days, in order to minimise confounding effects such as temporal changes in prey availability. Three TDRs deployed during the crèche stage were not retrieved. Devices were attached to the penguin's right leg with a temporary leg band (constructed from a cable tie and flexible plastic cable) using amalgamating tape and a cable tie (Booth 2011; Ratcliffe et al. 2014). The cylindrically shaped TDR devices measure 8 × 31 mm and weigh 1.3 g in seawater, equivalent to ca. 0.05% of the mean Northern Rockhopper Penguin body mass. This deployment technique was chosen due to the small size of the logger, allowing us to reduce any potential negative impact on foraging behaviour and the risk of device loss (Ratcliffe et al. 2014). The TDRs were programmed using the software G5 Host (Cefas Technology Limited) to record hydrostatic pressure (as a proxy
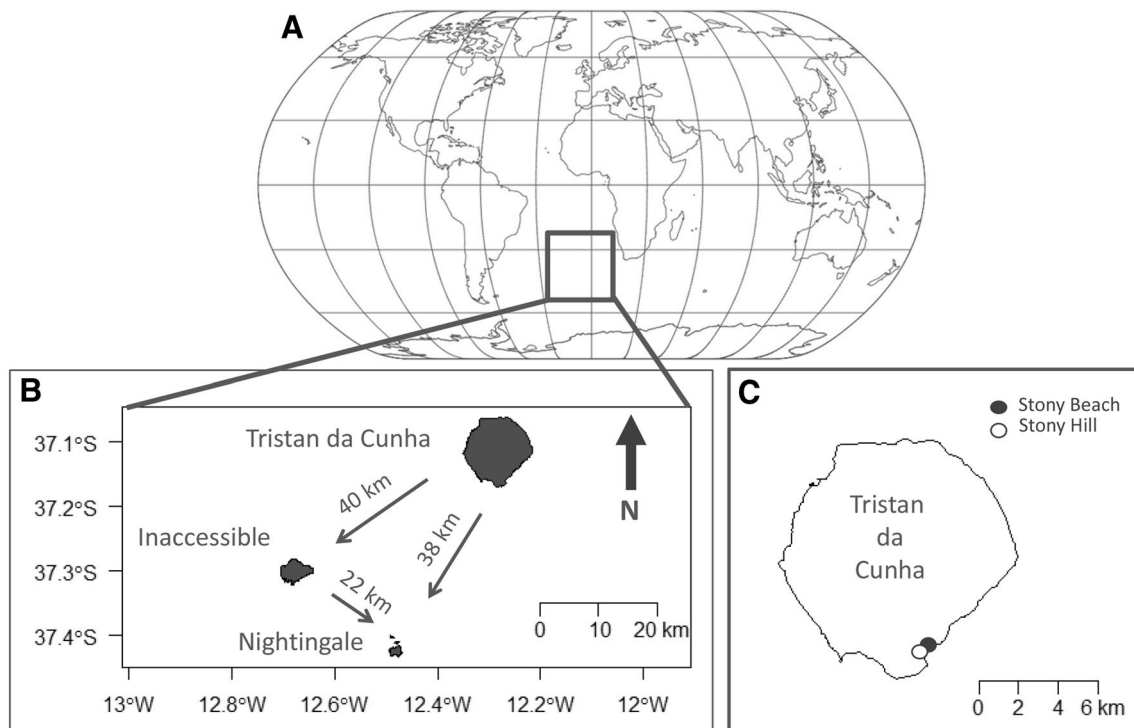
Fig. 1 Map of Tristan da Cunha displaying **a** the position of the archipelago in the South Atlantic Ocean, **b** the three main islands of Tristan, Inaccessible and Nightingale and **c** Tristan Island with the location of the study sub-colonies of Stony Beach and Stony Hill

for depth with a resolution of < 0.4 m) continuously at 1-s sampling intervals during the guard, or at 2-s intervals during the crèche stage when trips were expected to be longer, in order to secure complete data capture (Tremblay and Cherel 2005). Devices were set to start recording approximately 5 min after release of the bird. The handling of the bird, from capture to release, lasted ≤ 3 min. To further minimise stress and provide statistically independent data, different birds and nests were studied during each breeding stage. Study birds were individually marked with a waterproof animal marker ($^{©}$Porcimark) and nests numbered with paint on the nearest rock to avoid resampling. The colony and path to the colony were monitored continuously, from GMT 06:00 until approximately 22:00 h, and then sporadically throughout the night to maximise encounter of returning study birds. Birds were recaptured and devices retrieved upon their return to, or at, the nest prior to provisioning chicks. Diet sampling was conducted using the water-offloading technique (Gales 1987) on twenty device-equipped birds (guard $n = 17$, crèche $n = 3$). The day after deployment, the chicks of the TDR-equipped guard stage birds were weighed to the nearest 10 g.

Data analysis

Foraging trip and dive data

Dive data were analysed using MULTITRACE (Jensen software systems, Kiel, Germany). Prior to analysis, all data were corrected for a drifting surface level (recorded depth is adjusted so that the surface level is maintained at 0 m, Hagihara et al. 2011) and the dive threshold at which a foraging dive was deemed to occur was set to ≥ 3 m (in accordance with other studies of Rockhopper Penguins: Cherel et al. 1999; Tremblay and Cherel 2000, 2003; Dehnhard et al. 2016; Whitehead et al. 2016). Some birds were not recaptured after one foraging trip, and so consecutive trips were recorded over several days. In such cases, trips were separated when there was a gap in diving activity of ≥ 4 h (Pichegru et al. 2011).

For the comparison of diving behaviour between guard and crèche stage birds, each foraging trip was described by departure and arrival time (start and end time of first and last foraging dive, respectively), trip duration (time elapsed between first and last recorded foraging dive), vertical travel distance (VTD, the sum of the maximum dive depths for all

foraging dives during a trip, multiplied by two, Tremblay and Cherel 2003), total number of dives, dive rate (number of dives per foraging trip as a proportion of the foraging trip duration), and dive time (% of time spent underwater during foraging trip). Following Raya Rey et al. (2013), we calculated foraging activity as bottom time (min) per hour underwater. For each dive within a foraging trip, we calculated dive duration, maximum depth, bottom time and to determine prey pursuit events we used the number of undulations or 'wiggles' in the dive profile (Bost et al. 2007; Sala et al. 2012).

Feeding dives

Feeding dives were analysed from the same birds that provided diet data. To gain a comprehensive description of the diving behaviour of birds when feeding, we extracted all dives that contained wiggles in the dive depth profile (hereafter referred to as 'feeding dives') and examined an enlarged set of dive parameters to characterise prey pursuit strategy: dive duration, descent time, bottom time, ascent time, maximum depth, vertical descent rate, horizontal rate and vertical ascent rate. Hence, each feeding dive was analysed considering a minimum of one wiggle per dive. When multiple foraging trips were recorded for a bird, only dive data from the last trip were used, as these dives were the most likely to reflect the prey content of the obtained stomach sample (Wilson et al. 1989).

Meal mass and diet composition

Stomach content was sorted into principle prey items, weighed to obtain an estimate of proportion by wet mass (Cherel et al. 2007), and categorised according to the following wet mass contributions in the diet: zooplankton > 85%, fish > 85%, cephalopods 30–70% and zooplankton 30–70%, and mixed cephalopod 10–70%, zooplankton 10–70%, fish 10–70%. For further details of procedures, see Booth and McQuaid (2013).

Statistical analysis

R 2.12.1 (package 'nlme', R Development Core Team 2010) and PRIMER v. 6.1, PERMANOVA + (Anderson et al. 2008) were used to carry out all statistical analyses. Prior to analysis, all raw data were tested for normality of distribution and homogeneity of variances with the Kolmogorov–Smirnov test and Levene's test, respectively. In cases where data did not meet these assumptions after log transformation ($p > 0.05$), non-parametric statistical tests were used.

Foraging trip and dive analysis

A one-way permutational multivariate ANOVA or PERMANOVA (9999 permutations, dissimilarity matrix calculated using Euclidean distances) was used to compare breeding stages (fixed, orthogonal, 2 levels: guard and crèche) in terms of the foraging trip variables: trip duration, VTD, number of dives, dive time, dive rate, and foraging activity index. In cases where birds performed multiple trips, means for each trip and then a grand mean for each bird were calculated. MULTITRACE calculates a large number of dive parameters. Due to the nature of the diving variables measured, multi-collinearity was checked using the non-parametric Spearman correlation; none of the chosen variables had a correlation score higher than 0.85 (accepted threshold level of correlation; Clarke and Gorley 2006) and all were retained. Subsequently, we selected a set of variables to describe dive characteristics for comparison of the diving behaviour between guard and crèche stage birds (e.g. Tremblay and Cherel 2003; Crossin et al. 2015). Hence, running linear mixed effects models, using the package nlme in R (Pinheiro et al. 2009), we tested the three dependent variables: dive duration, maximum depth and bottom time. In all models, we used breeding stage (guard and crèche) as our explanatory variable with a fixed effect while 'trip' nested in 'bird identity' was included as a random effect. Following Ratcliffe et al. (2013), we conducted backwards-stepwise model selection, first identifying the best random-effects model structure by comparison of models with and without trip effect (nested in bird identity), which were fitted with restricted maximum likelihood (REML). We did not test for the performance of a model without bird identity, as removal would have violated the premise of independent data. For the variables dive duration and maximum depth, we applied a fourth square root transformation for normality and therefore used the function lme (Venables and Ripley 2002); while for the variable bottom time, we used a generalised mixed model specifying the family error Poisson (Breslow and Clayton 1993). As successive dives might not be independent, both models were fitted with a first-order autocorrelation structure using the function corAR1 (Box et al. 1994).

Multiple correlation analysis, calculated with Spearman's correlation, was used to examine possible correlations between guard stage chick weight and guard stage bird foraging trip variables (trip duration, VTD, number of dives, total number of dives and total dive time) using

the R package 'PerformanceAnalytics' (https://cran.rproj ect.org/package=PerformanceAnalytics).

Feeding dive analysis

Since not all prey categories were represented in both stages, samples were further categorised according to breeding stage to account for the effects of both stage and prey type. A one-way PERMANOVA (9999 permutations, dissimilarity matrix calculated with Euclidean distance) was performed to test the effect of stage/prey (fixed, orthogonal, 5 levels: crèche/fish; crèche/fish, cephalopod and zooplankton; guard/cephalopod and zooplankton; guard/zooplankton; and guard/fish, cephalopod and zooplankton) on the dive parameters: dive duration, descent time, ascent time, bottom time, maximum depth, vertical descent rate, horizontal rate and vertical ascent rate. Subsequently, a SIMPER analysis was performed to determine the parameters which contributed most to dissimilarities among groups, and PERMANOVA pairwise post hoc tests (p-pht) were used to test for significant differences among the levels of the factor stage/prey. Finally, we used linear models to examine the relationship between maximum dive depth and bottom time for each stage/prey category.

Results

Foraging trips

A total of 58 foraging trips were recorded for 27 guard stage birds and 35 foraging trips for 10 crèche stage birds. During both breeding stages, the majority of foraging trips had a duration of 14–16 h, with 83% of guard stage

Fig. 2 Frequency distribution of foraging trip duration (h) of Northern Rockhopper Penguins during the breeding season 2010/11 at Tristan da Cunha (guard $n = 58$, crèche $n = 35$)
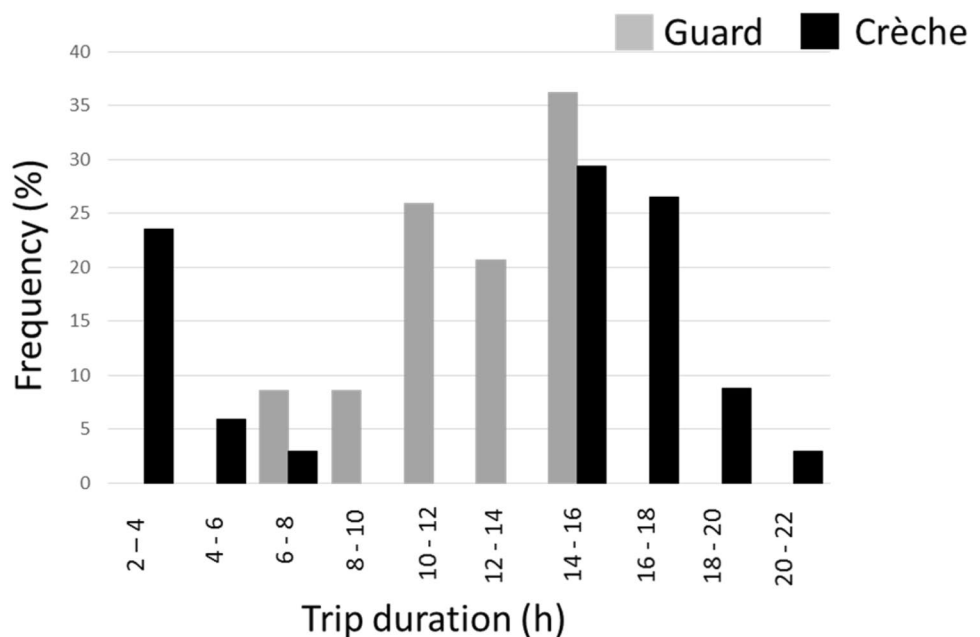

Table 1 Foraging trip and dive variables of Northern Rockhopper Penguins at Tristan da Cunha during the guard and crèche stages in 2010

Foraging trip variables	Guard	Crèche
Trip duration (h)	11.3 ± 2.8 (6.1–15.4)	12.1 ± 1.3 (2.0–21.0)
Number of dives	581.2 ± 195.3 (18–1223)	597.3 ± 112.7 (61–1002)
VTD (km)	17.2 ± 4.3 (0.4–35.7)	17.5 ± 1.2 (1.9–29.3)
Total dive time (%)	80.1 ± 8.9 (24.5–96.5)	74.7 ± 4.5 (48.7–93.5)
Foraging activity index	0.4 ± 0.1 (0.2–0.8)	0.3 ± 0.03 (0.2–0.5)
Dive rate (dives h^{-1})	51.7 ± 15.4 (7.6–96.1)	46.6 ± 4.9 (22.4–58.7)
Dive duration (s)	55.0 ± 0.2 (2–250)	52.1 ± 0.2 (4–244)
Maximum depth (m)	14.45 ± 0.05 (max: 88.97)	13.48 ± 0.06 (max: 94.02)

Values are mean ± SE, with ranges shown in brackets. Multiple trips by individual birds were pooled to obtain an overall mean. Sample sizes for foraging trip variables: guard $n = 27$, crèche $n = 10$ and for foraging dive variables: guard $n = 34439$, crèche $n = 26156$

trips lasting 10–16 h and 56% of crèche stage trips lasting 14–16 h. Crèche stage birds performed all trips longer than 16 h and all trips shorter than 6 h (Fig. 2), the shortest being 2.04 h. During these short trips, feeding activity was confirmed by the presence of wiggles so that these trips could be classified as foraging trips.

Mean values of foraging trip variables and dive parameters are presented in Table 1 together with standard errors and range of values. There was no significant difference between breeding stages in all examined foraging trip variables: trip duration, VTD, total number of dives, dive rate, total dive time or foraging activity index (PERMANOVA, $p > 0.05$). Similarly, there was no significant effect of breeding stage on the dive parameters: dive duration (LME, $p > 0.05$), maximum dive depth (LME, $p > 0.05$), and bottom time (GLMM, $p > 0.05$).

Within the guard stage, multiple correlation analysis showed that chick mass was not significantly correlated with trip duration, VTD, total number of dives or total dive time (Spearman correlation coefficients: 0.075, 0.14, -0.11, -0.24, respectively; $p > 0.05$ in all cases).

Feeding dives

Data for stomach content composition of 20 TDR-equipped birds returning from foraging trips are shown in Table 2, along with categorical diet classification for statistical analysis. Stomach contents retrieved ranged from 21.7 to 213.4 g wet weight and in each sample the digested component was dominant over the undigested component (Table 2). A significant effect of stage/prey (PERMANOVA, $F_{4,5526} = 147.62$, $p < 0.001$) was observed on the feeding dive parameters analysed: dive duration, descent time, bottom time, ascent time, maximum depth, vertical descent rate, horizontal rate and vertical ascent rate (Table 3). SIMPER analysis revealed that dive duration contributed more than 50% to dissimilarity between foraging dives made by birds to capture different prey types. Additionally, the variables bottom time and maximum depth together contributed to account for at least 26% further dissimilarity among foraging dives between all stage/prey categories.

The maximum depths of dives in different prey/stage categories were significantly different from each other (p-pht, $p = 0.0001$) with the exception of guard/mixed fish, cephalopod and zooplankton and guard/zooplankton (p-pht, $p > 0.05$; Fig. 3). Guard stage birds feeding on different prey

Table 2 Stomach content composition (by wet mass) of TDR-equipped Northern Rockhopper Penguins returning from foraging trips during the breeding season 2010 at Tristan da Cunha ($n = 20$; G guard, C crèche, ZP zooplankton, CEPH/ZP mixed cephalopod and zooplankton, MIX mixed fish, cephalopod, zooplankton, FISH fish)

Bird ID	Diet classification	Total mass (g)	Digested mass (%)	Fresh mass (%)	Fish (%)	Cephalopod (%)	Zoo-plankton (%)
G1	CEPH/ZP	73.6	69.7	30.3	0	33.9	66.1
G2	MIX	92.9	68.9	31.1	13.5	53.2	33.3
G3	CEPH/ZP	178.5	57.4	42.6	0.6	44.4	55
G4	CEPH/ZP	122.1	87.2	12.8	0	30	70
G5	CEPH/ZP	36.4	83.5	16.5	0	29.4	70.6
G6	ZP	71.5	99.7	0.3	1.8	3.8	94.4
G7	MIX	82	65.6	34.4	43.2	49	7.8
G8	MIX	91.6	63.3	36.7	32.8	10.9	56.3
G9	ZP	60.8	100	0	0	1.6	98.4
G10	ZP	181.2	91.8	8.2	3	10	87
G11	ZP	213.4	98.5	1.5	6.7	3.3	90
G12	ZP	191.1	99.8	0.2	0	0.9	99.1
G13	ZP	36.7	98.1	1.9	0	6	94
G14	ZP	45.2	98.9	1.1	0	1	99
G15	ZP	16.3	100	0	0	0	100
G16	ZP	92.2	100	0	0	0	100
G17	ZP	68.3	100	0	0	0	100
C1	MIX	12.7	88.2	11.8	33.1	11.8	55.1
C2	FISH	26.4	100	0	100	0	0
C3	FISH	29.9	95.3	4.7	98.3	0	1.7

Fig. 3 Notched box plots of the four diving parameters contributing most to dissimilarity of feeding dives made by Northern Rockhopper Penguins during the breeding season 2010/11 at Tristan da Cunha ($n = 5526$). The middle line indicates the median value and extreme values and quartiles are shown. Letters indicate homogenous groups (p-pht, $p < 0.05$). Abbreviations indicate breeding stage/diet category: CrecheFISH = Crèche stage, fish-dominated diet; CrecheMIX = crèche stage, mixed fish, cephalopod, zooplankton diet; GuardCEPHZP = guard stage, mixed cephalopod and zooplankton diet; GuardMIX = guard stage, mixed fish, cephalopod, zooplankton diet; GuardZP = guard stage, zooplankton diet
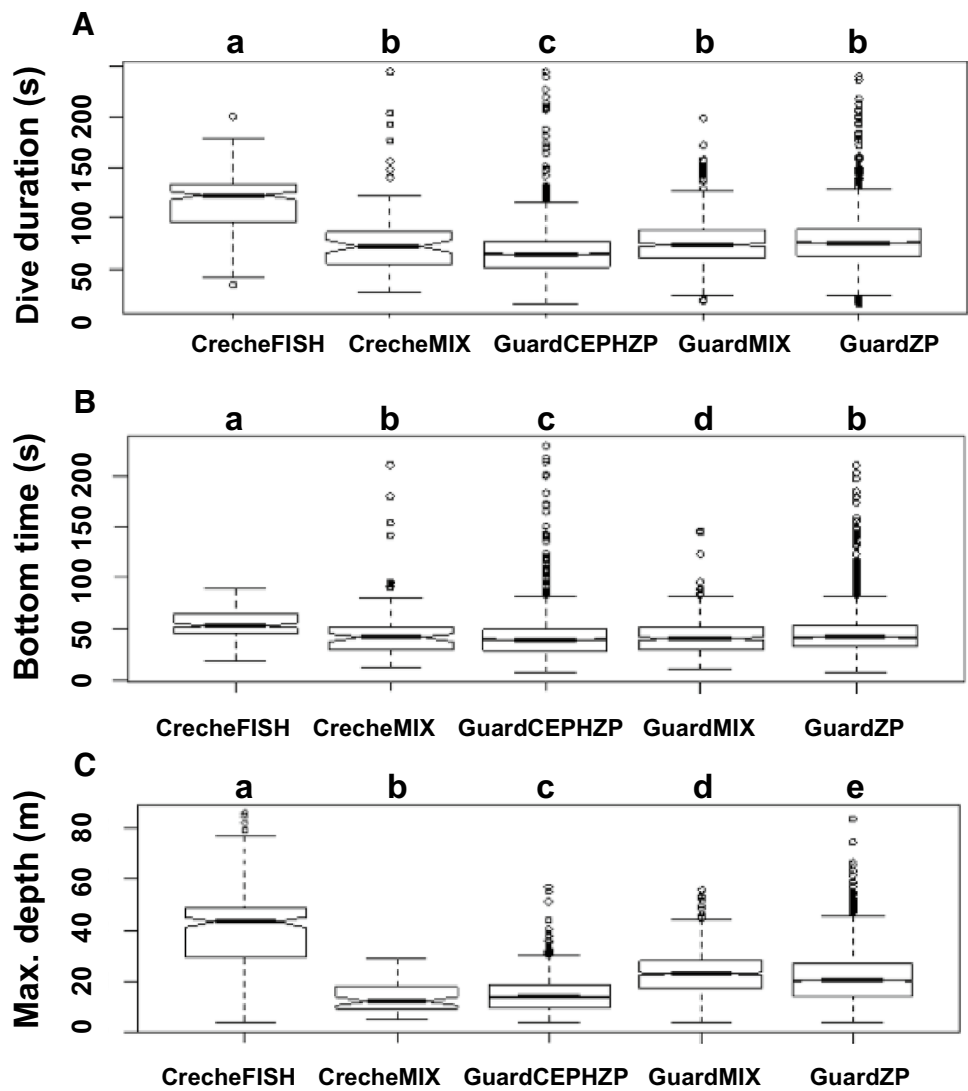

Table 3 Feeding dive variables of Northern Rockhopper Penguins at Tristan da Cunha during the guard and crèche stages in 2010

Feeding dive variables	CrècheFISH	CrècheMIX	GuardCEPHZP	GuardMIX	GuardZP
Dive duration (s)	112.9 ± 2.01	77.6 ± 4.8	66.7 ± 0.7	74.8 ± 0.9	76.5 ± 0.4
Descent time (s)	28.2 ± 0.9	14.1 ± 1.05	12.2 ± 0.2	16.5 ± 0.2	16.0 ± 0.1
Bottom time (s)	55.2 ± 0.9	50.4 ± 4.2	42.6 ± 0.6	42.4 ± 0.6	44.2 ± 0.3
Ascent time (s)	29.4 ± 1.02	13.1 ± 0.8	11.9 ± 0.2	16.1 ± 0.3	16.3 ± 0.1
Vertical descent rate (m s^{-1})	1.2 ± 0.02	0.9 ± 0.04	1.1 ± 0.01	1.2 ± 0.01	1.2 ± 0.01
Horizontal rate (m s^{-1})	0.1 ± 0.01	0.1 ± 0.01	0.07 ± 0.002	0.1 ± 0.003	0.08 ± 0.001
Vertical ascent rate (m s^{-1})	1.1 ± 0.02	0.8 ± 0.04	1.1 ± 0.01	1.1 ± 0.01	1.1 ± 0.01
Maximum depth (m)	38.6 ± 1.3	12.9 ± 0.6	15.1 ± 0.2	22.4 ± 0.3	20.9 ± 0.2
Number of wiggles	4.1 ± 0.1	3.9 ± 0.4	4.1 ± 0.1	4.4 ± 0.1	4.2 ± 0.04

Values are mean ± SE. (*ZP* zooplankton, *CEPH/ZP* mixed cephalopod and zooplankton, *MIX* mixed fish, cephalopod, zooplankton, *FISH* fish)

categories formed significantly different intermediate groups (Mean maximum depths: guard/cephalopod and zooplankton 15.1 m; guard/zooplankton 20.9 m; guard/mixed fish, cephalopod and zooplankton 22.4 m). The deepest dives were performed by crèche stage birds feeding on fish (mean maximum depth 38.6 m), while crèche birds feeding on

mixed prey performed the shallowest dives (mean maximum depth 12.9 m).

Guard stage birds feeding on a mixture of cephalopods and zooplankton performed the shortest dives (mean dive duration 66.7 s), while feeding dives made by crèche stage birds targeting fish were significantly longer than others (mean dive duration 112.8 s; Fig. 3). Dives in the categories crèche/mixed fish, cephalopod and zooplankton (mean dive duration 77.6 s), guard/mixed fish, cephalopod and zooplankton (mean dive duration 74.8 s) and guard/zooplankton (mean dive duration 76.5 s) formed a separate, intermediate group (p-pht, $p = 0.0001$; Fig. 3).

In terms of time spent at the bottom phase of the dive, similarly dives made by crèche stage birds feeding on fish had significantly longer bottom times than other feeding dives (mean bottom time 55.2 s), followed by crèche/mixed fish, cephalopod and zooplankton (mean bottom time 50.4 s) and guard/zooplankton (mean bottom time 44.2 s) feeding dives in an intermediate homogenous group. Guard/cephalopod and zooplankton (mean bottom time 42.6 s) and guard/mixed fish, cephalopod and zooplankton (mean bottom time 42.4 s) both formed significant individual groups (p-pht, $p = 0.0001$; Fig. 3), with the shortest bottom times during dives.

To confirm that the patterns observed in the examined parameters, bottom time and dive duration, were a true reflection of a difference in prey selection rather than purely reflecting the differences in dive depth, we performed a regression analysis of the bottom time against maximum dive depth for each of the prey/stage categories. While we found a significant relationship between the two dive parameters for guard stage birds feeding predominantly on zooplankton (guard/zooplankton) and on a mixed diet (guard/mixed fish, cephalopod and zooplankton) (LM, $F_{1,42220} = 124.1$, $p < 0.0001$ and LM, $F_{1,376} = 109.4$, $p < 0.0001$, respectively) there was no relationship for other stage/prey categories (LM, $p > 0.05$ in all cases).

Discussion

This study aimed to assess whether the foraging behaviour of a generalist predator mirrors a switch in its diet from a low to higher-energy prey species in order to meet the changing nutritional requirements of their young (Booth and McQuaid 2013). Given the increasing daily energy requirements of growing chicks during the breeding season, it can be expected that parental foraging strategies will be adjusted to maximise energy gain (Ydenberg et al. 1994). Brown (1987) estimated daily energy requirements of Southern Rockhopper chicks to increase more than fivefold from the first week of hatching to the midway point in their growth. Parents must meet this increasing demand in some manner,

to ensure successful breeding, either through an increase in provisioning frequency and amount (Trivelpiece et al. 1987; Jansen et al. 2002) or the selection of higher-energy-content prey (e.g. Gentoo Penguins in the Malvinas/Falkland Islands, Handley et al. 2017).

Being characterised as an opportunistic predator can be interpreted as implying naïve foraging behaviour, with random encounters of prey items (MacArthur and Pianka 1966; Orians and Pearson 1979), and it is still unclear whether foraging flexibility simply reflects prey availability and abundance (opportunistic behaviour) or if, in fact, the choice of prey is actively driven by modifying foraging behaviour to target specific prey items in order to match particular energetic needs through specialist behaviour (Gaston 2004; Ludynia et al. 2010). Of course, the two approaches are not mutually exclusive, but rather manifestations of the extreme flexibility in foraging behaviour required in a feeding environment made more unpredictable by the inability to fly. Not surprisingly, foraging strategies of generalist penguins are less well understood than those of specialists and the ultimate goal remains to disentangle the links among foraging behaviour, dietary shifts and prey availability.

In this study, despite the small sample size, we were able to confirm a shift in diet between guard and crèche stage Northern Rockhopper Penguins from a zooplankton to an energy-rich fish-dominated diet (corroborating the results of Booth and McQuaid 2013). Guard birds fed predominantly on zooplankton, comprising fish larvae and other crustaceans such as euphausiids, which form dense swarming aggregations close to the surface (Mauchline 1980), while crèche birds fed predominantly on small photichthyid fish as well as euphausiids. Fish are more energetically valuable than macrozooplankton (Mori 1998; Ainley et al. 2003). Myctophid fish are nutritionally more valuable than euphausiids (Van de Putte et al. 2006), and enriched in energy by 17–72% per unit mass compared to gravid female krill (Ichii et al. 1996). Although myctophids only contributed a small proportion of fish diet, they are closely related to photichthyids, which can be expected to have a similar nutritional quality. Cephalopods formed a similar contribution to diet in both breeding stages, and have a lower nutritional value than either fish or crustaceans (Heath and Randall 1985). Recognising the limitations of a small sample size, the fact that fish was only found in the diets of crèche bird's diet indicates a possible shift in diet across the season. This is supported by the same findings for a larger sample of birds in the same breeding season at Tristan da Cunha (Booth and McQuaid 2013). Furthermore, characteristic dive profiles associated with defined stage/prey categories were reflected in distinctive dive depths, bottom times and dive durations. Whilst dive depth is related to the distribution of prey within the water column, prey behaviour may dictate dive duration and bottom time (Lescroël and Bost 2005; Sala

et al. 2014). Prey exploitation strategies by penguins are dependent on a number of factors including the size and depth of prey patches and their abundance (Wilson et al. 2002). The strategies observed in our study were found to be linked to prey type, with birds targeting fish (> 90% mass in diet) performing longer, deeper dives, and those targeting zooplankton (> 90% mass in diet) performing shorter, shallower dives. Similar behaviour was observed in Macaroni Penguins, *E. chrysolophus,* which perform deeper dives to feed on fish than when feeding on crustaceans (Deagle et al. 2008). Although we interpret differences in dive parameters as changes in foraging behaviour, there were significant correlations between maximum dive depth and bottom time in the case of dives targeting zooplankton and those associated with a mixed diet. This suggests that, while changes in parameters were indeed generally related to the prey taken, rather than depth, in these two cases changes in dive behaviour may have been additionally influenced by depth. A shift in diet associated with plasticity in dive behaviour was detected in conspecifics at Amsterdam Island. In that case, birds performed deeper dives in the early part of the crèche stage compared to late crèche stage and this was associated with a shift in diet from one dominated by squid (44%) to one dominated by fish (64%) (Tremblay et al. 1997). This exemplifies the complexities of understanding prey capture strategies, in terms of behaviour, size and local distribution of the specific prey being targeted (Wilson et al. 2002), but nonetheless, corroborates our detection of prey switching and coupled behavioural changes in the species.

Although Northern Rockhopper Penguins are able to dive to depths greater than 90 m (this study; Cherel et al. 1999) they rarely did so, and the majority (83%) of dives recorded were concentrated in the upper 20 m of the water column. Such predominantly shallow diving behaviour is similar to that observed at Amsterdam Island, where birds mostly foraged at around 18 m (Cherel et al. 1999). Based on allometric equations, Cherel et al. (1999) predicted that Northern Rockhopper Penguins with a body mass of 2.3 kg would have a maximum dive duration of 124–176 s and a maximum dive depth of 77–89 m, values that were occasionally exceeded, but broadly similar to those recorded here (Table 1). However, birds generally avoided their physiological limits, and this likely reflects a behavioural strategy based on the distribution of prey within the water column (Wilson et al. 2002; Ropert-Coudert et al. 2006; Elliott et al. 2008).

During breeding, to successfully rear chicks, if penguins do not switch to a higher-energy prey they have to increase their foraging effort. Prey selection is constrained by availability, which in turn partially depends on foraging range. During the guard stage hatchlings require continuous parental attendance and the foraging range is consequently restricted, while the crèche stage, when chicks are able to thermoregulate themselves, allows greater flexibility for adults in acquiring food and delivering it to the nest. In many penguin species, this is manifested in an increase over the breeding period in either feeding frequency or the amount of food delivered to the chick (Zimmer et al. 2011) or increased foraging trip duration (e.g. Adelie Penguins, *P. adeliae*, Lyver et al. 2011). We observed no increase in foraging effort between breeding stages, in terms of foraging trip parameters (i.e. trip duration, total number of dives, VTD, total dive time, dive rate or foraging activity index). Dehnhard et al. (2016) similarly found no foraging differences between breeding stages for Southern Rockhopper Penguins, while others have recorded an increase over the breeding season (Schiavini and Raya Rey 2004; Raya Rey et al. 2007). We were unable to test the effect of sex on diving behaviour and diet during the crèche stage, since birds could not be blood-sampled for genetic sexing. While we acknowledge that in some species male and female penguins do display different foraging behaviours and diets (e.g. African Penguins, *Spheniscus demersus*, Pichegru et al. 2013 and Gentoo Penguins, Xavier et al. 2017), we highlight that no difference in diet was observed between the sexes in the crèche stage in a study of the same population of Northern Rockhopper Penguins during the same breeding season (Booth and McQuaid 2013). Furthermore, Dehnhard et al. (2016) observed similar foraging behaviour, in terms of dive depth, between crèche stage male and female Southern Rockhopper Penguins.

The Northern Rockhopper Penguin is an endangered species and very little information concerning the foraging ecology of the populations breeding in the South Atlantic Ocean, and their prey populations, are known. Despite the fact that there are limitations in our study, specifically the small sample size of crèche stage birds stomach content, the absence of sex data for crèche stage birds, and the fact that our data were collected during only one breeding season, this is the first account of the diving behaviour of the species at their South Atlantic breeding site, home to > 80% of the breeding population (Cuthbert et al. 2009; Robson et al. 2011). Thus, this study contributes valuable information on the marine ecology of this species and is particularly useful as a baseline for future studies of diving behaviour. There is clearly a close link between penguin dietary shifts and local prey abundance and often prey availability, rather than prey preference, is the driving force behind diet switching (Ludynia et al. 2010; Handley et al. 2017). In our study, the problem of separating the effects of prey selection and prey availability remains and future studies incorporating GPS location data and ideally at-sea surveys on prey distribution and abundance could separate these two possible explanations. For this reason, we cannot be certain if adults actively modify foraging behaviour according to increasing provisioning requirements of their brood or if the response

was mediated solely by environmental changes i.e. prey availability and abundance. However, we believe that it is unlikely that the shift in diet is related to altered prey density as a direct effect of prey depletion during the early stages of breeding, since the population of breeding birds on Tristan is small and their prey are highly mobile. Instead, we propose that our observations probably reflect the effects of prey switching between stages.

Thus, we conclude that these birds may have altered their diving strategies over the course of the breeding season, from shallower, shorter dives to longer, deeper dives between the guard and crèche stages in response to the energy requirements of their young rather than prey availability. The interpretation that this reflects a strategic dietary shift towards more energy-rich prey with the increasing energetic demands of chicks is supported by earlier work (Booth and McQuaid 2013). Northern Rockhopper Penguins, like most seabirds, live in a highly variable marine environment where behavioural plasticity is a fundamental trait of their life history. The ability to adjust foraging behaviour in response to changing physiological needs of the offspring may be of importance when presented with extrinsic constraints such as environmental changes.

Compliance with ethical standards

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

Animal rights Full permission for all methods used in this study and access to the penguin colonies were granted by the Tristan da Cunha government. Animal ethics approval was given by Rhodes University Ethics Committee (ZOOL-17-2010). All applicable international and institutional guidelines for the use of animals were followed.

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