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1 FORAGING PLASTICITY OF BREEDING NORTHERN ROCKHOPPER PENGUINS,
2 *EUDYPTES MOSELEYI*, IN RESPONSE TO CHANGING ENERGY REQUIREMENTS

3

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22 Running head: Foraging plasticity of Northern Rockhopper Penguins

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24 **Keywords:** Northern Rockhopper Penguin, *Eudyptes moseleyi*, Tristan da Cunha, Dietary shift,
25 Generalist, Foraging plasticity
26

27 ABSTRACT:

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

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INTRODUCTION

48 The foraging behaviour of seabirds is dictated by the dispersion, abundance and availability of
49 prey and, during breeding, also by the rate at which food must be delivered to the nest to
50 provision the brood (Lack 1968; Weimerskirch et al. 1994). While seabirds such as albatrosses
51 and petrels may exploit food resources distant from their breeding sites (Davis and Cuthbert
52 2001), penguins, being non-volant, are much more limited in their foraging ranges (Wilson
53 1985), making the proximity of their food crucial. This is particularly important during breeding,
54 when birds are constrained to act as central place foragers (Orians and Pearson 1979) and
55 obliged to catch enough food to provision both their chicks and themselves (Croxall and Davis
56 1999; Boersma et al. 2015). The inability of penguins to forage over long distances during this
57 phase of their life cycle can be partially compensated for by their ability to forage at depth (Elliot
58 et al. 2013). The chick-rearing period in particular is highly demanding due to the increasing
59 energetic requirements of the growing chick and, to meet these changing nutritional demands,
60 penguins must adjust their foraging behaviour by either increasing the amount of food ingested,
61 or their feeding frequency or by targeting higher-energy prey species (e.g. Gentoo Penguins,
62 *Pygoscelis papua*, Williams and Rothery 1990; Chinstrap Penguins, *P. Antarctica*, Jansen et al.
63 2002; Little Penguins, *Eudyptula minor*, Zimmer et al. 2011 and Magellanic Penguins,
64 *Spheniscus magellanicus*, Sala et al. 2012).

65 Prey-switching linked to changing circumstances has been observed in many penguin
66 species, ranging from some of the largest (King Penguins, *Aptenodytes patagonicus*, Charassin et
67 al. 1998) to the smallest species (Gentoo Penguins, Handley et al. 2016; Southern Rockhopper,
68 *Eudyptes chrysocome*, Schiavini and Raya Rey 2004 and Northern Rockhopper, *E. moseleyi*,
69 Penguins, Tremblay and Cherel 2003; Booth and McQuaid 2013). Understanding how predators

70 modify their diving behaviour with respect to prey type is, however, complex (Ropert-Coudert et
71 al. 2002; Wilson et al. 2002), and given that targeting different prey requires changing dive
72 characteristics, this is particularly true in generalist predators that feed on a variety of prey
73 species and lack a single behavioural search and capture pattern (Davoren et al. 2003; Wilson et
74 al. 2005). The combined use of time-depth recorders (TDRs) with subsequent detailed analysis
75 of dive characteristics and stomach contents has therefore proven to be useful in attempting to
76 disentangle the relationship between dive behaviour and prey selection in penguins (e.g. Ropert-
77 Coudert et al. 2006; Bost et al. 2007; Deagle et al. 2008).

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

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94

MATERIALS AND METHODS

95 **Study area and species**

96 Fieldwork was carried out during chick rearing, between November and December 2010, at the
97 Stony Beach colony on Tristan da Cunha, the main island of the archipelago (Fig. 1). The colony
98 is divided into two sub-colonies, approximately 500 m apart: Stony Hill (37° 09' 54'' S, 12° 16'
99 18''W) and Stony Beach (37° 09' 36'' S, 12° 16' 06'' W), with an estimated 280 and 260
100 breeding pairs respectively in the year of study (Tristan da Cunha Conservation Department
101 unpubl. data). Birds nest on rocky hillsides at both sites, using a single path to leave and return to
102 the rookery.

103 Like other *Eudyptes* penguins, Northern Rockhopper Penguins have a synchronised
104 breeding cycle with highly defined parental shifts in nest attendance. Once the eggs hatch, male
105 birds remain at the nest during the guard stage (2–3 weeks), whilst females undertake daily
106 foraging trips to provide food. After this period chicks form loose crèches (crèche stage), and are
107 provisioned by both parents until they fledge at the age of 63–70 days (Cuthbert 2013). Northern
108 Rockhopper Penguins display brood reduction and usually only a single chick is reared (Cuthbert
109 2013; Stein and William 2013).

110 **TDR deployment and diet sampling**

111 Time-depth recorders (TDR; model G5, Cefas Technology Limited, UK) were attached to 30
112 guard stage birds (all female) between November 1st and November 9th 2010 at the Stony Beach
113 sub-colony, and to 13 crèche stage birds (sex unconfirmed) between November 22nd and
114 December 3rd 2010 at Stony Hill. Within each breeding stage, data were collected over
115 approximately 10 days, in order to minimise confounding effects such as temporal changes in

116 prey availability. Three TDRs deployed during the crèche stage were not retrieved. Devices were
117 attached to the penguin's right leg with a temporary leg band (constructed from a cable tie and
118 flexible plastic cable) using amalgamating tape and a cable tie (Booth 2011; Ratcliffe et al.
119 2014). The cylindrically shaped TDR devices measure 8 x 31 mm and weigh 1.3 g in seawater,
120 equivalent to *ca.* 0.05% of the mean Northern Rockhopper Penguin body mass. This deployment
121 technique was chosen due to the small size of the logger, allowing us to reduce any potential
122 negative impact on foraging behaviour and the risk of device loss (Ratcliffe et al. 2014). The
123 TDRs were programmed using the software G5 Host (Cefas Technology Limited) to record
124 hydrostatic pressure (as a proxy for depth with a resolution of < 0.4 m) continuously at 1 s
125 sampling intervals during the guard, or at 2 s intervals during the crèche stage when trips were
126 expected to be longer, in order to secure complete data capture (Tremblay and Cherel 2005).
127 Devices were set to start recording approximately 5 min after release of the bird. The handling of
128 the bird, from capture to release, lasted ≤ 3 min. To further minimise stress and provide
129 statistically independent data, different birds and nests were studied during each breeding stage.
130 Study birds were individually marked with a waterproof animal marker (© Porcimark) and nests
131 numbered with paint on the nearest rock to avoid resampling. The colony and path to the colony
132 were monitored continuously, from GMT 06:00 until approximately 22:00 h, and then
133 sporadically throughout the night to maximise encounter of returning study birds. Birds were
134 recaptured and devices retrieved upon their return to, or at, the nest prior to provisioning chicks.
135 Diet sampling was conducted using the water-offloading technique (Gales 1987) on twenty
136 device-equipped birds (guard $n = 17$, crèche $n = 3$). The day after deployment, the chicks of the
137 TDR equipped guard stage birds were weighed to the nearest 10g.

138 **Data analysis**

139 **Foraging trip and dive data.** Dive data were analysed using MULTITRACE (Jensen software
140 systems, Kiel, Germany). Prior to analysis, all data were corrected for a drifting surface level
141 (recorded depth is adjusted so that the surface level is maintained at 0 m, Hagihara et al. 2011)
142 and the dive threshold at which a foraging dive was deemed to occur was set to ≥ 3 m (in
143 accordance with other studies of Rockhopper Penguins: Cherel et al. 1999; Tremblay and Cherel
144 2000, 2003; Dehnhard et al. 2016; Whitehead et al. 2016). Some birds were not recaptured after
145 one foraging trip, and so consecutive trips were recorded over several days. In such cases, trips
146 were separated when there was a gap in diving activity of ≥ 4 h (Pichegru et al. 2011).

147 For the comparison of diving behaviour between guard and crèche stage birds, each
148 foraging trip was described by departure and arrival time (start and end time of first and last
149 foraging dive, respectively), trip duration (time elapsed between first and last recorded foraging
150 dive), vertical travel distance (VTD, the sum of the maximum dive depths for all foraging dives
151 during a trip, multiplied by two, Tremblay and Cherel 2003), total number of dives, dive rate
152 (number of dives per foraging trip as a proportion of the foraging trip duration) and dive time (%
153 of time spent underwater during foraging trip). Following Raya Rey et al. (2013), we calculated
154 foraging activity as bottom time (min) per hour underwater. For each dive within a foraging trip
155 we calculated dive duration, maximum depth, bottom time and to determine prey pursuit events
156 we used the number of undulations or ‘wiggles’ in the dive profile (Bost et al. 2007; Sala et al.
157 2012).

158 **Feeding dives.** Feeding dives were analysed from the same birds that provided diet data. To gain
159 a comprehensive description of the diving behaviour of birds when feeding, we extracted all
160 dives that contained wiggles in the dive depth profile (hereafter referred to as ‘feeding dives’)
161 and examined an enlarged set of dive parameters to characterize prey pursuit strategy: dive

162 duration, descent time, bottom time, ascent time, maximum depth, vertical descent rate,
163 horizontal rate and vertical ascent rate. Hence, each feeding dive was analysed considering a
164 minimum of one wiggle per dive. When multiple foraging trips were recorded for a bird, only
165 dive data from the last trip were used, as these dives were the most likely to reflect the prey
166 content of the obtained stomach sample (Wilson et al. 1989).

167 ***Meal mass and diet composition.*** Stomach content was sorted into principle prey items, weighed
168 to obtain an estimate of proportion by wet mass (Cherel et al. 2007), and categorised according
169 to the following wet mass contributions in the diet: zooplankton > 85%, fish > 85%, cephalopods
170 30–70% and zooplankton 30-70%, and mixed cephalopod 10–70%, zooplankton 10–70%, fish
171 10–70%. For further details of procedures see Booth and McQuaid (2013).

172 **Statistical analysis**

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

178 ***Foraging trip and dive analysis.*** A one-way permutational multivariate ANOVA or
179 PERMANOVA (9999 permutations, dissimilarity matrix calculated using Euclidean distances)
180 was used to compare breeding stages (fixed, orthogonal, 2 levels: guard and crèche) in terms of
181 the foraging trip variables: trip duration, VTD, number of dives, dive time, dive rate, and
182 foraging activity index. In cases where birds performed multiple trips, means for each trip and
183 then a grand mean for each bird were calculated. MULTITRACE calculates a large number of
184 dive parameters. Due to the nature of the diving variables measured, multi-collinearity was

185 checked using the non-parametric Spearman correlation; none of the chosen variables had a
186 correlation score higher than 0.85 (accepted threshold level of correlation; Clarke and Gorley
187 2006) and all were retained. Subsequently, we selected a set of variables to describe dive
188 characteristics for comparison of the diving behaviour between guard and crèche stage birds (e.g.
189 Tremblay and Cherel 2003; Crossin et al. 2015). Hence, running linear mixed effects models,
190 using the package nlme in R (Pinheiro et al. 2013), we tested the three dependent variables: dive
191 duration, maximum depth and bottom time. In all models, we used breeding stage (guard and
192 crèche) as our explanatory variable with a fixed effect while ‘trip’ nested in ‘bird identity’ was
193 included as a random effect. Following Ratcliffe et al. (2013), we conducted backwards-stepwise
194 model selection, first identifying the best random-effects model structure by comparison of
195 models with and without trip effect (nested in bird identity), which were fitted with restricted
196 maximum likelihood (REML). We did not test for the performance of a model without bird
197 identity, as removal would have violated the premise of independent data. For the variables dive
198 duration and maximum depth, we applied a fourth square root transformation for normality and
199 therefore used the function lme (Venables and Ripley 2002); while for the variable bottom time,
200 we used a generalised mixed model specifying the family error Poisson (Breslow and Clayton
201 1993). As successive dives might not be independent, both models were fitted with a first-order
202 autocorrelation structure using the function corAR1 (Box et al. 1994).

203 Multiple correlation analysis, calculated with Spearman’s correlation, was used to
204 examine possible correlations between guard stage chick weight and guard stage bird foraging
205 trip variables (trip duration, VTD, number of dives, total number of dives and total dive time)
206 using the R package ‘PerformanceAnalytics’
207 (<https://cran.rproject.org/package=PerformanceAnalytics>).

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

220

221

RESULTS

222 Foraging trips

223 A total of 58 foraging trips was recorded for 27 guard stage birds and 35 foraging trips for 10
224 crèche stage birds. During both breeding stages, the majority of foraging trips had a duration of
225 14–16 h, with 83% of guard stage trips lasting 10–16 h and 56% of crèche stage trips lasting 14–
226 16 h. Crèche stage birds performed all trips longer than 16 h and all trips shorter than 6 h (Fig.
227 2), the shortest being 2.04 h. During these short trips feeding activity was confirmed by the
228 presence of wiggles so that these trips could be classified as foraging trips.

229

230 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

231 breeding stages in all examined foraging trip variables: trip duration, VTD, total number of
232 dives, dive rate, total dive time or foraging activity index (PERMANOVA, $p > 0.05$). Similarly,
233 there was no significant effect of breeding stage on the dive parameters: dive duration (LME, $p >$
234 0.05), maximum dive depth (LME, $p > 0.05$) and bottom time (GLMM, $p > 0.05$).

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

238 **Feeding dives**

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

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

254 depths: guard/cephalopod and zooplankton 15.1 m; guard/zooplankton 20.9 m; guard/mixed fish,
255 cephalopod and zooplankton 22.4 m). The deepest dives were performed by crèche stage birds
256 feeding on fish (mean maximum depth 38.6 m), while crèche birds feeding on mixed prey
257 performed the shallowest dives (mean maximum depth 12.9 m).

258 Guard stage birds feeding on a mixture of cephalopods and zooplankton performed the
259 shortest dives (mean dive duration 66.7 s), while feeding dives made by crèche stage birds
260 targeting fish were significantly longer than others (mean dive duration 112.8 s; Fig. 3). Dives in
261 the categories crèche/mixed fish, cephalopod and zooplankton (mean dive duration 77.6 s),
262 guard/mixed fish, cephalopod and zooplankton (mean dive duration 74.8 s) and guard/
263 zooplankton (mean dive duration 76.5 s) formed a separate, intermediate group (p-pht, $p =$
264 0.0001; Fig. 3).

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

273 To confirm that the patterns observed in the examined parameters, bottom time and dive
274 duration, were a true reflection of a difference in prey selection rather than purely reflecting the
275 differences in dive depth, we performed a regression analysis of the bottom time against
276 maximum dive depth for each of the prey/stage categories. While we found a significant

277 relationship between the two dive parameters for guard stage birds feeding predominantly on
278 zooplankton (guard/zooplankton) and on a mixed diet (guard/mixed fish, cephalopod and
279 zooplankton) (LM, $F_{1,42220} = 124.1$, $p < 0.0001$ and LM, $F_{1,376} = 109.4$, $p < 0.0001$, respectively)
280 there was no relationship for other stage/prey categories (LM, $p > 0.05$ in all cases).

281

282

DISCUSSION

283 This study aimed to assess whether the foraging behaviour of a generalist predator
284 mirrors a switch in its diet from a low to higher-energy prey species in order to meet the
285 changing nutritional requirements of their young (Booth and McQuaid 2013). Given the
286 increasing daily energy requirements of growing chicks during the breeding season, it can be
287 expected that parental foraging strategies will be adjusted to maximise energy gain (Ydenberg et
288 al. 1994). Brown (1987) estimated daily energy requirements of Southern Rockhopper chicks to
289 increase more than 5-fold from the first week of hatching to the midway point in their growth.
290 Parents must meet this increasing demand in some manner, to ensure successful breeding, either
291 through an increase in provisioning frequency and amount (Jansen et al. 2002; Trivelpiece et al.
292 1987) or the selection of higher energy-content prey (e.g. Gentoo Penguins in the
293 Malvinas/Falkland Islands, Handley et al. 2017).

294 Being characterised as an opportunistic predator can be interpreted as implying naïve
295 foraging behaviour, with random encounters of prey items (MacArthur and Pianka 1966; Orians
296 and Pearson 1979), and it is still unclear whether foraging flexibility simply reflects prey
297 availability and abundance (opportunistic behaviour) or if, in fact, the choice of prey is actively
298 driven by modifying foraging behaviour to target specific prey items in order to match particular
299 energetic needs through specialist behaviour (Gaston 2004; Ludynia et al. 2010). Of course, the

300 two approaches are not mutually exclusive, but rather manifestations of the extreme flexibility in
301 foraging behaviour required in a feeding environment made more unpredictable by the inability
302 to fly. Not surprisingly, foraging strategies of generalist penguins are less well understood than
303 those of specialists and the ultimate goal remains to disentangle the links among foraging
304 behaviour, dietary shifts and prey availability.

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

323 within the water column, prey behaviour may dictate dive duration and bottom time (Lescr el
324 and Bost 2005; Sala et al. 2014). Prey exploitation strategies by penguins are dependent on a
325 number of factors including the size and depth of prey patches and their abundance (Wilson et al.
326 2002). The strategies observed in our study were found to be linked to prey type, with birds
327 targeting fish (> 90% mass in diet) performing longer, deeper dives, and those targeting
328 zooplankton (> 90% mass in diet) performing shorter, shallower dives. Similar behaviour was
329 observed in Macaroni Penguins, *E. chrysolophus*, which perform deeper dives to feed on fish
330 than when feeding on crustaceans (Deagle et al. 2008). Although we interpret differences in dive
331 parameters as changes in foraging behaviour, there were significant correlations between
332 maximum dive depth and bottom time in the case of dives targeting zooplankton and those
333 associated with a mixed diet. This suggests that, while changes in parameters were indeed
334 generally related to the prey taken, rather than depth, in these two cases changes in dive
335 behaviour may have been additionally influenced by depth. A shift in diet associated with
336 plasticity in dive behaviour was detected in conspecifics at Amsterdam Island. In that case birds
337 performed deeper dives in the early part of the cr che stage compared to late cr che stage and
338 this was associated with a shift in diet from one dominated by squid (44%) to one dominated by
339 fish (64%) (Tremblay et al. 1997). This exemplifies the complexities of understanding prey
340 capture strategies, in terms of behaviour, size and local distribution of the specific prey being
341 targeted (Wilson et al. 2002), but nonetheless, corroborates our detection of prey-switching and
342 coupled behavioural changes in the species.

343 Although Northern Rockhopper Penguins are able to dive to depths greater than 90 m
344 (this study; Cherel et al. 1999) they rarely did so, and the majority (83%) of dives recorded were
345 concentrated in the upper 20 m of the water column. Such predominantly shallow diving

346 behaviour is similar to that observed at Amsterdam Island, where birds mostly foraged at around
347 18 m (Cherel et al. 1999). Based on allometric equations, Cherel et al. (1999) predicted that
348 Northern Rockhopper Penguins with a body mass of 2.3 kg would have a maximum dive
349 duration of 124 to 176 s and a maximum dive depth of 77 to 89 m, values that were occasionally
350 exceeded, but broadly similar to those recorded here (Table 1). However, birds generally avoided
351 their physiological limits, and this likely reflects a behavioural strategy based on the distribution
352 of prey within the water column (Wilson et al. 2002; Ropert-Coudert et al. 2006; Elliot et al.
353 2008).

354 During breeding, to successfully rear chicks, if penguins do not switch to a higher-energy
355 prey they have to increase their foraging effort. Prey selection is constrained by availability,
356 which in turn partially depends on foraging range. During the guard stage hatchlings require
357 continuous parental attendance and the foraging range is consequently restricted, while the
358 crèche stage, when chicks are able to thermoregulate themselves, allows greater flexibility for
359 adults in acquiring food and delivering it to the nest. In many penguin species, this is manifested
360 in an increase over the breeding period in either feeding frequency or the amount of food
361 delivered to the chick (Zimmer et al. 2011) or increased foraging trip duration (e.g. Adeliae
362 Penguins, *P. adeliae*, Lyver et al. 2011). We observed no increase in foraging effort between
363 breeding stages, in terms of foraging trip parameters (i.e., trip duration, total number of dives,
364 VTD, total dive time, dive rate or foraging activity index). Dehnhard et al. (2016) similarly
365 found no foraging differences between breeding stages for Southern Rockhopper Penguins, while
366 others have recorded an increase over the breeding season (Schiavini and Raya Rey 2004; Raya
367 Rey et al. 2007). We were unable to test the effect of sex on diving behaviour and diet during the
368 crèche stage, since birds could not be blood-sampled for genetic sexing. While we acknowledge

369 that in some species male and female penguins do display different foraging behaviours and diets
370 (e.g. African Penguins, *Spheniscus demersus*, Pichegru et al. 2013 and Gentoo Penguins, Xavier
371 et al. 2017), we highlight that no difference in diet was observed between the sexes in the crèche
372 stage in a study of the same population of Northern Rockhopper Penguins during the same
373 breeding season (Booth and McQuaid 2013). Furthermore, Dehnhard et al. (2016) observed
374 similar foraging behaviour, in terms of dive depth, between crèche stage male and female
375 Southern Rockhopper Penguins.

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

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

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

406

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417 **Compliance with ethical standards**

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

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

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598

599 **Figure Captions**

600 **Fig. 1** – Map of Tristan da Cunha displaying (A) the position of the archipelago in the South
601 Atlantic Ocean, (B) the three main islands of Tristan, Inaccessible and Nightingale and (C)
602 Tristan Island with the location of the study cub-colonies of Stony Beach and Stony Hill.

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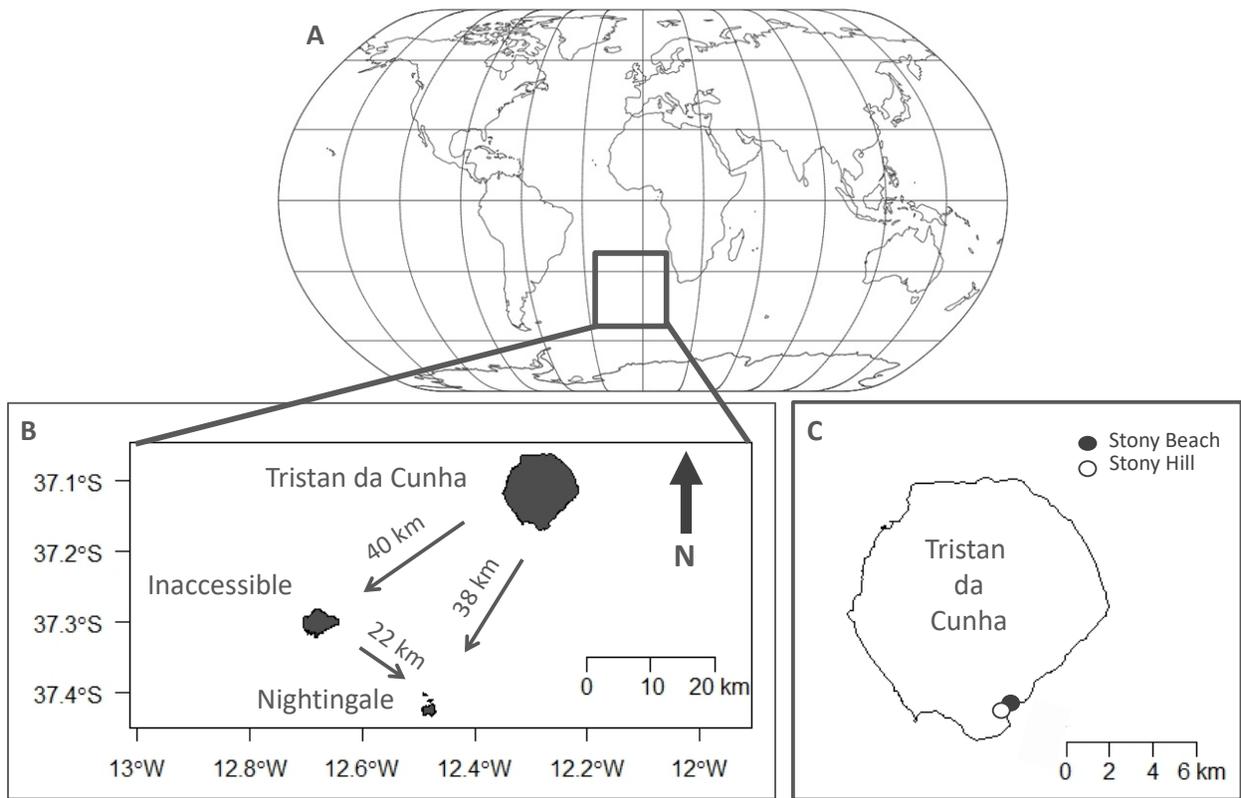
604 **Fig. 2** – Frequency distribution of foraging trip duration (h) of Northern Rockhopper Penguins
605 during the breeding season 2010/11 at Tristan da Cunha (guard $n = 58$, crèche $n = 35$)

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

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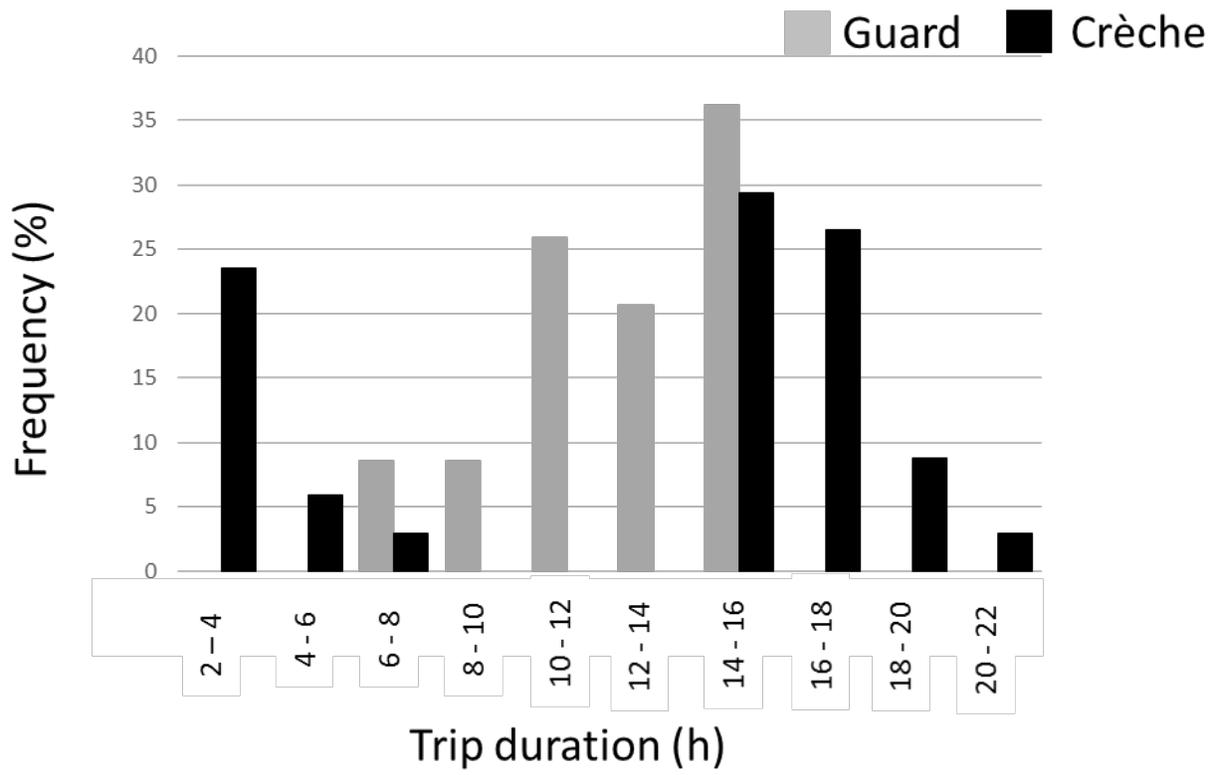
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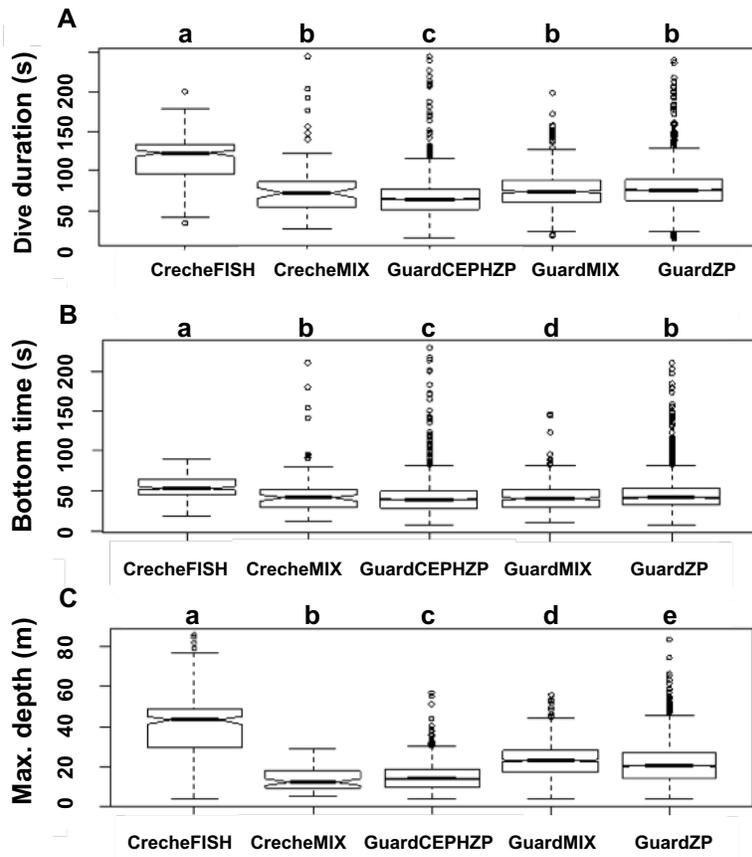
619 Fig 2



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625 **Table 1** – Foraging trip and dive variables of Northern Rockhopper Penguins at Tristan da
626 Cunha during the guard and crèche stages in 2010. Values are means +/- SE, with ranges shown
627 in brackets. Multiple trips by individual birds were pooled to obtain an overall mean. Sample
628 sizes for foraging trip variables: guard $n = 27$, crèche $n = 10$ and for foraging dive variables:
629 guard $n = 34439$, crèche $n = 26156$.

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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)

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633 **Table 2** – Stomach content composition (by wet mass) of TDR-equipped Northern Rockhopper
 634 Penguins returning from foraging trips during the breeding season 2010 at Tristan da Cunha (n =
 635 20; G: guard, C: crèche, ZP: zooplankton, CEPH/ZP: mixed cephalopod and zooplankton, MIX:
 636 mixed fish, cephalopod, zooplankton, FISH: fish).

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Bird ID	Diet classification	Total mass (g)	Digested mass (%)	Fresh mass (%)	Fish (%)	Cephalopod (%)	Zooplankton (%)
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

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640 **Table 3** – Feeding dive variables of Northern Rockhopper Penguins at Tristan da Cunha during
 641 the guard and crèche stages in 2010. Values are means +/- SE. (ZP: zooplankton, CEPH/ZP:
 642 mixed cephalopod and zooplankton, MIX: mixed fish, cephalopod, zooplankton, FISH: fish)

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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

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