

Long days, long trips: foraging ecology of female rockhopper penguins *Eudyptes chrysocome chrysocome* at Tierra del Fuego

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ABSTRACT: In rockhopper penguins *Eudyptes chrysocome*, the relationship between foraging effort and the daylight period is unclear. We studied the foraging ecology of female southern rockhoppers that were brooding chicks at Bahía Franklin (Staten Island) in December 2000. We compare our data with data presented for other subspecies and locations, analyzing the features of their foraging ecology and its relationship with the daylight period around Staten Island, the population size of different breeding locations and the marine environment. Southern rockhopper penguins performed longer trips (about 30 and 60 % longer for daily and overnight trips respectively) and between 5 and 7 more overnight trips (53 %) than the northern and eastern subspecies. Mean dive depth and dive duration were 28.9 ± 24.6 m and 79 ± 30 s respectively. The diving rate (30.4 ± 5.0 dives h^{-1}), and the proportion of trip duration underwater ($66.2 \pm 5.9\%$) confirmed the high foraging effort of rockhopper penguins. During the study period foraging trip duration increased, but dive parameters did not vary. Penguins traveled as much as 20 km to their foraging waters, either in shelf waters and/or in waters of a close shelf-break and slope. The diet was dominated in numbers by euphausiids, amphipods, cephalopods, fish larvae and juveniles, all prey species commonly found in Subantarctic waters. The long trips could be explained by the long twilight period and by diel vertical migration of prey, confirming the phenotypic plasticity of penguins in response to different marine environments. The extended foraging trip duration may contribute to sustaining the high level of the breeding population (167 000 breeding pairs) at Bahía Franklin, and account for differences in the recent history of different breeding colonies in the SW Atlantic Ocean.

KEY WORDS: *Eudyptes chrysocome chrysocome* · Southern rockhopper penguin · Foraging ecology · Diving behavior · Diet · Tierra del Fuego · SW Atlantic Ocean

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INTRODUCTION

Penguins constitute a large proportion of the top predator biomass in subantarctic and antarctic waters (Croxall 1984, Croxall & Lishman 1987). During the breeding time, when birds congregate in colonies and parents must provide food for both their offspring and themselves, foraging activity may be particularly great close to colonies. The rockhopper penguin *Eudyptes chrysocome* is one of the most abundant penguin species, and also the second smallest penguin species. The southern subspecies *E. chrysocome chrysocome* (here-

after referred to as *chrysocome*) breeds in southern South America and the Falkland (Malvinas) Islands. Staten Island, at the eastern tip of the Tierra del Fuego archipelago, holds 174 000 breeding pairs (26 % of the breeding population of this subspecies), with 167 000 nests located in a large colony recently discovered in Bahía Franklin (Schiavini 2000).

The diving and foraging behavior of rockhopper penguins during the brooding period has been studied in detail by Cherel et al. (1999) and by Tremblay & Cherel (1999, 2000, 2003) at Amsterdam, Crozet and Kerguel-

len Islands, and by Hull (2000) at Macquarie Island. The behavior described suggests that daylight duration represents a limiting factor as, in general, females make daily foraging trips, leaving the colony by dawn and returning by dusk. Cherel et al. (1999) and Tremblay & Cherel (2003) recorded high dive frequencies and percentage of trip duration underwater, concluding that brooding females operate at a high level of foraging effort, with little scope for increasing effort by an increase in the percentage of time underwater. They also suggested that foraging trip duration is the most likely foraging behavior characteristic of female rockhopper penguins that would vary during the brooding period. Despite these mentioned studies, the relationship between trip duration, foraging effort and daylight duration in rockhopper penguins remains unclear.

The Tierra del Fuego archipelago is one of the southernmost breeding areas of the species, with an extended daylight period during the breeding season compared to other breeding locations. By studying the foraging ecology in an area in which the daytime period is long and comparing the results with data for other localities, we explored the relationship between trip duration, foraging effort and daylight duration. Given the behavioral plasticity of the species (Tremblay & Cherel 2003) we hypothesize that, under longer daylight periods, foraging effort (as time spent underwater) decreases, but trip duration increases.

Ashmole (1963) proposed that pelagic seabird populations are limited by density-dependent competition for food around their breeding colonies. Cairns (1989) proposed that colony population size is a function of the size of the foraging habitat. The large size of the chrysocome colony on Staten Island raises questions about the levels of intraspecific competition that these birds would potentially experience. During the brooding period only the females feed the chicks, and their foraging range is constrained, increasing the potential for competition with other breeders, juveniles and failed breeders. In comparing the foraging behavior among different locations with different population sizes, it would be expected that larger rockhopper breeding colonies would tend to exploit farther foraging grounds or forage over longer periods than smaller populations.

This is the first report of the foraging ecology of female southern rockhopper penguins in the SW Atlantic Ocean during the brooding period. The large population size and location of the colony at Bahía Franklin, Staten Island, enabled us to investigate factors influencing the foraging ecology of rockhopper penguins. We compare our data with data presented for other subspecies and locations, i.e. northern rockhopper penguins *Eudyptes chrysocome moseleyi* (hereafter referred to as *moseleyi*) and eastern rock-

hopper penguin *E. chrysocome filholi* (hereafter referred to as *filholi*), analyzing the relationship between their foraging ecology, the daylight period, the population size at the different breeding locations and the marine environment around Staten Island.

MATERIALS AND METHODS

Study site. Fieldwork was undertaken at Bahía Franklin, Staten Island, Tierra del Fuego (54°50.0'S, 64°40.5'W, Fig. 1). Staten Island is situated at the southern extreme of the Patagonian shelf, where the 200 m isobath is located 12 km from the southern coast of Staten Island (Servicio de Hidrografía Naval 1993). Bahía Franklin is an open rectangular bay with a square mouth of 5.5 km width. It faces the Le Maire Strait, a 30 km wide passage that separates Staten Island from the Isla Grande de Tierra del Fuego. The sediments of the Le Maire Strait comprise sand, gravel and mud (Parker et al. 1997). The strait is famous for its strong tidal currents (up to 4 knots in the main axis) that interact with the Falkland (Malvinas) current, as well as with the prevailing western winds. Tide-rips and whirlpools are very common inshore close to headlands and points.

The waters around Staten Island are in the Subantarctic Zone, with the Subantarctic Front occurring at about 80 km SE of Staten Island (Orsi et al. 1995). Local oceanography includes waters from the Antarctic Circumpolar Current that generates the Falklands (Malvinas) Current after passing the Drake Passage, as well as shelf waters affected by continental discharges and tidal fronts (Sánchez et al. 1995, Bertolotti et al. 1996, Piola & Rivas 1997). To the east of Staten Island (110 km), waters are influenced by a shelf-break front, an area recognized to be of high productivity (González et al. 1997). Waters off Tierra del Fuego and Staten Island contain important biomasses of zooplankton and ichthyoplankton (Sánchez & Ciechomski 1995, Sabatini et al. 1999, 2001).

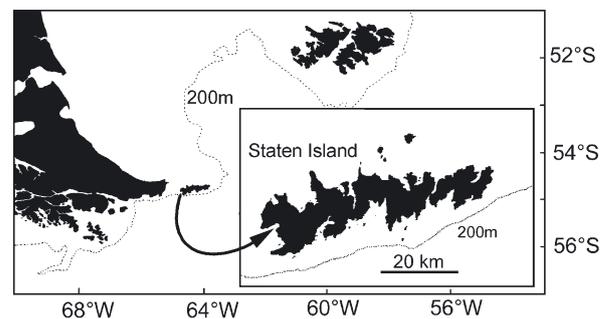


Fig. 1. Southern portion of SW Atlantic Ocean, showing location of study site

Instrument deployment. We equipped 11 females with 3 time-depth recorders (TDRs) from December 6 to 16, 2000, during the second half of the guard period (chicks started to hatch on November 27). At this time only the female provides food for the chick, while the male guards the nest. We used Lotek LTD-100 TDRs, also equipped with light sensors, to collect dive data. The devices had a 'nose-drop' shape to reduce hydrodynamic drag, presented a cylindrical section, measured 61×18 mm and weighed 16 g in air, corresponding to $<2\%$ of the cross-sectional area of the birds and $<1\%$ of their body mass. We deployed 3 devices consecutively on 11 females. TDRs were attached using Tesa® tape as described by Wilson et al. (1997a). The devices were deployed for 2.7 ± 0.8 d (range 1.8 to 3.8 d). During the first deployments we left the devices on the penguins for only 1 or 2 d, in the belief that penguins performed daily foraging trips. When we noticed that the birds stayed in the water overnight, we deployed devices for longer periods. TDRs were programmed to sample depth and light continuously at 2 s sampling intervals, allowing a total recording time of 6 d deploy⁻¹.

Diet analysis. Diet sampling was conducted using the water-offloading technique (Wilson 1984) on 11 females. For 4 birds, stomach samples were collected after recovering the TDRs. Birds were captured at the nest after display with their partner prior to deliver the food to chicks, weighed, sexed using bill depth and length, and lavaged. Diet samples were drained and preserved with 70% ethanol. In the laboratory, samples were weighted and sorted into the main components: fishes, squid and crustaceans. A subsample of $\frac{1}{8}$ of each sample was analyzed, and the results were extrapolated to the total. Identification of taxa was made using entire specimens for crustaceans, lower beaks for cephalopods and otoliths and cranial bones for fishes, and comparing them with the literature and our reference collection. Diet is described in terms of percentage frequency of occurrence, percentage by number and percentage by mass, to allow for the various biases of each of these techniques (Hyslop 1980, Duffy & Jackson 1986). The original weight of specimens ingested was estimated by applying regression equations relating squid beak size (lower rostral length) and euphausiid standard body length (anterior edge of eyeball to tip of telson) to body mass (Clarke 1986, Ridoux 1994).

Data analysis. We analyzed dive data using MULTITRACE (Jensen Software Systems). Data were corrected for a drifting surface level. A dive was deemed to occur when the maximum dive depth was ≥ 3 m (after Chappel et al. 1993, 1999, Tremblay & Cherel 2000, 2003). For each dive, the software calculated duration, onset, maximum depth, pre-dive interval

(from which we derived post-dive interval), bottom time (time spent at 75% of maximum dive depth attained during the dive: after Cherel et al. 1999, Tremblay & Cherel 2000, 2003), descent rate (from beginning of dive to start of bottom phase), and ascent rate (from end of bottom phase to end of dive). Vertical travel distance (VTD) was defined as 2 times the sum of the maximum dive depth for all dives performed during each trip (Horning & Trillmich 1997). Diving efficiency (proportion of bottom time over a complete dive cycle) was estimated following Ydenberg & Clark (1989) as diving efficiency = bottom time/(dive duration + post-dive interval). We compared our dive data with those reported by Hull (2000) in only a broad sense, as she considered dives >6 m depth for her analysis and her data for the 'chick rearing' period were pooled among sexes and included both the brooding and crèche period. We considered dives ≤ 5 m depth as traveling dives and dives >5 m depth as foraging dives, after Tremblay & Cherel (2003).

We assessed temporal changes in several parameters of foraging and diving behavior, considering the time elapsed since the first day of hatching (November 27) to the median point of each foraging trip as the independent variable (the date of hatching for chicks from to the studied females could not be recorded). We determined if an individual equipped with a TDR was either on land or in the water by the light-sensor readings: it was deemed to be on land when the readings presented a smooth profile, and to be resting on the sea surface when the readings presented an erratic profile (which we assumed represented movements of the penguins on the water surface). We confirmed this assumption with readings from individuals equipped with TDRs and also with implanted glass-encapsulated microchips with individual identification numbers (transponders, TIRIS 23 mm, Texas Instruments®), which were simultaneously detected by an automatic reading system.

Successive dive data are partially autocorrelated, as the maximum depth of a dive is influenced by the previous depths attained. As a consequence, data are temporally pseudoreplicated (Hurlbert 1984). To overcome this we followed the method of Tremblay & Cherel (2003). We performed a partial autocorrelation analysis, which verified that maximum dive depth failed to correlate after 4 successive dives. Thus, remaining 1 dive out of 4 would reduce the autocorrelation. On the other hand, all birds do not have the same statistical weight because of the unequal number of trips and of dives per trip recorded for the different individuals. Therefore, when examining dive parameters, we considered the bird as the sample unit and not the trip. Since the trip with the lowest number of dives contained 262 dives, we sampled 65 dives per

Table 1. *Eudyptes chrysocome*. Summary of foraging trip and dive characteristics for different subspecies of female rockhopper penguins at different localities. Values are means \pm SD. nr: not reported

Parameter	Staten Island ssp. <i>chrysocome</i> (this paper)	Macquarie Island ssp. <i>filholi</i> (Hull 2000)	Amsterdam Island ssp. <i>moseleyi</i> (Tremblay & Cherel 2003)	Kerguelen Island ssp. <i>filholi</i> (Tremblay & Cherel 2003)	Crozet Island ssp. <i>filholi</i> (Tremblay & Cherel 2003)
Dive depth	$\geq 3\text{m}$	$> 6\text{ m}$	$> 5\text{ m}$	$> 5\text{ m}$	$> 5\text{ m}$
Trip duration (h)					
Day trips	15.7 \pm 5.1 (n = 7)	153.4 \pm 108.0 (n = 7) ^a	12.2 \pm 2.57 (n = 107)	11.9 \pm 2.0 (n = 123)	11.2 \pm 3.6 (n = 125)
Overnight trips	34.8 \pm 8.7 (n = 7)		35.6 \pm 6.6 (n = 12)	–	28.6 \pm 5.0 (n = 13)
Overnight trips (%)	53% (n = 15)	nr	11% (n = 119)	–	10% (n = 138)
Outward travel time (h)					
Day trips	1.12 \pm 0.92	nr	0.51 \pm 0.29	0.21 \pm 0.30	0.41 \pm 0.45
Overnight trips	1.10 \pm 0.39		0.57 \pm 0.26	–	0.58 \pm 0.57
Inward travel time (h)					
Day trips	0.62 \pm 0.39	nr	0.56 \pm 0.40	0.69 \pm 0.85	0.38 \pm 0.44
Overnight trips	0.79 \pm 0.78		0.43 \pm 0.19	–	1.04 \pm 1.84
No. of traveling dives					
Day trips	53 \pm 34	nr	96 \pm 73	57 \pm 73	51 \pm 67
Overnight trips	103 \pm 54		210 \pm 109	–	226 \pm 116
No. of foraging dives					
Day trips	452 \pm 146	nr	362 \pm 129	292 \pm 69	247 \pm 76
Overnight trips	882 \pm 254		913 \pm 221	–	518 \pm 99
Dive rate (dives h ⁻¹)					
Day trips	32.7 \pm 5.7	14.8 \pm 9.4 ^a	37.2 \pm 9.5	29.6 \pm 8.9	27.1 \pm 5.9
Overnight trips	28.0 \pm 2.0		31.2 \pm 4.7	–	26.2 \pm 3.9
Maximum dive depth (m)	28.9 \pm 24.6	27.3 \pm 20.3	22.5 \pm 15.7	29.1 \pm 14.1	40.4 \pm 17.6
Deepest dive (m)	113	104	93	85	104
Vertical travel distance (km)					
Day trips	27.80 \pm 14.24	nr	16.02 \pm 3.97	17.38 \pm 4.68	20.06 \pm 7.47
Overnight trips	59.96 \pm 17.83		35.27 \pm 4.66	–	39.50 \pm 8.83
Dive time (% trip duration)					
Day trips	68.9 \pm 5.2 (n = 7)	36.6 \pm 9.3 ^{a,b}	63.9 \pm 8.1	61.9 \pm 8.8	64.2 \pm 8.5
Overnight trips	63.4 \pm 5.7 (n = 7)		49.7 \pm 3.9	–	26.2 \pm 3.9
Dive duration (s)	79 \pm 30	72 \pm 42	78.4 \pm 34.8	87.4 \pm 26.2	101.0 \pm 27.0
Post-dive interval (s)	20 \pm 11 ^c	nr	25.2 \pm 15.1	33.3 \pm 15.3	36.0 \pm 17.5
Bottom time (s)	35 \pm 17	30 \pm 6	41.8 \pm 20.8	54.7 \pm 20.8	57.4 \pm 19.1
Diving efficiency	0.34 \pm 0.14 ^c	nr	0.40 \pm 0.13	0.45 \pm 0.12	0.42 \pm 0.11
Descent rate (m s ⁻¹)	1.2 \pm 0.5	1.2 \pm 0.2	1.1 \pm 0.5	1.6 \pm 0.5	1.7 \pm 0.6
Ascent rate (m s ⁻¹)	0.8 \pm 0.5	1.0 \pm 0.2	0.9 \pm 0.5	1.3 \pm 0.5	1.3 \pm 0.5
Sample size	520	57 130	1632	1622	1693

^aDay and overnight trips pooled
^bBased on a 24 h period, not on the whole trip duration
^cPost-dive intervals $\leq 180\text{ s}$ (n = 509) were taken into account (the criteria used by Tremblay & Cherel 2003)

bird randomly. The resulting set (520 dives) was used to analyze the dive characteristics.

We estimated the distance traveled from the colony to where a penguin started to forage as the time elapsed between the initial dive to the first of the first 3 consecutive dives $\geq 10\text{ m}$ depth (after Cherel et al. 1999). We assumed that penguins travel continuously at a constant speed of 7.4 km h⁻¹ (Brown 1987) and in a

straight line. We estimated the return journey as the time elapsed between the last 3 consecutive dives $\geq 10\text{ m}$ depth and the final dive. The time of sunrise and sunset at the deployment locations were (for the mean date of device deployment on December 12) 04:35 and 21:49 h respectively (local time = GMT–3 h), giving a solar day length of 16.75 h. Dawn and dusk were at 01:28 and 01:00 h respectively following the nautical

definition, i.e. when the sun is 12° below the horizon. Thus, the twilight period (dawn and dusk together) lasted 6.78 h and nighttime was restricted to 0.47 h (28 min). The common names we use for the rockhopper subspecies follow the nomenclature of Ellis et al. (1998). All mean values are presented with \pm SD.

RESULTS

Trip characteristics

Depth and light data indicated that either 1 female did not return or its device was lost, and that 2 other females did not leave the colony. Data were thus obtained from 8 females during 15 foraging trips that included 11 819 dives performed during 390.3 h at sea. As 1 female was already in the water when the TDR started recording (at 00:00 h on December 10), its data was considered only for analysis of dive characteristics.

Of the foraging trips, 8 (53%) included overnight foraging, and 1 of these included 2 nights at sea. The duration of the foraging trips (excluding the incomplete trip) averaged 25.3 ± 12.0 h. Daily trips differed from overnight trips in duration (15.7 ± 5.1 h, $n = 7$ vs 34.8 ± 8.7 h, $n = 7$ respectively; Student's t -test, $t_9 = 5.00$, $p = 0.001$; Table 1). Most departures (71%, $n = 14$) occurred between 01:00 and 05:00 h, with a peak between 03:00 and 04:00 h (43%, $n = 14$). Arrival times occurred between 10:00 and 24:00 h, with 47% of them between 10:00 and 19:00 h and with a peak between 23:00 and 24:00 h (27%, $n = 15$). There was no difference in departure and arrival times between birds performing daily and overnight trips (t -test, departure times, $t_{12} = -1.20$, $p = 0.21$; arrival times, $t_{13} = 2.11$, $p = 0.05$). Periods on land (assessed for 7 trips) averaged 4.4 ± 1.9 h, with 4 stays during hours of darkness and 3 during daylight hours.

Travel time to foraging areas was 1.11 ± 0.81 h ($n = 14$ excluding the incomplete trip), and return time was 0.71 ± 0.61 h ($n = 15$). Outward and inward traveling times were not significantly different (t -test, outward trips, $t_{12} = 0.91$, $p = 0.38$; inward trips, $t_{11} = 0.97$, $p = 0.35$). Foraging ranges for the outward and return trips were estimated at 8.2 ± 6.2 and 5.3 ± 4.6 km with maxima of 20.2 and 16.4 km respectively.

The number of dives >3 m per foraging trip averaged 745 ± 339 and the average dive rate (based on trip duration) was estimated at 30.4 ± 5.0 dives h^{-1} (excluding the incomplete recorded trip with 1385 dives). Dive rate was 32.7 ± 5.7 and 28.0 ± 2.0 dives h^{-1} for daily and overnight trips respectively (Table 1) and were not significantly different (t -test, $t_7 = 2.05$, $p = 0.08$). Dives

made from dawn to dusk represented 99.6% of the 520 sampled dives. However, 121 of the sampled dives (23%) were performed under twilight conditions.

Dive characteristics

Among the sampled dives that were ≥ 3 m, the maximum dive depth was 113 m and the maximum dive duration was 164 s. Average maximum dive depth was 28.9 ± 24.6 m, the frequency distribution of dive depth presented 1 peak between 4 and 6 m depth (13%) and 50% of the dives were ≤ 19 m (Fig. 2). The mean proportion of foraging dives (>5 m depth) for all trips in *chrysocome* was $89.9 \pm 3.8\%$ ($n = 14$ excluding the incomplete trip).

Only 2 sampled dives were performed at night under the dawn and dusk times defined (reaching 5.4 and 6.1 m depth). During daylight hours, the mean maximum dive depth and its variation were relatively stable (Fig. 3), although maximum dive depths during twilight and night hours were shallow (Fig. 4). The mean dive duration was 79 ± 30 s, with 50% of the dives taking ≤ 78 s. The frequency distribution presented 1 peak at 62 to 64 s. Comparing twilight dives with daylight dives, twilight dives were shallower (9.6 ± 9.8 vs 34.8 ± 24.7 m, t -test: $t_{516} = 10.96$, $p < 0.001$), were shorter in dive duration (57 ± 21 vs 86 ± 30 s, t -test: $t_{516} = -9.75$, $p < 0.001$), and presented fewer foraging dives (>5 m depth) (76 vs 90%). The proportion of foraging dives (>5 m depth) per trip did not differ between day and overnight trips (Table 1) (t -test: $t_9 = -0.25$, $p = 0.8$).

Dive duration was positively related to dive depth (non-linear regression: duration = $[130.1 \times \text{depth}] / [\text{depth} + 11.5]$, $R^2 = 0.72$, Fig. 5a). Outliers represented

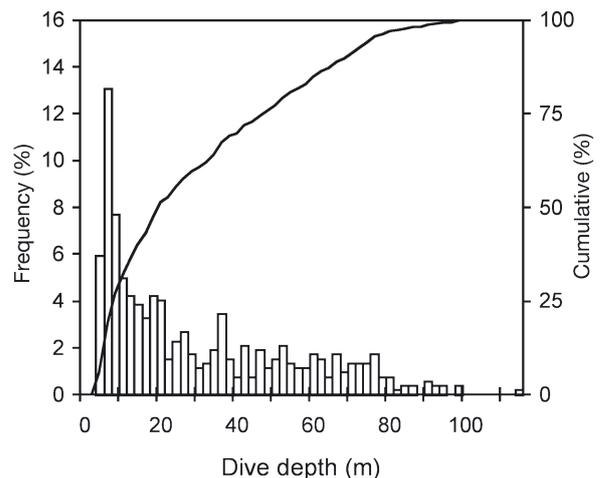


Fig. 2. *Eudyptes chrysocome chrysocome*. Frequency distribution of dive depth

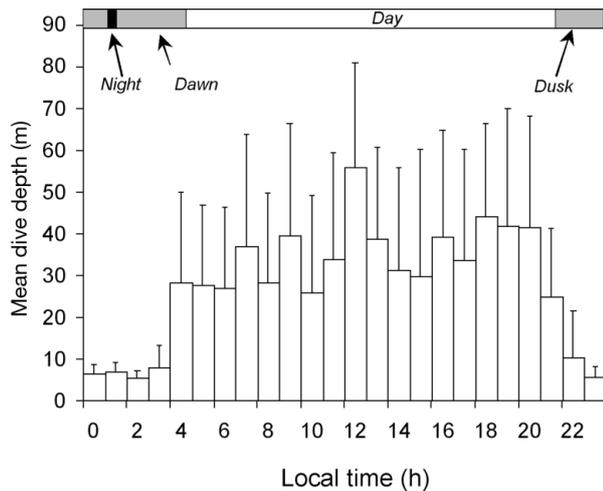


Fig. 3. *Eudyptes chrysocome chrysocome*. Dive depth (mean + SD) in relation to time of day for 520 randomly selected dives

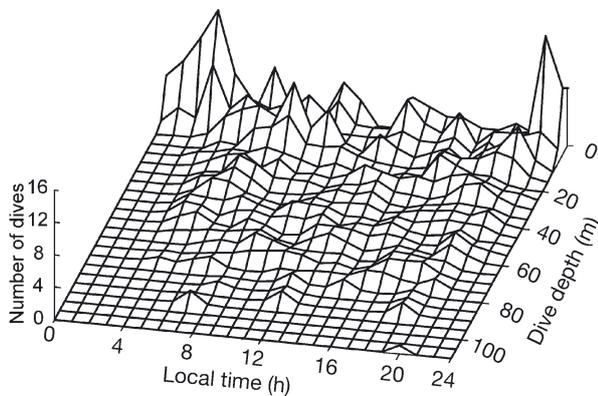


Fig. 4. *Eudyptes chrysocome chrysocome*. Distribution of number of dives in relation to time of day and dive depth for 520 randomly selected dives

by long dives (90 to 140 s) at shallow depths (3 to 10 m) were discarded for the analysis because of the software misinterpretation of several shallow dives (which were considered as 1 dive).

The penguins spent an average of $66.2 \pm 5.9\%$ of the trip duration underwater, with no significant difference between day and night trips (Table 1) (t -test: $t_{11} = -1.86$, $p = 0.09$). Bottom time peaked at 34 s and averaged 35 ± 17 s dive^{-1} , with 50% of the bottom times ≤ 33 s. The penguins spent 37% of their diving time between depths of 0 and 20 m. Diving efficiency averaged 0.34 ± 0.14 , and its maximum was attained at dive depths between 5 and 15 m (Fig. 5b). The distribution of post-dive intervals was unimodal, with a peak at 14 to 24 s, and with 50% of the post-dive intervals ≤ 19 s. Excluding intervals >180 s, post-dive intervals aver-

aged 20 ± 11 s ($n = 509$). Rockhopper penguins traveled an average VTD of 43.88 ± 22.78 km per foraging trip (excluding the incomplete trip). VTD differed between day and overnight trips (Table 1) (t -test: $t_{11} = -3.73$, $p = 0.003$). The mean descent and ascent rates were 1.2 ± 0.5 m s^{-1} and 0.8 ± 0.5 m s^{-1} respectively. Both rates increased with increasing dive depth (descent rate = $0.85 + 0.01 \times \text{depth}$, $F_{1,19} = 57.35$; ascent rate = $0.78 + 0.01 \times \text{depth}$, $F_{1,19} = 85.26$; $p < 0.001$ for both). Descent rates tend to be larger than ascent rates (t -test: $t_{487} = 47.9$, $p < 0.001$).

Temporal changes in foraging and diving behavior

Taking into account the time elapsed from the start of hatching (November 27) to the middle of each trip, trip length increased significantly (trip length = $3.11 \times \text{days} - 17.41$, $r^2 = 0.62$, $F_{1,12} = 20.18$, $p < 0.001$, Fig. 6a), but the duration of both the outward and the inward trip did not vary (p of linear regression: $p = 0.72$ and $p = 0.10$

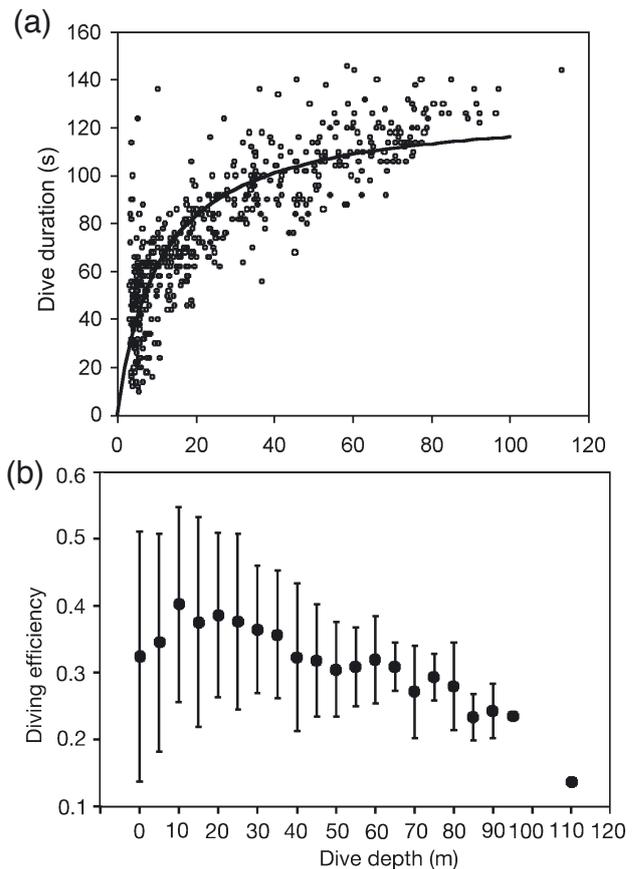


Fig. 5. *Eudyptes chrysocome chrysocome*. Relationship between (a) dive duration and dive depth, and (b) diving efficiency (bottom time/[dive duration + post-dive interval]) and dive depth (mean \pm SD) for 520 randomly selected dives

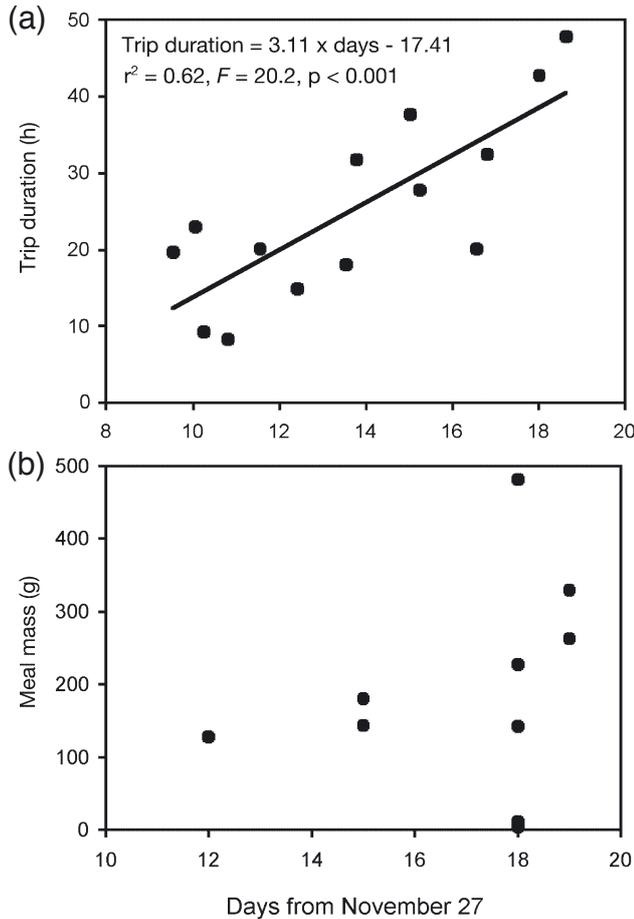


Fig. 6. *Eudyptes chrysocome chrysocome*. (a) Foraging trip duration in relation to days elapsed from start of hatching to the middle of the foraging trip; (b) mass of stomach content in relation to days elapsed from start of hatching

respectively). The basic dive parameters did not vary significantly for each trip over the study period (p of linear regression: $p > 0.1$ for all except for ascent rate, which was $0.05 > p > 0.04$). The mass of food brought ashore did not increase with time elapsed from the start of hatching (Fig. 6b) (p of linear regression: $p = 0.34$).

Diet composition

The 11 stomach contents weighed 203.6 ± 142.3 g. On average, female rockhopper penguins brought ashore 5 to 10% of their body weight as food. No relationship was found between the mass of stomach contents and trip duration (linear regression ANOVA: $F_{1,2} = 0.19$, $p = 0.703$). A total of 34 139 prey items were found in the contents, comprising a mixture of crustaceans, cephalopods and fishes. Crustaceans dominated the diet in terms of numbers (80%) followed by

cephalopods and fishes (15 and 3.6% respectively). However, cephalopods (mostly juveniles) contributed more to the diet in terms of mass (86%) than crustaceans (14%). *Gonatus antarcticus* dominated the diet in terms of mass (46%), followed by *Loligo gahi* (24%) and *Enteroctopus megalocyathus* (15%). Among the crustaceans, *Euphausia vallentini* was the dominant prey item in terms of numbers (34%), the amphipod *Themisto gaudichaudii* in terms of mass (7% mass, 18.4% numbers), and *Thysanoessa gregaria* contributed less than 1% to the diet. Due to the lack of functional relationships for the fish larvae and juveniles in the diet, we could not reconstitute the mass consumed. *Harpagifer bispinis* was by far the most numerous fish consumed (2.2%). There was a smaller proportion of *Salilota australis* (1.3%), only a few specimens of *Agonopsis chiloensis*, and an unidentified myctophid.

DISCUSSION

Foraging trips among subspecies and environments

Our data reveals that *chrysocome* performed more overnight trips than the other subspecies (Table 1), and performed extended foraging trips with a wide dispersion of departure and arrival times, as well as short periods on land. The average trip duration for day and night trips is comparable among subspecies (Table 1), but much shorter than the 7.0 ± 0.0 d ($n = 6$) or the 6.4 ± 4.5 d ($n = 7$) reported by Hull (1999a and 2000 respectively) for female *filholi* during the guarding period at Macquarie Island. This trip duration is remarkable, as only the female feeds the chick during the guarding period. However, Hull (1999a) described that rockhopper penguins from Macquarie forage in the Polar Frontal Zone, which contains abundant or predictable food sources such as myctophid fishes, a common prey item of rockhopper penguins from Macquarie Island. Another explanation could be that some *filholi* females actually stayed on land during night and that this was undetected by the depth readings of the TDRs (in our study, the light-channel readings of our TDRs helped us to distinguish between periods on land and at sea). Finally, another explanation could be a strong device effect on the birds equipped at Macquarie Island that induced very long foraging trips.

It is known that penguins are visual predators that depend on ambient light to locate prey (Wilson et al. 1989, 1993), that they dive shallower at night than during the day, and that even when successful in catching prey, their foraging success at night is reduced (Wilson et al. 1993, Jansen et al. 1998). The performance of overnight foraging trips and dives has been recorded

in several penguin species. Even in locations at a comparable latitude to Staten Island, penguins exhibit a variety of different foraging behavior. Rockhopper penguins breeding at Macquarie Island also dive at night, although the pooling of data precludes a detailed analysis (Hull 2000). At South Georgia, the king penguin *Aptenodytes patagonica* dives at night, but at much shallower depths than during the day (Kooyman et al. 1992). Female Macaroni penguins *Eudyptes chrysolophus* rearing chicks forage overnight, but at depths less than 20 m (Croxall et al. 1988). Gentoo penguins *Pygoscelis papua*, in which both parents feed the chick at brooding, forage only during the daytime (Croxall et al. 1988). At Signy Island, 26% of the total foraging trips of chinstrap penguins *Pygoscelis antarctica* were overnight trips, with nighttime dives as frequent as daytime dives but reaching shallower depths (nighttime defined as time between sunset and sunrise: see Fig. 7b of Takahashi et al. 2003). Royal penguins *Eudyptes schlegeli* from Macquarie Island dive both day and night, but at shallower depths at night (Hull 2000). In southern Chile, breeding Magellanic penguins *Spheniscus magellanicus* diving at night rarely dived deeper than 10 m (Radl & Culik 1999). In Antarctica, Adelie penguins *Pygoscelis adeliae* from Torgersen Island showed a lack of a strong circadian pattern in dive depth (Chappell et al. 1993). Chinstrap penguins at Seal Island performed overnight trips to enable chicks to grow at an adequate rate (Jansen et al. 1998).

Successful hunting during darkness hours is related to the ambient light available as well as to the available prey in the water column. Few papers define the term 'nighttime' (for examples see Cherel et al. 1999 and Takahashi et al. 2003), assuming that night represents the time between sunset and sunrise, and disregarding the twilight period, important in high latitudes. Several explanations (nonmutually exclusive) may be proposed for the high proportion of overnight trips and dive frequency in the hours of darkness by female *chrysocome* compared with the other subspecies. These explanations may be related to the different body sizes of the different subspecies, to the daylight regime of a specific locality in the particular study period, to the size of the breeding population and/or to the environmental conditions that influence food availability in the area.

It is known that the foraging capacities of marine mammals and seabirds are related to body size (Kooyman & Kooyman 1995, Schreer & Kovacs 1997). Among rockhopper penguins, *chrysocome* is the smallest in size (Cooper et al. 1990). However, measurements of bill length (38.3 ± 2.0 mm) and body weight (2.3 ± 0.2 kg) obtained during the 2000 season in 45 females from Staten Island are in the range of those reported

for *moseleyi* and *filholi* (Tremblay & Cherel 2003) and do not allow any conclusion about a relationship between body size and foraging trip duration.

The lengths of the day and of the twilight period are a function of latitude and of time of the year. If foraging trip duration is just a function of day length, a relationship between location of breeding grounds and foraging trip duration would be expected. This was not the case for rockhopper penguins. Birds from Kerguelen Island (at about Latitude 49° S) do not perform overnight trips whereas those from Amsterdam, Crozet, Marion, Macquarie and Staten Islands (at about Latitudes 38° S, 46° S, 49° S and 55° S respectively) do so (Brown 1987, Hull 1999a, 2000, Tremblay & Cherel 2003, this paper). Moreover, trip duration represented 93, 76 and 73% of the time between sunrise and sunset at Amsterdam, Kerguelen and Crozet respectively (Tremblay & Cherel 2003). Therefore, there was still some time available for increasing foraging trip duration at Kerguelen and the Crozet Islands.

The proportion of the sampled dives performed under twilight conditions in Staten Island (23.3%) and the proportion of foraging dives among the twilight dives (76%) imply that *chrysocome* may experience ambient light conditions during the extended twilight period that are sufficient to continue foraging instead of returning to the colony. This supposition is reinforced by their high dive rate and by the large proportion of time spent underwater for overnight trips compared to *moseleyi* and *filholi* (Table 1). This finding emphasizes the need to analyze diving under twilight conditions at high-latitude locations since, for *chrysocome*, it seems that during the brooding period they have almost permanent light conditions in which to forage.

Another potential explanation for the long trip duration is that foraging trip characteristics are related to colony size. As mentioned in the 'Introduction', the distance to the foraging grounds or trip duration should be proportional to the breeding population size. This would be reflected either in the proportion of overnight trips, in the foraging trip duration or traveling time and/or in the proportion of traveling versus foraging behavior. The available evidence suggests that none of these features may be related to colony size. The proportion of overnight trips recorded at Amsterdam, Crozet, Kerguelen and Staten Islands, 11, 10, 0 and 53% respectively (Tremblay & Cherel 2003, this paper) do not correlate with colony sizes of 24 890, 60 000, 85 500, and 174 000 breeding pairs respectively (Pearson correlation coefficient = 0.86, $p = 0.35$) (data from Woehler 1993, Guinard et al. 1998, Schiavini 2000). The population size at Macquarie Island is reported to be between 100 000 and 500 000 pairs and for that reason was not considered in this analysis. On the other hand, the large variation in traveling times

and trip duration among rockhopper subspecies precludes a conclusion about any relationship with colony size (Table 1). Finally, the mean proportion of foraging dives in *chrysocome* (>5 m depth, $89.9 \pm 3.8\%$) was comparable with that reported for Amsterdam, Crozet and Kerguelen Islands (79.6 ± 11.7 , 86.1 ± 12.7 , $85.0 \pm 13.3\%$ respectively, Tremblay & Cherel 2003).

A complementary explanation relates to the environment. Tremblay & Cherel (2003) compared characteristics of foraging trips of rockhopper penguins from Amsterdam, Crozet and Kerguelen and proposed that penguins foraging in more open waters (at Amsterdam and Crozet), perform some overnight trips, whereas those foraging in coastal waters at Kerguelen do not (birds breeding at Kerguelen forage in shallow and sheltered waters in the Gulf of Morbihan: Tremblay & Cherel 2003). In turn, *filholi* females from Macquarie Island foraged on oceanic waters of the Polar Frontal Zone for periods of 7.0 ± 0.0 d when guarding chicks (Hull 1999a) and also performed overnight trips. Birds from Staten Island foraged as far away as 20 km from the colony, in shelf waters of 100 to 200 m depth, but also in more pelagic waters of a shelf-break and slope located 12 km south of Staten Island. The foraging trip duration of *chrysocome*, which is able to feed either in shelf or in pelagic waters, may represent further evidence of phenotypic plasticity in response to different marine environments, as reported for the other subspecies by Tremblay & Cherel (2003).

The dietary data also suggest that *chrysocome* may forage either in shelf waters or in more pelagic waters off the shelf. The food mass brought ashore by the penguins at Staten Island (203.6 ± 142.3 g) is larger than that sampled from birds foraging in more open waters at Amsterdam and Crozet Islands (107.5 ± 47.5 and 150.6 ± 50.5 g respectively), but more similar to that at Kerguelen Island (214.8 ± 62.3 g, Tremblay & Cherel 2003). This suggests that foraging on shelf habitats (at Kerguelen and Staten Island) could be more productive than foraging in open waters (at Amsterdam or Crozet Islands). The large standard deviation of the mass obtained at Staten Island may be also a consequence of foraging either in shelf waters or in more open waters off the shelf. Southern rockhopper penguins at Staten Island feed opportunistically on shoaling or swarming zooplanktonic prey, as reported elsewhere (Croxall et al. 1985, Horne 1985, Brown & Klages 1987, Hindell 1988, Klages et al. 1988, 1989, Cooper et al. 1990, Hull 1999b, Pütz et al. 2001, Clausen & Pütz 2002). Gregarious crustaceans, juvenile squid and octopus, fish larvae and juveniles dominated the diet. The crustaceans in the diet are associated with subantarctic waters, although *Themisto gaudichaudii* is present also in antarctic waters (Vinogradov 1999). These crustaceans form interspecific

swarms or swarms within close vicinity to each other (Dadon & Boltovskoy 1982, Tarling et al. 1995). All are found in depths down to 100 m and are known to migrate vertically to the surface at night (Gibbons et al. 1999). The most common cephalopods consumed are known to be mid- to deep-water species present in the Subantarctic Zone (Rodhouse et al. 1992, 1996). Small specimens of *Gonatus antarcticus* were found in great numbers in the Polar Frontal Zone (Rodhouse et al. 1992), and the same study found that early life cycles of cephalopods (paralarvae and juveniles) are associated with major oceanographic features of the SW Atlantic Ocean. *Salilota australis* and *Sprattus fuegensis* inhabit the Patagonian shelf and are associated with the Falkland (Malvinas) Current. Moreover, Ehrlich et al. (1999) found densities of 102 to 1000 and 11 to 100 larvae 10 m^{-2} of *S. fuegensis* and *Agonopsis chiloensis* respectively around Staten Island.

The wide shelf waters of the southern Patagonian shelf sustain an important biomass of zooplankton and ichthyoplankton (Sánchez & Ciechomski 1995, Sabatini et al. 1999, 2001). The combined effect of diurnal vertical migration and advection of zooplankton due to the transition of bottom topography from the shelf slope to the shelf areas may contribute to the food availability for top predators. Perissinotto & McQuaid (1992) described such phenomena for the Prince Edwards archipelago, where large levels of zooplankton, migrating to the surface at night, become available to visual top predators such as seabirds. A similar phenomena may occur at Staten Island, with the shelf and slope located very close to penguin breeding grounds, and upstream of the branch of the Antarctic Circumpolar Current that enters the Patagonian shelf after leaving the Drake Passage to form the Falklands (Malvinas) Current. The macrozooplankton that rises in the water column during the long periods of dusk and dawn would be available for visual predators such as penguins. The zooplankton availability combined with the extended twilight periods in summer, may differentiate the marine environment close to Staten Island from that of Amsterdam, Crozet, Kerguelen and the Macquarie Islands.

Diving patterns

Most dive parameters for *chrysocome* (such as average maximum dive depth, dive duration, bottom time, descent and ascent rate) were comparable to those for the other subspecies (Table 1). The deepest dive among the 15 trips was 113 m and averaged 81.5 ± 18.5 m, being comparable among subspecies: 66 m for *filholi* at Crozet (Wilson et al. 1997b), 66 ± 28 m and 109 m for *moseleyi* at Amsterdam (Tremblay et al.

1997, Cherel et al. 1999, and this study Table 1). On the other hand, *chrysocome* presented a more even depth utilization than the other subspecies (Cherel et al. 1999, Hull 2000, Tremblay & Cherel 2003). The deepest dives by *chrysocome* were performed at noon, as reported for *moseleyi* (Cherel et al. 1999, Tremblay & Cherel 2003). Our data on dive depth and dive duration confirms that, for rockhopper penguins, as for the other subspecies (Wilson et al. 1997b, Cherel et al. 1999, Tremblay & Cherel 2003) most dives do not exceed the aerobic dive limit (sensu Chappel et al. 1993).

Eudyptes chrysocome spent almost $\frac{2}{3}$ of its foraging trips underwater, a proportion comparable to that of the other subspecies (Table 1) but larger than that reported for most other penguin species (Table 1 of Cherel et al. 1999 and references cited therein) and even for other top predators (Schreer et al. 2001). As Cherel et al. (1999) pointed out, the long time spent underwater is due mainly to the high dive rate of rockhopper penguins. Also, as one of the smallest penguin species, the size of its prey is limited by the size of its mouth, which is reflected in its diet. Therefore, rockhopper penguins need to develop a high dive rate in order to compensate for the capture of small prey. The distribution of diving efficiency with depth (Fig. 5a) reveals that *chrysocome* attains lower efficiencies for a given depth than do *moseleyi* and *filholi* (cf. present Fig. 5 with Fig. 7 of Tremblay & Cherel 2003), although this may be a characteristic of use of the water column rather than a physiological difference. The large average VTD per foraging trip for *chrysocome* in relation to *moseleyi* and *filholi* (Table 1) is readily explained by the former's homogeneous use of the water column and by the extended trip duration.

Rockhopper penguins foraging and breeding at Staten Island

Analysis of all the data on foraging trips and dive characteristics reveals that *chrysocome* differs from the other subspecies only in the extent of its foraging trips, with the other basic dive parameters being comparable. Our results confirm that rockhopper penguins from locations with different daylight and twilight periods share a high level of foraging effort, due to their high dive rate and percentage of time spent underwater, as pointed out by Cherel et al. (1999). This high effort is also consistent with the amount of food brought ashore at different localities. We conclude that an increase in the daylight period implies an increase in trip duration, but not in a reduction of foraging effort. Therefore, light would seem to be the main limiting factor of foraging behavior in rockhopper penguins. An exception could be the population at

Macquarie Island, with a daylight period similar to that at Staten Island, where Hull (2000) found dive rates of 14.8 ± 9.4 dives h^{-1} . The difference could be due to either differences in food availability and/or to an overestimation of trip duration caused by periods on land undetected from TDR readings.

During the study period, foraging trip duration increased in *chrysocome*, but the amount of food brought back to the colony did not (Fig. 6). However, chick age was not recorded when obtaining stomach contents and the variation in Fig. 6 could be due to some unknown dietary variation related to chick age. Based on trip duration and the outward and inward traveling times, *chrysocome* foraged for longer periods than the other subspecies with the exception of *filholi* from Macquarie Island. This supports the proposal of Cherel et al. (1999), who suggested that in view of the overall foraging and diving behavior of *moseleyi*, the only characteristic of foraging behavior most likely to vary in relation to energy demand and/or prey availability would be the duration of foraging trips.

Rockhopper penguins constitute the main diving seabird breeding at Staten Island, together with the Magellanic penguin *Spheniscus magellanicus* with ca. 100 000 nesting pairs (Schiavini et al. 1999). The nearest rockhopper penguin colonies are at the southern tip of the Tierra del Fuego archipelago or in the Falkland (Malvinas) Islands, far away from the foraging range of Staten Island birds during the brooding period. The diet of the Magellanic penguin in the southern SW Atlantic Ocean differs from the rockhopper penguin diet, because it includes fuegian sardine *Sprattus fuegensis*, southern blue whiting *Micromesistius australis*, silverside *Austroatherina* sp., Patagonian squid *Loligo gahi* and lobster krill *Munida* sp., with proportions varying according to location (Thompson 1993, Frere et al. 1996). Therefore, rockhopper penguins from Staten Island do not seem to compete for food with other penguins.

However, the large population of 167 000 breeding pairs at Bahía Franklin and the restricted foraging ranges of brooding females imply that foraging effort is confined to a relatively small area and time. This is emphasized by the fact that outward and inward traveling times (and thus foraging range) do not increase as the brooding period progresses. The question arises as to whether such a breeding population may compete for feeding space. It can be hypothesized that a combination of an extended twilight period and the plentiful food supply in shelf waters, which in turn is enhanced by the availability of zooplankton resulting from diurnal vertical migrations, may offer rockhopper penguins an extended time to exploit abundant food resources compared to other subspecies. This extra resource time may contribute indirectly to reduce

potential intraspecific competition. In order to test this hypothesis, our study would need to be repeated for other colonies of different sizes, located in similar areas of southern South America but in different environments, e.g. on more oceanic islands such as Islas Diego Ramírez or Isla Noir in the Pacific Ocean.

The large time-window for exploiting food resources available to rockhopper penguins may contribute to sustaining the high level of the breeding population in this area, and may also contribute to understanding differences in the recent history of the breeding colonies in the Falklands Islands and from Staten Island, whereby the former have undergone strong declines and recoveries during the last century (Bingham 1998, Pütz et al. 2001), while the latter appear to have been stable or increasing (Schiavini 2000).

Acknowledgements. This research was possible with the support of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), the Third World Academy of Sciences (Grant No. 99-193 RG/BIO/LAA to A.S.), the International Foundation for Science (grant A/2962-1 to A.S.), and of R. Portal (Total Austral SA). Special thanks to the Argentine Navy and to P. Grinberg for their transportation to Staten Island under difficult weather conditions, to P. Pérez Barros and M. Liljeström for their help in the field and with the English writing, to J. Lage, for arranging Multitrace to fit our needs, to R. Wilson for his advice on TDRs and software, and to K. Pütz, Y. Chereh, T. Martin and P. Trathan for their kind feedback.

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