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Diving behaviour of female northern rockhopper penguins, *Eudyptes chrysocome moseleyi*, during the brooding period at Amsterdam Island (Southern Indian Ocean)

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Abstract The pattern and characteristics of diving in 14 female northern rockhopper penguins, *Eudyptes chrysocome moseleyi*, were studied at Amsterdam Island (37°50'S; 77°31'E) during the guard stage, using electronic time–depth recorders. Twenty-nine foraging trips (27 daily foraging trips and two longer trips including one night) with a total of 16 572 dives of ≥ 3 m were recorded. Females typically left the colony at dawn and returned in the late afternoon, spending an average of 12 h at sea, during which they performed ~ 550 dives. They were essentially inshore foragers (mean estimated foraging range 6 km), and mainly preyed upon the pelagic euphausiid *Thysanoessa gregaria*, fishes and squid being only minor components of the diet. Mean dive depth, dive duration, and post-dive intervals were 18.4 m (max. depth 109 m), 57 s (max. dive duration 168 s), and 21 s (37% of dive duration), respectively. Descent and ascent rates averaged 1.2 and 1.0 ms^{-1} and were, together with dive duration, significantly correlated with dive depth. Birds spent 18% of their total diving time in dives reaching 15 to 20 m, and the mean maximum diving efficiency (bottom time:dive cycle duration) occurred for dives reaching 15 to 35 m. The most remarkable feature of diving behaviour in northern rockhopper penguins was the high percentage of time spent diving during daily foraging trips (on average, 69% of their time at sea); this was mainly due to a high dive frequency (~ 44 dives per hour), which explained the high total vertical distance travelled during one trip (18 km on average). Diving activity at night was greatly reduced, suggesting that, as other penguins, *E. chryso-*

come moseleyi are essentially diurnal, and locate prey using visual cues.

Introduction

Knowledge of the foraging ecology and diving performance of penguins has been revolutionized over the last decade by the use of miniaturized electronic time–depth recorders (Wilson 1995). Because of their size-linked ability to carry attached loggers, their use has mainly been restricted to the largest (genus *Aptenodytes*) and medium-sized (genera *Pygoscelis* and *Spheniscus*) species, one exception being a recent work on the little penguin *Eudyptula minor* (Bethge et al. 1997). Crested penguins (genus *Eudyptes*) are the most abundant penguins, both in number of individuals and number of species. Of the six *Eudyptes* species, only the diving behaviour of the macaroni *E. chrysolophus* and rockhopper *E. chrysocome* has been investigated in two studies using time–depth recorders (Croxall et al. 1993; Wilson et al. 1997). However, both studies were restricted to a fairly small number of birds (1 or 2) and one was conducted on a penguin that displayed abnormal behaviour: instead of regularly feeding its chick, the bird deserted it, and remained at sea for 21 consecutive days (Wilson et al. 1997).

The rockhopper penguin, *Eudyptes chrysocome*, is the smallest eudyptid, and one of the smallest penguins overall, being larger only than the little penguin and of about the same size as the Galápagos penguin *Spheniscus mendiculus*. Three subspecies are currently recognised; the southern rockhopper penguin that includes two subspecies (*filholi* and nominate *chrysocome*) and lives in the subantarctic zone, and the northern rockhopper penguin (*moseleyi*) inhabiting subtropical waters (Williams 1995). While the diet of rockhopper penguins had been investigated in several localities (see review in Cooper et al. 1990), little is known of the foraging ecology of the species. Two recent works using either capillary-tube depth gauges or time–depth recorders

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indicated, respectively, that northern rockhopper penguins forage in the top 150 m of the water column (Tremblay et al. 1997), and that most of the time spent diving by one southern rockhopper penguin was between 10 and 25 m (Wilson et al. 1997).

The aim of this study was thus to detail for the first time the diving behaviour of a species of crested penguin, the northern rockhopper penguin from Amsterdam Island (37°50'S; 77°31'E). We present information on diving patterns and performance (dive depth and duration, dive frequency, together with descent and ascent rates, and foraging effort) of birds fitted with electronic time–depth recorders. Since *Eudyptes chrysocome moseleyi* is a small penguin, and diving performance is mass-dependent (Schreer and Kovacs 1997; Wilson 1995), a comparison was made with diving characteristics of larger species. This description of the diving behaviour of rockhopper penguins represents the first part of an investigation on the plasticity in food and feeding ecology of the northern and southern subspecies in relation to various marine environments in the Southern Indian Ocean.

Materials and methods

Study site and birds

Field work was conducted at Pointe d'Entrecasteaux, Amsterdam Island (37°50'S; 77°31'E), from the 17 to 31 October 1995, at the end of the guard stage of *Eudyptes chrysocome moseleyi*. At this time, female rockhopper penguins perform daily foraging trips to feed their offspring, while males fast ashore, guarding the chicks. This behaviour is common to all crested penguins (Warham 1975), including the northern rockhopper penguin (Guinard and Tremblay unpublished data), although previous reports from Amsterdam Island (Duroselle and Tollu 1977) did not describe this behaviour. Females were selected opportunistically and captured in the late afternoon after chick-feeding. They were measured, weighed (accuracy ± 100 g), fitted with time–depth recorders (TDRs), and released at their nest 15 to 20 min following capture. This allowed the penguins to recover from the stress of capture and manipulation overnight before returning to sea to feed. The diving behaviour of 14 females was investigated over 1 to 3 consecutive days during the guard stage. On their return ashore, the birds were recaptured on the beach to avoid disturbance in the colony. The TDRs were removed; the birds were weighed, and the complete stomach contents of seven individuals were obtained by water off-loading (Gales 1987). In the laboratory, the samples were weighed and sorted into principal prey components which were weighed separately. The species composition of the food was determined from hard remains (fish otoliths and bones, squid beaks and crustacean exoskeletons) (Tremblay et al. 1997).

Time–depth recorders

Diving behaviour was studied using electronic TDRs (Mark V, Wildlife Computers, Woodinville, Washington, USA). The instruments were 9.5 cm long \times 3.7 cm wide \times 1.5 cm high, and weighed ~ 70 g in air, corresponding to $< 3\%$ of the bird's body mass. Because nonstreamlined devices have deleterious effects on crested penguins (Hull 1997), TDRs were shaped following indications given in Bannasch et al. (1994). The TDRs were attached to the most caudal position on the back of the birds using quick-set epoxy adhesive and plastic ties (Kooyman et al. 1992). The TDRs had a

data-storage capacity of 128 kilobytes. They were programmed to sample every 2 s at depths ≥ 2 m. This recording interval is $< 10\%$ of the mean dive duration, and thus cannot lead to errors in dive number and dive parameters (Wilson et al. 1995). Depth resolution was ± 1 m and the time base (quartz-controlled) was the same for all the recorders. At Amsterdam Island, local time is Universal Time + 5 h.

Diving-activity analysis and statistics

Dive-depth data were analysed using the software (Dive Analysis) provided by Wildlife Computers to determine dive depth, dive duration, bottom time (the time between the first and last readings $\geq 75\%$ of the dive's maximum depth), as well as ascent and descent rates. A dive was deemed to occur when the maximum depth was ≥ 3 m (Chappell et al. 1993).

Because of the unequal number of foraging trips recorded per penguin and the different number of dives per trip, the total number of dives recorded per individual bird varied from 274 to 2133. To give each penguin an equal statistical weight, we selected 250 dives randomly per bird, and the resulting data set ($n = 3500$) was used to analyse the characteristics of the dives.

Because luminosity is already high at sunrise and still elevated at sunset, daytime was calculated (following the nautical definition of dawn and dusk, i.e. when the sun is 12° below the horizon) as the time elapsed from dawn (45 min before sunrise) to dusk (45 min after sunset). Correlatively, nighttime was the time elapsed between dusk and dawn.

Data were statistically analysed using SYSTAT 7.0 for Windows. Means (\pm SD) are given.

Results

Timing and duration of foraging trips

Data was obtained from 14 female *Eudyptes chrysocome moseleyi* during 29 foraging trips which included a total of 16 572 dives during 385.5 h at sea. All foraging trips but two were completed on the same day. The duration of the 27 daily foraging trips averaged 12.15 ± 2.10 h (range 8.57 to 17.45 h), which represented 82% of the daytime (mean value from dawn to dusk for the study period = 14.89 h). The mean departure and return times were $04:40 \pm 00:46$ hrs (range 03:54 to 06:58 hrs) and $16:50 \pm 01:57$ hrs (range 12:46 to 21:42 hrs), respectively (Fig. 1). On average, departure was between dawn (04:08 hrs) and sunrise (04:53 hrs), and arrival back at the colony was ~ 2 h before dusk (19:01 hrs, sunset being at 18:16 hrs) (Fig. 2: Bird A).

Two foraging trips were longer, including one night spent at sea between two diurnal foraging periods (Fig. 2: Bird B). The two trips lasted for 21.72 and 35.57 h, with departure and return times at 13:14 and 04:22 hrs and at 10:57 and 15:56 hrs, respectively.

The mean body mass of the birds did not differ significantly at the beginning and the end of the experiment (2.25 ± 0.23 and 2.32 ± 0.19 kg, respectively; Student's paired t -test: $t = 1.258$, $P = 0.23$). This, together with the duration of foraging trips (13.29 ± 5.06 h, $n = 29$) which is similar to that previously reported for rockhopper penguins not carrying recording devices at the Falkland Islands (14.7 ± 4.0 h, $n = 43$: Thompson

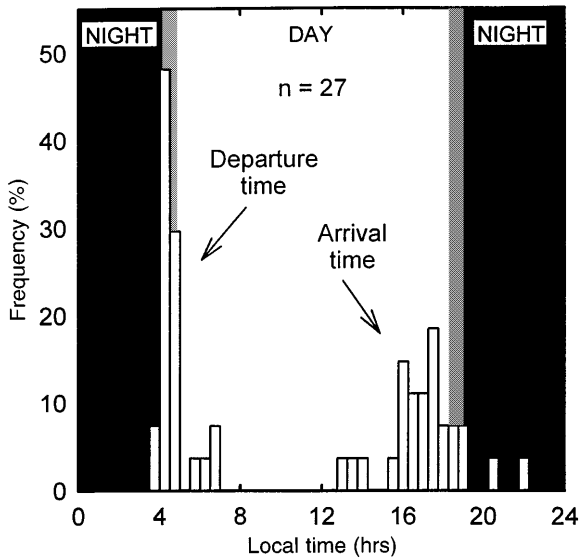


Fig. 1 *Eudyptes chrysocome moseleyi*. Frequency distribution of departure and arrival times of daily foraging trips during guard stage (Grey hatching dawn and dusk)

1989), suggests that the TDRs had a minimal effect on the foraging behaviour of penguins in the present study.

Travel time and foraging range

Foraging ranges, i.e. horizontal distances moved away from the colony, were estimated from the duration between the first recorded dive and the first group of at least three consecutive dives ≥ 10 m, assuming that penguins travelled continuously at a constant travelling

speed of 7.4 km h^{-1} (Brown 1987) and in a straight line. Similarly, the time between the last three consecutive dives ≥ 10 m and the last dive was calculated for the return journey.

The mean travel time to the foraging area was $0.76 \pm 0.35 \text{ h}$ (range 0.33 to 1.69 h, $n = 27$). The return travel time to the colony averaged $0.78 \pm 0.67 \text{ h}$ (range 0.11 to 3.01 h) and was not significantly different from the duration of the outward journey (Student's paired t -test: $t = 0.128$, $P = 0.90$). Consequently, the estimated foraging ranges on the outward and return journeys of daily foraging trips were identical and averaged $5.6 \pm 2.6 \text{ km}$ (range 2.5 to 12.5 km, $n = 27$) and $5.8 \pm 5.0 \text{ km}$ (range 0.8 to 22.3 km), respectively.

Number and frequency of dives

The number of dives per daily foraging trip was 545 ± 169 (range 274 to 943, $n = 27$). The average dive frequency during the daytime was $44.4 \pm 10.4 \text{ dives h}^{-1}$ (range 31.6 to 77.8). During the two longest trips (those that included one night), birds performed 578 and 1292 dives and had an overall dive frequency equal to 26.6 and $36.3 \text{ dives h}^{-1}$, respectively. However, only 58 and 40 dives occurred during the nighttime, and consequently dive frequency was higher during the daytime (42.0 and $47.2 \text{ dives h}^{-1}$) than at night (6.2 and 4.4 dives h^{-1}).

Of the 3500 dives, 99% were performed during the daytime (Fig. 3). The mean dive depth was greater during daytime dives than during nighttime dives ($18.5 \pm 14.7 \text{ m}$, $n = 3460$ vs $8.8 \pm 4.5 \text{ m}$, $n = 40$; Student's t -test: $t = 12.94$, $P < 0.001$) (Figs. 2 and 4). On average, rockhopper penguins dived to depths $>20 \text{ m}$ between 07:00 and 14:00 hrs, when the sun was at between 48 and 84% of its highest elevation (Fig. 4). The deepest dives occurred exclusively during the daytime, while in agreement with the outward and return journeys of the daily foraging trips, many shallow dives (probably travelling dives) occurred early in the morning and in the afternoon (Fig. 3).

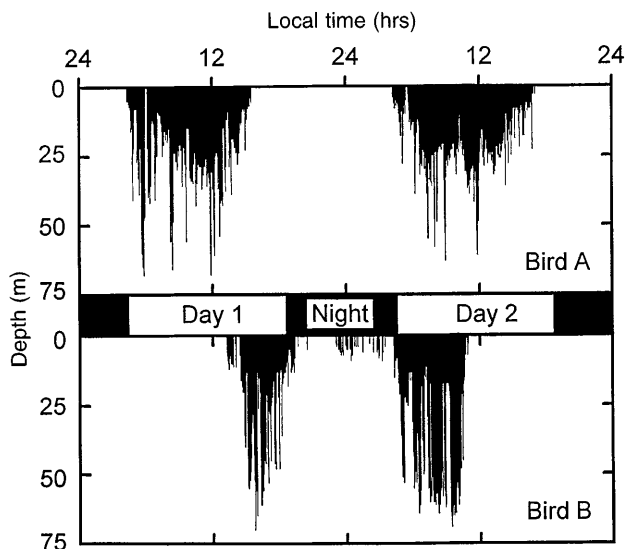


Fig. 2 *Eudyptes chrysocome moseleyi*. Diving records for individual penguin during two consecutive daily foraging trips (Bird A, upper panel), and for individual bird spending one night at sea (Bird B, lower panel)

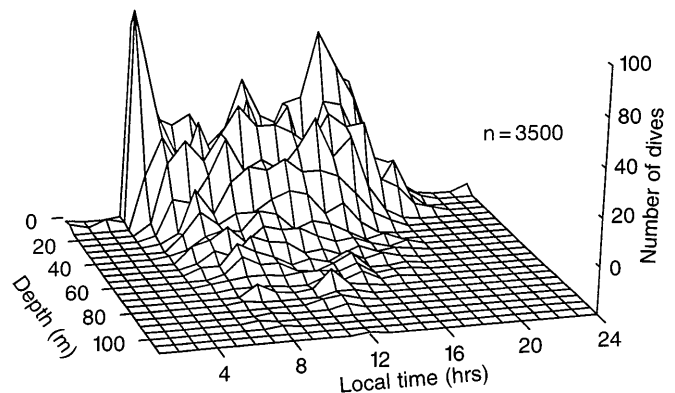


Fig. 3 *Eudyptes chrysocome moseleyi*. Distribution of number of dives in relation to time of day and dive depth

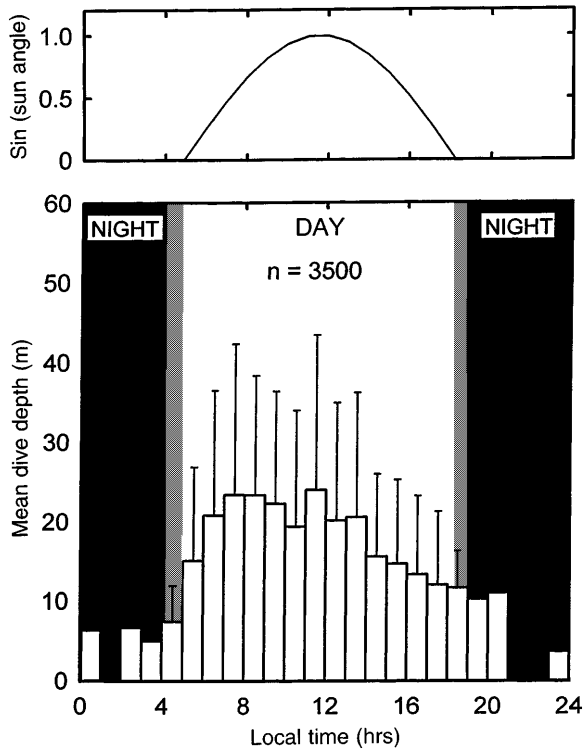


Fig. 4 *Eudyptes chrysocome moseleyi*. Variation in mean (+SD) dive depth in relation to time of day (Grey hatching dawn and dusk)

Dive depth, duration and surface intervals

Among the 16 572 recorded dives, the deepest dive reached 109 m and the longest dive lasted 168 s. The mean maximum depth of the 3500 dives analysed in detail was 18.4 ± 14.7 m, 50% of the dives being ≤ 15 m, 90% ≤ 38 m and 99% ≤ 71 m (Fig. 5). Mean dive duration was 57 ± 34 s, 50% of the dives being ≤ 57 s, 90% ≤ 105 s, and 99% ≤ 130 s. The distribution of both dive depth and duration was bimodal, with one peak at the shallowest depths (3 to 4 m) and shortest duration (3 to 8 s) and the second peak at 16 m and 68 s. Dive duration was positively related to dive depth (non-linear regression; equation: $\text{duration} = (187.87 \times \text{depth}) / (34.54 + \text{depth})$; ($R^2 = 0.79$) (Fig. 5).

Post-dive intervals were generally shorter than the preceding dives. The distribution of post-dive intervals was unimodal at 17 s, 50% of them being ≤ 20 s, 90% ≤ 36 s, and 99% ≤ 176 s (Fig. 5). Some dives were followed by extensive post-dive intervals (up to 1.04 h); excluding intervals >60 s ($n = 106$, 3% of the total), post-dive intervals averaged 21 ± 10 s ($n = 3394$).

Bottom time and diving efficiency

The bottom time of dives lasted on average 28.4 ± 19.3 s (range 0 to 98 s, $n = 3500$), 50% of bottom time being ≤ 26 s, 90% ≤ 54 s, and 99% ≤ 76 s. Diving efficiency in breath-hold divers has been defined

as the proportion of bottom time (during which predators presumably feed) over a complete dive cycle, following the equation of Ydenberg and Clark (1989): $\text{diving efficiency} = \text{bottom time} / (\text{dive duration} + \text{post-dive interval})$. The diving efficiency of rockhopper penguins averaged 0.34 ± 0.15 (range 0 to 0.84, $n = 3394$). The distribution of diving efficiency showed one mode at 0.40, 50% of efficiency being ≤ 0.35 , 90% ≤ 0.50 , and 99% ≤ 0.65 (Fig. 6). The mean maximum diving efficiency (0.38 to 0.39) occurred during dives that reached a maximum depth of 15 to 35 m (Fig. 6).

Descent/ascent rates

The descent and ascent rates for depths ≤ 5 m were high, with high standard deviations (2.65 ± 0.87 and 1.49 ± 1.13 ms^{-1} , respectively, $n = 653$) (Fig. 7). This resulted from methodological artifacts arising from the TDR's programming (see "Materials and methods—Time—depth recorders"). Excluding the dives of ≤ 5 m, mean descent and ascent rates were 1.22 ± 0.41 ms^{-1} and 1.00 ± 0.48 ms^{-1} , respectively, the descent rate being significantly higher than the ascent rate (Student's paired t -test: $t = 7.70$, $P < 0.001$, $n = 2847$). The rates of descent and ascent increased with increasing dive depth (Fig. 7), so that when penguins dived to 20 m they descended at 1.20 ± 0.38 ms^{-1} and ascended at 0.91 ± 0.40 ms^{-1} , and when they dived to 50 m they descended at 1.41 ± 0.20 ms^{-1} and ascended at 1.07 ± 0.27 ms^{-1} .

Foraging effort

On average, rockhopper penguins spent $68.6 \pm 6.7\%$ (range 52.9 to 79.1%, $n = 27$) of daily foraging trips diving (sum of durations of dives ≥ 3 m). During the two longer trips, the birds dived for 43.3 and 42.4% of their time at sea, including 56.6 and 54.4% during the daytime and 5.3 and 7.2% during the nighttime, respectively.

A good indicator of foraging effort is the total vertical travel distance (VTD), defined as the sum of the maximum depth of all dives multiplied by two (Horning and Trillmich 1997). During their daily foraging trips, the female rockhopper penguins travelled an average of 18.37 ± 3.80 km while diving (range 8.77 to 25.70 km, $n = 27$); this corresponds to a mean dive rate of 1.53 ± 0.29 km per hour (range 0.93 to 2.01 km h^{-1}). The VTD of the two birds which spent one night at sea was only 0.59 to 0.73 km during the nighttime, considerably less than the VTD during the daytime on the first (9.16 to 19.96 km) and second (15.12 to 12.02 km) days of the foraging trip.

The use of the water column by penguins is well represented by the total time devoted to dives reaching a given maximum-depth class expressed as a percentage of the total diving time. The overall distribution of depth utilization was skewed towards relatively shallow dives,

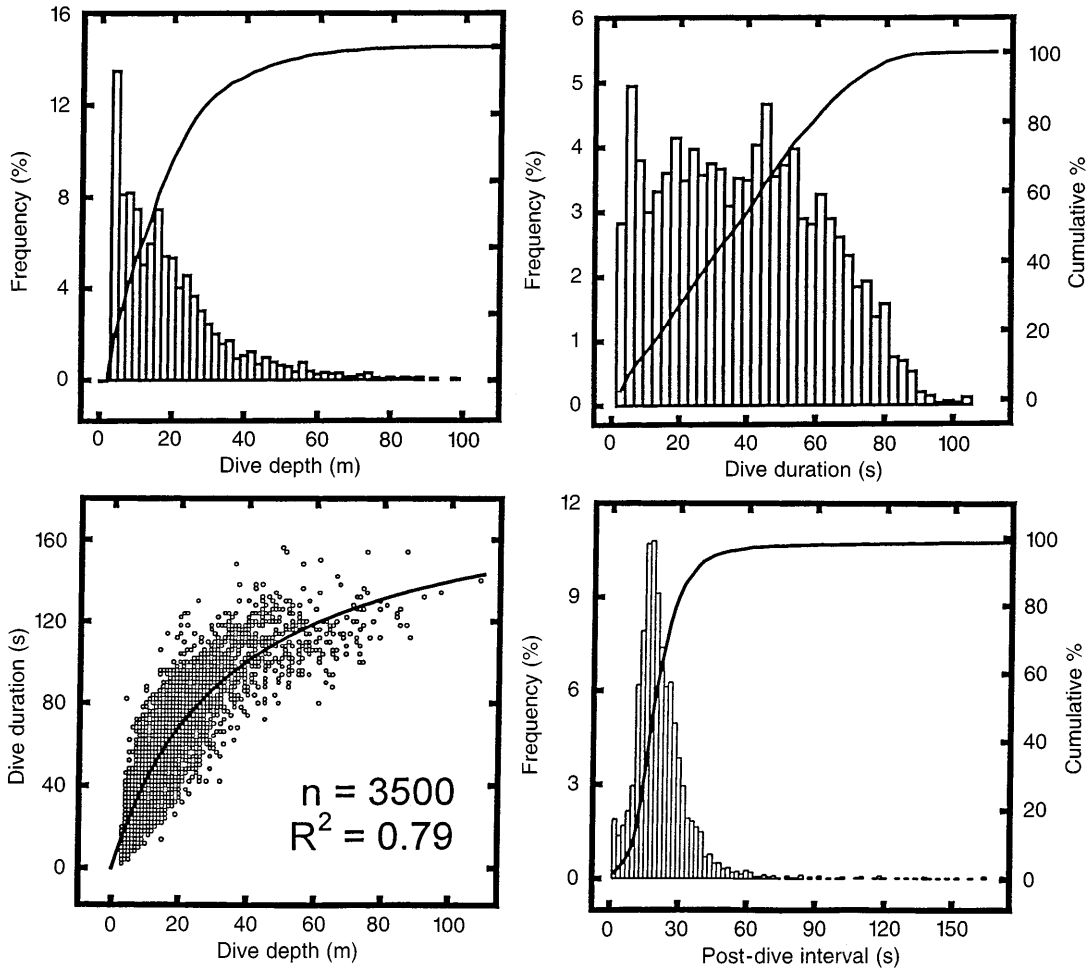
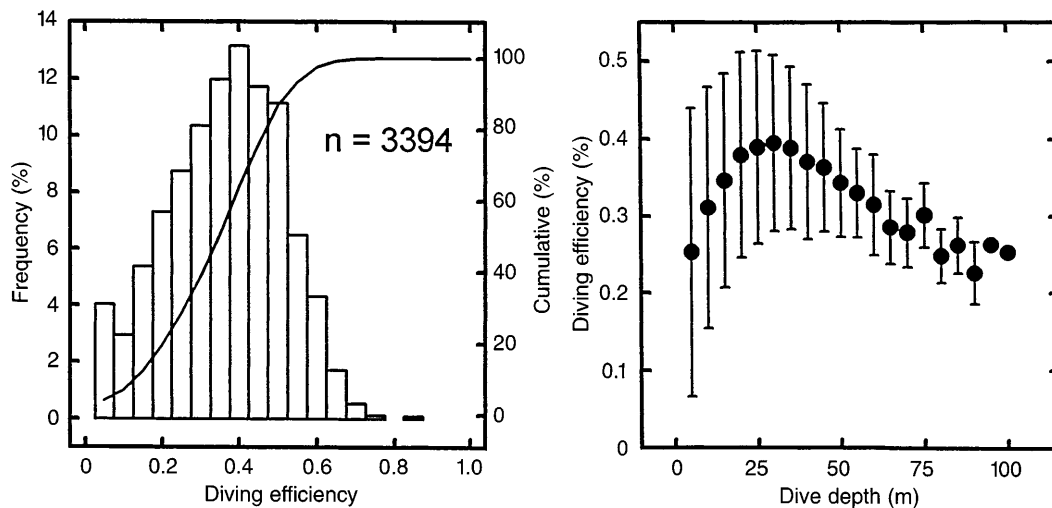


Fig. 5 *Eudyptes chrysocome moseleyi*. Frequency distribution of dive depth, dive duration and post-dive interval, and relationship between dive duration and dive depth

at the bottom for a given maximum-depth class expressed as a percentage of total bottom time showed the same distribution pattern (Fig. 8).

with a single mode: birds spent 17% of their diving time during dives down to 15 to 20 m, and 66 and 90% of their total diving time in 3 to 30 m dives and ≤ 50 m dives, respectively (Fig. 8). Accordingly, the time spent

Fig. 6 *Eudyptes chrysocome moseleyi*. Frequency distribution of diving efficiency (bottom time: dive duration + post-dive interval) and relationship between diving efficiency and dive depth (means \pm SD)



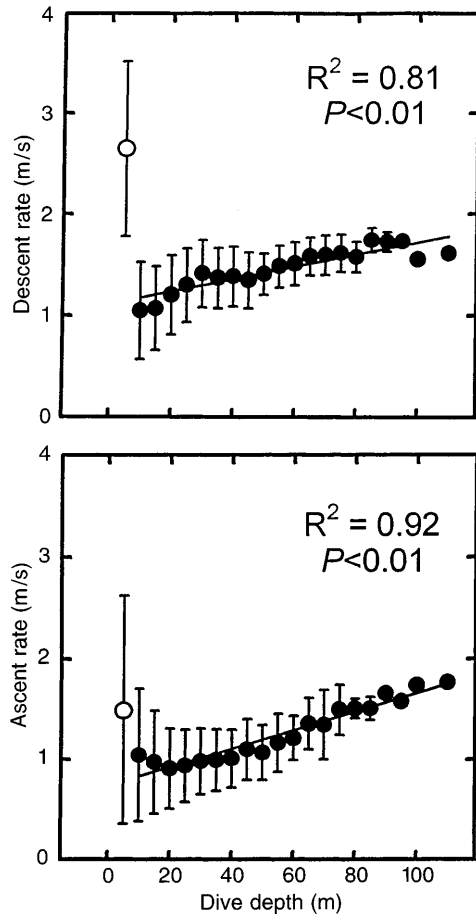


Fig. 7 *Eudyptes chrysocome moseleyi*. Average descent and ascent rates (means \pm SD) in relation to dive depth. Regression equations are: $y = 0.006x + 1.114$ and $y = 0.009x + 0.736$ for descent and ascent rates, respectively

Temporal changes in diving behaviour

The number of dives per foraging trip significantly increased and the mean dive depth significantly decreased during the brooding stage (Fig. 9). Consequently, depth utilization was different over the study period: it peaked for dives reaching 15 to 30 m (44% of total diving time) and 5 to 20 m (72%) at the beginning and the end of the study period, respectively. Penguins spent 13% of their diving time in dives > 50 m at the beginning, while no time was devoted to deep dives at the end of the period.

There was no change in the vertical distance travelled and total diving time during daily foraging trips ($n = 27$) over the two-week study period (Fig. 9).

Diet

The mass of stomach contents averaged 123.6 ± 83.7 g (range 12.3 to 200.3 g, $n = 7$). Overall, crustaceans dominated the diet by mass (58.1%), followed by fishes (28.1%) and squid (13.8%). By far, the most abundant prey was the euphausiid *Thysanoessa gregaria*, which

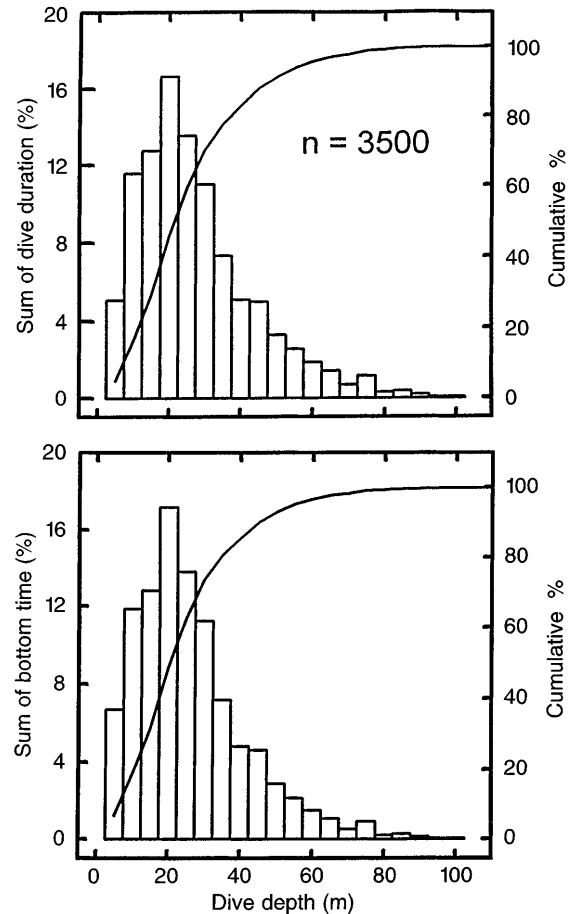


Fig. 8 *Eudyptes chrysocome moseleyi*. Frequency distribution of sum of dive durations (as percentage of total diving time) and sum of dive bottom times (as percentage of total bottom time) in relation to dive depth

represented 98.3% of the total number of prey. The fish diet included mainly several species of unidentified fish postlarvae (1.3%) and the photichthyid *Vinciguerria attenuata* (0.3%). An ommastrephid squid (probably *Todarodes filippovae*) was the main cephalopod prey (0.2%).

Discussion

Comparison with previous data on rockhopper penguins

There is little information available on the foraging behaviour of either northern (*Eudyptes chrysocome moseleyi*) or southern (*E. chrysocome chrysocome* and *E. chrysocome filholi*) rockhopper penguins. Using capillary-tube depth gauges, Tremblay et al. (1997) previously found that the maximum dive depth of northern rockhopper penguins during the crèche stage averaged 66 ± 28 m ($n = 49$), a value identical to that measured in this study (73 ± 18 m, $n = 14$) and to the maximum depth (66 m) reached by one southern rockhopper

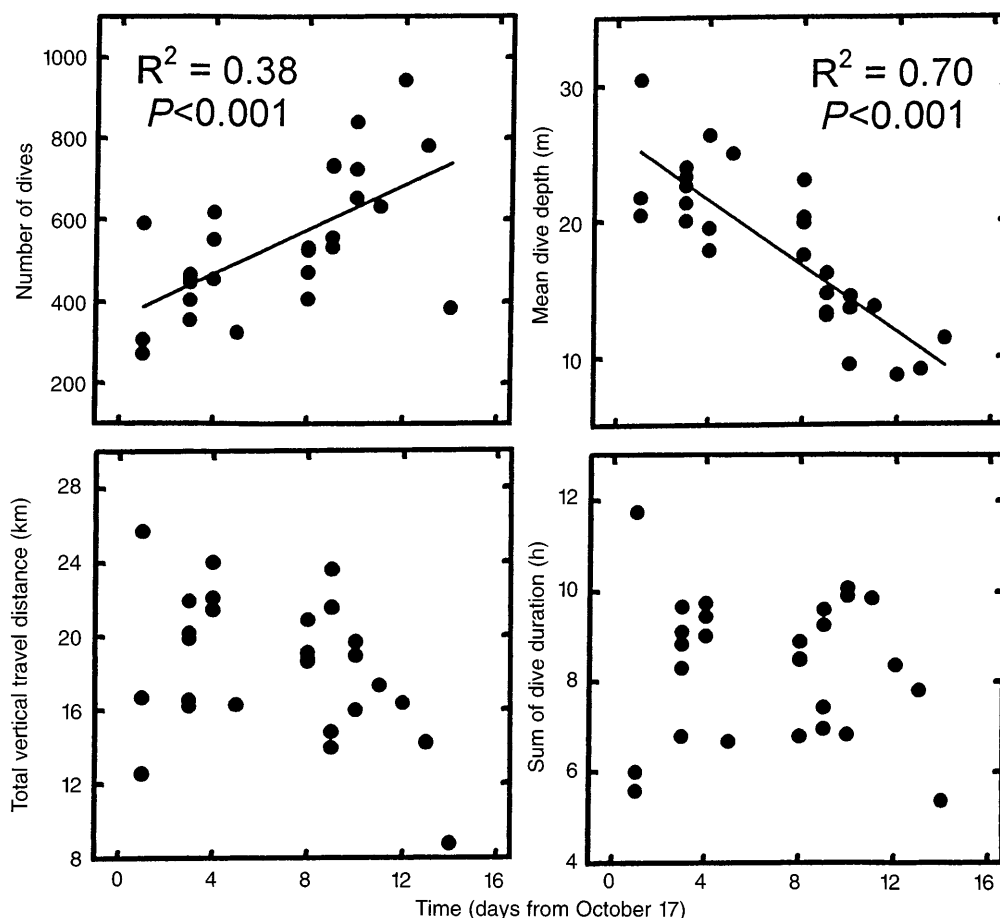


Fig. 9 *Eudyptes chrysocome moseleyi*. Number of dives, mean dive depth, total vertical travel distance and total time spent diving per foraging trip in relation to time during guard stage. Regression equations are: $y = 26.89x + 362.26$ and $y = -1.21x + 26.36$ for number of dives and mean dive depth, respectively

penguin from Crozet Islands (Wilson et al. 1997). The maximum dive duration in the latter study (180 s) was also similar to that determined here (168 s), suggesting that the two subspecies have similar maximum-dive capacities.

At Crozet, a remarkable feature of the foraging behaviour of rockhopper penguin was the relationship between dive duration and maximum depth achieved, i.e. the bird remained longer underwater for a given maximum depth than would be expected for a penguin of its size (Wilson et al. 1997). Results from the northern rockhopper penguins are not entirely consistent with this; for example the mean duration of a dive reaching 50 m was 111 s, a value much lower than the 167 s found for the southern subspecies. During a 50 m dive, birds from Amsterdam Island also spent less time at the bottom (53 vs 65 s) and had higher descent (1.41 vs 1.23 ms^{-1}) and ascent (1.07 vs 0.86 ms^{-1}) rates the Crozet bird (Wilson et al. 1997). Since Wilson et al.'s results were obtained from only one individual fitted with a TDR programmed with a low sampling frequency (every 8 s; Wilson et al. 1997), more information is

clearly needed on the foraging behaviour of the southern rockhopper penguins to assess the significance of the differences between the two subspecies.

Diving behaviour

The diving abilities of penguins are related to body mass, larger species being physiologically capable of longer and deeper dives (Kooyman and Kooyman 1995; Schreer and Kovacs 1997). The relationships between maximum dive duration and maximum dive depth with body mass for rockhopper penguins were examined using the allometric equations of Wilson (1995) and Schreer and Kovacs (1997). With a body mass of 2.3 kg, the predicted maximum dive duration and depth are 124 to 176 s and 77 to 89 m, respectively, for rockhopper penguins. The calculated maximum dive duration using the equation of Wilson agrees well with the recorded value (168 s), while both calculated maximum depths are below the diving ability of rockhopper penguins (109 m), as previously found from data obtained with capillary-tube depth gauges (Tremblay et al. 1997). The mean dive duration and mean dive depths of rockhopper penguins are in general agreement with values obtained for other penguin species. Rockhopper penguins dived longer and deeper than little penguins, *Eudyptula minor*, and they dived on average shorter and shallower

than penguins of larger size (Table 1), including the only other species of crested penguins so far investigated, the macaroni penguin *E. chrysolophus* (Croxall et al. 1993).

The mean dive duration and depth for penguins, including the rockhopper penguins, are much smaller than their maximum dive depth and duration (Table 1). This is thought to be related to the energetic cost of diving, very long dives being associated with anaerobiosis while shorter dives remain within the aerobic dive limit (ADL: Chappell et al. 1993). Since the surface intervals of rockhopper penguins were brief, averaging 37% of dive duration, most dives probably did not exceed the ADL. Assuming that only anaerobic dives were those with long post-dive intervals, the plot of post-dive intervals against dive durations, following Kooyman and Kooyman (1995), shows an inflection of the scattergram at a dive duration of ~ 110 s (data not shown). Our data on the dive durations of rockhopper penguin (Fig. 5) therefore indicate that these birds exceeded the estimated ADL in only 5% of the dives. Both the estimated behavioural ADL and frequency of anaerobic dives of rockhopper penguins are in general agreement with values obtained for the smallest and largest penguin species, namely the little (45 s and 2%) and the emperor (*Aptenodytes forsteri*: 8 min and 4%) penguins (Kooyman and Kooyman 1995; Bethge et al. 1997). More data are however needed on the behavioural ADL of medium-sized penguins for an accurate comparison among species.

The descent and ascent rates of rockhopper penguins are within the normal range for penguins (0.4 to 1.5 ms^{-1} : Wilson 1995). We also found that descent and ascent rates in the water column increased with increasing dive depth (Fig. 7). Since penguin swimming speed is more or less invariant during diving (Wilson 1995), this indicates that dive and return-to-the-surface angles increased with increasing dive depths in rockhopper penguins, as previously described for other species (Wilson 1995; Wilson et al. 1996). Penguins anticipate dive depth by increasing descent and ascent angles in deep dives to increase relative bottom (presumably feeding) time at the expense of travel time. Consequently, they spend less time searching for prey in the upper water strata during deep as opposed to shallow dives (Wilson et al. 1993).

Foraging effort

The most remarkable feature of foraging behaviour in female rockhopper penguins was the very high percentage of time spent diving (mean 69%; max. 79%) during their daily foraging trips (see also Fig. 2). This value is generally higher than those reported for other species (Table 1), except for one macaroni penguin that spent 71% of daytime diving during a two-day trip (Croxall et al. 1993). The long total diving time of the rockhopper penguin is more readily explained by its elevated dive frequency (44 vs 5 to 28 dives h^{-1} for other species), than

by the mean dive duration (that remained within the normal range for a penguin of its size: Table 1). Since a deeper diving organism can perform fewer (longer) dives during a given time than a shallower diver, a good indicator of foraging effort is the total vertical travel distance (Horning and Trillmich 1997). Due to their high dive-frequency during several consecutive hours, the total vertical travel distance by rockhopper penguins during a single daily foraging trip averaged 18 km, a value much higher than the estimated vertical distance covered by African *Spheniscus demersus* (1 km) and gentoo, *Pygoscelis papua* (10 km), penguins during daily trips at sea (Wilson et al. 1989).

In rockhopper penguins, diving efficiency peaked for dive depths between 15 and 35 m (Fig. 6). A decrease in diving efficiency with increasing dive depth (Fig. 6) was previously found in other penguin species, including the Adélie penguin *Pygoscelis adeliae* (Chappell et al. 1993), the king penguin *Aptenodytes patagonicus* (Kooyman et al. 1992), and the emperor penguin (Kooyman and Kooyman 1995). Rockhopper penguins spent 49% of their total diving time and total bottom time in dives down to 15 to 35 m (Fig. 8) that accounted for 37% of the total number of dives (Fig. 5). The numerous shallower dives (3 to 10 m) also accounted for 37% of the dives, but amounted to only 17 and 19% of the total diving time and total bottom time, respectively, with a lower diving efficiency (0.25 to 0.31). Rockhopper penguins spent more time underwater in dives with a high efficiency, i.e. in dives during which bottom time (feeding time) was maximized. There was, however, a slight shift between the peak in total diving time (which occurred for 15 to 20 m deep dives) and that in diving efficiency (15 to 35 m), indicating that birds mainly dived to the shallowest depths within the range of depths with a high efficiency. The depth distribution of prey may explain this shift to a given depth where euphausiids were probably concentrated.

Timing of foraging trips and foraging range

During the guard stage of crested penguins, the feeding of the chick devolves solely on the females, most of whom performing daily foraging trips for this purpose (Warham 1975). This pattern was observed in females equipped with TDRs in this study. Like females of the southern subspecies (Brown 1987; Thompson 1989), they spend the night ashore and forage during the day, usually leaving at dawn and returning in the afternoon (Fig. 1). Longer trips at sea including one night are not uncommon at that time, and have already been recorded for female macaroni penguins at South Georgia, the frequency of longer trips increasing as the chick grows (Croxall et al. 1988).

Female northern rockhopper penguins are obviously essentially diurnal foragers and visual predators, since not only did most of them stay ashore at night, but also their diving activity during darkness was low when they

Table 1 Diving performance of penguins (*N* number of birds; – not given)

Species	<i>(N)</i>	Dive depth (m)		Dive duration (s)		Dive frequency (dives h ⁻¹)	% total time at sea spent diving	Source
		mean	max.	mean	max.			
Little blue penguin, <i>Eudyptula minor</i>	(8)	3.4	27	21	88	28	60	Bethge et al. (1997)
Northern rockhopper penguin, <i>Eudyptes chrysocome</i> <i>moseleyi</i>	(14)	18	109	57	168	44	69	Present study
Southern rockhopper penguin, <i>Eudyptes chrysocome</i> <i>chrysocome</i>	(1)	bimodal, ≤3 and 18	66	–	180	–	45 ^a	Wilson et al. (1997)
Macaroni penguin, <i>Eudyptes chrysolophus</i>	(2)	29 ^b	115	90 ^b	377	19 ^b	48 ^b	Croxall et al. (1993)
Chinstrap penguin, <i>Pygoscelis antarctica</i>	(4)	bimodal, 2 and 31	121	bimodal, 10 and 72	180	13 ^c	–	Bengtson et al. (1993)
Adélie penguin, <i>Pygoscelis adeliae</i>	(50) (15)	26 5–21	98 –	73 72–138	160 –	– –	30–50 4–28	Chappell et al. (1993) Watanuki et al. (1993)
Gentoo penguin, <i>Pygoscelis papua</i>	(9)	bimodal, 4 and 80	156	bimodal, 14 and 150	–	17–23	52	Williams et al. (1992a)
	(3)	bimodal, 5–7 and 74–105	166	bimodal, 30–78 and 162–210	–	12–25	51–62	Williams et al. (1992b)
	(15)	bimodal, 10 and 80	212	–	378	15	37	Robinson and Hindell (1996)
	(7)	35	107	–	–	18	–	Wilson et al. (1996)
Magellanic penguin, <i>Spheniscus magellanicus</i>	(9)	20.2 mode 55–60	97	74, bimodal, 56–64 and 120–128	234	–	–	Peters et al. (1998)
King penguin, <i>Aptenodytes patagonicus</i>	(6) ^d	bimodal, 10–25 and 100–200	304	bimodal, 120 and 270	462	5–20 ^a	–	Kooyman et al. (1992)
Emperor penguin, <i>Aptenodytes forsteri</i>	(5)	mode 21–40	534	mode 240–300	948	9 ^a	–	Kooyman and Kooyman (1995)
	(14)	trimodal, 10–50, 100–200 and >300	477	204–240	912	6 ^c	–	Kirkwood and Robertson (1997)

^aIncluding nighttime

^bDaily foraging trips

^cDeep dives only (≥5 m or ≥20 s)

^dOnly birds equipped with Wildlife Computers time–depth recorders

^eFeeding dives only

stayed at sea during the nighttime. The two females engaged in longer trips had a lower dive frequency, dived at shallower depths, and consequently displayed a much lower total diving time and total vertical travel distance at night than during the daytime. These data confirm those obtained for southern rockhopper penguins by Wilson et al. (1997), and are in agreement with the general view that penguins are visual predators (see Wilson 1995 for discussion on the possible role of prey migration). Light intensity affects the depths to which penguins, including rockhoppers (Fig. 4) dive, as indicated by the consistent change in dive depths around dawn and dusk, and the achievement of deepest dives exclusively during the daytime (Wilson et al. 1993; Kirkwood and Robertson 1997). The role of light intensity in the foraging ecology of rockhopper penguins is moreover emphasized by the recently described synchronous diving behaviour of these birds, suggesting that they remain visually in contact underwater when foraging as a group (Tremblay and Cherel 1999).

Since many penguins, including the rockhopper penguin, display a diurnal foraging behaviour during chick-rearing, their foraging range is limited not only by swimming speed but also by day length. Accordingly, birds rarely forage >20 km away from the breeding colonies, most time being spent within 5 to 10 km of the islands (Wilson et al. 1989; Weavers 1992; Kerry et al. 1995; Robinson and Hindell 1996, Culik et al. 1998). Our estimated maximum foraging range (6 km average) agrees with this pattern, and indicates that northern rockhopper penguins are essentially inshore foragers during the guard stage.

Amsterdam Island is a volcanic oceanic island devoid of a peri-insular shelf. Within 5 to 10 km of the island, rockhopper penguins therefore forage not in neritic waters but in oceanic waters over deep depths (~1000 to 2000 m). They accordingly feed on mesopelagic oceanic prey such as the euphausiid *Thysanoessa gregaria* and the photichthid fish *Vinciguerria attenuata*. *T. gregaria* was previously found to be a main prey of northern rockhopper penguins both at Gough (Klages et al. 1988) and Amsterdam (Tremblay et al. 1997) islands. This swarming euphausiid occupies near-surface waters of the Indian Ocean, where it is abundant between 30 and 41°S (Brinton and Gopalakrishnan 1973; Mauchline 1980). *V. attenuata* was not previously reported as a prey of rockhopper penguins, but commonly occurred in the diet of birds at Amsterdam Island (Guinard and Cherel unpublished data). Together with myctophid fishes, *V. attenuata* is a major component of the mesopelagic fish fauna in subtropical waters (Young et al. 1996), including Amsterdam Island (Hulley and Duhamel 1990).

Changes in foraging behaviour over study period

During the 2 wk study period, northern rockhopper penguins increased the total number of dives per foraging trip while their mean dive depth decreased.

However, neither variations in the duration of the foraging trip nor in the sum of dive durations and in the total vertical travel distance per foraging trip were observed (Fig. 9). Taken together, these data indicate that there were no significant changes in the foraging effort during that period. They suggest that the observed variations in foraging characteristics were linked to changes in prey distribution or to a shift in prey items, as previously found for the crèche stage (Tremblay et al. 1997). This hypothesis cannot be confirmed because of the small number of diet samples, but *Vinciguerria attenuata* was the main prey in two samples collected the first day of the study, and *Thysanoessa gregaria* formed the bulk of the food ten days later.

The high dive frequency and percentage of time spent diving indicate that female rockhopper penguins operate at a high level of foraging effort, and that there is consequently little scope to increase effort through an increase in the percentage of time underwater. However, because penguins spent an average of 82% of daytime at sea, 18% thus remained potentially available for foraging; this suggests that the characteristic of foraging behaviour most likely to vary in relation to energy demand and/or prey availability is the length of foraging trips. More work is needed to understand how rockhopper penguins regulate their foraging effort; this can be achieved either by inter-annual comparison of diving behaviour in the same colony or by comparing feeding behaviour at different breeding localities in different marine environments.

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References

- Bannasch R, Wilson RP, Culik B (1994) Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J exp Biol* 194: 83–96
- Bengtson JL, Croll DA, Goebel ME (1993) Diving behaviour of chinstrap penguins at Seal Island. *Antarct Sci* 5: 9–15
- Bethge P, Nicol S, Culik BM, Wilson RP (1997) Diving behaviour and energetics in little penguins (*Eudyptula minor*). *J Zool, Lond* 242: 483–502
- Brinton E, Gopalakrishnan K (1973) The distribution of Indian Ocean euphausiids. *Ecol Stud Analysis Synth* 3: 357–382
- Brown CR (1987) Traveling speed and foraging range of macaroni and rockhopper penguins at Marion Island. *J Fld Ornithology* 58: 118–125
- Chappell MA, Shoemaker VH, Janes DN, Bucher TL (1993) Diving behavior during foraging in breeding Adélie penguins. *Ecology* 74: 1204–1215
- Cooper J, Brown CR, Gales RP, Hindell MA, Klages NTW, Moors PJ, Pemberton D, Ridoux V, Thompson KR, Van Hezik YM (1990) Diets and dietary segregation of crested penguins. In: Davis LS, Darby JT (eds) *Penguin biology*. Academic Press, San Diego, pp 131–156
- Croxall JP, Briggs DR, Kato A, Naito Y, Watanuki Y, Williams TD (1993) Diving pattern and performance in the macaroni penguin *Eudyptes chrysolophus*. *J Zool, Lond* 230: 31–47

- Croxall JP, Davis RW, O'Connell (1988) Diving patterns in relation to diet of gentoo and macaroni penguins at South Georgia. *Condor* 90: 157–167
- Culik BM, Luna-Jorquera G, Oyarzo H, Correa H (1998) Humboldt penguins monitored via VHF telemetry. *Mar Ecol Prog Ser* 162: 279–286
- Duroselle T, Tollu B (1977) The rockhopper penguin (*Eudyptes chrysocome moseleyi*) of Saint Paul and Amsterdam Islands. In: Llano GA (ed) Adaptations within Antarctic ecosystems, Proceedings of the third SCAR symposium on Antarctic biology. Smithsonian Institution, Washington, pp 579–604
- Gales RP (1987) Validation of the stomach-flushing technique for obtaining stomach contents of penguins. *Ibis* 129: 335–343
- Horning M, Trillmich F (1997) Ontogeny of diving behaviour in the Galapagos fur seal. *Behaviour* 134: 1211–1257
- Hull CL (1997) The effect of carrying devices on breeding royal penguins. *Condor* 99: 530–534
- Hulley PA, Duhamel G (1990) Report on prelevements RMT – fishes. In: Arnaud PM (ed) Les rapports des campagnes à la mer aux îles Saint-Paul et Amsterdam. Mission de Recherche des TAAF, Paris, pp 80–89 (No. 86-04)
- Kerry KR, Clarke JR, Else GD (1995) The foraging range of Adélie penguins at Bechervaise Island, Mac.Robertson Land, Antarctica as determined by satellite telemetry. In: Dann P, Norman I, Reilly P (eds) The penguins. Surrey Beatty & Sons, Chipping Norton, pp 216–243
- Kirkwood R, Robertson G (1997) The foraging ecology of female emperor penguins in winter. *Ecol Monogr* 67: 155–176
- Klages NT, Brooke M de L, Watkins BP (1988) Prey of northern rockhopper penguins at Gough Island, South Atlantic Ocean. *Ostrich* 59: 162–165
- Kooyman GL, Cherel Y, Le Maho Y, Croxall JP, Thorson PH, Ridoux V, Kooyman CA (1992) Diving behavior and energetics during foraging cycles in king penguins. *Ecol Monogr* 62: 143–163
- Kooyman GL, Kooyman TG (1995) Diving behavior of emperor penguins nurturing chicks at Coulman Island, Antarctica. *Condor* 97: 536–549
- Mauchline J (1980) The biology of mysids and euphausiids. *Adv mar Biol* 18: 1–681
- Peters G, Wilson RP, Scolaro JA, Laurenti S, Upton J, Galleli H (1998) The diving behavior of Magellanic penguins at Punta Norte, Peninsula Valdés, Argentina. *Colon Waterbirds* 21: 1–10
- Robinson SA, Hindell MA (1996) Foraging ecology of gentoo penguins *Pygoscelis papua* at Macquarie Island during the period of chick care. *Ibis* 138: 722–731
- Schreer JF, Kovacs KM (1997) Allometry of diving capacity in air-breathing vertebrates. *Can J Zool* 75: 339–358
- Thompson KR (1989) An assessment of the potential for competition between seabirds and fisheries in the Falkland Islands. Falkland Islands Foundation Project Report. Falkland Islands Foundation, Brighton
- Tremblay Y, Cherel Y (1999) Synchronous underwater foraging behavior in penguins. *Condor* 101: 179–185
- Tremblay Y, Guinard E, Cherel Y (1997) Maximum diving depths of northern rockhopper penguins (*Eudyptes chrysocome moseleyi*) at Amsterdam Island. *Polar Biol* 17: 119–122
- Warham J (1975) The crested penguins. In: Stonehouse B (ed) The biology of penguins. MacMillan, London, pp 189–269
- Watanuki Y, Kato A, Mori Y, Naito Y (1993) Diving performance of Adélie penguins in relation to food availability in fast sea-ice areas: comparison between years. *J Anim Ecol* 62: 634–636
- Weavers BW (1992) Seasonal foraging ranges and travels at sea of little penguins *Eudyptula minor*, determined by radiotracking. *Emu* 91: 302–317
- Williams TD (ed) (1995) The penguins Spheniscidae. Oxford University Press, Oxford
- Williams TD, Briggs DR, Croxall JP, Naito Y, Kato A (1992a) Diving pattern and performance in relation to foraging ecology in the gentoo penguin, *Pygoscelis papua*. *J Zool, Lond* 227: 211–230
- Williams TD, Kato A, Croxall JP, Naito Y, Briggs DR, Rodwell S, Barton TR (1992b) Diving pattern and performance in non-breeding gentoo penguins (*Pygoscelis papua*) during winter. *Auk* 109: 223–234
- Wilson RP (1995) Foraging ecology. In: Williams TD (ed) The penguins Spheniscidae. Oxford University Press, Oxford, pp 81–106
- Wilson RP, Bost CA, Pütz K, Charrassin JB, Culik BM, Adelung D (1997) Southern rockhopper penguin *Eudyptes chrysocome chrysocome* foraging at Possession Island. *Polar Biol* 17: 323–329
- Wilson RP, Culik BM, Peters G, Bannasch R (1996) Diving behaviour of gentoo penguins, *Pygoscelis papua*; factors keeping dive profiles in shape. *Mar Biol* 126: 153–162
- Wilson RP, Nagy KA, Obst BS (1989) Foraging ranges of penguins. *Polar Rec* 25: 303–307
- Wilson RP, Puetz K, Bost CA, Culik BM, Bannasch R, Reins T, Adelung D (1993) Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? *Mar Ecol Prog Ser* 94: 101–104
- Wilson RP, Pütz K, Charrassin JB, Lage J (1995) Artifacts arising from sampling interval in dive depth studies of marine endotherms. *Polar Biol* 15: 575–581
- Ydenberg RC, Clark CW (1989) Aerobiosis and anaerobiosis during diving by western grebes: an optimal foraging approach. *J theor Biol* 139: 437–449
- Young JW, Lamb TD, Bradford RW (1996) Distribution and community structure of midwater fishes in relation to the subtropical convergence off eastern Tasmania, Australia. *Mar Biol* 126: 571–584