

FORAGING BEHAVIOUR OF THE CHINSTRAP PENGUIN *PYGOSCELIS ANTARCTICA* AT ARDLEY ISLAND, ANTARCTICA

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SUMMARY

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The foraging behaviour of 20 Chinstrap Penguins *Pygoscelis antarctica* breeding at Ardley Island, King George Island, Antarctica was studied during the austral summers of 1991/2 and 1995/6 using stomach temperature loggers (to determine feeding patterns), depth recorders and multiple channel loggers. The multiple channel loggers recorded dive depth, swim speed and swim heading which could be integrated using vectors to determine the foraging tracks. Half the birds left the island to forage between 02h00 and 10h00. Mean time at sea was 10.6 h. Birds generally executed a looping type course with most individuals foraging within 20 km of the island. Maximum foraging range was 33.5 km. Maximum dive depth was 100.7 m although 80% of all dives had depth maxima less than 30 m. The following dive parameters were positively related to maximum depth reached during the dive: total dive duration, descent duration, duration at the bottom of the dive, ascent duration, descent angle, ascent angle, rate of change of depth during descent and rate of change of depth during ascent. Swim speed was unrelated to maximum dive depth and had mean values of 2.6, 2.5 and 2.2 m/s for the descent, bottom and ascent phases of the dive. The sequence of maximum depths reached in a dive series was not random, tending to be concentrated at a particular depth, irrespective of whether the penguins were feeding at that depth or not. Generally, sequential dives to a specific depth were abruptly terminated by a single dive to another depth which was characteristic in having no bottom phase and unusually steep descent and ascent angles. The maximum depth reached during this dive was then adhered to in the next dive sequence. There were peaks in feeding activity between 06h00 and 09h00 and 14h00 and 22h00. Although foraging effort and relative success decreased around midnight when light intensity was lowest, birds did dive up to 22 m at this time, considerably deeper than sympatric Adélie *P. adeliae* or Gentoo *P. papua* Penguins. These findings indicate that, in accordance with their small body size, Chinstrap Penguins forage inshore close to the surface during the chick-rearing phase. Apparent short-comings in the volume of water searched compared to sympatric congeners can be made good by intense diving activity during the period at sea, with no inter-bout rests, higher swim speeds and an apparent ability to be able to forage at lower light intensities which enables Chinstrap Penguins to forage better under twilight conditions.

INTRODUCTION

The Chinstrap Penguin *Pygoscelis antarctica* is the second most numerous species of penguin in the Southern Ocean ecosystem with a population numbering 7.5 million breeding pairs or c. 26% of the estimated total of 23.6 million breeding pairs of all penguin species in the region (Woehler 1995). As such, Chinstrap Penguins must be considered major consumers in the Southern Ocean. During breeding, this bird feeds almost exclusively on crustaceans, principally krill *Euphausia superba* and *E. crystallorophias* (Croxall & Furse 1980, Volkman *et al.* 1980, Jablonski 1985, Lishman 1985), which are caught during foraging trips lasting between 3 and 48 h (Jablonski 1985, Lishman 1985, Trivelpiece *et al.* 1987). Estimates of the foraging range lie between 33 km (Trivelpiece *et al.* 1987) and 114 km (Lishman 1985) depending on locality. Radio-telemetry and depth recorder data indicate that Chinstrap Penguins generally forage within the upper 40 m of the water column, rarely diving deeper than 100 m, and that dive durations rarely exceed 120 s (Lishman & Croxall 1983, Trivelpiece *et al.* 1986, Croll *et al.* 1991, Bengston *et al.* 1993).

In the King George Island area, the Chinstrap Penguin occurs sympatrically with two other congeners, the Adélie *P. adeliae* and Gentoo *P. papua* Penguins and, since in this region both other species feed predominantly on Antarctic Krill *E. superba* (for reviews see Trivelpiece *et al.* 1987 and Williams 1995), the three species are considered subject to inter-specific competition (Trivelpiece *et al.* 1987). Mechanisms by which competition may be reduced include staggered breeding seasons and differential depth utilisation (Trivelpiece *et al.* 1987). It has also been suggested that the birds may forage at different distances from the breeding sites (Trivelpiece *et al.* 1987).

We studied the foraging behaviour of Chinstrap Penguins breeding close to the Antarctic Peninsula using new technology to determine foraging areas, dive behaviour and feeding patterns. We hope that our data can be used to clarify the foraging niche of the Chinstrap Penguin so that its role as a predator in the Southern Ocean ecosystem may be better defined. Finally, we consider our data in the light of published information on congeners so as to determine inter-specific differences in marine ecology that might help reduce competition in areas of sympatry.

MATERIALS AND METHODS

Field work was conducted at Ardley Island (62°13'S, 58°55'W), King George Island, Antarctica during December 1991 to January 1992 and January 1996. A total of 20 Chinstrap Penguins attending chicks was caught at their nests and fitted with either multiple channel loggers (MCLs) or depth loggers (Table 1) (see below). Following suggestions made by Bannasch *et al.* (1994) to reduce hydrodynamic drag, the units were attached in the dorsal mid-line of the birds as close as possible to the tail without impeding the movement of the tail itself. Units were attached using tape passed under a few feathers and then around the body of the devices (see Wilson & Wilson 1989 for details). Seventeen of the device-fitted penguins were also given stomach temperature sensors (STLs)

(see below) to swallow. The complete attachment procedure took less than 10 minutes a bird.

After having been equipped, birds were released at the nest site and allowed to go to sea for at least one foraging trip. Upon their return after they were recaptured and the external units removed by taking off the tape, the STLs were recovered by stomach flushing (Wilson 1984).

Remote-sensing technology

All units were programmed and the recorded data accessed by computer using RS 232 interfaces. MCLs had a memory of 64 kbytes and were programmed to record at 10-s (and in two cases at 15-s) intervals, the depth loggers had a memory of

TABLE 1

Deployment of remote-sensing technology of Chinstrap Penguins breeding at Ardley Island during the austral summers of 1990/91 and 1995/96

Penguin	Unit	Date deployed	Date recovered	Number of trips	Sampling frequency (s)
Long nose	MCL	28 Dec 1991	29 Dec 1991	1	10
"	STL	28 Dec 1991	29 Dec 1991	1	16
Zacky	MCL	4 Jan 1992	5 Jan 1992	1	15
"	STL	4 Jan 1992	5 Jan 1992	1	16
Claudia	MCL	4 Jan 1992	5 Jan 1992	1	10
"	STL	4 Jan 1992	5 Jan 1992	1	16
Nippon	MCL	8 Jan 1992	9 Jan 1992	2	10
Carlito	MCL	9 Jan 1992	10 Jan 1992	1	10
"	STL	9 Jan 1992	10 Jan 1992	1	16
Round Robin	MCL	9 Jan 1992	10 Jan 1992	1	10
"	STL	9 Jan 1992	10 Jan 1992	1	16
Smiley	MCL	11 Jan 1992	12 Jan 1992	1	10
"	STL	11 Jan 1992	12 Jan 1992	1	16
Peter G.	MCL	11 Jan 1992	12 Jan 1992	2	10
Vibes	MCL	12 Jan 1992	13 Jan 1992	1	10
"	STL	12 Jan 1992	13 Jan 1992	1	16
Remington	MCL	16 Jan 1992	16 Jan 1992	1	10
"	STL	16 Jan 1992	16 Jan 1992	1	16
Zitter	MCL	16 Jan 1992	16 Jan 1992	1	10
"	STL	16 Jan 1992	16 Jan 1992	1	16
Thor	MCL	18 Jan 1992	19 Jan 1992	1	15
"	STL	18 Jan 1992	19 Jan 1992	1	16
A3	MCL	18 Jan 1992	19 Jan 1992	1	10
"	STL	18 Jan 1992	19 Jan 1992	1	16
Fang	MCL	19 Jan 1992	20 Jan 1992	1	10
"	STL	19 Jan 1992	20 Jan 1992	1	16
Yerasimus	MCL	19 Jan 1992	20 Jan 1992	1	10
"	STL	19 Jan 1992	20 Jan 1992	1	16
Charmed Qu	MCL	20 Jan 1992	20 Jan 1992	1	10
"	STL	20 Jan 1992	20 Jan 1992	1	16
Peter-John	MCL	20 Jan 1992	21 Jan 1992	1	10
Zügeli S.	Depth G	20 Jan 1996	23 Jan 1996	4	8
"	STL	20 Jan 1996	23 Jan 1996	4	10
Flip-hop	Depth G	20 Jan 1996	23 Jan 1996	3	8
"	STL	20 Jan 1996	23 Jan 1996	3	10
205305	Depth G	20 Jan 1996	25 Jan 1995	4	8
"	STL	20 Jan 1996	25 Jan 1996	3	10

128 kbytes and recorded data at 8-s intervals (hardware specified) and the STLs recorded data at intervals between 10 and 16 s in a 32 or 64 kbyte memory.

The MCLs (Driesen & Kern GmbH, Am Hasselt 25, D-24576 Bad Bramstedt, Germany) measured depth, speed and direction, weighed 200 g (maximum dimensions 99 × 54 × 20 mm) and were hydrodynamically shaped to minimize drag according to suggestions in Bannasch *et al.* (1994). Gas respirometry measurements made on conspecific, but marginally larger, Adélie Penguins in a swim canal indicated that the energetic costs of swimming with the MCLs exceeded those of non-equipped birds by *c.* 6% (Culik *et al.* 1994a). The MCLs recorded the following parameters:

1. Depth. This was determined by a pressure transducer for the range 0–200 m with 10-bit resolution. All units were calibrated in a pressure tank before and after deployment and found to be accurate to within one bit.
2. Speed. This was determined using a paddle wheel mounted to the aft of the MCL. The number of revolutions of the wheel per second was used as a measure of swim speed. All units were calibrated on birds swimming in a 21-m long covered canal (for details see Culik *et al.* 1994b). For speeds in excess of 0.4 m/s the paddle wheel measured swim speed with an accuracy of better than 10% of the recorded value.
3. Direction of travel. This was determined using two Hall sensors (both 8-bit resolution) placed at 90° to each other on the equator of a fluid-filled compass in a principle similar to that employed by Bramanti *et al.* (1988). Details of the system are given in Wilson *et al.* (1993). Accuracy of the determination of the direction of travel was better than 5° for swim angles (relative to the water's surface) of –14 to +14°. At greater angles the compass sometimes stuck and thus became less reliable although the heading was still correct to within 15°.

The depth loggers (Driesen & Kern GmbH) had a mass of 72 g (maximum dimensions 140 × 18 × 19 mm) and recorded pressure within the range 0–100 m with a resolution of 8 bit. Accuracy of the units was good to within one bit.

The STLs (Elkotec Electronic GmbH, D-8057 Eching, Germany and IDE GmbH, Hamburgerchaussee 53, D-24113, Kiel, Germany) had a total mass of 100 g (dimensions 101 × 21 mm diameter) (Wilson *et al.* 1992). The electronics was protected within a turned titanium housing with an O-ring-fitted lid. Temperature measurements (made with 8 bit resolution) were good to 0.8°C absolute accuracy and 0.1°C relative accuracy. All units were calibrated in a water bath before and after deployment.

Data from all loggers were analysed using programs from Jensen Software Systems (Lammertzweg 19, D-24235 Laboe, Germany). Dive patterns, integrated with swim speed underwater, were elucidated using ANDIVE6.0 where the following parameters are calculated for each dive: time of onset of each dive; durations of the total dive, the descent phase, bottom phase and ascent phase; swim angle with respect to the surface for the descent, bottom and ascent phases; swim speeds during descent, the bottom and ascent phases; the rate of change of depth during the descent, bottom and ascent phases. Dive to depths of less than 2 m were not included in the analysis due to difficulties in determining dive parameters related to the recording frequency of the loggers (Wilson *et al.* 1995a). Dives were classified as either 'V-shaped' or 'U-shaped' (see Le Boeuf *et al.* 1987, Schreer & Testa 1995,

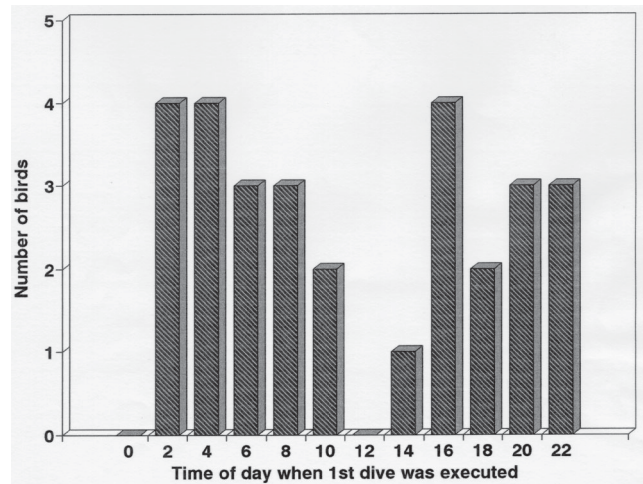


Fig. 1. Frequency of departures of Chinstrap Penguins leaving Ardley Island to forage as a function of time of day.

1996). During 'V-shaped' dives birds descended to a specific depth before returning immediately to the surface. These dives were classified as such when they had had no point of inflection in the dive profile other than the point of maximum depth and when this occurred within a maximum of 15 s (the maximum recording interval used – see Table 1). In order for dives to be considered 'U-shaped', the dive profile had to have a clear bottom phase with a duration in excess of 15 s delineated by two marked points of inflection (Schreer & Testa 1995, 1996). The program ROUTE10.0 allowed us to calculate the foraging routes of all penguins equipped with MCLs by vectorial integration of the swim speed, swim heading and dive depth (see Wilson *et al.* 1993). Feeding activity was determined using FEEDINT2.0 where temperature drops in excess of 0.2°C per 16-s recording interval were taken as indicative of ingestion (Wilson *et al.* 1995b). The integral of the temperature below the pre-temperature drop asymptote was taken to be linearly related to the mass of prey ingested (Wilson *et al.* 1995b).

RESULTS

A total of 20 Chinstrap Penguins was successfully equipped with external loggers during the study period (17 MCLs in 1990/1 and three depth loggers in 1995/6) recording information for a total of 30 foraging trips. Stomach temperature was logged in 24 of these trips (Table 1).

Foraging trips were most often initiated in the early morning or late afternoon. No birds initiated a foraging trip around midnight or midday (Fig. 1). Trips lasted for a mean of 10.6 ± 8.2 h and typically consisted of a looping course where the birds left the island travelling initially in a fairly straight line. Within the first hour, the course typically began to meander until eventually frequent doubling back was apparent. After a highly variable period of this less directional travel birds typically headed virtually straight back to their breeding island (Fig. 2). Mean foraging range was 11.5 ± 9.4 km (range 3.3–36.0 km, *n* = 17). At-sea area usage was essentially limited to the region south west of Ardley Island, extending out some 30 km beyond the entrance of the Maxwell Bay (Figs 2 & 3).

During foraging, diving was not organised into bouts where birds' periods of intense diving were separated by long resting

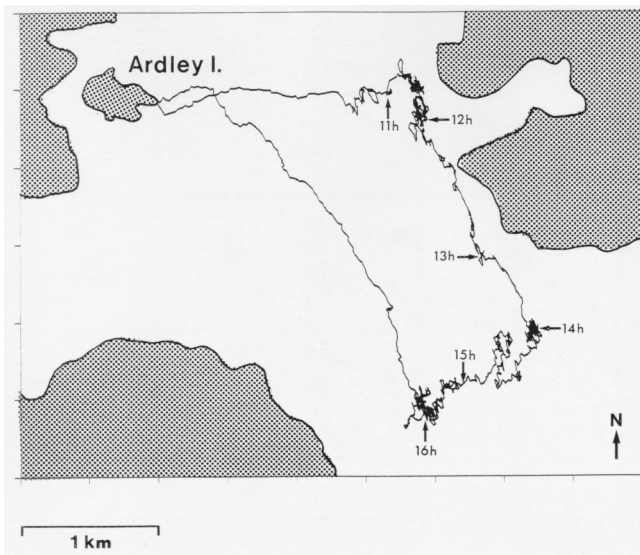


Fig. 2. Typical foraging trip of a Chinstrap Penguin departing from Ardley Island.

periods at the surface (*sensu* Williams *et al.* 1992). Rather, birds dived continuously throughout the time spent at sea (e.g. Fig. 4). V-dives accounted for 18.1% of all dives and did not differ significantly from U-dives in the angle of descent or angle of ascent as a function of max depth reached during the dive ($F = 2.3$, $P > 0.05$, ANOVA). Overall, maximum depth reached determined many of the dive parameters. Total dive duration, descent duration and ascent duration were all linearly related to maximum dive depth as was the descent angle (Table 2). The relationships between maximum depth reached and bottom duration, ascent angle and rate of change of depth during the descent and ascent phases of the dive were all logarithmic (Table 2). There was no apparent relationship between maximum depth reached and the rate of change of depth during the bottom phase (Mean = 0.01 ± 0.16 m/s, range 0–0.79 m/s, $n = 4545$), nor between maximum depth reached and bottom angle (Mean = $-0.3 \pm 4.5^\circ$, range -24.1 – 39.3 m/s, $n = 471$).

Swim speed was not related to maximum depth reached during the dive but significantly different between the different

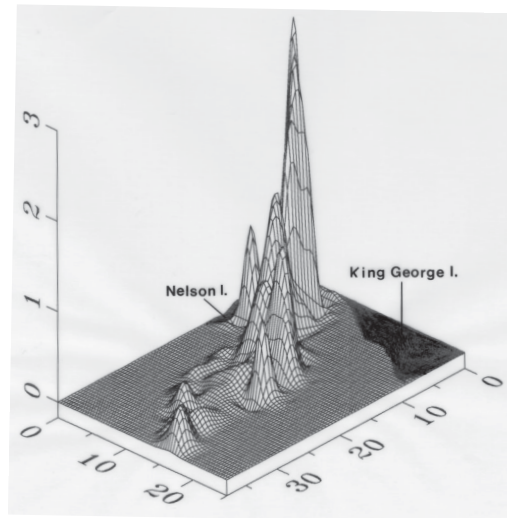


Fig. 3. At-sea area usage (long horizontal axis indicates distance (km) south of Ardley Island; short horizontal axis indicates distance (km) east of Ardley Island) of 17 Chinstrap Penguins breeding at Ardley Island during the 1990/1 austral summer. Values on the vertical axis refer to percentage time spent per km square quadrat.

phases of the dive (*t*-test, values between 2.36 and 20.38, $P < 0.05$) having a mean value of 2.63 ± 0.77 m/s (range 0.1–5.98 m/s, $n = 2734$) for the descent phase, 2.54 ± 0.74 m/s (range 0.5–5.48 m/s, $n = 471$) for the bottom phase and 2.18 ± 0.86 m/s (range 0.1–5.99 m/s, $n = 2734$) during the ascent phase.

The maximum depth reached during the dive was apparently limited by ambient light intensity. Although birds were often at sea at night when light intensity at the surface fell to values of 1-lux or less (depending on the date), no bird ever dived deeper than 22 m at such times. During the day maximum dive depth recorded from any individual was 100.7 m (Fig. 5). Overall, almost 60% of all dives did not exceed a depth of 10 m and c. 80% did not exceed 30 m (Fig. 6).

The sequence of maximum depths reached during a foraging trip was not random. A dive to a particular depth tended to

TABLE 2

Relationship between specified dive parameters (y) and maximum depth reached (x) (m)

Parameter	Relationship with max dive depth	r^2	P
Total dive duration (s)	$y = 34.14 + 1.39 \text{ Depth}$	0.81	<0.001
Descent duration (s)	$y = 11.89 + 0.40 \text{ Depth}$	0.53	<0.001
Bottom duration (s)	$y = -6.21 + 10.46 \ln(\text{Depth})$	0.48	<0.001
Ascent duration (s)	$y = 12.67 + 0.45 \text{ Depth}$	0.5	<0.001
Descent angle (degrees)	$y = -1.47 + 5.41 \text{ Depth}$	0.54	<0.001
Bottom angle (degrees)	–	<0.005	>0.05
Ascent angle (degrees)	$y = -0.22 - 9.05 \ln(\text{Depth})$	0.38	<0.001
Swim speed down (m/s)	–	<0.005	>0.05
Swim speed bottom (m/s)	–	<0.005	>0.05
Swim speed up (m/s)	–	<0.005	>0.05
Rate of change of depth (down) (m/s)	$y = (0.19 + 0.27 \ln(\text{Depth}))^2$	0.7	<0.001
Rate of change of depth (bottom) (m/s)	–	<0.005	>0.05
Rate of change of depth (up) (m/s)	$y = (0.19 + 0.25 \ln(\text{Depth}))^2$	0.71	<0.001

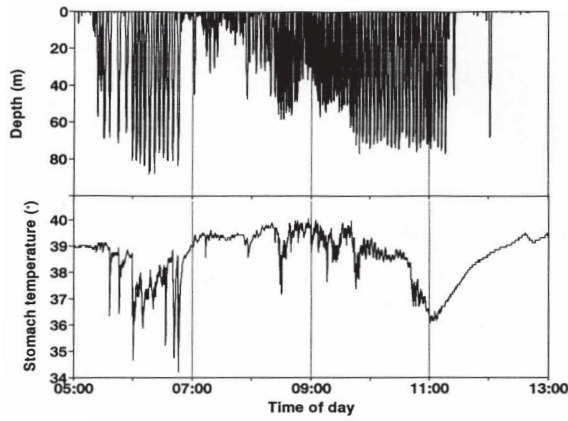


Fig. 4. Example of the diving behaviour (upper trace) of a Chinstrap Penguin foraging from Ardley Island in relation to feeding behaviour, as indicated by stomach temperature (lower trace).

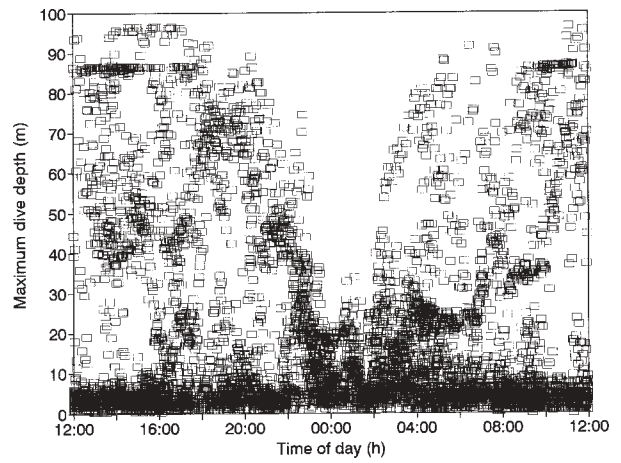


Fig. 5. Maximum depth reached during dives as a function of local time of day for Chinstrap Penguins foraging from Ardley Island.

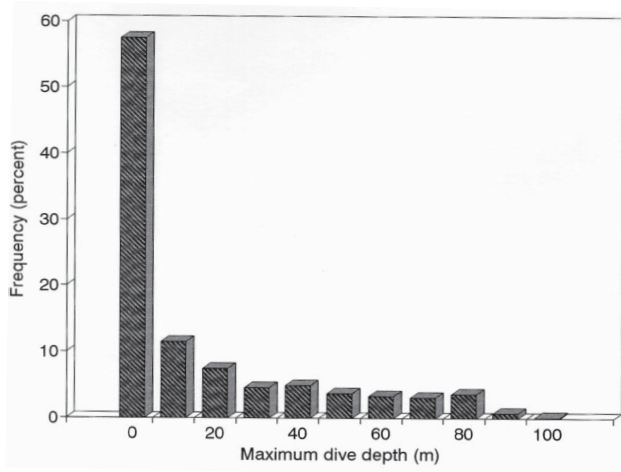


Fig. 6. Frequency of maximum dive depths for Chinstrap Penguins foraging from Ardley Island ($n = 6130$ dives).

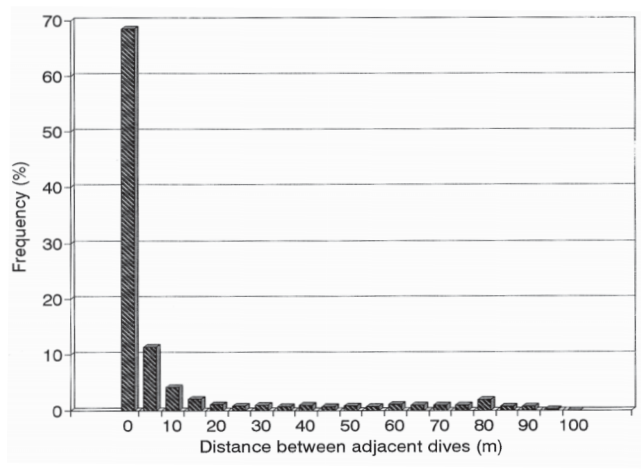


Fig. 7. Frequency of the difference in maximum dive depths between adjacent dives in Chinstrap Penguins foraging from Ardley Island.

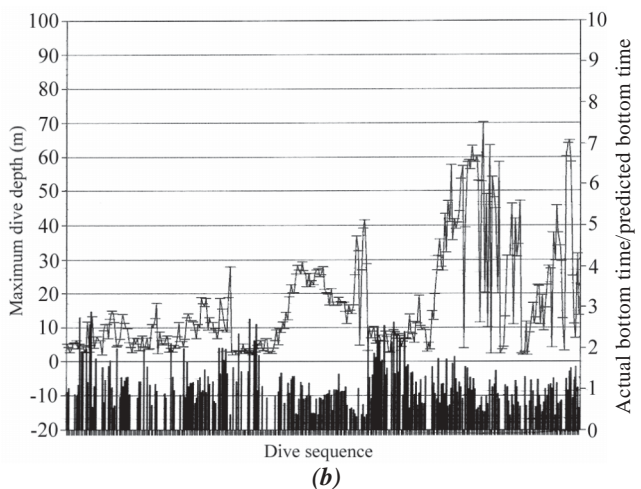
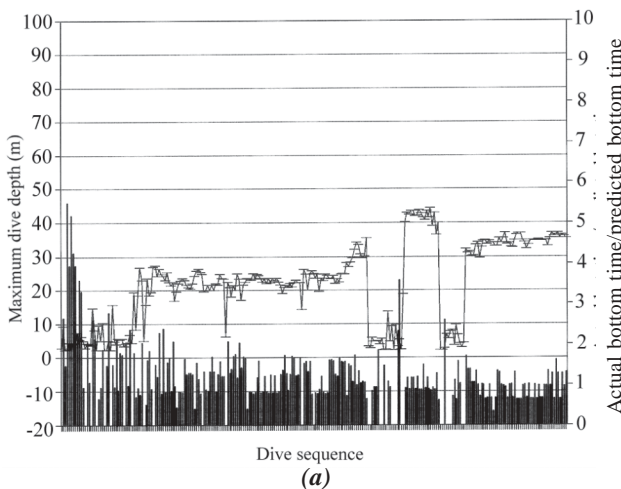


Fig. 8a and b. Sequence of maximum dive depths for two different Chinstrap Penguins during foraging trips. The bars at the bottom of the graphs indicate the extent to which the bottom duration of the relevant dives conforms to the general pattern of bottom duration vs maximum dive depth. This is derived by dividing the observed bottom duration by the predicted duration (determined from the relationship between bottom duration and maximum dive depth (Table 2)). Thus, for example, high bars indicate unusually long bottom durations.

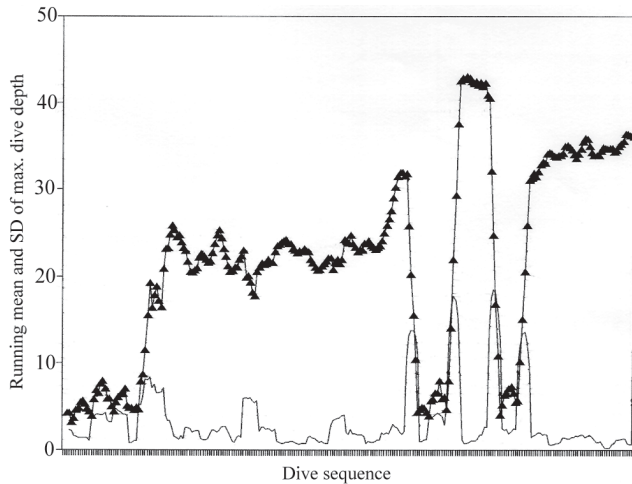


Fig. 9. The running mean (about 5 points) and running standard deviation (about 3 points) of the maximum depth sequence of Fig. 8a. The points where the two lines cross can be taken as junctions between two IBP (see text).

be followed by a dive to a similar depth (Fig. 7) for extended periods before the sequence of maximum depths abruptly changed to a new value (Fig. 8a). Time periods between such abrupt changes we refer to as intra-bout phases (IBPs). The temporal sequence of maximum dive depths within an IBP essentially varied according to one of three patterns:

1. maximum dive depth remained fairly constant over a series of dives (Fig. 8a);
2. maximum dive depth drifted, gradually increasing or decreasing over time although inter-dive differences in maximum dive depth were minimal (Fig. 8b); and
3. although the running mean of the maximum dive depth within an IBP was virtually constant, maximum dive depth was actually bi-modal, with deeper dives to one particular depth stratum being inter-spaced with shallow dives (Fig. 8b).

This latter pattern was most apparent during periods where dives exceeded 60 m, and was particularly marked in dives exceeding 80 m. Although it is fairly easy to determine subjectively what constitutes an IBP within a sequence of depth measurements (cf. Fig. 8), it should be possible to define IBPs mathematically to facilitate analysis and to create clear cut working rules. Consideration of our data showed that if a running mean of five points of the maximum depths reached in a series is plotted against a running standard deviation of three points from the same series, the beginning and end of IBPs are well defined as the points where the line defining the standard deviation crosses the line defining the mean (Fig. 9). The series within two such crossings can be considered an intra-bout phase if there are four or more points within the defined limits (cf. Fig. 9).

Stomach temperature data did not show the fine, temporal resolution necessary to be certain during which dive birds had actually ingested food, especially towards the end of the foraging trip (Fig. 4) (cf. Wilson *et al.* 1995b). This is likely to be due to variation in stomach churning as a result of having to delay digestion of ingested food for the chicks (Peters 1997), which affects the rate of warming of stomach contents (Wilson *et al.* 1995b). However, relatively coarse analysis showed that Chinstrap Penguins did not feed equally at all hours of the day. There was a peak in feeding activity between 06h00 and 09h00 followed by a marked lull at mid-

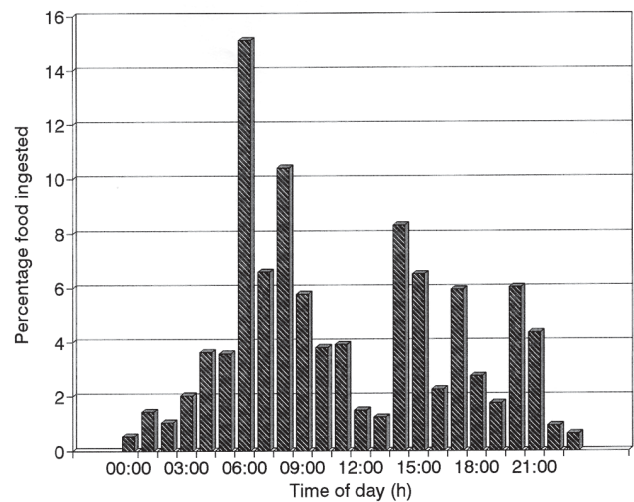


Fig. 10. Amount of prey ingested as a function of time of day by Chinstrap Penguins foraging from Ardley Island.

day. After 14h00 feeding activity generally increased to a higher level which was maintained until 21h00 whereupon it decreased thereafter to a daily minimum around midnight (Fig. 10).

DISCUSSION

Device effects

There have been several studies which clearly demonstrate the extent to which externally-attached devices affect the way penguins forage. Device attachment can reduce swim speed (Wilson *et al.* 1986), dive depth (Wilson 1989), time spent away from the colony to forage (Croll *et al.* 1991, Watanuki *et al.* 1992) and chick-provisioning rate (Watanuki *et al.* 1992). Although the use of device cross-sectional area might give some idea as to the potentially detrimental effects of the system on the birds, it is overly simplistic because it does not account for device shape. We are certain that our MCLs affected foraging behaviour (see below) and it would be naïve to assume that the depth recorders did not do so, although perhaps to a lesser extent. Comparison of dive parameters between MCL- and depth recorder-fitted birds showed that animals carrying the considerably smaller depth recorders diving to specific depths remained underwater for longer by some 10%, having significantly longer descent, bottom and ascent durations (R.P. Wilson & G. Peters unpubl. data). For the purposes of this study, however, this has been ignored and all data lumped. We consider that the patterns presented here represent minimum performances and results should be interpreted as such.

Foraging ranges, areas and track format

Little work has been done on the specific foraging areas of Chinstrap Penguins with chicks. Using foraging trip length and projected swim speed Trivelpiece *et al.* (1986a) suggested that Chinstrap Penguins breeding at Point Thomas (62°10'S, 58°30'W), King George Island have a maximum foraging range of 31 km. Similarly, Lishman (1985) calculated that Chinstrap Penguins breeding at Signy Island, South Orkney Islands have maximum foraging ranges of between 66 and 132 km, depending on the breeding stage. Based on measured distances travelled and a rather speculative factor to correct for

distance acquired due to diving (vertical movement) and non-directional swimming, Wilson *et al.* (1989a) calculated that Chinstrap Penguins from Anvers Island (64°47'S, 64°27'W) had a mean foraging range of only 3 km. The data in the current study show that there can be immense variability in the foraging range of Chinstrap Penguins, this presumably being related to the local availability of krill. Krill appears abundant within Maxwell Bay, because all three *Pygoscelis* species breeding at Ardley Island predominantly feed there (Wilson 1995, cf. Heinemann *et al.* 1989). There are, however, some inter-specific differences in foraging areas for the sympatric *Pygoscelis* penguin species breeding at Ardley Island which might help reduce competition. Gentoo Penguins apparently never move out of Maxwell Bay, not ranging more than 10 km during foraging trips for their chicks (Wilson *et al.* 1998). Both Chinstrap and Adélie Penguins occasionally move out of the bay to forage, travelling up to 40 km away from their breeding island (Wilson 1995).

The looping courses used by the Chinstrap Penguins in our study appear similar to those of Magellanic Penguins *Spheniscus magellanicus* (Wilson *et al.* 1996b) and King Penguins *Aptenodytes patagonicus* (Jouventin *et al.* 1994). Both these penguin species were, however, absent for considerably longer periods. Since prey density is likely to increase with increasing distance from the breeding site due to inter- and intra-specific competition (Birt *et al.* 1987) it is reasonable that during the initial phases of the foraging trip birds should move away from the island fairly rapidly. At some point, however, increasing prey density with increasing distance from the colony will be balanced by increased travelling time and the energetic costs associated with this. This might explain why penguin foraging tracks eventually become much less directional although birds still do tend to move away from the island. When appropriately satiated, birds move directly back to the island, although deep dives may occur on the return route suggesting that birds are still foraging opportunistically.

Diving behaviour

The diving behaviour of Chinstrap Penguins from Ardley Island was very similar to that reported for the species at Seal Island (61°S, 55° 25'W), South Shetland Islands, by Bengston *et al.* (1993, see also Trivelpiece *et al.* 1986). Birds essentially exploited the top 100 m of the water column although most dives were not deeper than 30 m which is fairly typical for a penguin of this size (Wilson 1995). Increases in dive duration with increasing maximum dive depth were also found by Bengston *et al.* (1993) and seem to be a standard feature of penguin foraging behaviour (e.g. Gentoo Penguins (Williams *et al.* 1992, Wilson *et al.* 1996a), Adélie Penguins (Chappell *et al.* 1993), King Penguins (Kooyman *et al.* 1992, Pütz 1994), Emperor Penguins *A. forsteri* (Kooyman & Kooyman 1995, Kirkwood & Robertson 1997), African Penguins *Spheniscus demersus* (Wilson & Wilson 1995), Humboldt Penguins *S. humboldti* (Luna & Culik 1999), Rockhopper Penguins *Eudyptes chrysocome* (Wilson *et al.* 1997), and Little Penguins *Eudyptula minor* (Bethge *et al.* 1997). Results from other species also suggest that dive and return-to-surface angles increase with increasing maximum dive depth which increases descent rate because swim speeds remain essentially constant (Wilson & Wilson 1995, Wilson *et al.* 1996a, R.P. Wilson unpubl. data).

Allometry is important in consideration of penguin diving capacities. Large body size seems to confer a number of advantages with respect to foraging in penguins in that larger

species stay underwater for longer, dive deeper, and appear to be able to swim faster (summarized in Wilson 1995, Schreer & Kovacs 1998). Chinstrap Penguins are the smallest of the *Pygoscelis* penguins and are thus expected to be the most restricted in their diving and swimming abilities, something that would apparently give them a competitive disadvantage when compared to Adélie or Gentoo Penguins (Wilson 1995). In fact, although the diving performance of Chinstrap Penguins conforms to the allometric trend (Wilson 1995), these birds swim markedly faster than do other similarly-sized, and even larger, species. Only the 35-kg Emperor Penguin habitually appears to swim faster at 3 m/s (Kooyman *et al.* 1992). Of the congeners, the normal swim speed of Adélie Penguins is 2.2 m/s and that of Gentoo Penguins is only 1.8 m/s (Culik *et al.* 1994). Values for other species range from 1.8 m/s for Little Penguins (Bethge *et al.* 1997) to 2.2 m/s for King Penguins (Kooyman *et al.* 1992) (other values are summarized in Wilson 1995). It is perhaps worth pointing out that Culik *et al.* (1994) found the lowest cost of transport in Chinstrap Penguins to be at speeds of 2.4 m/s, again, the highest of the *Pygoscelis* species, and a figure that accords well with that found in our study.

Intra-bout phases

The observation that Chinstrap Penguins dive in well-defined intra-bout phases raises questions as to the role of such behaviour and implies particular foraging interest at specific depths. Depths at which particular foraging interest occurs can be examined by looking at bottom durations (the time the birds spend at the bottom in 'U-shaped' dives) because Wilson & Wilson (1995) noted that African Penguins only execute dives with an appreciable bottom phase when prey are captured. This is not the case, however, in Adélie Penguins where birds execute a considerable number of U-dives without ingesting prey (Wilson *et al.* 1993, cf. Chappell *et al.* 1993) and the situation appears similar in Chinstrap Penguins. Nonetheless, the fact that birds remain for extended periods at specific depths indicates a disproportional interest in these depths which is likely to enhance their chances of prey location or capture (Wilson *et al.* 1996a). For this reason we created a bottom-phase index to determine which bottom phases were unexpectedly short or long; First we used our regression of bottom duration against maximum depth (Table 2) to predict the expected bottom duration for any particular dive. We then divided the observed bottom duration by the expected duration (e.g. Figs 8a,b). Mathematically, the bottom duration index

$$(BDI) = O_{bd}/(10.46\ln(\text{Depth}))$$

where O_{bd} = Observed bottom duration.

Values above 1 constitute longer than expected bottom durations, values less than 1 being shorter than expected for the given depth. Consideration of this in relation to IBPs showed strikingly that the bottom duration index fell virtually to zero every time a IBP began, irrespective of the value of the bottom duration index within adjacent IBPs (e.g. Fig. 8a). In other words, a change from one IBP to another was always marked by V-dives. In order to determine whether the characteristics of these V-dives were different to those of other dives, we regressed the mean of the descent plus the ascent angles in all dives against maximum depths reached and found the best fit to be:

$$\text{angle} = -1.06 + (5.86 \text{ Depth}) (r^2 = 0.47, P < 0.001).$$

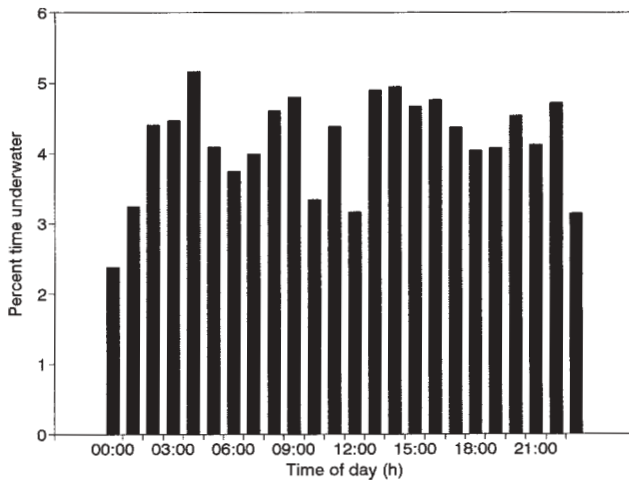


Fig. 11. Percentage time spent underwater as a function of time of day in Chinstrap Penguins foraging from Ardley Island.

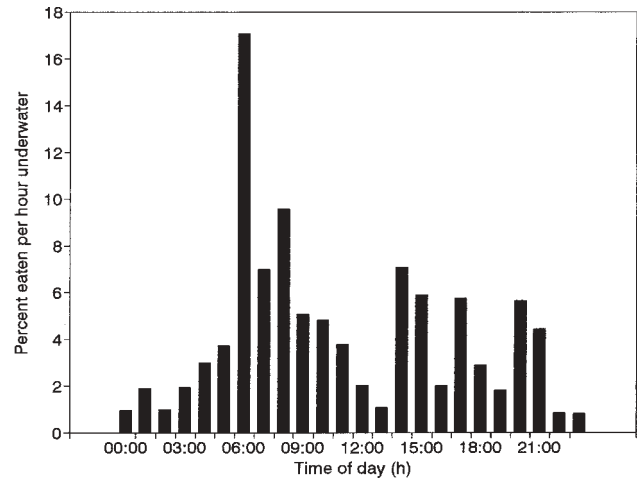


Fig. 12. Relative catch per unit effort in Chinstrap Penguins foraging from Ardley Island as a function of time of day. Catch is the total amount ingested per hour and effort is the total time spent underwater per hour.

As above, we then divided the observed mean of the descent and ascent angles by the predicted angle to obtain an angle index. Consideration of this angle index with the bottom duration index and IBPs showed that it was also unusually high, coincident with the low bottom duration indices at the point where one IBP changed into another. Mean angle index at IBP junctions was 1.4 ± 0.47 , $n = 57$, significantly higher than the mean angle index within IBPs (Mean = 1.07 ± 0.37 , $n = 443$, for a random selection of dives within IBPs; t -test, $P < 0.05$). The actual value for the mean of the dive and return to the surface angles for dives at IBP junctions was not related to maximum depth reached during the dives and was 32.2° (SD 12.7). It would thus appear that when an IBP is terminated, birds begin a very particular type of searching behaviour which determines to a large extent the depth likely to predominate in the following IBP.

During most dives, it is clear that the birds 'know' to which depth they will dive from the moment they leave the water surface, this being indicated by both the dive angle and (consequently) the rate of descent. There are clear advantages to this as it allows the penguins to be physiologically prepared for the dive in question. The initial dives in an IBP do not conform to this. The mean dive angle adopted by Chinstrap Penguins at the onset of a new IBP was $32.2 \pm 12.7^\circ$ to a mean dive depth of 21.4 ± 12.7 m. A dive angle of 32.2° would normally be adopted for dives to 42 m. Furthermore, subsequent to such dives birds immediately select a depth corresponding approximately to the point of maximum depth of the steeply-angled V-dive and begin executing apparently normal searching/foraging dives with expected bottom durations and appropriate dive angles. Thus, it would appear that during the execution of the initial dive of an IBP a decision is made about the depths to be exploited over the course of the IBP. It is unlikely that prey are actually sighted during such dives since penguins only encounter prey during a rather low percentage of dives and, in any event, there is nothing in the dive profile or swim speeds to indicate prey capture (cf. Wilson and Wilson 1995). Rather, it may be that birds somehow look for cues within the water column that might indicate the likely presence of prey at particular depths. The unusually steep angles in these dives may occur because Chinstrap Penguins do not yet know the depth to which they will dive, although a steep angle ensures that they can dive deeply if no appropriate cues occur in shallower depth strata.

The pattern of change of maximum depths within IBPs is difficult to explain. It is conceivable that both changes in mean dive depth (cf. Fig. 8b) as well as a series of relatively constant depths (cf. Fig. 8a) could be attributed to krill vertical movement, or lack of it. Neither case is apparently consistently indicative of feeding if the bottom duration index is to be used as a measure of prey ingestion. Consideration of STL data in conjunction with variation in maximum depth over an IBP is equivocal due to lags in the response of the system, especially if birds have already ingested prey (cf. Wilson *et al.* 1995). The case of bi-modality in the frequency of maximum dive depths within an IBP (cf. Fig. 8b) is perplexing. Because this pattern occurs more commonly when one of the modes is particularly deep (Fig. 7) it may serve a physiological function (G. Peters unpubl. data). Certainly, given the patchy distribution of krill down the water column (cf. Everson 1982, Godlewska & Klusek 1987), such bimodality is unlikely to represent feeding at both represented depths, quite apart from the fact that it would seem an inappropriate strategy for air-breathers to exploit krill at great depths if they are also close to the surface.

Feeding rhythms

It has been suggested that the change in depth utilisation by marine endotherms, whereby animals systematically dive deeper during the hours of daylight, is linked to the movements of prey species since many pelagic prey exhibit marked diel vertical migration, moving closer to the surface at night (e.g. Croxall *et al.* 1985, Kooyman *et al.* 1992). In doing so they not only become more accessible for air-breathing predators, but also increase in density which should facilitate their capture (Kooyman *et al.* 1992). However, movement of plankton close to the surface at night is thought to allow these animals to feed while being difficult to locate for visually-dependent predators (Gliwicz 1986). Our data indicate that if krill in the Maxwell Bay area did indeed exhibit diel vertical migration according to the classic schema (cf. Godlewska & Klusek 1987) there were no immediately obvious benefits to Chinstrap Penguins at night (Fig. 10). However, it is clear that Chinstrap Penguins do occasionally ingest prey during hours of darkness. The ease with which the birds can do this can be alluded to by electing some measure of catch per unit effort.

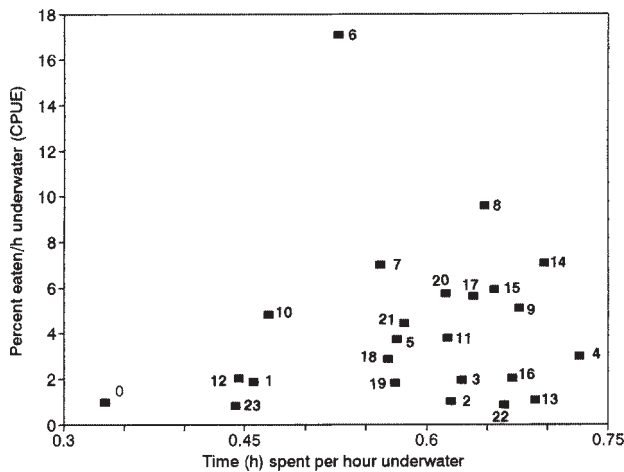


Fig. 13. Percent mass ingested per hour underwater (CPUE) as a function of time spent underwater (effort) for that relevant time period. Numbers next to the squares indicate the relevant hour of the day to which the data correspond.

Here, we consider that the time spent underwater per hour of the day can be used as a measure of effort and the amount ingested corresponds to the catch. Thus, Chinstrap Penguins breeding at Ardley Island apparently reduce their foraging effort at night (both in the number of dives per hour as well as in the total amount of time spent underwater per hour) (Fig. 6) which accounts, in part, for the reduced feeding rate at night. However, despite this, dividing the catch per hour (Fig. 10) by the effort (Fig. 11) shows that birds forage markedly less successfully at night than during the day (Fig. 12). The simplest explanation for this is that the birds are visual predators (e.g. Howland & Sivak 1984, Martin & Young 1984) and are unable to see prey well enough at night to be able to forage effectively. Whether the few prey that they ingest are detected by bioluminescence or star- or moonlight remains to be determined.

A similar situation has been proposed for Adélie and Gentoo Penguins breeding at Ardley Island. Both these species dive at night although neither appears to feed (Wilson *et al.* 1993). It is notable, however, that the maximum depths reached during periods of maximum darkness during January (<10 m for both species) are considerably less than those reached by Chinstrap Penguins. As is the case for the Chinstrap Penguin, it has been suggested that both species are primarily visual predators and that they cannot effectively forage at night, their lower critical limit in light levels being 1 lux (Wilson *et al.* 1993). In this respect, therefore, it would appear that Chinstrap Penguins can forage more effectively than either congener during periods of twilight because Chinstraps dive deeper at this time, despite the fact that catch per unit effort is relatively low. This ability may give Chinstrap Penguins a competitive advantage over sympatric congeners when prey are scarce.

The extent to which birds tailor foraging effort to tie in with apparent prey accessibility (cf. Figs 10, 11) can be examined by regressing CPUE against effort (Fig. 13). Here, the drop in CPUE around midnight is mirrored by a substantial reduction in time spent underwater. That birds dive at all at this time may rather be a reflection of birds commuting to or from the feeding sites than a genuine attempt to forage (cf. Heath 1985, Wilson *et al.* 1993, Pütz 1994). The drop in the amount of food ingested at mid-day is perplexing and not atypical in penguins.

A similar pattern has been noted in African (Wilson & Wilson 1995), King (Pütz 1994) and Adélie Penguins (Wilson *et al.* 1993). Since, in all the above cases, birds were foraging for chicks it is conceivable that the birds forage for themselves during the early phase of the foraging trip, digesting fast, before foraging for their chicks at a later time when digestion must be slowed or stopped (cf. Wilson *et al.* 1989b). Moreno & Sanz (1996) have ascertained that Chinstrap Penguins foraging for chicks need to ingest *c.* 1670 g of krill per foraging trip in order to support their brood and their own energetic needs. Since Chinstrap Penguin stomachs only hold a maximum of *c.* 550 g (unpubl. data), it is clear that digestion must be rapid, at least during the initial phase of the foraging trip (Peters 1997). In addition, stomach temperature traces from *Pygoscelis* penguins foraging for chicks show patterns indicative of rapid, complete stomach mixing during the first part of a foraging trip, followed by little, or no, mixing later on (Wilson *et al.* 1995, Peters 1997).

Otherwise, the lull in feeding activity at mid-day might be simply a reflection of the fact that the vertically-migrating krill have moved to depths beyond which Chinstrap Penguins can effectively hunt. This explanation is, however, difficult to equate with the situation at 13h00 where birds invested an enormous amount of effort foraging with little return. A more insidious explanation of this would be that although the device-equipped birds attempted to forage just after mid-day, the recording units precluded them from reaching the necessary greater depths (cf. Wilson 1989, Wilson & Culik 1992). Certainly our equipped birds in this study dived deeper and longer when equipped with the smaller depth recorders than with the MCLs (R.P. Wilson & G. Peters unpubl. data).

In conclusion, the Chinstrap Penguin at Ardley Island foraging for chicks is an inshore feeder and conforms with penguin allometric tendencies in being a rather shallow diver. This would appear to put the bird at a competitive disadvantage compared to the larger, deeper-diving sympatric Adélie and Gentoo Penguins. However, Chinstrap Penguins swim markedly faster than either conspecific, which presumably enables them to search water volumes at a higher rate. In addition, Chinstrap Penguins can apparently forage at lower light intensities than the other two species, which enables them to exploit greater depths at night. Chinstrap Penguins show a number of peculiarities in their diving behaviour, such as very specific intra-bout phases, which indicate that the process of prey location is non-random and likely to be extremely complex.

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