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The diving behaviour of brooding king penguins (*Aptenodytes patagonicus*) from the Falkland Islands: variation in dive profiles and synchronous underwater swimming provide new insights into their foraging strategies

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Abstract The diving behaviour of king penguins (*Aptenodytes patagonicus*) was studied on the Falkland Islands, where a small population (ca. 300 fledglings year⁻¹) is located at the geographical limit of their breeding range. King penguins rearing newly hatched chicks were equipped with time-depth recorders before leaving for sea. In total, 20,175 dives > 3 m were recorded from 12 birds during 15 foraging trips with a mean duration of 5.7 ± 2.3 days. The majority of the trips was directed up to 500 km to the northeast of the breeding colony in slope waters of, and oceanic waters beyond, the Patagonian shelf. Mean time spent underwater accounted for 42 ± 9% of the foraging trip. Mean dive depth achieved was 55 ± 16 m; maximum dive depth recorded was 343 m. Mean dive duration was 159 ± 25 s; maximum dive duration was 480 s. The mean vertical distance covered was 140 ± 65 km trip⁻¹; and on average birds covered 25 km day⁻¹. Synchronous diving behaviour was observed in two birds for a period of about 24 h after leaving the colony. Dive depth correlated positively with: (1) light intensity, (2) dive duration and (3) vertical velocities, thus confirming previous findings obtained from conspecifics at other breeding sites and indicating comparable diving behaviour. However, separation of dives according to their profile—V-, U-, or W-shaped—revealed signifi-

cant differences between certain dive parameters. For a given depth range, bottom time was longer and vertical velocities higher in W-dives than in U-dives. This, together with a higher number of W-dives at dawn and dusk, suggests that foraging is more effective during W-dives than U-dives, and during twilight. These findings imply that king penguins have to make more complex decisions, individually and socially, on the performance of the subsequent dive than previously thought.

Introduction

King penguins (*Aptenodytes patagonicus*) breed on sub-Antarctic islands within the vicinity of the Antarctic Polar Front (APF). With a population of > 2 million breeding pairs (Woehler 1993), they are recognised as a major consumer in the Southern Ocean. Many aspects of their foraging ecology have been intensively studied at various breeding sites, including their diving behaviour (Kooyman et al. 1992; Charrassin et al. 1998, 1999; Pütz et al. 1998; Moore et al. 1999; Charrassin and Bost 2001; Charrassin et al. 2002; Wienecke and Robertson 2002) and diet (for summary see Cherel et al. 2002).

Over the past 50 years, concurrently with a general population increase (Woehler and Croxall 1997; Weimerskirch et al. 2003), a small king penguin population has become established on the Falkland Islands. Over the last decade, it has had an average annual breeding success rate of about 300 chicks (Clausen and Huin 2003; Pütz, unpublished data). Apart from some breeding pairs found amongst colonies of gentoo penguins (*Pygoscelis papua*), one single king penguin breeding colony is situated at Volunteer Beach (East Falkland). This site differs in many respects from other king penguin breeding locations, because the Falkland

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Islands are: (1) the most temperate of all breeding sites; (2) furthest from the birds' main summer foraging grounds at the Antarctic Polar Front (Pütz 2002), situated >500 km to the southeast (Peterson and Whitworth 1989); (3) located on the south-eastern edge of the highly productive Patagonian Shelf; and (4) located in an area where a major multinational fishing fleet has been targeting squid and finfish since the early 1980s (Barton 2002).

Dives of air-breathing marine top predators such as turtles (e.g. Hochscheid et al. 1999; Houghton et al. 2002), seals (e.g. Campagna et al. 1995; Schreer and Testa 1996) and penguins (e.g. Kooyman et al. 1992) are commonly classified according to their shape. In penguins, three different dive types have been identified: V-, U- and W-shaped dives (Wilson 1995). V-dives are believed to be purely exploratory (Wilson 1995), whereas U- and W-dives represent different prey-capturing strategies, with prey pursuit occurring predominantly during the ascent and bottom phases, respectively (Kirkwood and Robertson 1997; Ropert-Coudert et al. 2000). The recent development of data loggers with sufficient memory has allowed researchers to monitor the diving behaviour in great detail over extended periods. Thus, diving data can now be closely analysed in terms of the different dive types and their relationships to other parameters such as, for example, time of day and dive duration, in order to further explain the diving behaviour of these animals in relation to their environment. The aim of this study was to: (1) describe, for the first time, the diving behaviour of king penguins from the Falkland Islands and (2) establish their different diving strategies.

Materials and methods

Field work was carried out at Volunteer Beach in the northeast of East Falkland (51°29'S; 57°50'W) between 5 and 20 February 2001 (Fig. 1). Birds (*Aptenodytes patagonicus*) were selected from pairs in a partner role exchange, where individuals freshly returned from foraging at sea take over brooding duties. During the partner role exchange, sex was determined acoustically by comparing the calls of both birds (Derenne et al. 1979). Those that were due to depart to sea after the exchange were followed visually and captured outside the colony. After covering the head and immobilising the penguin to minimise disturbance, devices were attached on the mid-line of the back as far distally as possible without impairing the preen gland, using black tape (Tesa, Beiersdorf, Hamburg, Germany) and two-component neoprene glue (Deutsche Schlauchbootfabrik, Eschershausen, Germany) according to the method described by Wilson et al. (1997). The devices were then covered with a layer of quick epoxy (Loctite 3430, Loctite Deutschland, Munich, Germany) to prevent the birds from removing the tape with their beaks. The whole process took <20 min per bird.

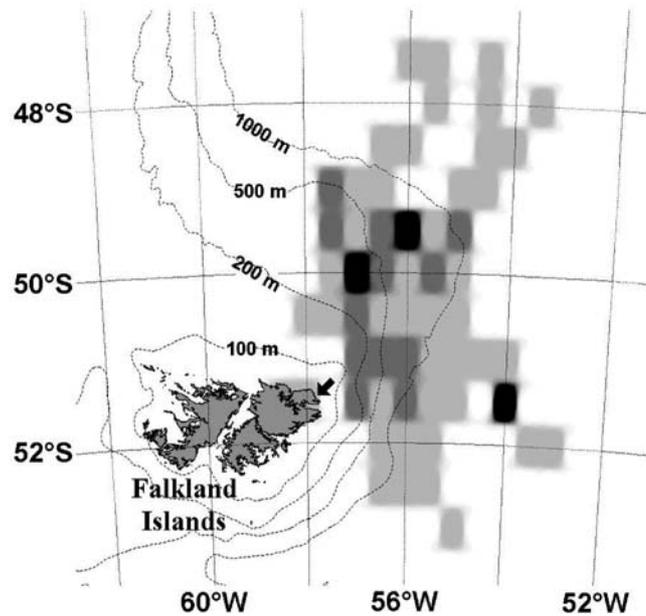


Fig. 1 *Aptenodytes patagonicus*. Density plot of the foraging area of king penguins breeding at Volunteer Beach (indicated by an arrow) on the Falkland Islands. The darker the shading, the more locations were obtained for that specific grid square (0.5° latitude × 0.5° longitude)

Technical details of TDRs

The time-depth recorders (TDRs) used (MK7, Wildlife Computers, Redmond, USA) were embedded in epoxy resin and hydrodynamically shaped following the recommendations by Bannasch et al. (1994). The devices weighed approximately 30 g, equivalent to <0.3% of the average penguin body mass (Williams 1995), and their maximum dimensions were 98.5 × 20 × 10 mm. They were programmed with MK7HOST (Wildlife Computers) and set to record every 5 s while the bird was in contact with salt water. Data were stored in a 2 Mb Flash EPROM chip, which could record up to 2 million data points. The TDRs were each equipped with a pressure sensor, a light sensor and a temperature sensor. The pressure sensor recorded dive depth between 0 and 350 m, accurate to within 0.5 m (range 0–20 m), 1 m (range 20–200 m) and 5 m (range 200–350 m). The light sensor recorded light intensity on a logarithmical scale ranging between $2 \times 10^{-10} \text{ W cm}^{-2}$ and $1 \times 10^{-2} \text{ W cm}^{-2}$. Data collected by the temperature sensor were not considered in this study.

Data analysis

Measurement of ambient light intensity can be used to determine the geographic position of the device, because day length and the time of midday, compared to Greenwich mean time, are a function of geographic locality and date (Wilson et al. 1992; Hill 1993). Light data were analysed for position using GEOLOCATION

(Wildlife Computers, USA). As the error associated with individual positions can be of the order of several tens of kilometres (Welch and Eveson 1999; Wilson et al. 2005), the positional data obtained were smoothed and then transferred into MAPINFO (MapInfo, USA) to create a density distribution plot. During the study period, time of sunrise moved from 0538 to 0602 hours and sunset from 2032 to 2007 hours local summer time, with civil twilight beginning and ending about 40 min before and afterwards, respectively.

Dive data were first corrected for potential drift using the programme ZOC (Zero Offset Correction, Wildlife Computers) and then analysed with DIVE ANALYSIS (Wildlife Computers). Only dives exceeding 3 m were considered, because dives < 3 m were unlikely to be reliably resolved with the settings chosen. For each dive the following parameters were determined: date and time, maximum dive depth, total dive duration, descent and ascent velocities, bottom time (i.e. time spent at 85% of the maximum depth), number of depth undulations (i.e. spontaneous deviations ≥ 2 m from the mean dive depth) during the bottom time, and post-dive time (i.e. surface recovery period after individual dives). For further analysis, dives were classified according to their shape into V-dives (no bottom time), U-dives (bottom time, but no undulations) and W-dives (undulations occurring during bottom time) (cf. Wilson 1995).

Following Ydenberg and Clark (1989), the diving efficiency DE can be calculated as: $DE = \text{bottom time} / (\text{dive duration} + \text{post-dive time})$.

Post-dive time is dependent on the amount of oxygen used during the preceding dive. However, other factors may also contribute to this parameter, for example resting periods or oxygen deficits built up over a number of previous dives. In order to eliminate all but the purely physiological factors contributing to the surface time, calculation of diving efficiency was restricted to dives

followed by a post-dive time of < 1,000 s (corresponding to about 2.5×maximum dive duration).

Statistical analysis to show the differences between U- and W-dives was carried out on a subsample containing 750 randomly selected dives from one of each bird's foraging trips. These dives were pooled and classed into 50-m categories to perform Mann–Whitney *U*-tests.

Results

Foraging area

The king penguins (*Aptenodytes patagonicus*) studied foraged to the east and northeast of the breeding colony beyond the Patagonian shelf slope, where water depth rapidly increases from 200 m to over 1,000 m (Fig. 1). The maximum distance from the breeding colony was estimated to be about 500 km. However, all birds with a trip duration of < 5 days (Table 1) foraged not further away than 300 km from the colony in water depths between 200 and 1,000 m.

General characteristics of the foraging and diving behaviour

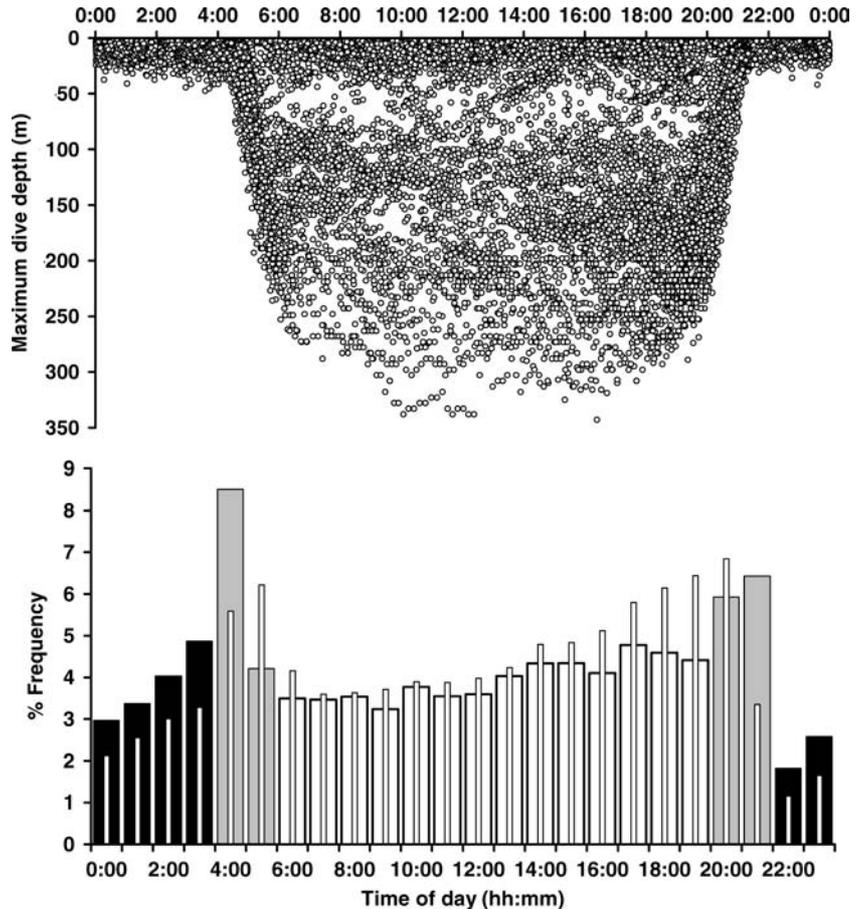
The diving activities of 12 king penguins were monitored during 15 foraging trips with a mean duration of 5.7 ± 2.3 days (Table 1). Overall, 20,175 dives > 3 m were recorded. The distribution of maximum dive depths in relation to time of day indicated that night dives never exceeded 50 m, whereas maximum dive depth increased with sunrise and decreased again at sunset (Fig. 2a). During the day, dive depth ranged between 3 and 343 m.

With respect to time of day (Fig. 2b), nearly twice as many dives were performed during twilight hours (25%

Table 1 *Aptenodytes patagonicus*. Summary of diving parameters for king penguins equipped with time-depth recorders at Volunteer Beach, Falkland Islands, during the brooding period (M male; F female)

Bird no.	Sex	First dive		Trip duration (days)	Total no. of dives (<i>n</i>)	Time spent underwater (%)	Vertical distance covered (km)	Dive depth (m)		Dive duration (s)	
		Date	Time					Max.	Mean	Max.	Mean
K66	M	8 Feb	1558 hours	6.0	1,475	50.4	155.4	343	53	460	165
K67	M	7 Feb	1857 hours	9.5	2,994	57.7	266.2	248	45	360	132
K68	M	7 Feb	1003 hours	9.2	2,198	44.3	233.5	292	53	460	168
K69	M	8 Feb	1202 hours	4.8	1,137	42.5	134.4	305	59	455	182
K72	F	7 Feb	1447 hours	3.6	590	22.3	33.9	171	29	355	121
		14 Feb	1124 hours	4.0	837	38.8	103.3	274	62	455	167
K73	F	6 Feb	1601 hours	4.1	1,029	45.6	115.6	303	56	435	152
		15 Feb	1714 hours	4.2	887	45.3	166.1	338	94	460	195
K74	M	7 Feb	0802 hours	2.5	450	33.0	50.9	233	57	395	153
		14 Feb	1516 hours	4.0	1,149	55.8	138.1	278	60	425	165
K75	M	6 Feb	1739 hours	7.1	1,788	42.4	176.7	289	49	455	151
K76	F	7 Feb	0807 hours	6.3	1,475	36.5	119.1	288	40	480	130
K77	M	6 Feb	1508 hours	4.8	756	39.6	123.5	243	82	460	213
K79	F	6 Feb	1437 hours	5.0	895	30.3	74.2	273	42	395	131
K80	F	7 Feb	1846 hours	9.7	2,515	48.2	212.8	238	42	445	159

Fig. 2a, b *Aptenodytes patagonicus*. **a** Maximum dive depth and **b** frequency of the number of dives (*thick bars*) and time spent underwater (*thin bars*) as a function of time of day. Night time is indicated by *black*, twilight by *grey* and daylight by *open bars*



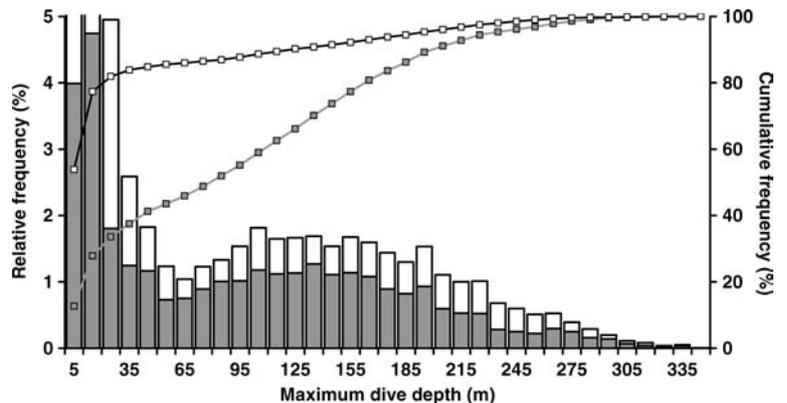
of all dives within 4 h, corresponding to $6.25\% \text{ h}^{-1}$ at twilight) as were undertaken during daylight (55% of all dives within 14 h, corresponding to $3.9\% \text{ h}^{-1}$ in daylight). The number of dives was lowest during the night (20% within 6 h, corresponding to $3.3\% \text{ h}^{-1}$ in darkness).

The mean time spent underwater during the foraging trips recorded was $42.2 \pm 9.4\%$ (Table 1). With regard to specific hours of the day, time spent underwater was also lowest during the night (total 14% or $2.3\% \text{ h}^{-1}$), whereas during daylight twice as much time was spent underwater (total 64% or $4.6\% \text{ h}^{-1}$). Again, the time

spent underwater was highest during twilight hours (total 22% or $5.5\% \text{ h}^{-1}$).

As regards the dive profile, nearly two-thirds of all dives were U-shaped (63%), with W-shaped dives making up 31%. Only 6% of all dives were V-dives, which never exceeded a depth of 30 m and were excluded from further analysis. Frequency analysis of maximum dive depths indicated a bimodal distribution (Fig. 3), with a preference for shallow dives up to 30 m in depth and another preference for dives ranging between 100 and 200 m. A minimum occurred between 60 and 70 m. However, in dives exceeding 40 m, the proportion of

Fig. 3 *Aptenodytes patagonicus*. Relative (*bars*) and cumulative (*line*) frequencies of the number of U-dives (*open*) and W-dives (*grey*) in relation to maximum dive depth. The relative frequency of U-dives in 5-, 15- and 25-m depth classes was calculated to be 37.0%, 16.1% and 3.2%, respectively



W-dives was always higher than U-dives. Accordingly, the mean maximum dive depth during U-dives was 35.6 ± 62.9 m, whereas the mean maximum dive depth during W-dives was 94.0 ± 78.7 m, this difference being significant (Kruskal–Wallis H -test, $P < 0.001$).

With regard to time of day, most dives during hours of twilight were W-dives, whereas the percentage of W-dives was lower in dives performed during daylight (Fig. 4). At night, only around 20% of all dives were W-dives. The mean number of undulations in W-dives was 1.5 ± 0.9 min^{-1} bottom time, the maximum number of nine undulations during a single dive was achieved independently by three different birds.

The frequency distribution of the dive durations also showed a bimodal distribution, with one maximum obtained between 60 and 110 s and a second, smaller one, between 250 and 310 s (Fig. 5). Dive duration was positively correlated to maximum dive depth (based on all dives: $y = 68.407 \ln(x) - 46.468$; $r^2 = 0.87$), whereas bottom time duration increased up to dive depths of about 90 m and thereafter remained more or less constant (Fig. 6). Based on 50-m classes, the duration of dives < 50 m was significantly longer in W-dives (Mann–Whitney U -test, $P < 0.001$), while U-dives > 150 m lasted significantly longer than W-dives (Mann–Whitney U -test, $P \leq 0.01$). However, over the entire depth range bottom time duration was significantly longer in W-dives than in U-dives (Mann–Whitney U -test, $P < 0.001$).

The mean vertical distance covered was 140.2 ± 64.6 km per foraging trip. The relationship between vertical distance covered and foraging trip duration was linear (constrained to pass through the origin) and best described by: vertical distance (km) = 24.7 foraging trip duration (days); $r^2 = 0.75$, $P < 0.001$, indicating that the birds travelled on average 25 km day^{-1} in a vertical direction.

Vertical velocities were divided into descent and ascent phases. Towards both extremes of the dive range, i.e. very shallow and very deep dives > 300 m, descent

and ascent rates were similar, whereas in between descent velocity was generally higher than ascent velocity (Fig. 7). This difference became even more pronounced when data were separated into U- and W-dives (Fig. 8). Notably, vertical velocities in U-dives, during both descent and ascent, were in each depth class significantly lower than the vertical velocities calculated for W-dives (Mann–Whitney U -test, $P < 0.001$).

Diving efficiency (DE) was calculated to be 0.25 ± 0.12 for all dives; however, separate calculations for U- and W-dives revealed significantly different values of 0.21 ± 0.09 and 0.33 ± 0.12 , respectively (Mann–Whitney U -test, $P < 0.001$). DE was also highest during hours of twilight (0.27 ± 0.17), whereas it was more or less similar during day (0.22 ± 0.10) and night (0.23 ± 0.13).

Synchronous diving behaviour was observed in two birds, K72 and K79, while departing from the colony (Fig. 9). Both birds dived simultaneously for a period of about 24 h before K79 made some shallow dives interspersed with deep dives, which separated the two birds for the rest of their respective foraging trips. Usually, king penguins gathered on the beach before departing in groups, whereas birds returned from foraging trips alone (authors' personal observations).

Discussion

Foraging area

Positional data derived from light intensity data are subject to considerable bias (for review see Welch and Eveson 1999; Wilson et al. 2005). However, circumstantial evidence strongly suggests that the king penguin (*Aptenodytes patagonicus*) foraging area identified in the eastern and north-eastern slope waters of the Falklands (Fig. 1) in fact represented their true foraging grounds. The main oceanographic feature in the area is the Falkland Current (Glorioso and Flather 1995), which

Fig. 4 *Aptenodytes patagonicus*. Proportion of W-dives in relation to maximum dive depth for night time (black bars), twilight (grey bars) and daylight (open bars)

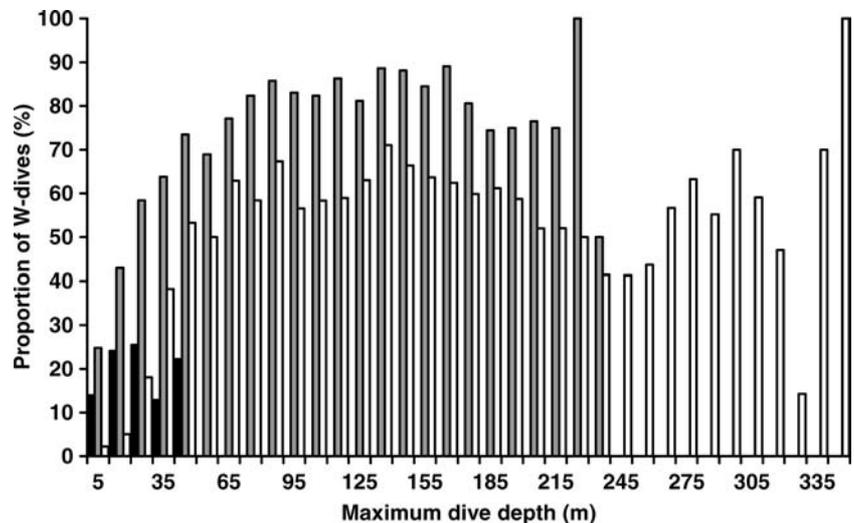


Fig. 5 *Aptenodytes patagonicus*. Relative (bars) and cumulative (line) frequency distribution of the dive duration of U-dives (open; $n=12,636$) and W-dives (grey; $n=6,339$)

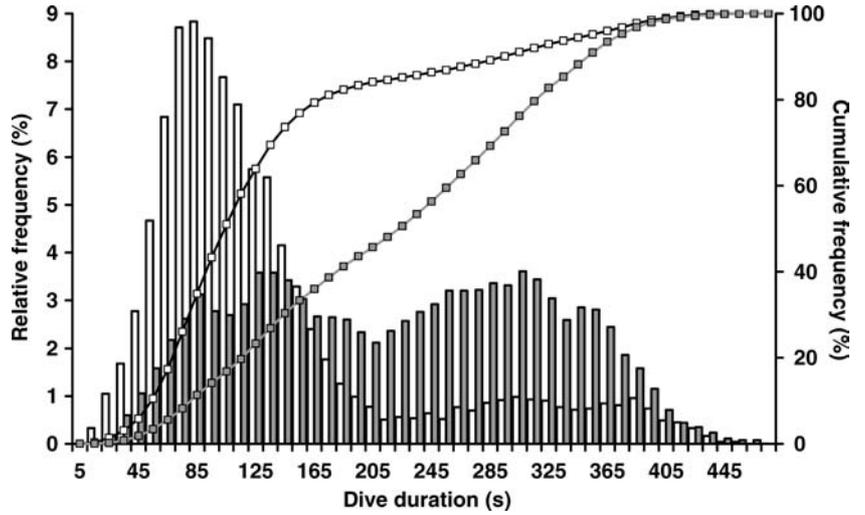
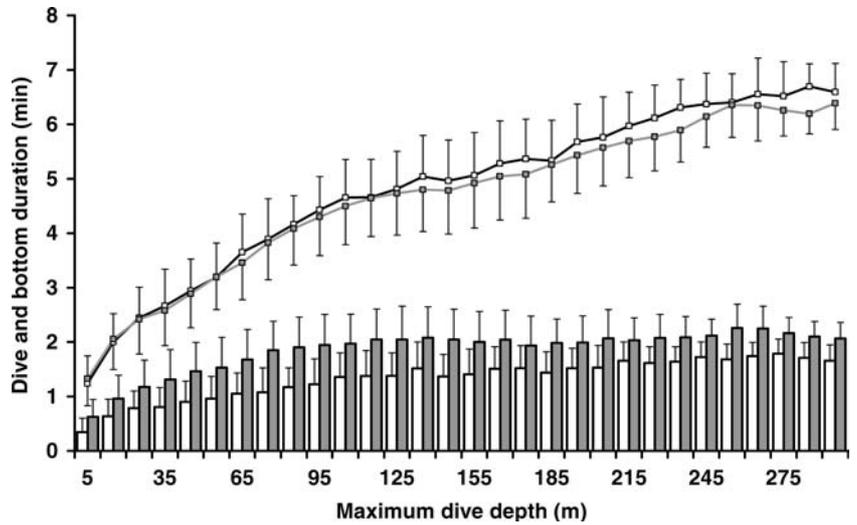


Fig 6 *Aptenodytes patagonicus*. Total dive (lines) and bottom time (bars) duration of U-dives (open) and W-dives (grey) in relation to maximum dive depth



corresponds to the Sub-Antarctic Front (SAF) elsewhere (Peterson and Whitworth 1989). These waters are known to be nutrient-rich and contain a high biomass,

including myctophid fish. King penguins are recognised as mesopelagic predators that feed predominantly on myctophids (see review in Cherel et al. 2002). In fact, in a simultaneous study it was confirmed that king penguins from the Falkland Islands feed predominantly on the myctophid *Protomyctophum choriodon* (Cherel et al. 2002), which is widely distributed between the Sub-tropical Front and the Antarctic Polar Front (APF) and is abundant in slope waters in the Southwest Atlantic (Hulley 1981; Konstantinova et al. 1994). Foraging over slope waters was recently described for birds from the same colony in austral spring and king penguins breeding at Kerguelen (Pütz 2002), but, to our knowledge, the present study is the first to show king penguins foraging consistently at the SAF. Indeed, the main summer feeding ground elsewhere is located further south, near or at the APF (see review in Pütz 2002), with only a few Crozet birds reaching the SAF at that time (Guinet et al. 1997). The most likely explanation of this difference is the geographical location of the Falkland Islands, which are the only breeding area of king penguins north of the SAF; all the other populations breed

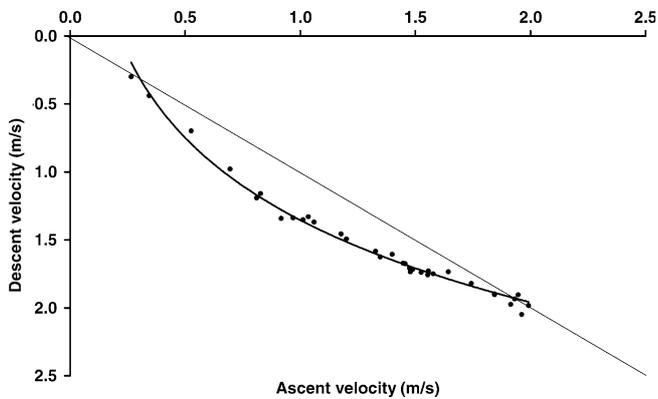
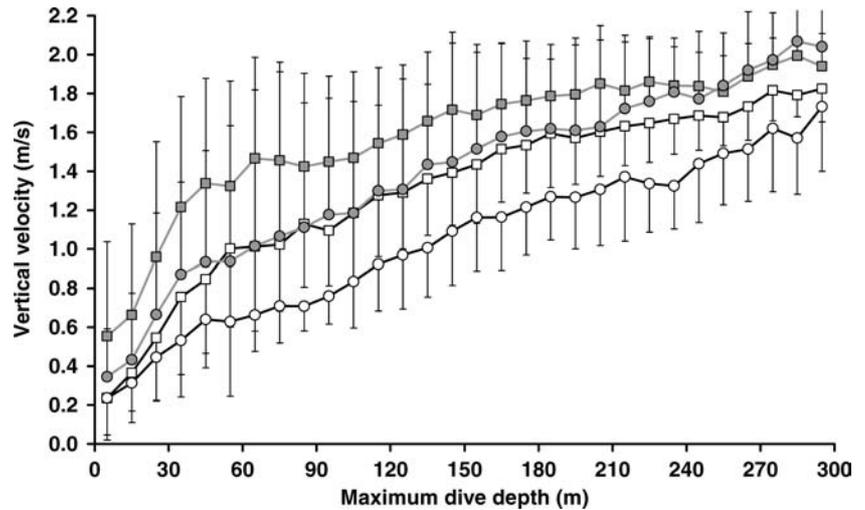


Fig. 7 *Aptenodytes patagonicus*. Relationship of descent to ascent velocity as a function of maximum dive depth (in 10-m classes). The thin diagonal line hypothetically indicates equal values; the thick line indicates the best fit to the values ($y = -0.8734 \ln(x) - 1.3542$; $r^2 = 0.99$)

Fig. 8 *Aptenodytes patagonicus*. Vertical velocity in relation to maximum dive depth (in 10-m classes) in U-dives (black line, open symbols) and W-dives (grey line and symbols), separated for descent (squares) and ascent (circles)



south of it. The ecological importance of that foraging area is underlined by the fact that it is also frequented by Magellanic penguins (*Spheniscus magellanicus*, Pütz et al. 2002) and rockhopper penguins (*Eudyptes chrysocome*, Pütz et al. 2003) from the Falkland Islands at the onset of the breeding season, as well as other marine top predators breeding in South Georgia (Croxall and Wood 2002).

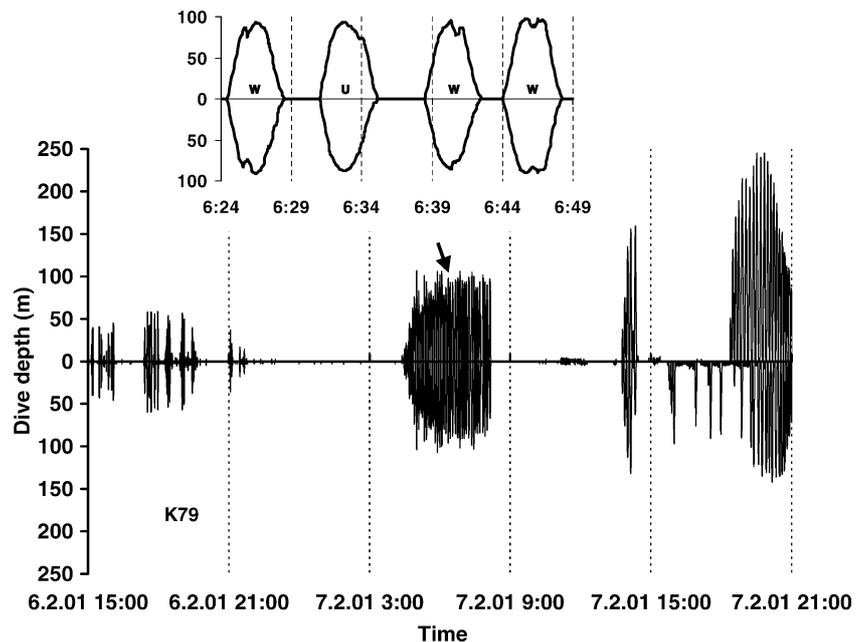
General diving behaviour

In general, the diving pattern of king penguins from the Falkland Islands closely resembled that found in birds from other breeding sites, for example, the diurnal dive pattern (Fig. 2), and the positive relationships between maximum dive depth and total dive duration (Fig. 6)

and vertical velocities (Fig. 8), respectively (Kooyman et al. 1992; Pütz et al. 1998; Charrassin et al. 2002). The diurnal dive pattern has been attributed to the fact that penguins are visually orientated predators that need a certain amount of light to encounter prey, whose vertical distribution is also dependent on ambient light intensity (Wilson et al. 1993). Accordingly, myctophids make diurnal migrations and can be found in dense aggregations at greater depths during the day, migrating to the surface at night, where they are more equally distributed (Gjosaeter and Kawaguchi 1980; Zasel'slyi et al. 1985; Torres and Somero 1988).

Our study, however, highlights the importance to king penguins of foraging during the twilight hours. Birds maximised their time underwater around sunrise and sunset (Fig. 2b), and DS was also highest during twilight. This strongly suggests that king penguins for-

Fig. 9 *Aptenodytes patagonicus*. Depth profiles of king penguins K72 and K79 after departing the colony. Both profiles show synchronous diving behaviour for 24 h; thereafter profiles run out of phase. Detailed insert shows W-dives (dives 1, 3 and 4) interspersed with one U-dive (dive 2)



age most effectively in the transition period when their prey is migrating from the upper water column to greater depths and vice versa. Our data also suggest that foraging at night is greatly reduced, which agrees with the determination of the timing of prey ingestion in king penguins (Pütz and Bost 1994; Pütz et al. 1998). In the latter studies, however, no clear difference was found between twilight and daylight foraging. This may have been due to the fact that food intake was investigated using stomach temperature sensors (Pütz and Bost 1994; Pütz et al. 1998). These loggers accurately determine the timing of prey ingestion, but are particularly insensitive to multiple prey ingestions, thus inducing considerable errors in mass estimates (Wilson et al. 1995). This is the most likely explanation for the lack of clear differences in food intake between daylight and twilight hours. More information from birds equipped with oesophageal—not stomach—sensors (Charrassin et al. 2001) is therefore needed to test our hypothesis about the importance of prey intake at dawn and dusk.

There were pronounced differences between the descent and ascent rates of any particular dive, with the former being higher than the latter, except at both extremes of the depth range (Fig. 7). To our knowledge, these differences have not been described before in king penguins and have rarely been noted in other penguin species (Tremblay and Cherel 2003; Wilson and Liebsch 2003). This may be due to the large scatter associated with pooling many individuals in the interest of describing the behaviour of the species and to the lack of detailed analysis over certain depth ranges as was performed in our study.

King penguins, like other penguin species, usually maintain a constant swimming speed, at which the energy invested is minimal in relation to the distance covered (Culik et al. 1996; Ropert-Coudert et al. 2000), and changes in vertical velocity are mainly achieved by adjusting dive angles (Wilson 1995; Pütz et al. 1998; but see Wilson et al. 1996). However, previous studies have shown that during the ascent phase, flipper beat frequency decreases or even ceases and the return to the surface is passively facilitated through buoyancy (Sato et al. 2002; Wilson and Liebsch 2003). Sato et al. (2002) have even suggested that penguins actively regulate their air volume according to the intended dive depth, to optimise the costs and benefits of their buoyancy. Given these different types of propulsion, it is not surprising to observe differences in descent and ascent rates. The similar values for descent and ascent rates at the extreme of the depth range may be explained by the fact that: (1) shallow dives are usually travelling dives that contain no prey-searching component and (2) after extended periods underwater, oxygen stores are depleted and need to be replenished.

Specific dive patterns

To our knowledge, the present study is the first to investigate in detail the characteristics of different dive

profiles in king penguins (but see the preliminary work of Ropert-Coudert et al. 2000). The specific analysis of dives according to their shape revealed some striking differences in certain dive parameters. V-shaped dives are believed to be purely exploratory (Wilson 1995; Ropert-Coudert et al. 2000), which is supported by our results, whereas V-dives accounted for only 6% of all dives and never exceeded 30 m. However, there is strong evidence that U- and W-shaped dives contain a feeding component, which occurs at different phases in each type of dive. In a study simultaneously recording dive depth and swimming speed in king penguins, it was suggested that feeding occurs mainly during the ascent phase of U-dives (Ropert-Coudert et al. 2000). In contrast, prey capture in W-dives seems to occur mainly during the bottom phase, as has been shown by speed and beak-opening measurements (Ropert-Coudert et al. 2000; Wilson et al. 2002; Simeone and Wilson 2003).

A new finding, however, is that our data suggest that king penguins forage more effectively during W-dives than during U-dives. Firstly, in dives exceeding 40 m, the proportion of W-dives was always higher (Fig. 3), and king penguins are known to feed almost exclusively during deep dives (Pütz et al. 1998). Secondly, compared with U-dives, W-dives contained significantly longer bottom time (Fig. 6) and higher vertical velocities (Fig. 8). It is advantageous for pelagic feeders to spend less time in transit between the sea surface and the depth at which a food patch is located and to maximize bottom time to increase the time available for prey capture. Thirdly, most dives during hours of twilight were W-dives (Fig. 4), which is probably a main feeding time for king penguins over the diurnal cycle (see discussion above). It is notable that the highest DE values were also recorded at dawn and dusk. Seasonal changes in DE calculated for king penguins have been noted before by Charrassin et al. (2002), but, to our knowledge, this is the first study to report changes in DE with regard to time of day. Generally, we suggest that a higher proportion of W-dives is probably a behavioural hunting response to more dispersed prey at a time when myctophids undertake their nycthemeral vertical migration.

It is known that penguins adjust their dive angle according to the maximum dive depth anticipated (see above), which already implies that penguins predict their dive depth and adjust their dive angle accordingly (Wilson 1995). As mentioned before, it has also been suggested that the air volume is actively regulated depending on the expected dive depth (Sato et al. 2002). Furthermore, Wilson (2003) found that Magellanic penguins (*Spheniscus magellanicus*) also anticipate their foraging success in terms of the number of prey they are likely to catch and inhale accordingly before the dive. Given the differences between U- and W-shaped dives found in this study, we suggest that, in addition, birds adjust the overall performance of the subsequent dive depending on the expected prey distribution: they either optimise their bottom time and spend less time on commuting to specific depths (i.e. W-dive), or reduce

their bottom time to the benefit of the time spent commuting (i.e. U-dive). Both strategies may reflect differences in prey distribution; however, further research on the distribution of myctophid prey and on the diving behaviour of king penguins is needed to shed more light on this phenomenon.

Synchronous diving behaviour

Synchronous diving behaviour, as has been observed in our study, has been postulated for many different penguin species and has been found to occur in rockhopper (Tremblay and Cherel 1999), chinstrap (*Pygoscelis antarctica*) and Adelie (*P. adeliae*) penguins (Takahashi et al. 2004a, 2004b). Like most penguins, eudyptids and pygoscelids perform short foraging trips (mainly daily trips) during chick rearing, while species of the genus *Aptenodytes* (including king penguins) have a different strategy, undertaking much longer trips. Our data thus suggest that travelling and/or feeding in groups is a general characteristic of penguins at sea, whatever the length of the foraging trip. Synchrony in king penguins was recorded at the beginning of the trip only, which is in accordance with penguins leaving the colony in groups. Penguins can also meet at sea and dive in synchrony, before going their own way again, as previously shown in rockhopper penguins (Tremblay and Cherel 1999).

Synchrony was observed during one long bout of deep dives (Fig. 9); in addition, king penguins are known to begin to feed a few kilometres from the colony during their first day at sea (Pütz and Bost 1994; Bost et al. 1997). This suggests that the two birds were already engaged in feeding, diving in synchrony to target prey in the same place at the same time. Interestingly, synchrony was also recorded during bouts with almost no diving activity or with shallow dives only. This indicates that penguins were resting and most likely travelling together at and near the surface, a behaviour also previously recorded in rockhopper penguins (Tremblay and Cherel 1999).

The probability of recording synchronous diving activity in penguins is very low, due to the small number of birds equipped with TDRs and thus the dilution effect of a large colony size. However, visual observations of birds swimming in the water in rafts (see discussion in Tremblay and Cherel 1999), the recent use of penguin-mounted cameras (Takahashi et al. 2004b), together with the fortuitous—but fruitful—recording of synchronous diving activity, all suggest that this behaviour is common during penguin foraging. This would imply that penguins predict their diving performance not only on an individual, but also on a group basis, which, in turn, raises a number of questions about social coordination and communication that invite further investigation.

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