Polar Biol (2007) 30:133–142
DOI 10.1007/s00300-006-0168-8

ORIGINAL PAPER

Extreme dives by free-ranging emperor penguins

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Received: 6 January 2006 / Revised: 16 May 2006 / Accepted: 20 May 2006 / Published online: 19 July 2006

Abstract We examined the incidence of extreme diving in a 3-year overwintering study of emperor penguins *Aptenodytes forsteri* in East Antarctica. We defined extreme dives as very deep (> 400 m) and/or very long (> 12 min). Of 137364 dives recorded by 93 penguins 264 dives reached depths > 400 m and 48 lasted > 12 min. Most (65%) very long dives occurred in winter (May–August) while 83% of the very deep dives took place in spring (September–November). The two most extreme dives (564 m depth, 21.8 min duration) were separate dives and were performed by different individual penguins. Penguins diving extremely deeply may have done so as part of their foraging strategy whereas penguins diving for very long times may have been forced to do so by changes in the sea-ice conditions.

Introduction

Many species of seabirds and all species of marine mammals hunt prey at or below the water surface and some species are capable of diving to remarkable depths. Among marine mammals, Weddell seals *Leptonychotes weddelli* (Plötz et al. 2001) are capable of reaching 450 m and Southern elephant seals *Mirounga leonina* can exceed 1,400 m (Slip et al 1994). Among seabirds, penguins are the most proficient divers and emperor penguins A*ptenodytes forsteri* are the world's deepest diving species of seabird with maximal dive depths of > 500 m (Kooyman and Kooyman 1995).

Diving to great depths is a behaviour that exposes the divers to increases in pressure and decreases in temperature and light availability. To perform deep dives efficiently, special adaptations needed to evolve for animals to cope with these constraints. Examples of physiological adaptations include the ability to collapse the lungs to avoid decompression sickness (Kooyman et al. 1972), to store oxygen in blood and muscles rather than the respiratory system (Kooyman and Ponganis 1998), and to adjust abdominal temperature and heart rate to conserve the core temperature (Green et al. 2003; Ponganis et al. 2003). These physiological adaptations provide deep divers with the capacity to exploit prey at depths that are out of the reach of many other species of top predators.

When diving, air-breathing divers rely entirely on the oxygen stored in their bodies for energy generation. Many animals (seals and penguins included) appear to dive longer than their oxygen stores should allow them. Changes in their heart rates, a reduction of their metabolic rates and even a reduction in body temperature appear to be mechanisms that enable them to remain submerged for extended periods (see Butler 2004).

But animals also exhibit flexibility in their behaviours in response to physiological changes. For example, when diving deep they may reduce their actual foraging time to stay within their aerobic dive limits (Schreer et al. 2001). To understand the extent to

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which physiology limits behaviour requires an understanding of the at-sea behaviour of free-ranging animals in their natural environment (e.g. Kramer 1988; Costa and Sinervo 2004). Empirical studies of the behaviour of free-living animals demonstrate how animals apply these special physiological adaptations on a daily basis in their quest to survive. Diving, for example, forms a complex set of behaviours and physiological functions that influence each other and ultimately limit what animals are able to achieve.

Extreme dives, i.e. dives that far exceed the average, both in terms of depth and duration, are in all likelihood performed near the physiological limits of divers. By observing these extreme behaviours, insights can be gained into the maximal capacity of deep divers and the potential of a species' ability to respond to environmental changes (see Costa and Sinervo 2004).

Here we report the incidence of extreme dives by emperor penguins during a 3-year study of the foraging ecology of these birds throughout their breeding cycle (May–December). We present data on a subset of dives that includes the maximal depths attained and longest breath-holds recorded for emperor penguins to date, as well as the frequency of such dives in the penguins' diving repertoire. Our findings are discussed in terms of the foraging environment of emperor penguins and the relevance to survival of being able to perform extremely deep and extremely long dives.

Methods

Study location and periods

The study was conducted at the emperor penguin colony at Auster (67°26′S, 63°49′E; 13,500 breeding pairs) in the breeding seasons of 1988, 1993 and 1994. In 1988, we deployed time–depth recorders on departing breeding adults from the start of the chick-rearing period in July until late October when chicks were old enough to thermoregulate themselves. In 1993 and 1994, adults were instrumented from May to October; this included the foraging period of female penguins during winter. Dives recorded in winter were performed by females that departed the colony after laying. For the spring deployments, the gender of the equipped penguins was unknown.

In 1988, we deployed 'Paddlewheels' ($n = 9$; Platypus Engineering, Tasmania) that sampled depth every 2 s. These instruments weighed ~200 g and had a frontal area equivalent to 2.7% of the cross-sectional area of a 24 kg emperor penguin. In 1993 and 1994, we deployed Mk7 TDRs ($n = 45$ and 39, respectively; Wildlife Computers, Redmond, USA) that sampled every 5 s. Note that this sampling interval in conjunction with the 3 m depth minimum may lead to a slight underestimation of depths and durations. The Mk7 data loggers were set in special streamlined housings with bollards at either end of the instruments and were attached to the penguins' feathers with hose clamps. A TDR with housing and hose clamps weighed approximately 100 g and had an frontal area of 4 cm^2. This was < 1% of the cross-sectional area of a 24 kg emperor penguin. All instruments had a resolution of 1 m. In all years, instruments were attached with an industrial strength contact glue (Loctite 401) to the lower back feathers of the birds. The penguins were intercepted on their return to the colony to recover the devices.

Extreme dives

Dive data were analysed by using zero offset correction and dive analysis software supplied by the manufacturer. The depth threshold was set to 3 m depth because of the drift of the instruments in the detection of the surface and because of the possible influence of waves on the pressure transducers. Two types of dives were defined as being extreme: (a) very deep dives that went to > 400 m, and (b) very long dives that lasted > 12 min (irrespective of depth). For the purpose of this paper, we chose 400 m as the minimal depth for an extremely deep dive as this is about twice the mean maximal depth of the continental shelf; penguins could not dive extremely deeply if they were limited by the depth of the continental shelf. Also a depth of 400 m is within the known dive depth range of emperor penguins (Kooyman and Kooyman 1995). A duration of 12 min was selected as the minimum for very long dives because this length of time equates approximately to twice the measured aerobic dive limit (5.6 min; ADL) for emperor penguins (Ponganis et al. 1997). The ADL is the time during which emperor penguins rely on aerobic metabolism for energy. There appears to be a "transition zone" of dive durations during which anaerobic metabolism increases (Ponganis et al. 1997). Our chosen cut-off point of 12 min is well outside this transition period.

Extreme dives were assessed in terms of maximal depth and duration, as well as 'bottom time' (time from the first to the last depth recording at > 85% of the maximum depth; default setting of the dive analysis program, Wildlife Computers 1998), and the length of the surface intervals following extreme dives.

The post-dive surface interval is the time from the end of an extreme dive to the start of the next dive regardless of whether or not the following dive was a foraging dive. Surface intervals following both types of extreme dives occasionally lasted > 25 min (0.5–16.7 h, $n = 11$ for deep dives; 0.5–18.5 h, $n = 5$, for long dives). When no further activity was recorded during this period, we assumed that the penguins had emerged from the water onto the sea ice or were engaged in non-foraging activities (e.g. preening). Because of this, surface intervals of > 25 min following extreme dives were not included in our analysis.

Extreme dives were also examined in terms of their frequency of occurrence including both the number of penguins performing such dives, and the number of times individuals repeated them.

Since environmental factors that may influence the dive depth change with time of year, we investigated the frequency of occurrence of extreme dives during two broadly defined seasons: the austral winter (May–August) which includes the period from egg laying to brooding, and the spring (September–early November) when chicks undergo a period of growth, requiring an increased foraging intensity by parents. Major seasonal changes occur in the degree of light penetration through the water column (affects visibility) and the degree of ice cover (affects light penetration and may influence access to the ocean).

Data are presented as means ± 1 SD and as medians. We compared medians statistically using Mann–Whitney *U* tests or Mann–Whitney rank sum tests.

Table 1 Summary of parameters describing very deep and very long dives performed by emperor penguins from Auster

Variable	Very deep dives	Very long dives
Number of dives	264	48
Percent of all dives recorded	0.20	0.04
Number of penguins performing dives	15	24
Depth (m)		
Average	426 ± 30	76 ± 37
Maximum	564	250
Minimum	402	18
Median	414	66
Dive duration (min)		
Average	8.3 ± 0.8	14.0 ± 2.1
Maximum	10.9	21.8
Minimum	6.0	12.0*
Median	8.4	13.4
Bottom time (min)		
Average	2.4 ± 0.5	4.4 ± 3.7
Median	2.4	3.4
Maximum	3.8	15.0
Minimum	1.1	0.3
Percent bottom time of total dive time		
Average	29 ± 5	31 ± 22
Median	29	26
Maximum	43	87
Minimum	15	3
Surface interval (min)		
Average	5.8 ± 4.5	3.5 ± 3.3
Median	4.4	2.6
Maximum[a]	23.9	21.5
Minimum	0.07	0.03

Means are given ± 1 SD. Minima of extreme dives are as defined in this paper. [a]Surface intervals > 25 min were excluded (see text)

Results

General

The 93 equipped penguins recorded a total of 137,364 individual dives of which the large majority (129,789 or 94.5%) reached < 200 m, and only 264 (0.2%) exceeded 400 m. Similarly, the durations of 129,946 (94.6%) dives lasted up to 6 min, 7,370 (5.4%) lasted 6–12 min and 48 (0.04%) were > 12 min. Thus, a total of 312 dives qualified for our definition of extreme. These dives are discussed below.

Very deep dives

Since none of the very deep dives exceeded 12 min duration and none of the very long dives reached > 400 m these two groups were considered to be independent. The 264 very deep dives averaged 425 ± 30 m with a median of 414 m and a maximum of 564 m (Table 1). Some 174 dives (66% of very deep dives) went to < 420 m (Fig. 1a). Only 12 dives (5%) exceeded 500 m and all of these dives were performed by the same penguin.

Very deep dives averaged 8.3 ± 0.8 min (range 6.0–10.9 min) and the median duration was 8.4 min. The majority of very deep dives (41%) lasted 8–9 min (Fig. 1b) and only eight dives (2.3%) were > 10 min (Table 1).

Very long dives

Dives lasting > 12 min occurred even more rarely than very deep dives. Only 48 (0.04% of all dives recorded) very long dives were performed. These dives averaged 14.0 ± 2.1 min with a median of 13.4 min. More than half of the very long dives ($n = 29$) lasted up to 14 min while three dives were exceptionally long with durations of 17.1, 21.3, and 21.8 min (Fig. 2a).

The average depth achieved on very long dives was 76 ± 37 m with a median depth of 66 m (Table 1). Forty-two of the 48 very long dives were to < 100 m. The majority (58.3%) of very long dives (including the

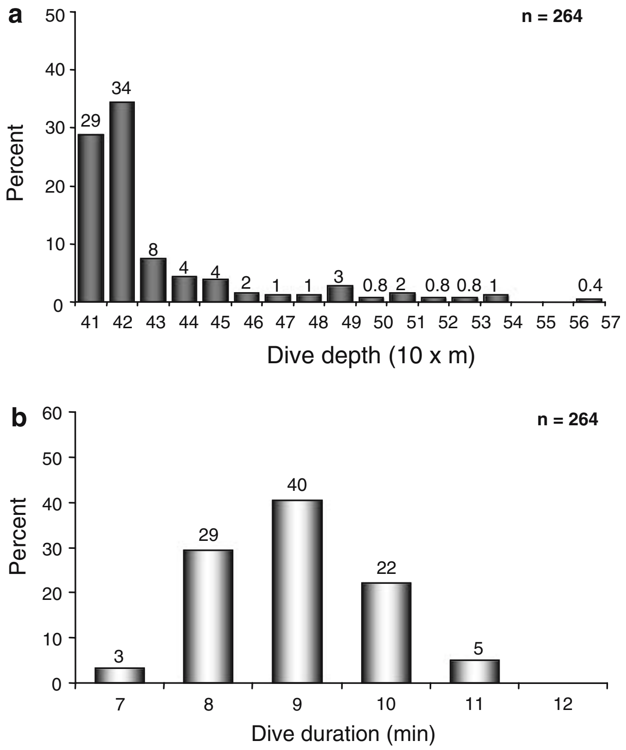


Fig. 1 Frequency distribution **a** of dive depths and **b** of durations of very deep dives (> 400 m) performed by emperor penguins from Auster over three seasons

three longest dives recorded) reached 60–80 m depth (Fig. 2b). The deepest dive of this group reached 250 m and lasted 13.0 min and was the only very long dive to > 200 m depth. The shallowest very long dive reached 18 m and lasted 12.7 min (Table 1).

Frequency of occurrence of extreme dives

Very deep dives (> 400 m) were performed by 15 of the 93 emperor penguins studied. Two individuals performed a single very deep dive while the other 13 achieved at least 4 very deep dives during a single foraging trip. When several very deep dives were made, they occurred either on the same day or on 2 or 3 consecutive days. Two penguins achieved the highest repetition rate of very deep dives per day exceeding 400 m on 21 occasions in one day. One of these two penguins dived to > 400 m on four consecutive dives (performed at 0755–0853 h, and at 1110–1255 h). Overall these two penguins performed 33 and 61 very deep dives, respectively, contributing 13 and 23% of all very deep dives recorded.

Only one penguin dived to > 500 m. In early November 1994, this penguin reached a depth of 564 m making it the deepest diving emperor penguin on record to date. This very deep dive was the second dive exceeding 400 m and was followed by a 2.5 h break (Fig. 3). When the penguin commenced diving again it dive > 400 m 15 more times on the same day. Overall, this individual passed 500 m on 12 occasions over 3 consecutive days and contributed ~16% (n = 43 dives) of all very deep dives. Thus, three penguins (the two with the greatest deep diving repetition rate and the deepest diver in our study group) were responsible for 137 or 52% of all very deep dives recorded.

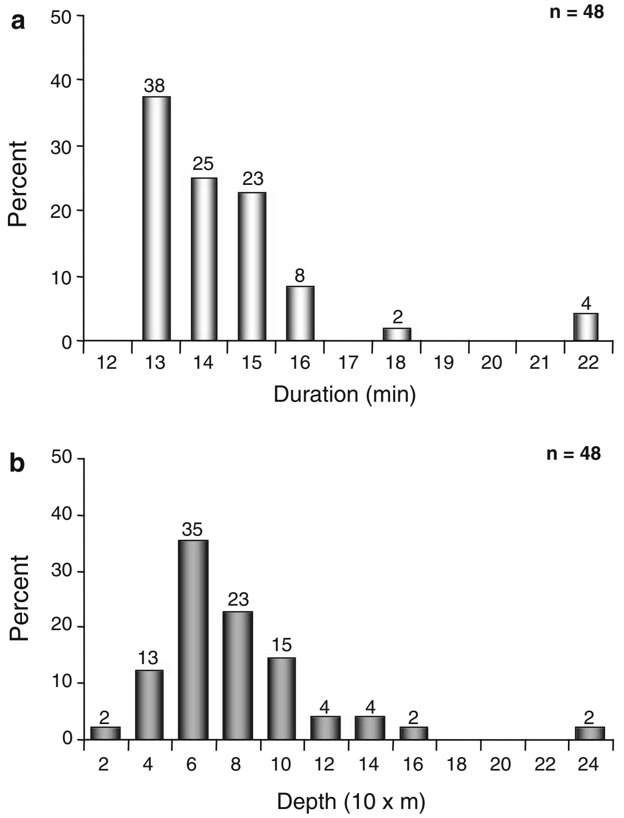


Fig. 2 Frequency distribution **a** of dive depths and **b** of durations of very long dives (> 12 min) performed by emperor penguins from Auster over three seasons

Twenty four of the 93 penguins performed very long dives (> 12 min) and 10 of those did so only once. The maximum number of very long dives performed in a day was four. This occurred only once; the emperor penguin was foraging in August 1994. All four very long dives were made on the same day from ~1030 to 1400 h when the bird dived 25 times to various depths.

Two dives lasting > 20 min were recorded by two different individuals. One of the extremely long dives was the fourth dive to exceed 12 min on the same day (Fig. 4), while the other was the only very long dive performed by the diver on its entire foraging trip (see insert, Fig. 4).

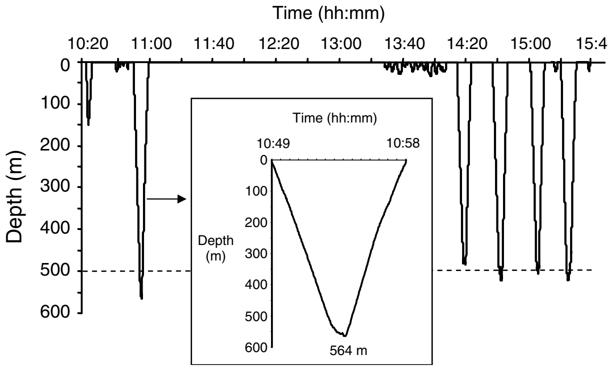


Fig. 3 Partial dive profile of the emperor penguin that performed the deepest dive recorded to date for the species in November 1994. The *insert* shows the deepest dive in detail

Bottom times and post-dive surface intervals

The bottom times of very long dives ranged from 0.3 to 15.0 min and were more variable than those of very deep dives (range 1.1–3.8 min, Table 1). Median durations of bottom times were 2.4 min for very deep dives and 3.4 min for very long dives (Mann–Whitney Rank Sum $U = 6636.500$, $P = 0.003$).

The percentage that bottom times represented in each dive averaged 29 ± 5% (median 29%) in very deep dives and 31 ± 22% (median 26%) in very long dives (Table 1). With a range from 3 to 87% bottom time percentages were more variable in the very long dives compared to the very deep dives (range 15–43%).

Surface intervals following very deep dives averaged 5.8 ± 4.5 min (range 0.07–23.9 min) compared to 3.5 ± 3.3 min (range 0.03–21.5 min) for very long dives (Table 1). Median durations were 4.4 min for deep dives and 2.6 min for long dives and were statistically significantly different ($U = 3394.000$, $P < 0.001$). There was a strong correlation between surface interval and dive duration in very deep dives (Pearson's $r = 0.286$, $P < 0.001$) but no in very long dives (Pearson's $r = 0.118$, $P = 0.457$; Fig. 5).

Characteristics of follow-up dives

The average depth for the dives that followed very deep dives was 163 ± 193 m (median = 27 m, maximum = 536 m). Sixty five (28%) of consecutive dives were also to extreme depths, a further 7% (16) were to > 300 m while the remaining 65% (149) of dives reached < 200 m. The durations of these follow-up dives averaged 3.7 ± 3.6 min with a median of 2.0 min. The longest dive duration immediately following a very deep dive was 10.6 min (Table 2).

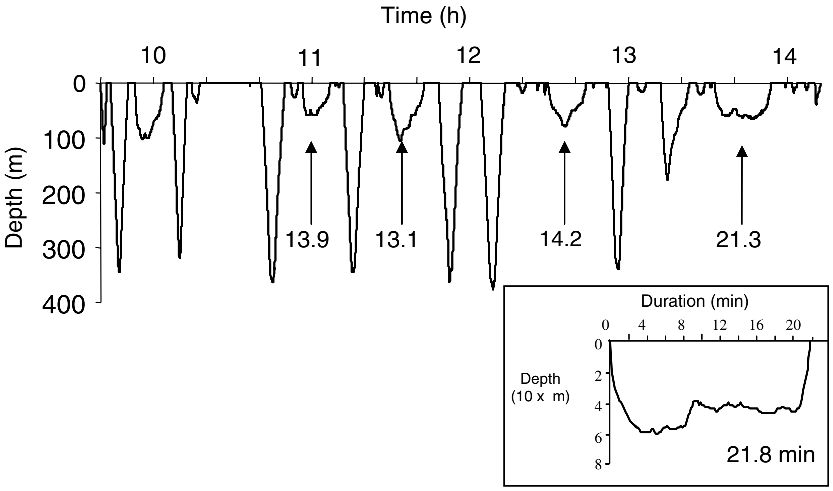
Dives following very long dives lasted 2.9 ± 3.5 min (median 1.7 min), i.e. they averaged about one quarter the duration of the preceding long dive. However, two penguins performed dives that were followed by dives that were longer than the preceding very long dives.

The depths of dives following very long dives averaged 40 ± 63 m (median = 21 m). In 28 of the 48 following dives, depths attained were < 50% of the depths reached on the very long dives and on only five dives was the maximal depth greater than on the previous dive.

Extreme dives in winter and spring

There was a seasonal change in the length of the instrument deployments. In winter (June/July), the emperor penguins carried the instruments from 72 to 82 days. As the seasons progressed, foraging trips became shorter lasting from 22 to 49 days in late winter (August) compared to 13–32 days in spring (September–November).

Fig. 4 Partial dive profile of a male emperor penguin performing several very long dives on the same day in August 1994. Dive times are indicated below very long dives. The *insert* shows a dive performed by a male emperor penguin in August 1988; this is the longest dive recorded to date for this species



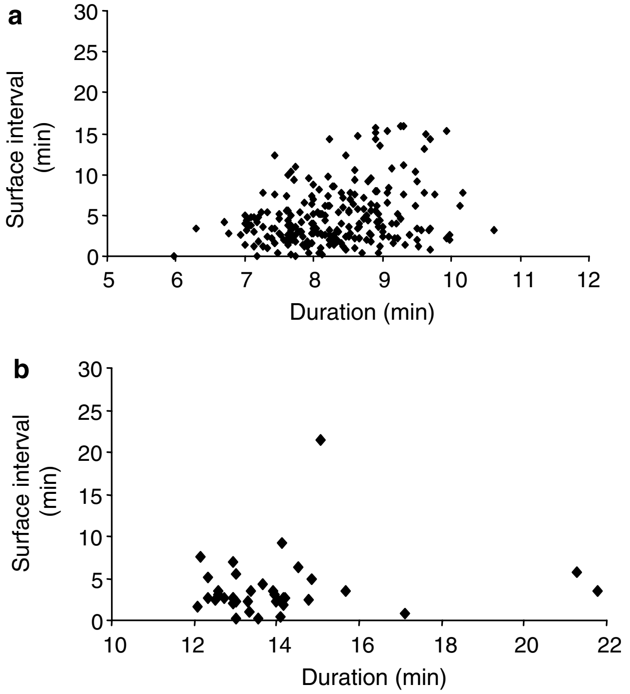


Fig. 5 Post-dive surface intervals versus dive duration **a** of very deep and **b** of very long dives of emperor penguins

The majority of very deep dives (*n* = 224 or 85%) occurred in spring and averaged 429 ± 31 m. In comparison, very deep dives performed in winter (15%) averaged 411 ± 7 m (*n* = 40). The maximal depths of very deep dives recorded in winter and spring were 435 and 564 m, respectively (Table 3). Median dive depths were 408 m in winter and 417 m in spring (*U* = 3485.000, *P* < 0.001). All of the deep winter dives were to < 450 m compared to the spring dives of which 84% reached < 450 m, and 16% went to > 500 m (Fig. 6a, *U* = 384.000, *P* = 0.003).

Very deep dives averaged 8.3 ± 0.6 and 8.4 ± 0.9 min in winter and spring, respectively. Median dive durations were 8.2 min in winter and 8.3 min in spring (*U* = 4970.500, *P* = 0.460). Ninety percent of very deep dives in winter lasted < 9 min compared to 77% of dives in spring (*U* = 26.000, *P* = 0.841).

The majority (65%) of very long dives occurred in winter (Fig. 6b) but the durations of long dives in winter and spring did not differ significantly (winter 13.7 ± 2.1 min, median 13.3; spring 14.1 ± 1.1 min, median 14.0; *U* = 493.5, *P* = 0.099, Table 3). The frequency distribution of dive durations varied between winter and spring but was not significant: in winter, 47% of very long dives lasted from 12–13 min and 36% lasted 14–15 min compared to 8 and 83% in spring, respectively (*U* = 173.000, *P* = 0.918).

The depths of very long dives averaged 67 ± 30 m in winter and 78 ± 45 m in spring with respective maxima of 150 and 250 m. The median dive depths were 63 and 60 m for winter and spring, respectively (*U* = 446.0, *P* = 0.532).

Table 2 Characteristics of dives immediately following extreme dives

Variable	Dives after very deep dives	Dives after very long dives
Dive depth (m)		
Average	163 ± 193	40 ± 63
Maximum	536	363
Minimum	6	3
Median	27	21
Dive duration (min)		
Average	3.7 ± 3.6	2.9 ± 3.5
Maximum	10.6	14.1
Minimum	0.3	0.1
Median	2.0	1.7

Discussion

The data presented here are a subset of a larger set of dive data obtained over 3 years of research on emperor penguins and comprise only dives that fitted our definitions of 'extreme'. The limits of what constitutes extreme dives in terms of depth and duration were

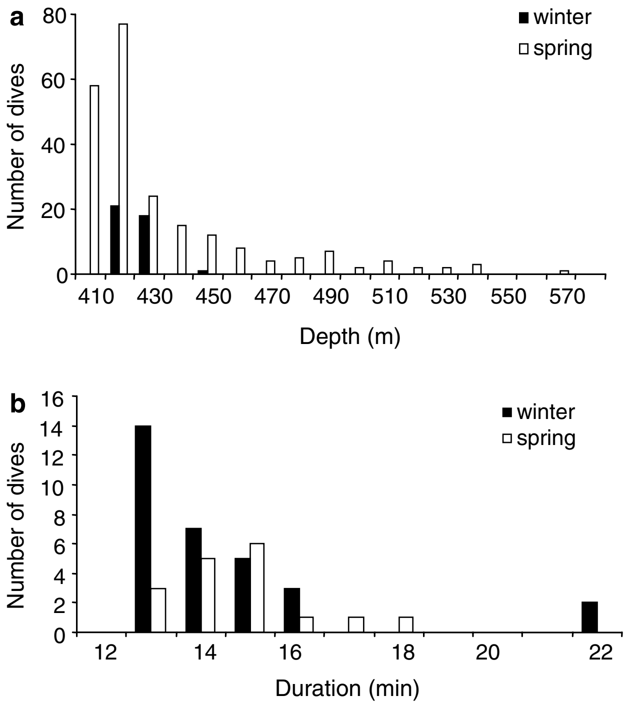


Fig. 6 Frequency distribution **a** of depths of very deep dives and **b** of dive durations of very long dives in summer and winter

arbitrary. However, we attempted to put them into a logical context that would allow us to explore the importance of such dives to emperor penguins with regard to their foraging strategies and habitat use in their natural environment. This is the context in which following discussion should be viewed.

Very deep dives

Our observations confirm emperor penguins as the unchallenged deep divers among seabirds. However, while dives to extreme depths are impressive, they were performed rarely. At Auster, only 0.2% of all dives recorded over 3 years exceeded 400 m. These dives were also uncommon in terms of the number of penguins performing them: 15 of the 93 individuals dived to 400 + m and only one penguin dived to > 500 m. This individual reached a maximal depth of 564 m; this is to date the deepest dive on record for the species. Some 52% of very deep dives were made by only three penguins. Nevertheless deep dives are a normal feature of the diving repertoire of emperor penguins and may be performed frequently at times, at least by some individuals.

Attempts to explain why only a few emperor penguins dived to extreme depths need to consider the penguins' environment and the conditions under which they forage. Clearly a number of preconditions need to be met for emperor penguins to perform very deep dives. First, the opportunity must be there, i.e. the birds need to forage in areas where the water is deep enough for them to be able to reach extreme depths. Emperor penguins foraging over the continental shelf are unlikely to reach great depths since the seafloor here is only approximately 200 m deep. Of the 93 penguins we studied, 14 carried satellite trackers that located their position at sea (Wienecke and Robertson 1997). These birds were 11 females that left Auster after laying in June 1994 and three males that departed the colony in August 1994. Since the fast-ice excluded the penguins from foraging over the continental shelf, they foraged on the shelf slope where the water reaches depths well beyond that of the shelf. The satellite-tracked emperor penguins had the opportunity to dive to extreme depths as they foraged in waters > 400 m deep. However, 70% of the dives of the females reached 50–200 m, and only 1% exceeded 300 m. The deepest dive recorded by females in winter was 372 m. All three males also foraged on the continental shelf slope but only one dived extremely deep. This bird reached depths of up to 435 m on three consecutive days (see Wienecke and Robertson 1997 for more details). For the other emperor penguins in the current study no information is available on foraging locations regarding water depth. Thus, we do not know whether the penguins did not perform very deep dives because they dived in relatively shallow water or whether other factors prevented them from doing so.

A second factor determining whether penguins dive to extreme depths is the availability of prey in very deep water. Some profiles of very deep dives showed "wiggles" (fluctuations in depth during bottom phase) indicating potential prey pursuit. The flat bottom profiles of other very deep dives suggest that the penguins reached the seafloor. Demersal and bentho-pelagic fish, such as *Gymnodraco acuticeps*, *Chaenodraco wilsoni* and *Trematomus bernacchii* are known to live at depths of 550–800 m and formed part of the diet of emperor penguins from Auster (e.g. Robertson et al 1994; Kirkwood and Robertson 1997). This indicates that the penguins frequented extreme depths to hunt. While some benthic fish bury themselves in the sand or hide under rocks other species may spend considerable periods on the substratum (Eastman 1993). This behaviour may make them easy prey for emperor penguins.

A third factor that may influence whether penguins can achieve great depths is physical ability. It is not known in how far differences in physical capabilities and/or experience of individuals vary and determine an individual's capacity to perform these remarkable dives. The age of the birds is initially a factor: young emperor penguins whose dives usually reached depth < 100 m in their first few months at sea acquire the deep diving capacity with time (see Ponganis et al. 1999). Although the physical and physiological constraints of deep diving are not yet fully understood, individual differences in the ability to perform extreme dives may be a factor. A study of common eider ducks *Somateria mollissima* suggested the variability in diving behaviour within and between individuals reflected differences in individual ability and physiology (Guillemette et al. 2004). The same may be the case with emperor penguins—some may have the innate ability to dive very deeply and some may not.

Very long dives

In our study, only 20 of the 93 emperor penguins surveyed performed very long dives. With an average depth of 76 m, most very long dives were shallow and no two very long dives were performed consecutively. When an individual performed more than one very long dive, the dives usually occurred on the same day. Also, very long dives tended to be interspersed among much deeper dives (e.g. Fig. 5).

There were two common patterns of very long dives. The first showed that a penguin dived to a certain depth, spent some time there, ascended to shallower waters and stayed at that depth for the remainder of the dive. The dives ended with an abrupt return to the surface. The second, less common, pattern showed that the penguins reached the maximal dive depth and remained there for most of the dive. While the first profile type occasionally showed wiggles in the initial part of the dive, the second type was characterised by smooth undulations rather than rapid changes in depth.

The first type of behaviour had been observed among emperor penguins in the Ross Sea by Kooyman and Kooyman (1995) who considered this behaviour to be a consequence of diving in heavy pack-ice. In our study, 31 of 48 very long dives, including the two longest dives recorded for emperor penguins to date (21.3 and 21.8 min, Fig. 5), occurred in winter when the penguins were thought to forage in dense pack-ice. The two longest dives on record probably occurred when the exit holes in the pack-ice closed while the birds were submerged. Pack-ice is mobile and floes continuously change their position and density due to wind and wave actions. A gap in the ice that provided access to a foraging penguin can quickly close forcing the penguin to exit elsewhere. Although the two 20+ min dives were recorded several years apart and were performed by different individuals, they were remarkably similar. On both dives, the penguins remained at 40–60 m depth (close to the maximal depth they attained on these dives) for approximately 60–75% of the total dive time. By remaining at a relatively shallow depth, they would have increased the search area for an exit hole both in terms of the extent of sea-ice they were able to survey, as well as the time they were able to remain submerged. Both dives were characterised by sudden and steep ascends indicating that light, and hence a break in the ice, may have been detected.

On most very long dives, the margin by which the penguins exceeded the 2× ADL was relatively small. Nearly half of the dives lasted < 13 min and the average dive duration of very long dives of 14.0 min was 17% longer than our 12 min limit while the median dive duration (13.4 min) lasted 12% longer than our threshold for extreme dives. Twenty nine of the 48 very long dives lasted up to 14 min. Thus, the majority (60%) of very long dives exceeded our threshold duration by < 20%.

Emperor penguins did not appeared to incur a great cost given that the median surface interval following the very long dives was 2.7 min. Note however, that depths of dives following very long dives were generally shallower than the preceding dives. Thus, a combination of tolerance to anaerobic metabolism (Ponganis and Kooyman 2000) and diving to shallow depths may enable emperor penguins to cope with lactate build-up after very long dives while continuing to dive.

Bottom times and post-dive surface intervals

The average bottom time for very deep dives (2.4 ± 0.5) was about half that for very long dives (4.4 ± 3.7) but the coefficient of variation was much smaller in very deep dives than in very long dives. This difference in variability may be related to the different purposes of very deep and very long dives. The profiles of the very deep dives indicate that the penguins were actively pursuing prey (undulating bottom profiles) or examining the seafloor (flat bottom profiles) probably in search of prey. In addition, the bottom times were similar irrespective of the depth within the 400–564 m depth range. This indicates that emperor penguins dive very deeply to hunt and that over the roughly 150 m depth range of very deep dives the penguins did not compromise their foraging time.

Compared to very deep dives, on very long dives the bottom times of the penguins were much longer and highly variable. The profiles of very long dives were more diverse (see above) than those of very deep dives. Some penguins appeared to hunt (as indicated by wiggles in the profile) while others may have travelled, searched for holes in the ice, interacted with conspecifics or fed on small shoaling prey in the shallower depth strata. Because of this multitude of possible behaviours, it is difficult to interpret bottom time on extended pelagic dives. Similar profiles, particularly of dives where penguins spent a considerable time at a relatively shallow depth before returning to the surface, were also observed among emperor penguins in the Ross Sea (Kooyman and Kooyman 1995). The suggestions that these profiles occurred because the penguins were trapped underneath the sea-ice is supported by our data and seems a plausible explanation for at least some of the very long dives.

Post-dive surface intervals provide an indication of the time taken to restore oxygen levels after anaerobic dives. Generally, the longer a dive lasts the longer the oxygen restoration period at the surface. However, surface intervals are highly variable and not all the time spent at the surface can be attributed to oxygen replenishment (Kramer 1988; Boyd 1997). Penguins also exhibit behaviours, such as resting, preening, sheltering from blizzards, etc between dives. Thus, the time spent at the surface after a dive is not exclusively related to the duration of the preceding dive (see Schreer et al. 2001).

Post-dive surface intervals were highly variable after both types of extreme dives. However, surface intervals following very deep dives were on average 1.7 times longer than those following very long dives. Ponganis et al. (1997) showed that blood lactate concentrations in emperor penguins increased in dives lasting > 7 min and also that 7–12 min after the return to the surface lactate levels virtually returned to predive concentrations. Thus, physiologically emperor penguins appear to be able to recover relatively quickly from the oxygen debt sustained when exceeding their ADL. However, in our study median post-dive surface intervals after both the very deep and very long dives lasted only 4.4 and 2.6 min, respectively. Therefore, the total recovery period may not necessarily be spent on the surface in free-ranging emperor penguins. Given that the dive depths and durations of dives following the extreme dives tended to be short and shallow (see Table 2), the recovery period may be extended beyond the estimated time of 7–12 min by continuing to dive but only to shallow depths. Continuing to dive even though some degree of oxygen debt may have been sustained may reflect the intent to exploit prey before it escapes, or to avoid predators near the surface, or a combination of both.

Table 3 Comparison of dive depths and durations of very deep and very long dives in winter and spring

Variable	Winter	Spring	Statistics
Very deep dives	*n* = 40	*n* = 224	
Depth (m)			
Average	411 ± 7	429 ± 31	
Median	408	417	$U = 3485.000$ $P < 0.001$
Maximum	435	564	
Duration (min)			
Average	8.3 ± 0.6	8.4 ± 0.9	
Median	8.2	8.3	U = 4970.500 $P = 0.460$
Maximum	9.7	10.9	
Minimum	7.4	6.0	
Very long dives	*n* = 31	*n* = 17	
Depth (m)			
Average	67 ± 30	78 ± 45	
Median	63	60	$U = 446.000$ $P = 0.532$
Maximum	150	250	
Minimum	18	38	
Duration (min)			
Average	13.7 ± 2.1	14.1 ± 1.1	
Median	13.3	14.0	$U = 493.500$ $P = 0.099$
Maximum	21.8	17.1	

Extreme dives in winter and spring

Seasonal variations in environmental conditions, such as changes in light levels through the water and pack-ice, appeared to play a role in the penguins. Of the very deep dives, only 40 (15%) were performed in winter and the remaining 224 (85%) dives occurred in spring. None of the very deep dives occurred in June or July and the earliest one took place in the second week of August in all years. In addition, the median dive depths of extremely deep dives were significantly different in winter and spring. In the middle of winter (June), the sun transits at an altitude of 0° and is not visible above the horizon. There are < 3 h of twilight from noon until ~1500 h at the latitude of Auster. By mid-August, the sun is visible again for approximately 8 h. However, as it transits at only 12° altitude solar influx occurs at a highly oblique angle. All but four extremely deep dives recorded in winter took place when maximal light was available (0940–1640 h). Only 5 of the 15 very deep diving penguins exceeded 400 m in winter and all did so in mid- to late August.

In spring, emperor penguins increased the number of very deep dives and performed them virtually at all hours of the day and night although 80% occurred when maximal light was available (~0800 to 1800 h,

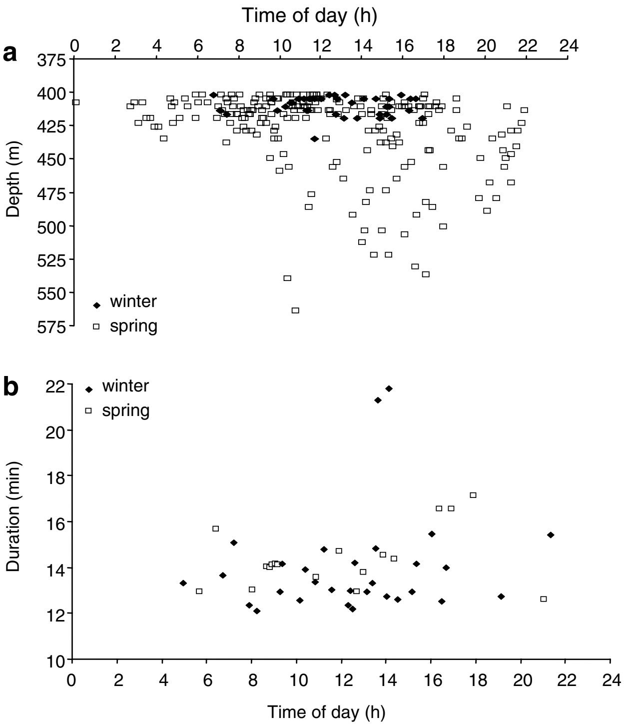


Fig. 7 Distribution **a** of very deep and **b** of very long dives performed by emperor penguins in winter and spring versus time of day

Fig. 7). This finding supports results of an earlier study of emperor penguins in the Ross Sea where dives to > 300 m were reported only during hours of maximal light availability (Kooyman and Kooyman 1995).

Extremely long dives occurred mainly in winter. This included the two longest dives recorded. In contrast to the very deep dives, extremely long dives occurred over a much wider time period spanning about 16 h (0500–2100 h) both in winter and spring. However, 17 of the 31 very long dives recorded in winter were performed after 1000 h and before 1500 h. This temporal distribution of very long dives is further evidence that these dives are driven by environmental changes rather than being performed deliberately. Although emperor penguins are most active during the time of day when maximal light is available they can enter the water at any time of the day and thus can be trapped under the ice at any time.

In conclusion, most emperor penguins did not perform extreme dives. With regard to very deep dives, they may not have had the opportunity to reach great depths because of the depth of the ocean floor in their foraging area. However, when the opportunity arises they may choose to perform very deep dives if they have the capability to do so. In contrast, very long dives appear to be the result of changes in the environment, particularly the pack-ice conditions. Pre-moulting adult emperor penguins foraged up to 6° latitude north of their colony in oceanic waters > 3,000 m deep (Wienecke and Robertson 2004). Further research will have to show whether when hunting in oceanic waters emperor penguins dive to extreme depths more frequently.

Acknowledgements We gratefully acknowledge the help and support of the three overwintering teams at Mawson Station in 1988, 1993 and 1994. Without their help and support in the field this work would not have been possible. We thank two anonymous referees for their instructive and in depth comments that helped improve the manuscript. This study was part of the Australian Antarctic Division's scientific program and was approved by the Australian Animal Ethics Committee (Department for the Environment and Heritage).

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