

Original paper

Deep dives and aortic temperatures of emperor penguins: new directions for bio-logging at the isolated dive hole

Paul J. Ponganis*, Robert P. van Dam, Torre Knowler,
David H. Levenson and Katherine V. Ponganis

Center for Marine Biotechnology and Biomedicine, Scripps Institution of
Oceanography, University of California San Diego, La Jolla, CA 92093-0204, USA
(*pponganis@ucsd.edu)

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Abstract: In order to document deep (> 100 m) dives and aortic temperature responses of emperor penguins (*Aptenodytes forsteri*) at an isolated dive hole, and also to evaluate a new catheterization technique, three birds were equipped with time depth recorders, temperature data loggers, and percutaneously-inserted aortic thermistors. After recovery from anesthesia, they were provided access for one day to the dive hole. The birds tolerated the experiment without complication. Mean diving duration (\pm SE) of 83 dives was 5.9 ± 3.1 min; 55% of dives were > 5.6 min, the previously determined aerobic dive limit; 36% were > 100 m in depth. Mean aortic temperatures during 3-h rest periods ranged from $37.3 \pm 0.2^\circ\text{C}$ to $38.0 \pm 0.1^\circ\text{C}$. Mean dive temperature did not correlate with dive duration, and the grand mean of mean dive temperatures in each bird ranged from $38.3 \pm 0.2^\circ\text{C}$ to $39.0 \pm 0.2^\circ\text{C}$; there was no evidence of core hypothermia during dives. Reliable, safe catheterizations, and the large percentage of deep/long dives of these birds should provide the basis both for future studies of pressure adaptation and hypoxic tolerance in diving emperor penguins, and for investigation of deep-dive foraging behavior.

key words: aorta, dive, emperor penguin, temperature

Introduction

In order to investigate the diving physiology and behavior of emperor penguins (*Aptenodytes forsteri*), bio-logging research projects have been conducted during austral springs since 1987 on penguins diving at an isolated dive hole in McMurdo Sound. Initial studies, with time-depth recorders (TDRs) and microprocessor-based heart rate (R wave detectors) and swim velocity (paddlewheel velocity sensor) recorders, documented diving heart rates at or below resting levels and mean swim speeds near 3 m/s during predominantly shallow (< 60 m) dives of up to 12-min duration (Kooyman *et al.*, 1992). During these dives, the birds typically ascend from depth to capture the sub-ice fish, *Pagothenia borchgrevinki*, near the platelet ice layer on the undersurface of the sea ice (Ponganis *et al.*, 2000). Although emperors use a stroke-glide wing beat pattern for propulsion, it was found that prolonged gliding, a potential energy-conservation mechanism (Williams *et al.*, 2000), did not occur during these dives under the ice (van Dam *et al.*, 2002). Under such conditions,

the measured aerobic dive limit (ADL_M or diving lactate threshold) is 5.6 min (Ponganis *et al.*, 1997), more than twice the calculated ADL (ADL_C , Nagy *et al.*, 2001). The difference between the ADL_M and ADL_C does not appear secondary to core hypothermia and hypothermic prolongation of aerobic dive time (Ponganis *et al.*, 2001, 2003). Although temperatures in peripheral tissues (limbs, subcutaneous tissue, anterior abdomen) often decreased dramatically during dives, temperatures in central sites (vena cava and deep veins, pectoral muscle) were conserved.

Dive patterns at the isolated dive hole range from serial to sporadic dives, and, almost always, the birds exit the water and stand on the sea ice between dives (Kooyman *et al.*, 1992; Ponganis *et al.*, 2001, 2003). Since post-dive intervals are in the same range as those of emperors on foraging bouts at sea during chick-rearing periods (Kooyman and Kooyman, 1995), we suggest that these findings are most applicable to the shallow dives of emperors foraging in pack ice. During foraging bouts at sea, more than 50% of all dives are < 50 m in depth, and 25% of foraging dives are < 40 m in depth (Kooyman and Kooyman, 1995). In addition, however, deep dives of 100- to 500-m depth are also considered to be significant for foraging.

Comparison to the deep dives of emperors and to other patterns of diving, such as the serial, deep dives with no out-of-water exit of king penguins (*A. patagonicus*; Handrich *et al.*, 1997), would be valuable. Therefore, we report here the first observations of deep-diving behavior (> 100 m) of emperor penguins at the isolated dive hole, present our initial investigations of aortic temperature responses during such dives, and outline future directions of research afforded by these findings and techniques.

Materials and methods

Emperor penguins were captured at the McMurdo Sound ice edge in October, 2001, were maintained and allowed to forage at an isolated dive hole in a corral on the sea ice for two months, and were then released. As part of an initial study to record data from a sensor implanted in the aorta, three birds, under general isoflurane-oxygen anesthesia (Ponganis *et al.*, 2001), were instrumented with a Mk5 TDR (Wildlife Computers, Redmond, WA, 1×3.5×8 cm, 50 g), and a temperature logger (UFI, Morro Bay, CA, 13×4×3.5 cm, 350 g). Both devices were attached to feathers on the back with Loctite glue, a velcro patch, and cable ties. Depth sensitivity of the TDR was: 0.25 m (0 to 20 m), 1 m (20–55 m), 5 m (50–250 m), and 10 m (250–420 m). A YSI 554 thermistor (Yellow Springs Instruments, Yellow Springs, OH, 95% response time 0.2 s, 0.05°C sensitivity), calibrated as previously described (Ponganis *et al.*, 2001), was inserted percutaneously with a peel-away introducer (Cook, Bloomington, IN) via the femoral artery into the aorta (as confirmed by a $P_{O_2} > 85$ torr during anesthesia (i-STAT, East Windsor, NJ). Temperature was recorded every 15 s; depth and light intensity, every second. After overnight recovery, birds were allowed access to the dive hole. Devices were removed under general anesthesia after one day of diving.

Data were downloaded to a personal computer, and analyzed with Excel, and Origin software. Start and end of dive times were determined by depth change from baseline, and were confirmed by appropriate changes in light intensity. Submergences of < 1 min were not considered dives; consequently, intervals between dives were termed post-dive intervals. Results are expressed as mean ± standard error unless otherwise stated. Statistical signifi-

cance was assumed at $p < 0.05$.

Results

Access to the experimental dive hole was limited by overnight recovery from anaesthesia, weather constraints, and the need to stop food intake 8 h prior to general anaesthesia. Consequently, EP36 had 14-h access to the dive hole (0900–2300), EP37, 3 h (1730–2030), and EP41, 15 h (0900–2400). Prior to these experiments, these and seven other captive penguins had been exposed to nearly around-the-clock access to the dive hole (0800–0200). Mean diving duration of 83 dives by the three instrumented birds was 5.9 ± 3.1 min; 55% of dives were > 5.6 min; 36% were > 100 m in depth. Dive duration correlated significantly with maximum depth ($r = 0.61$, $p < 0.001$), as did the post-dive interval with dive duration ($r = 0.38$, $p < 0.001$, see Fig. 1). Individual dive statistics for each bird are in Table 1.

Mean temperatures during 3-h rest periods (0100–0400) ranged from $37.3 \pm 0.1^\circ\text{C}$ to $38.0 \pm 0.1^\circ\text{C}$, and the grand mean of mean dive temperatures of each bird, from $38.3 \pm 0.2^\circ\text{C}$ to $39.0 \pm 0.2^\circ\text{C}$ (Table 1). Mean temperatures of individual dives ranged from 37.7 to 39.3°C . Correlations of individual dive mean temperatures and dive durations in each animal were not significant (Table 1). There were also no significant correlations of dive duration and the difference between the last pre-dive temperature and the highest temperature recorded during a dive in any bird (Table 1).

Depth and aortic temperature profiles of EP41 during 15 h at the isolated dive hole (Fig. 2) demonstrate the fluctuations in aortic temperature during both isolated and serial, and, deep and shallow dives throughout the day. Intra-dive temperature typically increased (range: 0.1 to 3.5°C for all dives) above the immediate pre-dive level; this occurred during both serial (EP41, Fig. 3) and isolated (EP36, Fig. 4) deep dives. It is notable that the highest

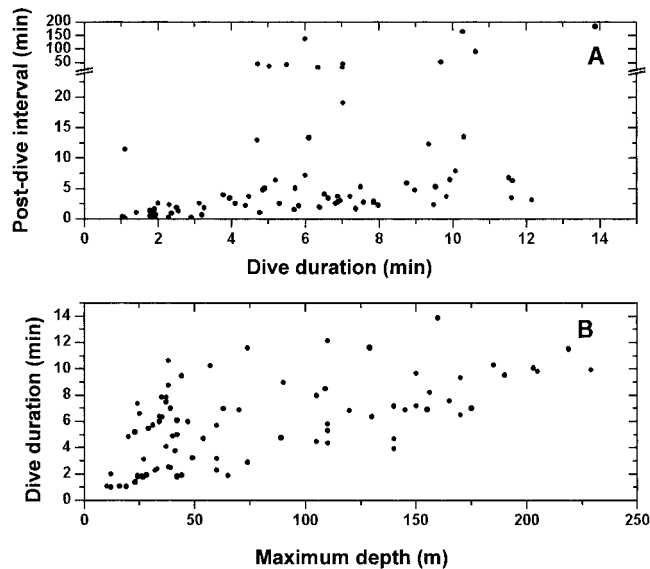


Fig. 1. (A) Post-dive interval–dive duration distribution of three emperor penguins at the isolated dive hole, excluding the last dive of each bird, when access to the dive hole was stopped ($r = 0.38$, $n = 80$, $p < 0.001$). (B) Dive duration–dive depth distribution for all dives ($r = 0.61$, $n = 83$, $p < 0.001$).

temperatures during a dive often occurred transiently during descent, a time associated with highest wing beat frequencies (Van Dam *et al.*, 2002). This could occur at the beginning of a dive or during a later descent during a dive (Fig. 3).

Table 1. Dive and aortic temperature data of individual emperor penguins. Aortic temperature was sampled every 15 s; temperature at rest was determined over 3-h periods from 0100 to 0400. Dive mean temperature is the mean of all 15-s values during a given dive. Max T is the maximum individual 15-s value recorded during a dive. ΔT is the difference between max T and the last pre-dive temperature value for that dive. The correlation coefficient, r , was not significant in any of the analyses ($p > 0.05$).

Bird identification	EP36	EP37	EP41
Body mass (kg)	25.5	26.3	25.2
# Dives	34	12	37
Dive duration (min, mean \pm SE)	6.3 \pm 3.6	4.1 \pm 2.7	6.1 \pm 2.6
Maximum duration (min)	12.2	8.9	13.9
% > ADL _M (5.6 min)	50%	42%	65%
% > 100 m	29%	25%	46%
Maximum depth (m)	230	140	175
Temperature at rest (3 h) ($^{\circ}$ C, mean \pm SE)	37.7 \pm 0.1	38.0 \pm 0.1	37.3 \pm 0.1
Diving temperature ($^{\circ}$ C, grand mean \pm SE of individual dive mean temperatures)	38.3 \pm 0.3	39.0 \pm 0.2	38.3 \pm 0.2
Dive mean temperature range ($^{\circ}$ C)	37.6–38.8	38.7–39.3	37.8–38.5
r (mean dive temperature to dive duration)	0.08	0.19	0.13
Range of max T during each dive ($^{\circ}$ C)	37.9–39.1	39.0–40.0	38.2–40.1
Range of ΔT for each dive ($^{\circ}$ C)	0.1–1.3	0.1–1.3	0.4–3.5
r (ΔT to dive duration)	0.25	0.35	0.26

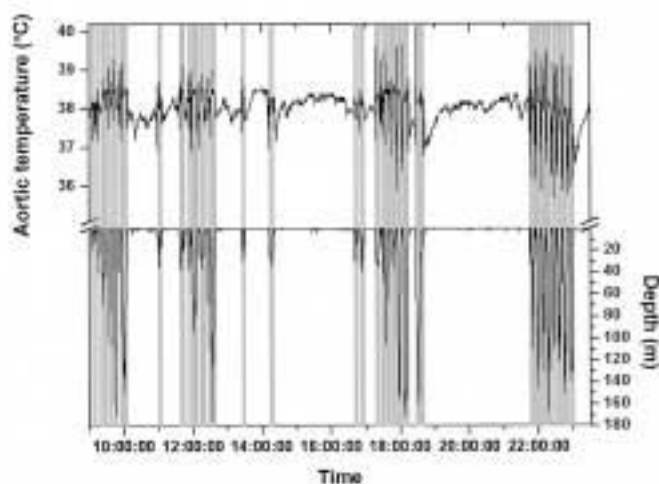


Fig. 2. Aortic temperature and depth profiles of EP41 during 15 h at the isolated dive hole. Gray-shaded background indicates dive period.

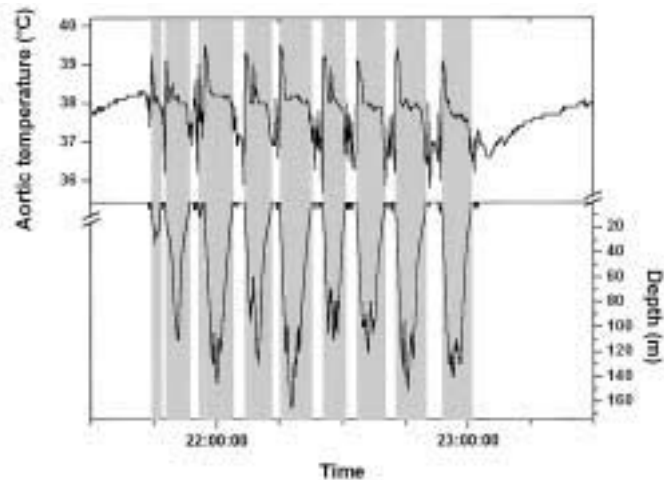


Fig. 3. Two-hour record of aortic temperature and depth of EP41 during a series of deep dives. Note transient elevations in temperature during descent periods.

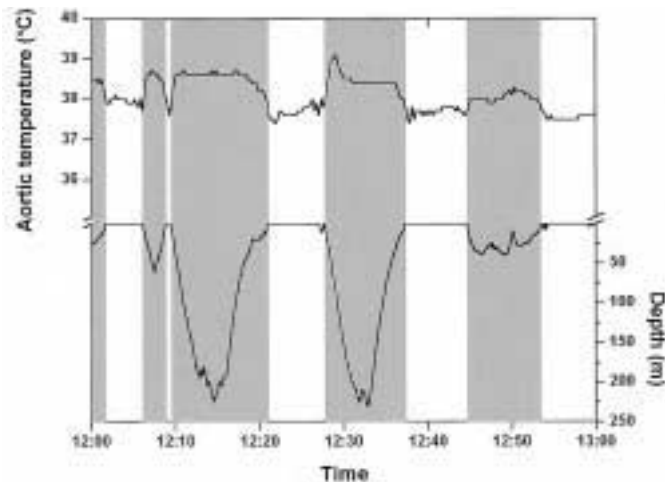


Fig. 4. One-hour record of isolated, long-duration dives to 230 m depth by EP36.

Discussion

Deep dive behavior

Deep dive behavior (> 100 m) occurred in emperor penguins at the isolated dive hole once they were allowed late-night access to the dive hole. In previous studies, and initially in the 2001 season, birds were generally allowed access to the dive hole only from 0800 to 1700. Under those conditions, all dives were predominantly shallow. Deep dives occurred in 2001 once the birds were allowed to dive between 1700 and 0200. All the birds (including those not in the study) appeared to shift to this pattern as evidenced by more diving activity in the evening period, the occurrence of long dives as recorded by observation and stopwatch both during the evening and the day, and a change in guano color/composition. Otolith analysis suggests that the prey is the Antarctic silverfish, *Pleuragramma antarcticum* (G.L. Kooyman, unpublished obs.). The jagged depth profiles at the bottom of deep dives

(Figs. 3, 4) also suggest such prey capture at depth. It is unclear what caused the change in dive behavior, *i.e.*, lack of surface prey at night, availability of deeper prey at night, or preference for deeper prey once discovered. During foraging at sea, it should be noted that deep dives do occur throughout the day, although dives > 400 m occur between 0500 and 1900 hrs (Kooyman and Kooyman, 1995).

As in studies of emperor penguins foraging at sea (Kooyman and Kooyman, 1995), dive duration of these three birds at the isolated dive hole correlated with maximum depth ($r = 0.61$, Fig. 1). Eighty-three percent of dives >100 m in depth were beyond the previously determined 5.6-min ADL_M (Ponganis *et al.*, 1997). However, long dives also occurred at shallow depths. Similar to prior studies of shallow dives at the isolated dive hole (Ponganis *et al.*, 2001), approximately one-third (37%, Fig. 1) of dives <50 m in depth were > the ADL_M determined for such dives. Although the increase in post-dive interval with dive duration ($r = 0.38$, Fig. 1) suggests a need for some metabolic recovery after longer dives, there was a wide scatter of data, and other factors (*i.e.*, satiety) may also play a role in the determination of post-dive interval durations.

Aortic temperature

Aortic temperature profiles provided no evidence of core hypothermia, even during dives as long as 14 min and as deep as 230 m (Figs. 2, 4). These aortic temperatures are consistent with prior findings of normothermia in the vena cava, deep veins, and pectoral muscle of emperor penguins diving under sea ice (Ponganis *et al.*, 2001, 2003). The decreased temperatures observed during post-dive intervals between serial dives (Fig. 3) are consistent with rewarming of a cooled periphery and stomach contents as previously observed during post-dive periods (Ponganis *et al.*, 2001, 2003). Thus, there is no evidence in these data that core hypothermia extends aerobic dive time of deep dives of emperor penguins diving under sea ice at the isolated dive hole.

Implications for bio-logging at the isolated dive hole

The large percentages of both deep dives (37% >100 m) and long dives (55% > ADL_M) of these birds at the isolated dive hole, and the development of safe, reliable vascular access techniques for both the aorta and vena cava (this study, Ponganis *et al.*, 2001) are significant because they provide the basis to begin examination of pressure adaptation and hypoxemic tolerance in diving emperor penguins. The mechanisms by which emperors avoid decompression sickness and nitrogen narcosis during their 100- to 500-m dives at sea are unknown (Kooyman and Kooyman, 1995; Kooyman and Ponganis, 1998; Ponganis *et al.*, 1999). Performance of dives as deep as 230 m by catheterized birds at the isolated dive hole should allow investigation of this question. In addition, the frequent occurrence of both shallow and deep long dives should enable us to 1) assess O₂ store management and depletion during such dives, and 2) determine if the ADL_M of deep dives is equivalent to or greater than that of shallow dives. It has already been hypothesized that prolonged gliding during deep dives may be a mechanism to extend the ADL for deep dives since prolonged gliding does not occur during shallow dives at the isolated dive hole (Van Dam *et al.*, 2002). This hypothesis is supported by observations of gliding behavior during ascent in both king and Adélie (*Pygoscelis adeliae*) penguins (Sato *et al.*, 2002).

The occurrence of deep dives at the isolated dive hole also provides the basis to further

study foraging behavior of emperors. Application of the Crittercam camera has successfully documented foraging strategy and prey intake during shallow dives of emperors at the isolated dive hole. It is anticipated that these deep dives will provide the opportunity to evaluate and refine newer and smaller camera technologies (video, digital) to allow documentation of foraging behavior not only at the isolated dive hole but also eventually at sea.

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