RESEARCH ARTICLE

Stroke rates and diving air volumes of emperor penguins: implications for dive performance

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SUMMARY

Emperor penguins (*Aptenodytes forsteri*), both at sea and at an experimental dive hole, often have minimal surface periods even after performance of dives far beyond their measured 5.6 min aerobic dive limit (ADL: dive duration associated with the onset of post-dive blood lactate accumulation). Accelerometer-based data loggers were attached to emperor penguins diving in these two different situations to further evaluate the capacity of these birds to perform such dives without any apparent prolonged recovery periods. Minimum surface intervals for dives as long as 10 min were less than 1 min at both sites. Stroke rates for dives at sea were significantly greater than those for dives at the isolated dive hole. Calculated diving air volumes at sea were variable, increased with maximum depth of dive to a depth of 250 m, and decreased for deeper dives. It is hypothesized that lower air volumes for the deepest dives are the result of exhalation of air underwater. Mean maximal air volumes for deep dives at sea were approximately 83% greater than those during shallow (<50 m) dives. We conclude that (a) dives beyond the 5.6 min ADL do not always require prolongation of surface intervals in emperor penguins, (b) stroke rate at sea is greater than at the isolated dive hole and, therefore, a reduction in muscle stroke rate does not extend the duration of aerobic metabolism during dives at sea, and (c) a larger diving air volume facilitates performance of deep dives by increasing the total body O_2 store to $68\,ml\,O_2\,kg^{-1}$. Although increased O_2 storage and cardiovascular adjustments presumably optimize aerobic metabolism during dives, enhanced anaerobic capacity and hypoxemic tolerance are also essential for longer dives. This was exemplified by a 27.6 min dive, after which the bird required 6 min before it stood up from a prone position, another 20 min before it began to walk, and 8.4 h before it dived again.

Key words: aerobic dive limit, diving air volume, emperor penguin, oxygen stores, stroke rate, surface interval.

INTRODUCTION

The concept of an aerobic dive limit (ADL) emphasizes the efficiency of aerobic energy production as the metabolic basis for the performance of routine, frequent, repetitive dives to depth (Kooyman et al., 1983; Kooyman et al., 1980). Defined as the dive duration associated with the onset of post-dive lactate accumulation, the ADL has become fundamental to the interpretation of diving physiology, dive behavior and foraging ecology (Butler and Jones, 1997; Kooyman and Ponganis, 1998). Dives beyond the ADL are less frequent and are associated with prolonged surface intervals, presumably because of the recovery period required after long duration dives.

However, emperor penguins (*Aptenodytes forsteri*, Gray 1844), both at sea and at an isolated experimental dive hole (Kooyman and Kooyman, 1995; Ponganis et al., 2007), routinely dive beyond the 5.6 min measured ADL (ADL_M) determined by post-dive blood lactate analyses in emperor penguins diving at an isolated dive hole (Ponganis et al., 1997b). In addition, surface intervals after dives even as long as 10 min are often less than 1–2 min in both situations (Ponganis et al., 2007; Wienecke et al., 2007). Such repetitive diving ability beyond the ADL_M raises questions about the duration of

aerobic metabolism during individual dives of emperor penguins, the post-dive metabolism of lactate, anaerobic capacity, and the tolerance of high lactate levels in these birds.

To address this remarkable capacity for long dives in emperor penguins, we applied dive recorders (depth, speed, 2-D acceleration) to emperor penguins diving at the isolated dive hole and to emperor penguins making foraging trips to sea from the Cape Washington colony in Antarctica. First, we wanted to evaluate the relationship of surface interval to dive duration, especially at the isolated dive hole. We wished to determine whether prolongation of minimum surface intervals occurred near the 5.6 min ADL_M. Second, we hypothesized that stroke rates for dives of given duration were lower at sea than at the isolated dive hole. Because an at-sea behavioral ADL (ADL_B) of 8 min had previously been estimated on the basis of a prolongation of post-dive intervals (Kooyman and Kooyman, 1995), we postulated that stroke rate, an index of muscle workload and the depletion rate of the muscle O_2 store, would be 40% lower at sea. Such a reduction in stroke rate could account for the 2.4-min difference between the ADL_B at sea and the ADL_M at the isolated dive hole as well as for the relatively short surface intervals after long dives at sea. Third, we hypothesized that the magnitude

of the respiratory O_2 store was greater during deep dives than during shallow dives of emperor penguins. Increased air volumes during deep dives had previously been observed in both king (*A. patagonicus*) and Adélie (*Pygoscelis adeliae*) penguins (Sato et al., 2002). Because the ADL_M was determined during shallow diving at the isolated dive hole (Ponganis et al., 1997b), such an increase in the respiratory O_2 store during deep dives could contribute to prolonged aerobic metabolism during long, deep dives at sea. An increase in the respiratory O_2 store might then contribute to the repetitive diving ability of emperor penguins at sea and to the differences between the ADL_B at sea and the ADL_M at the isolated dive hole.

MATERIALS AND METHODS
Field studies
The first field study was conducted in McMurdo Sound, Antarctica during the period from 14 November to 4 December 2004. Three emperor penguins, ranging from 24.4 to 27.4 kg, were captured near the sea ice edge of eastern McMurdo Sound. They were maintained in a corral at a research camp (Penguin Ranch) on the McMurdo sea ice (77°43′S, 166°07′E). The penguins foraged daily beneath the sea ice with entry and exit through two 1.2 m wide dive holes drilled inside the corral. A data logger was attached to the central back of each penguin with waterproof Tesa™ tape (Beiersdorf AG, Hamburg, Germany) and glue (Loctite epoxy, Henkel, Westlake, OH, USA) while the bird was under hand restraint. The bird was allowed to dive, and the data logger was retrieved 38–60 h after attachment. Each bird was instrumented one to three times.

The second field study was conducted at the breeding colony at Cape Washington (74°39′S, 165°24′E) during the chick-rearing period from 26 October to 24 November 2005. All deployments of data loggers were conducted on 28 October. Fourteen birds departing for foraging trips were captured at the edge of the colony. Data loggers were attached to the central back feathers using waterproof tape and stainless steel cable ties. VHF transmitters (Model MM130, ATS, Isanti, MN, USA) were attached to the lower back with cable ties. Body mass was measured to the nearest 100 g at deployment and recapture, using a balance (Pesola 50 kg). After release, every bird walked toward open water. Handling time was less than 30 min.

Instruments
3-D loggers (W1000L-3MPD3GT, Little Leonardo Ltd, Tokyo, Japan) were used for the first field study at the isolated dive hole. The W1000-3MPD3GT was 26 mm in diameter, 174 mm in length, had a mass of 120 g in air, and recorded 3-axes magnetism (1 Hz), speed (1 Hz), depth (1 Hz), temperature (1 Hz) and 3-axes acceleration (either 16 or 32 Hz for each deployment). These data allowed construction of underwater 3-D dive paths (Shiomi et al., 2008); however, only dive parameters, such as dive depth and duration, swim speed and stroke rate were used in the present study. Acceleration data loggers (W1000L-PD2GT and W1000L-PD2GT, Little Leonardo Ltd) and 3-D loggers (W1000L-3MPD3GT, Little Leonardo Ltd) were used for the second field study to obtain detailed information at sea (depth, speed and acceleration) during the foraging trip. In the second field study, nine W1000-PD2GT were used and data were obtained from seven of them. The W1000-PD2GT was 22 mm in diameter, 122 mm in length, had a mass of 73 g in air, and recorded speed (1 Hz), depth (1 Hz), temperature (1 Hz) and 2-axes accelerations (16 Hz). The devices were set to start recording 4–96 h (4 days) after deployment (Table 1). Data length of W1000-PD2GT ranged from 3.9 to 4.1 days (Table 1). Two W1000L-PD2GT (capacity of memory was larger than W1000-

PD2GT) were used and data were obtained from them. The W1000L-PD2GT was 27 mm in diameter, 128 mm in length, had a mass of 101 g in air, and recorded speed (1 Hz), depth (1 Hz), temperature (1 Hz) and 2-axes acceleration (16 Hz). Data lengths of the W1000L-PD2GT were 14.3 and 14.5 days (Table 1). Three W1000L-3MPD3GT (3-D logger) were used and data were obtained from one of them at sea. Data length of W1000L-3MPD3GT was 11.5 days, which covered the whole foraging trip.

Loggers were positioned so as to detect longitudinal and dorso-ventral acceleration. In this paper, 3-axes magnetism is not considered. Acceleration output values from the recorders were converted into acceleration ($m s^{-2}$) with linear regression equations. To obtain the calibration equations, values recorded by each sensor at 90 and –90 deg from the horizontal were regressed on the corresponding acceleration (9.8 and $-9.8 m s^{-2}$, respectively). Loggers measured both specific acceleration (such as wing stroking activity) and gravity-related acceleration. Low-frequency components (<0.5 Hz) of the fluctuation in longitudinal acceleration, along the long axis of the body, were used to calculate the pitch angle of the animal (Sato et al., 2003). The depth criterion for a dive was 1 m.

To test the effect of dive depth on dive duration, linear mixed models were fitted with dive duration as a response variable, dive depth as a fixed effect, and individual as a random effect at each study site (at sea and at the isolated dive hole). Then, to test the effect of site on slope, two generalized linear mixed models were fitted with Poisson error distribution and a logarithm link function, in which dive duration was a response variable with dive depth as an offset term, and individual as a random effect. One model included place (at the isolated dive hole or at sea) as a fixed effect, the other did not. Akaike information criteria (AIC) were used to select the most parsimonious model. For the model fitting, R 2.10 (R Development Core Team, 2009) was used with glmer function in R package lme4 (Bates and Maechler, 2009).

Stroke rate analysis
In order to examine the difference in stroke rate between birds at the isolated dive hole and birds foraging at sea, the number of strokes during a dive was calculated with the longitudinal acceleration data, in which stroking activities were presented as regular peaks (Sato et al., 2005; van Dam et al., 2002). Then, two types of generalized linear mixed models were fitted with Poisson error distribution and a logarithm link function, in which the total number of strokes during a dive was a response variable with dive duration as an offset term and individual as a random effect. One model included place (at the isolated dive hole or at sea) as a fixed effect, the other did not. AIC were compared between the two fitted models. For the model fitting, R 2.10 (R Development Core Team, 2009) was used with glmer function in R package lme4 (Bates and Maechler, 2009).

Diving air volume analysis
Swim speed during the prolonged glide period during final ascent was used to estimate diving air volume in dives at sea following the methods of a previous study (Sato et al., 2002). The diving air volumes were estimated for dives selected at random ($N=425$ dives by 10 birds). Using the biomechanical model (Sato et al., 2002), the model simulation was conducted for each dive under several values of air volume. The simulated speeds were then compared with the measured speed to select an appropriate value of the air volume for each dive. The estimated air volume was compared with dive depth. To test the effect of dive depth on the estimated air volume, both a linear mixed model and a quadric mixed model were

Table 1. Field study of emperor penguins at a breeding colony in Cape Washington

ID	Logger	Delay time (h)	Initial body mass (kg)	Place and status when recaptured	Final body mass (kg)	Mass gain (kg)	Trip duration (days)	Data length (days)
CW1	W1000-PD2GT	8	29.0	In colony	No data	No data	7.9	4.0
CW2	W1000-PD2GT	8	23.0	On the way to the colony	25.5	2.5	10.0	4.1
CW3	W1000-PD2GT	8	21.5	In colony	25.5	4.0	17.8	4.1
CW4	W1000-PD2GT	48	23.5	In colony	25.5	2.0	13.5	3.9
CW7	W1000-PD2GT	96	24.0	On the way to the colony	26.5	2.5	16.1	4.0
CW8	W1000-PD2GT	96	27.5	In colony	30.5	3.0	13.7	3.9
CW9	W1000-PD2GT	96	24.0	In colony with chick	26.5	2.5	15.0	4.0
CW10	W1000L-PD2GT	4	25.5	In colony	30.5	5.0	19.7	14.3
CW11	W1000L-PD2GT	4	22.0	In colony with chick	22.5	0.5	16.5	14.5
CW13	W1000L-3MPD3GT	4	26.0	In colony	30.0	4.0	11.5	11.5

fitted with diving air volume as a response variable, dive depth as a fixed effect, and individual as a random effect. AIC was used to select the most parsimonious model from the model including random effect only, the linear mixed model and the quadric mixed model. For the model fitting, R 2.10 (R Development Core Team, 2009) with glmer function in R package lme4 (Bates and Maechler, 2009) and Matlab (MathWorks, Natick, MA, USA) with nlmefit function were used.

RESULTS
Cape Washington deployments
Measured masses of the Cape Washington birds were between 21.5 and 29.0 kg, in the same range as those of the penguins (24.4–27.4 kg) at the isolated dive hole (Table 1). Two of the 14 birds were recaptured near the colony 3 days later. The two birds seemed to be non-breeding birds because they did not depart for the foraging trip and wandered around the colony. Another bird was not recaptured because it was never relocated. The other 11 birds were recaptured at the colony and the instruments were retrieved. One of the 11 instruments did not work because of mechanical trouble. Data were obtained from the other 10 birds. According to the body mass measurements, net mass gain ranged from 0.5 to 5.0 kg (N=10 birds) (Table 1) after foraging trip durations of 7.9 to 19.7 days. Small mass gains (0.5 kg) might be secondary to feeding of chicks prior to recapture. We succeeded in recapturing two birds on the way back to the colony. Their mass gains were both 2.5 kg.

General description of dives
All 10 birds at sea performed dives during the sampling periods of their recorders. Mean dive duration ranged from 1.7 to 2.9 min, and the maximum dive duration was 27.6 min (CW8, Table 2), which is now the longest recorded dive of any avian diver. The maximum dive depth for each bird ranged from 357.5 to 513.5 m, and mean dive depths were between 28.3 and 71.9 m. Mean dive durations for three birds at the isolated dive hole ranged from 1.8 to 3.0 min, similar to those of free-ranging birds at sea, but mean dive depths at the isolated dive hole were between 13.0 and 15.8 m, and the maximum dive depth of each bird was shallower than 100 m (Table 2). According to the histograms in Fig. 1A, most dives at sea were also shallower than 100 m; however, 18.3% of dives were deeper than 100 m. Most dives at sea and at the isolated dive hole were shorter than 10 min (99.7 and 92.3% were ≤10 min, respectively; Fig. 1C,D).

Dive duration increased with dive depth at sea (Fig. 2A). AIC of the model with dive depth as a fixed effect (AIC: 235,995) was smaller than that of the model including a random effect only (AIC: 259,668). However, dive duration of shallow dives varied considerably (Fig. 2A). Some shallow dives at sea were long, and the extreme long dives (>10 min) were shallow, near 100 m (Fig. 2A). The longest recorded dive duration (27 min 36 s) of this species was attained in a shallow dive of 110 m by a free-ranging bird (CW8) at sea. There was also a positive relationship between dive depth and dive duration at the isolated dive hole. AIC of the model with dive depth as a fixed effect (AIC: 23,463) was smaller

Table 2. Diving characteristics of emperor penguins at sea (Cape Washington) and the isolated dive hole (Penguin Ranch)

| ID	N	Dive duration (min)		Dive depth (m)	
		Mean ± s.d.	Max.	Mean ± s.d.	Max.
Cape Washington					
CW1	906	2.0±1.9	8.4	28.3±48.8	357.5
CW2	1479	1.7±2.5	12.2	42.8±78.7	418.0
CW3	1153	2.0±2.3	12.7	38.4±55.9	423.0
CW4	1264	2.1±2.5	11.5	39.1±74.4	513.5
CW7	1376	2.1±2.5	12.5	49.6±95.0	475.8
CW8	1167	2.0±2.5	27.6	38.2±78.4	501.8
CW9	953	2.8±2.7	10.9	68.3±101.7	499.5
CW10	3447	2.9±2.3	12.1	71.9±76.1	458.8
CW11	5859	1.7±2.1	12.7	30.6±50.1	400.3
CW13	2959	2.6±2.4	17.3	43.3±68.2	509.2
Total	20430	2.2±2.4	–	44.8±71.4	–
Penguin Ranch					
PR1	420	3.0±4.3	19.8	15.8±16.7	80.3
PR2	1213	1.8±3.9	19.1	13.0±15.6	95.8
PR3	274	2.7±5.1	22.1	14.7±17.4	69.8
Total	1907	2.0±3.9	–	13.5±16.5	–
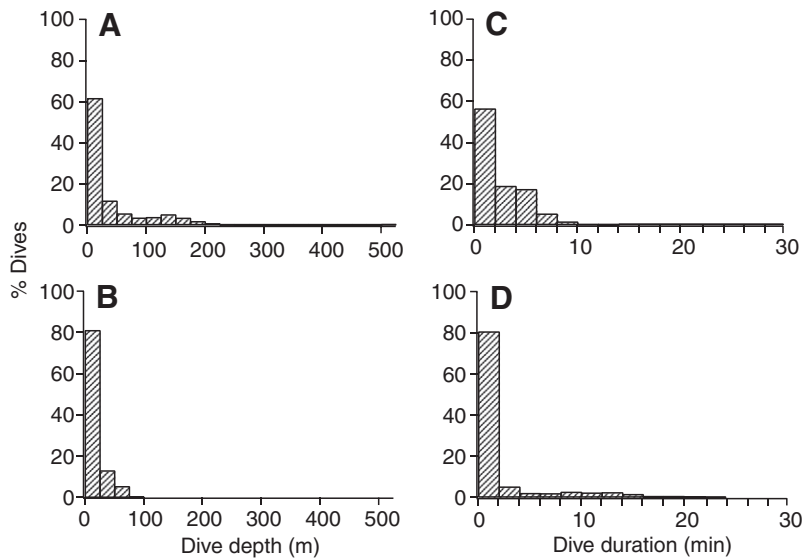
Fig. 1. Histograms of dive depth (A,B) and duration (C,D). Data were obtained from 10 birds (*N*=20,430 dives) at sea (A,C) and three birds (*N*=1907 dives) at the isolated dive hole (B,D).

than that of the model including a random effect only (AIC: 26,193). AIC of the model with place (at the isolated dive hole or at sea) as a fixed effect was smaller than that of the model not considering place as an effect (AIC: 965,921 and 965,943, respectively). Birds at the isolated ice hole also performed shallow, long dives (Fig. 2B).

Surface interval analysis

Surface intervals varied considerably for any given dive duration both at sea and at the isolated dive hole (Fig. 3A,B). Minimum surface intervals were less than 1 min even after dives as long as 10 min at both sites. There was no apparent distinct inflection point toward longer surface intervals. After classification of dives of <2 min or <50 m as part of the post-dive interval at sea (Kooyman and Kooyman, 1995), re-analysis demonstrated that the minimum post-dive interval began to increase above 1 min after dives of 6–7 min duration (Fig. 3C). The minimum post-dive interval was near 2 min at dive durations of 9–10 min except for two points (Fig. 3C). Similar analysis of post-dive intervals at the isolated dive hole with a filtering criterion of dives <2 min suggested that minimum post-dive interval began to increase above 1 min at dive durations of 6–7 min (Fig. 3D). However, as at sea, there were dives of >10 min duration with post-dive intervals less than 2 min (Fig. 3D).

Stroke rate

The total number of strokes per dive increased with dive duration at both sites (Fig. 4). AIC of the model with place as a fixed effect was smaller than that for the model not considering place as an effect (AIC: 65,997 and 66,003, respectively). The estimated slope (calculated as number of strokes s^{-1}) was smaller for birds at the isolated dive hole than for free-ranging birds at sea (0.38 and 0.59, respectively), which means that stroke rates were different between sites and were less for birds diving at the isolated dive hole.

Detailed behavior of the longest dive

Fig. 5 illustrates the entire data record of the longest reported dive by a 27.5 kg emperor penguin (CW8). The bird reached a maximum depth of 110 m and then swam at depths ranging between 30 and 60 m. Mean swim speed in the descent phase was 2.1±0.1 m s^{-1}; mean swim speed decreased to 1.7±0.3 m s^{-1} during the later, shallower

portion of the dive. The penguin adopted a stroke-and-glide method during most of the dive, and stopped flipper beating during the final ascent at a depth of 48 m, after which it glided up to the sea surface in 37 s (Fig. 5B). Swim speed increased from 1.5 to 3.1 m s^{-1} during the passive ascent period. After this longest dive of 27.6 min, the
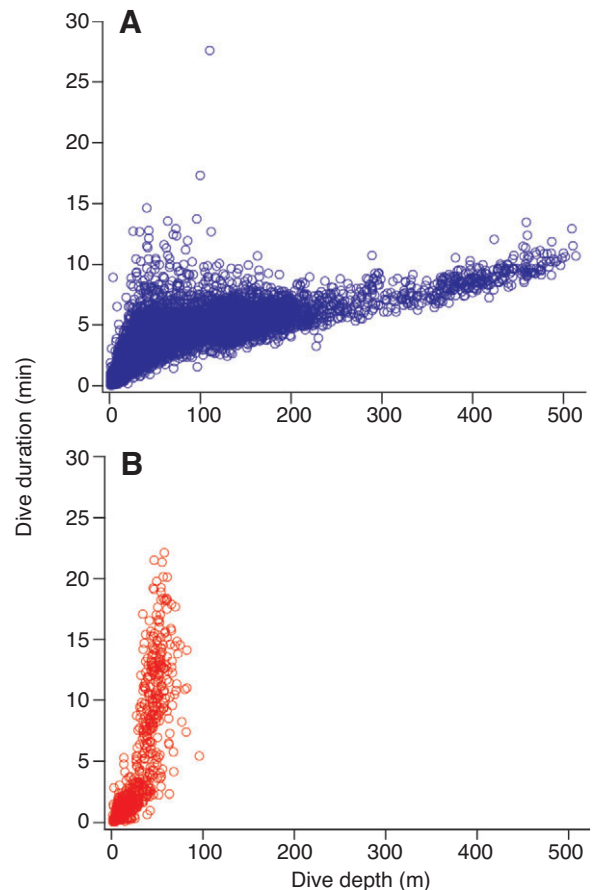

Fig. 2. Relationship between dive depth and duration. Data were obtained from 10 birds (*N*=20,430 dives) at sea (A) and three birds (*N*=1907 dives) at the isolated dive hole (B).
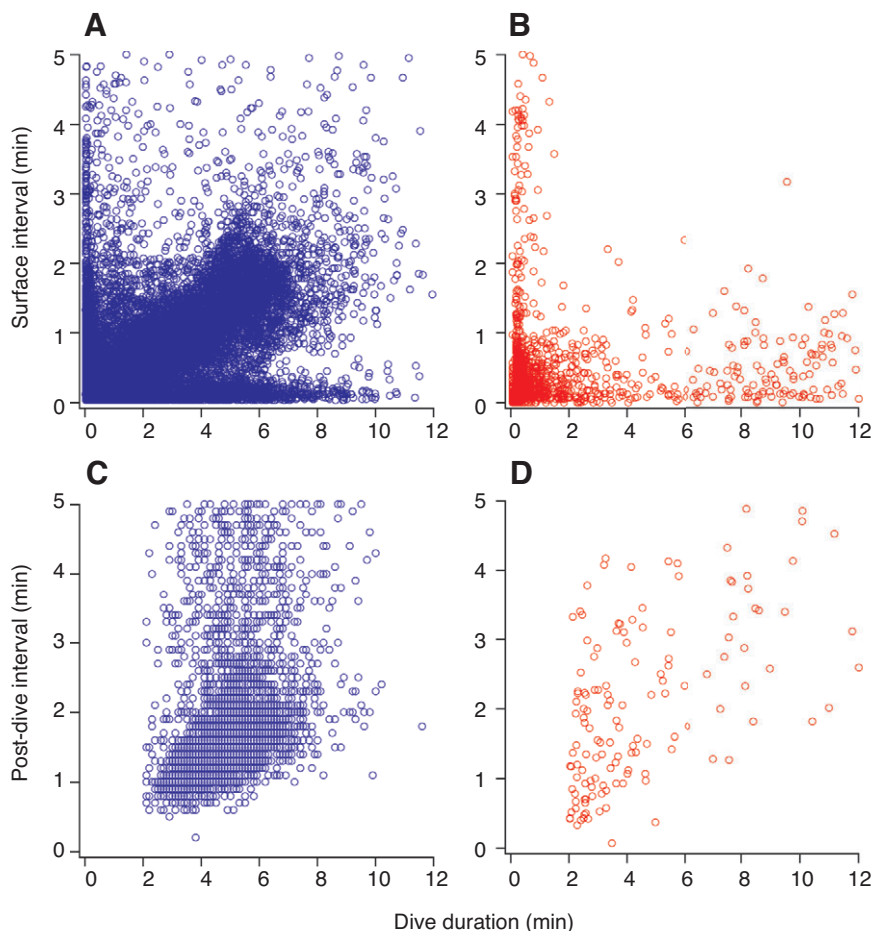
Fig. 3. Relationship for dives of up to 12 min duration between dive duration and surface interval or post-dive interval at sea (A, *N*=20,420; C, *N*=5415) and at the isolated dive hole (B, *N*=1901; D, *N*=365). Analogous to prior research (Kooyman and Kooyman, 1995), post-dive intervals at sea included surface time as well as dives <2 min or ≤50 m. At the isolated dive hole, post-dive intervals included surface times and dives <2 min.

penguin remained in a prone position (lying horizontal on its abdomen) for 5.9 min (Fig. 5C), and then stood quietly (pitch 70–80 deg) for 20 min. During the initial prone position, periodic movements were apparent in both dorso-ventral acceleration and pitch angle (Fig. 5C). We assume these movements are indicative of breathing. The overall respiration rate during the 5.9 min post-dive prone period was 17.8 breaths min^{-1}. The respiratory rate was 22 breaths min^{-1} during the first minute; it gradually decreased over 2.5 min to 15 breaths min^{-1} (Fig. 5C).

Diving air volume

All penguins at sea stopped stroking during ascent and made prolonged glides to the surface. Durations of the prolonged glides were relatively short, less than 9% of dive durations. Examples of the swim speed simulation results for passive ascents of shallow and deep dives are shown in Fig. 6. The calculated speeds under the conditions of 1.6 and 4.2 l diving air volume (at 1 atm pressure, ~101 kPa) accorded well with the measured speeds of the shallow (43.3 m) and deep (411.3 m) dives, respectively (Fig. 6). They indicate that the penguin could ascend passively at the recorded speeds if 1.6 and 4.2 l of air, respectively, were retained in the body.

The estimated air volumes of shallow dives were small. Air volume increased with dive depth up to 250–300 m and decreased in deep dives of 400–500 m (Fig. 7). AIC of the quadric mixed model ($V=-0.0009D^2+0.4396D+63.5482$, AIC: 3832) was smaller than that of the model including random effect only (AIC: 4010) and the linear mixed model ($V=0.02861D+89.56698$, AIC: 4007), where V is diving air volume (ml kg^{-1}) and D is dive depth (m).

The calculated diving air volume is the volume of air in the body during the final phase of each dive. That value has been assumed to reflect the inspiratory air volume at the start of the dive (Sato et al., 2002). However, variation in the magnitude of air volumes during the final ascent may at least in part be the result of exhalation of
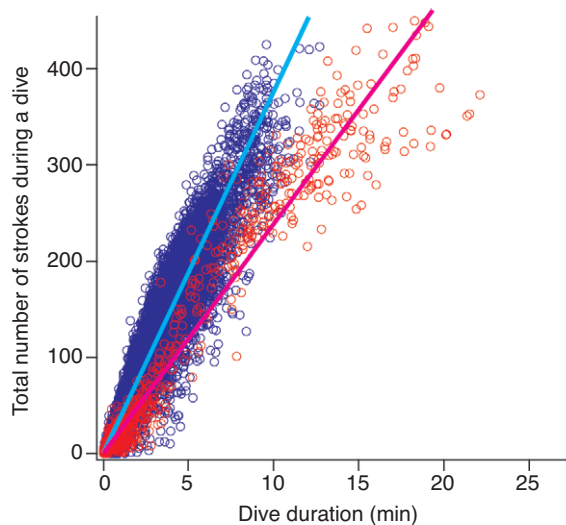

Fig. 4. Relationship between dive duration and total number of strokes during a dive. Data from nine birds at sea are represented as blue circles (*N*=16,546) and data from three birds at the isolated dive hole are indicated as red circles (*N*=1907). Regression lines are represented as light blue (at sea) and pink (at the isolated dive hole).
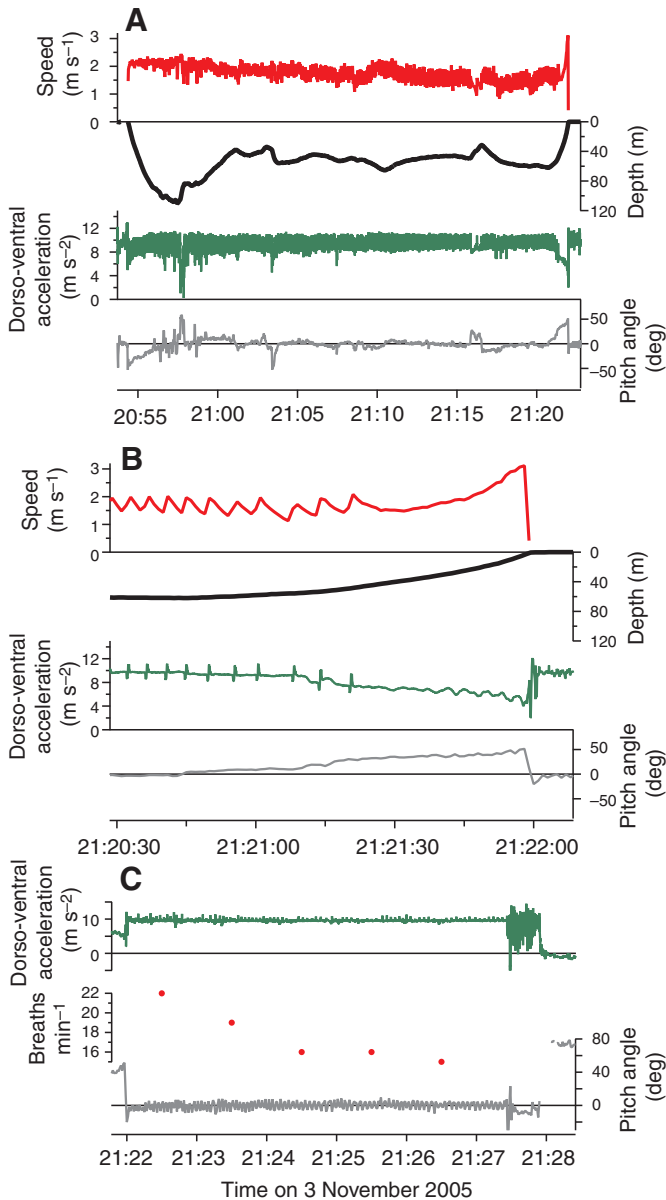
Fig. 5. Detailed behavior of an emperor penguin (CW8, Cape Washington 2005) diving for 27.6 min, which is the longest recorded dive for avian divers. The entire record (A), an enlargement of the final segment of the dive (B) and subsequent time on the ice (C). Breaths per minute (red dots) were counted from pitch angle every minute.
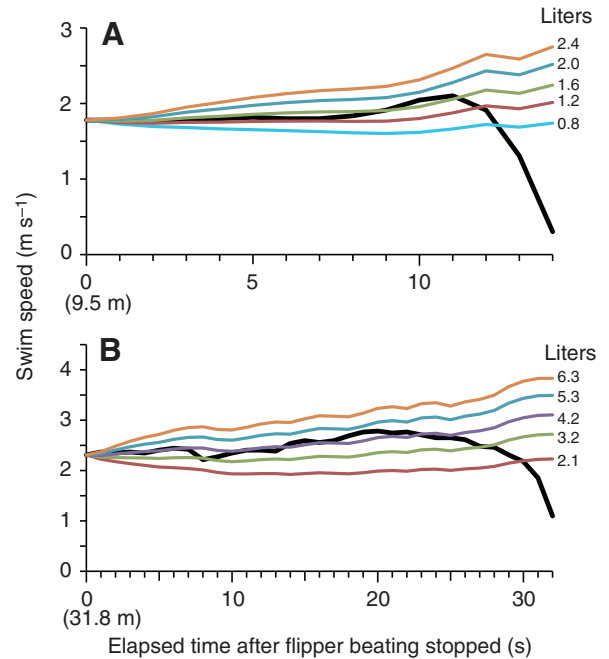

Fig. 6. Relationship between measured swim speed (thick black line) and simulated speed (colored lines) during the passive ascent periods of dives 155 (A) and 612 (B) of an emperor penguin (CW2). Values beside the colored lines are diving air volumes (at 1 atm, ~101 kPa) used in the model simulation. The depths at which the bird stopped flipper beating are indicated in parentheses.

air during the dive prior to the glide phase of the ascent. To examine this possibility, the initial descent stroking pattern of one bird was used as a relative index of inspiratory air volume. At the same swim speed, stroke effort should be proportional to buoyancy, and, hence, the inspiratory air volume. Fig. 8 illustrates the initial stroking patterns of a 23.0 kg penguin (CW2) in the first 10 s of four dives. Each example (Fig. 8A–D) corresponds with the points indicated in Fig. 7. In the case of a shallow dive with a small estimated air volume (Fig. 8A), stroke rate was 1.1 Hz at the beginning of the dive. The dive in Fig. 8B was also shallow, but both estimated diving air volume (4.3 l) and initial stroke rate (1.7 Hz) were high while swim speed was low in this dive. In the case of deep dives (Fig. 8C,D), estimated air volumes were 3.5 and 1.6 l; however, initial stroke

rates were 1.7 and 1.9 Hz, respectively (Fig. 8C,D), implying that the inspiratory air volume in the dive shown in Fig. 8D may have been greater than that calculated during the final ascent. Such a difference may be the result of exhalation of air during the dive prior to the gliding ascent. Such exhalations may account for the 40–170 ml kg^{-1} range of estimated diving air volumes of deep dives (>300 m) (Fig. 7).

DISCUSSION
Dive behavior

Maximum depths of dive and dive durations of emperor penguins during foraging trips to sea (Table 2, Fig. 1) were similar to those obtained in previous studies during foraging trips to sea in the chick-rearing period (Kirkwoods, 2001; Kirkwood and Robertson, 1997; Kooyman and Kooyman, 1995; Robertson, 1995). Of note is the longest recorded dive of an emperor penguin to date; a 27.6 min dive by CW8. Although maximum dive depths were generally shallower at the isolated dive hole, the distribution of dive durations was shifted towards longer dives (Figs 1 and 2). The shallow dives at the isolated dive hole are a consequence of the availability and hunting of prey fish beneath the surface of the sea ice (Ponganis et al., 2000). At the isolated dive hole, 12.6% of dives were >5.6 min (ADL$_M$), and 10.3% were >8 min (ADL$_B$).

It is remarkable that emperor penguins foraging from Cape Washington (this study) and Coulman Island (Kooyman and Kooyman, 1995) dive to depths >400 m much more routinely than those diving in East Antarctica (Wienecke et al., 2007). In 137,364 dives by 93 penguins in East Antarctica, only 15 birds performed dives >400 m, and only one dived deeper than 500 m. In contrast, in our study, 9 of 10 birds dived deeper than 400 m, and three birds dived >500 m.
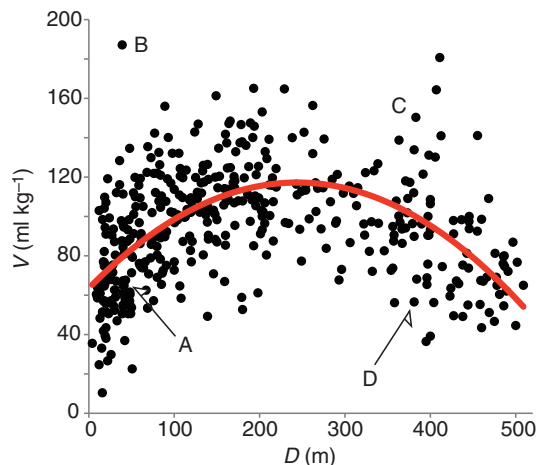
Fig. 7. Relationship between dive depth (D) and estimated air volume (V) of 10 emperor penguins (N=425). Thick red curve indicates the most parsimonious model selected by mixed model analysis ($V=-0.0009D^2+0.4396D+63.5482$). Letters A–D indicate values used in Fig. 8.
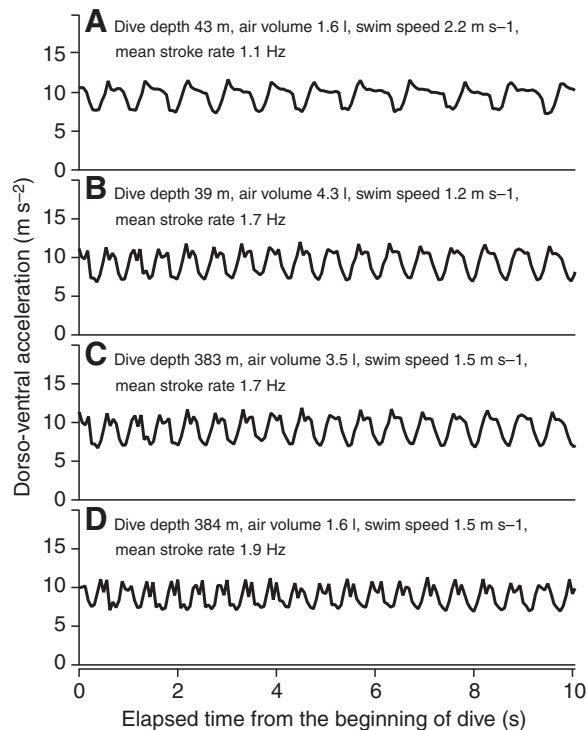

Fig. 8. Stroking patterns in the first 10 s of dives by an emperor penguin (CW2). (A) A shallow dive with a low calculated diving air volume, (B) a shallow dive with a large air volume, (C) a deep dive with a larger air volume, and (D) a deep dive with a small calculated air volume. Stroke rates were 1.1, 1.7, 1.7 and 1.9 Hz in dives A–D, respectively. The letters A–D correspond to the dives with the marked air volumes A–D in Fig. 7.

The relationship of dive duration to maximum depth of dive during foraging trips to sea was also similar to that in prior studies of foraging emperor penguins (Fig. 2A). If one considers that dives <2 min or <50 m are probably not foraging dives at sea (Kooyman and Kooyman, 1995), the majority of foraging dives at sea are between 5 and 10 min, and 50–500 m (Fig. 2A). Dives longer than 5.6 min (ADL_M) were 10.1% of all dives or a ~2100 dives; dives greater than 8 min (ADL_B) in duration were 1.9% of all dives (approximately 400 dives).

Surface interval–dive duration relationships

Examination of the surface interval to dive duration relationship both at sea and at the isolated dive hole demonstrated that minimum surface interval did not increase for dives beyond the ADL_M (Fig. 3A,B). It is possible that prolongation of surface intervals only occurs after a much greater lactate accumulation than that necessary for detection of an initial small elevation of post-dive blood lactate (the ADL_M) (Kooyman and Kooyman, 1995; Ponganis et al., 1997b). As demonstrated previously in both Weddell seals (*Leptonychotes weddellii*) and Baikal seals (*Phoca sibirica*), animals can have short surface intervals and continue to dive despite elevated blood lactate concentrations; in addition, elevated blood lactate concentrations can decrease during the breath-hold period (Castellini et al., 1988; Ponganis et al., 1997a). The relatively rapid decline measured in post-dive blood lactate concentrations of emperor penguins would also facilitate repetitive diving activity (Ponganis et al., 1997b).

The surface interval and dive duration data were also filtered to obtain post-dive interval. In this process (Kooyman and Kooyman, 1995), dives at sea were considered recovery dives and, therefore, part of the post-dive interval if the dives were <2 min in duration or <50 m in depth. Because most dives at the isolated dive hole were shallow, only dives <2 min in duration were considered recovery dives. After such data processing (Fig. 3C,D), minimum post-dive interval increased above 1 min after dives of 6–7 min duration both at the isolated dive hole and at sea, i.e. in the general range of the previously determined 5.6 min ADL_M and 8 min ADL_B. For dive durations of 10 min, the minimum post-dive interval was near 2 min. Thus, in our study, for 99.7% of all dives at sea, and 92.5% of dives

at the isolated dive hole (i.e. those under 10 min dive duration), the minimum post-dive intervals were less than 2 min.

From these minimum surface interval and minimum post-dive period analyses, it appears that emperor penguins can successfully perform many dives at sea without the need for an extended surface interval or even an extended post-dive period. This is similar to previous analyses of long and deep dives of emperor penguins diving in East Antarctica (Wienecke et al., 2007). Indeed, most minimum surface intervals are ≤1 min, the mean time for replenishment of blood and air sac O_2 stores (Ponganis et al., 2009). Thus, recovery from any elevation in blood lactate concentration is either rapid or does not always require a significant increase in the post-dive interval. Conversely, different physiological responses during different types of dive may prolong the duration of aerobic metabolism and delay the onset of lactate accumulation.

Stroke rate

A lower stroke rate at sea than at the isolated dive hole is one mechanism that could account for a longer ADL at sea and for the performance of repetitive, long deep dives at sea. However, in contrast to this hypothesis, stroke rates of dives at sea were actually greater than those of dives at the isolated dive hole (Fig. 4). This was unexpected because dives of penguins at sea typically have a period of prolonged gliding during ascent (Sato et al., 2002) whereas prolonged gliding does not occur during dives at the isolated dive hole (van Dam et al., 2002) (present study). Despite this lack of prolonged gliding, the total number of strokes per dive at the isolated dive hole was less than that for a dive of similar duration at sea (Fig. 4).

Table 3. Magnitude and distribution of oxygen stores in penguins

Dive type	Respiratory volume (ml kg^{-1})	Oxygen store (ml kg^{-1})			
		Air	Blood	Muscle	Total
Shallow dives	64	12.2	21.1	24.4	57.7
Deep dives	117	22.2	21.1	24.4	67.7

The maximum respiratory oxygen extraction during a dive was assumed to be 19% (Ponganis et al., 2010). Respiratory volumes are calculated as described in Materials and methods.

Assuming stroke rate is an adequate index of muscle workload and metabolic rate (Williams et al., 2000; Williams et al., 2004), muscle O_2 consumption is greater at sea than at the isolated dive hole. Based upon the mean number of strokes for dives at sea, stroke rate and muscle workload are about 1.6 times greater than those for dives of similar duration at the isolated dive hole. If the onset of post-dive lactate accumulation were solely dependent on the depletion of a muscle O_2 store isolated from the circulation, the ADL_M at sea would be less than at the isolated dive hole. Our hypothesis that a decreased stroke rate and muscle workload at sea could account for a longer ADL (behavioral or measured) at sea is not correct. For birds at the isolated dive hole, we suspect that the shift towards longer durations of dives (Fig. 1) is supported by a lower diving metabolic rate afforded by the lower stroke rates and muscle workloads (Fig. 4) as well as by the extreme bradycardias during these dives (Meir et al., 2008). It should also be noted that we have assumed that stroke rate is an adequate index of muscle workload. It is possible that stroke thrust and amplitude may vary with individual strokes, and also contribute to muscle workload (Williams et al., 2011). These parameters await further investigation.

Diving air volume

Diving air volume was estimated on the basis of body angle and swim speed during the prolonged gliding phase of the final ascent of a dive. As explained previously (Sato et al., 2002), and again reviewed in Fig. 6, this is the volume of air at surface air pressure, which, when compressed at depth, converted to buoyancy and combined with body angle, can best approximate the swim speed profile observed during the gliding ascent. Penguins do not appear to exhale during most of this gliding ascent because the observed speed profile should otherwise shift to that predicted by a lesser air volume. Such a shift in swim speed as evidence for exhalation of air or for other breaking maneuvers only occurs during the last 3–7 s of the ascent (Fig. 6). Exhalations at the end of ascent have been observed in penguins at sea (G.L.K. and P.J.P., unpublished observations). Consequently, the calculated air volume is considered to be the air volume (corrected to surface air pressure) that is in the body during that portion of the gliding ascent during which the observed swim speeds follow the predicted profile (i.e. prior to those last 3–7 s of the ascent).

Provided the bird does not exhale or otherwise lose air earlier in the dive (i.e. prior to the start of the gliding ascent), this calculated air volume should be representative of the initial air volume at the start of a dive. If the bird does exhale prior to the start of the gliding ascent, the initial start-of-dive air volume would be underestimated by this calculation. Note also that the calculated diving air volume includes both plumage air and respiratory air (lungs and air sacs). Loss of plumage air during a dive prior to the gliding ascent may also contribute to a lower-than-expected calculated diving air volume. However, plumage air is only about 10% of the diving air volume in simulated dives under restraint conditions, and diving air volumes of simulated dives appear to be at the low end of the range

of diving air volumes at sea (Kooyman et al., 1973; Sato et al., 2002; Sato et al., 2006). Consequently, with these caveats in mind and as in past papers, the entire diving air volume will be used for respiratory oxygen store calculations in this paper.

Diving air volume of emperor penguins increased with maximum depth of dive to about 200–300 m depth (Fig. 7). An increase in the estimated diving air volume with maximum depth is consistent with data from other penguin species (Sato et al., 2002). However, unlike in other penguin species, there was a decrease in diving air volume for dives at greater depths (especially between 400 and 500 m depth). This decline may be consistent with air volumes at the start of these deepest dives that are lower than those of the 200–300 m deep dives. The values for these deepest dives are closer to those for the dives of less than 100 m (Fig. 7).

However, the low values for 400–500 m deep dives in Fig. 7 suggest to us that the birds may be exhaling prior to the start of the gliding ascent during these very deep dives. Indeed, the variation in diving air volumes at all depths (Fig. 7) may be due either to use of different inspiratory air volumes during dives to the same depth and/or to exhalation of air prior to the start of the gliding ascents during all dives. Such exhalations may affect maneuverability, speed and hunting strategy. Weddell seals, for example, have been observed to flush fish out of the sub-ice platelet layer with exhalations (Davis et al., 1999). Exhalation of air has also been reported during early ascents of Antarctic fur seals (*Arctocephalus gazella*) (Hooker et al., 2005).

To assess the possibility of exhalation of air prior to the gliding ascent, initial stroke rates during dives were examined in one bird (Fig. 8). Interpretation of initial stroke rates during dives in Fig. 8 is dependent on the assumption that those values are a relative index of buoyancy and, hence, initial diving air volume (see Materials and methods). For the shallow dives in Fig. 8A and B, the difference in initial stroke rate supports the dive volume calculation, and suggests that even for shallow dives, there may be a wide range of inspiratory volumes. The high stroke rate during the deep dive in Fig. 8C was also consistent with the dive volume calculation and supported the hypothesis that inspiratory air volumes are large for deep dives. For the deep dive in Fig. 8D, the high stroke rate, but low calculated air volume suggest that the bird dived with a large inspiratory air volume (high stroke rate), but that the bird exhaled during the dive prior to the ascent, the time for which the air volume was calculated. Therefore, although initial diving air volume is variable for a given depth, we think that inspiratory air volume generally increases with depth of dive and is even elevated for dives to 500 m. We attribute the inverted U-shaped relationship of diving air volume to maximum dive depth to exhalation of air prior to the start of the gliding ascent during the deepest dives. In addition, the variability in the air volume data at all depths may be at least partially secondary to such exhalations. Possible exhalation of air represents a limitation of the use of diving air volume to estimate inspiratory air volume. Evaluation of this possibility awaits future application of animal-borne camera technology to emperor penguins at sea.

If we assume the mean values of calculated diving air volumes in Fig. 7 are representative of the initial diving air volume, then the inspiratory air volumes of 200–400 m deep dives are near 117 ml kg^{-1} (Fig. 7). Given the possible early exhalation of air during a dive and the subsequent potential limitations of these estimations, it is remarkable that this mean value is 98% of the mean respiratory capacity (120±2 ml kg^{-1}) predicted for the body masses of these penguins by an allometric equation (Lasiewski and Calder, 1971). Maximum diving air volumes of king and Adélie penguins are also in the same range as those predicted by the allometric equation (Sato et al., 2002). These findings reinforce the concept that penguins dive on inspiration. However, given the variability in data (the highest values near 160 ml kg^{-1} in Fig. 7), and the possibility of air exhalation, this mean value may underestimate the true start-of-dive air volume. Nonetheless, at this time, this 117 ml kg^{-1} value appears to be the best available estimate of the inspiratory air volume for deep dives.

Based on this analysis of the diving air volume data, mean initial air volumes of emperor penguins increase significantly from 64 to 117 ml kg^{-1} between shallow dives (<50 m) and deep dives (100–400 m). The former is the mean diving air volume of the quadric model for the shallowest dives; the latter is the maximum value of the quadric model. The shallow dive value is similar to the mean 69 ml kg^{-1} value measured in king penguins during simulated dives (Ponganis et al., 1999). The difference in diving air volumes between shallow and deep dives at sea represents an 83% increase in the size of the respiratory O$_2$ store (Table 3).

Respiratory and total body O$_2$ stores

With 19% maximum respiratory O$_2$ extraction during a dive (Ponganis et al., 2010), and diving air volumes of 64 and 117 ml kg^{-1} for shallow and deep dives, respectively, the available mass-specific respiratory O$_2$ store ranges from 12.2 to 22.2 ml O$_2$ kg^{-1} during dives of emperor penguins at sea. Use of the previous 69 ml kg^{-1} air volume of king penguins during simulated dives (Ponganis et al., 1999) and a 19% O$_2$ extraction, yields a respiratory O$_2$ store of 13.1 ml O$_2$ kg^{-1} (Ponganis et al., 2010). Thus, the maximum respiratory O$_2$ store resulting from larger diving air volumes in deep dives is 69% greater than past estimates based on air volumes during simulated dive studies.

With these estimates of respiratory O$_2$ stores, total body O$_2$ stores can be calculated for deep and shallow dives of emperor penguins. Given the new estimates of blood O$_2$ extraction and the differential distribution of myoglobin in the pectoralis–supracoracoideus muscles *versus* other muscles in the body (Ponganis et al., 2010), current best calculations of the mass-specific blood and muscle O$_2$ stores in emperor penguins are 21.1 and 24.4 ml O$_2$ kg^{-1}, respectively. These results and the 22.2 ml O$_2$ kg^{-1} respiratory O$_2$ store for deep dives yield a total body O$_2$ store of 68 (67.7) ml O$_2$ kg^{-1}, with 33, 31 and 36% of O$_2$ in the respiratory system, blood and muscle, respectively, for a diving air volume of 117 ml kg^{-1}. In contrast, for a diving air volume of 64 ml kg^{-1}, the total body O$_2$ store is 58 (57.7) ml O$_2$ kg^{-1}, with 21, 37 and 42% of O$_2$ in the respiratory system, blood and muscle, respectively.

In addition to a difference in the magnitude of the body O$_2$ stores during different types of dive, we suspect that emperor penguins exhibit a spectrum of cardiovascular responses dependent on the nature and depth of a dive. Variable rates of air sac and blood O$_2$ depletion and highly variable venous P_{O_2} and Hb saturation profiles in dives at the isolated dive hole have all suggested that the severity of bradycardia, degree of peripheral ischemia (especially to muscle) and utilization of arterio-venous shunting are not fixed (Meir and Ponganis, 2009; Meir et al., 2008; Ponganis et al., 2009; Ponganis

et al., 2007; Stockard et al., 2005). This capacity to alter the magnitude and distribution of blood flow during dives underlies the management of O$_2$ stores, and potentially increases the duration of aerobic metabolism and delays the onset of lactate accumulation.

Lastly, we point out that, despite our emphasis on aerobic diving, exceptionally long dives also occur at sea. The physiological capacity to perform such dives is essential to the success and survival of emperor penguins. The longest dives are shallow dives, usually less than 100 m in maximum depth (Kooyman and Kooyman, 1995; Wienecke et al., 2007). In the 27.6 min dive in Fig. 5, the longest recorded dive of an emperor penguin, the estimated diving air volume was 2.4 l or 87 ml kg^{-1}, providing 17 ml O$_2$ kg^{-1} of respiratory O$_2$, and a total body O$_2$ store of about 63 ml O$_2$ kg^{-1}. Clearly, some dives are anaerobic, as evidenced by the prolonged post-dive recovery in respiratory rate in Fig. 5C, and the 8.4 h period before this bird began to dive again. Although such dives may be rare, exquisite O$_2$ store management and exceptional hypoxemic and ischemic tolerance are essential to survive such incidents. Extreme bradycardia, near-complete depletion of the blood O$_2$ store and exceptional anaerobic tolerance undoubtedly contributed to the successful performance of this dive (Meir and Ponganis, 2009; Meir et al., 2008; Ponganis et al., 2009; Ponganis et al., 2007).

Perspectives

Analysis of surface interval–dive duration relationship confirms that emperor penguins can perform dives greater in duration than their ADL without prolongation of the surface interval. This occurs both at sea and at an isolated dive hole, where the 5.6 min ADL$_M$ has been determined with post-dive blood lactate measurements. After conversion of short duration (<2 min) dives into part of the post-dive interval, minimum post-dive intervals are still near 1 and 2 min, respectively, after 6–7 min and 10 min dive durations at both sites.

The ability to perform repetitive dives at sea is not afforded by a lower stroke rate. The total number of strokes per dive for dives of equivalent duration is actually higher at sea than at the isolated dive hole. Performance of deep dives at sea is probably facilitated, however, by an increased diving air volume (117 ml kg^{-1}) and respiratory O$_2$ store. Management of this enhanced body O$_2$ store is probably optimized by cardiovascular adjustments to prolong the duration of aerobic metabolism during dives.

Despite our emphasis on aerobic metabolism during dives, enhanced anaerobic capacity and hypoxemic tolerance undoubtedly also contribute to the performance of longer dives (Mill and Baldwin, 1983; Ponganis et al., 2007). This was exemplified by a 27.6 min dive, recovery from which required 6 min before the bird stood up from a prone position, another 20 min before it began to walk, and 8.4 h before it dived again.

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