

Stroke frequencies of emperor penguins diving under sea ice

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Summary

During diving, intermittent swim stroke patterns, ranging from burst/coast locomotion to prolonged gliding, represent potential energy conservation mechanisms that could extend the duration of aerobic metabolism and, hence, increase the aerobic dive limit (ADL, dive duration associated with onset of lactate accumulation). A 5.6 min ADL for emperor penguins had been previously determined with lactate measurements after dives of <50 m depth. In order to assess locomotory patterns during such dives, longitudinal acceleration was measured with an attached accelerometer in 44 dives of seven adult birds diving from an isolated dive hole in the sea ice of McMurdo Sound, Antarctica. Detection of wing strokes in processed accelerometer data was verified in selected birds with analysis of simultaneous Crittercam underwater video footage. Mean dive duration of birds equipped with the accelerometer and a time-depth recorder (TDR) was 5.7±2.2 min; 48% of these dives were greater than the measured 5.6 min ADL (ADL_M). Highest stroke frequencies (0.92±0.31 Hz, N=981) occurred during the initial descent to 12 m depth. Swimming effort was

reduced to a mean stroke frequency <0.70 Hz during other phases of the dive (while traveling below 12 m depth, during foraging ascents/descents to and from the sub-ice surface, and during final ascents to exit). The longest stroke interval (8.6 s) occurred during a feeding excursion to the undersurface of the ice. In dives >ADL_M, mean stroke frequency during travel segments was significantly less than that in dives <ADL_M (P<0.05). Mean stroke frequency of the entire dive correlated inversely (P<0.05) with diving duration (r=-0.67) and with mean dive depth (r=-0.43). Emperor penguins did not exhibit any significant (>10 s) periods of prolonged gliding during these shallow (<60 m) foraging dives. However, a stroke/glide pattern was evident with more than 50% of strokes associated with a stroke interval >1.6 s, and with lower stroke frequency associated with increased dive duration.

Key words: accelerometer, aerobic dive limit, *Aptenodytes forsteri*, Crittercam, dive, emperor penguin, stroke frequency.

Introduction

Burst swimming (stroke and glide) has long been considered an efficient form of aquatic locomotion (Weihs, 1974). More recently, another form of intermittent locomotion, prolonged gliding, has been observed in several marine mammal species (Skrovan et al., 1999; Williams et al., 2000; Nowacek et al., 2001). In addition, in Weddell seals *Leptonychotes weddellii*, prolonged gliding has been associated with decreased diving metabolic rates (Williams et al., 2000). Thus, in addition to hydrodynamic adaptations and buoyancy changes, intermittent locomotory patterns probably play a significant role in energy conservation during diving (Williams, 2001). As a consequence, the aerobic dive limit of a species (ADL; dive duration associated with post-dive lactate accumulation) may vary according to the depth profile and swimming behavior during dives.

The measured ADL (ADL_M), or diving lactate threshold (DLT) as determined by blood lactate measurements (Butler

and Jones, 1997) of emperor penguins *Aptenodytes forsteri* is 5.6 min (Ponganis et al., 1997). That ADL study involved relatively shallow dives (<50 m) of emperors foraging from an isolated dive hole. Depth profiles of these dives typically include descent to depth, travel at depth, hunting ascents to the undersurface of the ice to catch fish, and then return to depth for travel and eventual exit at the dive hole (Ponganis et al., 2000). Although shallow dives (<60 m) comprise about 60% of all dives during foraging trips to sea, emperors also routinely dive to 500 m depth, and frequently have diving durations greater than the ADL_M (Kooyman and Kooyman, 1995; Kirkwood and Robertson, 1997). Given the large diving air volume of penguins (Kooyman et al., 1973; Ponganis et al., 1999; Sato et al., 2002) and the potential role of buoyancy changes and intermittent locomotion patterns in affecting the magnitude of the ADL, it is unknown if swim behaviors during deep and shallow dives differ, and if the aerobic dive limit of

deep-diving emperors is the same as that of the shallow-diving birds at the experimental dive hole. In order to begin to assess these possibilities, we sought to measure stroke frequency and determine the locomotory pattern during the shallow dives of emperor penguins foraging from an isolated dive hole.

Materials and methods

Emperor penguins *Aptenodytes forsteri* Gray were maintained for 2 months (October–November) in a corral and allowed daily access to an isolated dive hole on the sea ice of McMurdo Sound, Antarctica (Ponganis et al., 1997, 2000). The birds were captured at the McMurdo Sound ice edge.

Forward acceleration was measured in seven birds with an accelerometer datalogger unit attached to the back. The accelerometer was oriented to measure acceleration in the direction of the penguin's spine. The datalogger consisted of a microprocessor (5F, Onset Computer, Pocasset, MA, USA) measuring the low-pass output (<10 Hz) of a single-axis acceleration sensor (ADXL105, Analog Devices, Norwood, MA, USA) at a rate of 20 Hz. The sensor was calibrated statically against the earth's gravitational acceleration at five inclinations.

The acceleration datalogger was attached to the penguins for 1 h periods in two configurations: (1) inside a streamlined

aluminum housing (275 g, 14 cm × 6 cm × 3 cm) secured with cable ties to a previously glued Velcro strip on the central back of the birds; or (2) incorporated into a National Geographic Crittercam underwater video camera worn by harness (approximately 1 kg, neutral buoyancy, 9 cm diameter, 25 cm length, 63 cm² frontal area, 3.6 s depth sampling rate; see Ponganis et al., 2000). In configuration (1), a time depth recorder (TDR, Mk7, Wildlife Computers, Redmond, WA, USA; 41 g, 9.3 cm × 2.4 cm × 1.3 cm, 0.5 m resolution, 1 s sampling rate) was simultaneously deployed on the bird's back behind the accelerometer datalogger. Underwater observations of departures and returns to the dive hole were made from a sub-ice observation chamber (Ponganis et al., 2000).

Penguin swim strokes observable in the Crittercam video footage were correlated with the acceleration record to guide the design of an automated stroke detection algorithm from the accelerometer measurements. Stroke frequency was determined in a subset of Crittercam footage with customized software, which detected, in each video frame (29.97 frames s⁻¹), the vertical location of the horizontal scan line with the highest luminance. Assignment of a single location value to each video frame yielded a frame-accurate, time series that tracked the vertical movement associated with swim strokes as visible in the video sequence (see Fig. 1).

In order to detect wing strokes from the accelerometer data,

a customized peak detection software program was applied to the data after first processing it with a five-sample moving average. Analysis of three randomly selected dives of birds equipped with both the Crittercam and accelerometer revealed that 68 and 97% of wing strokes detected by algorithm from the accelerometer data coincided, within 100 and 200 ms, respectively, with strokes detected by the video frame analysis. Stroke rates above 2 beats s⁻¹ were considered to be artifacts; they constituted less than 1% of detected wing beats, and were excluded from the data analysis.

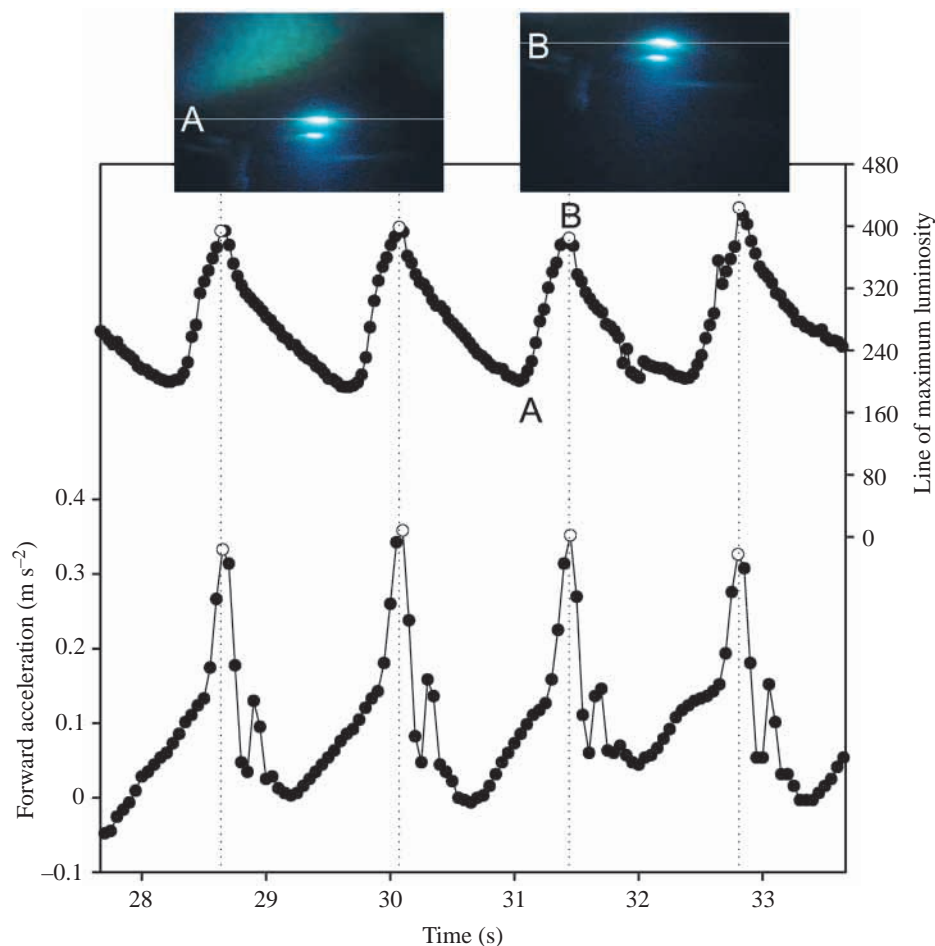


Fig. 1. Swim strokes of an emperor penguin approaching two through-ice dive holes (bright spots in the video frames). In this view, the bird is swimming toward the dive holes. A and B indicate the horizontal line with greatest luminosity for the video frames shown, as an example of the frame luminosity time-series (upper graph). Open circles show that peaks in the curves generated by video analysis correspond with peaks in the measured longitudinal acceleration (lower graph), allowing for calculation of stroke frequencies from either source.

Table 1. Body mass, instruments deployed, and dive characteristics of emperor penguins

Bird	Body mass (kg)	Instruments	Number of dives	Mean dive duration (min) (range)	Max. dive depth (m)
14	24.8	Acc+TDR	2	4.37 (4.17–4.57)	33.0
16	27.0	Acc+TDR	4	5.63 (2.32–9.08)	42.0
17	24.3	Acc+TDR	2	3.38 (1.52–5.25)	30.0
19	26.8	Acc+TDR	8	6.00 (4.23–7.35)	49.0
20	29.5	Acc+TDR	10	5.46 (1.33–10.35)	37.0
23	25.0	Acc+TDR	6	7.02 (5.5–9.57)	53.0
		Acc+Cam	9	4.42 (1.44–8.57)	48.2
24	24.7	Acc+Cam	3	3.61 (2.28–4.61)	26.2

Max., maximum; Acc, accelerometer; TDR, time–depth recorder; Cam, Crittercam.

For comparison of stroke frequencies during different dive phases in birds with the accelerometer/TDR, stroke frequency data were separated into six dive segment categories: initial descent (0–12 m depth), travel (>12 m depth), foraging ascent (12–2 m depth), foraging descent (2–12 m depth), final ascent (12–0 m depth), and other (shallow ascents and descents near the ice holes). The 12 m criterion corresponds to the maximum depth of the shallowest dive examined; the underside of the sea ice was at 2 m depth.

Values are expressed as means \pm s.d. unless otherwise indicated. Statistics were considered significant at $P < 0.05$.

Results

Penguin swim stroke data were obtained for a total of 44 dives >1 min duration. The mean diving duration of all birds was 5.3 ± 2.2 min (range 1.3–10.4 min), and the maximum depth was 53 m (Table 1). 18 dives were of longer duration than the 5.6 min ADL measured for emperor penguins under similar conditions (Ponganis et al., 1997). Penguins fitted with the Crittercam system made significantly shorter dives than those carrying the smaller accelerometer and TDR instruments (mean dive durations 4.2 ± 2.1 versus 5.7 ± 2.2 min; t -test).

Swim stroke frequencies in birds equipped with the accelerometer/TDR varied by dive segment (Fig. 2). Mean stroke rates were highest (0.92 Hz) during the initial descent from the dive hole, and lowest (0.61 Hz) during the travel segments of dives (Table 2). Travel segments constituted on average 66.4% of the birds' dive time (Table 2). For dives of greater duration than the ADL_M, mean travel segment stroke frequencies were significantly lower than those during the travel segments of shorter dives (t -test on $1/f$ transformed data, 0.56 ± 0.07 versus 0.69 ± 0.11 Hz). Histogram analysis (Fig. 3) revealed that

>50% of wing beats were associated with a stroke interval >1.6 s.

Mean stroke frequencies while foraging were similar for both ascent and descent segments above 12 m depth. Analysis of the stroke frequency during the entire foraging ascent (from depth to under the ice) resulted in a mean value of 0.54 ± 0.23 Hz ($N=88$ ascents). Feeding excursions to the underside of the sea ice also yielded the longest measured wing beat interval of 8.6 s. However, no significant periods (>10 s) of wing inactivity interpretable as prolonged gliding behavior were observed in any of the dives.

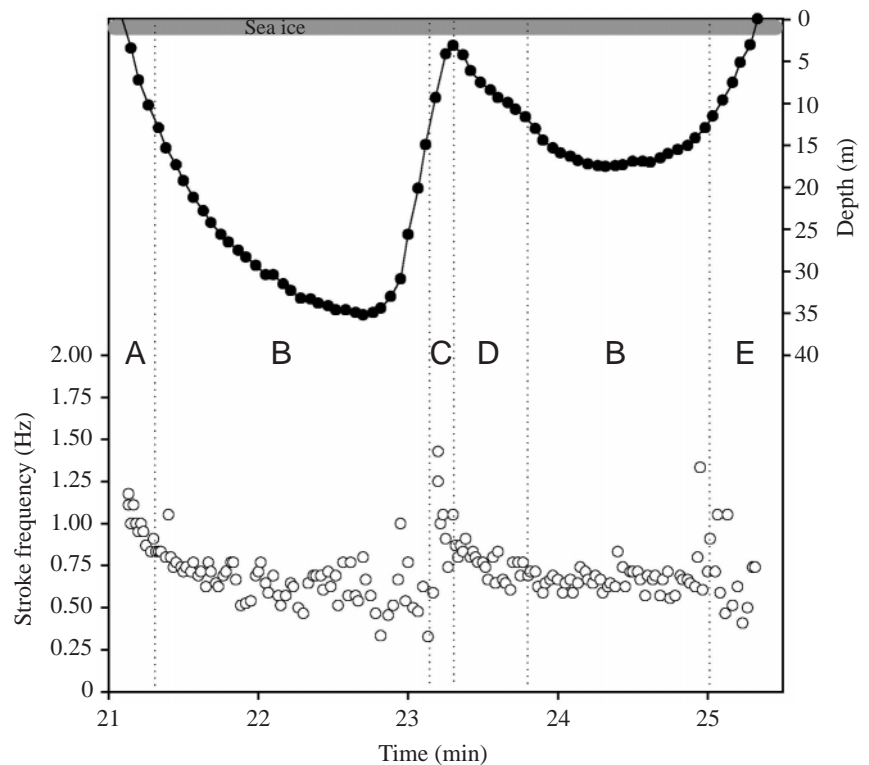


Fig. 2. Depth profile (filled circles) and measured stroke frequencies (open circles) of an emperor penguin. Identified segments of the dive are: A, initial descent; B, travel; C, foraging ascent; D, foraging descent, E, final ascent.

Table 2. Emperor penguin swim stroke frequencies by dive phase

	Wing beat frequency (Hz)			Total swim strokes	Proportion of dive time (%)
	Mean \pm s.d.	Min.	Max.		
Initial descent	0.92 \pm 0.31	0.22	1.82	981	8.9
Travel	0.61 \pm 0.24	0.12	2.00	4873	66.4
Foraging ascent	0.70 \pm 0.38	0.14	1.82	311	9.8
Foraging descent	0.69 \pm 0.32	0.12	1.82	737	3.8
Final ascent	0.66 \pm 0.30	0.16	1.82	774	8.9
Other	0.87 \pm 0.44	0.16	2.00	233	2.2

Min., minimum; Max., maximum.

Descents and ascents were limited to those portions of dives <12 m depth.

Total swim strokes, number of strokes in each dive phase for all birds.

Mean dive stroke frequencies (i.e. of the entire dive) of birds equipped with an accelerometer/TDR were not significantly different from those of birds carrying the Crittercam (*t*-test on $1/f$ transformed data, 0.68 ± 0.12 versus 0.74 ± 0.12 Hz, respectively), although the stroke frequency distributions were slightly different (Fig. 3). In both circumstances, mean dive stroke frequencies correlated significantly with dive duration ($r=-0.57$ and -0.58 , respectively, Fig. 4) and with mean dive depth ($r=-0.50$ and -0.40 , respectively).

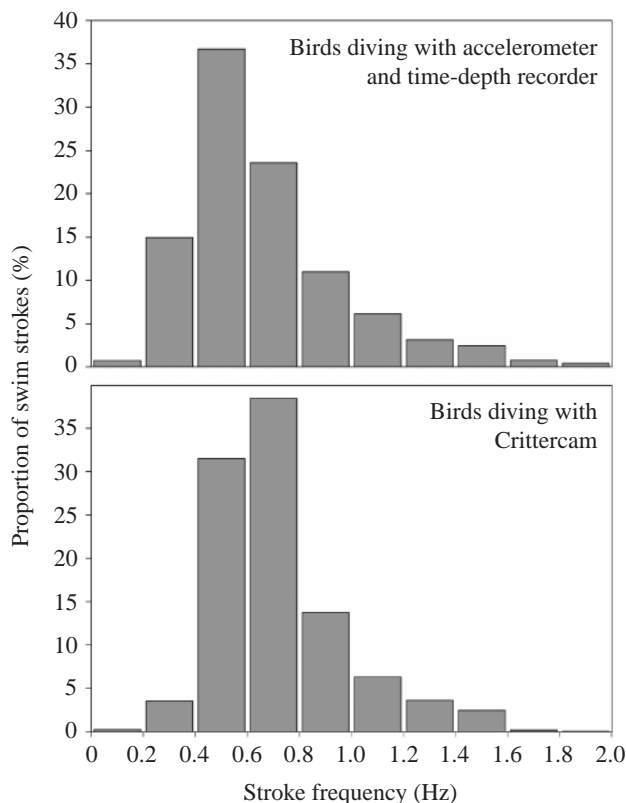


Fig. 3. Histograms of swim stroke frequencies for emperor penguins diving with each of the two instrument configurations used in this study.

Discussion

Although a penguin's propulsion is also dependent on wing span, thrust, angle of attack, and stroke amplitude in addition to stroke frequency (Clark and Bemis, 1979; Hui, 1988; Bannasch, 1995), we hypothesized that different wing-beat frequencies would at least partially reflect work effort to overcome buoyancy as depth changed. Other factors, of course, could also affect stroke frequency. These include horizontal versus vertical travel, and changes in swim velocity and direction during hunting, prey capture and maneuvering beneath the dive hole. However, with increasing depth, upward buoyancy forces are reduced as compression reduces the volume of air contained in the lungs, in the air sacs and under the feathers. In addition, buoyancy may be decreased by air loss from beneath the feathers, although the magnitude of such loss is undocumented in emperors. Therefore, we expected that wing-beat frequency would be decreased at depth, but whether prolonged glide time, as in marine mammals (Williams et al., 2000), constituted 10–80% of descent time was another question.

Earlier observations of emperor penguins in the near-surface zone made from a submerged observation chamber, yielded wing-beat frequencies of around 0.75 Hz (Kooyman and Ponganis, 1994). These observations correspond to those parts of dives classified in our study as initial descent and final ascent segments, and the reported value falls within the range of stroke frequencies we measured for these segments. Although drag secondary to the recorders may have contributed to slight differences between the chamber observations of birds without recorders and the measurements in this study, the accelerometer/TDR unit weighed less than 1.5% of the body mass of these birds and constituted less than 3% of the frontal cross-sectional area, i.e. less than the criteria cited as significant by most investigators (Wilson et al., 1986).

We attribute the high stroke frequencies we measured for penguins during their initial descent phase of dives to the need to overcome substantial initial buoyancy. The buoyancy of a typical 23 kg emperor penguin with a 69 ml kg^{-1} diving air volume (Ponganis et al., 1999) calculated with the equation of Sato et al. (2002) is 17.5 N. By 10 m depth, this initial

buoyancy would be reduced by 46%. A reduction in buoyancy is consistent with the high stroke frequencies during initial descents, and with the lower stroke frequencies during travel segments. Low stroke frequencies during the entire foraging ascent (from depth to the sub-ice surface) are also consistent with an increase in buoyancy during ascent. The role of buoyancy in energetic costs of diving penguins has also been emphasized by Sato et al. (2002). Those investigators documented prolonged gliding behavior during ascents from depth in both Adelie *Pygoscelis adeliae* and king penguins *Aptenodytes patagonicus*, and reported that calculated diving air volume increased with maximum dive depth, suggesting that a smaller diving air volume during shallow dives of penguins reduced the cost of overcoming buoyancy during shallow dives. The findings in the present study and that of Sato et al. (2002) are therefore consistent with a significant role for diving air volume and buoyancy in the diving energetics of penguins. The actual diving air volume of emperor penguins is unknown; the above calculation utilized a value measured during simulated dives of king penguins, a value which is also in the range of values estimated by Sato et al. (2002) for shallow dives of free-diving king penguins. The role of buoyancy may be even more important in birds than in marine mammals since diving air volume is 3–7 times greater in birds (Butler and Jones, 1997). In the lesser scaup *Aythya affinis*, for example, buoyancy contributes to about 75% of the mechanical cost of underwater locomotion (Stephenson, 1994).

In contrast to the findings of Sato et al. (2002), in which gliding was also observed during ascents from shallow depths, prolonged gliding was never observed in emperor penguins foraging under sea ice. This may be partially accounted for by the nature of such dives at the isolated dive hole, and the necessity of horizontal travel beneath fast ice. The majority of distance traveled was horizontal for the emperors, and they returned to a small dive hole, not an open surface. However, a stroke/glide swim pattern, similar to that reported for horizontal swimming in marine mammals (Williams, 2001), was evident in the stroke frequency distribution of these birds. More than 50% of strokes were associated with a glide period (stroke interval) greater than 1.6 s; almost 20% of strokes had intervals greater than 2.5 s.

Stroke frequencies of entire dives correlated inversely, although weakly, with both dive duration and mean dive depth. In addition, stroke frequencies during travel segments of dives $>ADL_M$, were significantly less than those of dives $<ADL_M$. In addition to longer glide periods during such dives, this implies that the distance traveled per stroke was greater in longer/deeper dives, or that swim velocity was lower. If one assumes similar swim speeds near 3 ms^{-1} (Kooyman et al., 1992) during the travel segments of all dives, then the average distance traveled per stroke ranges from approximately 3 to 5 m. Swim speeds, however, were not measured. Regardless of this, lower stroke frequencies in longer dives could decrease locomotory work, due to both a decreased work rate and

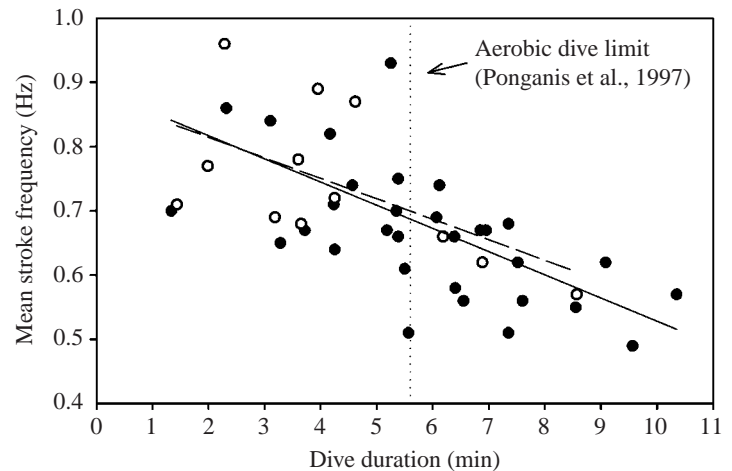


Fig. 4. Correlation of mean stroke frequencies during travel segments to total dive durations for 44 emperor penguin dives. Open circles, dives by birds carrying the Crittercam system (broken line, $r = -0.58$). Filled circles, dives made with the smaller accelerometer and time-depth recorder instruments (solid line, $r = -0.57$).

decreased drag secondary to the reduction in limb movement (Williams, 2001).

The increased workload imposed on the penguins equipped with the larger Crittercam system had a significant negative effect on dive duration, but not on mean stroke frequencies. This suggests that the Crittercam birds compensated for the increased drag either through reduced swim speed, or by augmenting propulsion power through means other than wing-beat frequency. Neither swim speed nor wing-beat parameters such as stroke amplitude and angle of attack were measurable with our instruments. The observation that the Crittercam-equipped penguin, when sighted swimming with a group of birds, would typically return last suggests that swim speed was reduced. The correlation of lowered stroke frequencies with increasing dive duration implies that the birds most likely followed a strategy of reduced swim effort, resulting in lower velocities and decreased induced drag.

A stroke/glide swim pattern, consistent with energy efficiency in diving, has now been demonstrated in emperor penguins. Stroke frequencies in these free-diving penguins were less than the 1–1.2 Hz stroke frequencies observed in emperor penguins swimming in a flume at a metabolic rate of $20\text{ ml O}_2\text{ kg}^{-1}\text{ min}^{-1}$ (Kooyman and Ponganis, 1994). Since heart rates were also lower in free-diving penguins (Kooyman et al., 1992) than in birds swimming at $20\text{ ml O}_2\text{ kg}^{-1}\text{ min}^{-1}$ (Kooyman and Ponganis, 1994), all the evidence suggests that the O_2 consumption rate during the submerged period of the dive is lower than that swim flume metabolic rate. However, other factors also affecting energy output, such as stroke amplitude and thrust, were not measured in either the flume study or this study.

The lack of prolonged gliding during shallow foraging dives both $<ADL_M$ and $>ADL_M$ has several implications. First, prolonged gliding may not be a significant mechanism of

energy conservation in 60% of dives at sea and in the longest duration dives recorded in emperor penguins, since these dives are predominantly shallow (<60 m). The lack of gliding may be secondary to buoyancy effects as well as the necessity of horizontal travel during such dives. Second, since recent data from king penguins indicates that gliding during ascent may begin as deep as 125 m (Sato et al., 2002), prolonged gliding in deep dives may represent a potential mechanism to decrease locomotory effort and increase the ADL of deep dives of emperor penguins.

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References

- Bannasch, R.** (1995). Hydrodynamics of penguins – an experimental approach. In: *The Penguins* (ed. P. Dann, I. Norman and P. Reilly), pp. 141-176. Sydney: Surrey Beatty & Sons.
- Butler, P. J. and Jones, D. R.** (1997). Physiology of diving of birds and mammals. *Physiol. Rev.* **77**, 837-899.
- Clark, B. D. and Bemis, W.** (1979). Kinematics of swimming of penguins at Detroit Zoo. *J. Zool., Lond.* **188**, 411-428.
- Hui, C. A.** (1988). Penguin swimming. I. Hydrodynamics. *Physiol. Zool.* **61**, 333-343.
- Kirkwood, R. and Robertson, G.** (1997). Seasonal change in the foraging ecology of emperor penguins on the Mawson coast, Antarctica. *Mar. Ecol. Prog. Ser.* **156**, 205-223.
- Kooyman, G. L. and Kooyman, T. G.** (1995). Diving behavior of emperor penguins nurturing chicks at Coulman Island, Antarctica. *Condor* **97**, 536-549.
- Kooyman, G. L. and Ponganis, P. J.** (1994). Emperor penguin oxygen consumption, heart rate and plasma lactate levels during graded swimming exercise. *J. Exp. Biol.* **195**, 199-209.
- Kooyman, G. L., Ponganis, P. J., Castellini, M. A., Ponganis, E. P., Ponganis, K. V., Thorson, P. H., Eckert, S. A. and LeMaho, Y.** (1992). Heart rates and swim speeds of emperor penguins diving under sea ice. *J. Exp. Biol.* **165**, 161-180.
- Kooyman, G. L., Schroeder, J. P., Greene, D. G. and Smith V. A.** (1973). Gas exchange in penguins during simulated dives to 30 and 68 m. *Am. J. Physiol.* **225**, 1467-1471.
- Nowacek, D. P., Johnson, M. P., Tyack, P. L., Shorter, K. A., McLellan, W. A. and Pabst, D. A.** (2001). Buoyant balaenids: the ups and downs of buoyancy in right whales. *Proc. Roy. Soc. Lond. B* **268**, 1811-1816.
- Ponganis, P. J., Kooyman, G. L., Starke, L. N., Kooyman, C. A. and Kooyman, T. G.** (1997). Post-dive blood lactate concentrations in emperor penguins, *Aptenodytes forsteri*. *J. Exp. Biol.* **200**, 1623-1626.
- Ponganis, P. J., Kooyman, G. L., van Dam, R. P. and LeMaho, Y.** (1999). Physiological responses of king penguins during simulated diving to 136 m depth. *J. Exp. Biol.* **202**, 2819-2822.
- Ponganis, P. J., van Dam, R. P., Marshall, G., Knower, T. and Levenson, D. H.** (2000). Sub-ice foraging behavior of emperor penguins. *J. Exp. Biol.* **203**, 3275-3278.
- Sato, K., Naito, Y., Kato, A., Niizuma, Y., Watanuki, Y., Charrassin, J. B., Bost, C.-A. and Le Maho, Y.** (2002). Buoyancy and maximal diving depth in penguins: do they control inhaling air volume? *J. Exp. Biol.* **205**, 1189-1197.
- Skrovan, R. C., Williams, T. M., Berry, P. S., Moore, P. W. and Davis, R. W.** (1999). The diving physiology of bottlenose dolphins (*Tursiops truncatus*) II. Biomechanics and changes in buoyancy at depth. *J. Exp. Biol.* **202**, 2749-2761.
- Stephenson, R.** (1994). Diving energetics in the lesser scaup, *Aythya affinis*. *J. Exp. Biol.* **190**, 155-178.
- Weih, D.** (1974). Energetic advantages of burst swimming of fish. *J. Theor. Biol.* **48**, 215-229.
- Williams, T. M.** (2001). Intermittent swimming by mammals: a strategy for increasing energetic efficiency during diving. *Amer. Zool.* **41**, 166-176.
- Williams, T. M., Davis, R. W., Fuiman, L. A., Francis, J., Le Boeuf, B. J., Horning, M., Calambokidis, J. and Croll, D. A.** (2000). Sink or swim: strategies for cost-efficient diving by marine mammals. *Science* **288**, 133-136.
- Wilson, R. P., Grant, W. S. and Duffy, D. C.** (1986). Recording devices on free-ranging marine animals: does measurement affect foraging performance. *Ecology* **67**, 1091-1093.