

RESEARCH ARTICLE

Point of no return in diving emperor penguins: is the timing of the decision to return limited by the number of strokes?

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Accepted 4 October 2011

SUMMARY

At some point in a dive, breath-hold divers must decide to return to the surface to breathe. The issue of when to end a dive has been discussed intensively in terms of foraging ecology and behavioral physiology, using dive duration as a temporal parameter. Inevitably, however, a time lag exists between the decision of animals to start returning to the surface and the end of the dive, especially in deep dives. In the present study, we examined the decision time in emperor penguins under two different conditions: during foraging trips at sea and during dives at an artificial isolated dive hole. It was found that there was an upper limit for the decision-to-return time irrespective of dive depth in birds diving at sea. However, in a large proportion of dives at the isolated dive hole, the decision-to-return time exceeded the upper limit at sea. This difference between the decision times in dives at sea *versus* the isolated dive hole was accounted for by a difference in stroke rate. The stroke rates were much lower in dives at the isolated hole and were inversely correlated with the upper limit of decision times in individual birds. Unlike the decision time to start returning, the cumulative number of strokes at the decision time fell within a similar range in the two experiments. This finding suggests that the number of strokes, but not elapsed time, constrained the decision of emperor penguins to return to the surface. While the decision to return and to end a dive may be determined by a variety of ecological, behavioral and physiological factors, the upper limit to that decision time may be related to cumulative muscle workload.

Key words: dive path, acceleration, *Aptenodytes forsteri*.

INTRODUCTION

Breath-holding divers are always in a dilemma during submergence: while they benefit by exploring and traveling underwater, they must return to the water surface to replenish oxygen stores and to remove accumulated carbon dioxide. Longer dives could provide more prey or increase distance traveled, but might also require longer recovery times at the surface (Kooyman and Kooyman, 1995; Kooyman et al., 1980). Therefore, deciding when to end a dive may not be straightforward. For a variety of animals, factors affecting the decision have been investigated both theoretically and empirically in terms of foraging ecology and behavioral physiology (Houston and Carbone, 1992; Mori et al., 2002; Thompson and Fedak, 2001). In these studies, dive duration was almost always used as a temporal parameter, which is important to estimate optimal time budgets and to examine physiological capacities. However, given that divers must decide to return to the surface well before the end of a dive, the start time to return may also be worth investigating in this context.

Emperor penguins (*Aptenodytes forsteri* Gray 1844) are consummate avian divers, which have been reported to dive deeper than 550 m (Wienecke et al., 2007) and for longer than 27 min (Sato et al., 2011). In deep dives, the time lag between the decision to return the surface and the end of a dive is inevitably long and, therefore, examination of dive duration alone may not be sufficient to understand their diving strategies. In the present study of emperor

penguins, we investigated the decision time defined as the time into a dive at which the animal begins to return to the surface. The major constraints on diving behaviors are likely to be physiological ones (Butler and Jones, 1997; Kooyman and Ponganis, 1998). We hypothesized that, as a physiological factor, cumulative muscle work, and not time *per se*, determined the time limit of the decision to return to the surface. Because the number of swim strokes has been shown to relate strongly to oxygen consumption and muscle stroke effort (Williams et al., 2011; Williams et al., 2004), the number of strokes at the decision time was investigated as a reasonable index of muscle workload.

MATERIALS AND METHODS

Field experiments

We used the data sets of dives under two different conditions: during foraging trips at sea and at the artificial isolated dive hole (hereafter, experiments A and B, respectively). These are the same data as used in our previous papers (Sato et al., 2011; Shiomi et al., 2008).

Experiment A was conducted at a breeding colony of emperor penguins near Cape Washington, Antarctica (74°39'S, 165°24'E), during the period from 28 October to 17 November 2005. Ten birds were captured at the edge of the colony, and either of two types of data logger was attached to the lower central back feathers using waterproof tape (TesaTM tape, Beiersdorf AG, Hamburg, Germany),

instant glue (Loctite epoxy, Henkel, Westlake, OH, USA), and stainless steel cable ties. One type recorded swim speed (1 Hz), depth (1 Hz) and 2-axis acceleration (16 Hz) (W1000-PD2GT or W1000L-PD2GT; 122 or 128 mm in length, 22 or 27 mm in diameter, 73 or 127 g in air; Little Leonardo Ltd, Tokyo, Japan). The other type recorded swim speed (1 Hz), depth (1 Hz), 3-axis acceleration (8 Hz) and 3-axis magnetism (1 Hz) (W1000L-3MPD3GT; 174 mm in length, 26 mm in diameter, 120 g in air; Little Leonardo Ltd). Using a data set recorded by W1000L-3MPD3GT, three dimensional (3-D) dive paths can be reconstructed (Shiomi et al., 2008). VHF transmitters (Model MM130, ATS, Isanti, MN, USA) were also deployed on all the birds at sea to locate them when they returned to the dense colony. The birds were recaptured at the colony 7.9–19.7 days after the deployment, and the instruments were retrieved.

Experiment B was conducted from 15 November to 4 December 2004 in McMurdo Sound, Antarctica (77°43'S, 166°07'E). Loggers (W1000L-3MPD3GT, see above) were attached to three penguins. Three-axis accelerations were recorded at 16 or 32 Hz, and other parameters at 1 Hz. The birds were enclosed within an isolated corral on the fast sea ice and allowed to dive freely through the artificial dive hole (Kooyman et al., 1992). One to three deployments were done for each penguin, and the loggers were retrieved 1.6–2.5 days after attachment.

Decision-to-return time

A dive was defined as any submersion deeper than 2 m and longer than 3 s. As our interest was in the time at which the bird decided to return to the water surface, we analyzed the elapsed time after the start of a dive until a continuous final ascent started (Fig. 1A). The ascent start time (AST) was obtained from time-series depth data as the elapsed time until the last positive change of depth occurred at a depth deeper than half of the maximum depth of a dive.

In addition, 3-D dive paths of one bird (CW13) in experiment A and of three birds in experiment B were calculated using a customized macro (Narazaki and Shiomi, 2010; Shiomi et al., 2010) compliant with Igor Pro (WaveMetrics, Lake Oswego, OR, USA). In dive path analyses, only dives in which mean swim speed was greater than 1 m s^{-1} were considered as reliable data. This is because mean cruising swim speed of emperor penguins was around 2 m s^{-1} (Sato et al., 2010). In dives with swim speeds less than 1 m s^{-1} , it is highly possible that rotation of the propellers, which is used for measuring swim speeds, probably stopped or slowed as a result of ice accumulation around the propeller. For each dive path, the farthest horizontal distance (FHD) from the starting point and the

elapsed time (farthest horizontal time, FHT) until the bird reached the farthest horizontal point were calculated (Fig. 1B).

Number of strokes

Emperor penguins perform stroke and glide swimming (van Dam et al., 2002). As an index of muscle workload at the decision to return, the number of strokes during the period from the start of a dive to the AST or the FHT was calculated using the longitudinal acceleration data, which reflect stroking activity as regular peaks (van Dam et al., 2002). We recognized a set of up- and down-beats as one stroke, and calculated stroke rate as the number of strokes per second. To determine a difference between the two experiments and to calculate the stroke rate in each experiment, two types of generalized linear mixed model were fitted to the pooled data with Poisson error distribution and logarithm link function, in which the number of strokes was a response variable with the AST or the FHT as an offset term, and 'bird identity within an experiment' as a random effect. One model included 'experiment' (during foraging trips or at the isolated ice hole) as a fixed effect, the other did not. Akaike information criteria (AIC) were compared between the two fitted models. Stroke rates were presented as the slopes of the models. For the model fitting, R 2.10 (R Development Core Team, 2009) was used with the *glmer* function in R package *lme4* (Bates and Maechler, 2009).

RESULTS

Dives during foraging trips (experiment A)

In total, 15,978 dives were recorded from 10 free-ranging birds breeding near Cape Washington. On visual examination of the plot of the AST against dive depth, the upper boundary of the AST conditional on dive depth seemed asymptotic (Fig. 2A). Therefore, non-linear quantile regression (Koenker and Park, 1996) was applied to estimate the asymptotes. A similar approach was adopted in a previous study to estimate the asymptotes of dive duration in leatherback turtles (Bradshaw et al., 2007). Quantile regression gives a functional relationship between variables for a certain portion of a probability distribution (Cade and Noon, 2003; Koenker and Bassett, 1978). It is useful for investigating limiting factors, providing an estimate of the upper boundary of the conditional distribution of responses (Cade and Noon, 2003). Because this method is robust to the presence of outliers (Cade et al., 1999), it seemed suitable for our data, which had some exceptional data points (large AST) in relatively shallow dives (Fig. 2A). We fitted an exponential-rise model:

$$Y = a [1 - \exp(-bX)], \quad (1)$$

on the 95th percentile of the AST (Y , in min) against maximum dive depth (X , in m) (Fig. 2A). For the model fitting, R 2.10 (R

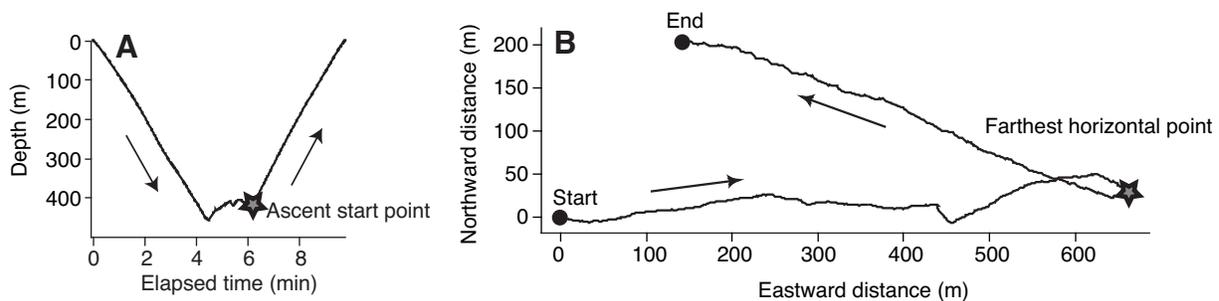


Fig. 1. Illustration of the point of decision to return the surface in non-U-turn dives (A; time-series depth data) and in U-turn dives (B; an aerial view of a dive path). The onset of ascent and U-turn were considered as the decision point in A and B, respectively.

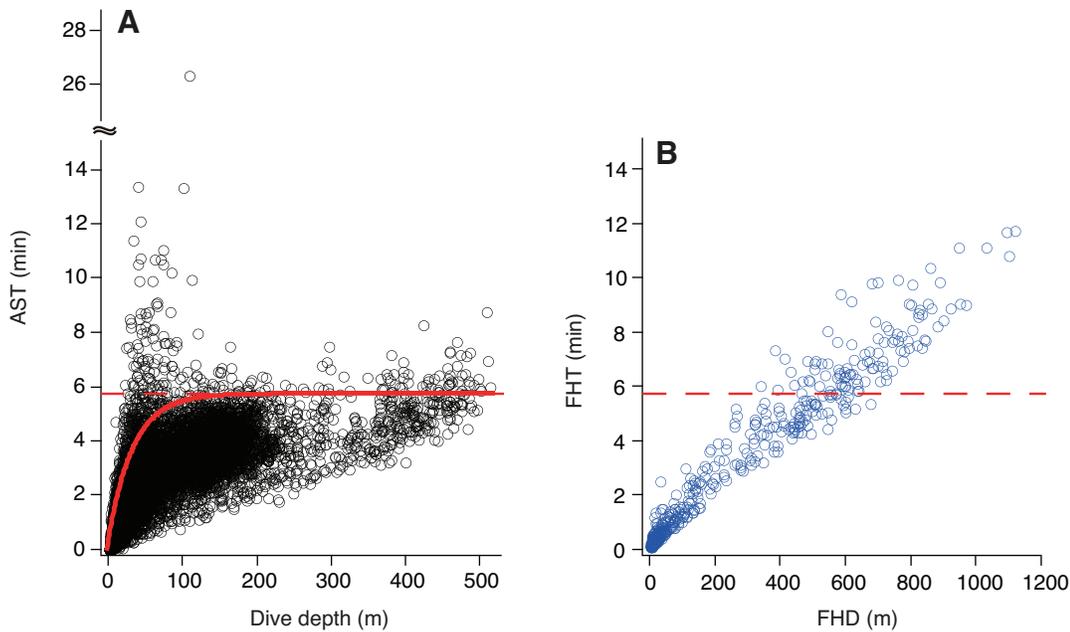


Fig. 2. Relationships between the decision-to-return time and vertical or horizontal distance from the starting point of the dive. (A) Plots of ascent start time (AST) against dive depth obtained from birds diving during foraging trips (experiment A; $N=15,978$ dives from 10 birds) and (B) those of farthest horizontal time (FHT) against the farthest horizontal distance (FHD) obtained from birds diving at the isolated dive hole (experiment B; $N=495$ dives from three birds). A red line represents the 95th percentile regression line, $AST=a(1-\exp[-b(\text{dive depth})])$, using average regression coefficients from 10 birds in experiment A; dashed lines represent an average asymptote (5.7 min) estimated in experiment A (see Table 1).

Development Core Team, 2009) was used with the *nls* function in R package *quantreg* (Koenker, 2009). The regression coefficient (a) for each bird, which corresponded to an estimated asymptote value of the AST, was 5.7 ± 0.56 min (mean \pm s.d., range 4.9–6.7 min; Table 1). Of dives in which the AST exceeded the asymptote of each bird, $42.2 \pm 25.4\%$ (mean \pm s.d., range 14.3–100%) were shallower than 100 m (Fig. 2A).

For one bird (CW13), 3-D dive paths of 2411 dives were reconstructed. Dives appeared to be divided roughly into two groups; in group I, the FHT nearly equaled the end times of the dive (i.e. dive duration), and those of group II were less than the dive duration. A histogram of the ratio of the FHT to the dive duration had a prominent peak just below 1 and a low peak between 0.4 and 0.75, corresponding to group I and II, respectively (Fig. 3A). The dive paths of group II indicated that the bird began to return toward the starting point of the dive after the FHT (see Fig. 1B). For these U-turn dives, the FHT should be more indicative of the timing of the decision to return than the AST. If we define U-turn dives as dives in which the ratio of the FHT to dive duration was between 0.4 and

0.75 and in which the FHD was greater than the dive depth, the FHT of these U-turn dives, ranging up to 9.5 min, positively correlated with the FHD (Pearson's correlation coefficient $r_c=0.96$, $P<0.0001$, $N=217$ dives; green circles in Fig. 3B). The maximum FHD was 865.2 m. By replacing the AST and dive depth with the FHT and the FHD for the U-turn dives, respectively, the outliers of shallow dives in the plot of the AST against dive depth disappeared (compare Fig. 2A and Fig. 3B).

Dives at the isolated ice hole (experiment B)

In experiment B, all the dives were U-turn dives because there was neither another ice hole nor an ice crack through which to exit within several kilometers around the artificial hole. Therefore, the same analyses as for U-turn dives of bird CW13 were applied. 3-D paths of 495 dives were reconstructed for three birds. For comparison with dive paths of bird CW13 in experiment A, the ratio of the FHT to dive duration in dives in which birds clearly performed U-turns ($FHD>100$ m) was calculated. The histogram had a peak around 0.5 (Fig. 3B), similar to the U-turn dives of bird CW13 (Fig. 3A). The

Table 1. Results of 95th percentile regression analyses on the ascent start time (AST) and the cumulative number of strokes at the AST against dive depth for birds in experiment A

Bird	No. of dives	AST (min)		Number of strokes at the AST		Stroke rate (beats s^{-1})	s.e.
		Coefficient a	Coefficient b	Coefficient a	Coefficient b		
CW1	676	5.7	0.05	196	0.05	0.60	0.007
CW2	994	5.9	0.02	257	0.03	0.70	0.005
CW3	876	4.9	0.04	236	0.04	0.78	0.007
CW4	875	6.3	0.03	271	0.03	0.69	0.005
CW7	997	5.6	0.03	294	0.03	0.83	0.005
CW8	852	5.9	0.03	295	0.02	0.63	0.008
CW9	818	5.4	0.04	239	0.05	0.72	0.005
CW10	3061	5.1	0.04	256	0.03	0.82	0.004
CW11	4156	5.1	0.04	255	0.04	0.80	0.003
CW13	2673	6.7	0.03	–	–	–	–
Mean		5.7	0.03	255	0.03	0.73	
s.d.		0.6	0.01	31	0.01	0.08	

The regression equation was $Y=a[1-\exp(-bX)]$, where Y is the AST or the number of strokes at the AST and X the dive depth. Stroke rates were obtained as a slope of the linear regression line to predict the number of strokes from the decision-to-return time.

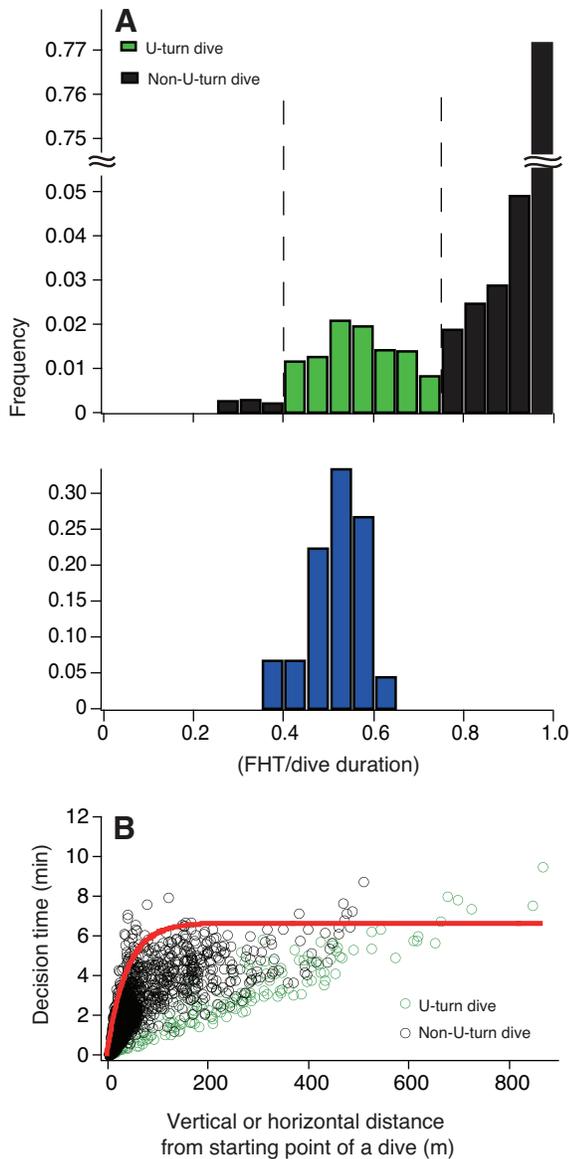


Fig. 3. Classification of U-turn dives using dive paths of bird CW13. (A) Histogram of the ratio of the FHT to dive duration (top). For reference, a histogram obtained from bird PR3 in experiment B is also presented (bottom). (B) Relationship between decision-to-return time (i.e. AST for non-U-turn dives, FHT for U-turn dives) and vertical or horizontal distance from the starting point of the dive for non-U-turn dives (black) and U-turn dives (green). The red line presents the 95th percentile regression line obtained from bird CW13.

FHT correlated with the FHD for all birds (Pearson's correlation coefficient $r_c=0.96$ to 0.98 , $P<0.0001$, Fig. 2B). While dive depth did not exceed 100 m, the maximum value of the FHD in each bird was 1047.8 ± 108.6 m (mean \pm s.d.) in experiment B. In $23.7\pm 7.7\%$ (mean \pm s.d., range 18.4–32.5%) of the dives in each bird, the FHT exceeded the average upper limit of the AST (5.7 min) in birds in experiment A (Fig. 2B).

Number of strokes

The following results of stroke analyses do not include data from bird CW13, because acceleration was recorded at the lower sampling frequency (8 Hz), and the algorithm to detect strokes did not appear

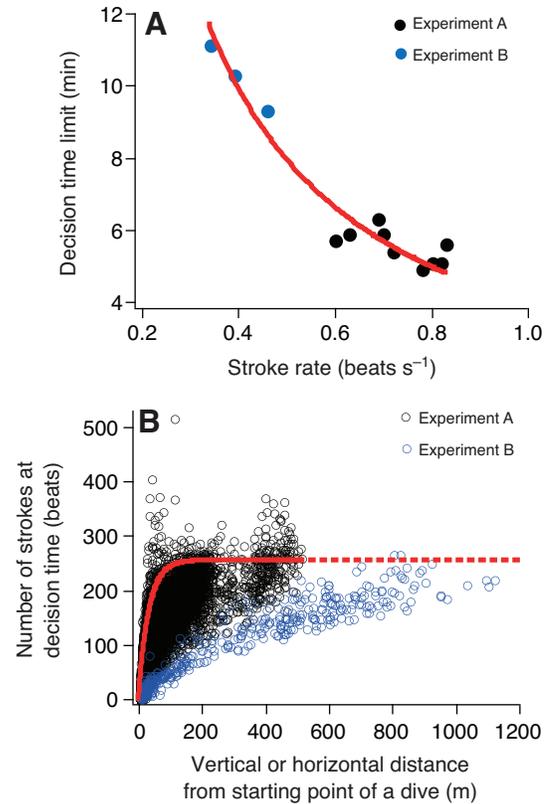


Fig. 4. Results of stroke analyses. (A) Relationship between the upper limit of the decision-to-return time (decision time limit) and stroke rate in each bird in experiment A (black) and B (blue). The decision time limit was estimated by 95th percentile regression on AST in experiment A, and as the maximum FHT multiplied by 0.95 in experiment B. The red line indicates the regression line: decision time limit=3.97/stroke rate. (B) Relationship between the number of strokes at the decision to return and the vertical or horizontal distance from the starting point (black, birds in experiment A; blue, birds in experiment B). The red line presents the 95th percentile regression line averaged for birds in experiment A.

to work well when using the same threshold as for the other data sampled at 16 or 32 Hz. In all the other 12 birds from both experiments A and B, the number of strokes significantly increased with the decision time, i.e. the AST and the FHT (linear regression: $r^2=0.89$ to 0.97 for each bird, $P<0.0001$). AIC of the model with 'experiment' as a fixed effect, which was fitted on the number of strokes against the decision time, was smaller than the one not considering 'experiment' (AIC: 35,556 and 35,575, respectively). This means that the number of strokes for dives of similar duration was different between experiments. The estimated slope (calculated as the number of strokes s^{-1}) was smaller for birds in experiment B than in experiment A (0.45 and 0.79 beats s^{-1} , respectively), as previously reported (Sato et al., 2011). In addition, stroke rate of individual birds estimated by linear regression (range 0.34–0.83 beats s^{-1} ; $P<0.0001$; Tables 1 and 2) was inversely related with the upper limit of the decision time (hereafter, decision time limit) obtained by 95th percentile regression on the AST against dive depth in experiment A and by the maximum FHT multiplied by 0.95 in experiment B (linear regression using reciprocals of stroke rate: $r^2=0.995$, $P<0.0001$, $N=12$ birds, decision time limit=3.97 \times (1/stroke rate); Fig. 4A).

Table 2. Decision time limit and results of stroke analyses for birds in experiment B

Bird	No. of dives	Maximum FHT (min)	Maximum number of strokes at the FHT	Stroke rate (beats s ⁻¹)	s.e.
PR1	158	10.8	218	0.39	0.009
PR2	254	9.8	267	0.46	0.006
PR3	83	11.7	225	0.34	0.008
Mean		10.8	237	0.40	
s.d.		1.0	27	0.06	

FHT, farthest horizontal time.

Stroke rates were obtained as a slope of the linear regression line to predict the number of strokes from the decision-to-return time.

In experiment A, the number of strokes at the AST also appeared asymptotic, conditional on dive depth (Fig. 4B). Fitting an exponential model to estimate the 95th percentile conditional on dive depth, the estimated upper limit of the number of strokes at the AST was 255 ± 31 beats (range 196–295 beats) in each bird (Table 1). The number of strokes at the FHT in experiment B was 237 ± 27 beats at maximum (Table 2), which distributed within a similar range to that of birds in experiment A (Fig. 4B).

DISCUSSION

Although the AST in experiment A was variable for a given depth (Fig. 2A), there appeared to be both lower and upper boundaries. While the linear increase in the lower limit with dive depth reflected V-shaped dives with no bottom times, the asymptotic distribution of the upper limit suggested that there was a decision time limit independent of dive depth. There were some shallow dives (dive depth <100 m) in which the AST largely exceeded the estimated decision time limit (Fig. 2A), but fine-scale 3-D dive paths of bird CW13 yielded a possible explanation. In most of those shallow dives, the bird traveled horizontally a far distance and then returned toward the starting point of the dive (see Fig. 1B). This shape of the dive paths was similar to those of birds diving at the isolated dive hole in experiment B, where they dived shallower than 100 m, probably for foraging fish beneath the surface of the sea ice (Ponganis et al., 2000), and always returned to the ice hole because the fast sea ice prevented them from surfacing at other places. Also, in shallow and long dives during foraging trips at sea, birds might dive under the sea ice and explore not vertically but horizontally (Kooyman and Kooyman, 1995; Watanuki et al., 1997; Wienecke et al., 2007). Under such circumstances, they might decide to return toward the starting point of a dive unless another exit is found. Considering that replacing the AST with the FHT for the U-turn dives of bird CW13 eliminated the outliers among shallow dives in the plot of AST against dive depth (Fig. 3B), there appeared to be a decision rule irrespective of whether dives were vertical or horizontal. Those inferences from the results in bird CW13 are likely applicable to shallow and long dives of the other nine birds in experiment A as well, although their dive paths were unknown.

However, it was found that the FHT of birds in experiment B often exceeded the decision time limit, mean 5.7 min, obtained in experiment A (Fig. 2B). This did not fit the hypothesis that there is a common decision time limit to return. Stroke analyses helped to address this inconsistency. In experiment B, the combination of the lower stroke rate and the higher value of the maximum FHT than in experiment A resulted in the maximum number of strokes on the FHT for each bird, ranging from 218 to 267 beats, which were within the range of the upper limit of the number of strokes at the AST in experiment A, 196–295 beats (Fig. 4B). These results suggest that the accumulated number of strokes, but not the elapsed time, was

related to their decision time limit to return. This concept was also supported by the decision time limits of individual birds, which were longer for birds with a lower stroke rate (Fig. 4A). The limit of the number of strokes expected from the regression line, decision time limit = $3.97 \times (1/\text{stroke rate})$, is 238 beats ($=3.97 \times 60$), which is consistent with the empirical value for each bird presented in Tables 1 and 2.

The cost of diving consists of basal metabolic cost and locomotor cost, and the number of strokes is a reasonable index of the latter, i.e. muscle workload (Williams et al., 2011; Williams et al., 2004). Our results suggest that the cumulative work in muscle triggered the onset of the return to the surface. Comparison between experiments A and B and among individuals indicated that a decrease in stroke rate prolonged the decision time limit, which increased the maximum distance traveled by the time of the decision (up to more than 1 km in experiment B). Intermittent stroking of aquatic animals has been elucidated as a swimming strategy to save locomotor cost (Weihs, 1974; Williams, 2001). In emperor penguins, this locomotion pattern was reported as a potential energy conservation mechanism to achieve long dives (van Dam et al., 2002) in addition to physiological adaptations, such as bradycardia and peripheral vasoconstriction reducing the basal metabolic cost of diving (Meir et al., 2008; Ponganis et al., 2003). We show here that stroking patterns may affect the decision to end a dive and consequently the dive duration.

CONCLUSION

In the present study, it was found in experiment A that emperor penguins at sea had a decision time limit to return the water surface that was independent of the distance to the surface (vertical or horizontal). However, in combination with the results from experiment B at the isolated dive hole, we suggest that the decision was constrained not by elapsed time but by the number of strokes and, thus, perhaps cumulative muscle work. These new insights were revealed by focusing on the start time to return to the surface and by reconstructing fine-scale dive paths. Some previous studies reported asymptotic distributions of dive duration (Bradshaw et al., 2007), and postulated that total oxygen stores and oxygen consumption rate constrain dive duration (Hansen and Ricklefs, 2004; Hays et al., 2000). However, most of those studies considered only dive duration as a temporal parameter. The duration of a dive is a consequence of the prior decision to return to the surface. Therefore, it may be important to investigate the timing of the initiation of the return as well as dive duration to fully understand diving strategies.

ACKNOWLEDGEMENTS

We thank the staff of McMurdo Station, especially Fixed Wing Operations, for their support, T. Stockard, K. Ponganis, J. Meir, T. Zenteno-Savin, J. St Leger and E. Stockard for their assistance at Penguin Ranch, and Dr N. Miyazaki for his sponsorship (UTBLS: Bio-Logging Science, University of Tokyo). We are grateful to C. Williams for comments on an early draft of this paper.

FUNDING

This study was supported by a grant from Research Fellowships of the Japan Society for the Promotion of Science (JSPS) for Young Scientists [grant no. 23-2916 to K. Shiomi], by a research grant from JSPS [grant no. A19255001 to K. Sato], and by the National Science Foundation [grants OPP 0229638, 0538594 and 0944220 to P.J.P.].

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