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Emperor penguins adjust swim speed according to the above-water height of ice holes through which they exit

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Summary

Emperor penguins leap from the water onto the sea ice. Their ability to reach above-water height depends critically on initial vertical speed of their leaping, assuming that the kinetic energy is converted to gravitational potential energy. We deliberately changed the above-water heights of ice hole exits, in order to examine whether penguins adjusted swim speed in accordance with the above-water height of the ice. Penguins were maintained in a corral on the fast ice in Antarctica, and voluntarily dived through two artificial ice holes. Data loggers were deployed on the penguins to monitor under water behavior. Nine instrumented penguins performed 386 leaps from the holes during experiments. The maximum swim speeds within 1 s before the exits through the holes correlated significantly with the above-water height of the holes. Penguins adopted higher speed to exit through the higher holes than through the lower holes. Speeds of some failed exits were lower than the theoretical minimum values to reach a given height. Penguins failed to exit onto the sea ice in a total of 37 of the trials. There was no preference to use lower holes after they failed to exit through the higher holes. Rather, swim speed was increased for subsequent attempts after failed leaps. These data demonstrated that penguins apparently recognized the above-water height of holes and adopted speeds greater than the minimal vertical speeds to reach the exit height. It is likely, especially in the case of higher holes (>40 cm), that they chose minimum speeds to exit through the holes to avoid excess energy for swimming before leaping. However, some exceptionally high speeds were recorded when they directly exited onto the ice from lower depths. In those cases, birds could increase swim speed without strokes for the final seconds before exit and they only increased the steepness of their body angles as they surfaced, which indicates that the speed required for leaps by emperor penguins were aided by buoyancy, and that penguins can sometimes exit through the ice holes without any stroking effort before leaping.

Supplementary material available online at
http://jeb.biologists.org/cgi/content/full/208/13/2549/DC1

Key words: data logger, leap, kinetic energy, gravitational potential energy, buoyancy, Emperor penguins.

Introduction

The dependence of emperor penguins on diving and foraging in the marine environment necessitates frequent exits from the ocean onto the sea ice, on which they breed, rear chicks and rest. Because of the presence of predators at the ice edge, there is considerable pressure for emperor penguins exit the sea safely and efficiently. They should leap to exit onto the sea ice. Their ability to reach above-water height depends critically on the angle and speed of their leaps. In a video study of Adélie penguins exiting the water, Yoda and Ropert-Coudert (2004) concluded that Adélie penguins adjust their take-off angle according to the reflected image of the height of ice above the water. However, it is not known whether penguins also alter their swim speeds proportionately to the required height of the exit.

We deliberately changed the above-water heights of two ice holes through which emperor penguins exited. Swim speed, stroke frequency, body angle and depth were monitored using animal-born recorders. Time of exit and hole choice of penguins were simultaneously monitored by observers on the ice. We obtained the first field data to test the hypothesis that penguins adjust swim speed according to the above-water height of holes. We also described their behavior after failed exits onto the sea ice and determined whether they change holes after failed exits

Table 1. *Summary of jump out performance in 13 deployments by nine Emperor penguins*

Year	2003						2004						
Deployment	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	13th
Bird number	313	311	314	304	311	313	426	429	418	427	429	420	429
Body mass (kg)	25.4	29.5	24.5	23.3	28.9	25.7	23.5	27.4	25.9	22.2	27.0	23.5	27.2
Mean height (cm)													
Lower	25.1	28.0	15.4	9.8	9.1	9.2	29.0	28.0	24.2	18.0	16.0	15.9	13.4
Higher	41.4	40.8	33.1	23.0	23.8	24.0	33.0	33.0	26.9	26.9	28.0	29.4	29.5
Height difference (cm)	16.3	12.8	17.7	13.2	14.7	14.8	4.0	5.0	2.7	8.9	12.0	13.5	16.1
Number of exits													
Lower	27	10	37	14	58	20	13	7	17	4	5	13	7
Higher	5	16	18	2	15	12	11	20	8	11	10	9	17
Success:Failure													
Lower	20:7 }*	9:1	37:0 }*	13:1	57:1	19:1	12:1	6:1	15:2	4:0	5:0	13:0	7:0
Higher	1:4 }	15:1	15:3 }	2:0	14:1	10:2	8:3	20:0	7:1	8:3	8:2	9:0	15:2

First six deployments were conducted in 2003 and the others in 2004.
*$P<0.05$; Fisher's exact probability test. See text for details.

and/or whether they increase their swim speed in the subsequent trials.

Materials and methods

Emperor penguins *Aptenodytes forsteri* Gray were captured near the ice edge of McMurdo Sound, Antarctica and additionally, in 2003, four penguins were collected when they passed near our study site. A total of 14 birds in 2003 and 16 birds in 2004 were maintained in a corral at a sea ice camp for 2 months prior to release. The sea ice camp was located on the fast ice of McMurdo Sound, approximately 8 km and 100 km away from the ice edge in 2003 and 2004, respectively. Two ice holes, 1.2 m in diameter and 8 m apart were drilled through the 2.3–2.5 m thick ice in the corral. The holes were plugged by corks during the night to prevent Weddell seals from hauling out on the ice. When the holes were open, birds voluntarily dove through the two dive holes to forage beneath the sea ice.

Recordings

Multi-sensor data loggers (W1000L-PD2GT: 22 mm diameter, 124 mm length; 80 g in air; Little Leonardo Corp., Tokyo, Japan) were used to record swim speed at 0.25-s intervals for six deployments in 2003 and 0.125 s intervals for seven deployments in 2004, depth at 1 s intervals, two-dimensional accelerations (for detecting flipper movement from heaving acceleration and body angle from surging acceleration; see Sato et al., 2004) at 1/16 or 1/32 s intervals, and ambient temperature at 10 s intervals. The data loggers were attached to the back of penguins using waterproof Tesa tape (Wilson and Wilson, 1989) and plastic cable ties. Swim speed was recorded as rotations of an external propeller. It was converted to swimming speed using the calibration method of Sato et al. (2003). The data loggers were deployed on the birds for 26.1–60.9 h. During the deployment, birds repeatedly entered and exited through the holes with the other non-instrumented birds.

Behaviors of the instrumented birds were monitored [time (h:m:s) of exit and hole choice by birds] and recorded. A total of six deployments on four birds were monitored from November 12 to Dececember 6 in 2003 and seven deployments on five birds were monitored from November 14 to December 5 in 2004. Body masses were measured using a platform scale at deployment and retrieval of the recorder. Body mass at deployment, ranging from 22.2 kg to 29.5 kg (Table 1), were used for analysis. Food intake during the daily dives has been inferred from guano deposition on the ice (Ponganis et al., 1997) and confirmed by animal-born video cameras (Ponganis et al., 2000). They usually gained weight during the daytime and lost weight during the night.

The above-water heights of the two ice holes (between the edge of the ice and sea surface) were purposefully changed between two holes and among deployments in 2003 (Table 1). At the beginning of the second year (from 7th to 10th deployments), the above-water heights of the holes were purposefully adjusted within 10 cm difference (Table 1). The heights were modified with a chainsaw and ice chisel. Positions of higher and lower holes were occasionally changed between deployments. Underwater observations of departures and returns to the dive hole were made from a sub-ice observation chamber (Kooyman, 1968).

Analyses and graphics were performed with IGOR Pro (version 3.1) and StatView (version 5.0). The results of statistical tests were assumed to be significant at $P<0.05$.

Calculations

Consider a penguin of mass M_b that exits for a leap with initial vertical velocity V. As the penguin rises to the highest

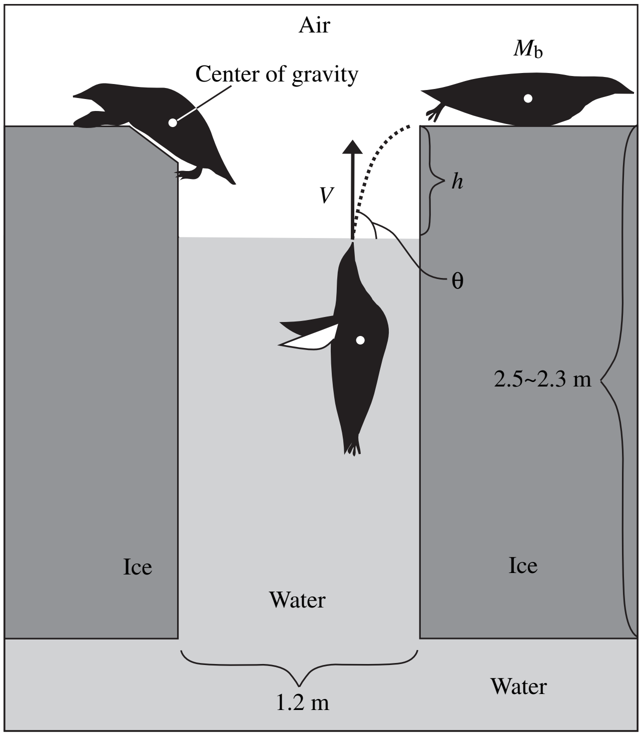

Fig. 1. Schematic diagram of exit options for the penguins. As shown on the left, the bird could climb onto the ice if the center of gravity reached the height of the ice around the hole, or the exit speed was sufficient to project the bird onto the ice (the right-hand bird).

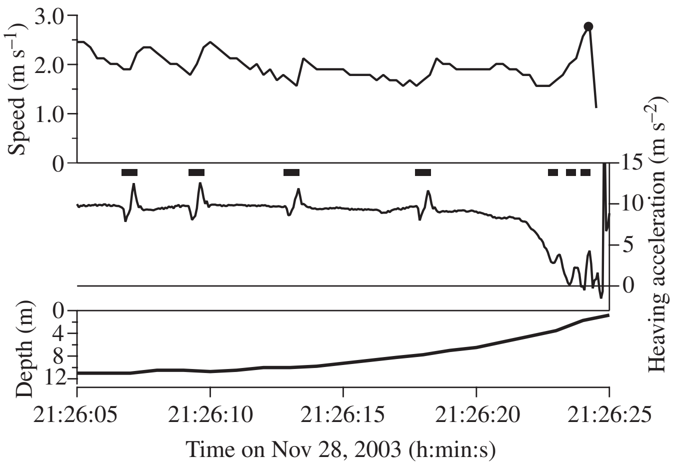

Fig. 2. Typical profiles for last 20 s before exit through the ice hole in 6th deployment by bird no. 314. The closed circle indicates the maximum swim speed before exit. Horizontal bars indicate strokes based on acceleration.

point in its leaping and lands on the ice on its belly, the vertical velocity falls to zero, and the associated kinetic energy just under the sea surface is converted to gravitational potential energy on the ice:

$$0.5M_\text{b}V^2 = M_\text{b}\boldsymbol{g}h\,, \tag{1}$$

where $\boldsymbol{g}$ is the gravitational acceleration (=9.807 m s^{-2}) and h is the above-water height of the hole (Fig. 1). The initial vertical velocity to reach the highest point is given by:

$$V = \sqrt{2\boldsymbol{g}h}\,. \tag{2}$$

When Yoda and Ropert-Coudert (2004) developed a similar model for Adélie penguin's leaping, they considered the distance between the center of gravity of a penguin and its feet, because Adélie penguins land on the ice on their feet. Emperor penguins land prone on their belly. According to the observation, they could climb on the ice using their flippers and feet if the center of gravity reached the height of the ice surface (see the left penguin in Fig. 1). This is the reason that we did not consider the distance between the center of gravity and its belly. The maximum swim speed within 1 s before the exit was compared with the theoretical vertical velocity. Considering the narrow diameter of the hole (1.2 m), body angles of penguins were close to vertical. However, they could sometimes leap with a non-vertical body angles (θ in Fig. 1), especially when the above-water height of the ice at the hole was low. The theoretical vertical velocity could be considered to be the minimal swim speed to reach the above-water height of the ice. Note that the required speed is independent of the mass of bird in Eq. 2. This is why data from all birds were pooled when comparing measured speeds and the above-water heights of the ice at the holes.

Results

The nine instrumented-penguins performed 232 exits from the lower hole and 154 exits from higher hole in 13 deployments (Table 1; see supplementary material). They failed to exit onto the ice in 37 of a total of 386 exits (10%). Comparing the success:failure ratio of higher and lower holes, there were significant differences in two deployments (first and third) in which the difference in heights between two holes was the largest (Table 1, Fisher's exact probability test). In the other cases, there was no significant difference in the success:failure ratio between higher and lower holes (Table 1, Fisher's exact probability test).

Swim speeds in relation to the above-water heights of holes

Fig. 2 shows typical depth, acceleration and swim speed profiles before an exit from the ice hole. The bird adopted a stroke-and-glide method as it approached the hole. Gliding phases between wing strokes were observed. Swim speed fluctuated around 2 m s^{-1} in correspondence with the stroke pattern. The final acceleration with three strokes enabled the penguin to reach a speed of 2.8 m s^{-1} in less than 2 s. The final decrease in speed indicates that the bird leapt out of the water, because the propeller does not rotate in the air. The maximum swim speeds within 1 s before exit, which is represented by a closed circle in Fig. 2, were used for further analyses.

The maximum swim speeds before exits were significantly correlated with the above-water heights of the holes (Fig. 3,

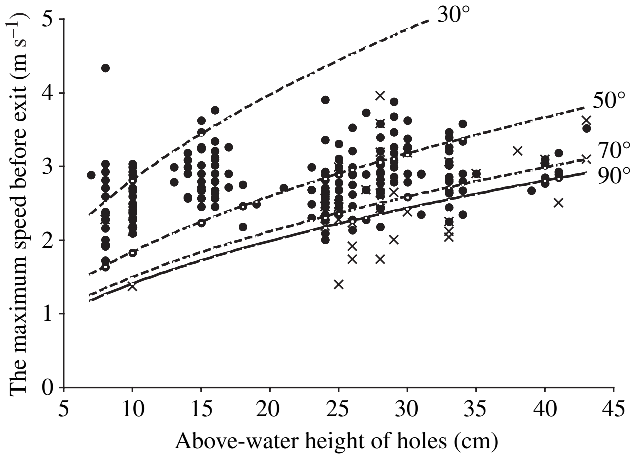

Fig. 3. Relationship between above-water height and the maximum speed before exit. Observed data (386 exits in 13 deployments by nine birds are pooled) are represented by closed circles (successful exit) and crosses (failed exit). The solid curve is the theoretical line for initial vertical speed to reach the height, assuming a take-off angle (θ) of 90° (see text for details). If penguins adopt non-vertical body angles, higher swim speeds were needed to obtain the necessary vertical speeds for the height, which are represented by dotted curves for various take-off angles.

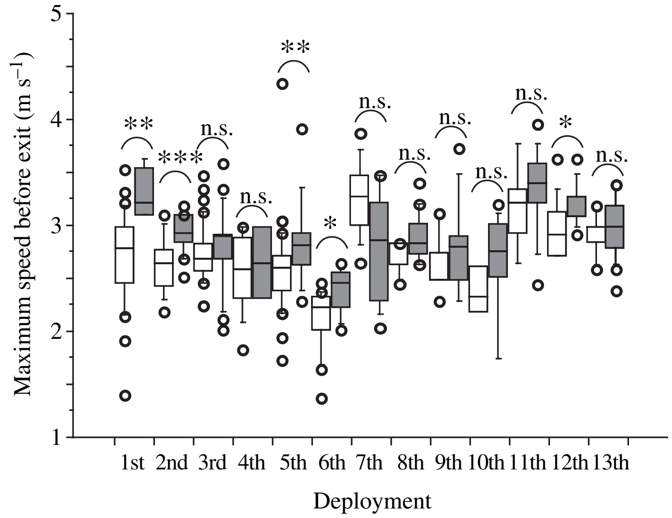

Fig. 4. Box plots for the comparison in the maximum speed before exit between lower (white bars) and higher (gray bars) holes for each deployment. The differences in the above-water height of holes were less than 10 cm in four deployments (from 7th to 10th). *$P<0.05$; **$P<0.01$; ***$P<0.001$; two-tailed Mann–Whitney *U* tests; n.s., not significant.

N=386 exits in 13 deployments by nine birds; Spearman R=0.421, $P<0.0001$). Most speeds of successful exits were above the minimum vertical velocity theoretically needed to reach the height (solid curve in Fig. 3). Swimming speeds of failed exits were sometimes lower than the theoretical minimum values (Fig. 3).

In the first six deployments in 2003, the differences in the above-water height of holes were larger than 10 cm (Table 1). The maximum swim speeds before exits from higher holes were greater than those of lower holes and there were significant differences in the speeds between holes in four of the six deployments in 2003 (two-tailed Mann–Whitney *U* tests; Fig. 4). In following four deployments from the 7th to the 10th in 2004, the above-water heights of the two holes were almost the same level (to within 10 cm; Table 1). There was no significant difference in the four deployments (two-tailed Mann-Whitney *U* tests; Fig. 4). In the last three deployments, the differences in the heights between the two holes were larger than 10 cm (Table 1). In these last deployments, the swim speeds in higher holes were greater than those of lower holes and there were significant differences in the speeds between higher and lower holes in one of the three deployments (two-tailed Mann-Whitney *U* tests; Fig. 4).

Behavior after failed leaps

Penguins failed to exit onto the ice, in total, 37 times, and tried the next exit within 1 min in 27 of those 37 cases. In these second exit attempts, there was no tendency for them to choose the lower hole after they failed in the higher hole. In these second attempts, there were 17 failed exits, the birds selected the lower hole eight times, and the same higher hole nine times. Ten initial failed leaps occurred at the lower hole. After these failures, the birds tried the next exits in the higher holes in four cases. They tried to exit at the same lower hole in the other six cases. There was a significant difference between swim speeds for the failed exits and the velocities for subsequent attempts ($P<0.05$, Wilcoxon signed-rank test). Penguins adopted significantly higher speeds in the subsequent attempts after failed exits.

Discussion

Data from this study demonstrate that penguins apparently recognize the above-water height of ice holes and adjusted their swimming speeds before the exit according to the height required to clear the ice around the hole. There were no significant differences in speeds when the differences in height were smaller than 10 cm (from the 7th to the 10th deployments in Fig. 4). However, they adopted higher speeds to exit through the higher holes than those through the lower holes when the height differences were larger than 10 cm (Fig. 4). There were significant differences in exits speed through higher and lower holes in five deployments but there was no significant difference in the other four deployments, which might be because of the small number of exits in the 4th, 12th and 13th deployments (Table 1).

Pooled data from all 13 deployments indicate that the swim speed increased significantly as the above-water height increased (Fig. 3). When the above-water heights were smaller than 20 cm, most observed swim speeds were much greater than the minimal theoretical values (the solid curve in Fig. 3). This might be because of the shallow body angles of penguins.

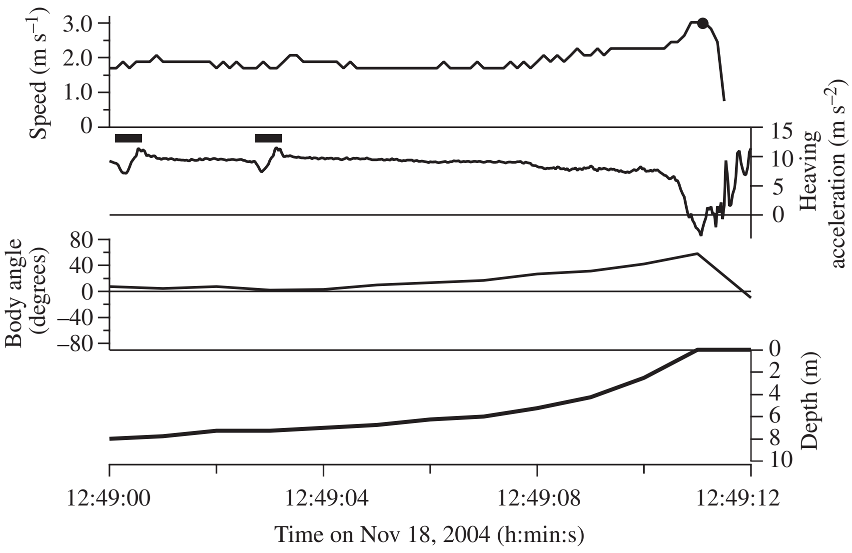

Fig. 5. An example of the last 12 s before exit through the ice hole in the 8th deployment by bird no. 429. The closed circle indicates the maximum swim speed before exit. Horizontal bars indicate strokes based on acceleration.

If penguins adopt shallow body angles for lower ice heights, they need higher swim speeds to obtain the necessary vertical speeds for the heights (as indicated by dotted curves in Fig. 3). It is likely that penguins chose vertical take-off angles and minimum speeds to exit through the holes, especially for the higher holes (>40 cm), to avoid using excess energy for swimming before leaping (Fig. 3).

According to observation from a sub-ice observation chamber, the birds sometimes directly exited onto the sea ice from deep below the surface. Some exceptionally high speeds (Fig. 3) were recorded in such cases. Fig. 5 gives one example of the direct exit from depth. This bird dived for 17 min 25 s, reached a maximum depth of 53.3 m and directly exited through the higher hole (33 cm in height) onto the sea ice. According to the theoretical calculation (Eq. 2), a swimming speed of 2.5 m s^{-1} was needed to exit through this hole. However, the bird reached a maximum speed of 3.0 m s^{-1} before the leap (Fig. 5). The bird did not stroke for the final 7 s before leaping and it only increased the steepness of its body angle to 58 degrees as it surfaced (Fig. 5). Sato et al. (2002) demonstrated that surfacing king and Adélie penguins could increase swim speed using buoyant force without any stroking effort. Van Dam (2002) reported that, in emperor penguins, the mean stroke frequency during final ascent to exit (<0.70 Hz) was lower than that during the initial descent (0.92 Hz). The present study indicates that leaps by emperor penguins were aided by buoyancy and that they can sometimes exit through the ice hole without any stroking effort before the leap. It appears that penguins might know that they do not need to stroke if they reach enough speed in accordance with the above-water height of the hole.

Several factors may contribute to the range of exit speeds observed in this study. In some instances, birds were chased by a Weddell seal (observation from a sub-ice chamber), so escape from predators might be one reason of some of the high speeds. In addition, the kinetic energy of swimming penguins may be converted not only to gravitational potential energy but also to the creation of waves at the surface, and to kinetic energy of some amount of splash. However, the present study could not deal with these aspects because of the difficulty in obtaining quantitative information.

The birds may obtain information on the above-water height of each ice hole before leaps because they repeated dives and commuted frequently between the water and the ice throughout the deployments. According to our observation, they sometimes surfaced in the ice hole for a while, looked at their surroundings, and then made a brief excursion below the surface before exiting through the hole. Yoda and Ropert-Coudert (2004) demonstrated that Adélie penguin adjusted their take-off angle to move out of the water onto the ice. This study indicates that emperor penguins also have a capacity to adjust swim speed before exits according to the above-water height of the holes, and that they decided to increase swim speed for subsequent trials after failed exits, instead of selecting the lower holes.

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