J. Zool., Lond. (2004) **263**, 1–5 Printed in the United Kingdom DOI:10.1017/S0952836904004820

Decision-rules for leaping Adélie penguins (*Pygoscelis adeliae*)

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(Accepted 14 October 2003)

Abstract

Adélie penguins *Pygoscelis adeliae* were tested as to whether they jump with optimal energy efficiency when moving out of the sea to the land. Adélie penguins risk predation if the jump fails. Swimming penguins usually launch up the side of sea ice to a surface higher than sea level. Analysis of jumping behaviour recorded by a video camera showed that the trajectory of the centre of gravity of the birds during the aerial phase of jumping was parabolic, indicating that the success of landing depends on three parameters at the time of take-off from water: speed, angle and distance from the point of emergence to the ice edge. There was a negative relationship between distance and the take-off angle, suggesting that penguins adjust their take-off angle to the distance from the ice edge. The comparison among hypotheses revealed that penguins did not jump with optimal energy efficiency. Instead, they aimed for the refracted image of the edge of the cliff, which from underwater appears higher than it actually is. This direction-dependent rule seems to be more robust and reliable than the optimal energetic strategy.

Key words: bird locomotion, boundary, decision-rule, Adélie penguin, *Pygoscelis adeliae*, leaping

INTRODUCTION

Many animals frequently move through the boundary between water and air, but refraction of light across this boundary could cause confusion as animals move through the boundary. This may be why plunge-diving seabirds enter the sea vertically (e.g. gannets or terns; Shealer, 2002) because this reduces distortion of the position of subsurface prey due to refraction (Azuma, 1997). Similar problems are encountered by animals moving from water to air.

Penguins sometimes leap out of the sea onto land that is above sea level. In the case of Adélie penguins *Pygoscelis adeliae*, they may reach a height of 2–3 m above sea level (Reilly, 1994; McGonigal & Woodworth, 2001; Ainley, 2002). As penguins repeatedly travel between sea and land during the breeding season (Stonehouse, 1975) and since falling back into the water carries increased risk of predation by leopard seals (Ainley, 2002), natural selection may have led to decision-making about jumping that ensures success. As penguins cannot generate any propulsion in the air, the success of landing depends on three factors at the time of take-off from the water: take-off speed, angle and distance from the point of emergence to the ice. We tested three hypotheses concerned with how penguins adjust these factors:

(1a) Penguins jump with optimal energy efficiency. At a given position of emergence, penguins may select the take-off angle to minimize the take-off speeds. This strategy also has the advantage of decreasing the impact of landing on their body. However, as light is refracted through the boundary between air and water, the height of the target cliff appears higher than the real height, when viewed from under water (Denny, 1993). If this hypothesis is upheld, penguins would need to know the height of the ice edge in advance.

(1b) If the height of the ice edge is estimated from underwater, it appears higher than the actual height. Penguins may select the take-off angle to minimize speeds for this apparent height of the cliff from under water. This is not optimal energetic strategy, although the aerial trajectory is energetically efficient for the apparent height. This strategy indicates that penguins measure the refracted height of the ice edge from under water.

(2) Penguins do not jump with optimal energy efficiency. As the direction is often more accurately judged than the distance to a specific point (Kamil & Cheng, 2001), penguins may simply set their take-off angle from under water to aim for the refracted vision of edge of the cliff.

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Hypothesis 1(a,b) is concerned with the currency energy, while the hypothesis 2 is concerned with the currency fitness that penguins are using (see Discussion). This study tested how Adélie penguins control their leaping behaviour.

METHODS

This study was conducted in Dumont D'Urville, Terre Adélie (66.7°S, 140.0°E), during the austral summer 2001/2002. To calculate the length from the centre of gravity of a bird to its feet, we measured the body length (the length from top of the head to the feet) for 21 unfilmed penguins. The length from the centre of gravity of a bird to its feet was calculated to be half of the body length. The centre of gravity was assumed to remain constant as the penguin leaps, or at least only moves minimally as the penguin alters its body shape on take-off and when in the air.

The behaviour of penguins jumping out from the water was recorded using a video camera (30 frames/s). The camera was fixed on a tripod on land and placed so as to monitor the entire trajectories laterally. No one stood nearby the camera during recording so that the behaviour of jumping penguins was not likely to have been altered by observers. The plane of the ice edge was horizontal, so that the height of ice was the same for each bird.

We analysed data from 23 filmed individuals. The analysis of video data was performed on Apple Macintosh personal computers using NIH Image 1.6.2 (U.S. National Institutes of Health, Springfield, Virginia). The trajectory must be parabolic, neglecting the forces other than the gravity such as lift/thrust by flippers and the air resistance due to air density (see Discussion). The trajectory of the geometric centre of gravity of jumping penguins was described frame by frame. A second-order polynomial function was fitted to the trajectories.

The maximum height penguins reached was described as:

$$H = v_0 t_H - (1/2)\, g t_H^2 \qquad (1)$$

where H is the maximum height of the centre of the penguins leaping from water surface, v_0 is the vertical speed of take-off, t_H is the time taken to reach the maximum height from emergence (Fig. 1) and g is the gravitational acceleration (9.8 m/s^2). The law of conservation of energy states that,

$$(1/2)mv^2 = mgH + (1/2)mv_x^2 \qquad (2)$$

where m is the body mass of a bird, v is the take-off speed, v_x is the horizontal speed. Here, $v^2 = v_x^2 + v_0^2$, so that equation (2) is:

$$(1/2)mv_0^2 = mgH \qquad (3)$$

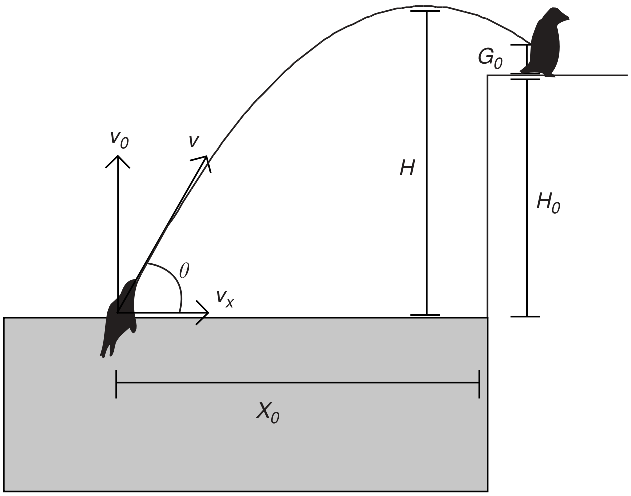

Fig. 1. Definitions of the parameters used in this study for leaping Adélie penguins *Pygoscelis adeliae*: v (take-off speed), v_0 (vertical take-off speed), v_x (horizontal take-off speed), θ (take-off angle), H (maximum height reached during the leap), G_0 (the distance between the centre of gravity of a pengin and its feet), H_0 (the height of the ice edge) and X_0 (the distance from the point of emergence to the cliff).

Here, t_H was extracted from the video data, so that H and v_0 could be calculated from equations (1) and (3). Defining the height of the cliff as H_0 and the distance between the land and the centre of gravity of a bird standing on land as G_0, $(G_0 + H_0)$ is expressed as:

$$(G_0 + H_0) = v_0 t_L - (1/2) g t_L^2 \qquad (4)$$

where t_L is the time taken from emergence to landing obtained from video data. Assuming that G_0 is equal for each bird, $(G_0 + H_0)$ is equal for all birds. Defining the take-off angle as θ,

$$v_x = v_0 / \tan\theta \qquad (5)$$

We calculated $\tan\theta$ as the inclination of the function fitted to the jumping trajectory when penguins emerged from the water. Thus, v_x can be calculated from equation (5). The horizontal distance from the point of emergence to the cliff was defined as X_0. After X_0 was measured as the number of pixels at the video for each bird, X_0 was converted into metres using H_0. The X_0 slightly changes with relation to the third dimension, so we corrected X_0 for each bird since the height of cliff H_0 is constant in spite of the third dimension.

Hypothesis 1a

Penguins jump with optimal energy efficiency: penguins may adjust their take-off speeds to minimize the energy used. In this case, penguins should land when their centre of gravity reaches the extreme of the parabolic trajectory. Thus, the optimal vertical speed v_0^* is expressed as:

$$v_0^* = [2g(H_0 + G_0)]^{0.5} \qquad (6)$$

The optimal horizontal speed v_x^* is expressed as:

$$v_x^* = X_0 g / v_0^* \qquad (7)$$

The optimal take-off angle θ^* is calculated as:

$$\theta^* = \arctan(v_0^*/v_x^*) \tag{8}$$

This model assumes that penguins have information on the height of the ice edge.

Hypothesis 1b

If the height of the ice edge is estimated from underwater, it appears higher than the actual height. In this model, penguins are assumed to estimate the height of the ice edge from underwater. Defining the apparent height, penguins should leap according to:

$$H_a = X_0 \tan\theta \tag{9}$$

Using a refractive power for air and water of 1 and 1.333, respectively, defining the angle of incidence and refraction of light as θ_2 and θ_1, respectively, and defining α by the equations:

$$\theta = \pi/2 - \theta_1 \tag{10}$$

$$\alpha = \pi/2 - \theta_2 \tag{11}$$

Snell's law, which gives the relationship between angles of incidence and refractive powers of two media (Denny, 1993), indicates that:

$$\sin\theta_2 = 1.333 \sin\theta_1 \tag{12}$$

Substituting (10) and (11) to (12),

$$\sin(\pi/2 - \alpha) = 1.333 \sin(\pi/2 - \theta) \tag{13}$$

Therefore,

$$\cos\alpha = 1.333 \cos\theta \tag{14}$$

Tan α is equal to $(H_0 + G_0)/X_0$, therefore, α is arctan $\{(H_0 + G_0)/X_0\}$.

Thus, H_a was calculated as:

$$\begin{aligned} H_a &= X_0 \tan\{\arccos(1/1.333 \cos\alpha)\} \\ &= X_0 \tan(\arccos\{1/1.333 \cos(\arctan[(H_0 + G_0)/X_0])\} \end{aligned} \tag{15}$$

Thus, if penguins jump with optimal energy efficiency for the apparent height, the optimal vertical speed v_{0a}^* for the apparent height H_a is calculated as:

$$v_{0a}^* = [2g(H_a)]^{0.5} \tag{16}$$

The optimal horizontal speed v_{xa}^* is expressed as:

$$v_{xa}^* = X_0 g / v_{0a}^* \tag{17}$$

The optimal take-off angle θ_a^* for the apparent height is calculated by:

$$\theta_a^* = \arctan(v_{0a}^*/v_{xa}^*) \tag{18}$$

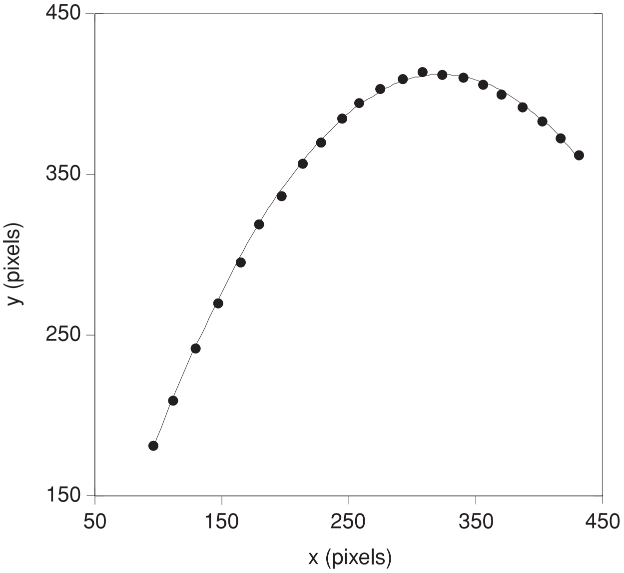

Fig. 2. Example of the trajectory of the centre of gravity of a leaping Adélie penguin *Pygoscelis adeliae*: take-off and in-air sequence. The plots of the trajectory were fitted by the second-order polynomial function ($y = -58.0 + 2.91x - 0.00450x^2, R^2 = 0.9997$). The time between data points is 1/30 s.

Hypothesis 2

Penguins may aim directly toward the ice edge. In this case, the take-off angle is:

$$\theta_a^* = \arctan(X_0/H_a) \tag{19}$$

RESULTS

Body length of unfilmed birds was 0.42 ± 0.03 m ($n = 21$). Thus, G_0 was calculated to be 0.21 m.

One of 23 filmed penguins crashed into the ice edge. This individual had the smallest distance from the emergence point to the cliff. Twenty-two birds landed on their feet and then tobogganed.

The trajectory of jumping penguins was clearly parabolic (Fig. 2; $R^2 = 0.999 \pm 0.001$, mean ± SD, $n = 22$). The height of the cliff plus the distance between the land and the centre of gravity of a bird standing on land ($H_0 + G_0$) was 1.10 ± 0.06 m for 22 penguins. Therefore, H_0 was calculated at 0.89 m. The maximum height reached by penguins was 1.32 ± 0.16 m for 22 birds.

There was a significant negative correlation between the distance and the take-off angle (Spearman rank correlation coefficient: $r_s = -0.542, n = 23, P < 0.05$). There was no correlation between the speed and the distance (Spearman rank correlation coefficient: $r_s = 0.141$, $n = 22$, NS) and the speed and take-off angle (Spearman rank correlation coefficient: $r_s = -0.138$, $n = 22$, NS).

There was a significant difference of the take-off angles among the experiment and hypotheses (ANOVA, d.f. = 3,88, $F = 29.837$, $P < 0.0001$; Fig. 3). Further multiple comparisons using Scheffé's test showed significant

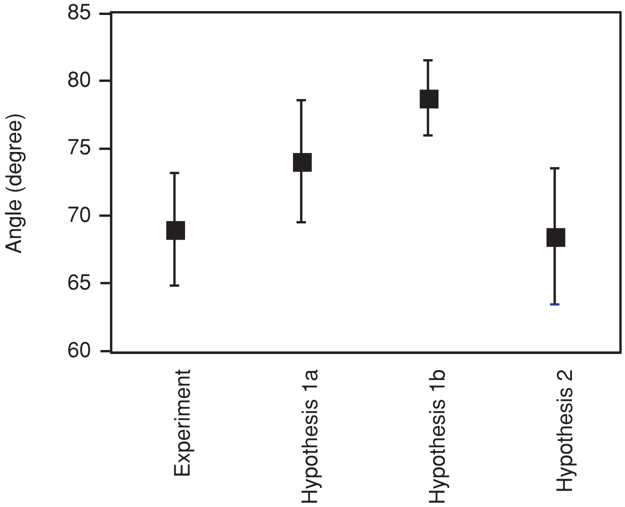

Fig. 3. Comparison among emergence angles from the field data, hypothesis 1a, 1b and 2 (mean ± SD). There was a significant difference among the take-off angles (ANOVA, d.f. = 3,88, $F = 29.837$, $P < 0.0001$; Fig. 4). Further multiple comparisons using Scheffé's test showed significant differences between the experiment and hypotheses 1a and 1b (both $P < 0.01$), but not between the experiment and hypothesis 2 ($P = 0.9756$).

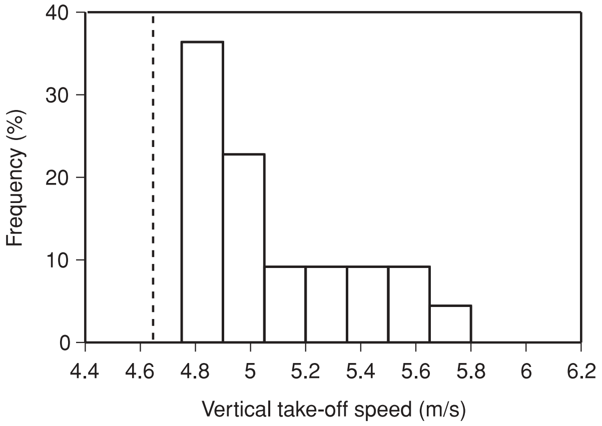

Fig. 4. Distribution of vertical take-off speeds of leaping Adélie penguins *Pygoscelis adeliae*. The dashed line shows the minimum vertical speed for take-off so as to reach the upper level of the ice shelf (4.64 m/s).

differences between the experiment and hypothesis 1a, 1b (both $P < 0.01$), but not between the experiment and hypothesis 2 ($P = 0.9756$).

The vertical take-off speed was skewed to the minimum speed to reach the upper level of the ice shelf (Fig. 4). The average take-off speed and optimal speed in hypothesis 1a was 5.45 ± 0.30 m/s and 4.85 ± 0.12 for 22 birds, respectively.

DISCUSSION

The trajectory for birds leaving the water was clearly parabolic (Fig. 2), indicating no mechanisms for useful lift or thrust by the flippers and little influence of air resistance. As Adélie penguins can jump up to 2–3 m (McGonigal & Woodworth, 2001; Ainley, 2002), the birds in this study did not reach their maximum height. Thus, penguins do not always jump at a maximum speed, but apparently adjust their jumping behaviour to the circumstances.

At a given distance from the point of emergence to the ice edge, it is optimal energetic efficiency for penguins to adjust take-off angle to minimize speed (hypothesis 1a). This hypothesis is not supported by the data (Fig. 3). Also, penguins do not apparently select the take-off angle to minimize the energy for the refracted vision of the target ice edge (hypothesis 1b; Fig. 3).

One possible explanation for this is that penguins have imperfect information about the exact height of the ice edge in advance of the leap. Imprecise information about the height and/or distance of the ice edge could lead to the penguins being precautionary about the risks of failing in their jump. One of 23 penguins, whose distance from the point of emergence to the cliff was smallest, crashed, indicating that this bird overestimated the distance. Evidence from the skewed distribution of vertical take-off speed in Fig. 4 suggested that penguins were usually over-compensating in order to avoid errors.

Alternatively, penguins may choose the take-off angle so as to aim for the ice edge as predicted by hypothesis 2 (Fig. 3). This may be because direction can be judged more accurately than distance (Kamil & Cheng, 2001). The height of the ice edge appears greater due to the refraction of light (Denny, 1993): the apparent height being more than 1.333 times greater than reality, changing the take-off angle and distance of the point of emergence from the ice edge. As a result, if penguins aimed at this apparent height, the birds will land successfully. This strategy does not minimize energy expenditure because it costs about 1.26 times more than the optimal energetic strategy (hypothesis 1a). However, the refracted image of the edge of the cliff must be reliable for jumping to compensate for this energetic disadvantage. Since penguins that fall back after hitting the wall are at risk of being captured by a leopard seal (Ainley, 2002), penguins appear not to adopt the energy-saving strategy but instead opt for the one that is most likely to maximize long-term fitness.

In conclusion, penguins may use the refraction of light to adopt the simple rule for leaping. This rule is a robust way of avoiding failure. This study provides the example of animals being risk averse rather than being energy efficient.

Acknowledgements

Drs G. L. Kooyman, Y. Mori, K. Sato and R. P. Wilson are warmly thanked for their advice and critical reading of this manuscript. This study was supported by National Institute of Polar Research and the XXth Mission in DDU and Institut Paul-Emile Victor (IPEV). This study was supported by Research Fellowships from the Japan Society for the Promotion of Science for Young Scientists and by a

Grant-in-Aid for the 21st Century COE Research (Kyoto University, A2).

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