The Journal of Experimental Biology 204, 685–690 (2001)
Printed in Great Britain © The Company of Biologists Limited 2001
JEB3214

A NEW TECHNIQUE FOR MONITORING THE BEHAVIOUR OF FREE-RANGING ADÉLIE PENGUINS

K. YODA[1,2,*], Y. NAITO[2], K. SATO[2], A. TAKAHASHI[3], J. NISHIKAWA[4], Y. ROPERT-COUDERT[3], M. KURITA[5] AND Y. LE MAHO[6]

[1]*Department of Zoology, Graduate School of Science, Kyoto University, Kitashirakawa, Sakyo, Kyoto 606-8502, Japan,* [2]*National Institute of Polar Research, 1-9-10 Kaga, Itabashi, Tokyo 173-8515, Japan,* [3]*Graduate University of Advanced Studies, Department of Polar Sciences, National Institute of Polar Research, 1-9-10 Kaga, Itabashi, Tokyo 173-8515, Japan,* [4]*Ocean Research Institute, University of Tokyo, Minamidai, Nakano, Tokyo 146-8639, Japan,* [5]*Port of Nagoya Public Aquarium, 1–3 Minato-machi, Minato, Nagoya 455-0033, Japan* and [6]*Centre d'Ecologie et Physiologie Energétiques, Centre National de la Recherche Scientifique, 23 rue Becquerel, 67087 Strasbourg Cédex, France*

*e-mail: yoda@ci.zool.kyoto-u.ac.jp

Accepted 4 December 2000; published on WWW 1 February 2001

Summary

Measurement of the time allocation of penguins at sea has been a major goal of researchers in recent years. Until now, however, no equipment has been available that would allow measurement of the aquatic and terrestrial behaviour of an Antarctic penguin while it is commuting between the colony and the foraging grounds. A new motion detector, based on the measurement of acceleration, has been used here in addition to current methods of inferring behaviour using data loggers that monitor depth and speed. We present data on the time allocation of Adélie penguins (*Pygoscelis adeliae*) according to the different types of behaviours they display during their foraging trips: walking, tobogganing, standing on land, lying on land, resting at the water surface, porpoising and diving. To illustrate the potential of this new technique, we compared the behaviour of Adélie penguins during the chick-rearing period in a fast sea-ice region and an ice-free region. The proportion of time spent standing, lying on land and walking during foraging trips was greater for penguins in the sea-ice region (37.6±13.3 % standing, 21.6±15.6 % lying and 5.9±6.3 % walking) than for those in the ice-free region (12.0±15.8 % standing, 0.38±0.60 % lying and 0 % walking), whereas the proportion of time spent resting at the water surface and porpoising was greater for birds in the ice-free region (38.1±6.4 % resting and 1.1±1.1 % porpoising) than for those in the sea-ice region (3.0±2.3 % resting and 0 % porpoising; means ± S.D., *N*=7 for the sea-ice region, *N*=4 for the ice-free region). Using this new approach, further studies combining the monitoring of marine resources in different Antarctic sites and the measurement of the energy expenditure of foraging penguins, e.g. using heart rates, will constitute a powerful tool for investigating the effects of environmental conditions on their foraging strategy. This technique will expand our ability to monitor many animals in the field.

Key words: *Pygoscelis adeliae*, Adélie penguin, acceleration data logger, remote monitoring, behaviour, time budget, allocation, foraging strategy.

Introduction

During the last decade, the study of the foraging behaviour of marine animals has been made possible by the development of new technologies resulting from the miniaturization of electronic devices (Naito et al., 1990; Kooyman et al., 1992; Williams et al., 1992; Croxall et al., 1993; Wilson and Wilson, 1995). Logging of dive depth and swimming speed has provided useful data about the swimming behaviour of penguins. Such results have revealed that penguins are marvellous divers: king penguins (*Aptenodytes patagonicus*) forage at depths of over 300 m (Kooyman et al., 1992) and Adélie penguins forage at a maximum depth of 180 m (Watanuki et al., 1997).

Until now, however, no equipment has been available to monitor the many possible behaviours of a penguin while it is commuting between the colony and the foraging grounds. To determine in detail their time allocation has been one of the three major goals of researchers studying penguins in recent years (others are the precise measurement of marine resources and of the energy expenditure of foraging penguins). Inter-dive behaviour is important for the elucidation of the time budgets of penguins during foraging trips, because the time spent at the surface accounts for a large part of the foraging trip (e.g. 65–70 %, Chappell et al., 1993; 52–73 %, Watanuki et al., 1997).

We have used a new motion detector, which measures acceleration, in addition to previously available methods of inferring behaviour using data loggers, i.e. monitoring depth and speed. Unlike the previous data, acceleration data permit behaviour to be recorded directly. We present data on the time allocation of Adélie penguins, categorized into the different types of behaviours they display during their foraging trips: walking, tobogganing, standing on land, lying on land, resting at the water surface, porpoising and diving. To illustrate the potential of this new technique, we compared the time allocation of Adélie penguins, during the chick-rearing period, in a fast sea-ice region and an ice-free region.

Materials and methods

Field experiments

This study was conducted at Hukuro Cove (69°00′S, 39°39′E) south of Syowa station and at Adélie Land (66°07′S, 140°00′E) near Dumont d'Urville station in Antarctica from December 1998 to January 1999. At Hukuro Cove, the bay was covered with fast sea-ice approximately 1 m thick throughout the study period; the fast sea-ice had completely disappeared before the beginning of the study at Adélie Land.

The behaviour of breeding Adélie penguins was monitored using a 12-bit resolution, 16 Mbyte memory, four-channel UWE-PD2G logger (weighing 60 g, 20 mm in diameter, 122 mm in length; Little Leonardo, Tokyo, Japan) that recorded depth, speed (from the number of rotations of a propeller) and acceleration. Depth and swimming speed data were recorded at a frequency of 1 Hz. Acceleration data were recorded at a frequency of 16 Hz at Hukuro Cove and at 3.3 Hz at Adélie Land, respectively, using two piezo-resistive accelerometers (model 3031, IC Sensors). The logger was attached to the back of the penguin, where it recorded acceleration in two axes of three directions; surging acceleration measured along the longitudinal body axis of the penguin, heaving acceleration measured dorso-vertically and swaying acceleration measured transversely crossing the penguin's body from right to left (Fig. 1).

Adélie penguins captured at their nests were rapidly equipped with the loggers at Hukuro Cove (*N*=17) and Adélie Land (*N*=8). The data loggers were attached caudally on the bird's back to minimize drag (Bannasch et al., 1994; Culik et al., 1994) using tesa tape (Wilson et al., 1997) at Hukuro Cove and epoxy adhesive at Dumont d'Urville. The penguins were recaptured after their foraging trip, and the data loggers were retrieved. The exact position of the logger on the back of a bird varied slightly from one individual to another in relation to the curvature of its back. To reduce the effects of differences in attachment among individuals as much as possible, at the start of the analysis of data, surging acceleration was individually calibrated as being equal to 9.8 m s^{-2} when the bird was standing still after attachment of the logger.

Categorization of behaviour from acceleration

The activities of penguins during a foraging trip is divided into the following seven major categories; walking, tobogganing, standing on land, lying on land, resting at the water surface, porpoising and diving; tobogganing penguins lie on their belly and push themselves forward with alternating foot movements (Wilson et al., 1991), and porpoising penguins jump briefly out of the water (Yoda et al., 1999). We defined diving behaviour as swimming at a depth of more than 1 m. The acceleration profiles for specific types of behaviour were categorized during a calibration experiment conducted on two captive Adélie penguins in the Port of Nagoya Public Aquarium and on each wild penguin equipped with a data logger during movements from their nest to the sea, where we could observe the birds directly. Penguins were recorded (at 30 frames s^{-1}) using a video camera, and the acceleration profiles were compared by visual analysis of the videotapes. The relationships between the behaviour and acceleration profiles of penguins walking, tobogganing, standing on land, lying on land and resting on the water surface were confirmed near their colony in field experiments, and the relationship for porpoising penguins was calibrated in the aquarium.

The acceleration sensors measure both accelerations related to changes in the movements of birds and gravitational acceleration (9.8 m s^{-2}). Thus, the amplitude of surging acceleration when the penguin is not moving represents the component of gravitational acceleration that changes in response to the posture of the bird. This enabled us to determine the posture of the penguins, i.e. whether they were standing, lying on land or resting at the water surface. To remove the acceleration of the movement, the surging acceleration data were smoothed using a moving average over 111 points, which was appropriate for discriminating the dynamic activities in order to determine posture. The threshold at which the three postures would best be distinguished from each other was identified. Below this threshold, the acceleration spectra were analyzed automatically.

Dynamic behaviour, i.e. walking, tobogganing and porpoising, were categorized by examining the acceleration

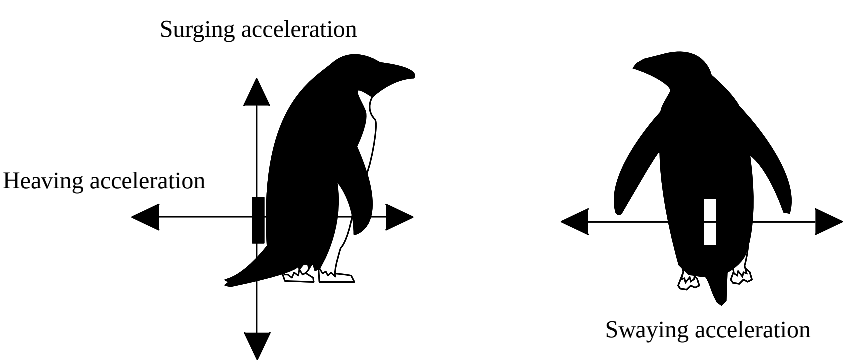

Fig. 1. Schematic diagram showing the direction of surging, heaving and swaying accelerations recorded by a data logger on the back of an Adélie penguin.

profiles by eye. The periodic properties of the acceleration signal obtained from walking and tobogganing behaviour allowed a Fourier analysis to be applied, enabling us to determine the frequency of walking and tobogganing.

Results are presented as means ± S.D. Comparisons were evaluated using a Mann–Whitney *U*-test. Differences were accepted as significant when $P<0.05$.

Results

Penguins had a mean mass of 4.4±0.43 kg (mean ± S.D., N=11). In the sea-ice region, all the recorders were recovered, but seven loggers were missing after one foraging trip, one acceleration sensor was broken and two penguins did not dive at all. In the ice-free region, all the loggers were also recovered, but two penguins did not dive and two recorders was not attached appropriately. Therefore, seven of the PD2G loggers delivered reliable data for one foraging trip in the sea-ice region and four of the loggers for one foraging trip in the ice-free region. Fig. 2 gives examples of the raw data. The duration of a foraging trip in the sea-ice region (10.4±6.8 h, mean ± S.D., range 3.0–21.5 h, N=7 birds) was shorter than that in the ice-free region (27.3±10.5 h, mean ± S.D., range 13.0–38.1 h, N=4 birds; $P<0.05$, Mann–Whitney *U*-test).

The distribution of surging accelerations in relation to the posture of penguin was bimodal, with higher values (⩾5.0 m s^{-2}) corresponding to upright and lower values (<5.0 m s^{-2}) to horizontal positions (Fig. 3A,B). Values ⩾1.5 m s^{-2} corresponded to lying on land and values <1.5 m s^{-2} corresponded to resting at the water surface (Fig. 3A,B), although this value did not always allow a definitive separation between lying on land and resting at the water surface. Therefore, changes in heaving acceleration due to sea waves when the bird is at sea were used in combination with the inclination angles of the loggers for an accurate discrimination (Fig. 3B).

The large lateral swings of walking penguins (Pinshow et al., 1977) and the dash-and-stop movements of tobogganing penguins affected the surging and swaying acceleration pattern

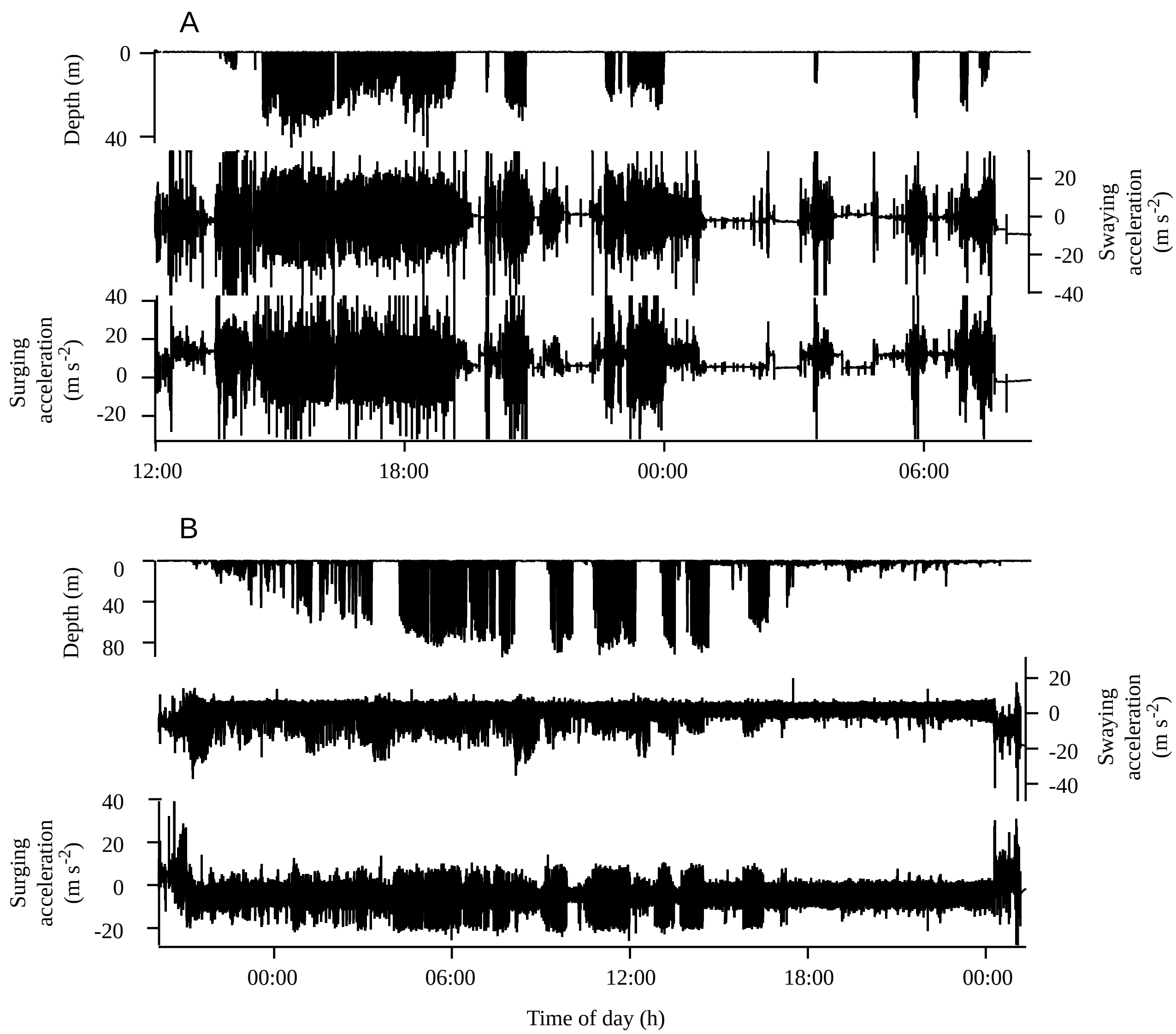

Fig. 2. Examples of acceleration and diving profiles of Adélie penguins foraging in an area covered by sea-ice (A) and in an ice-free area (B).

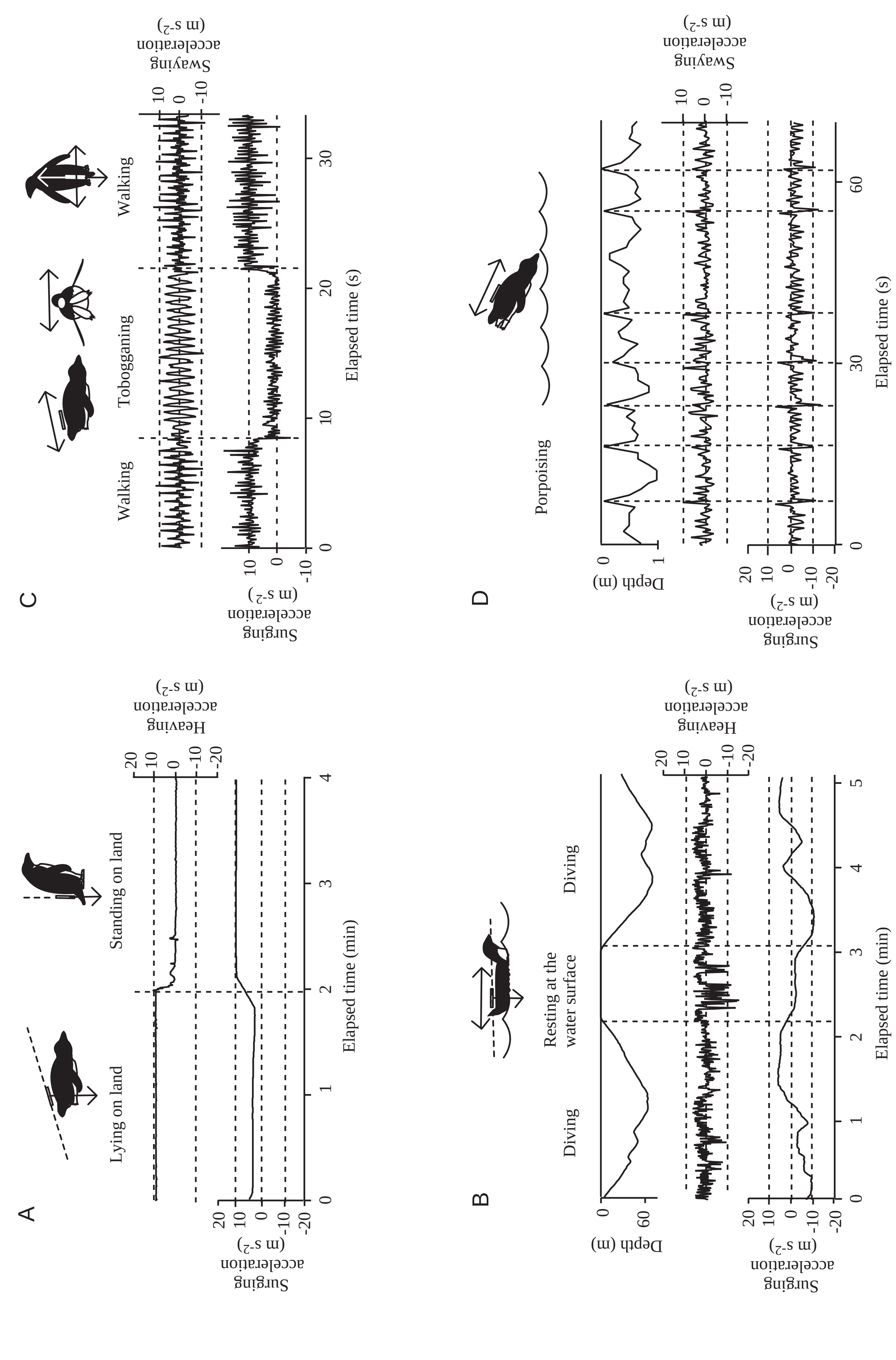

Fig. 3. Profiles of surging, heaving and swaying acceleration and depth for Adélie penguins (A) lying and standing on land, (B) diving and resting at the water surface, (C) walking and tobogganing and (D) porpoising. Surging acceleration in A and B was smoothed using the procedure described in the text to differentiate the three types of posture. Leaps during porpoising are indicated by vertical broken lines in D.

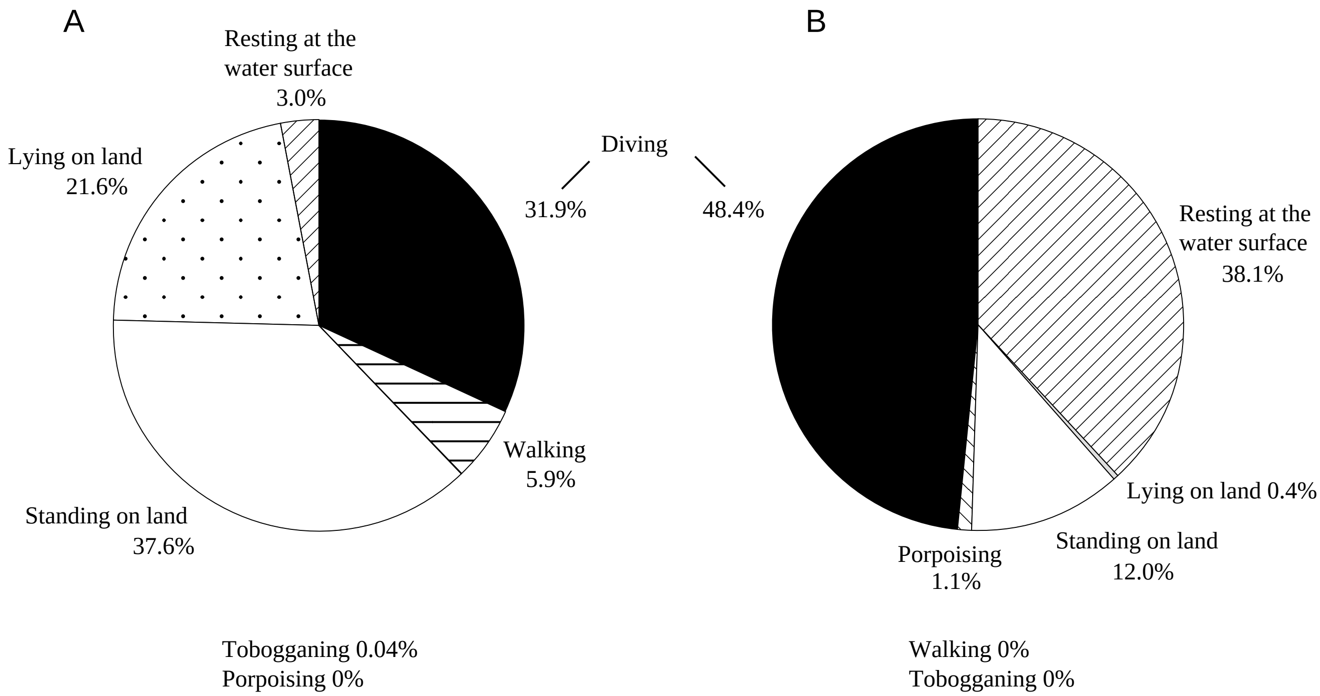

Fig. 4. Behavioural time budgets of Adélie penguins foraging in an area covered by sea-ice (Hukuro Cove; *N*=7 birds) (A) and in a ice-free area (Adélie Land; *N*=4 birds) (B).

recorded by the loggers (Fig. 3C). These two behaviours could be distinguished using the posture of the birds indicated by the surging acceleration profile: walking penguins stand up, whereas tobogganing penguins lie down (Fig. 3C).

When penguins leapt into the air during porpoising, the amplitude of surging acceleration increased briefly up to almost $10\,m\,s^{-2}$ before decreasing to $-10\,m\,s^{-2}$ (Fig. 3D). This might be caused by the change of posture in relation to jumping into the air and then plunging into the water and to the impact of the movement.

The difference in sampling frequency between the penguins at the sea-ice region and the ice-free region did not affect these categorizations of behaviour. The differences between individual penguins were barely detectable when these seven types of behaviour were distinguished.

The frequency of the different behaviour types was calculated for the two study sites (Fig. 4). There was no significant difference between the two colonies in the proportion of time spent diving during foraging trips (P=0.06, Mann–Whitney U-test). The proportion of time spent standing, lying on land and walking was greater for birds in the sea-ice region (37.6±13.3 % standing, 21.6±15.6 % lying and 5.9±6.3 % walking, means ± S.D.; P<0.05, Mann–Whitney U-test) than for those in the ice-free region (12.0±15.8 % standing, 0.38±0.60 % lying and 0 % walking, means ± S.D.; P<0.05, Mann–Whitney U-test) and the proportion of time spent resting at the water surface and porpoising was greater for birds in the ice-free region (38.1±6.4 % resting and 1.1±1.1 % porpoising, means ± S.D.) than for those in the sea-ice region (3.0±2.3 % resting and 0 % porpoising, means ± S.D.; P<0.05, Mann–Whitney U-test).

The stride frequencies of walking and tobogganing penguins in the sea-ice region were calculated as 1.7±0.3 Hz (mean ± S.D., range 1.0–2.8 Hz, N=233) and 1.7±0.2 Hz (mean ± S.D., range 1.4–1.9 Hz, N=5), respectively.

Discussion

Motion detectors and accelerometers have been used to monitor objectively the behaviour of ambulatory humans (Bussmann et al., 1998). Moreover, the use of accelerometers to monitor the swimming activities of free-ranging animals has recently been reported for penguins (Yoda et al., 1999; Arai et al., 2000) and for seals (Davis et al., 1999; Williams et al., 2000). In the present study, accelerometers were used to monitor the behaviour of a free-ranging animal both at sea and on land.

In this study, seven behaviour patterns of penguins during foraging trips were distinguished. It may also be possible to obtain information to sub-divide these behaviours further, e.g. jumping on rocks, which is a common activity of rockhopper penguins (*Eudyptes chrysocome*), and which may be special interest for specific research, although the present study categorized general behaviour during foraging trips. Three postures (standing on land, lying on land and resting on water) could be automatically distinguished by using appropriate thresholds, although changes in acceleration caused by sea waves were also used to discriminate between two lying positions. A method by which walking, tobogganing and porpoising activities can be automatically distinguished from other behaviours is still under investigation. However, these dynamic behaviours seemed to be clearly distinguishable by eye (Fig. 3). Once the behaviour/acceleration profiles had been calibrated at an aquarium or in the field, where the behaviour can be recorded by video camera, this system proved to be highly reliable for continuous automatic monitoring.

The short sampling interval enabled us not only to monitor high-speed behaviour, such as porpoising, but also to calculate the frequency of walking and tobogganing, using mathematical methods such as Fourier analysis. These analyses will enable us to study the energetic efficiency of walking and tobogganing (Wilson et al., 1991) during foraging trips in the natural condition.

Using this new approach, further studies combining the monitoring of marine resources in different Antarctic sites and the measurement of the energy expenditure of foraging penguins, e.g. by measuring heart rates (Bevan et al., 1995), will constitute a powerful tool for examining the foraging strategy chosen in the different environmental conditions, such as sea-ice conditions. In the present study, the behaviour of penguins in the sea-ice region and the ice-free region was quite different because of the difference in resting site between dives, i.e. on the sea-ice in the sea-ice region and at the water surface in the ice-free region, and the type of locomotion, i.e. walking and tobogganing in the sea-ice region and swimming and porpoising in the ice-free region. These differences in behaviour require different energy expenditures, which may lead to different strategies of time allocation during foraging trips. The possible flexibility of the behavioural strategy of penguins will be revealed by a combination of measurements of behaviour and energy expenditure.

This method could be used to monitor not only the behaviour of aquatic animals, such as penguins, but also the activities of terrestrial animals. For example, the behaviour of flying slaty-backed gulls (*Larus schistisagus*) has been monitored as a periodical profile using an acceleration data logger (K. Yoda, Y. Watanuki and Y. Naito, unpublished data). The overall design of this system offers high flexibility for the study of many different animals and enables the behaviour of the animal to be analysed precisely in its natural environment.

This work was supported by the fortieth JARE and Grant-in-aid for International Scientific Research. We thank J. Baudat and all the 1998/1999 team in Dumont d'Urville French station and Syowa station for their assistance in the field, T. Akamatsu, National Research Institute of Fisheries Engineering, M. Kuroki, Graduate University of Advanced Studies, for calibration experiments of the propeller data logger, M. Fukuda, Tokyo Sea Life Park, and I. Uchida, Port of Nagoya Public Aquarium, for their assistance in the aquarium investigations and M. Imafuku, A. Mori, Y. Mori, Kyoto University, R. P. Wilson, Institut für Meereskunde, and two anonymous reviewers for comments on the manuscript.

References

Arai, N., Kuroki, M., Sakamoto, W. and Naito, Y. (2000). Analysis of diving behavior of Adélie penguins using acceleration data logger. *Polar Biosci.* **13**, 95–100.

Bannasch, R., Wilson, R. P. and Culik, B. (1994). Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J. Exp. Biol.* **194**, 83–96.

Bevan, R. M., Woakes, A. J., Butler, P. J. and Croxall, J. P. (1995). Heart rate and oxygen consumption of exercising gentoo penguins. *Physiol. Zool.* **68**, 855–877.

Bussmann, J. B. J., van de Laar, Y. M., Neeleman, M. P. and Stann, H. J. (1998). Ambulatory accelerometry to quantify motor behaviour in patients after failed back surgery: a validation study. *Pain* **74**, 153–161.

Chappell, M. A., Shoemaker, V. H., Janes, D. N., Bucher, T. L. and Maloney, S. K. (1993). Diving behaviour during foraging in breeding Adélie penguins. *Ecology* **74**, 1204–1215.

Croxall, J. P., Briggs, D. R., Kato, A., Naito, Y., Watanuki, Y. and Williams, Y. D. (1993). Diving pattern and performance in the macaroni penguin *Eudyptes chrysolophus*. *J. Zool., Lond.* **230**, 31–47.

Culik, B. M., Bannasch, R. and Wilson, R. P. (1994). External devices on penguins: how important is shape? *Mar. Biol.* **118**, 353–357.

Davis, R. W., Fuiman, L. A., Williams, T. M., Collier, S. O., Hagey, W. P., Kanatous, S. B., Kohin, S. and Horning, M. (1999). Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* **283**, 993–996.

Kooyman, G. L., Cherel, Y., Le Maho, Y., Croxall, J. P., Thorson, P. H., Ridoux, V. and Kooyman, C. A. (1992). Diving behavior and energetics during foraging cycles in king penguins. *Ecol. Monogr.* **62**, 143–163.

Naito, Y., Asaga, T. and Ohyama, Y. (1990). Diving behavior of Adélie penguins determined by time–depth recorder. *Condor* **92**, 582–586.

Pinshow, B., Fedak, M. A. and Schmidt-Nielsen, K. (1977). Terrestrial locomotion in penguins: it costs more to waddle. *Science* **195**, 592–594.

Watanuki, Y., Kato, A., Naito, Y., Robertson, G. and Robinson, S. (1997). Diving and foraging behaviour of Adélie penguins in areas with and without fast sea-ice. *Polar Biol.* **17**, 296–304.

Williams, T. D., 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.

Williams, T. D., Kato, A., Croxall, J. P., Naito, Y., Briggs, D. R., Rodwell, S. and Barton, T. R. (1992). Diving pattern and performance in nonbreeding gentoo penguins (*Pygoscelis papua*) during winter. *Auk* **109**, 223–234.

Wilson, R. P., Culik, B., Adelung, D., Coria, N. R. and Spairani, H. J. (1991). To slide or stride: when should Adélie penguins (*Pygoscelis adeliae*) toboggan? *Can. J. Zool.* **69**, 221–225.

Wilson, R. P., Püts, K., Peters, G., Culik, B., Scolaro, J. A., Charrassin, J.-B. and Ropert-Coudert, Y. (1997). Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Soc. Bull.* **25**, 101–106.

Wilson, R. P. and Wilson, M.-P. T. (1995). The foraging behaviour of the African Penguin *Spheniscus demersus*. In *The Penguins: Ecology and Management* (ed. P. Dann, I. Norman and P. Reilly), pp. 244–265. Australia: Surrey Beatty & Sons Pty Limited.

Yoda, K., Sato, K., Niizuma, Y., Kurita, M., Bost, C. A., Le maho, Y. and Naito, Y. (1999). Precise monitoring of porpoising behaviour of Adélie penguins determined using acceleration data loggers. *J. Exp. Biol.* **202**, 3121–3126.