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Source: Ardea, 107(3) : 333-339

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/arde.v107i3.a12

Homing ability of Adélie Penguins investigated with displacement experiments and bio-logging

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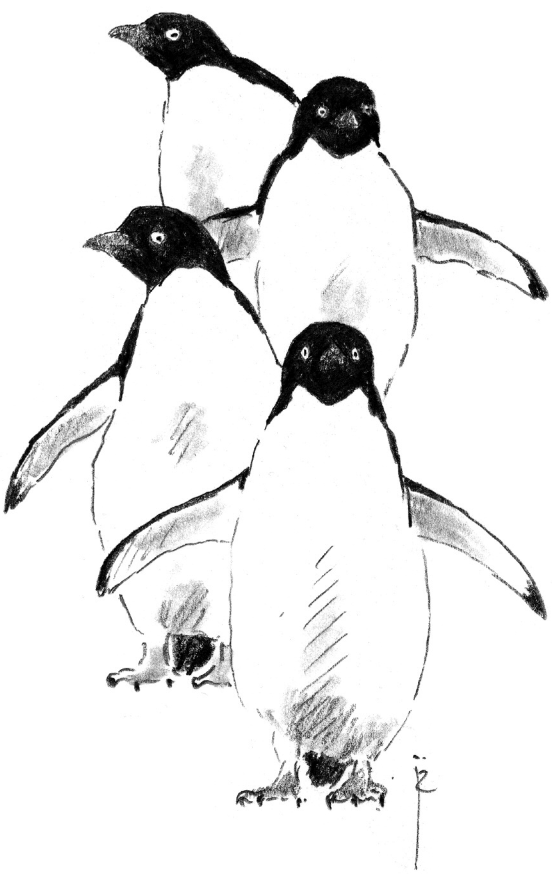

Shiomi K., Kokubun N., Shimabukuro U. & Takahashi A. 2019. Homing ability of Adélie Penguins investigated with displacement experiments and bio-logging. Ardea 107: 333–339. doi:10.5253/arde.v107i3.a12

Adélie Penguins *Pygoscelis adeliae* live exclusively in Antarctica and commute between the sea for foraging and the land for breeding. During these movements, they must navigate various environments: underwater, on sea ice and on land; an unusual set of challenges among animals. Navigation mechanisms of this species were intensively studied about 50 years ago, but technological limitation at that time made it hard to fully understand movement patterns under experimental as well as natural conditions. Recent developments in animal-borne data loggers have enabled us to record movement paths and activities of such birds. In this paper, we report the results of displacement experiments combined with bio-logging on Adélie Penguins, conducted for the first time since initial experiments more than 50 years ago. Two chick rearing birds were caught at their nests and data loggers with GPS and accelerometers were deployed on their backs. The birds were artificially displaced and released approximately 1 km from the breeding colony. From the release point, their options to return to the nest were either walking over land or swimming in the sea. The birds successfully returned to the colony 6.0 h and 8.1 h after release, taking 44 min and 41 min, respectively, from the onset of homeward movement. Both individuals took what appeared to be the straightest and shortest course crossing over land. They spent most of the homing phase (51.2% and 66.2%) walking and only entered the water – in the same place – in the last stretch homewards. The results of our study demonstrate the homing ability of Adélie Penguins from a distant location after artificial displacement and the potential use of positional and acceleration data to study the navigation of penguins that travel by both land and sea.

Key words: acceleration, GPS, homing, navigation, penguin, walk

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During the breeding season, penguins travel tens or sometimes hundreds of kilometres between their nesting colony on land and foraging areas at sea (e.g. Ancel *et al.* 1992, Bost *et al.* 1997, Ryan *et al.* 2004, Cottin *et al.* 2012). For these movements, they use two locomotion modes with different speeds and costs of transport, i.e. swimming and walking (Pinshow *et al.* 1977, Culik & Wilson 1991). In addition, species living in Antarctica must navigate through particularly variable environments, including open water, on top of and underneath sea ice and on land. However, the manner in which they achieve this navigation remains unclear.

Intensive research on the navigation mechanisms of Adélie Penguins *Pygoscelis adeliae* was carried out over 50 years ago. Large-scale experiments using displacement by airplane were conducted, moving animals up to 2700 km from the breeding colony (Emlen & Penney 1964, Penney & Emlen 1967). The results of these studies showed that Adélie Penguins released from unknown places free of landmarks headed northwards, probably relying on a time-compensated sun compass, trying to reach the sea irrespective of the colony's position. However, due to technological limitations at that time, only initial orientation after release was investigated and it was not possible to track movement paths and activities all the way to the nests.

Recent progress in bio-logging technology has advanced studies of animal navigation through the ability to record behaviours under natural and manipulated conditions, beyond previously achievable observation ranges (Rutz & Hays 2009). Soon after GPS data loggers were sufficiently miniaturised to be applied to birds (Steiner *et al.* 2000, von Hünerbein *et al.* 2000), they started to be used in displacement experiments to investigate navigation ability and mechanisms (e.g. Lipp *et al.* 2004, Vyssotski *et al.* 2006, Gagliardo *et al.* 2013). In addition, acceleration data reflecting body posture and activity (Yoda *et al.* 2001, Sakamoto *et al.* 2009, Watanabe *et al.* 2012) could be used to estimate the proportion of time spent on each mode of locomotion and behavioural responses to varying environments during goal-oriented movements. However, no studies, to date, have used GPS and accelerometers in displacement experiments with penguins, while a few previous studies using GPS-loggers mentioned navigation and orientation of penguins during foraging trips (Mattern *et al.* 2007, 2013).

In the present study, displacement experiments using animal-borne data loggers were conducted on two Adélie Penguins. Our aim was to examine their route selections and behavioural time allocation after release and explore how GPS and acceleration data can contribute to our understanding of the homing behaviour of penguins.

Methods

Displacement experiments

Field experiments on Adélie Penguins were conducted on 17 January 2018 at the Hukuro Cove colony (Figure 1; 69.21°S, 39.63°E; 150–200 pairs) in Lützow-Holm Bay in Antarctica. This field site is about 23 km south of the Japanese Syowa (Showa) Station. Two Adélie Penguins breeding at this colony were caught by hand during the late guarding stage, during which one parent guards its chick at the nest, while the other forages at sea. Both nests had one chick. We caught the two birds just after they returned to their nest at the end of a foraging trip and before their mates left the nest to forage, thereby avoiding leaving the chick alone. The experimental birds were determined to be a

Adélie Penguins walking overland (photo Kozue Shiomi, 12 December 2017, near a breeding colony in Lützow-Holm Bay in Antarctica).

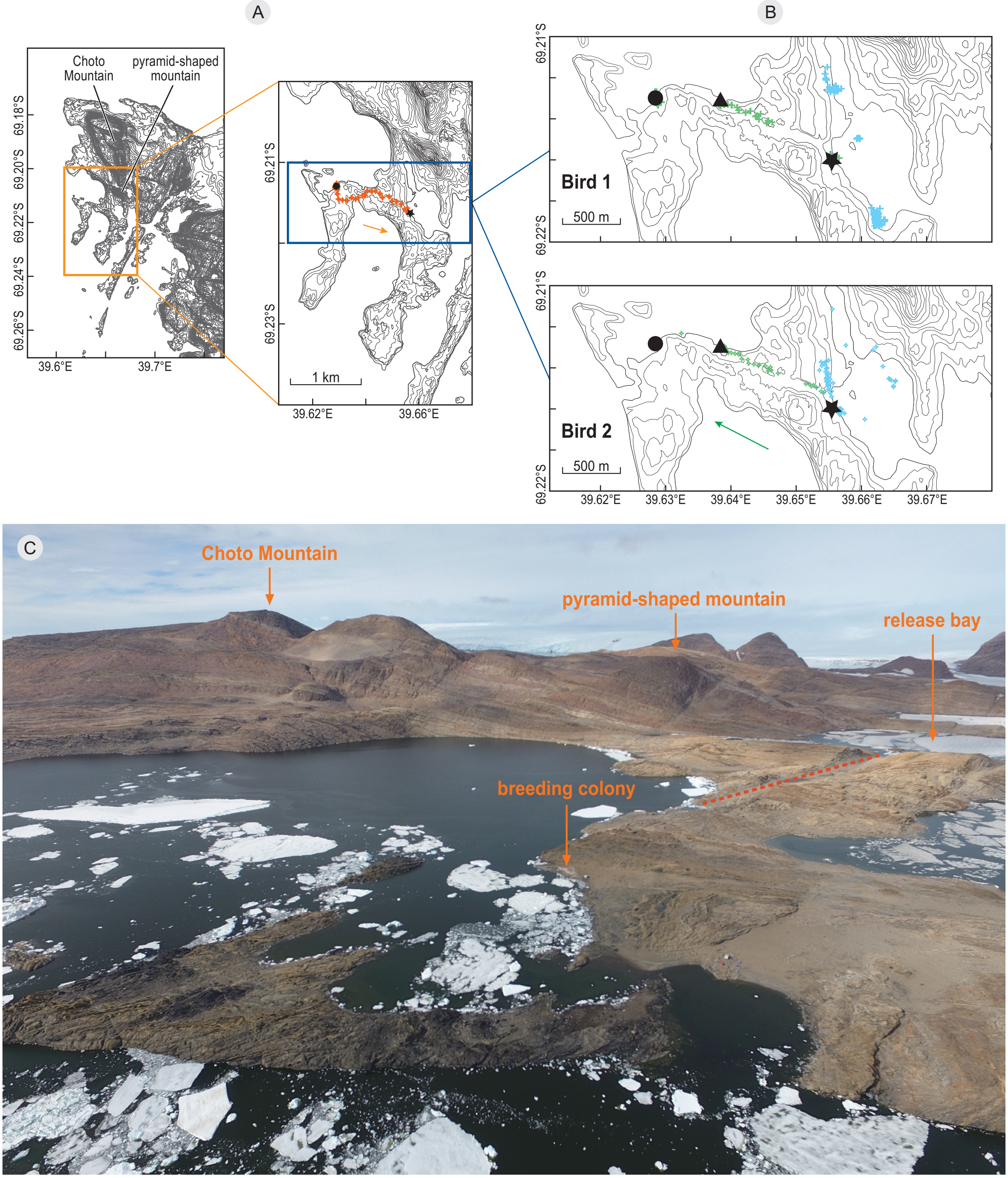

Figure 1. Map of the field site showing (A) our path during displacement of two Adélie Penguins and (B) the positions of the penguins after release. Contour interval on the maps is 10 m. The position of the breeding colony and the release point are indicated with a filled circle and star, respectively. In (B), light blue and green points indicate those before and after the onset of homing, respectively; triangles indicate the place where they entered the sea during the last phase of homing. Note that there were some gaps in the positional records due to an interruption of satellite signals. (C) Landscape around the field site. Arrows indicate Choto Mountain, the pyramid-shaped mountain, the release bay where the birds were released and the breeding colony. The dashed line shows a straight path between the bay and the place where the birds dived into the sea. The photo was taken using a drone (Phantom 4, DJI) on the day of the displacement experiments.

male (Bird 1) and a female (Bird 2) based on their bill length, bill depth and flipper width (Kerry *et al.* 1992). A data logger (c. 25 g, Axy-Trek with 450 or 600 mAh battery, TechnoSmart, Italy) was attached to the lower back using waterproof tape. Instant glue and plastic cable ties were also used to prevent the tape from detaching. The loggers recorded GPS positions every minute, 3-axis acceleration at 25 Hz and depth and temperature at 1 Hz. Each bird was placed in a cloth bag, held under the arm, and then displaced to a position about 1 km east of the colony (Figure 1; 69.22°S, 39.66°E). The cloth bag had a hole for air. The walk to the release location was approximately 20 min and our path was not completely straight (Figure 1A). Bird 1 was released around 11:00 and Bird 2 around 17:00, both in overcast conditions. When released at the coastline of the bay (hereafter called the release bay), the penguins immediately ran into the water and started swimming. We returned to the colony after the releases and awaited the return of the birds.

Data analyses

Data were analysed using IGOR Pro (WaveMetrics, Inc., Lake Oswego, OR, USA) with the software Ethographer (Sakamoto *et al.* 2009). All positional fixes were plotted on a contour map using the Universal Transverse Mercator (UTM) coordinate system. The contour map was downloaded from the website of the Geospatial Information Authority of Japan (http://antarctic.gsi.go.jp/download_01_25000.html). The homing phase was considered to have started when the penguins stopped diving in the release bay and began walking towards the colony (Figure S1, S2).

The total duration of walking, resting and diving after the onset of homing was estimated using the lateral acceleration and depth data. First, the duration spent underwater was calculated based on depth values. Second, continuous wavelet transformation was applied to time series data of lateral acceleration recorded during the period spent on land, which provided a behavioural spectrum (Sakamoto *et al.* 2009). Based on the k-means algorithm, the spectrum for each second were clustered into three categories (Figure 2A; Sakamoto *et al.* 2009). According to the characteristics of the generated clusters, two of the three categories appeared to correspond with walking and resting (Yoda *et al.* 2001, Watanabe *et al.* 2012), while the third could not be interpreted as any specific behaviour (possibly body shaking to remove water; Figure 2). Finally, the time allocated to each behaviour (cluster) was calculated.

Familiarity of penguins with release area

To evaluate how familiar Adélie Penguins breeding at this colony are with the release bay area, tracking data for foraging trips were examined. The data were obtained from 48 birds between 28 December 2017 and 15 January 2018, i.e. the guard stage, using three types of data loggers (17-g Axy-Trek, TechnoSmart, Italy, c. 37-g CatLog2, Mr. Lee, USA, and 57-g GPL-D3GT, Little Leonardo, Japan). Each logger recorded GPS positions every second, every minute or every 5 min. We visually checked if the penguins passed the release bay and whether it was by the same route as the released birds.

Results and discussion

The two penguins, Bird 1 and Bird 2, were found and recaptured at their nest, respectively, 8.1 and 16.6 h after being released. Their mates continued to guard the chick at the nest until the experimental birds returned. The recovered data loggers had recorded all parameters. There were some gaps in the positional data, however, probably due to interruptions of the satellite signals by large rocks and water during dives (Figure S1, S2).

According to the positional fixes, the birds arrived at the colony, respectively, 8.1 and 6.0 h after the release. They spent several hours within the release bay, before beginning to move towards the colony. During this pre-homing period, the penguins dived intensively (43.7% and 64.7% of the total pre-homing duration, respectively) and landed on two or three different locations between dives (Figure S1, S2). It is unclear why the birds did not start homing soon after being released or what the purpose of diving and landing was. They might have been lost and searching for homing routes, resting for recovery and/or foraging underwater. After the onset of homing, it took 41 and 44 min for Bird 1 and Bird 2, respectively, to reach the colony.

Time series acceleration data showed that the largest proportion of time during homing was spent walking for both individuals (51.2% and 66.2%, respectively; Figure 2B). Whilst walking on land, the dominant stride frequency was 1.6 Hz for both individuals (Figure 2A). This value is similar to that reported for Adélie Penguins walking on sea ice (1.7 Hz; Yoda *et al.* 2001); therefore, the released birds were considered to have been walking in the usual manner. The birds stopped walking more often in the later part of homing, before diving into the sea (Figure 2B). These stops might have been to rest or for collecting information to find a route home.

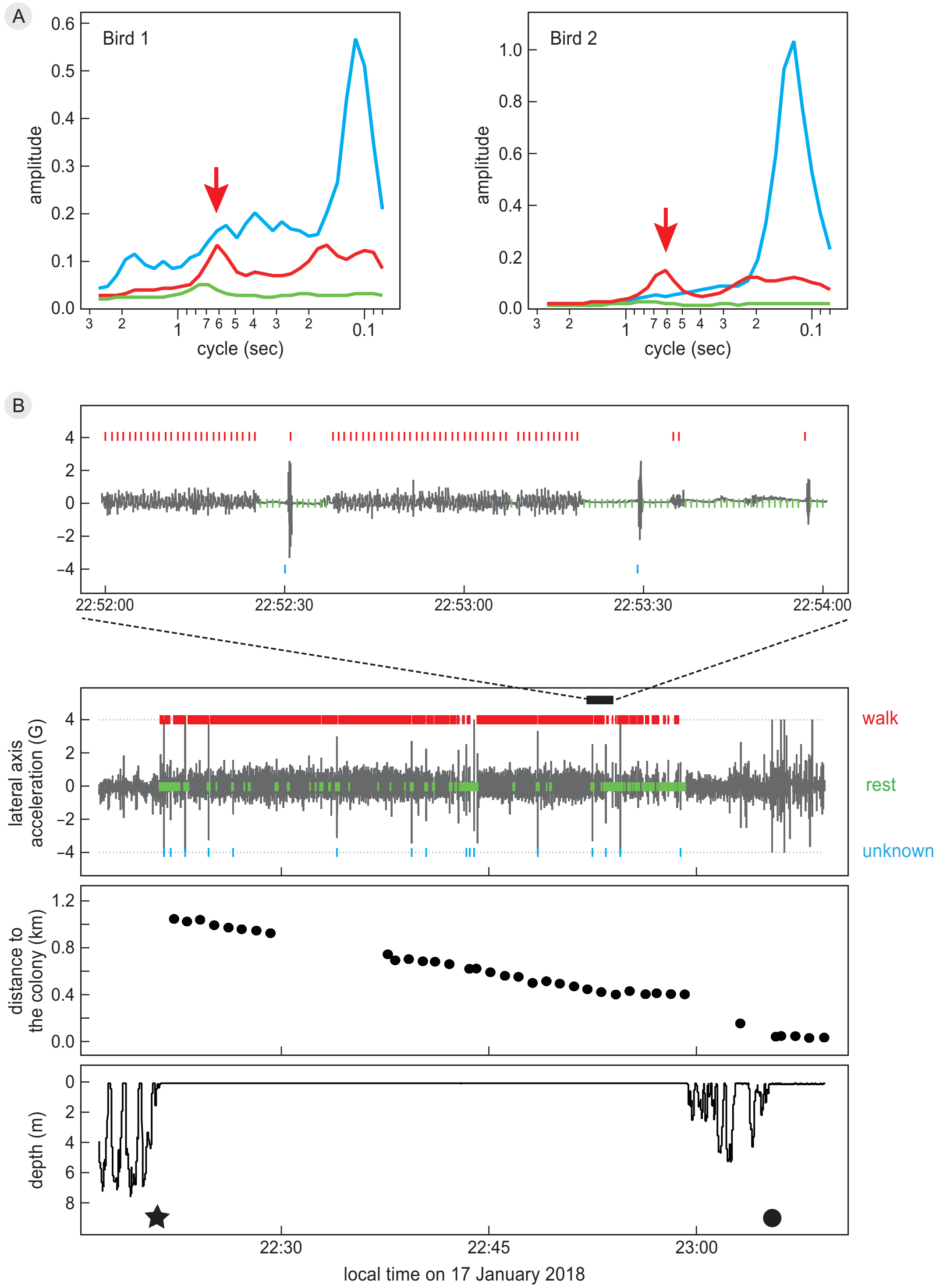

Figure 2. (A) Ethograms obtained from the lateral axis acceleration data during homing of the two Adélie Penguins. Each category was interpreted as walk (red), rest (green) and unknown (blue). Arrows indicate the peak of cycle duration (0.614 s) to calculate stride frequency of walking. (B) Time series data of lateral axis acceleration, distance to the colony and depth during homing of Bird 2. Coloured vertical bars show behavioural modes estimated based on the behavioural spectra for each second. A filled star and circle on the time axis indicate the start and end of the homing phase, respectively.

During homewards travel, rather than walking along the coastline or swimming, both individuals took an overland course. Even though there are conflicting reports of walking speeds for Adélie Penguins (Taylor 1962), walking speeds reported for a level snow field (0.53 m/s, Wilson *et al.* 1991) are about 0.25 times slower than those for swimming (2.1 m/s; Sato *et al.* 2010). The cost of travelling per unit distance is about 4.6 times greater for walking than swimming in Adélie Penguins (1.1 ml O_2/kg/m for walking at 0.83 m/s, Pinshow *et al.* 1977; 0.24 ml O_2/kg/m for swimming at 2.2 m/s, Culik *et al.* 1994). Assuming that the proportion of time spent resting does not change between locomotion modes, at-sea routes would be a better option in terms of travel time when the swimming route is shorter than 4.0 times the route on land. Additionally, in terms of energetic cost, swimming would be beneficial when the travel distance is shorter than 4.6 times that of the overland route. If our birds travelled exclusively by swimming, the travel distance to the colony would be at least about 6.5 km (Figure 1). Therefore, only walking or a combination of walking and swimming appeared to be efficient.

The path taken by the penguins from the release bay was roughly the same as that we used to displace them. The route was rocky but relatively flat without steep slopes, which would be the least resistant path towards the colony (Figure 1B, C). After walking almost in a straight path over land, both penguins dived into the sea from the same location (Figure 1B). Following some shallow dives (<6 m; Figure 2B), the birds reached the colony. This movement pattern contrasted somewhat with the path that we took during displacement of the penguins; we were forced onto a circuitous route to avoid steep slopes instead of the at-sea route (Figure 1A). Thus, the birds used the shortest option to get back to their nests.

The movement paths of 48 other Adélie Penguins breeding at the Hukuro Cove colony indicated that the release bay and the overland route to the colony were not usually used during foraging trips in that year (Figure S3). Although we cannot conclude that the displaced birds had never been to the area and used the route before based only on these data, the release bay seemed to be an irregular location, at least for that season. For homing from an unfamiliar location after artificial displacement, the penguins might have relied on various local environmental cues, including visual as well as olfactory and auditory cues. Choto Mountain and the pyramid-shaped mountain north of the colony (Figure 1), for example, might serve as landmarks for penguins. We also cannot exclude the possibility that penguins gathered useful information for homing during the actual displacement, especially considering that both birds returned largely via the same route that we used to displace them.

Our experiment shows the ability of Adélie Penguins to achieve accurate homing following release at a distant location beyond a hill. In addition, the results demonstrate the potential use of tracking devices with an accelerometer and depth sensor for navigation studies of penguins. We used only two birds in this study, but such small-scale trials are also necessary to see how displaced birds and the mate birds respond to experimental procedures. To further understand route selection and the mechanisms of homing in penguins, long-distance displacements combined with biologging, experiments under various geographic/weather conditions and sensory manipulations should be helpful. In parallel, detailed analyses of regular homing movement patterns during foraging trips and evaluation of individual familiarity with areas around the colony are also essential.

Acknowledgments

This study was financially supported by JSPS KAKENHI Grant Numbers 16H06541, 16K16185 and 17H05983 and the Japanese Antarctic Research Expedition (AP0922, JARE59). We are grateful to members of JARE 58, JARE 59 and NIPR Antarctic centre for their logistic support, to Carlo Catoni (TechnoSmart) for his support with data loggers and to two anonymous reviewers and the editor for their constructive comments. All procedures in our experiments were approved by the Ministry of the Environment, Japan, and Animal Care and Use Committee, National Institute of Polar Research.

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Samenvatting

De Adéliepinguïn *Pygoscelis adeliae* komt uitsluitend in Antarctica voor. De vogels pendelen hier heen en weer tussen het land (waar ze broeden) en de zee (waar ze foerageren). Ze worden daarbij geconfronteerd met verschillende microhabitats (onderwater, zeeijs, land), wat een uitzonderlijke situatie bij dieren is. In dit artikel beschrijven we de resultaten van verplaatsingsexperimenten met twee Adéliepinguïns. Beide vogels werden bij hun nest met jongen gevangen en voorzien van een datalogger met GPS en versnellingsmeters op hun rug. De vogels werden op ongeveer één km van de broedkolonie vrijgelaten. Vanaf het punt van loslaten waren er twee opties om terug te keren naar het nest, namelijk door over land te lopen of via zee te zwemmen. De vogels keerden 6,0 uur respectievelijk 8,1 uur na vrijlating met succes terug naar de kolonie. Ze deden er 44 respectievelijk 41 minuten over vanaf het moment dat zij aan de terugtocht waren begonnen. Beide vogels volgden de rechtstreekse, kortste weg over land. Ze brachten 51,2% respectievelijk 66,2% door met lopen en gingen pas in het laatste stuk naar het nest het water in; beide vogels deden dit op dezelfde plaats. Ons experiment demonstreert het navigatievermogen van de Adéliepinguïn en laat zien dat door gebruik van positie- en versnellingsgegevens de verplaatsingen van pinguïns die zich zowel over land als over zee voortbewegen goed te volgen zijn.

Corresponding editor: Wouter Vansteelant
Received 4 March 2019; accepted 4 November 2019

Supplementary Material is available online
www.ardeajournal.nl/supplement/s107–333–339