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Speed consensus and behavioural coordination of Adélie penguins travelling on sea ice in groups

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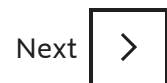
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Highlights

- The process of behavioural coordination affects the cost of collective behaviour.
- We used biologgers to study the collective behaviour of travelling Adélie penguins.
- Penguins maintained their group cohesion by regulating their speed with each other.
- Movement speed was adjusted by coordinating rest timings and locomotion mode.

Group-living animals must coordinate their behaviour to maintain group cohesion. Therefore, documenting when and how wild animals coordinate their behaviour in groups is important for inferring the cost of collective behaviour. However, previous field studies focused on certain species exhibiting strong social relationships, and limited information is available on species that form fluid groups, which may show different behavioural coordination. Here, using biologging, we examined the stability and mechanism of group cohesion in Adélie penguins, *Pygoscelis adeliae*, travelling on sea ice. GPS tracking showed that two or three birds in each of three groups departed the colony at the same time, travelled together for several hours and reached the ice edge simultaneously. In all groups, penguins achieved a consensus on travelling speed, maintaining group cohesion until reaching the ice edge. We collected records of three-axis acceleration for a group of three birds, which allowed us to classify their behaviours (resting, walking or tobogganing) and examine behavioural coordination among the group members in detail. Two possible mechanisms of synchronous travelling were speculated. First, the group members match their timing of resting, suggesting that the onset of resting of an individual is followed by that of the others. Second, locomotion modes (walking/tobogganing) and locomotion speed in each mode while travelling in groups differ between individuals. To maintain group cohesion, penguins may adjust either the speed in each locomotion mode or the proportional use of the locomotion mode to match the overall travelling speed. Additionally, the tracked penguins alternated their relative spatial positions and the order of synchronous resting initiation, suggesting mutual social influences. Overall, Adélie penguins actively maintain group cohesion with occasional members by mutually coordinating their behaviours while travelling in groups on sea ice.



Keywords

behavioural classification; behavioural coordination; biologging; collective behaviour; locomotion behaviour; penguin; social interaction

Living in a group offers a variety of benefits, including reduced predation risk, increased foraging efficiency and decreased energetic costs of movement (reviewed in [Krause & Ruxton, 2002](#)). However, individuals must reach a consensus on their behaviour to maintain group cohesion. In a travelling group, individuals must coordinate the direction

(where), timing (when) and speed (how fast) of movement ([Conradt & Roper, 2009](#); [Couzin et al., 2005](#); [Sankey et al., 2019](#)), and such behavioural coordination can be costly ([Conradt & Roper, 2005](#); [Sankey et al., 2019](#)) because individual preferences or interests may differ between group members during decision making ([Biro et al., 2006](#); [King et al., 2008](#)). For instance, pigeons, *Columba livia*, flying in groups must match their flight speed, requiring some individuals to fly at a suboptimal speed, which differs from their preferred solo speed and incurs additional energy costs ([Sankey et al., 2019](#)). Therefore, to infer the cost of collective behaviour, understanding how each of the group-living animals with different characteristics coordinates its behaviour in a group is important ([Herbert-Read, 2016](#)).

Recent advances in biologging or image tracking have allowed researchers to record the movements of individuals and infer the processes of collective decision making in moving groups ([Hughey et al., 2018](#)). For instance, [Strandburg-Peshkin et al. \(2015\)](#) tracked the movement of a group of olive baboons, *Papio anubis*, and tested how individuals reached a consensus on movement direction. According to the authors, baboons made decisions on movement direction democratically rather than following the leadership of a particular individual. Similar studies on other species have shown that animals living in groups adjust their movements in response to the movements and positions of the other individuals in the group (reviewed in [Herbert-Read, 2016](#)). However, previous empirical studies have mainly focused on species that form relatively stable social groups, such as primates ([Farine et al., 2017](#); [King et al., 2008](#)) and hand-reared birds ([Pettit et al., 2013](#); [Portugal et al., 2014](#); [Sankey et al., 2019](#)). Although group living is a phenomenon found in a range of animal taxa ([Krause & Ruxton, 2002](#)), limited information is available on species that form fluid groups with unstable social relationships in the wild (but see [Daniel et al., 2007](#); [Fischhoff et al., 2007](#); [Jones et al., 2020](#)).

Seabirds are a suitable target for studies of collective behaviour because over 95% of seabird species breed colonially ([Schreiber & Burger, 2002](#)) and potentially have access to rich social information ([Evans et al., 2016](#)). However, a limited number of biologging studies have examined the group behaviour of seabirds during travelling and foraging ([Cook et al., 2017](#); [Thiebault et al., 2014, 2016](#)). This is because seabirds tend to form large colonies with many individuals, and it is often difficult to deploy enough biologging devices to record interactions among individuals. A previous study ([Jones et al., 2020](#)) revealed spatiotemporal dynamics in the social associations of Australasian gannets, *Morus serrator*, based on extensive GPS tracking; however, little is known regarding behavioural coordination among group members.

In the present study, we investigated the collective movements of Adélie penguins, *Pygoscelis adeliae*, walking in groups, by using a combination of GPS and acceleration data. We conducted our fieldwork at a breeding colony of Adélie penguins on Mamejima Island in East Antarctica from early to late December. During this period, individuals in pairs alternate between foraging trips and incubation. Penguins dive from the ice edge and forage in open water areas (i.e. cracks and polynyas) to feed on krill and fish. In this region, the fast sea ice expands around the colony, often reaching several tens of kilometres. Therefore, penguins need to travel on sea ice for several hours (Cottin et al., 2012), and such foraging trips last several days (Watanuki, 1993).

During a study on the foraging behaviour of incubating penguins, we fortuitously obtained GPS records of penguin groups that walked together over sea ice from the colony to the ice edge. This offered us the opportunity to examine how penguins achieve consensus on travelling speed by coordinating their behaviour. Penguins breed in colonies and frequently interact with individuals surrounding their nests (Penney, 1968; Williams, 1995). In addition, penguins exhibit collective behaviour at sea, such as diving and foraging together (Hinke et al., 2021; Pütz & Cherel, 2005; Sutton et al., 2015; Takahashi et al., 2004; Tremblay & Cherel, 1999). However, the dynamics of group members and their behavioural coordination remain unknown, particularly during travel between the colony and the foraging site (Daniel et al., 2007; Hinke et al., 2021). Adélie penguins are often observed to form groups consisting of one to tens of individual(s) when they leave the colony for foraging. However, it remains unclear whether and how penguins maintain these groups for extended periods until reaching the ice edge.

To this end, we examined the stability and behavioural mechanism of group cohesion in Adélie penguins travelling on sea ice, by using a combination of GPS tracking and behavioural monitoring with accelerometers. Specifically, we examined (1) whether the birds maintain the group formed on departure until they reach the ice edge, (2) which behavioural coordination allows these birds to maintain group cohesion, and (3) how the birds are spatially located in the group and how they influence each other's behaviour.

Methods

Data Collection

We conducted fieldwork in a breeding colony of Adélie penguins on Mamejima Island (69°2'S, 39°28'E) in Lützow-Holm Bay, Antarctica, in December 2017. In that year, 157 pairs of penguins were observed breeding in this colony as of 1 December, and the nests were

spread out within a radius of 100m. To avoid disturbing the breeding of the penguins, we had to choose cases where both individuals of a pair were present in the colony. Therefore, immediately after they had switched incubation with the partner returning from the foraging trip, we caught 17 male penguins with a hand net and equipped them with one or two types of data loggers on 5–7 December. Five birds were equipped with Axy-Trek (TechnoSmArt, Rome, Italy; 48×24×13 mm, weight 23 g, with a 450 mAh battery), which was set to record the GPS position every 5 min, three-axis acceleration at 25 Hz, and depth and temperature at 1 Hz. We equipped 12 other birds with CatLog2 (Catnip Technologies, Hong Kong; 55×32×15 mm, weight 26 g, with an 800 mAh battery), which recorded the GPS position every 5 min. In addition, we equipped three of the 12 birds with Axy-Depth (TechnoSmArt, Italy; 35×14×13 mm, weight 7 g), which recorded three-axis acceleration at 10 Hz and depth and temperature at 1 Hz, and equipped four of the 12 birds with BLS DT (Biologging Solutions, Tokyo, Japan; 30×11×11 mm, weight 6 g), which recorded depth and temperature at 1 Hz, respectively. The loggers were attached to the lower back using Tesa tape, mastic tape and instant glue to secure the ends of the tape and plastic cable ties (Wilson *et al.*, 1997). The total weight of the loggers was 23–33 g, accounting for <1% of the body weight of each bird. The average (\pm SD) handling time was 14.0 \pm 2.8 min per bird, ranging from 11 to 20 min. The nests of the tracked birds were distributed throughout the colony.

Processing of Location Data

We processed GPS tracks using the ‘foieGras’ package (Jonsen *et al.*, 2020) in R version 4.2.0 (R Core Team, 2022) to estimate the most likely locations at the recorded times taking measurement error into account. We fitted a correlated random walk model and ignored data points with a 5.0 m/s speed filter because Adélie penguins swim at 2.0 m/s (Sato *et al.*, 2010) and walk at a slower speed (Wilson *et al.*, 1991). Since the time when GPS position was recorded differed slightly between the loggers on study birds, we derived the predicted locations of each individual every 5 min and used them to calculate distances between individuals and compare travelling speeds at the same time. We defined the ‘transit’ phase as the period after the penguins moved further than 150 m from the nest and just before they began diving. We considered penguins to be diving when the depth data were available and the depth exceeded 0.5 m or estimated them to be at sea based on locations overlaid on satellite imagery (Terra, MODIS, True Color, Corrected Reflectance, NASA Worldview Snapshots, <https://wvs.earthdata.nasa.gov>; image recorded on 6 December 2017) when the depth data were unavailable. We defined travelling groups so that all tracked birds that had started a ‘transit’ within 5 min belonged to the same group. Therefore, since we did not track all the birds in the breeding colony, the groups of tracked

birds may have travelled together with other birds that were not tracked. The GPS tracks were projected onto satellite imagery using the Quantarctica package ([Matsuoka et al., 2018](#)) in QGIS version 3.26 ([QGIS Development Team, 2022](#)). Moreover, to discuss the potential benefit of group formation, we calculated the straightness of the tracks by dividing the straight-line distance between the start and end points of the transit by the total travelling distance.

Behavioural Classification Based on Acceleration

We obtained acceleration records from three birds moving in a group during transit (see Results) and analysed these records using Ethographer ([Sakamoto et al., 2009](#)) in Igor Pro version 8.0 (WaveMetrics, Inc., Lake Oswego, OR, U.S.A.). The behaviour of penguins during transit to the ice edge was distinguished as resting, walking or tobogganing (moving on their bellies using their feet and flippers for propulsion; [Williams, 1995](#); [Yoda et al., 2001](#)). We classified penguin behaviour at every second into these three categories based on acceleration data analysis in the following two steps. First, the swaying acceleration was analysed to determine resting or moving (by either walking or tobogganing) based on the calculation of a behavioural spectrum with continuous wavelet transformation. The behavioural spectrum was clustered into four categories based on the k-means algorithm ([Sakamoto et al., 2009](#)). One cluster with no fluctuations in swaying acceleration was considered resting, and three other clusters with fluctuations in swaying acceleration were considered moving. Next, we calculated the pitch angle from the surging acceleration to identify whether the penguins were walking or tobogganing. Loggers measure both dynamic and gravitational acceleration ([Yoda et al., 2001](#)). High-frequency components are related to animal movement; therefore, to eliminate these, we used a filter (two-band low-pass filter) for surging acceleration ([Sato et al., 2003](#)). The end of the first filter and the start of the second were set as 0.1 and 0.5 Hz, respectively ([Watanuki et al., 2005](#); [Yoda & Ropert-Coudert, 2007](#)). The filtered surging acceleration was converted into the pitch angle of the birds ([Sato et al., 2003](#)). A pitch angle of 30° or greater during movement was used as the criterion for walking (otherwise tobogganing). After classification, we obtained the dominant cycle of the change in sway acceleration every second based on the peak tracer function in Ethographer to estimate stride cycles during walking and tobogganing.

Estimation of Locomotion Speed During Walking and Tobogganing

GPS positions were collected every 5 min, during which the penguins moved by both walking and tobogganing (see Results). Therefore, it was impossible to measure walking

speed and tobogganing speed directly. Instead, to estimate locomotion speeds in each mode, we performed generalized least square (GLS) analysis on the relationship between locomotion speed and the percentage of time spent tobogganing/walking while taking the temporal correlations into account as follows.

We first calculated 'speed during locomotion' by dividing the horizontal distance between two consecutive GPS positions by the time spent in locomotion behaviour (i.e. time classified as moving based on swaying acceleration). We then calculated the 'percentage of tobogganing in locomotion' as the percentage of time spent on tobogganing in the total time spent in locomotion behaviour for each GPS interval.

In GLS analysis, we constructed the model as follows: 'speed during locomotion' was used as our response variable, which was modelled as a function of 'percentage of tobogganing in locomotion', individual ID, and an interaction term between them. Accounting for potential autocorrelation in our data, we employed an ARMA (autoregressive moving average) correlation structure with both autoregressive and moving average orders of 1 nested within the identity of individuals. The fitting method we used was maximum likelihood ('ML'), which estimates the parameters in our model that make our observed data the most probable. Using the fitted regression equation, we can estimate each individual's walking (or tobogganing) speed by assigning 0 (or 100) to the 'percentage of tobogganing in locomotion'. We conducted this analysis with the 'nlme' package ([Pinheiro et al., 2023](#)) in R.

Analysis of Resting Synchrony

We assessed whether the group members rested or moved together more often than expected by chance, by calculating the proportion of time when a pair of individuals was resting or moving simultaneously in the total transit time based on behavioural classification at every second. We defined this proportion as the index of concurrence and used it as an indicator of whether the resting/moving states of two individuals were synchronized (see [Gautrais et al., 2007](#)). To assess this value, we estimated the expected range (95% confidence interval) of the index of concurrence, assuming that each individual independently switched between the resting and moving states using Monte Carlo simulations (for details see the [Appendix](#)). We compared the index of concurrence from the actual data with the confidence interval of simulated values to determine whether the individuals' timing of resting/moving matched more than expected by chance. We examined the validity of this method by calculating and simulating the index of concurrence of individuals in different groups.

Inference of Group Structure and Social Influence

Based on predicted locations every 5 min, we calculated two indicators of group structure: polarization order parameter and bearing angles. The polarization order parameter indicates whether the direction of movement is consistent among the group and takes a range from 0 (no alignment) to 1 (all individuals are aligned) ([Tunstrøm et al., 2013](#)). The bearing angle is the angle between the vector of moving direction and the vector from the focal individual to another individual at each time ([Götze et al., 2020](#)), which is an indicator of the position of the focal individual in the group relative to the travelling direction.

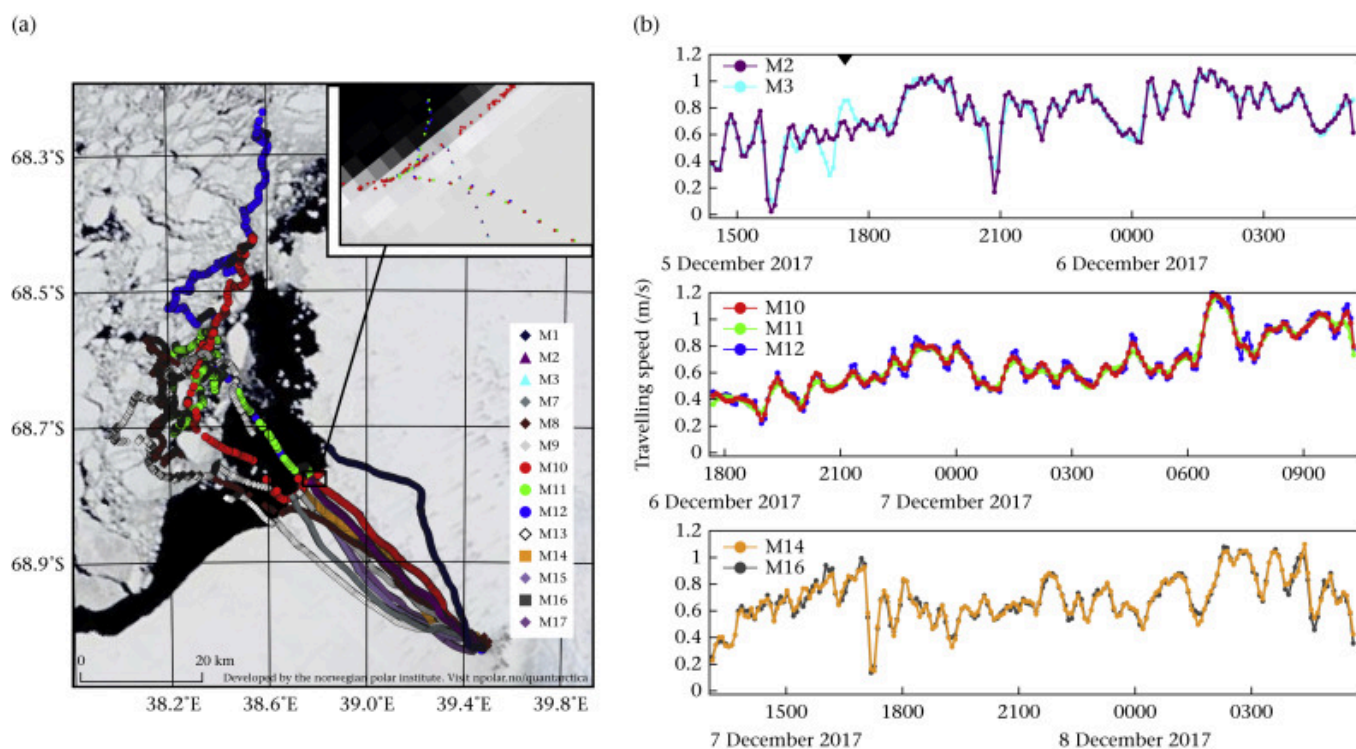
We then examined the social influence among the tracked individuals travelling in groups using two approaches. First, we examined the spatial positions of individuals in the groups ([Strandburg-Peshkin et al., 2018](#)). We identified the individual walking at the frontmost position among tracked birds every 5 min to estimate forward and backward positions relative to the travelling direction. The travelling direction was estimated based on a vector whose starting point was the original position, and endpoint was the position after 5 min. The travelling direction for each group was determined by averaging the travelling direction of each tracked individual. Second, we examined the order of synchronous resting initiation among tracked birds ([Strandburg-Peshkin et al., 2018](#)). From the order of initiation of synchronous behaviour, we can infer the direction of social interaction ([Krause & Ruxton, 2002](#); [Nagy et al., 2010](#); [Petit & Bon, 2010](#)). In the present study, by examining synchronous resting events, we can determine the direction of the social influence regarding the resting behaviour for each event. We here defined a resting bout as a cluster of rest periods interrupted by a short moving period below the 'bout-ending criterion'. For each synchronous resting event, we compared the start time of the resting bout among individuals and ranked the time when the resting bout was initiated. We performed curve fitting in Igor Pro and derived the bout-ending criterion, assuming that the length of the moving period is generated by two Poisson processes ([Sibly et al., 1990](#)). In the present study, the bout-ending criterion was 4.26s (for details see the [Appendix](#)).

Ethical Note

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 (Permit No. NIPR-ACUC-H29-1). We adhered to the ASAB/ABS Guidelines for the Use of Animals in Research. All penguins were placed in a bag during logger attachments/retrievals to reduce stress and handled for less than 20 min. Loggers were mounted on the lower back to reduce drag in the water. After attaching loggers, we visited the colony intermittently to retrieve them because of logistical constraints but failed to retrieve three loggers. We did not observe breeding failure in any nests of tracked birds.

Results

We recovered loggers from 14 of the 17 equipped birds 12–22 days after deployment ([Table A1](#)). Tracking data were collected from all 14 birds, depth and temperature data from nine birds and acceleration data from eight birds. All records ended in the middle of the foraging trip but covered the entire transit to the ice edge. The birds travelled 41.1 ± 1.8 km over 16.9 ± 2.8 h, with high straightness of tracks (mean \pm SD = 0.96 ± 0.02) on sea ice that was newly formed in the preceding winter ([Table A2](#), [Fig. 1a](#)). The birds departed together in three groups: one group included M2 and M3, another group included M14 and M16 and another group included M10, M11 and M12. In all cases, birds reached the ice edge simultaneously. The birds moved continuously close to one another; specifically, the average distance between tracked individuals (mean \pm SD) of the three groups was 27.0 ± 36.0 , 39.6 ± 23.1 and 20.0 ± 15.4 m, respectively, based on GPS locations. During transit, the travelling speed fluctuated, although the fluctuations were consistent among the group ([Figs. 1b](#) and [A1](#)). The GPS tracks of the two tracked pairs (M2 and M3, M14 and M16) ended at the ice edge ([Fig. 1a](#)). The tracks of the third group of three birds (M10, M11 and M12) continued from the ice edge to the open water. Two birds, M11 and M12, swam along the same path for approximately 29 km and dived synchronously over 15 h ([Figs. 1a](#) and [A2](#)), but M10 separated from them near the ice edge ([Fig. 1a](#)). The distance between M2 and M3 had temporarily increased but declined as the delayed individual (M3) increased its travelling speed (a ‘catch-up’ event; [Figs. 1b](#) and [A3](#)).

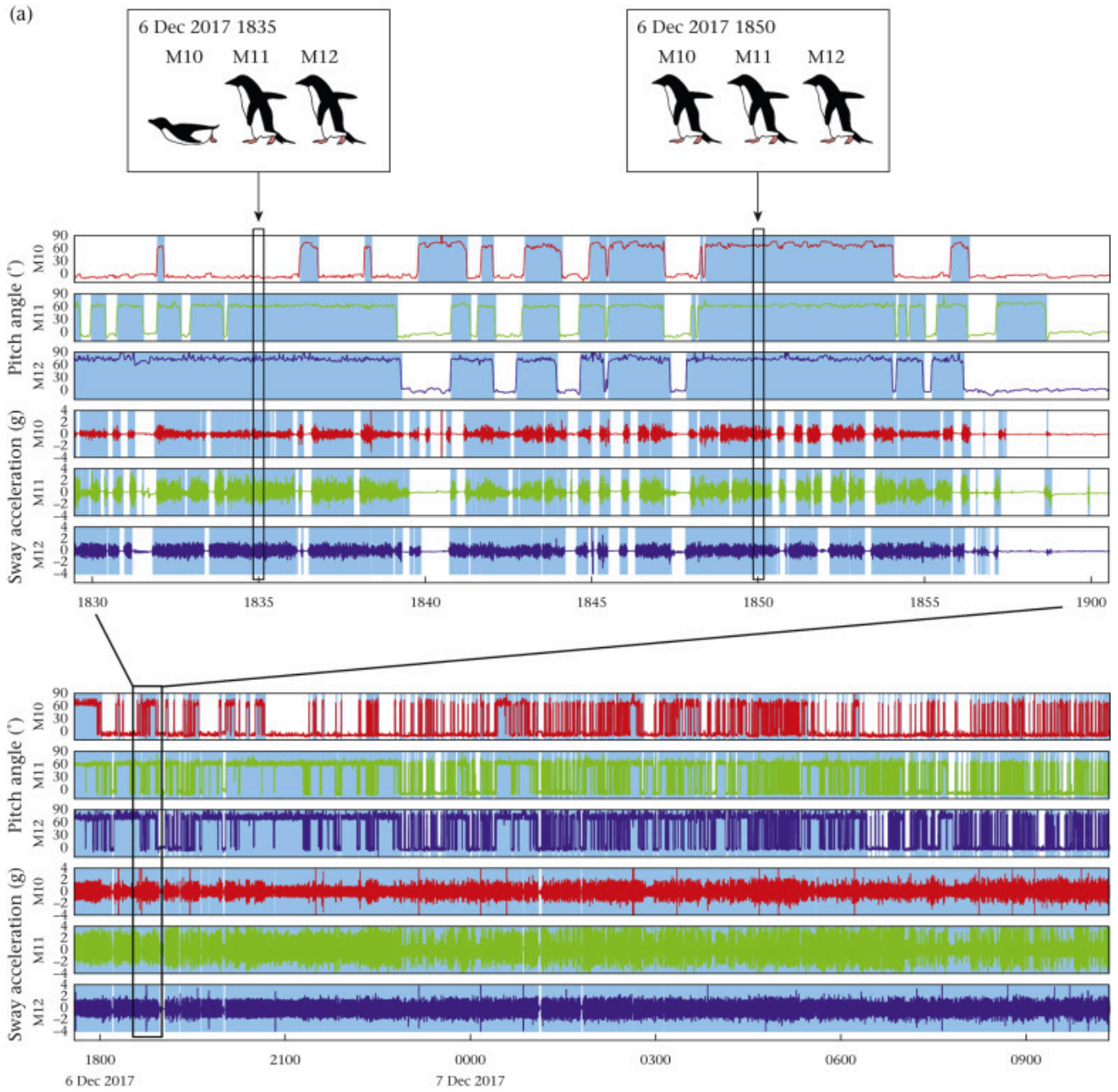


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Figure 1. Results of GPS tracking. (a) GPS tracks of penguins on foraging trips. The background satellite imagery was obtained on 6 December 2017. (b) Changes in the speed of individuals travelling together during transit. The estimation of speed is based on the predicted locations of individuals at the same time every 5 min. The inverted triangle for M3 indicates a 'catch-up' event (see text).

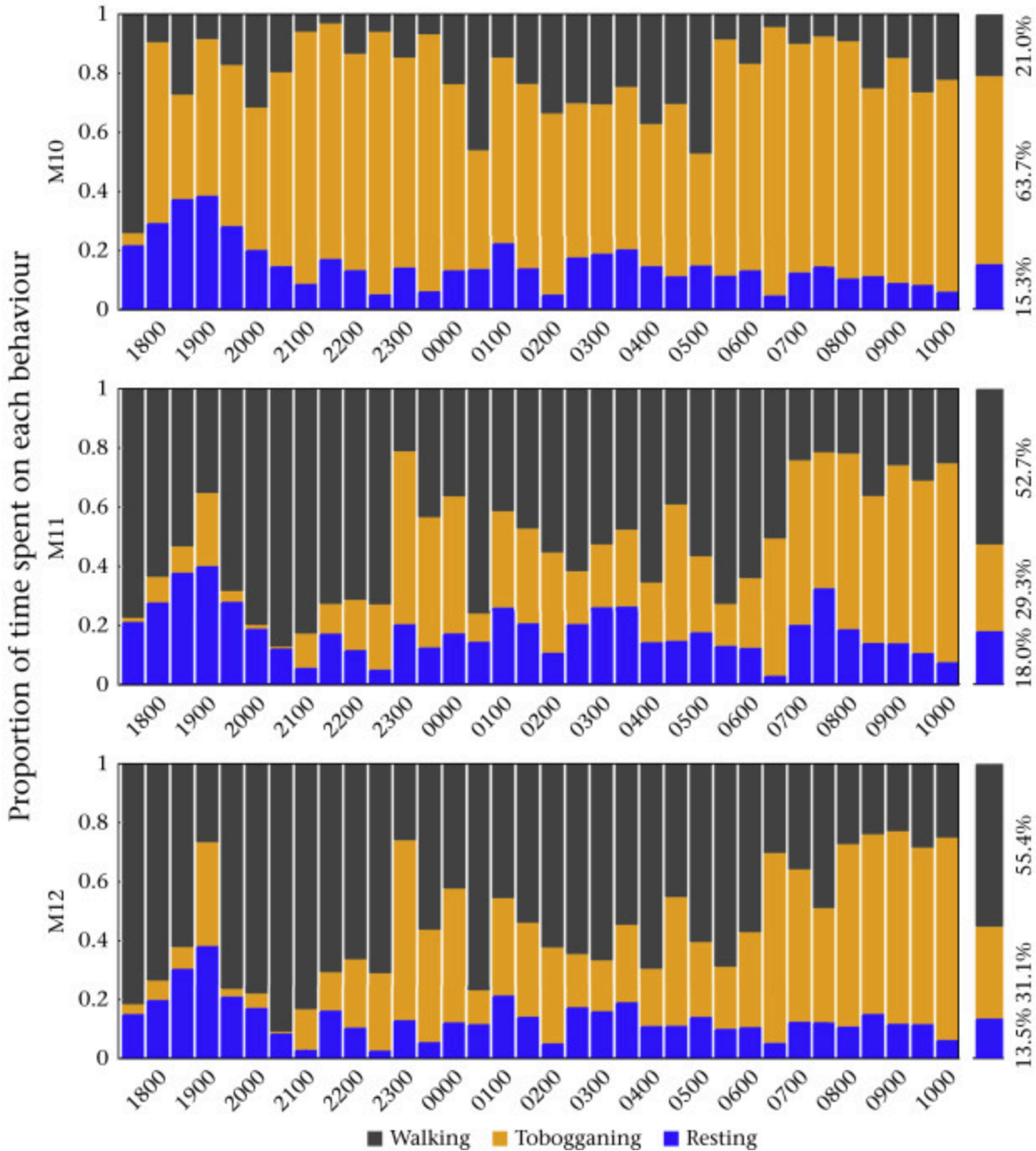
We successfully collected acceleration data from three birds, namely M10, M11 and M12, travelling together, which enabled behavioural classification ([Fig. 2a](#)). On average, the birds rested 15.6% of the time during transit ([Fig. 2](#)). M10 tobogganed for longer than the others throughout the transit ([Fig. 2b](#)). In the frequency distribution of the dominant cycles of change in sway acceleration during tobogganing and walking for each individual, the largest peak appeared around 0.5–0.6s ([Fig. A4](#)). This possibly corresponded to the one-stride cycle (side-by-side body movement) of penguins during tobogganing and walking (see [Yoda et al., 2001](#)).



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(b)



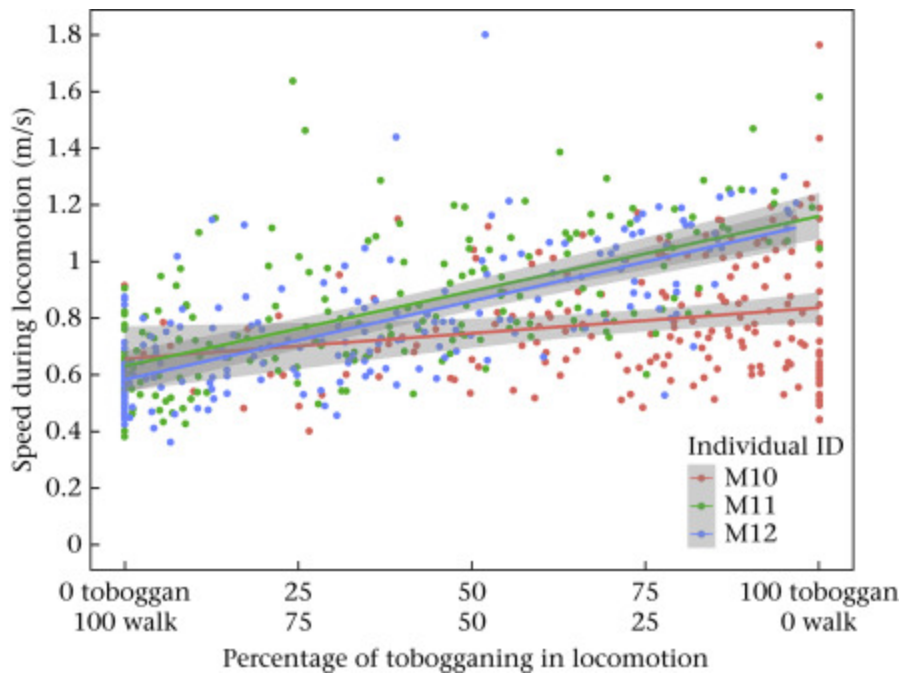
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Figure 2. (a) Pitch angle and sway acceleration of three individuals travelling together during the transit. The blue background in the graph of pitch angle indicates the period when a penguin was estimated to be standing. The blue background in the graph of sway acceleration indicates the period when a penguin was estimated to be moving. Illustrations show the estimated behaviour (tobogganing or walking) of each bird at each time point. (b) Time series changes in the proportion of time spent in each behaviour over 30min. The

horizontal axis indicates the start time of the corresponding column. The rightmost column shows the proportion of time spent on each behaviour during the transit as a whole.

Speed during locomotion increased with tobogganing time for all individuals (Fig. 3). GLS analysis showed that the slopes of the regression lines for M11 and M12 were significantly larger than that for M10 ($P=0.005$ and 0.0001 , respectively; Table A3), which means that the tobogganing speeds of these two individuals were greater than that of M10. The estimated walking and tobogganing speeds based on the regression lines for each individual were 0.75 and 0.81 m/s, 0.71 and 0.90 m/s, and 0.66 and 0.92 m/s, respectively. Using the time and estimated locomotion speed, we calculated the percentage of distance travelled by tobogganing; M10, M11 and M12 travelled by tobogganing for 77%, 41% and 44% of the entire distance of transit (M10=31.1 of 40.6 km; M11=15.9 of 38.5 km; M12=17.3 of 39.5 km), respectively.

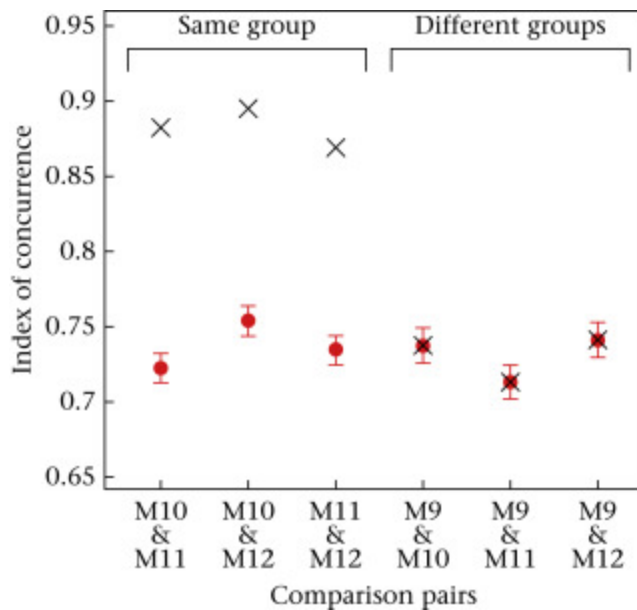


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Figure 3. Relationship between the locomotion mode and the speed during locomotion. Each point corresponds to a penguin's movement every 5 min. The lines represent linear regressions for each individual, and the shaded areas indicate the 99% confidence intervals.

The index of concurrence from the real data set exceeded the upper 95% confidence interval limit of the simulated values for the pairs of birds travelling in the same group (Fig. 4). In contrast, in the pairs of birds in different travelling groups, the index of concurrence from the real data set fell within the 95% confidence intervals predicted by simulations (Fig. 4).

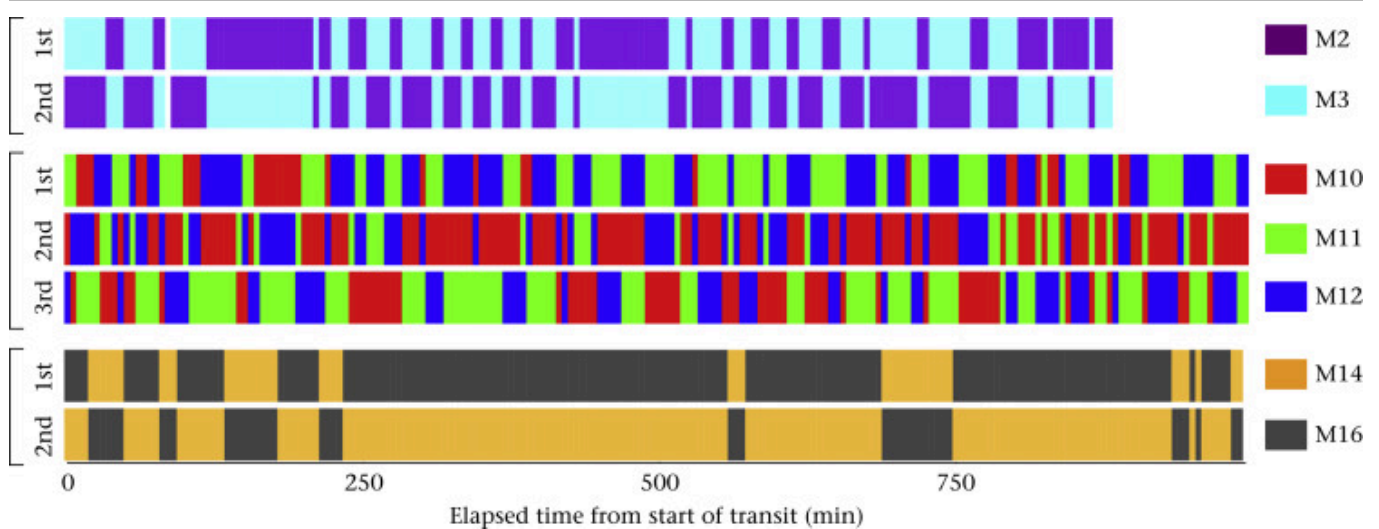


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Figure 4. Resting synchrony between pairs from the same and different travelling group(s). The cross mark indicates each pair's index of concurrence from the real data set. The red circle and bar indicate the mean value and 95% confidence interval of the index of concurrence estimated from Monte Carlo simulations, assuming that individuals in each pair change states (moving/resting) independently (i.e. no coordination).

In all three groups, the polarization order parameter was always high, except for the 'catch-up event' in the group of M2 and M3 (Fig. A5). Each individual took turns at the front position during transit (Fig. 5), and bearing angles in the group of M10, M11 and M12 fluctuated greatly (Fig. A6). In one group (M10, M11 and M12), where we classified the behaviour based on acceleration data, one bird (M12) often initiated the resting bout first when a synchronous resting event occurred (52%; Fig. A7). Nevertheless, all birds took turns initiating the resting bouts.



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Figure 5. Changes in the relative position of the recording individual among the group. Brackets include individuals in the same group.

Discussion

Our observations indicated that Adélie penguins that departed from the colony at the same time maintained group cohesion by constantly reaching a consensus on travelling speed during transit to the ice edge. Below, we discuss the possible behavioural mechanisms of this adjustment of travelling speed as well as the group structure in the three groups examined. We speculate that in groups of Adélie penguins, speed consensus is achieved by fine-scale coordination of resting and locomotion behaviours, and the group structure is not stable. Finally, we discuss the costs and benefits of behavioural coordination to maintain group cohesion while travelling to foraging sites.

In all three groups, each individual moved at a closely regulated travelling speed and maintained a small interindividual distance. Although the travelling speed fluctuated temporally for each individual during transit, the temporal patterns of fluctuation matched among individuals. Since the penguins travelled on newly formed, flat sea ice with little undulation, the effect of topography on travelling speed is likely to be minor. Rather, we suggest that the matching of travelling speeds results from penguins' active adjustment. In addition, in one group (M2 and M3), where the distance between individuals temporarily increased and the polarization decreased, a 'catch-up event' was observed where one individual subsequently increased its movement speed. This suggests an active adjustment of travelling speed.

Penguins interact with other birds around their nests ([Williams, 1995](#)); however, in the present study, the nests of birds that formed the group were not adjacent to one another. Moreover, a male penguin's departure likely depends on the timing of its partner's return ([Watanuki, 1993](#)). Therefore, the groups tracked in the present study were probably formed by individuals that coincidentally departed for foraging at the same time. Nevertheless, we found speed consensus in all groups, suggesting that penguins can maintain group cohesion with occasional members on each trip.

Penguins likely achieved speed consensus through two types of behavioural coordination. The first is synchronous resting. In general, resting is thought to arise from the internal demands of each individual (e.g. [Watanabe et al., 2012](#)). None the less, the timing of resting and moving of the three individuals in the same group matched more often than expected by chance. Therefore, penguins coordinated their resting behaviour depending on the resting behaviour of the other penguins, such as initiating resting following the resting onset of the other individuals or immediately terminating resting when the other individuals were not resting at the same time.

The second type of behavioural coordination is the adjustment of locomotion behaviours. Penguins move fast and energetically efficiently by tobogganing under most conditions ([Wilson et al., 1991](#)); however, they may encounter difficulties over irregular surfaces. Hence, the locomotion behaviour of penguins on ice may depend on the condition of the ice surface ([Yoda & Ropert-Coudert, 2007](#)). Therefore, we expected travel time, distance, tobogganing and walking speed to be consistent among individuals in the same group. However, in the present study, even though penguins in the group travelled in close proximity and were thought to have experienced broadly similar environments, their locomotion modes often differed. Consequently, the travel time in each locomotion mode differed between individuals, with one individual (M10) tobogganing for a longer period and distance. In addition, we found that M10 tobogganed at a lower speed than the other individuals (albeit at a faster pace than the walking speed). These individual differences in locomotion behaviour can be explained by differences in preferences for the use of locomotion mode (i.e. M10 preferred tobogganing while the others preferred walking) or in the preferred speed for each locomotion mode (i.e. M10 preferred tobogganing at a slower pace than M11 and M12). Based on our first explanation, the relatively slow tobogganing speed of M10 may be due to tobogganing at walking speed when the other individuals were walking. Based on our second explanation, the relatively long tobogganing distance of M10 was likely required to catch up with the other individuals. These explanations are not mutually exclusive and difficult to distinguish based on our results. However, the following two observations suggest the importance of the second explanation. First, the stride cycle of tobogganing of

M10 was smaller than that of the other individuals (Fig.A4); therefore, M10 moved a smaller distance per stride, possibly reflecting the relatively low body weight (and perhaps small body length) of this individual (TableA1). Therefore, to increase the tobogganing speed to the same level as that of other individuals, M10 had to further increase stride frequency, which would incur additional energy expenditure. This supports the second explanation by suggesting a limit to which small individuals can increase their tobogganing speed. Second, M10 was often positioned towards the back of the tracked individuals (Fig.5) and often initiated resting later than the others (Fig.A7), based on the analysis of social influence. This suggests that M10 tobogganed longer to catch up with the group from behind, although the exact relationship between the penguin's relative position within the group and locomotion behaviour was not known, due to the long GPS positioning interval (every 5 min), compared to behavioural classification based on acceleration (every second).

The two locomotion modes, walking and tobogganing, have advantages and disadvantages; while tobogganing has greater speed and is more energy efficient on smooth ice, it results in loss of oil from ventral feathers or feather wearing and requires additional feather care (Wilson *et al.*, 1991). Hence, penguins have been thought to switch locomotion modes in response to environmental conditions. However, in this study, penguins might have switched locomotion modes to maintain group cohesion by compensating for individual differences in locomotion speed. In this case, when other individuals are tobogganing, an individual with a slower tobogganing speed is thought to lag behind the group during the period. Therefore, it would be necessary for the slower individual to travel by tobogganing, even in environments where other individuals switch to walking, and tobogganing under inappropriate conditions may entail the cost of consensus. That is, individuals with slower locomotion speeds may be required to spend more time self-maintaining to keep up with the group.

Although we cannot exclude the possibility of the presence of some other nontracked birds in each group, our results imply that penguins mutually coordinate their behaviour based on nonfixed group structure. In general, behavioural coordination among animals in a group is achieved either through a single individual or a few individuals having a significant influence on the others (unshared decision; King *et al.*, 2008; Nagy *et al.*, 2010) or through individuals coordinating their behaviour with one another (shared decision; Gall *et al.*, 2017; Strandburg-Peshkin *et al.*, 2015). We examined the social influence among individuals in the studied groups of Adélie penguins based on their spatial positions during transit and the initiation of synchronous resting. Individuals in the frontmost position generally have a more dominant effect on the movement of following individuals (Nagy *et al.*, 2010; Pettit *et al.*, 2013, 2015); therefore, our two approaches are expected to represent different

aspects of social influence. In all groups, the birds in the frontmost position among tracked animals or the first initiator of the synchronous resting varied during transit, suggesting their mutual social influences, as observed in king penguin, *Aptenodytes patagonicus*, chicks returning to their crèches under experimental conditions (Nesterova et al., 2014). In groups comprising fixed members, certain individuals, as determined by age, sex and other factors, often dominate the group choice (King et al., 2008; McComb et al., 2011). In contrast, through observation of plains zebras, *Equus quagga burchellii*, Fischhoff et al. (2007) hypothesized that specific individuals would not be able to assume dominant roles consistently if group membership changes frequently. Our results suggest that this hypothesis may also be valid for seabirds, animals of different taxa and animals with different social structures.

Penguins continuously maintained group cohesion, suggesting that they benefit from grouping during transits. Several benefits of grouping in foraging trips have been proposed: predator vigilance, efficient travelling and cooperative foraging (Daniel et al., 2007; Sutton et al., 2017; Takahashi et al., 2004). Here, we discuss their relative importance, although we are aware that our empirical results do not allow us to directly verify whether these benefits exist because our tracked birds might have travelled with other nontracked birds. First, penguins may benefit from grouping by reducing the risk of predation. This hypothesis is supported by several studies which have shown that Antarctic penguins dive synchronously when entering the sea (Ainley, 1972; Takahashi et al., 2004; Watanabe et al., 2012), while seals tend to aggregate at the ice edge, so predation risk is probably highest there and seals pose no threat during transit over sea ice (Ainley, 1972; Penney & Lowry, 1967). The observed behaviour in the present study allowed the penguins to reach the ice edge in a group; therefore, they may have benefited through predator avoidance after reaching the ice edge. However, the initiation of synchronous dives often results from gathering at the ice edge (Watanabe et al., 2012). In the present study, penguins in a group showed behavioural coordination throughout their trip to the ice edge. This implies that there are other benefits of grouping. Second, the grouping may improve navigation. Birds in a group are expected to travel on an efficient track by following knowledgeable leaders (Flack et al., 2012; Mueller et al., 2013) or by averaging their routes (the 'many wrongs' hypothesis; Biro et al., 2006; Codling et al., 2007; Simons, 2004). Our results indicate that all seven individuals that formed groups took an efficient route to the foraging site (straightness > 0.95). We studied the males' first trips when they may have relatively limited a priori knowledge of the foraging habitat which will vary with seasonal changes in sea ice conditions. In such conditions, penguins may benefit from improved navigation by grouping for efficient travelling to the ice edge. However, since we did not track all individuals in the colony, we have no evidence that individuals that used the less

efficient route (e.g. M1) were travelling alone. Therefore, information on actual group size (including both tracked and nontracked birds) is needed to test this hypothesis. Third, grouping on land may be related to cooperative foraging. Penguins dive synchronously, which is expected to increase foraging success (Sutton *et al.*, 2015). Such foraging groups have been reported to form before diving in little penguins, *Eudyptula minor* (Sutton *et al.*, 2017) and chinstrap penguins, *Pygoscelis antarcticus* (Hinke *et al.*, 2021). Our results also show that two (M11 and M12) of the three birds in a group, which formed at departure, travelled together for several hours after reaching the ice edge (Fig.A2). Since the two birds dived synchronously, these birds likely targeted the same prey and might have benefited from group foraging. Therefore, group formation and maintenance during travelling on ice may benefit individuals by increasing foraging efficiency thereafter.

Group coordination has been studied in detail in a limited number of species with strong social interactions, partly because of methodological limitations; however, interaction rules may differ between taxa, situations or individuals (Herbert-Read, 2016). Here, we have demonstrated the possibility of inferring how individuals make decisions to maintain group cohesion from fortuitous data collection and detailed analysis of biologging data in seabirds forming temporary travelling groups. In the future, as biologging devices become smaller, lighter and less expensive, researchers will be able to collect records on behavioural coordination in a wide variety of species under natural conditions. Accumulation of knowledge on collective behaviour across diverse animal species will allow us to better understand the ecological drivers of the evolution of collective behaviour.

Conclusions

Through detailed analysis of GPS tracking and acceleration data, we obtained evidence that Adélie penguins actively maintain group cohesion by achieving a consensus on travelling speed while walking on ice to distant foraging sites. The penguins maintained group cohesion by resting synchronously and adjusting their locomotion behaviours.

Author Contributions

Toshitaka Imaki: Conceptualization, Methodology, Formal analysis, Writing – Original draft.

Nobuo Kokubun: Conceptualization, Investigation, Writing – Review & editing. **Kozue**

Shiomi: Conceptualization, Investigation, Writing – Review & editing, Funding acquisition.

Akinori Takahashi: Conceptualization, Writing – Review & editing, Supervision, Funding acquisition.

Data Availability

The data sets analysed during the current study are available at the Arctic and Antarctic Data archive System (ADS) of the National Institute of Polar Research (<https://ads.nipr.ac.jp/dataset/A20230911-001> ↗).

Declaration of Interest

None.

Acknowledgments

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Appendix.

Simulations for the Analysis of Rest Synchrony

We considered the every-second transitions between the resting and moving states of each individual as Markov processes, as described by [Gautrais et al. \(2007\)](#). We calculated the transition probabilities between the two states using the actual data of each individual. Using the model, we obtained virtual time series data of the behaviour (moving/resting) of each individual under the null hypothesis that penguins independently switch between resting and moving states and calculated the index of concurrence. We determined the initial states and length of the virtual time series based on the portion of the actual data for which both individuals in the pair were available during transit. We obtained the mean value and 95% confidence interval of the index of concurrence by conducting 10 000 Monte Carlo simulations ([Fig.A8](#)). We ran the simulations using Igor Pro.

Resting Bout Criterion

First, we classified travelling into resting/moving every second based on heaving acceleration data (as described in the main text). We assumed that successive moving periods within 1 min could be split into two categories: activity derived from temporary body movements during resting bouts (short process) and continuous movement separating resting bouts (long process). We assumed that the Poisson process generated moving periods in each category. Thus, we fitted the following model to the log frequency distribution of the length of moving periods, as described by [Sibly et al. \(1990\)](#):

$$y = \ln (N_s \lambda_s e^{\lambda_s x} + N_l \lambda_l e^{\lambda_l x}) \quad (\text{A1})$$

where N_s and N_l are the numbers of short and long processes, and λ_s and λ_l are the lengths of short and long processes, respectively; y indicates the log frequency and x indicates the length of the moving period.

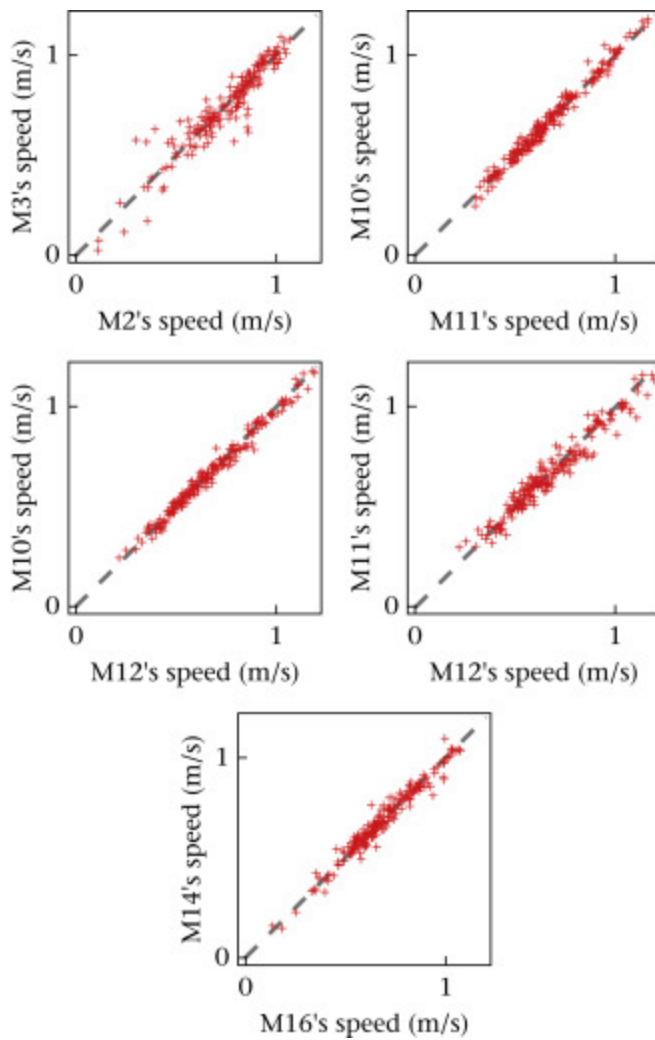
We fitted the model using Igor and obtained all converged parameters ([Fig.A9](#)). Using these parameters, we calculated the bout ending criterion (BEC), the length of the moving time that distinguishes the resting bouts, using the following equation:

$$\text{BEC} = \frac{\log_e \left(\frac{N_s \lambda_s}{N_l \lambda_l} \right)}{\lambda_s - \lambda_l} \quad (\text{A2})$$

The calculated BEC minimizes the number of moving periods assigned to the wrong category ([Slater & Lester, 1982](#)). From this equation, the activity time of 4.26s was calculated as the criterion for bout classification. In other words, any activity lasting less than 4s was considered a temporary movement within a single resting bout. The actual resting bouts were determined based on this criterion for each individual.

To examine the sensitivity of their results to changes in the BEC, we checked the synchronous resting initiator when BEC=2.5s and 10.5s. When BEC=2.5s, M10, M11 and M12 were estimated to be the initiator in 16, 29 and 54% of the synchronous resting events. When BEC=10.5s, M10, M11 and M12 were estimated to be the initiator in 16, 26 and 58% of the synchronous resting events. These results show that the estimation of the initiator is

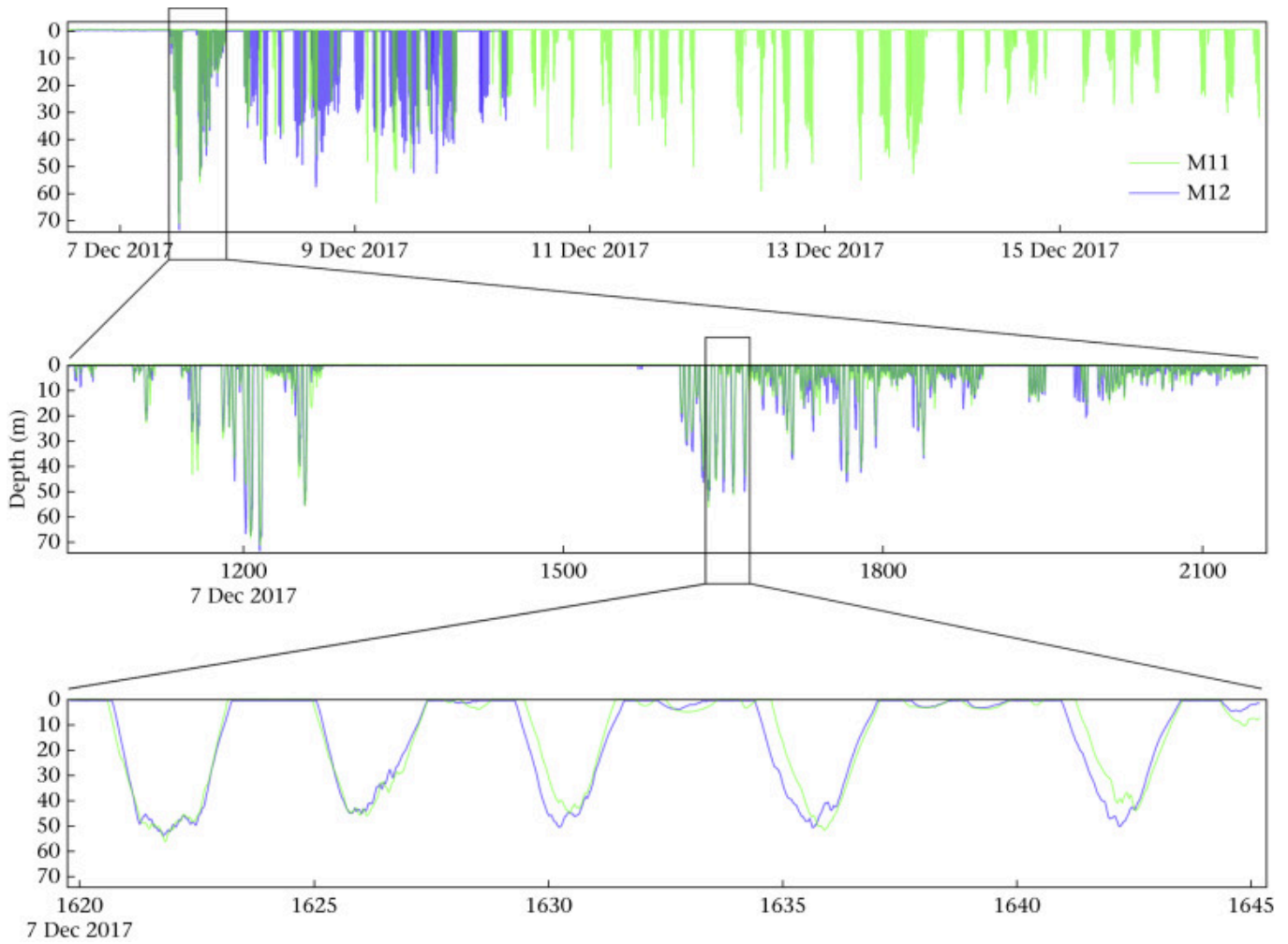
robust to the change in BEC.



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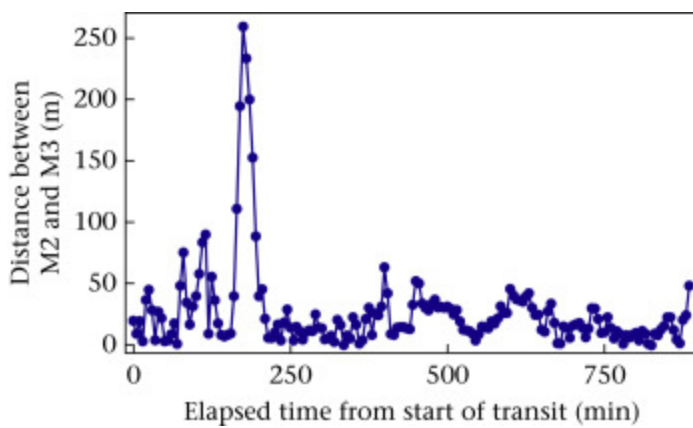
FigureA1. Comparison of speeds within individuals of the same group. Plots correspond to travelling speeds per 5 min. Black dashed lines indicate $x=y$.



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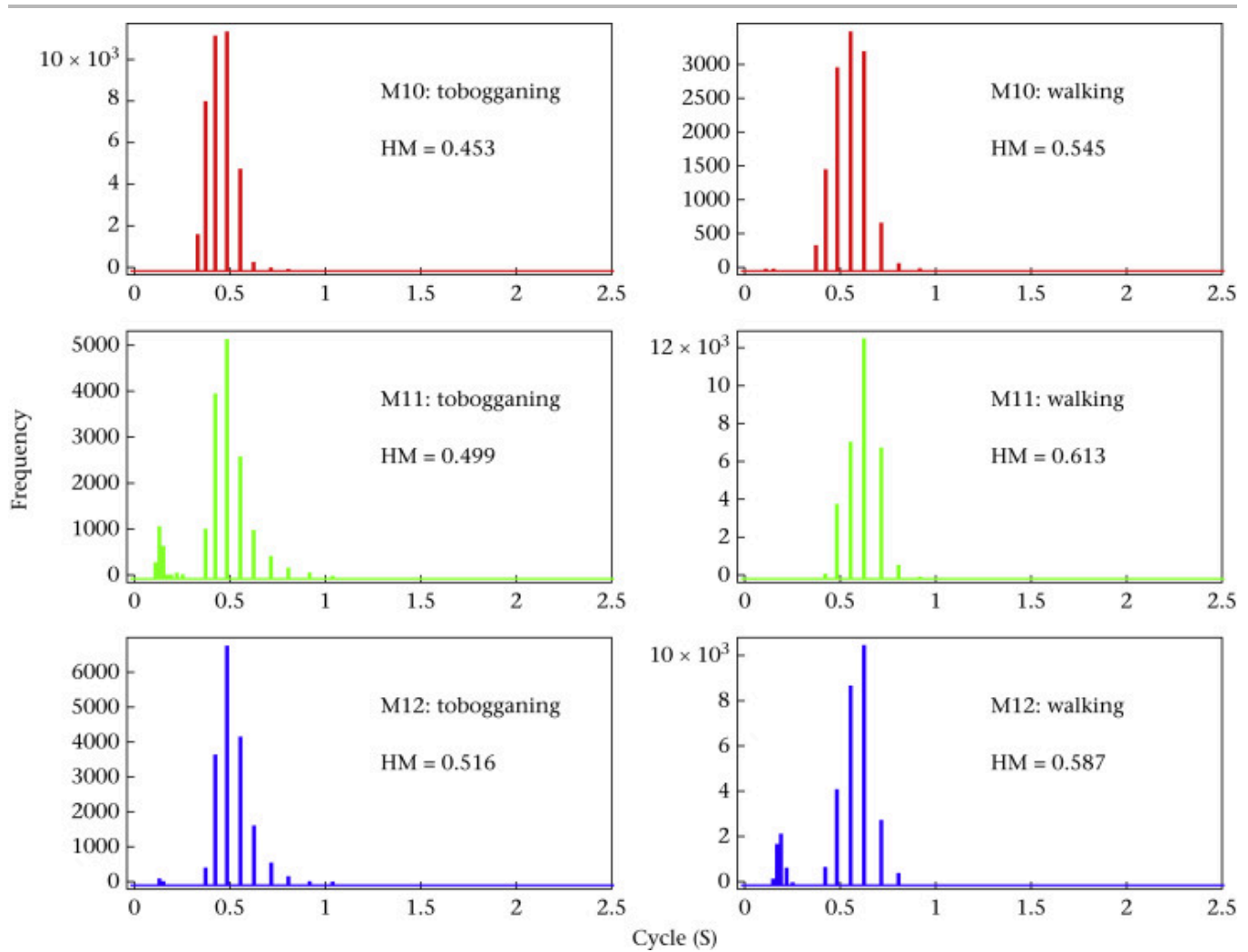
FigureA2. Diving records of M11 and M12 which dived synchronously after reaching the ice edge.



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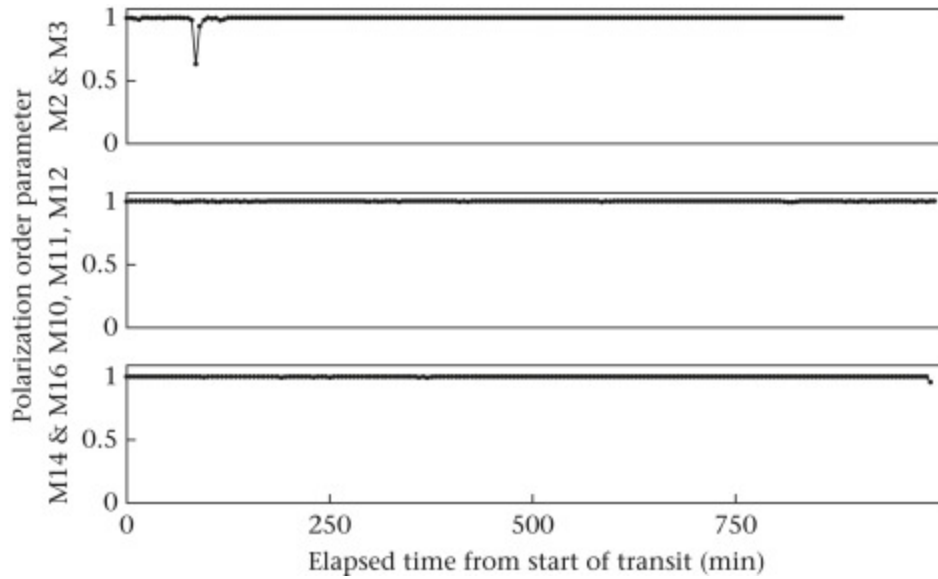
FigureA3. Changes in interindividual distance between M2 and M3.



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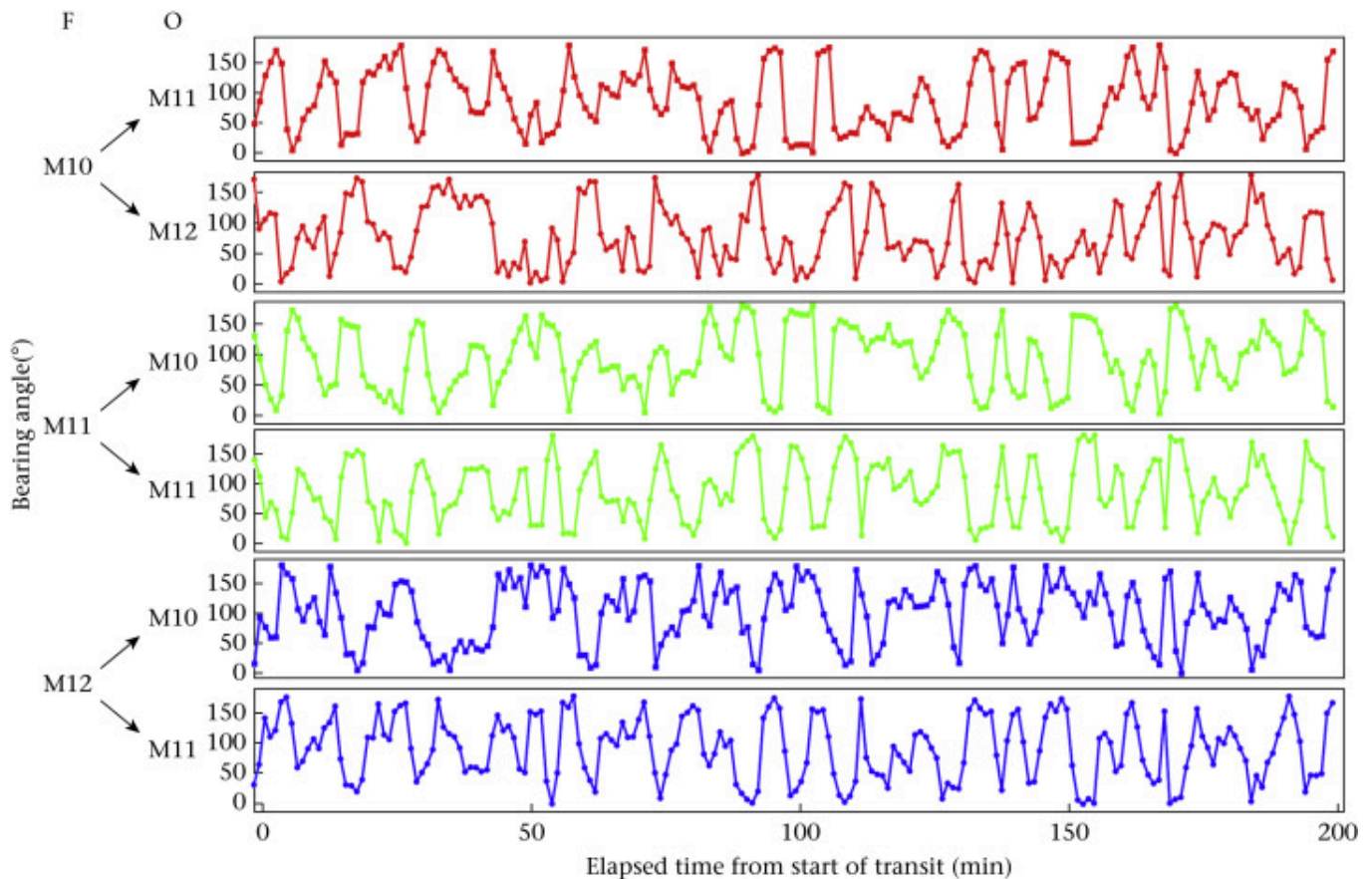
FigureA4. Frequency distribution of the dominant cycles of change in sway acceleration during tobogganing and walking for each individual. HM represents the harmonic mean between 0.3 and 1.5s.



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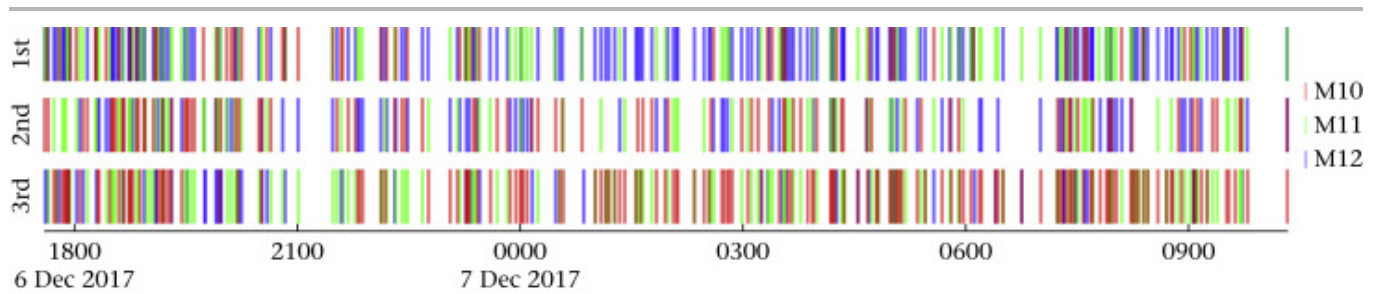
FigureA5. Changes in polarization order parameter in each group. This parameter indicates whether the direction of movement is consistent among the group.



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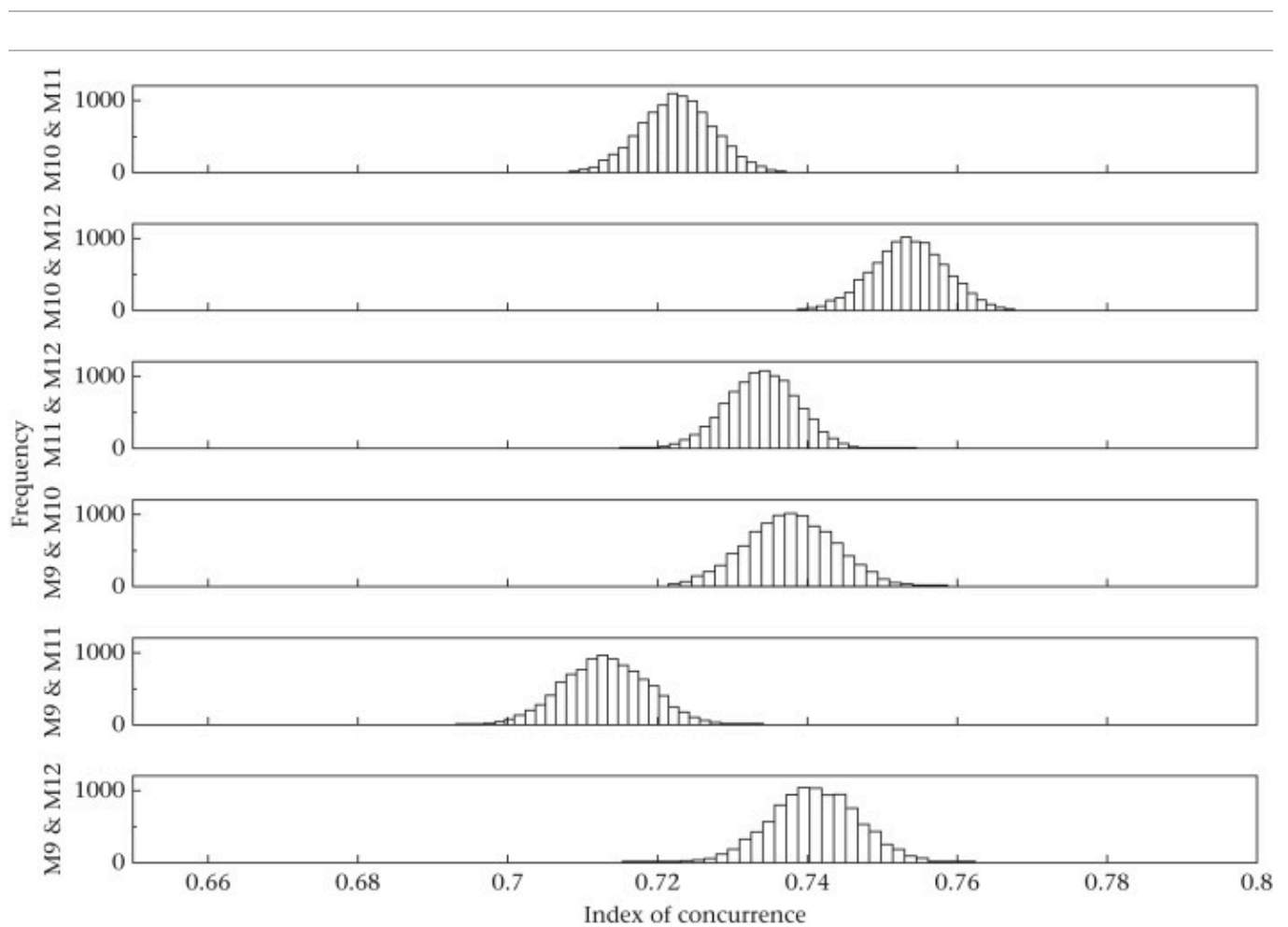
FigureA6. Bearing angles between M10, M11 and M12 during transit. 'F' indicates focal individuals and 'O' indicates other group members.



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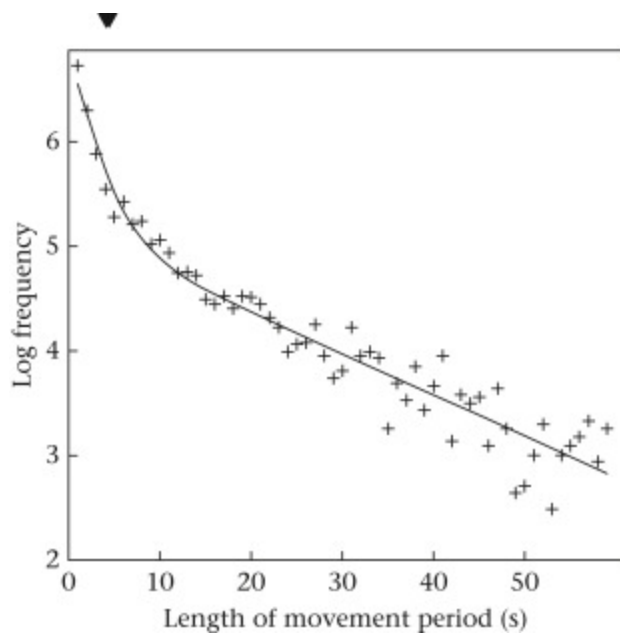
FigureA7. Estimated initiator of synchronous resting during transit.



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FigureA8. Results of Monte Carlo simulations for the index of concurrence between individuals from the same or different group(s).



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FigureA9. Model fitting for the log frequency of moving periods for each duration of movement. Black triangle indicates the bout-ending criterion (BEC=4.26s).

TableA1. Summary of morphological data and capture/recapture times (date/time of day) of recorded individuals

Bird ID	Capture			Recapture			
	Time of capture	Time of release	BM at capture (g)	Time of recapture	Time of release	BM at recapture (g)	BM change (g)
M1	5 Dec 2017 0928	5 Dec 2017 0946	4400	25 Dec 2017 1119	25 Dec 2017 1140	5350	950
M2	5 Dec 2017 1009	5 Dec 2017 1024	4350	17 Dec 2017 1124	17 Dec 2017 1139	5500	1150
M3	5 Dec 2017 1043	5 Dec 2017 1103	3950	25 Dec 2017 1439	25 Dec 2017	-	-

Bird ID	Capture			Recapture			
	Time of capture	Time of release	BM at capture (g)	Time of recapture	Time of release	BM at recapture (g)	BM change (g)
						1445	
M4	5 Dec 2017 1133	5 Dec 2017 1149	3900	Not recaptured			
M5	5 Dec 2017 1313	5 Dec 2017 1327	4400	Not recaptured			
M6	5 Dec 2017 1343	5 Dec 2017 1356	3900	Not recaptured			
M7	5 Dec 2017 1507	5 Dec 2017 1524	3900	27 Dec 2017 1351	27 Dec 2017 1402	4750	
M8	6 Dec 2017 1131	6 Dec 2017 1145	4250	25 Dec 2017 1529	25 Dec 2017 1535	–	–
M9	6 Dec 2017 1158	6 Dec 2017 1211	4550	16 Dec 2017 1545	16 Dec 2017 1558	5550	1000
M10	6 Dec 2017 1233	6 Dec 2017 1244	3850	25 Dec 2017 1045	25 Dec 2017 1106	4600	750
M11	6 Dec 2017 1354	6 Dec 2017 1406	4350	25 Dec 2017 1545	25 Dec 2017 1550	–	–
M12	6 Dec 2017 1421	6 Dec 2017 1433	4650	17 Dec 2017 1519	17 Dec 2017 1533	6250	1600
M13	6 Dec 2017 1504	6 Dec 2017 1515	3450	25 Dec 2017 1426	25 Dec 2017 1432	–	–

Bird ID	Capture			Recapture			
	Time of capture	Time of release	BM at capture (g)	Time of recapture	Time of release	BM at recapture (g)	BM change (g)
M14	6 Dec 2017 1527	6 Dec 2017 1539	4600	25 Dec 2017 1452	25 Dec 2017 1458	–	–
M15	6 Dec 2017 1551	6 Dec 2017 1602	4400	25 Dec 2017 945	25 Dec 2017 1007	5250	850
M16	7 Dec 2017 0932	7 Dec 2017 0943	4100	25 Dec 2017 1500	25 Dec 2017 1509	–	–
M17	7 Dec 2017 1554	7 Dec 2017 1605	3950	25 Dec 2017 1015	25 Dec 2017 1031	5100	1150

BM: body mass.

TableA2. Summary of travelling behaviour during transit to the ice edge

Bird ID	GPS recording periods corresponding to the transit ¹		Travelling distance (km)	Straightness	Transit duration (h)	Average travelling speed (m/s)
	Start	End				
M1	5 Dec 2017 161250	6 Dec 2017 143836	47.4	0.88	22.4	0.59
M2	5 Dec 2017 141811	6 Dec 2017 050820	39.7	0.98	14.8	0.74
M3	5 Dec 2017 142041	6 Dec 2017 050602	39.7	0.98	14.8	0.75
M7	6 Dec 2017 144203	7 Dec 2017 062458	41.7	0.95	15.7	0.74

Bird ID	GPS recording periods corresponding to the transit ¹		Travelling distance (km)	Straightness	Transit duration (h)	Average travelling speed (m/s)
	Start	End				
M8	8 Dec 2017 144008	9 Dec 2017 140125	41.7	0.94	23.4	0.50
M9	6 Dec 2017 214014	7 Dec 2017 170008	39.8	0.97	19.3	0.57
M10	6 Dec 2017 173537	7 Dec 2017 102005	40.0	0.98	16.7	0.66
M11	6 Dec 2017 173506	7 Dec 2017 102009	39.8	0.98	16.8	0.66
M12	6 Dec 2017 173509	7 Dec 2017 102019	40.2	0.97	16.8	0.67
M13	7 Dec 2017 004102	7 Dec 2017 140938	41.0	0.96	13.5	0.85
M14	7 Dec 2017 131303	8 Dec 2017 055627	41.3	0.96	16.7	0.69
M15	6 Dec 2017 210601	7 Dec 2017 104149	40.8	0.96	13.6	0.83
M16	7 Dec 2017 131301	8 Dec 2017 054237	40.7	0.96	16.5	0.69
M17	7 Dec 2017 173641	8 Dec 2017 085314	41.2	0.95	15.3	0.75

1

Date and time of day of start and end are given.

TableA3. Summary of the results of GLS analysis. 'loemode_prop' indicates the percentage of time spent on tobogganing in the total time spent in locomotion behaviour

	Value	SE	t	P
(Intercept)	0.750305	0.098188	7.64155	0
locmode_prop	0.059887	0.045787	1.307937	0.191
ID M11	-0.03976	0.136494	-0.29126	0.771
ID M12	-0.08605	0.136536	-0.63022	0.529
locmode_prop:ID M11	0.189639	0.067028	2.829264	0.005
locmode_prop:ID M12	0.257452	0.065803	3.912477	<0.001

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