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## Resolution of navigational conflict in king penguin chicks



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Conflicts may arise within a moving animal group if its members have different preferred destinations. Many theoretical models suggest that in maintaining group cohesion conflicting preferences can have an overwhelming influence on decision making. However, empirical studies, especially on wild animals, remain limited. Here, we introduce a new study system for investigating collective decision making: king penguins, *Aptenodytes patagonicus*. Their gregarious lifestyle, the colony's organization into subgroups and group travel make king penguins especially interesting for studying collective movements. Chicks spend their first year of life in groups with other chicks (crèches), and if displaced will return to their crèche. We examined how different levels of navigational conflict affect such homing, by comparing the performance of pairs of chicks from the same crèche with pairs from different crèches. The majority of chicks in both treatments travelled at least part of the journey together; when doing so they were more efficient and faster than individuals travelling alone. Chicks took turns in leading and following. Chicks with a common destination (same-crèche pairs) were more precise at homing and less likely to split up than those with a conflict over preferred destinations (different-crèche pairs). Our results support some, but not all, predictions derived from theoretical models.

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Group movements and collective navigation are widespread among group-living animals and can take place on many different spatial and temporal scales (Kerth, 2010). Given the variety of challenges associated with group coordination, many examples in the animal world raise fascinating questions about the organization underpinning such collective motion phenomena, and about the decision-making mechanisms responsible for successful group movement (Conradt & Roper, 2005; Dyer, Johansson, Helbing, Couzin, & Krause, 2009; Sumpter, Krause, James, Couzin, & Ward, 2008; Sumpter & Pratt, 2009). Group members have to reach a consensus on where to go and what to do so as to maximize the benefit of the conspecifics surrounding them. Maintaining proximity can be crucial for survival (Ioannou, Guttal, & Couzin, 2012). However, conflicts of interest may lead to reduced navigational efficiency or group fragmentation even for animals that have a strong affinity to travel in groups (Conradt, Krause, Couzin, & Roper, 2009). Thus, collective decisions are strongly influenced by information uncertainty and conflicting preferences (Conradt, 2012). Several studies have developed models on the mechanisms of

group movement and decision making (e.g. Conradt & Roper, 2005; Johnstone & Manica, 2011; Rands, Cowlishaw, Pettifor, Rowcliffe, & Johnstone, 2003). For example, combining preferences from several group members can reduce overall error and increase the decision accuracy of the group (Simons, 2004). However, arriving at a non-preferred destination might be costly for some individuals. Consequently, many decision-making models have explored the trade-off between maintaining group cohesion and individual preferences (Conradt, 2012).

The topic of collective decision making has seen an explosion of interest among mathematical biologists in recent years, but empirical studies are still limited. Conradt (2012) reviewed models and experimental studies on animal collective decision making, while highlighting the need for more experimental tests. A comprehensive overview of empirical work in the area of decision making is also provided by Kerth (2010). The main aim of our work is to provide much-needed empirical data on group navigation to complement the existing theoretical framework. We propose a new system to study collective decision making in the context of group navigation: wild king penguins, *Aptenodytes patagonicus*. While much is known about the biology of this species and the first steps have been made towards understanding how they navigate, the group aspects of king penguin movements have never been

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explored before. On land, these birds form large colonies (e.g. ca. 500 000 breeding pairs at the largest known colony, Ile aux Cochons, Crozet Archipelago; Guinet, Jouventin, & Malacamp, 1995) that can stretch over several kilometres, and they are known to move in groups on land and in water (Aubin & Jouventin, 1998; Stonehouse, 1960; Weimerskirch, Stahl, & Jouventin, 1992).

Chicks, in particular, provide a useful system for investigating the processes of group decision making during navigation. They show a very strong affinity to stay in groups, both as an antipredator defence mechanism and for thermoregulation during winter (Le Bohec, Gauthier-Clerc, & Le Maho, 2005). Several weeks after hatching, chicks are left unattended by their parents; these chicks form groups with other young known as crèches (Le Bohec et al., 2005; Stonehouse, 1960). Both parents leave for foraging trips that can last from several days to several weeks. The exact locations of the crèches within these large colonies are crucial for chicks' survival because they serve as meeting places where parents find and feed their chicks after a foraging trip (Dobson & Jouventin, 2003). Hence, chicks must remain within the general area of their crèches in order to be found by their parents. However, this is a highly challenging task because bad weather and predators can drive crèches over a hundred metres away from their original location. Crèches can fragment or merge and chicks can end up in a group whose members originate from different crèches.

Here, we investigated the dynamics of decisions made by individuals navigating together to common or different destinations. Specifically, we looked at the homing of the smallest possible groups: pairs of king penguin chicks. We based our experiments on chicks' strong motivation to return to their crèches if displaced (Nesterova, Mardon, & Bonadonna, 2009). To manipulate the levels of conflict faced by pairs experimentally, we captured individual chicks either at the same crèche (SC) or from two different crèches (DC). We displaced these pairs away from the colony and observed their homing. Consequently, SC pairs had no conflict over their desired destinations, while DC pairs experienced within-group conflict over their destinations. With our experiments we set out to address the following questions. (1) Do king penguin chicks derive navigational benefits when travelling in pairs? (2) Is navigation of chick pairs affected by a conflict over preferred destination? (3) How do king penguin chicks resolve navigational conflict?

## METHODS

### Field Experiments

Field experiments took place at Ratmanoff colony, Kerguelen Islands (70°33'E, 49°14'S) during November–December 2011. This large colony is around 100 m wide and stretches over 1 km in the north–south direction on Courbet Peninsula. We used 10–11-month-old chicks from two similar-sized crèches in the tests. The chicks' age was estimated based on their size and moulting condition (Stonehouse, 1960; Weimerskirch et al., 1992). During experiments, chick pairs were captured and transported to an experimental arena (see below) from where they were released later on. To capture a chick, an experimenter slowly approached a chick of interest and held it against her legs. Immediately after, she placed a cotton hood over the chick's head. Blindfolded chicks usually remain stationary. Pairs of chicks were captured simultaneously by two experimenters. In the 'same crèche' (SC) treatment, two neighbouring chicks, standing within 1–2 m from each other, were captured in the same crèche ( $N = 15$  pairs). The SC pairs came either from crèche A or crèche B. In the 'different crèche' (DC) treatment, two chicks were captured from two different crèches ( $N = 16$  pairs) that appeared as two distinctive groups, separated by space with no chicks, at the moment of capture (see Fig. 1 for the

experimental set-up). The distances between capture locations for chicks from different crèches ranged between 18.7 m and 80.3 m ( $43.6 \pm 5.7$  m).

To eliminate the use of any internally generated cues during homing, blindfolded chicks were rotated three times at the capture site, carried by hand along an indirect path to the arena, and rotated there again. The circular experimental arena, bordered by a fabric barrier (radius: 5.2 m; barrier height: 1 m), was situated south from the colony on a small plateau, 111–176 m ( $139.3 \pm 1.87$  m) from the capture locations. The crèches from where the chicks originated were not visible from the arena.

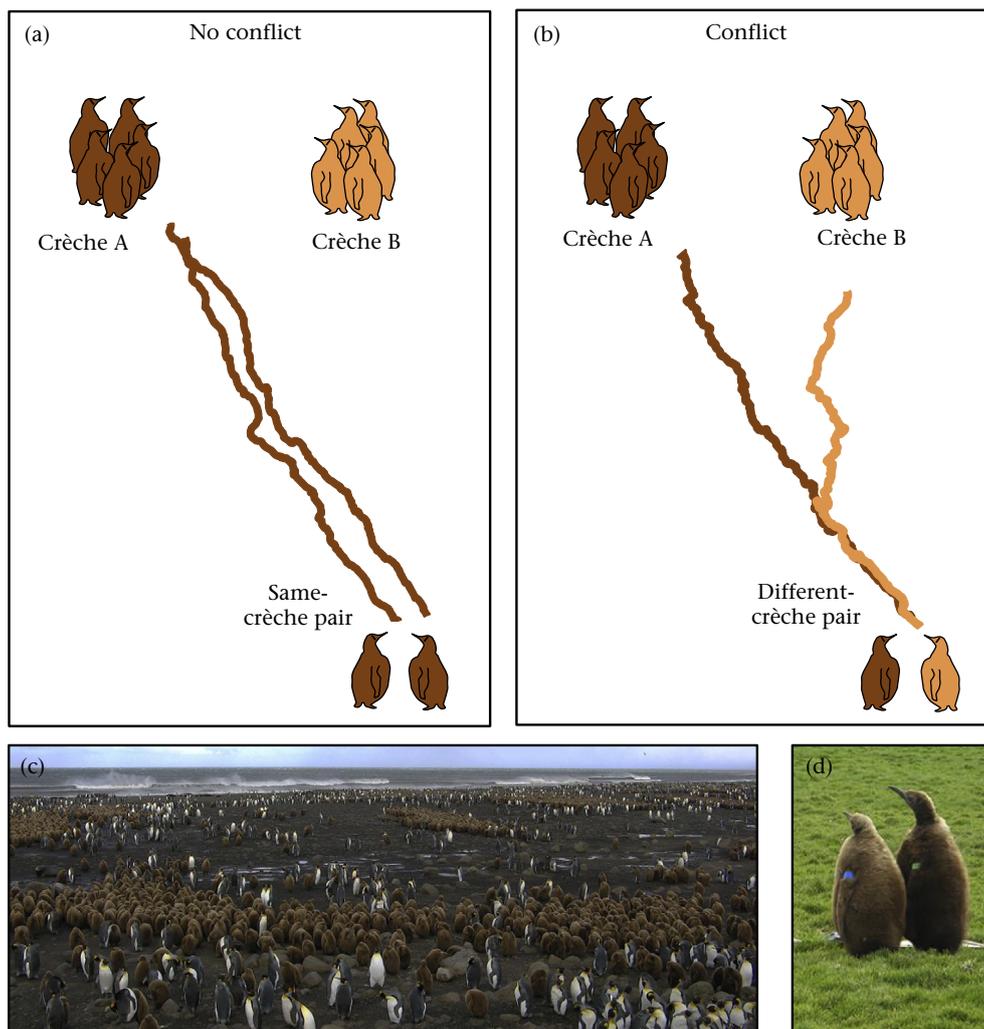
Chicks were fitted with a 17 g miniature GPS logger (Qstarz International Co., Ltd., Taiwan) constituting less than 0.2% of the chick's mass. GPS loggers were attached to Darvic plastic bands that were placed at the base of one flipper for the duration of the trial. Coloured Tesa tape was attached to the other flipper to help with visual identification during the test. In addition, to avoid accidental recapture, chicks were marked with the green Porcimark (KRUUSE, Langeskov, Denmark) on their chest. The loggers were set to acquire positional fixes (geographical longitude and latitude, error  $\pm 4$  m) at 5 Hz resolution. At the end of fitting, the hood was removed from the chick's head. To avoid any possible directional biases generated by the experimenter during release and to allow chicks to recover from any potential stress associated with capture, chicks spent the first 10 min of testing in the arena. After 10 min, the arena barrier was lowered, and chicks were free to return to their crèches. Chicks' homing was observed remotely with binoculars and was videotaped when possible. After 1 h, chicks were recaptured to remove the GPS loggers and Tesa bands and released back into their crèches. Each chick was tested only once.

Temperature, cloud cover, wind directions and speed measurements were taken at the time of each release. Trials for SC and DC treatments were conducted in a random order, under the constraint that no more than two trials of the same treatment could be run in a row, and were intermixed with trials for other experiments. This study was performed according to the guidelines of ASAB/ABS, IPEV, Comité d'éthique pour l'expérimentation animale Midi-Pyrénées (MP/05/26/05/11) and the Oxford University Ethical Review committee.

### Statistical Analysis

For analyses, the positional data were converted from degrees to metres by projecting the polar on to a Cartesian coordinate system, using a Universal Transverse Mercator projection. The tracks (a track is a chronologically ordered series of locations for an individual in one trial) were smoothed by using the moving average method over 1 s. The starting point for the tracks was set at 4 m outside the arena barrier, and the tracks ended after 1 h of testing. We used different parts of the tracks (complete and 30 m trimmed) for our analyses. The complete tracks were used to measure how closely chicks approached their capture location. The minimum distance between a chick's track and its capture location is referred to as homing precision. For all other analyses, we used tracks until the point where a chick reached a 30 m radius of its capture location or complete 1 h tracks for nonhoming individuals. When the experiments were conducted, the crèches were very spread out because of the extremely mild weather conditions; hence chicks arriving within 30 m of the capture location were usually within their crèches and the 30 m cutoff appears to be a suitable endpoint of the homing path. Consequently, a homed chick was a chick that arrived within 30 m radius from its capture location within 1 h.

From the tracks we derived the following measures. Speed was the average of the instantaneous speeds calculated between two consecutive GPS fixes. Efficiency was defined as the ratio of the



**Figure 1.** Experimental set-up. Individual chicks were captured either (a) in the same crèche or (b) at two different crèches. Consequently, same-crèche (SC) pairs had no conflict, while different-crèche (DC) pairs experienced within-group conflict over their desired destinations. Chick pairs were displaced to an experimental arena, ca. 140 m away from the colony, equipped with miniature GPS loggers and released. SC pairs were captured in either crèche A or crèche B. We analysed GPS tracks of chicks returning to their crèches. (c) An overview of the colony showing different crèches. (d) A pair of chicks equipped with GPS loggers at the release location.

shortest distance between start and end points of the track (or segment of interest, see below) to the total track (segment) length. The track length was the sum of the distances between all consecutive pairs of GPS fixes in a track. A chick was considered to be at a stop if its speed was less than 0.05 m/s for more than 1 s. Total number of stops was divided by the total track length to estimate number of stops/m. We also measured the instantaneous distance between synchronized tracks of two partners. Based on these intertrack distances we classified chick tracks into two types of segments: walking together, when chicks were walking  $\leq 11$  m from each other, and separate, when chicks were walking  $> 11$  m from each other. To determine the 11 m threshold we looked at pairs from different crèches, where the distance between chicks fluctuated widely. The full separation of 75% of pairs could be clearly predicted by the 11 m threshold. The remaining 25% of pairs were seen to come closer again after they exceeded the 11 m threshold; however, all these pairs diverged again shortly after. We did not consider higher thresholds owing to limited visibility in the crowded colony.

To express the similarity of the movements between two chicks walking as a pair, we calculated the dynamic interaction index (DI; Calenge, 2006; Long & Nelson, 2013). The DI index measures the interaction between two individuals by estimating their correlation

in movement direction and distance. For our comparisons we used the overall DI index which combines both displacement and direction in one value. DI\_func.R script was downloaded from the website <http://www.geog.univ.ca/spar/DynamicInteraction/>. For the segments of tracks when chicks were walking together, we calculated which chick occupied a frontal position with respect to the pair's direction of movement. Leaders were those chicks that occupied a frontal position and whose movements were related to its partner's as measured by the DI index. In addition, we calculated efficiency and speed for 'together' and 'separate' segments.

Linear mixed models (LMM) were used to compare: (1) speeds of chicks walking together or separately (fixed effect: together/separate; random effect: pairs); (2) speeds of SC and DC chicks (fixed effect: SC/DC; random effect: pairs); (3) efficiencies of chicks walking together or separately (fixed effect: together/separate; random effect: pairs). Generalized linear mixed models (GLMM) were used to compare: (1) efficiencies of SC and DC chicks (fixed effect: SC/DC; random effect: pairs; gamma distribution with log link function), (2) homing precision of SC and DC chicks (fixed effect: SC/DC; random effect: pairs; gamma distribution with log link function) and (3) number of stops/m of SC and DC chicks (fixed effect: SC/DC; random effect: pairs; gamma distribution with log

link function). The DI index of chicks walking together or separately was compared by means of paired *t* tests. A *t* test was used to compare means of (1) the DI index of SC and DC chicks, (2) the proportion of the track walked together by SC and DC chicks and (3) the proportion of time one chick was in front of its partner. To compare frequencies of SC and DC pairs homing together all the way/homing together part of the way/homing independently, a Fisher exact test was used. Pearson correlations were calculated to explore the relationship between (1) distance between partners and distance travelled together, (2) distance between capture locations and distance travelled together and (3) angle between capture locations and distance travelled together. Throughout the text we report mean values with associated SEs. Analyses were conducted in Matlab (Mathworks, Natick, MA, U.S.A.), R (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>) and SPSS (IBM, Armonk, NY, U.S.A.).

## RESULTS

### Do Chicks Benefit from Travelling in Pairs?

Most chick pairs (30/31 pairs) homed as a group for at least a part of the journey. When chicks walked together with a partner, they were faster ( $0.30 \pm 0.01$  m/s) than those that walked alone ( $0.22$  m/s  $\pm 0.02$ ; LMM:  $N = 62$  chicks,  $F_{1,50} = 12.50$ ,  $P < 0.001$ ; Fig. 2). In addition, chicks were more efficient in pairs ( $0.41 \pm 0.04$ ) than as individuals ( $0.19 \pm 0.02$ ; LMM:  $N = 62$  chicks,  $F_{1,54} = 21.39$ ,  $P < 0.001$ ; Fig. 2). For the chicks that homed, the longer partners walked together the more efficient their return was (Pearson correlation:  $r_{22} = 0.622$ ,  $P = 0.001$ ). The closer partners were to each other for the duration of their joint travel, the further they walked together (Pearson correlation:  $r_{28} = -0.564$ ,  $P < 0.001$ ; Fig. 3).

### Is Navigation Affected by Conflict over Preferred Destination?

Homing precision was different between the two experimental conditions. SC chicks came on average within  $9.8 \pm 2.8$  m of their

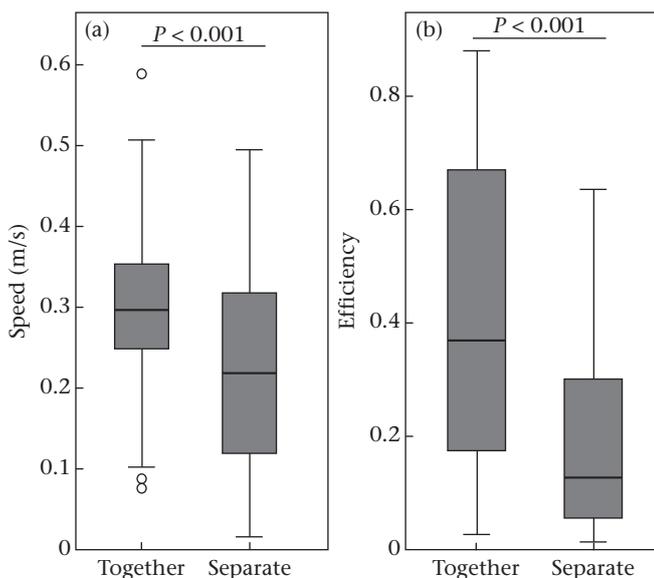
capture location during the 1 h experimental period. This final distance was significantly shorter than that of the DC chicks, which approached their crèches only up to  $29.1 \pm 7.0$  m (GLMM:  $N = 62$  chicks,  $F_{1,29} = 6.619$ ,  $P = 0.015$ ; Fig. 4). Most of the DC pairs on average split  $94.9 \pm 6.4$  m before they arrived at one of the crèches. In the SC group, 28 chicks homed, and only two chicks from different pairs never arrived within 30 m of their capture locations. In the DC group, 24 chicks homed and eight chicks did not. These nonhoming chicks were from three pairs in which both partners did not home, and two chicks whose partners did home.

We found no evidence that overall speed, efficiency and number of stops of chicks that homed were different between SC and DC pairs (speed: LMM:  $N = 52$  chicks,  $F_{1,24} = 0.127$ ,  $P = 0.725$ ; efficiency: GLMM:  $N = 52$  chicks,  $F_{1,24} = 0.526$ ,  $P = 0.476$ ; stops/m, GLMM:  $N = 52$  chicks,  $F_{1,26} = 0.078$ ,  $P = 0.782$ ; Table 1).

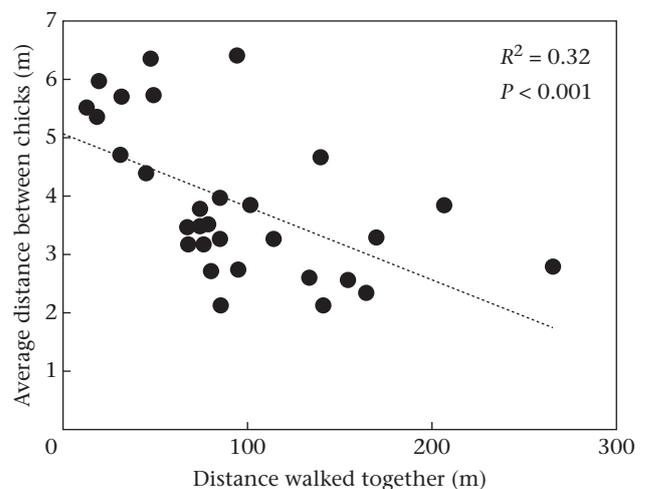
### How do Chicks Resolve Navigational Conflict?

We observed three different types of group homing: (1) chicks walked with their partner to a common capture location (or at least to one of the capture locations in the case of DC pairs), (2) they split up along the way, or (3) both birds walked completely independently all the way (Fig. 5). However, the frequencies of each of these behaviours were different between SC and DC pairs.

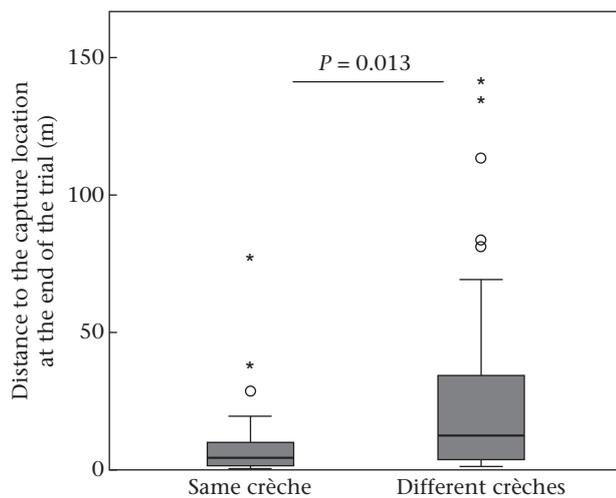
A conflicting goal had a clear effect on the chick pairs' group homing performance. Only two of the 16 DC pairs remained together all the way. These two comprised a pair of chicks that were lost and never reached the colony and a pair of chicks whose capture locations were only 18.7 m away from each other, the minimum distance among all DC pairs. On the other hand, seven of 15 SC pairs walked home together (Fisher exact test: together versus partially together + separate,  $N = 31$  pairs,  $P = 0.038$ ; Fig. 6). The proportion of the trip that chicks walked together was higher for the SC pairs ( $0.75 \pm 0.05$ ) than for DC pairs ( $0.50 \pm 0.05$ ; *t* test:  $N = 31$  pairs,  $t_{29} = 2.342$ ,  $P = 0.026$ ). The majority of SC pairs that split did so at the end of their trip, except one pair that split at the beginning and two pairs that split and then came back together in the middle of their journeys. DC pairs were seen to separate both in the first and the second half of their journeys. Among DC pairs, we found no evidence that the size of the conflict, measured as distance or angle between capture locations, affected the distance chicks would travel together. For instance, the distances between



**Figure 2.** Box plots of (a) speed and (b) efficiency of chick pairs walking together or separately. Efficiency was calculated as the ratio of the shortest distance between the start and the end of the track segment (together or separate) to the total segment length. Boxes indicate medians and upper and lower quartiles; vertical lines extend to 1.5 times the upper and lower quartiles and circles indicate outliers. All outliers were included in the analysis.



**Figure 3.** Correlation between the distance chicks walked together and the distance between chicks in the pair when walking together. The dashed line is the least squares regression relation between the two variables.



**Figure 4.** Box plots of how close chicks approach their capture locations within 1 h of testing. Boxes indicate medians and upper and lower quartiles; vertical lines extend to 1.5 times the upper and lower quartiles. Circles indicate outliers from 1.5 to 3 times the upper and lower quartiles; stars indicate outliers  $>3$  times the upper and lower quartiles. All outliers were included in the analysis.

capture locations ranged between 18.7 m and 80.3 m ( $43.6 \pm 5.7$  m) and were not correlated with the distances chicks travelled together (Pearson correlation:  $r_{14} = -0.274$ ,  $P = 0.305$ ). The angle between two capture locations at the release point (i.e. initial conflict angle) ranged between  $6.20^\circ$  and  $31.42^\circ$  ( $15.62 \pm 2.44$ ). Again, we did not observe any correlation between the initial conflict angles and the distances chicks travelled together (circular–linear correlation:  $N = 16$  pairs,  $r = 0.251$ ,  $P = 0.603$ ). As chicks approached the colony, the conflict angle changed progressively for each pair. The angle between the two capture locations at the split point ranged from  $7.25^\circ$  to  $41.91^\circ$  ( $20.69 \pm 3.36$ ).

We measured the degree of similarity between the movements of two chicks in a pair with the DI index that took into account both direction and displacement distance of movement. When two chicks were walking together, their movements showed a higher degree of similarity ( $0.325 \pm 0.04$ ) than when they were walking independently ( $0.164 \pm 0.03$ ; paired  $t$  test:  $N = 22$  chicks,  $t_{21} = 3.738$ ,  $P = 0.001$ ). On the other hand, whether chicks came from the SC ( $0.302 \pm 0.04$ ) or DC ( $0.378 \pm 0.04$ ) groups did not affect how similar their movements were when walking together ( $t$  test:  $N = 30$  pairs,  $t_{28} = -1.256$ ,  $P = 0.220$ ).

Given the similarity of movements of chicks walking together, we next investigated whether given chicks could be classified as either leaders or followers based on their position in the pair with respect to the pair's direction of movement. In the majority of pairs, chicks took turns in taking the frontal position (Fig. 7). No differences were observed in the proportion of the time one chick was in front of its partner between SC and DC pairs (mean<sub>SC</sub> =  $0.50 \pm 0.06$ , mean<sub>DC</sub> =  $0.48 \pm 0.07$ ;  $t$  test:  $N = 30$  pairs,  $t_{28} = 0.275$ ,  $P = 0.785$ ).

**Table 1**  
Track speed, efficiency and number of stops/m for same- and different-crèche pairs

	Same crèche		Different crèches	
	Mean $\pm$ SE	N	Mean $\pm$ SE	N
Speed (m/s)	0.26 $\pm$ 0.01	28	0.25 $\pm$ 0.02	24
Efficiency	0.73 $\pm$ 0.02	28	0.69 $\pm$ 0.03	24
Stops/m	0.12 $\pm$ 0.02	28	0.13 $\pm$ 0.02	24

Only chicks that homed were considered.

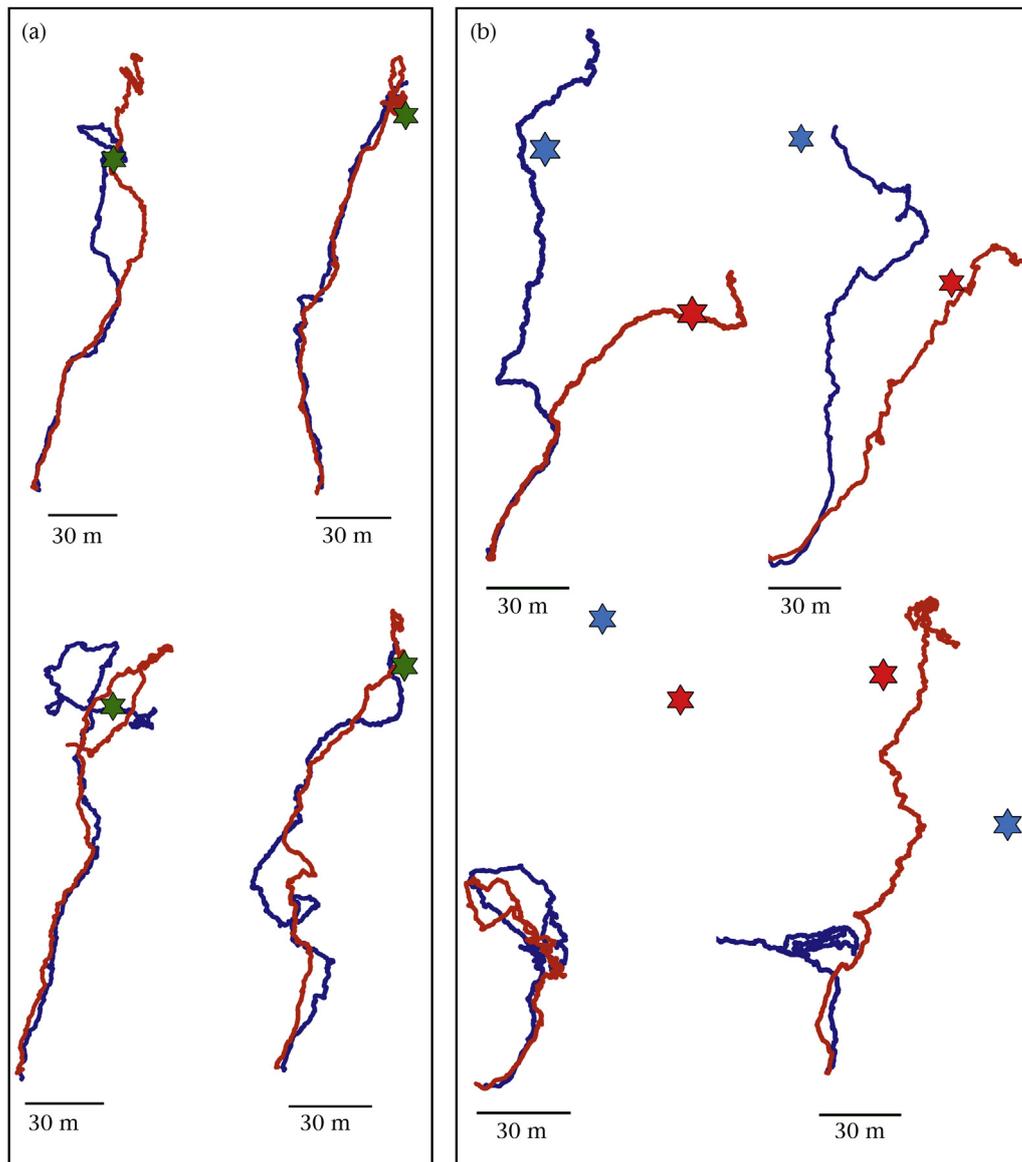
## DISCUSSION

Our experiments demonstrated that king penguin chick pairs released away from the colony can home collectively. Chicks walking together with a partner were faster and more efficient than chicks that walked alone. However, homing behaviour was strongly affected by the composition of the group. When intragroup conflict was present, chicks' attraction to their destination was stronger than that to their partner. Different-crèche pairs tended to split up earlier than same-crèche pairs. Moreover, homing precision was higher for same-crèche pairs which experienced no conflict over their preferred destination.

Moving as a group potentially provides navigational advantages to the individual chicks. While individual performance was not tested directly in our experiments, the fact that chicks were faster and more efficient when they walked together with a partner indirectly supports the idea that chick pairs do better than individuals. Higher speeds and more direct routes allowed chick pairs to reduce their time outside the colony. Increased navigational performance of groups compared with that of individuals has been previously demonstrated empirically in several other species. For example, pigeons, *Columba livia*, released in pairs or small flocks were faster and more efficient during homing than individuals (Biro, Sumpter, Meade, & Guilford, 2006; Dell'Arciccia, Dell'Omo, Wolfer, & Lipp, 2008). Similarly, schools of mosquitofish, *Gambusia holbrooki*, were faster and more accurate at selecting an appropriate arm in a Y-maze than individuals (Ward, Herbert-Read, Sumpter, & Krause, 2011). It remains for future studies to compare navigation performance of individuals with that of pairs over the entire journey towards the colony. It is possible that the higher density of penguins closer to the colony forces chicks to reduce their walking speed irrespectively of whether they are travelling alone or in groups. The larger number of conspecifics in and around the colony could also affect their ability to detect their partners. As chicks in the pair move further away from each other within crowded areas, they are more likely to lose sight of each other. This might also explain our result that the partners' proximity to each other predicted their duration of travelling as a group.

The need to navigate to two different destinations did not interfere with the chicks' overall speed and efficiency. None the less, the lack of conflict improved homing performance. For instance, homing precision was different between the two experimental treatments: SC chicks arrived closer to their capture locations than DC chicks, even after DC chicks had split from their partner. Such differences in homing precision were unexpected given the strong selection pressure on chicks to be able to return to their specific place in the colony. Because most of the DC pairs split before they arrived at one of the crèches, it is unlikely that chicks had a direct influence on each other during the last stages of homing. Our results appear to be in accordance with the predictions of the 'many wrongs' principle, which states that navigational accuracy increases with group size (Simons, 2004). In the case of DC pairs, the majority of chicks arrived close to the capture location individually (group size = 1), while SC chicks often arrived together with a partner (group size = 2) which seemed to improve their homing precision. Studies on humans also showed the improvement in navigational accuracy, measured as angular deviation towards the target from the direction of movement, for groups of 10, but performance of human pairs was similar to individual performances (Faria, Codling, Dyer, Trillmich, & Krause, 2009). To test directly the 'many wrongs' principle in king penguins, it would be interesting to compare the performance of chicks released individually or in groups of different sizes.

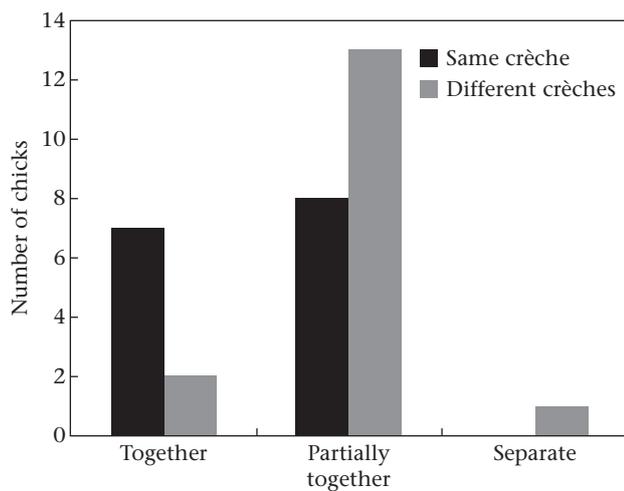
A conflicting goal had a clear effect on group homing performance, and the majority of king penguin chicks solved the



**Figure 5.** Examples of chicks' homing tracks. Stars indicate capture locations. (a) Same-crèche pairs, for which all chicks arrived near their capture locations. (b) Different-crèche pairs: the examples include two pairs for which both chicks arrived near their capture locations, one pair that never reached its capture location and another pair in which one chick never reached its capture location.

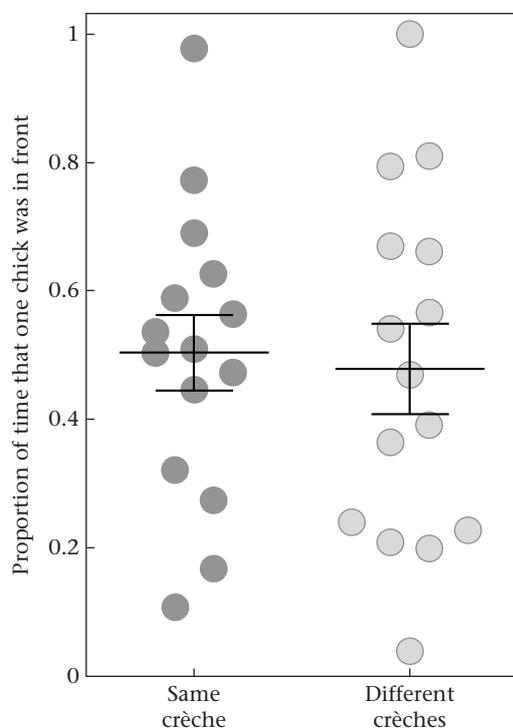
navigational conflict by splitting. We predicted that chicks with a smaller initial conflict would maintain group cohesion longer. Indeed, SC chicks walked together longer than DC chicks. However, among DC pairs, we found no evidence that the size of the conflict affected the distance chicks would travel together. Moreover, given the wide range of the conflict angles at the split point, we could not determine whether there was a threshold in the level of conflict beyond which animals would not travel together. Work on pigeons, on the other hand, demonstrated that the level of conflict predicted whether birds stayed together or not (Biro et al., 2006). We did not observe differences in the outcome among DC pairs with respect to the size of the conflict probably because for chicks it is more important to be within a correct crèche (but the exact position in the crèche is less relevant). However, the costs of approaching the colony alone during the day seem to be negligible, because for chicks of this age in good body condition predation is highly unlikely.

Several models that focus on the collective decision making of groups, including pairs, have been put forward (reviewed in Conradt, 2012). The model developed by Johnstone and Manica (2011) is of particular interest to our study. It predicts that when the conflict within a group is relatively small, a mix of leaders and followers would be maintained in the population. Moreover, the best levels of coordination within pairs are achieved when partners have clearly distinctive temperaments: leaders and followers. On the other hand, at intermediate levels of conflict, the intrinsic tendency of group members to adopt the role of leaders will be highest. Empirical studies on sticklebacks, *Gasterosteus aculeatus*, supported the predictions of this model. Pairs that had no conflict over a foraging location showed emergence of clear leaders and followers (Harcourt, Ang, Sweetman, Johnstone, & Manica, 2009), whereas pairs with conflicting destinations took turns at visiting different foraging sites (Harcourt, Sweetman, Manica, & Johnstone, 2010).



**Figure 6.** Distribution of chick pairs walking together all the way (or towards at least one of the capture locations in the case of different-crèche pairs), part of the way together or completely separately for same- and different-crèche pairs.

Our results, on the other hand, provide only partial support to Johnstone and Manica's model. In the no-conflict situation, SC pairs showed high levels of coordination by maintaining group cohesion longer. This is in accordance with one of the model's predictions stating that a high degree of common interest will lead to a greater level of coordination. However, we did not see the emergence of clear leaders and followers. Instead, chicks shared their leadership along the way. They alternated in being at the front of the pair when walking together. This suggests that collective movements of king penguin pairs are governed primarily by an overall democratic



**Figure 7.** Each circle represents data for a pair of chicks showing the proportion of time ( $x$ ) one chick, randomly chosen, was in front of its partner. The proportion of time its partner was leading is equal to  $1 - x$ , and not shown on the figure. Dark grey and light grey circles correspond to same-crèche and different-crèche pairs, respectively. Black lines correspond to mean  $\pm$  SEM.

principle in which the two partners alternate in taking the leadership role as they progress through the journey. When a conflict over destinations was present, DC pairs resolved it by splitting, suggesting that each chick adopted a leader role, effectively 'refusing' to follow its partner, as would be predicted by Johnstone and Manica's model for intermediate levels of conflict. Before the split, DC chicks shared their leadership just like SC chicks. Perhaps larger group sizes of chicks would stimulate emergence of clear leaders and followers.

Our present experiments have focused on navigation and conflict resolution in pairs, the simplest of groups. King penguins, as a study system, have great potential for further studies of group navigation. Future experiments could examine navigation in groups of different sizes and composition to determine the effects of these factors on conflict resolution and leadership. Coordination and decision making may become more challenging in larger groups (e.g. 6–10 individuals). Pairs take turns when it comes to leadership, but this kind of mechanism may become inefficient and costly in cases where the directional decisions of many members have to be integrated. Successful homing may depend upon the emergence of well-defined leaders in larger groups of chicks. Alternatively, chick groups could exhibit a hierarchical organization similar to that observed in pigeons in which each individual follows a particular group member (Nagy, Akos, Biro, & Vicsek, 2010). To change group composition one could vary the proportion of chicks from the same/different crèches or locations of crèches from where chicks were taken. Both of these scenarios could happen under natural conditions when crèches intermix. In addition, one could alter the level of individual experience of group members. It has been shown that in pigeons leadership is influenced by the level of homing experience (Flack, Pettit, Freeman, Guilford, & Biro, 2012), and it would be interesting to test whether experienced king penguin chicks are more likely to lead others. Other behavioural, morphological or physiological features may also alter an individual's tendency to influence the movement of a group (King & Sueur, 2011; Petit & Bon, 2010). For example, empirical studies have observed that familiarity between individuals can modulate an individual's tendency to follow the movements of a preferred partner (Boissy & Dumont, 2002; Flack, Freeman, Guilford, & Biro, 2013; Griffiths & Magurran, 1999; Ramseyer, Boissy, Thierry, & Dumont, 2009; Toth et al., 2009). Crèches are relatively stable units with many opportunities for repeated interactions between the same individuals. On the other hand, no well-defined hierarchy within a crèche has been identified so far, and there are no foraging excursions at this stage of development. Understanding the mechanisms of group dynamics in such systems will provide a valuable addition to a growing body of knowledge on collective movements.

### Conclusions

Here, we have provided much-needed empirical evidence on how wild animals resolve conflict over preferred destinations under natural conditions. When walking as a group king penguin chicks derived navigational benefits and shared their leadership, but they solved conflict over destinations by splitting. Our results support some, but not all, theoretical predictions, suggesting that the generality of existing models needs to be re-evaluated and additional parameters may need to be considered in order to increase their applicability.

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