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## The effect of experienced individuals on navigation by king penguin chick pairs



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Group members' individual experience can have important influences when navigating collectively. However, how exactly they structure group travel performance is still not fully understood. This study investigated how navigation and leadership dynamics are affected by the presence of an experienced individual in king penguin, *Aptenodytes patagonicus*, chick pairs. We tested pairs of chicks in which two partners differed in their level of prior navigational experience. Naïve pairs consisted of two chicks that had no previous homing experience. In mixed pairs, one chick was naïve, but the other chick had previous homing experience. Our results showed that in mixed pairs the navigational performance of naïve chicks improved if they travelled together with an experienced partner compared to when they walked alone. Experienced chicks, however, maintained their relatively high speeds and efficiencies irrespective of whether they walked with a partner or independently. We also observed a shift in leadership dynamics: in naïve pairs, both chicks took turns in leading and following, while in mixed pairs, experienced chicks tended to lead throughout. Our work provides a valuable empirical system in which to test theoretical models of leadership and information transfer within groups.

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Group movements are essential parts of many animals' lives. Moving collectively can present individuals with many advantages such as reduced risk of predation (Krause & Ruxton, 2002), an ability to reach previously unknown food resources (Laland & Williams, 1997), finding and deciding on the best sleeping sites (Fleischmann et al., 2013), increasing navigational accuracy (Faria, Codling, Dyer, Trillmich, & Krause, 2009), or even the avoidance of potential intergroup conflicts (McComb, Moss, Durant, Baker, & Sayialel, 2001). While moving collectively could be beneficial to all members of the group, the decisions regarding initiation, coordination, duration and termination of the movement could be taken by a small minority of the group. Who contributes to collective decisions will have direct fitness consequences for all members of the group.

Emergence of leaders, i.e. individuals who initiate and/or direct group movements, can be spontaneous, arising from the needs (e.g. energetic requirements) of group members (Conradt, Krause, Couzin, & Roper, 2009; Rands, Cowlshaw, Pettifor, Rowcliffe, & Johnstone, 2003). In other cases, individual characteristics of a group member can predispose its leader/follower status. For example, an individual's knowledge and previous experience can influence its capacity to assume leadership. In turn, this will have important effects on the group's navigational performance. Trained meerkats, *Suricata suricatta*, can successfully initiate group departures in the direction of a food source known only to them (Bousquet & Manser, 2011). More experienced pigeons, *Columba livia*, lead their less experienced partners on homing journeys (Flack, Pettit, Freeman, Guilford, & Biro, 2012). In golden shiners, *Notemigonus crysoleucas*, an informed minority can lead its shoal towards a food source (Reebs, 2000). In some cases, experience can even overshadow the effect of personality differences (Nakayama, Stumpe, Manica, & Johnstone, 2013). Moreover, dominance status and age often correlate with levels of experience, such that their specific effects on leadership and group navigation may be hard to disentangle.

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Thus, increasing group members' knowledge can clearly improve the efficiency of a moving group, and the underlying processes have become a focus of intense scientific interest. Couzin et al.'s (2005) mathematical model of collective motion suggests that information can propagate through a group even when group members are not aware of who has relevant information. Also, democratic decision making that results in less extreme decisions is predicted to be more beneficial and widespread among animal groups (Conradt & Roper, 2003). While a strong theoretical framework dealing with questions of experience and group navigation has been developed, empirical validations of model predictions, in particular experiments using wild subjects, remain limited (but see Banks & Guilford, 2000; Bousquet & Manser, 2011; Flack et al., 2012; Guilford & Chappell, 1996). Thus, one of our aims was to provide a qualitative assessment of these theories based on experimental results from a natural system.

The main focus of the present study was to investigate how navigation and leadership dynamics are affected by the presence of an experienced individual in conavigating groups. To address this we performed homing experiments with king penguin, *Aptenodytes patagonicus*, chicks. King penguins, especially chicks that form young-only subgroups within the colony, are of particular interest to studies of group dynamics. These birds live in large and crowded colonies that can stretch over several kilometres, and are often seen travelling in groups (Aubin & Jouventin, 1998; Chamailé-Jammes, Guinet, Nicoleau, & Argentier, 2000; Stonehouse, 1960; Weimerskirch, Stahl, & Jouventin, 1992). Navigation within a colony can present many challenges, yet chick survival and adult reproductive success depend on the birds' ability to locate precisely a particular place within a colony (Dobson & Jouventin, 2003; Lengagne, Jouventin, & Aubin, 1999). Chicks, from the age of several weeks, form groups, known as crèches, with other youngsters. Owing to predator attacks or adverse weather conditions, these crèches can become displaced or intermixed. Nevertheless, chicks must be able to return to their place in the colony to allow their parents to find and feed them.

While we know that crèching behaviour is essential for chick survival (Le Bohec, Gauthier-Clerc, & Le Maho, 2005), dynamics of interactions between crèche members have been largely overlooked and unexplored. Previous experiments demonstrated that chicks are highly motivated to return to their crèches if displaced, and they do so successfully both during the day and at night, and both individually and in groups (Nesterova, Mardon, & Bonadonna, 2009; Nesterova et al., 2014). Crèches are social units in which there are many possibilities for information transfer. For example, chicks can have different levels of experience with their surroundings. Just before fledging, chicks make excursions outside of their crèches alone or in small groups (personal observation). Consequently, if chicks are displaced, it may pay them to follow more experienced members of the group when attempting to return to the original crèche location. Whether such individuals can be recognized by others and whether recognition is, indeed, at all necessary for information transfer are fascinating questions that remain to be investigated.

To address whether and how the presence of experienced individuals affects the navigational performance of a group of king penguin chicks, we experimentally created two types of groups in which chicks differed in their level of navigational experience. We focused our efforts on the simplest kind of group, i.e. pairs. Naïve pairs (NP) were composed of two chicks that had not been displaced before. Mixed pairs (MP) consisted of one naïve chick and one experienced chick. The 'experienced' chick was designated as such because it had had previous experience in navigating back to its crèche individually after an experimental displacement. Naïve chicks had never previously been moved from their crèches.

To examine the effect of experience on group navigation, we performed three types of comparisons between naïve and experienced chicks. First, to measure the effect of homing experience, we compared the performance of the experienced chicks from MP to that of the naïve chicks from NP. We hypothesized that the experienced chicks would exhibit better homing performance than naïve individuals. Second, we compared the performance of MP and NP chicks to test whether the presence of an experienced individual improves the navigation of its naïve partner and the entire group. We hypothesized that experienced chicks would lead their naïve partners towards the colony, given their extra navigational experience with the area, and that MP would outperform NP in terms of efficiency and speed. Finally, we compared the navigational performance of an experienced chick and its naïve partner within each pair. We tested whether an experienced chick influenced its partner, resulting in increased naïve chick performance when the two birds walked together, compared with parts of homing journeys when they walked independently.

## METHODS

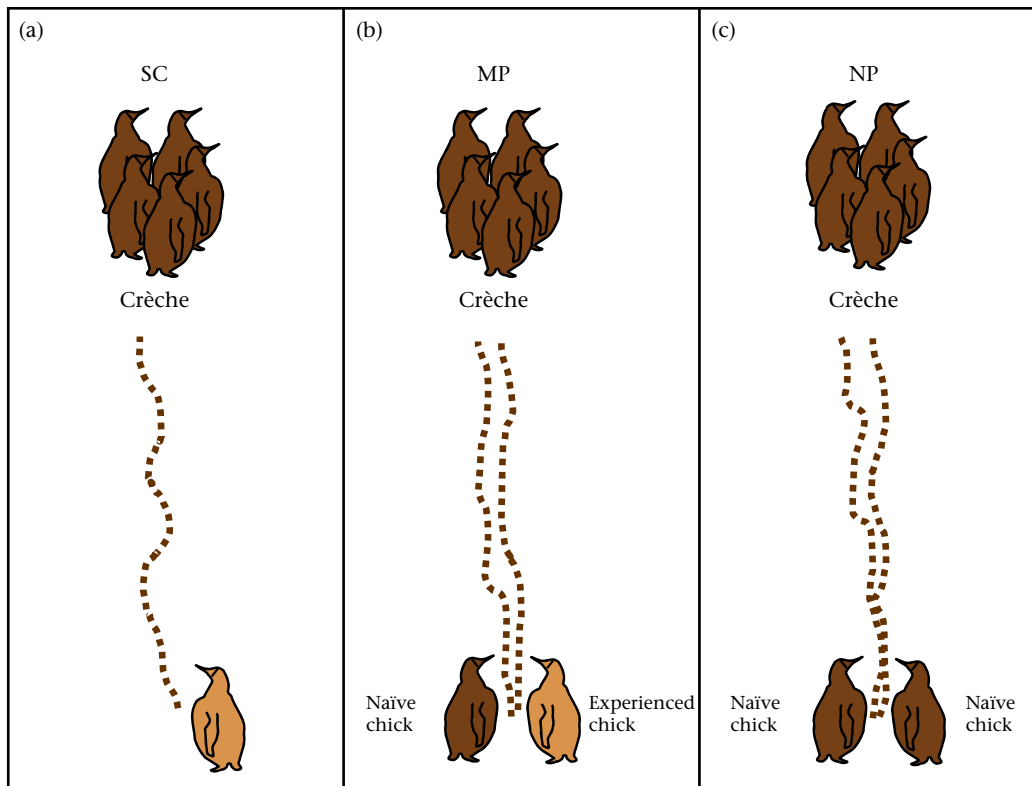
### Field Experiments

We conducted our experiments on 10–11-month-old king penguin chicks at Ratmanoff colony, Kerguelen Island (70°33'E, 49°14'S) during November–December 2011. The chicks' age was estimated based on their size and moulting condition (Stonehouse, 1960; Weimerskirch et al., 1992). During experiments, we captured chicks at their crèches and transported them to an experimental arena from where they were later released. The circular arena, bordered by a fabric barrier (radius: 5.2 m; barrier height: 1 m), was situated south from the colony on a small plateau. The distance between the arena and the capture locations ranged from 111 m to 185 m, with a mean  $\pm$  SE of  $141 \pm 2.19$  m. Crèches from which chicks originated were not visible from the arena.

Immediately after capture, we covered the chicks' eyes with a cotton hood, rotated them three times at the capture site, transported them to the arena along a nondirect path, and rotated them again three times. These procedures were performed to eliminate the use of internally generated cues during the return journey to the crèche. In the arena, we fitted chicks with a 17 g (<0.2% of body weight) GPS logger (Qstarz International Co., Ltd., Taiwan) at the base of one flipper and a coloured Tesa tape band on the other flipper to help with visual identification during the test. The GPS loggers acquired positional fixes (geographical longitude and latitude, error  $\pm 4$  m) at 5 Hz resolution. We marked chicks with green Porcimar (KRUUSE, Lageskov, Denmark) on the chest to identify individuals that had already been part of an experiment.

Chicks spent the first 10 min in the arena to recover from any potential stress associated with the capture and to prevent any bias in the release direction. Then the arena barrier was lowered and chicks were free to leave. We observed chicks' homing remotely by means of binoculars, and we videotaped trials when possible. After 1 h, we recaptured the chicks to remove GPS loggers and Tesa bands. We kept Tesa bands on the chicks that were scheduled to be tested twice (see below). All Tesa bands were removed after the second trial. After recapture, chicks were released in their crèches.

To investigate the effect of experience on navigation, chicks were subjected to three treatments: solo chick (SC), mixed pair (MP) and naïve pair (NP) releases (Fig. 1). In the SC treatment, naïve chicks (chicks that had not previously participated in any releases) were captured and released individually in the arena ( $N = 10$  chicks). All chicks that were released individually later participated in the MP releases. In the MP treatment, two chicks were captured simultaneously and released in pairs; one of the chicks in the pair



**Figure 1.** Experimental set-up. Chicks were displaced from their crèches and released as (a) solo chicks, released for the first time (SC), (b) as mixed pairs (MP) composed of an experienced (released for the second time) and a naïve chick (released for the first time) and (c) as naïve pairs (NP).

was an ‘experienced’ chick (in that it had previously successfully completed a solo release), while the second chick was a naïve chick that was found within 1–2 m of the experienced chick at the moment of capture ( $N = 10$  pairs). Among the experienced chicks, the period between the two subsequent captures (first capture for SC release and second capture for MP release) was 3–12 days, with a mean  $\pm$  SE of  $6.7 \pm 0.99$  days. In the NP treatment, two naïve chicks that were standing within 1–2 m of each other were captured and released together in the arena ( $N = 15$  pairs). Across all the treatments, experienced chicks were released twice (SC then MP); all other chicks (naïve chick in MP and naïve chicks in NP) were released only once.

Trials for the SC, MP and NP treatments were conducted in random order, with the constraint that (1) an experienced chick in the MP treatment should by definition have previously completed its solo release, and (2) that no more than two trials of the same treatment were conducted in a row. The trials were intermixed with trials for other experiments.

#### Data Analysis

Before processing, tracks were smoothed by calculating a moving average with a 1 s window. For all analyses we trimmed tracks to start once chicks had reached 4 m outside the arena barrier and ended when the chicks arrived within a 30 m radius of their capture location. At the time of experiments the crèches were spread out due to mild weather conditions. Consequently, chicks that arrived within 30 m of their capture location were usually within their crèches already, and we considered them as ‘homed chicks’ (Nesterova et al., 2014). For chicks that never reached the 30 m boundary, we used the full hour of track data prior to recapture and manual return to the colony.

From the track data we calculated the following variables. Speed was defined as the average of the instantaneous speeds calculated between all consecutive pairs of GPS fixes. The total track length was calculated as the sum of the distances between all consecutive pairs of GPS fixes. Homing precision measured how precisely a chick returned to its capture location. It was defined as the minimum distance to the capture location reached within 1 h after the release. If a chick returned exactly to its capture location, its homing precision was said to be 0. Efficiency was calculated as the ratio of the shortest distance between the start and end points of the track to the total track length. To investigate leader–follower relationships in moving pairs, we determined which individual was in front (with respect to the pair’s direction of movement) at any given point during the homing journey, and calculated the pair’s dynamic interaction index (DI). A DI index measures the degree of dynamic interaction in movement direction and movement displacement between individuals in a pair (Calenge, 2006; Long & Nelson, 2013). In our analyses we used an overall DI index that includes both displacement and direction. The `DI_func.R` script used in our calculations can be found within the `wildlifeDI` package ([cran.r-project.org/web/packages/wildlifeDI/index.html](http://cran.r-project.org/web/packages/wildlifeDI/index.html)).

To test whether proximity to the colony affected homing, the tracks of solo chicks were partitioned into two segments of approximately equal length. Chicks usually encountered conspecifics during the second half of their journey, but not in the beginning. The first segment included part of the track that lay between 4 and 60 m from the arena barrier, and the second segment 60 m from the arena barrier to 30 m from the capture location. We then compared speed and efficiency of these segments.

The distance between chicks in a pair varied throughout their journey. A threshold of 11 m, established in our previous study

(Nesterova et al., 2014), determined whether chicks were said to be walking together or not by examining the instantaneous interchick distances. As a result, two tracks, matched in time, that are part of a given paired release can be broken down into segment-pairs where the two chicks are considered to be walking together ( $\leq 11$  m apart) and segment-pairs where they are considered to be walking independently ( $> 11$  m). In our analyses, we analysed full tracks as well as segments together and separately.

To quantify whether chicks released twice showed any similarity between their routes, we looked at the difference in inter-route distances within and between individuals. Inter-route distance was measured as the mean distance from each point of one track (the focal track) to the nearest neighbouring point of the other track (the reference track). The calculations were then repeated reciprocally (i.e. the focal track became the reference track, and vice versa), and the values were averaged to give a single inter-route distance value for the two tracks. If repeated releases of the same chick showed track similarity, we expected inter-route distances within individuals (i.e. when comparing the second, MP release of an experienced chick with its first, SC, release,  $N = 10$ ) to be smaller than inter-route distances of two different individuals (MP release of an experienced chick compared to any SC release other than its own,  $N = 90$ ). To quantify the differences, we used route similarity values (RSV) defined as a difference between 'different chick inter-route distances' and 'same chick inter-route distances'. Consequently, for each experienced chick, its 'same chick inter-route distance' was paired with each of the nine 'different chick inter-route distances', resulting in 90 paired routes. Smaller RSVs would correspond to relatively little similarity between two routes of the same individual. We used a two-tailed Wilcoxon signed-rank test to determine whether the median RSV was significantly different from zero. We explored the similarity of routes in the beginning (first segment), middle (second segment) and end (third segment) of a homing journey. The track segments were defined as follows: the first segment included part of the track between 4 and 34 m from the arena barrier, the second segment was 34–64 m from the arena barrier and the third segment included the rest of the track, 64 m from the arena barrier to 30 m from the capture location.

Paired  $t$  tests were used to compare (1) speeds and (2) efficiencies of the first and second segments of SC tracks. We used  $t$  tests to compare (1) speeds and (2) efficiencies of experienced chicks in MP and chicks in NP (one randomly chosen partner in each pair); (3) speeds and (4) efficiencies of naïve chicks in MP and chicks in NP (one randomly chosen partner in each pair); (5) DI indices between MP and NP; (6) proportions of a journey when a chick was in front between MP and NP; and (7) distances travelled together between MP and NP. Linear mixed models (LMM) were used to compare (1) speeds of experienced and naïve chicks walking together or alone in MP (fixed effects: experienced/naïve chick, together/alone; random effect: pairs; repeated measurements: together/alone) and (2) speeds of MP and NP (fixed effect: MP/NP; random effect: pairs). Generalized linear mixed models (GLMM) with a gamma error distribution and a log-link function were used to compare (1) efficiencies of experienced and naïve chicks walking together or alone in MP (fixed effects: experienced/naïve chick, together/alone; random effect: pairs; repeated measurements: together/alone), (2) efficiencies and (3) homing precision of MP and NP (fixed effect: MP/NP; random effect: pairs). Generalized linear models (GLM) with gamma distribution and log-link function were used to compare interpartner distances in MP and NP. We used a linear model (LM) to explore relationships between mean speed differences and the distances chicks travelled together. Pearson correlation was used to relate the changes in

efficiency between the first and second release of experienced chicks and inter-route distances. As the comparisons of (1) naïve chicks in MP with naïve chicks in NP and (2) all chicks in MP with all chicks in NP test the same hypothesis, we applied a Bonferroni correction. Consequently, the significance of these tests was assessed at the 0.025 level.

Throughout the paper we report mean values with associated SEs;  $P$  values are for two-tailed tests. 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.). The GPS track data associated with this experiment are available in the [Appendix](#).

#### Ethical Note

This study adhered to the ASAB/ABS, IPEV, Comité d'éthique pour l'expérimentation animale Midi-Pyrénées (MP/05/26/05/11) and the Oxford University Ethical Review committee's guidelines.

## RESULTS

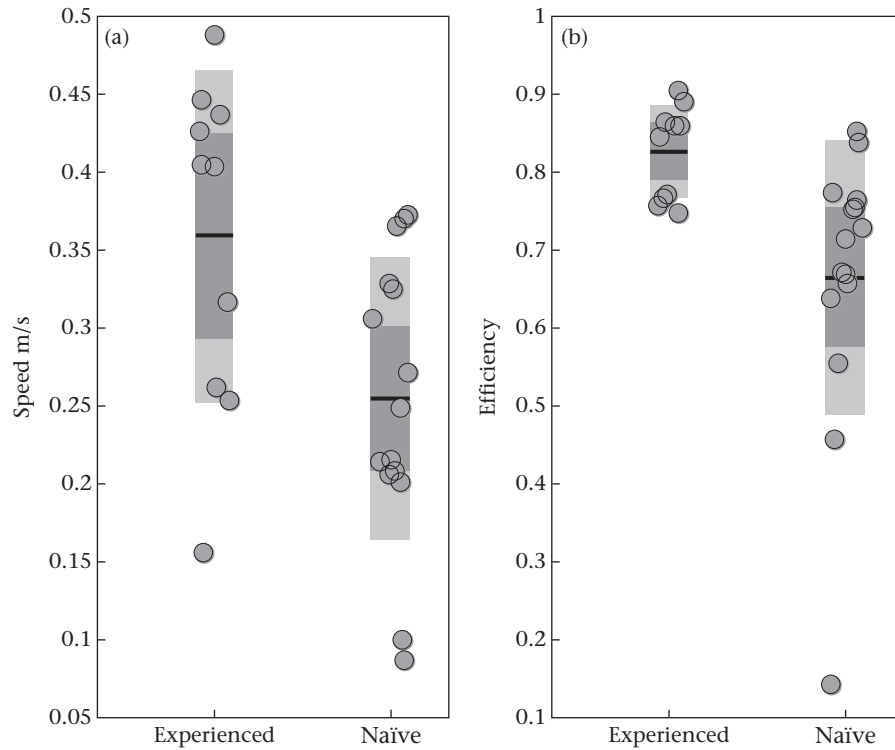
### *How Does Experience Change Navigational Performance of a Chick?*

Nine of 10 SC homed after their first release. The chick that did not home approached its capture location to within 33 m. The average homing efficiency of SC was  $0.695 \pm 0.038$ , and speed was  $0.216 \pm 0.026$  m/s. When released in pairs, experienced chicks in MP were considerably faster (Fig. 2a) and more efficient (Fig. 2b) than naïve chicks in NP (speed:  $t$  test:  $t_{23} = 2.632$ ,  $P = 0.015$ ; efficiency:  $t$  test:  $t_{23} = 2.778$ ,  $P = 0.011$ ). Moreover, experienced chicks had a tendency to recapitulate their previous solo routes during their second MP release. In particular, they showed significant self-similarity at the beginning and the end of their routes, while showing more variation in the middle ( $N = 90$  paired routes; beginning segment:  $RSV = 2.23 \pm 1.23$ ; Wilcoxon signed-rank test:  $Z = -2.018$ ,  $P = 0.044$ ; middle segment:  $RSV = 0.62 \pm 3.23$ ; Wilcoxon signed-rank test:  $Z = -0.718$ ,  $P = 0.473$ ; end segment:  $RSV = 6.31 \pm 2.36$ , Wilcoxon signed-rank test:  $Z = -2.477$ ,  $P = 0.013$ ; see also Fig. 3). Chicks that had a particularly inefficient route during the first release changed their routes, leading to a relatively large improvement in efficiency. This is evidenced by the positive correlation between change in efficiency and inter-route distance among two releases (Pearson correlation:  $r_9 = 0.655$ ,  $P = 0.040$ ).

### *How Does an Experienced Chick Affect Group Performance?*

Both MP and NP showed collective homing for at least part of their journeys (Appendix Figs A1, A2). Only one MP never walked together, and the naïve chick in this pair did not reach its crèche during the 1 h experimental time. MP chicks tended to split up earlier along their homing journeys than NP chicks which walked collectively most of the way ( $t$  test:  $t_{23} = -2.232$ ,  $P = 0.036$ ; Tables 1, 2). As expected, the distances that two chicks travelled together depended on their speed differences (LM:  $N = 25$  pairs (MP + NP),  $F_{1,23} = 7.099$ ,  $P = 0.014$ ; Table 2). Homing precision was similar for MP and NP chicks (GLMM, log link, gamma:  $F_{1,48} = 2.308$ ,  $P = 0.135$ ; Table 2).

Figure 4 shows individual speeds and efficiencies of SC, MP and NP chicks over their entire homing journeys. MP partners (Fig. 4a, b) showed greater differences in their navigational performance than NP partners (Fig. 4c, d). However, we wanted to determine the effect of the experienced individual on the navigation of a group, which is why we then focused only on the parts of the tracks where chicks were walking together. For these track segments, efficiencies

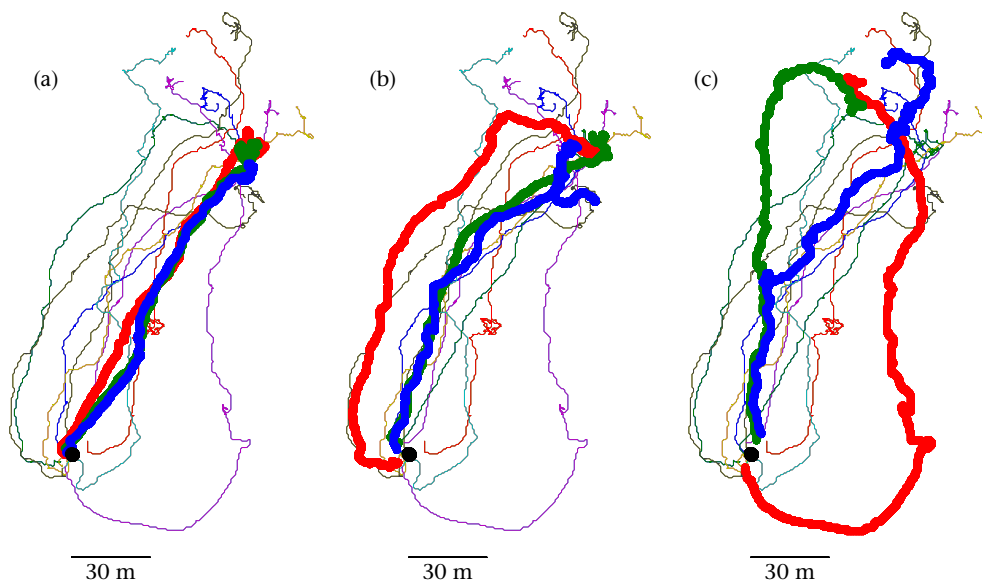


**Figure 2.** (a) Speed and (b) efficiency of experienced chicks in MP ( $N = 10$ ) and naïve chicks in NP ( $N = 15$ ). Circles give the observed values, black lines indicate means, dark grey boxes 95% confidence intervals around the mean and light grey boxes standard deviations.

of naïve chicks in MP and naïve chicks in NP (one randomly chosen partner from each pair) were not significantly different ( $t$  test:  $t_{22} = 0.111$ ,  $P = 0.912$ ; naïve MP =  $0.788 \pm 0.034$ , NP =  $0.784 \pm 0.018$ ), but naïve chicks in MP were faster than NP chicks ( $t$  test:  $t_{22} = 2.608$ ,  $P = 0.016$ ; naïve MP =  $0.360 \pm 0.029$ , NP =  $0.262 \pm 0.023$ ). Similar results were obtained when all individuals in each pair were considered. The presence of an

experienced chick had an effect on the walking speed of the pair, and MP chicks were faster than NP chicks (LMM:  $F_{1,22} = 8.494$ ,  $P = 0.008$ ; Fig. 5a, Table 2) but the efficiencies of MP and NP chicks were not different (GLMM, log link:  $F_{1,46} = 2.617$ ,  $P = 0.113$ ; Fig. 5b, Table 2).

Guidance by experienced chicks can further be detected when examining the spatial organization of the group. Experienced chicks



**Figure 3.** Individual tracks showing different degrees of route similarity between a given chick's first and second release. Thick red lines correspond to the tracks during the first release of a chick (SC), thick green lines to the second release of the same chick (experienced chick in MP) and thick blue lines to the partner of an experienced chick (naïve chick in MP). Thin lines represent tracks of all solo chicks. A black dot indicates the release location, the arena centre. Tracks of the same individual during the first and the second release show (a) high similarity (mean inter-route distance = 3.7 m), (b) some similarity (mean inter-route distance = 17.9 m) and (c) little or no similarity (mean inter-route distance = 51.0 m).

**Table 1**  
Pair homing parameters (mean  $\pm$  SE) for MP chicks ( $N = 10$  pairs) and NP chicks ( $N = 15$  pairs)

	Distance together (m)	DI
MP	75.6 $\pm$ 12.3	0.470 $\pm$ 0.048*
NP	118.9 $\pm$ 13.5	0.302 $\pm$ 0.043

DI was calculated for the part of tracks when chicks travelled together.

\*  $N = 9$  pairs; one MP pair never walked together and therefore was not included in the analyses.

spent more than 50% of the time in front (one-sample  $t$  test:  $t_8 = 2.702$ ,  $P = 0.027$ ; Table 2) during segments when MP walked together (see Supplementary video). In NP, on the other hand, the two naïve partners spent roughly equal proportions of time in front (one-sample  $t$  test:  $t_{14} = 0.006$ ,  $P = 0.996$ ; Table 2). Moreover, chicks' movements were less correlated as measured by the DI index when both partners were naïve compared to when the pair included an experienced individual ( $t$  test:  $t_{22} = 2.537$ ,  $P = 0.019$ ; Table 2, Fig. 5c).

#### How Does an Experienced Chick Affect Partner's Performance?

The fact that 90% of MP split up before reaching their destination allowed us to examine further how naïve chicks were affected by their experienced partners. Consequently, we examined the performance of a chick within a journey by comparing its speed and efficiency before and after splitting from its partner. Walking with an experienced partner increased both the speed and efficiency of naïve chicks (Fig. 6). The speed of naïve chicks dropped significantly after they separated from their experienced partners (LMM: effect of experience:  $F_{1,8} = 10.215$ ,  $P = 0.013$ ; effect of walking together:  $F_{1,15} = 13.762$ ,  $P = 0.002$ ; interaction:  $F_{1,16} = 5.417$ ,  $P = 0.033$ ). Similarly, the efficiency of naïve chicks decreased after separation from their experienced partners (GLMM, log link: effect of experience:  $F_{1,32} = 8.057$ ,  $P = 0.008$ ; effect of walking together:  $F_{1,32} = 3.584$ ,  $P = 0.067$ ; interaction:  $F_{1,32} = 4.501$ ,  $P = 0.042$ ; Fig. 6b). Experienced chicks, on the other hand, maintained relatively high speeds and high efficiencies even when they were walking independently.

To test the possibility that differences observed in speeds and efficiencies were due to the different level of chick experience or presence of a partner and not to the fact that chicks were closer to the colony during the second half of the journey, we compared speeds and efficiencies of SC during the first and second halves of their journey and found no differences ( $N = 10$  SC; speed: first part =  $0.282 \pm 0.047$  m/s, second part =  $0.213 \pm 0.023$  m/s; paired  $t$  test:  $t_9 = 1.240$ ,  $P = 0.246$ ; efficiency: first part =  $0.767 \pm 0.041$ , second part =  $0.727 \pm 0.033$ ; paired  $t$  test:  $t_9 = 1.010$ ,  $P = 0.339$ ).

## DISCUSSION

Our study examined how the presence of an experienced individual affected navigation in king penguin chick pairs. We found that chicks' navigational performance improved with repeated releases. When released in pairs, experienced chicks were faster and

more efficient than naïve chicks that were also released in pairs. Moreover, experienced chicks tended to take a leading position when travelling with a naïve partner. Overall, mixed pairs moved faster than naïve pairs, but the efficiencies of the two groups were not significantly different. Detailed examination of individual tracks over entire journeys revealed that the navigational performance of naïve chicks improved if they stayed with their experienced partners: they were faster and more efficient than when they walked alone. Experienced chicks, on the other hand, maintained their relatively high speeds and efficiencies irrespective of whether they walked with a partner or independently.

Our results suggest that chicks remember and learn from the previous homing experience. It should be noted that in this particular study, we focused on how different levels of experience affect navigation within a group, and we did not examine how navigational performance would change with repeated solo releases. When released in pairs, experienced chicks moved considerably faster and more efficiently than naïve individuals also released in pairs. Moreover, chicks that had particularly inefficient routes during their first journey improved these during their second release. Otherwise, chicks showed a tendency to follow their own routes, in particular by recapitulating the beginning and the end of their trips. The lack of similarity for the middle portion of the track is probably due to the presence of the transitory adult groups that often change their location in space and time and might have affected the chicks' paths. Given the short displacement distances, it is hard to estimate the immediate advantages of chicks' ability to retrace their own route or their ability to follow the familiar landmarks, which could also result in the route similarity. However, this might become important later on in life when an individual has to find its breeding place within the crowded colony.

Many pairs walked part of the way together and then split. When walking collectively, mixed pairs travelled faster than fully naïve pairs. The differences in efficiencies between the two groups were less pronounced, but became more evident when tracks were examined in more detail. Specifically, we compared the performance of the same individuals in mixed pairs as they walked collectively and independently. The results revealed that naïve chicks were not only considerably faster but also more efficient when they travelled together with an experienced partner. Experienced chicks, on the other hand, maintained relatively high speeds and efficiencies regardless of whether they walked with a partner or alone. Thus, while navigation of naïve chicks in mixed pairs was influenced by their experienced partner, the naïve chicks themselves had, in contrast, no effect on their partner's movements. Route familiarity appears to override any physical or social cues from a partner during homing, and the benefits of returning faster to the colony seem to outweigh any advantages of collective homing.

When comparing naïve and mixed pairs, we observed an interesting shift in leadership dynamics. In naïve pairs, in which chicks had similar levels of experience, leadership was divided more or less equally between group members, and both chicks took turns in leading and following. Such leadership dynamics were also observed previously for naïve pairs whose members originated

**Table 2**  
Individual homing parameters (mean  $\pm$  SE) for MP chicks ( $N = 10$  pairs) and NP chicks ( $N = 15$  pairs)

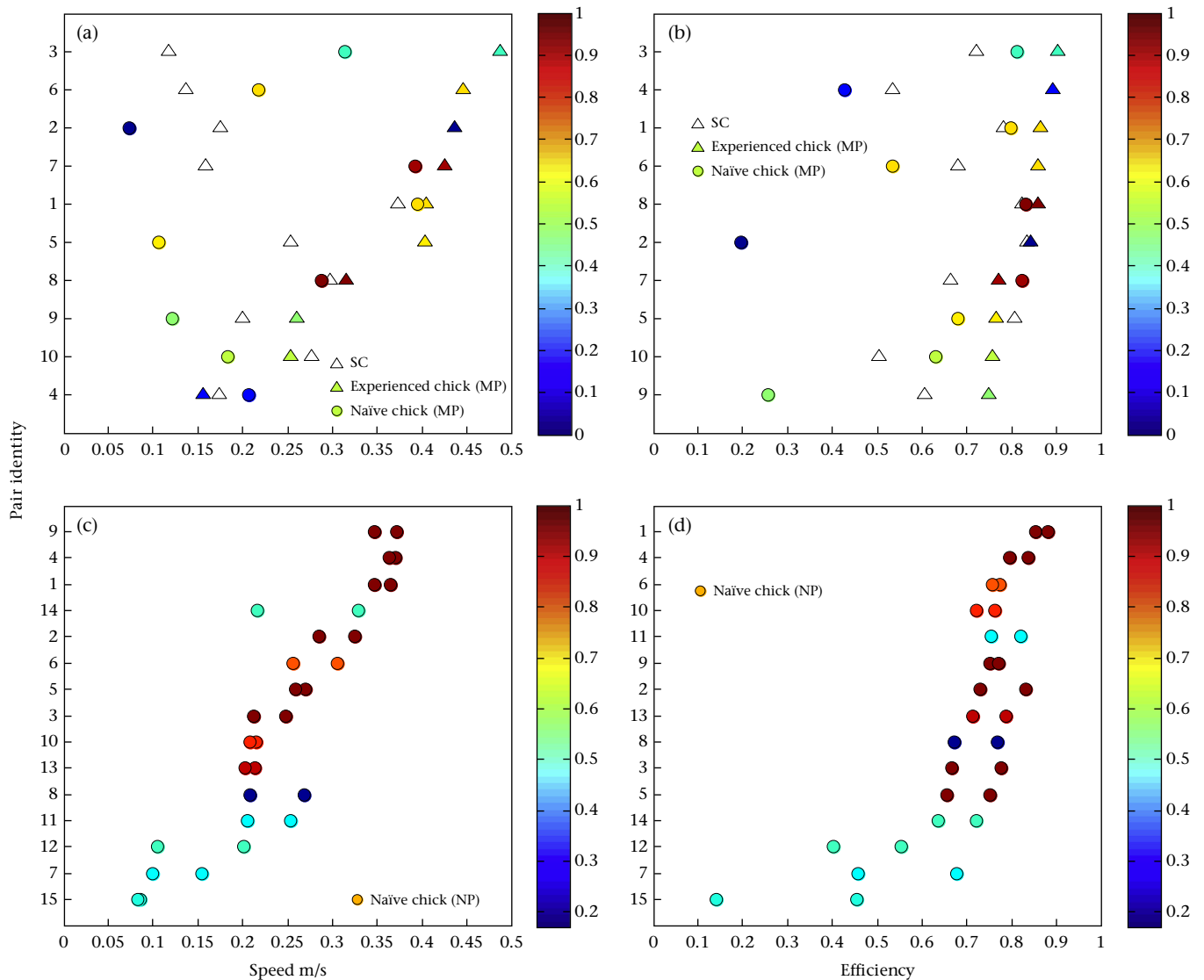
	Homing precision (m)	Speed (m/s)	Efficiency	Proportion of time in front	Proportion of trip distance walked together
MP	16.3 $\pm$ 6.0	0.376 $\pm$ 0.021*	0.806 $\pm$ 0.020*	0.694 $\pm$ 0.071 <sup>†,‡</sup>	0.555 $\pm$ 0.064*
NP	9.8 $\pm$ 2.8	0.274 $\pm$ 0.016	0.756 $\pm$ 0.017	0.500 $\pm$ 0.045 <sup>‡</sup>	0.730 $\pm$ 0.050

Speed and efficiency were calculated for the part of tracks when chicks travelled together.

\*  $N = 9$  pairs; one MP pair never walked together and therefore was not included in the analyses.

<sup>†</sup> Calculated for the experienced chick.

<sup>‡</sup> Calculated for one randomly chosen partner in each NP.



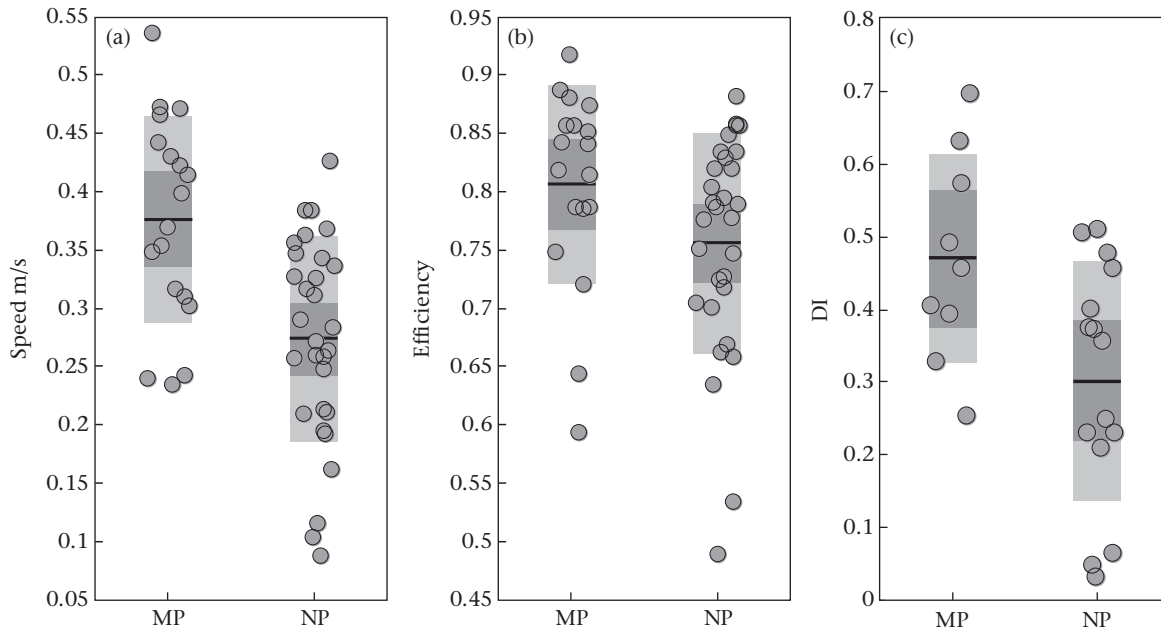
**Figure 4.** (a) Speeds for SC and MP chicks, (b) efficiencies for SC and MP chicks, (c) speeds for NP chicks and (d) efficiencies for NP chicks. Triangles correspond to solo releases (SC), and circles represent paired releases (MP and NP). The colour of the symbols indicates the proportion of time a pair of chicks walked together, from dark blue when chicks spent no time together to dark red when chicks walked together all the way. Pairs are ordered from the lowest to highest speed or efficiency of an experienced chick in MP or one randomly chosen naïve chick in NP.

from different crèches (Nesterova et al., 2014). Yet, in mixed pairs, the experienced chicks took the lead most of the time. This is not surprising given their higher speeds. In pigeons, faster ground speeds are known to correlate with leadership (Pettit, Perna, Biro, & Sumpter, 2013), with higher speeds allowing birds to ‘get out in front’ and dominate collective movements. In addition, simulations performed by Pettit, Perna, et al. (2013) suggest that speed differences alone can be responsible for the emergence of leadership. Having a consistent leader for most of the journey in penguin chick pairs could also explain why the movements of two partners in mixed pairs were more correlated than in naïve pairs. Our findings that experienced individuals tend to lead are in agreement with previous experimental work. Flack et al. (2012) demonstrated that pigeons with less experience tended to follow more experienced partners, as long as the difference between the two birds’ levels of experience was large enough. Similarly, naïve female guppies have been shown to follow their trained partners to a food source and to learn the particular route demonstrators were using (Laland & Williams, 1997).

One of the unexpected results of our study is the relatively early split of mixed pairs compared to naïve pairs. Travelling alone outside of the colony is dangerous for a chick. Giant petrels (*Macronectes* spp.) hunt king penguin chicks by separating an individual from a group and then attacking it (Le Bohec, Gauthier-Clerc, Gendner, Chatelain, & Le Maho, 2003). Therefore, we would expect chicks to try to minimize their time alone by travelling together to their crèches. We have observed similar splitting behaviour previously in pairs of naïve chicks where two partners came from different crèches and, therefore, had a conflict over their preferred destinations (Nesterova et al., 2014). However, in the present experiment, both partners of each pair were captured at the same location, and thus had the same destination. Therefore, they could have potentially travelled together to their crèches as many naïve pairs did. Yet, in mixed pairs, naïve chicks did not maintain the high speeds throughout their journey and often fell behind their experienced partners.

There are several explanations that could potentially account for the early split of mixed pairs. First, experienced chicks could have

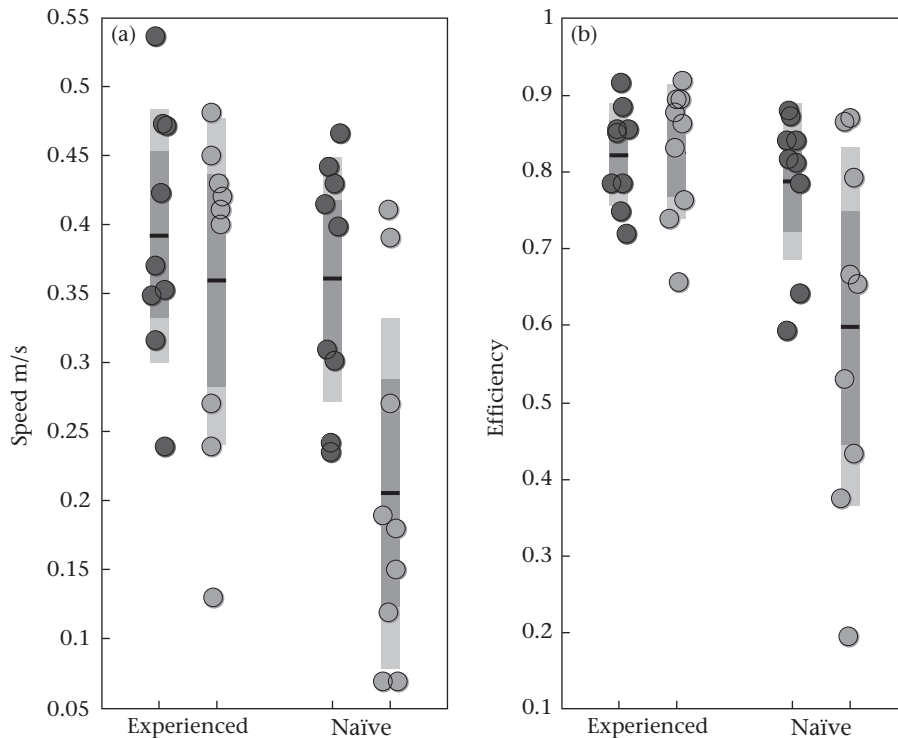




**Figure 5.** (a) Speeds, (b) efficiencies and (c) dynamic interaction (DI) indices of MP and NP chicks when they walked together. Circles give the observed values, black lines indicate means, dark grey boxes 95% confidence intervals around the mean and light grey boxes standard deviations.

simply outpaced their naïve partners. However, there is no reason to assume that naïve chicks were not able to keep up with their experienced partners. In fact, not travelling alone and reducing the time outside of the colony would have been beneficial for naïve chicks. Second, splitting in mixed pairs could have been associated with proximity to the colony. As chicks approached the colony, naïve individuals could have been distracted by the presence of other conspecifics, could have felt safer, or could have seen their crèches and, consequently, stopped following their partners. Yet,

when we compared navigational performance of chicks released individually during their first and second parts of the journey, we did not find differences in their speeds and efficiencies. In addition, many naïve pairs continued to travel together even as they approached the colony. Third, naïve chicks took an active role in navigation, and did not always choose to follow their partners. Naïve chicks might have required more time to decide on the direction of movement, while experienced chicks were already familiar with the landscape and moved ahead without waiting for



**Figure 6.** (a) Speeds and (b) efficiencies of experienced and naïve chicks in MP as a function of whether they walked together (dark grey circles) or separately (light grey circles). Black lines indicate means, dark grey boxes 95% confidence intervals around the mean and light grey boxes standard deviations.

their partner. As chicks approached the colony the importance, for a naïve individual, of providing input into the direction of movement might have outweighed the benefits of being in a pair, leading to the pair splitting. In naïve pairs, on the other hand, both chicks had similar speeds and both chicks could have contributed to the direction of movement. It has been reported that naïve pigeons also have an input in determining a pair's route when flying together with a more experienced individual (Pettit, Flack, Freeman, Guilford, & Biro, 2013).

Whether animals can benefit from their experienced partners depends on release distance. For example, in experienced/naïve pigeon pairs released 10 km from the loft, naïve birds benefited from their experienced partners and performed better than pigeons in naïve/naïve pairs (Banks & Guilford, 2000). In that study, half of the experienced/naïve pigeon pairs and no naïve/naïve pairs arrived together at the loft (i.e. they split up at some point during the journey, although in the absence of tracking data we cannot be sure when splits happened). However, when such pigeon pairs were released 25 km from the loft, naïve birds in mixed pairs did not follow their experienced partners (Guilford & Chappell, 1996). Very few pairs arrived at the loft together (0.08% of naïve/naïve pairs, 0.16% of experienced/naïve pairs). What we observed in king penguins is rather different: many naïve pairs walked almost all the way collectively, while mixed pairs stayed together only for a part of the journey. Release distances used in our experiment are typical of the displacement distances that king penguin chicks can encounter on a daily basis, owing to weather or predator-induced disturbance. Whether group behaviour would change at the longer release distances or in larger groups remains to be investigated.

In their model Couzin, Krause, Franks, and Levin (2005) demonstrated that effective information transfer within a group can take place even when the identities of informed individuals are unknown to the rest of the group; hence explicit signalling is not necessary for relevant information to exert an influence on the collective. In the present study, information transfer within mixed pairs seemed to happen only for a part of the journey before pairs split up. These findings raise questions regarding individual recognition and its advantages for information transfer within groups. Can king penguin chicks recognize their crèche mates and their level of experience? In our experiments, it would have been beneficial for naïve chicks to travel all the way with their experienced partner if they recognized their crèche mates. Otherwise, the potential costs of arriving at a wrong place inside the colony might outweigh the immediate benefit of arriving there quickly.

In conclusion, our results suggest that naïve king penguin chicks travel faster when they home collectively with an experienced individual. However, chick pairs tend to split up when only one individual is leading, even if the leader is the individual that is the better informed of the pair. Experience alone is sufficient in determining leadership within pairs.

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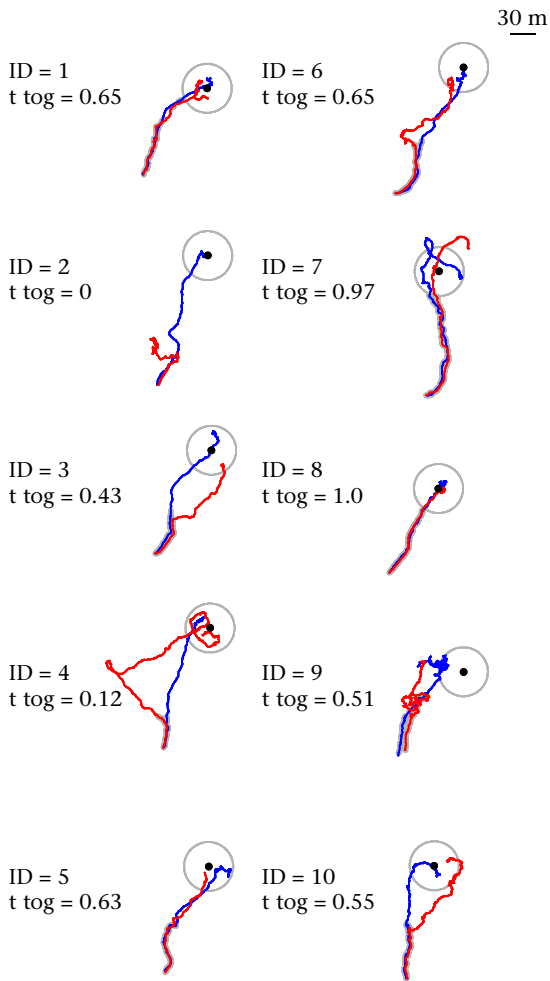
## Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2015.03.008>.

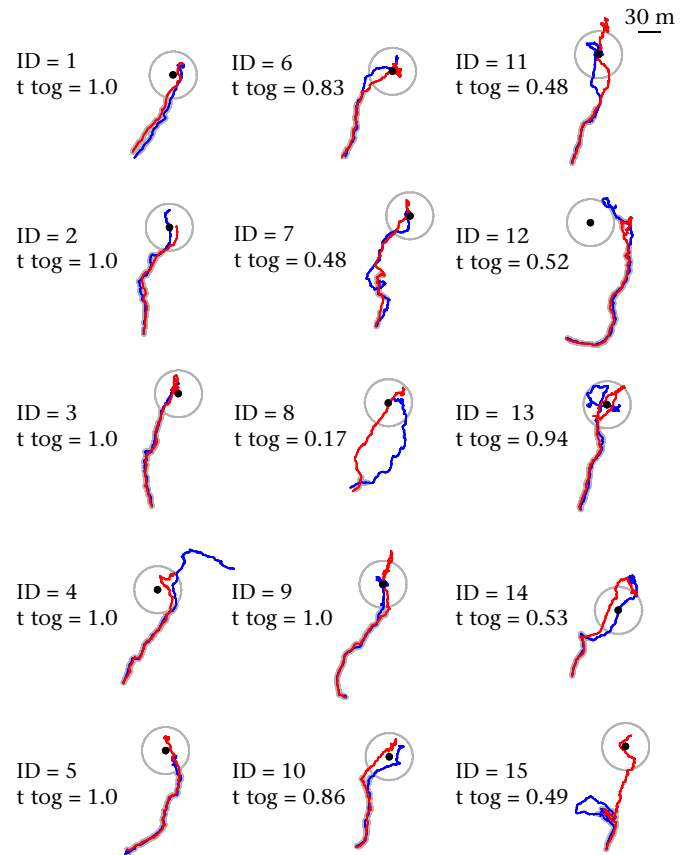
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## APPENDIX



**Figure A1.** Complete individual chick tracks during MP releases. Tracks of experienced chicks are shown in blue, tracks of naïve chicks are shown in red and capture locations are indicated as black dots. Grey circles indicate a 30 m radius around the capture locations. The track segments where chicks were walking together are highlighted in grey. Proportions of trip time that chicks travelled together (from release until they arrived within a 30 m radius from their capture location) are given next to each pair of tracks (t tog). ID = pair identity.



**Figure A2.** Complete individual chick tracks during NP releases. Tracks of two partners in each pair are shown in blue and red and capture locations are indicated as black dots. The track segments where chicks were walking together are highlighted in grey. Grey circles indicate a 30 m radius around the capture locations. Proportions of trip time that chicks travelled together (from release until they arrived within a 30 m radius from their capture location) are given next to each pair of tracks (t tog). ID = pair identity.