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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.

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, Cowlishaw, 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; Chamaillé-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 ± SE of 141 ± 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 ±4 m) at 5 Hz resolution. We marked chicks with green Porcimark (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