

Orientation in a crowded environment: can King Penguin (*Aptenodytes patagonicus*) chicks find their crèches after a displacement?

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SUMMARY

For seabird species, the presence of conspecifics in a crowded breeding colony can obstruct locally available orientation cues. Thus, navigation to specific locations can present a challenging problem. We investigated short-range orientation in King Penguin (*Aptenodytes patagonicus*) chicks that live in a large and densely populated colony. The two main objectives were to determine whether chicks displaced to a novel location away from the colony (i) can orient towards the colony and return to their crèche and (ii) rely on visual or non-visual cues for orientation. To address these questions, a circular arena was constructed 100 m away from the colony. Chicks were released in the arena during the day and at night. After the orientation experiment in the arena, chicks were allowed to return to their home crèche, if they could. Our results showed that, during day trials, chicks preferred the half of the arena closer to the colony, but not at night. However, at night, birds spent more time on ‘the colony half’ of the arena if the wind blew from the colony direction. When animals were allowed to leave the arena, 98% of chicks homed during the day but only 62% of chicks homed at night. Chicks that homed at night also took longer to find their crèche. The experiments suggest that King Penguin chicks can find their crèche from a novel location. Visual cues are important for homing but, when visual cues are not present, animals are able to make use of other information carried by the wind.

Key words: short-range orientation, King Penguin, *Aptenodytes patagonicus*, chick, visual landmark.

INTRODUCTION

Navigation in many colonial species poses a riddle, given the current understanding of short-range navigation. Once an animal arrives closer to its goal, it must rely on local methods of orientation that allow fine-scale positioning (reviewed in Shettleworth, 1998). For example, pigeons (*Columba livia*), when arriving in the familiar area of the loft, pay attention to the visual features of the landscape around it; and birds that have been prevented from learning these features have problems in locating the loft (Gagliardo et al., 2007). Several species of nocturnal petrels (*Procellariiformes*) are known to use olfactory cues at the last stages of homing when they look for their burrows at night (Bonadonna and Bretagnolle, 2002). However, the presence of many conspecifics in dense colonies can obstruct any locally available cues, whether they be visual, olfactory or auditory, making short-range orientation especially challenging. The sun, stars and the Earth’s magnetic field seem to be unaffected by the proximity of many conspecifics but such types of cues usually provide useful information for orientation over larger distances (at least several kilometres) (Lohmann et al., 2007; Wiltschko and Wiltschko, 1999; Wiltschko and Wiltschko, 2003; Wiltschko and Wiltschko, 2005) (but see Phillips et al., 2002). In spite of these challenges, colonial animals are successful at homing within a colony.

This conundrum of orientation is especially apparent in the case of King Penguins (*Aptenodytes patagonicus*). King penguins live in densely populated colonies that can stretch for over several kilometres along the shore and sometimes consist of as many as 300,000 breeding pairs (Aubin and Jouventin, 1998; Weimerskirch et al., 1992). The flightless nature of penguins adds an additional layer of complexity for orientation in the terrestrial breeding colony.

Unlike other colonial birds, King Penguins cannot hover above the colony to obtain an aerial view of its structure and its potential landmarks. King penguins do not build nests; instead, they incubate a single egg and brood a chick on the top of their feet. Mates alternate parental duties, with one foraging at sea while the other attends to the egg or young chick. Once chicks become capable of self-thermoregulation, they are left alone in the colony while both parents forage and periodically come back for feedings. While waiting for their parents to return, chicks form groups called ‘crèches’ (Barrat, 1976; Stonehouse, 1960). As a result, each parent returning from a foraging trip at sea is faced with the complicated task of finding its partner on the egg or on a young chick, or an older chick in a crèche in the colony. Chicks, as well as adults, are faced with navigational challenges. In order to be found by the parents, they must remain in the crèche. These places are known as ‘rendezvous’ zones, and are the locations where the chicks were last fed (Dobson and Jouventin, 2003; Stonehouse, 1960). Within these zones, parents and chicks are extremely efficient at identifying each other based on their individual vocalizations (Aubin and Jouventin, 1998; Jouventin, 1982; Jouventin et al., 1999). However, it is not a trivial task for a chick to maintain fidelity to a rendezvous zone. Extensive rainfall can cause flooding, which forces chicks to temporarily abandon their places. Giant petrels (*Macronectes* spp.) that prey on chicks can split and drive crèches away from their original location or separate individuals from a crèche (Descamps et al., 2005; Le Bohec et al., 2003; Stonehouse, 1960). In addition, colony growth, disturbances created by elephant seals (*Mirounga leonina*) passing through and inclement weather conditions can all force chicks to move away from a rendezvous zone (A.P.N., J.M. and F.B., unpublished observations).

Possession of an ability to find a specific place in the colony is crucial for the survival of King Penguins but little is known about their orientation on land. On the flat relatively featureless beaches, densely distributed individuals obstruct most of the local visual cues. Sound from the colony can be a good guiding cue as King Penguins approach the colony. However, the sound has been shown to be ineffective at distances of more than ~8.8 m for individual recognition (Dobson and Jouventin, 2003; Lengagne et al., 1999). Therefore, we still do not understand the orientation mechanisms used by colonial sea birds to reach their place in the colony.

The goal of the present study was to investigate the short-range orientation abilities in King Penguin chicks and to analyse the mechanisms involved. We hypothesised that visual cues are important for orientation and designed two experiments to test this. In the arena experiment, we manipulated visual cues and observed the directional preference of chicks (towards vs away from the colony). Then, in the homing experiment, we tested the ability of chicks to home during the day (all visual cues present) and during the night (limited visual cues present).

METHODS

Animals and study area

We studied King Penguins (*Aptenodytes patagonicus* Miller 1778) from December 2007 to January 2008 at a colony situated at Cape Ratmanoff, Courbet Peninsula, Kerguelen Island (70 deg. 33' E, 49 deg. 42' S). This large colony stretches for over a kilometre from north to south on a flat sandy beach. Experiments were performed on chicks that were approximately 10 months old and had not yet moulted into adult plumage. We used the size and moulting condition to estimate the age of the chicks (Stonehouse, 1960; Weimerskirch et al., 1992). We based our experiments on the fact that chicks are motivated to remain in the crèches in order to be fed by the parents and to reduce predation risks (Le Bohec et al., 2005). On multiple occasions, we observed chicks that participated in the experiments being fed by a parent. It is unlikely that removal of the chicks from a crèche had an affect on their feeding. Chicks were removed from a crèche only for relatively short periods of time, never more than 90 min. During this time of the year, parents usually come to feed chicks at intervals of several days, and adults can also remain on shore for several days (Weimerskirch et al., 1992). If a parent cannot find its chick right away, it repeats its efforts (Dobson and Jouventin, 2003).

Experimental arena

A circular arena (radius 3.2 m) was located 100 m south of the three experimental crèches (94 m from crèche 1, 101 m from crèche 2 and 107 m from crèche 3, Fig. 1). It was located on a small plateau that was elevated ~2 m above the colony level, and as a result the colony was not visible from inside or just outside the arena. The arena barrier was made from fabric, with a 1 mm mesh size, that was supported by metal poles. Raising or lowering the barrier during experiments allowed manipulation of the availability of visual cues. The ground in the arena was divided into four quadrants with painted lines running through the middle of the arena in north–south and east–west directions. A release box (0.8×0.55×0.4 m) was located at the west end of the arena. This box had two opposite doors to allow the introduction of the animal inside the box through the outside door and its release inside the arena through the other door. Two observation posts were established 5 m west and 5 m east of the arena. Such placement of the experimenters minimized the potential effect on the behaviour of the chicks as no bias was introduced in a chick's choice between the north and the south sides of the arena. The observer at the west post carried out the video recording and weather measurements. The observer at the east post timed animal movements in the arena. No chicks were seen in the arena location before the experiments.

Experimental procedure

Chicks were captured with a net at their crèches and fitted with a cotton hood that prevented them from seeing. We marked and recorded the coordinates of the capture location. Animals were hand-carried towards the arena along one of two L-shaped routes (Fig. 1). At the arena, chicks were rotated three times in order to prevent chicks from using path integration on their return. Indeed, other birds such as domestic geese (*Anser* spp.) are able to home after passive displacement if they have been able to see during their outward journey but not if the view has been shielded, presumably by using path integration (Von Saint Paul, 1982).

Chicks were then marked with colored Tesa tape on their chest and back and fitted with a global positioning system (GPS) collar on the neck. The GPS collar consisted of a Velcro band to which a 13 g GPS (TechnoSmArt) was attached, which constitutes approximately 0.1% of the mass of a bird. A 1.5 m string was also attached to allow removal of the collar without recapturing birds.

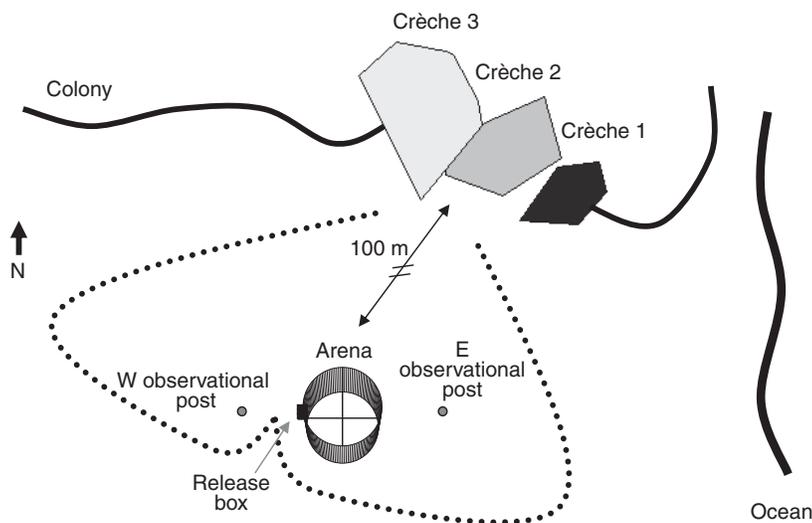


Fig. 1. Experimental arena. A circular arena was constructed 100 m away from the three experimental crèches. Chicks were carried from the crèches to the arena along one of the two routes (dotted lines) and were later released through the release box (black rectangle at the west end of the arena). The observations were conducted from two observational posts – east and west (gray circles). The thick gray line represents the edge of the colony, and the thick black line indicates the ocean. Drawing is not to scale.

Marked chicks were placed into a release box. The hood was removed once chicks were in the box, and the first door was closed. After 1 min, the second door – allowing access to the arena – was opened from a distance using a system of strings. The timing of the trial started once the chick stepped out of the box.

Before each trial, we measured the extent of any cloud cover and the direction and speed of wind at the height of the chick. Sky conditions were visually assessed using a 0–8 scale, where 0 represented a completely clear sky and 8 a completely overcast sky. To determine the direction of the wind, we used a weather vane and compass, while the wind speed was measured with a digital anemometer to the nearest decimetre per second.

Trials were organised in two parts. The first part tested the orientation of the chick in the arena, and the second part tested the ability of the chick to home to its crèche. We manipulated the availability of visual cues in two ways: (i) by conducting trials during day and night and (ii) by using different heights of the arena walls (high vs low barrier) during day trials. With the ‘high-barrier night’ configuration, the view of any landmarks was extremely limited. The ‘high-barrier day’ configuration (0.9 m) prevented animals from seeing the detailed landscape during the day but potentially allowed them to see the very general features of the environment, such as the land–sky outline, through the fabric mesh. The ‘low-barrier day’ configuration (0.7 m) was lower than the height of a chick and allowed the animal to see all the features of the landscape. Trials were partially videotaped.

Day trials

Each day trial started with the high-barrier configuration. During a 15 min period, we noted movements of the chick between quadrants and the amount of time it spent in each quadrant. After the first 15 min in the arena, the high barrier was lowered to 0.7 m (low-barrier treatment). When lowering the barrier, two researchers simultaneously approached the arena at the east and west ends and pushed the fabric down the metal poles while moving clockwise. Chicks were observed for another 15 min with the low barrier. Then the barrier was lowered completely and chicks were allowed to leave the arena. The homing chick was focally observed at a distance of approximately 50 m until it got to what was considered a homing distance from the capture location in its crèche (20 m). We also ensured that chicks remained in their home crèche for 5 min before ending the trial. At the end of the trial, one observer crawled towards the chick and pulled on the string to retrieve the GPS collar.

A total of 42 chicks were tested in day trials. All chicks expressed searching behaviour in the arena. On a few occasions, chicks escaped the arena before the end of the low-barrier test. These tended to be bold individuals that repeatedly pushed on the barrier, and eventually they were able to fall over it. As a result, 37 chicks completed high-barrier trials, and 26 completed both high- and low-barrier trials.

Night trials

Night trials were conducted between 23:30 h and 02:30 h when no sunlight was present. These trials were similar to the day trials, with a few exceptions. Animals were not subjected to the lower barrier treatment and were released after the first 15 min in the arena. Reflective tape was used to mark chicks and important locations in the colony such as crèches and capture locations.

At night, birds are more wary and removal of the GPS collar could have disturbed them. Therefore, chicks were not fitted with the GPS collar. Instead, an observer carrying the GPS device

followed each chick at a distance of approximately 15 m, retracing its path. Chicks did not show any reaction to observers at such a distance. Particular care was also taken not to disturb other birds in a crèche, and the observers always walked very slowly. In the arena, chick movements were monitored by a camcorder with infrared lamps (Sony DCR-HC38 night shot and IRLamp6 from Bat Conservation and Management, Carlisle, PA, USA). Night-vision binoculars were used to follow animals outside of the arena. A total of 22 chicks were tested at night.

Any animals that failed to come back to their crèche within 1 h were recaptured and returned to their crèche.

Data analysis

To determine whether chicks can orient towards the colony, we analysed the amount of time they spent on the north and south halves of the arena as the colony was located north of it (Fig. 1). The chick was said to prefer the north half of the arena if it spent more than half of the total testing time (>450 s) there. A chi-square test was used in this analysis.

To compare the performance of the chicks between different treatments such as ‘high-barrier day’ *versus* ‘high-barrier night’, we analysed the number of seconds animals spent in the north half of the arena using Mann–Whitney tests. When the same animal performed in several treatments, such as in ‘high-barrier day’ and ‘low-barrier day’ treatments, a Wilcoxon signed ranks test was used. We also analysed whether northerly winds (coming from north, north-west or west directions), blowing approximately from the direction of the colony, and southerly winds (coming from south, south-east or south-west) had an influence on the behaviour of chicks (no north-east winds were recorded during experiments; west winds were grouped together with north and north-west winds because they also carried the noise from the colony, based on the perception of a human observer). As in the previous comparisons, we analysed the number of seconds chicks spent in the north half of the arena by means of Mann–Whitney tests.

The level of activity of a chick in the arena was assessed based on the number of transitions between each quadrant it made. A chick was considered to have moved from one quadrant to another if it had completely crossed the line separating the quadrants. The activity level was compared between different treatments by means of Mann–Whitney or Wilcoxon signed ranks tests.

After chicks left the arena, we noted whether they homed and how long it took them to reach their crèche. We compared the ability to home (Fisher exact test) and homing duration (Mann–Whitney test) between the day and night trials. To investigate the influence of sky conditions on homing, we compared homing time under a partially cloudy sky (1–7) with the homing time under a completely overcast sky (8) (Mann–Whitney test).

GPS trajectory data were collected for 33 chicks during the day and 18 chicks at night. From GPS homing data, we extracted the total length of the path (D_t) and the beeline distance (D_s) between the starting point (arena) and the end-point of the path. As a measure of the ‘straightness’ (optimality) of the path of a chick, we used the ‘linearity index’, LI, defined as $LI = D_s/D_t \leq 1$. Consequently, LI values approaching 1 would indicate animals following a path close to the shortest one. We also analysed the distribution of chicks at 10 m and 30 m from the arena, distances at which the colony was still not visible (Rayleigh and Watson U^2 tests).

Non-parametric tests were chosen for the analysis because not all data satisfied normality assumptions. All reported tests are two tailed.

RESULTS

Orientation in the arena

All chicks walked freely around the arena upon release. During day trials, more chicks preferred the north half of the arena: in the high-barrier treatment, 27 out of 36 animals and in the low-barrier treatment 21 out of 26 animals (χ^2 test, day trials, high barrier: $N=36$, $\chi^2_{1}=9$, $P=0.003$; day trials, low barrier: $N=26$, $\chi^2_{1}=9.846$, $P=0.002$, Fig. 2). This preference for the north side was less pronounced during night trials, where 14 out of 20 animals preferred the north half (χ^2 test, night trials, high barrier: $N=20$, $\chi^2_{1}=3.2$, $P=0.074$, Fig. 2). The obstruction of visual cues with the high barrier during the day did not affect the behaviour of chicks in the arena. The amount of time chicks spent on the north side of the arena during high- or low-barrier treatment was not significantly different (Wilcoxon signed ranks test, $N=26$, $Z=-1.486$, $P=0.137$, Fig. 2). The activity levels of chicks were similar during day and night trials (Mann–Whitney test, $N_{\text{day}}=33$, $N_{\text{night}}=22$, $U=294.5$, $P=0.238$) and between low- and high-barrier treatments during the day (Wilcoxon signed ranks test, $N=25$, $Z=-1.458$, $P=0.145$).

Indeed, the direction of the wind affected the position of chicks in the arena during night trials, but not during day trials (Fig. 3). At night, birds spent more time in the north half of the arena if they experienced northerly winds (Mann–Whitney test, night trials, high barrier: $N_N=16$, $N_S=6$, $U=18.500$, $P=0.030$). During day trials, the wind direction did not significantly influence the orientation of the chicks (Mann–Whitney test, day trials, high barrier: $N_N=26$, $N_S=11$, $U=100.0$, $P=0.153$; day trials, low barrier: $N_N=16$, $N_S=10$, $U=76.0$, $P=0.856$).

Homing

The ability to home was drastically different between daytime and night-time. During the day, 98% of animals reached their crèche, whereas only 62% of animals homed at night (Fisher exact test, $N=63$, $P<0.0001$). Chicks that were able to return to their crèches at night took longer compared with the chicks that homed during the day (median_{night}=27 min, IR=41.50; median_{day}=14 min, IR=15.75; Mann–Whitney test, $N_{\text{day}}=42$, $N_{\text{night}}=13$, $U=153.0$,

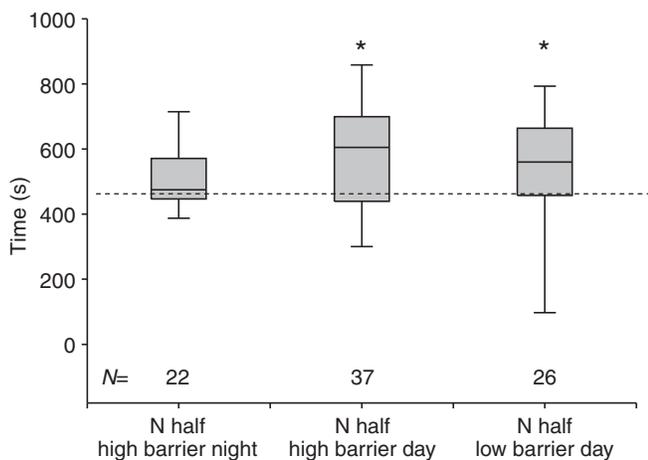


Fig. 2. Time spent in the north half of the arena. Box plots show medians and interquartile ranges for the time (s) chicks spent in the north half of the arena for the high-barrier night, high-barrier day and low-barrier day treatments. The dashed line indicates 450 s, one half of the testing time. Numbers above the x-axis indicate the number of animals that completed the test. The medians for each condition are the following: high-barrier night northern half=475, high-barrier day northern half=605, low-barrier day northern half=560. Significant effects are indicated with an asterisk (*).

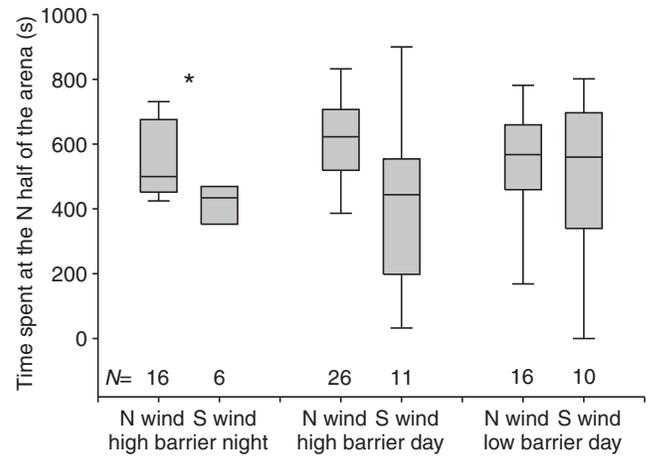


Fig. 3. The effect of wind on the orientation of chicks in the arena. Box plots show medians and interquartile ranges for the time (s) chicks spent in the north half of the arena when winds blew from the north or from the south directions for the high-barrier night, high-barrier day and low-barrier day treatments. Numbers above the x-axis indicate the number of animals that completed the test. The medians for each condition are the following: high-barrier night northerly wind=500, southerly wind=434; high-barrier day northerly wind=622.5, southerly winds=444, low-barrier day northerly wind=567, southerly wind=560. The significant effect is indicated with an asterisk (*).

$P=0.017$). Examples of some paths of chicks during the night and day are shown in Fig. 4. Northerly winds coming from the colony did not improve homing time during the day (Mann–Whitney test, $N_N=27$, $N_S=14$, $U=187.5$, $P=0.968$). The effect of the wind during the night could not be determined owing to a low sample size.

We also investigated the influence of sky conditions on the orientation of chicks. At night, we compared the homing abilities of chicks under completely overcast (8) and partially overcast skies (1–7). Sky conditions did not seem to affect their performance (Fisher exact test, $N=21$, $P=0.377$). Some birds were able to home even under completely overcast conditions (four chicks out of six homed), whereas others did not find their crèches with star or moonlight present (four chicks out of 15 did not home). In addition, homing time was not affected by the level of cloud cover during the day (Mann–Whitney test, day trials: $N_{1-7}=33$, $N_8=9$, $U=126.5$, $P=0.507$). The effect of the sky condition during the night could not be determined owing to the low sample size.

Neither during day nor during night did chicks go to their crèche along straight paths (day trials: $N=33$, LI median=0.32, IR=0.20; night trials: $N=18$, LI median=0.27, IR=0.30). Linearity index comparison for chicks that reached their crèches gave no indication that day and night paths differ in their straightness (Mann–Whitney test, $N_{\text{day}}=33$, $N_{\text{night}}=11$, $U=135.0$, $P=0.216$). Already at 10 m and 30 m away from the arena chicks were oriented towards their crèches (Rayleigh test, 10 m: $N_{\text{day}}=34$, $Z=11.16$, $P<0.001$; $N_{\text{night}}=18$, $Z=3.644$, $P=0.024$; 30 m: $N_{\text{day}}=34$, $Z=20.624$, $P<0.001$; $N_{\text{night}}=18$, $Z=5.608$, $P=0.003$; Fig. 5). There was no significant difference in the distributions of homing animals at 10 m (or 30 m) during the day and during the night (Watson U^2 test, 10 m: $N_{\text{day}}=34$, $N_{\text{night}}=18$, $U^2=0.074$, $0.5>P>0.2$; 30 m: $N_{\text{day}}=34$, $N_{\text{night}}=18$, $U^2=0.115$, $0.5>P>0.2$).

Once in their crèches, chicks often stopped near the capture site (median_{day}=9.0 m, IR=10.0; median_{night}=5.0 m, IR=5.5). Chicks approached their capture site more closely at night than during the day (Mann–Whitney test, $N_{\text{day}}=36$, $N_{\text{night}}=13$, $U=148.0$, $P=0.050$).

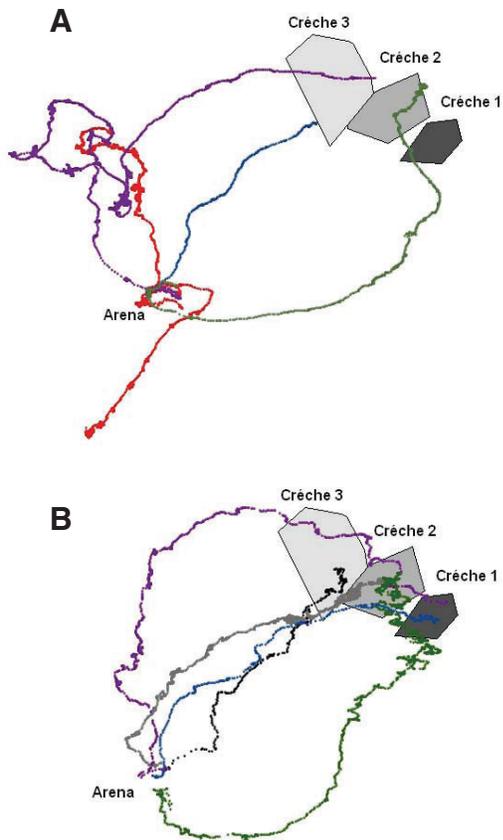


Fig. 4. The homing paths of chicks. (A) Five paths undertaken during the night and (B) five paths undertaken during day trials. Three crèches are represented by the gray polygons. In red are two paths of chicks that did not home at night. All chicks homed during the day.

Visual examination of homing trajectories revealed no dependence of the shape of the homing path on the particular crèche from which chicks were taken or on the route along which chicks were transported to the arena.

DISCUSSION

Our experiments showed that, during day trials (high- or low-barrier configurations), more chicks preferred the half of the arena that was closer to the colony. This preference was less pronounced during night trials. However, at night, birds spent more time on the north half of the arena if the wind blew from the direction of the colony. During the day, homing success was higher, and chicks homed faster than at night. Chicks homing at night stopped closer to their original capture location than chicks homing during the day.

Our results suggest that chicks at the age of ten months can orient towards the colony and find their specific place after a passive displacement. They remain close to the colony and do not usually wander away so far inland. Accidental displacement, however, due to bad weather or predation can occur, but over smaller distances [10–40 m (A.P.N., J.M. and F.B., unpublished observations)] than our experimental displacement (100 m). In this situation, the ability to home is adaptive for survival.

At night, crèches are more condensed for thermoregulatory purposes (Le Bohec et al., 2005) and, probably, owing to nocturnal predation by giant petrels (A.P.N., J.M. and F.B., unpublished observations). This might account for the observed differences

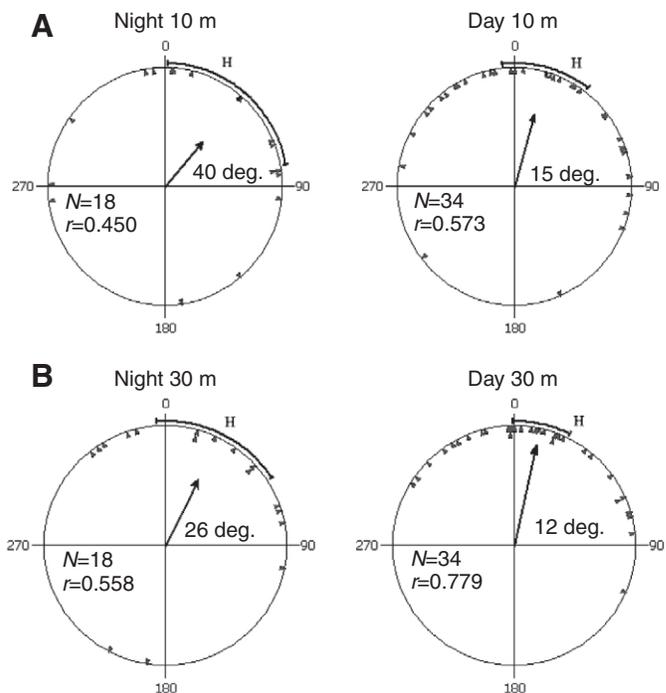


Fig. 5. Homing directions at distances of 10 m and 30 m away from the arena. Circular diagrams show the heading of chicks (blue triangles at the periphery) at (A) 10 m and (B) 30 m away from the arena during night and day trials. The arrow from the centre of the diagram indicates the mean heading direction vector. H, homing direction; N, number of birds; r, length of mean vector.

in homing accuracy between the day and night. Interestingly, the distance between the point where a chick stopped its homing trip and the original capture location is close to the average range of vocal recognition of 8.8 m reported for King Penguins (Lengagne et al., 1999). This suggests that chicks tended to return to their rendezvous zone where they could hear their parents. Chicks did not approach their crèches in a straight path, either during the day or during the night. When possible, they tried to join small groups of resting or moulting adults that could be found all around the colony. Moving from one group to another while homing might reduce predation risk through a dilution effect (Hamilton, 1971).

The drastic difference in homing rate between the day and night trials suggests that some cues that are available only during day time are especially important for orientation. The potential candidates are the sun and visual cues provided by the landscape. Our results suggest that the visibility of the sun did not affect the homing abilities of chicks. Even under completely overcast conditions during the day, chicks homed as fast as when the sky was visible. These findings are different from what was observed with Adélie Penguins (*Pygoscelis adeliae*) (Penney and Emlen, 1967; Penney and Riker, 1969). When released 340–1500 km away from the colony, Adélie Penguins were disoriented and lost under overcast skies but headed in the direction of their colony if the sun was visible. However, in the case of Adélie Penguins, the homing took place over a much larger scale – several hundreds of kilometres, whereas King Penguin chicks had to cover only 100 m. Many species of birds are known to use the sun for orientation but it usually functions as a compass to get the general bearings and not for fine-scale positioning (reviewed in Wiltschko and Wiltschko, 2003). At

the fine scale, information provided by the sun is presumably not useful or is not precise enough.

Most likely, King Penguin chicks relied on the visual cues of the landscape for orientation. The colony itself can serve as a visual landmark for the general direction of travel. However, in our experiments, chicks could not see the colony from the arena. The colony was also not visible at 10 m and 30 m away from the arena; nevertheless, the majority of the chicks headed in the correct direction.

Visual landscape landmarks other than the colony itself appear to be important for both initial orientation and homing. Even a limited view of the landscape was sufficient for initial orientation. During day trials with a high barrier, animals could potentially see through the fabric only the most prominent features of the landscape. A human observer could distinguish the outline of the horizon when looking through the fabric. The full view of the landscape, as with the low-barrier configuration, did not increase the amount of time chicks spent in the half of the arena that was closer to the colony. However, the presumably drastic reduction in visual cues due to darkness affected the behaviour of the chicks. The preference for the north half of the arena was more pronounced during day than night. Also, not all chicks homed at night, and homing time at night was longer.

The reduced ability to home and slow homing speed at night are unlikely to be explained by the difference in the activity levels as chicks were as active in the arena during day and night. Non-homing behaviour might also be attributed to the difference in the motivation to come back to a crèche. For example, chicks that were recently fed by the parents might not be as eager to return. We do not think that this is the case for two reasons. First, being in a crèche reduces predation risks (Le Bohec et al., 2005) and this should provide a strong motivation to home under any circumstances. Second, this potential bias and our random choice of birds for the experiment during the day and night should have affected the homing motivation of some chicks during the day as well but this was not observed.

Some chicks were able to home at night, and this ability seemed to be unaffected by the sky conditions. A few chicks homed even under completely overcast conditions, whereas other failed even with a moon and star light. This suggests that visual cues are not the only cues that penguins attend to. When visual cues were limited by the darkness, animals probably paid more attention to cues that were carried by the wind. At night, chicks spent more time in the north half of the arena if the wind blew from the colony direction. On the day trials with few visual cues available (high barrier), there was also a tendency for chicks to spend more time in the north half of the arena when the northerly (colony) winds blew, suggesting integration of visual and other cues whenever possible. This trend completely disappeared when full view of visual cues became available (low barrier), and the behaviour of animals was no longer influenced by the direction of the wind (Fig. 3). Surprisingly, wind direction affected the initial orientation but had no effect on the speed of homing. It is possible that cues carried by the wind are useful for choosing the general direction but are not useful for fine-scale homing.

The cues that can be carried by the wind are auditory and olfactory. Large colonies, as at Ratmanoff, produce a lot of noise. Humans can hear this colony as far as a kilometre away under favourable meteorological conditions. Knowing the superior auditory abilities of King Penguins, it seems likely that they use the colony noise as a compass, at least for initial orientation. Observations of Emperor Penguins suggest the same as later arrivals

in the season have little trouble finding the colony, probably because they are guided by its sound (Jouventin, 1971). Similarly, nocturnally migrating passerines such as Eurasian Reed and Sedge warblers (*Acrocephalus* spp.) pay attention to acoustic stimuli, such as songs of conspecifics, when they look for stopover sites at night (Mukhin et al., 2008).

It is harder to assess the importance of olfactory cues as little is known about the ability of King Penguins to perceive odours. In Adélie penguins (*Pygoscelis adeliae*), the olfactory bulb constitutes 17% of the cerebral hemisphere. Other species with an olfactory bulb of similar size such as diving petrels (*Pelecanoides georgicus*) and pigeons (*Columba livia*) – both 18% – have been known to use olfaction for orientation (Bonadonna et al., 2003; Wallraff, 2004). If the olfactory bulbs of King Penguins are alike, they potentially can use odours for orientation as well. Furthermore, preliminary Y maze experiments with African Penguins (*Spheniscus demersus*) suggest that they can orient towards dimethyl sulfide (Cunningham et al., 2006).

At the scale of movements we described, information of high resolution is necessary for the animals to home. We have demonstrated that visual cues are of primary importance as their absence at night cannot be completely compensated by the other cues present. Also, the present experiments proved that chicks can use different cues for orientation, probably by integrating information from all the sources. Future experiments will test the homing abilities of chicks during the day and night when the ears of the birds are covered or when chicks are made anosmic. The systematic removal of each set of cues should reveal its relative importance for orientation.

Another interesting aspect of chick homing that remains to be investigated is the development of orientation abilities. The need to find rendezvous zones in the crèches seems to be ever present because chicks have to be fed by their parents. There must be a strong selection pressure on the development of these abilities from a very early age. However, in order to home, birds might need to develop a cognitive apparatus or simply require time to learn the surroundings of the colony. Also, it would be interesting to know whether knowledge of the colony landscape (visual, auditory or olfactory) acquired during the crèching period is used later when the adults come back to breed at the colony.

Our experiments were the first of short-range orientation in a colonial seabird. King Penguin chicks demonstrated a strong ability to home to their crèches, and, at a finer scale, to find their rendezvous zone within the crèches. Even at the age of ten months, before chicks moult and first go to sea, they already have a well-developed orientation system.

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