Emperor penguin mates: keeping together in the crowd

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As emperor penguins have no breeding territories, a key issue for both members of a pair is not to be separated until the egg is laid and transferred to the male. Both birds remain silent after mating and thereby reduce the risk of having the pair bond broken by unpaired birds. However, silence prevents finding each other if the pair is separated. Huddles—the key to saving energy in the cold and the long breeding fast—continuously form and break up, but not all birds are involved simultaneously. We studied the behaviour of four pairs before laying. Temperature and light intensity measurements allowed us to precisely detect the occurrence of huddling episodes and to determine the surrounding temperature. The four pairs huddled simultaneously for only 6 per cent of the time when weather conditions were harshest. Despite this asynchrony, the huddling behaviour and the resulting benefits were similar between pairs. By contrast, the huddling behaviour of mates was synchronized for 84 per cent of events. By coordinating their huddling behaviour during courtship despite the apparent confusion within a huddle and its ever-changing structure, both individuals save energy while securing their partnership.

Keywords: huddling; synchronization; pairing; temperature; Antarctica

1. INTRODUCTION

Group formation is a widespread phenomenon throughout the animal kingdom, occurring in a wide range of taxa (Parrish & Edelstein-Keshet 1999) both in wild and domestic animals (Webster & Hurnik 1994; Brockett *et al.* 1999; Ruckstuhl 1999). Evolutionary theories suggest that joining a group increases the organisms' fitness (Parrish & Edelstein-Keshet 1999) by reducing the chance of being caught by a predator, increasing the foraging efficiency and reducing energy costs (Ruckstuhl & Neuhaus 2001; Krause & Ruxton 2002).

Synchronized behaviours occur when two or more animals perform behaviour switches at the same time (Dostálková & Špinka 2007). Breeding synchrony is a characteristic of colonial birds (Coulson 2002; Jovani & Grimm 2008) and emperor penguins (*Aptenodytes forsteri*) fit this picture. They reach their colony site in columns of hundreds. At Pointe Géologie colony, most birds arrive by early April, peak mating occurs in early May, peak laying follows in mid-May and peak hatching is in late July (Prévost 1961; Isenmann 1971). In contrast to other colonial birds, emperor penguins are unique in that they do not defend a territory once they have paired. The lack of territoriality and mobility is essential in enabling them to huddle together (Jouventin 1971), and huddling is the key to their ability to reduce their metabolic rate and therefore sustain prolonged fasts (Ancel *et al.* 1997). They breed during the Antarctic winter in a few favourable coastal areas where sea ice is secure. The colonies, such as the one located at Dumont d'Urville, may be 100 km from the

pack ice or polynyas where they feed (Ancel *et al.* 1992). The female fasts for approximately 45 days until she lays the egg and leaves the colony after passing it to the male. The male entirely assumes the task of incubation and fasts for approximately 120 days (Prévost 1961; Isenmann 1971). Without huddling, the males could fast only for approximately 60 days and therefore would not be able to incubate the egg until hatching (Ancel *et al.* 1997). A point usually not considered is that emperor penguins also huddle during periods of harsh weather, which occur during pairing.

The absence of an individual breeding territory enables the birds to huddle, but it presents the problem of a considerably higher risk of mates being separated once they are paired. Moreover, at Dumont d'Urville the females of emperor penguins outnumber the males, presumably because of a lower survival of males due to their long winter fast (Isenmann 1971; Jenouvrier *et al.* 2005). Once paired, emperor penguins do not sing until the egg is laid and this silence avoids unpaired females trying to disrupt the couple (Jouventin 1971). Since the songs of emperor penguins aid their individual identification, mates have to find other ways to avoid losing each other when moving into the colony. The exaggerated waddling gait of the first bird to go makes it easier for the partner to follow (Jouventin 1971). But what happens to the mates in the crowd of a huddle remains unknown.

Huddling is a complex phenomenon (Gilbert *et al.* 2006) involving adjustments in body temperature and a reduction of the exposed surface area of the body (Gilbert *et al.* 2007). The duration of huddles is very short, lasting only approximately 1.6 hours on average. The birds alternate in getting close to each other in huddles and breaking apart (Gilbert *et al.* 2006). However, it is rare

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that all birds present in the colony huddle together in one group. They usually form groups of varying sizes, especially during pairing. The density of huddles varies among and within groups; while some birds of one group are tightly huddling (ten birds a square metre; [Prévost 1961](#)), others are standing nearby in a loose aggregation. It was therefore of particular interest to find out whether the mates behaved similarly (i.e. showed synchrony) in such a heterogeneous and continuously evolving structure.

Many studies are devoted to synchrony within groups, such as arrival on the colony site ([González-Solís *et al.* 1999](#); [Gunnarsson *et al.* 2004](#)), breeding ([Emlen & Demong 1975](#); [Yom-Tov 1975](#); [Jovani & Grimm 2008](#)), egg-laying ([Kattan 1997](#); [Mermoz & Reboreda 1999](#)), vigilance ([Pays *et al.* 2007](#)), foraging ([Tremblay & Cherel 1999](#); [Ruckstuhl & Neuhaus 2001](#); [Rands *et al.* 2003](#); [Stone *et al.* 2003](#); [Takahashi *et al.* 2004, 2008](#); [Pütz & Cherel 2005](#); [Gautrais *et al.* 2007](#)), etc. However, the simple case when two animals attempt to coordinate a single behaviour switch has been poorly investigated ([Engel & Lamprecht 1997](#)) except for mathematical models of behaviour synchronization ([Rands *et al.* 2003](#); [Dostálová & Špinka 2007](#)). Group formation necessitates the cooperation of individuals and this reaches a high level in huddling emperor penguins. Thus our main goals were to determine whether emperors huddle in synchrony or not, both between and within pairs, and whether both pairs and mates get similar access to the warmth of the huddles.

2. MATERIAL AND METHODS

At Pointe Géologie colony (Adélie Land, 66°40' S, 140°01' E) four of the approximately 3000 emperor penguin breeding pairs were captured between 20 April and 2 May 2005, equipped with data loggers and then released in the colony to resume their breeding activities. Data loggers (Mk9, Wildlife Computers, Redmond, WA, USA, 30 g, 6.7 × 1.7 × 1.7 cm) were glued to the back feathers of all eight birds to record temperature (range: −40 to +60°C) and light intensity (arbitrary units, arb. units) of their environment at a sampling rate of 5 s. Internal clocks of the Mk9s were set to universal time. Around mid-May, females were recaptured when leaving the colony after having transferred their eggs to their mate and data loggers were removed. In late July, the equipped males were recaptured on their first post-incubation departure from the colony. A meteorological station (Météo France), situated 500 m away from the colony, provided wind speed (m s^{−1}) and temperature (°C) data. Wind chill (°C) was calculated according to the formula of [Osczevski & Bluestein \(2005\)](#).

Data were downloaded from data loggers and analysed first with HEXDECODE software (Wildlife Computers) and second with MT-DIVE software (Jensen Software Systems, Munich, Germany). Information from the light sensors indicated complete darkness (from 0 to 40 arb. units) when the birds were inside huddles. Combining the information from both temperature and light sensors ([Kirkwood & Robertson 1999](#); [Gilbert *et al.* 2006](#)), a bird's position was defined as 'isolated' (temperature approx. −10 to −15°C, i.e. corresponding to the environmental conditions in the colony, and light intensity approx. 80–100 and approx. 150–160 arb. units at night and during daylight, respectively) or 'grouped' (temperature higher than 0°C and light intensity lower than 40 arb. units). Civil night was defined as the time when the Sun was between 0 and 6 degrees below the horizon. When a bird was part of a

Figure 1. Representative example of temperature and light recordings on an emperor penguin's back (female 1 on 27 April) for two consecutive huddling bouts (between dotted lines). The first episode occurs during the night and the second at the onset of the day (see text for explanations).

huddle, the temperature rose and light levels suddenly decreased, indicating the onset of a huddling bout. Abruptly rising light levels and falling temperatures corresponded to the end of a huddling bout. We analysed the onset and the exit time of huddles, the duration of huddling bouts, the maximum temperature ($T_{\max}$) surrounding the bird, the mean temperature (T_{mean}) during the huddling bout and the temperature under the curve area (T_{uca}), which indirectly represents warmth benefits associated with huddling ([figure 1](#)). We also counted the number of huddling bouts per day and the total time spent huddling per day.

We compared these six parameters on inter- and intra-pair scales. For comparisons at the inter-pair scale, we analysed the 14 common days of data for the four pairs, from 2 to 15 May. For each pair, we took into account the latest onset and the earliest exit of a huddling bout held in common for both the male and the female. We then tested differences between pairs for the six huddling parameters using Kruskal–Wallis ANOVAs (distribution not normal). The same test was also used to investigate the influence of weather conditions on huddling synchrony between pairs, which was followed by a *post hoc* Dunn test. Five categories were defined: 0–4 pairs simultaneously engaged in huddling bouts. For intra-pair comparisons, we took into account the whole dataset for each pair (from 21 April to 19 May), encompassing all huddling episodes in common or not by both mates, and performed *t*-tests (normal distribution of data) and Mann–Whitney tests (when data distribution was not normal) for differences between males and females.

Statistical analyses were performed using SIGMASTAT (v. 2.03). Means are given $\pm$ s.d. in the text. Differences were considered significant when $p < 0.05$.

3. RESULTS

Equipped females laid eggs between 16 and 19 May, which coincides with the average egg-laying date at the Pointe Géologie colony ([Prévost 1961](#); [Isenmann 1971](#)). The breeding success of the four pairs was similar to that of non-instrumented pairs: of the four pairs studied, all but one were feeding their chick until October 2005. Mean wind chill at the colony during the study period (from late April until the end of the pairing period) was $-26.4 \pm 4.1^\circ\text{C}$. Equipped emperor penguins were part of huddles for relatively short periods

Figure 2. (a) Huddling bout durations from 2 to 15 May, representing the asynchrony between pairs; (b) detail showing huddling bouts recorded for the four pairs, held in common by both partners, revealed by external temperature during 6 May. Grey areas stand for civil night (black, pair 1; red, pair 2; green, pair 3; blue, pair 4).

(1 h 48 min $\pm$ 1 h 27 min, $n=905$). A high percentage of huddling episodes (503 out of 905, i.e. 56.7 $\pm$ 11.0%, $n=8$ pairs) were associated with considerable increases in ambient temperature to 20–37°C. Birds were exposed to temperatures above 20°C for 48 $\pm$ 8% of the time. Also, 72 per cent of the huddling events were strictly nocturnal, whereas only 13 per cent were strictly diurnal, the remaining 15 per cent straddling civil night and day (civil night averaging 73 $\pm$ 4% of time, $n=28$ days).

(a) Huddling behaviour at the inter-pair scale

To compare between pair behaviours, we analysed the huddling bouts that all pairs had in common. Huddling was highly asynchronous among pairs (figure 2) and they were huddling in unison only for 6 per cent of the time, while the categories '1 pair huddling' and '2 pairs huddling simultaneously' represented 61 per cent of huddling events and 53 per cent of time huddling, respectively (figure 3). In addition, weather conditions significantly influenced the inter-pair synchrony: when conditions were the harshest (mean wind chill of $-31.4 \pm 4.4^\circ\text{C}$), the four pairs huddled in unison and, at the other extreme, no pair was engaged in huddling bouts when conditions were more favourable ($-28.1 \pm 5.0^\circ\text{C}$; $H=35.2$, d.f. = 4, $p < 0.001$; figure 3).

Given this high degree of asynchrony, we examined whether pairs gained similar or different energetic benefits from huddling (table 1). The pairs engaged in an average of 4.3 ± 2.0 huddling bouts per day ($n=112$ days for the

Figure 3. Percentages of events (black bars) and time (grey bars) as a function of the number of pairs simultaneously engaged in huddling bouts and according to wind chill (top). Different letters indicate significant differences. Means $\pm$ s.e.m.

four pairs), T_{max} in the huddles averaged $26.2 \pm 9.7^\circ\text{C}$, T_{mean} was $15.6 \pm 9.2^\circ\text{C}$ and T_{uca} was $6.5 \pm 5.3^\circ\text{C}$.s ($n=482$ for the last three parameters). Huddling bouts lasted approximately 2 hours (135 ± 90 min, $n=482$) and the time spent huddling was on average 41 $\pm$ 15% per day ($n=112$ days for the four pairs). There were no significant differences between the four pairs for any of the parameters tested (table 1).

(b) Huddling behaviour at the intra-pair scale

At the intra-pair scale, we first aimed to determine whether mates huddled in unison or not (figure 4). During the study period, 762 out of 905 huddles were common to both members of a pair (i.e. 381 at the scale of the pair: 108, 111, 97 and 65 for pairs 1, 2, 3 and 4, respectively). Thus, in total, 84 per cent of huddling bouts were shared by the two mates, meaning that 16 per cent of huddling bouts occurred independently between partners of a pair. However, these independent huddling bouts were of a shorter duration than those for the common bouts (34 ± 29 and 122 ± 87 min, respectively; $U=23\,802$, $p < 0.001$). Moreover, of the 143 independent huddling bouts, only 60 (42%) were undertaken by females compared with 83 (58%) by males.

With regard to mutual huddling episodes, we tried to determine whether one member of the pair could be a potential leader by investigating the time difference in the onset and exit of huddling episodes between the two mates. For the onset, total synchrony occurred for 10 bouts and in 69 per cent of all cases the time difference in the onset of huddling between both mates was less than 5 min, with a mean time lag of 8.5 ± 16.9 min ($n=381$). The mean time lag of males entering huddles before females was 10.1 ± 19.1 min, whereas it was 7.0 ± 14.2 min ($U=29\,730$, $p=0.07$) for females. For the exit, total synchrony occurred for 41 bouts and in 94 per cent of all cases the time difference for both birds to end huddling occurred in less than 5 min, with a short mean exit time lag of 2.2 ± 11.7 min ($n=381$). Males initiated huddling more often than females (in 201 episodes versus 170 for females) while females ended huddling more often than males (in 193 cases versus 147 for males). There were no significant differences for the four pairs in the number of onsets and exits undertaken either by males or females ($t=1.97$, $p=0.14$ and $t=-1.35$, $p=0.27$, respectively).

Table 1. Parameters depicting the huddling behaviour for the four pairs (P1, P2, P3 and P4) and related statistics. (Means $\pm$ s.e.m. (n)). Temperature under curve area (T_{uca}) in product of temperature and time ($^{\circ}\text{C}\cdot\text{s}$); maximal temperature ($T_{\max}$) in $^{\circ}\text{C}$; mean temperature (T_{mean}) in $^{\circ}\text{C}$; number of huddling bouts per day ($H\text{ d}^{-1}$); percentage of huddling bouts per day ($\%H\text{ d}^{-1}$) and huddling bout duration (H_{dur}) in hours and minutes.)

	P1	P2	P3	P4	mean	H	F	d.f.	p -value
T_{uca}	6.8 ± 0.5 (108)	7.2 ± 0.6 (110)	6.0 ± 0.4 (134)	6.1 ± 0.5 (130)	6.5 ± 0.2 (482)	1.55		3	0.67
$T_{\max}$	25.2 ± 1.0 (108)	27.6 ± 0.9 (110)	27.0 ± 0.8 (134)	25.0 ± 0.9 (130)	26.2 ± 0.4 (482)	2.75		3	0.43
T_{mean}	14.4 ± 0.9 (108)	16.5 ± 0.9 (110)	16.8 ± 0.8 (134)	14.5 ± 0.8 (130)	15.6 ± 0.4 (482)		$F_{3,239} = 1.28$		0.28
$H\text{ d}^{-1}$	3.9 ± 0.4 (28)	3.9 ± 0.3 (28)	4.8 ± 0.4 (28)	4.6 ± 0.4 (28)	4.3 ± 0.2 (482)	3.25		3	0.35
$\%H\text{ d}^{-1}$	39.1 ± 2.7 (28)	40.4 ± 3.0 (28)	41.0 ± 3.3 (28)	42.0 ± 2.5 (28)	40.6 ± 1.4 (112)		$F_{3,55} = 0.13$		0.94
H_{dur}	2 h 26 min $\pm$ 0 h 09 min (108)	2 h 28 min $\pm$ 0 h 09 min (110)	2 h 02 min $\pm$ 0 h 07 min (134)	2 h 10 min $\pm$ 0 h 08 min (130)	2 h 15 min $\pm$ 0 h 04 min (482)	2.66		3	0.45

In view of this high synchrony, we investigated whether both mates get equivalent access to the warmth of huddles. No significant differences were found between the male and the female of each pair (table 2). Considering all pairs, males and females spent on average $38 \pm 16\%$ of their time huddling per day ($t = -0.69$, $p = 0.49$, $n = 180$ days for all pairs). Similarly, there were no significant differences between males and females in the number of huddling bouts per day (5.0 ± 2.5 ; $U = 7909$, $p = 0.50$, $n = 180$ days for all pairs), the mean duration of huddling episodes (1 h 48 min $\pm$ 1 h 27 min; $U = 201\,203$, $p = 0.72$), the temperature under curve area ($5.0 \pm 5.1\text{ }^{\circ}\text{C}\cdot\text{s}$; $U = 200\,331$, $p = 0.89$) and in the maximum ($21.7 \pm 11.6\text{ }^{\circ}\text{C}$; $U = 202\,105$, $p = 0.55$) and mean ($12.3 \pm 9.9\text{ }^{\circ}\text{C}$; $U = 197\,463$, $p = 0.557$) temperatures during huddling ($n = 905$ for the last four parameters).

4. DISCUSSION

Almost all penguin species breed in colonies (Reilly 1994) where synchrony occurs (Jovani & Grimm 2008), but the literature on synchronous behaviour rarely mentions these seabirds (but see Kirkwood & Robertson 1999), except in the context of foraging behaviour (Tremblay & Cherel 1999; Takahashi *et al.* 2004, 2008; Pütz & Cherel 2005). The pairing period of penguins is of particular interest since it is the only phase of the breeding cycle during which both sexes are present together in the colony for a long time (approximately 45 days in emperor penguins; Isenmann 1971). Usually, once penguins are paired, their partnership is secured by their breeding territory, which corresponds to their nest or burrow. King penguins (*Aptenodytes patagonicus*), the closest relatives of emperor penguins, share the peculiarity of having no nest. However, they stay in the same area of the colony where they vigorously defend a small territory (Challet *et al.* 1994; Côté 2000; Viera *et al.* 2008). The lack of breeding territory among emperor penguins, together with the mobility of the colony and of birds within the colony, introduces major constraints for a successful partnership. At the Pointe Géologie colony, females outnumber males by approximately 10 per cent (Jouventin 1971; Bried *et al.* 1999; Jenouvrier *et al.* 2005) and therefore the earlier a female returns at the beginning of the breeding cycle, the higher the probability that she will get a mate (Isenmann 1971). However, unpaired females increase the risk of splitting up pairs already formed. For females whose partner is taken by another female, the time to secure a new

Figure 4. (a) Huddling bout durations from 21 April to 14 May; (b) detail showing huddling bouts revealed by external temperature recorded for pair 1 (black, male; grey, female) during 5 May. Grey areas stand for civil night.

partnership extends the duration of an already long fast. This in turn increases the risk of breeding failure since abandonment is triggered once a threshold in body reserves has been reached (Groscolas 1986, 1988; Robin *et al.* 1988). For these reasons, birds remain silent once paired, until laying and egg exchange have been completed. This reduces the risk of a pair splitting up, as well as of breeding failure. While this silence avoids unpaired individuals disrupting the couple, it precludes any vocal identification by partners in case they lose each other. Indeed, the song of emperor penguins is the key to their individual identification (Jouventin *et al.* 1979; Aubin *et al.* 2000). It allows the mates to find each other for the short changeover of attendance duties, to take care and feed the chick from the time of hatching to the departure of the chick to the sea.

territoriality, the discontinuation of singing once mated and the fact that females outnumber males in the colony may explain the high intra-pair huddling synchrony.

In summary, the unique absence of territoriality among emperor penguins allows them to huddle and cope with long periods of fast. Emperor penguins may also be unique among colonial birds in their ability to synchronize their pair behaviour to avoid separation in the crowd and thereby secure both partnership and breeding success.

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