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New insights into the huddling dynamics of emperor penguins

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Social thermoregulation is a cooperative strategy in which animals actively aggregate to benefit from the warmth of conspecifics in response to low ambient temperatures. Emperor penguins, *Aptenodytes forsteri*, use this behaviour to ensure their survival and reproduction during the Antarctic winter. An emperor penguin colony consists of a dynamic mosaic of compact zones, the so-called huddles, included in a looser network of individuals. To maximize energy savings, birds should adjust their huddling behaviour according to environmental conditions. Here, we examined the dynamics of emperor penguin aggregations, based on photo and video records, in relation to climatic factors. Environmental temperature, wind and solar radiation were the main factors contributing to huddle formation. The analysis of individual movements showed that birds originating from loose aggregations continually joined huddles. Sometimes, a small number of birds induced a movement that propagated to the entire huddle, causing its breakup within 2 min and releasing birds, which then integrated into looser aggregations. Different parts of the colony therefore appeared to continually exchange individuals in response to environmental conditions. A likely explanation is that individuals in need of warmth join huddles, whereas individuals seeking to dissipate heat break huddles apart. The regular growth and decay of huddles operates as pulses through which birds gain, conserve or lose heat. Originally proposed to account for reducing energy expenditure, the concept of social thermoregulation appears to cover a highly dynamic phenomenon that fulfils a genuine regulatory function in emperor penguins.

Coloniality is the aggregation of individuals of the same species on a breeding ground remote from foraging sites (Kharitonov & Siegel-Causey, 1988). This kind of social reproduction is used by many species of vertebrates, and especially by seabirds among which more than 95% nest in colonies (Brown, Stutchbury, & Walsh, 1990). Living within a colony may entail costs in terms of intraspecific competition, spread of pathogens or travel distances (e.g. Kharitonov & Siegel-Causey, 1988; Krause & Ruxton, 2002). To be adaptive, coloniality has to bring fitness benefits that offset these costs (e.g. Danchin & Wagner, 1997; Dubois, Cézilly, & Pagel, 1988; Siegel-Causey & Kharitonov, 1991).

For some species, one main advantage of group living is social thermoregulation (Gilbert et al., 2010). This is a cooperative strategy that operates through both physiological and behavioural processes. It can be defined as the active aggregation of individuals to benefit from the warmth of conspecifics in response to low temperatures (Alberts, 1978; Gilbert et al., 2010; Martin, Fiorentini, & Connors, 1980). Huddling animals maximize energy savings by reducing the body surface area exposed to cold, thus decreasing heat loss, and by warming their surrounding environment. Huddling occurs in vertebrates as diverse as rodents, bats, primates and penguins (e.g. Gilbert, Blanc, Le Maho, & Ancel, 2008; Hayes, 2000; Ostner, 2002; Willis & Brigham, 2007). Huddles of emperor penguins, *Aptenodytes forsteri*, and crèches of king penguin chicks, *Aptenodytes patagonicus*, can involve thousands of birds, which cooperate to share warmth and decrease predation risk (Ancel, Visser, Handrich, & Le Maho, 1997; Gilbert, Robertson, Le Maho, Naito, & Ancel, 2006; Le Bohec, Gauthier-Clerc, & Le Maho, 2005; Prévost, 1961).

Huddling is probably a key factor allowing the colonization of particularly cold habitats by endotherms. Emperor penguins

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represent the most extreme example, as they are the only animals able to breed during the Antarctic winter, far from the open sea where they feed (Prévost, 1961). Their thermoneutral zone ranges from −10 to +20 °C, and they can withstand negative ambient temperatures only to a certain extent before increasing their metabolism to generate heat (Le Maho, Delclitte, & Chatonnet, 1976; Pinshow, Fedak, Battles, & Schmidt-Nielsen, 1976). However, when conditions deteriorate further (at −25 °C, the probability of huddling is ca. 80% for a wind speed of 0 m/s and 98% for a wind speed of 15 m/s, Gilbert, Robertson, Le Maho, & Ancel, 2008), behavioural strategies complement physiological strategies, which allows emperor penguins to save energy (Le Maho, 1977). Under similar weather conditions, free-ranging males that huddled maintained a metabolic rate 16% lower than captive males that were experimentally prevented from forming dense aggregations (Ancel et al., 1997).

When wind chill increases the cooling rate, emperor penguin colonies move downwind (Gilbert, Robertson et al., 2008; Prévost, 1961; Robertson, 1990). By contrast, when wind chill decreases, colonies move against the wind, presumably because birds tend to return to their usual sites to avoid areas of unstable ice. Therefore, colonies move back and forth under the influence of winds (Gilbert, Robertson et al., 2008). It is known that a major part of energy saving in loosely grouped birds is from mutual wind protection (Ancel et al., 1997). Low ambient temperatures, however, appear more influential than wind speed in inducing the formation of huddles (Gilbert, Le Maho, Perret, & Ancel, 2007; Gilbert, Robertson et al., 2008), but we do not know to what extent other meteorological factors can affect the grouping patterns of emperor penguins.

A colony of emperor penguins is spatially heterogeneous, consisting of several parts of varying densities (Gilbert et al., 2006). In the tighter aggregations called huddles, density can reach 8–10 birds/m^2 (Prévost, 1961), individuals step in a synchronized way (Gerum et al., 2013; Zitterbart, Wienecke, Butler, & Fabry, 2011) and the birds most exposed to the wind move along the opposite flank of the huddle for protection (Birr, 1968; Prévost, 1961; Robertson, 1990; Waters, Blanchette, & Kim, 2012). As heat loss is limited within huddles (as heat can dissipate only by inhalation of cold air and through the head) ambient temperature can reach 37.5 °C (Gilbert et al., 2006), well above the birds' +20 °C upper critical temperature (Le Maho et al., 1976; Pinshow et al., 1976). As a consequence, birds face the paradox that in a cold physical environment they sometimes need to dissipate excess heat (Gilbert et al., 2007, 2006). At present, we do not know how emperor penguins deal with these apparently contradictory requirements since the factors influencing the process of huddle formation and breakup have never been studied in detail with regard to environmental variables. Most studies have examined the effects of weather conditions on emperor penguin colony structure only during incubation, but since energetic constraints are likely to differ between the breeding stages it is important to examine them also during pairing and chick rearing. For instance, penguins have to fast for a prolonged time during incubation when weather conditions are most severe, while they only stay in the colony for short periods when rearing chicks, when weather conditions are more favourable. Consequently, forming huddles may be more critical during incubation relative to other breeding stages to maximize energy savings.

To understand the dynamics of social thermoregulation in emperor penguins according to environmental variables (ambient temperature, wind speed, wind direction, relative humidity, atmospheric pressure or solar radiation), we investigated the huddling behaviour of an entire colony during pair formation, incubation and chick rearing, that is, from winter to summer. We aimed to test the following predictions: (1) as dense aggregations protect emperor penguins from inclement weather conditions and help individuals to save energy, meteorological variables that have the potential to lower body temperature should result in an increase in huddle formation and duration, (2) as social thermoregulation is based upon the need of individuals to save energy by forming huddles and the need to shed excess heat by leaving huddles, this should lead to the regular formation and breakup of huddles, and (3) as a colony of emperor penguins is made of aggregations of different densities, individuals should move between loose aggregations and huddles to control body temperature.

METHODS

Subjects

We studied the emperor penguin colony of Pointe Géologie Archipelago (Dumont d'Urville, Terre Adélie, Antarctica, 66°40′S, 140°01′E) where about 3000 pairs breed each year on the fast-ice between islands and the Antarctic continent (Prévost, 1961). We collected data in 2005, 2006 and 2008, over three reproductive periods: pairing (from arrival of the birds in late April to mid-May), incubation (from mid-May to mid-July) and chick rearing (from mid-July to mid-September). Fieldworkers counted the birds in the colony at each season, once a week depending on the weather conditions (good visibility, low wind). There were a maximum of 3253, 3350 and 3160 breeding males during the incubation periods in 2005, 2006 and 2008, respectively.

Definitions

To analyse the distribution of emperor penguins within the colony, we differentiated between two different grouping patterns: huddles and loose aggregations. A huddle was defined as a part of a group in which individuals were closely assembled; typically, individuals had flippers held against the body and the head tucked into the shoulders, and each bird hid its beak between the necks of others. Note that movements within a huddle are limited, birds being only able to move the head or to make limited steps in a synchronized way (Gerum et al., 2013; Zitterbart et al., 2011). Sometimes a huddle broke down when its members became more active (Fig. 1). A group could contain one or several huddles. Loose aggregations consisted of all the individuals in a group that did not belong to huddles. These birds were stationary or mobile, and had limited if any physical contact with their neighbours or were apart from each other. They engaged in different activities such as grooming, lifting the abdominal skin fold covering the egg, consuming snow or performing courtship displays when females were present. During the pairing period, both males and females were present in the huddles but during the incubation period, only males were present.

Climatic and Seasonal Influences on Huddling Patterns

To investigate huddling patterns, we photographed the colony every day (weather permitting) from late April to mid-September 2008. Several photos were taken within three different time windows (morning: 0930–1130 hours; midday: 1130–1330 hours; afternoon: 1330–1530 hours; local time i.e. UTC + 10 h), each time from three vantage points located on nearby hills (from two points on Le Mauguen Island and from one point on Rostand Island). The different photographs of the colony were collated to get a single picture of the entire colony using PTGui software (www.ptgui.com). Each picture was visually analysed on a computer screen using the zoom function. This led to a database of 118 panoramic pictures: 20