



Socially-induced variation in physiological mediators of parental care in a colonial bird



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ABSTRACT

Social facilitation of reproduction occurs in humans and animals, and may represent one of the bases of reproduction in groups. However, its underlying physiological mechanisms remain largely unexplored. Here, we found in a colonial bird, the Adélie penguin (*Pygoscelis adeliae*), that the number of parental interactions (nest relief ceremonies) performed by breeding individuals on the colony was positively related to prolactin levels in other breeding individuals exposed to these interactions (*i.e.* focal individuals). As prolactin is typically involved in the expression of parental behaviour in birds, this suggests that parental interactions by conspecifics represent social cues that might increase parental motivation in focal individuals. Moreover, parental interactions were not related to corticosterone levels in focal individuals, suggesting that these social cues were not stressful for penguins. However, social stimulation still had a cost for focal individuals, as it was negatively related to their antioxidant defences (a component of self-maintenance). As social stimulation was also positively related to prolactin levels, this highlights the fact that social stimulation acts on the trade-off between reproduction and self-maintenance. For the first time, the results of the current study shed light on the physiological factors potentially underlying social facilitation of parental care. Importantly, they suggest that, even though social facilitation of parental care may increase breeding performance, it can also negatively affect other fitness components.

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1. Introduction

Reproductive behaviour is socially facilitated when the reproductive behaviour of an individual augments the rate at which conspecific individuals perform the same behaviour or related behaviours (Zajonc, 1965). For instance, in humans, transition to parenthood increases after siblings, friends or colleagues have become parents (Balbo and Barban, 2014; Lois and Arránz Becker, 2013; Pink et al., 2014). Social facilitation of reproduction may therefore give the impression that the decision to reproduce spreads ‘contagiously’ within social groups. The most probable explanation for this phenomenon in humans is social learning, which is the process by which decisions are altered by new information obtained from observation of other individuals (Heyes, 1994). In that case, social learning provides potential new parents with information on the feasibility of becoming a parent, thereby minimizing the risk of taking the wrong decision. Social facilitation of reproduction is, however, not restricted to humans, as social stimulation can also hasten reproduction within animal groups (Danchin, 1988; Waas, 1988).

Studies on social facilitation of reproduction have so far mostly focused on the decision to reproduce and become a parent but have not examined whether such a phenomenon occurred later when parents have to care for their offspring. This is important, as social facilitation of parental care may enhance the development and the survival of young within groups. Moreover, studies on social facilitation of reproduction have overlooked its underlying physiological mechanisms and its potential costs. Uncovering the physiological basis of social facilitation could be of particular importance in an evolutionary context, since we do not know if and how it could impact life history trade-offs.

In mammals, oxytocin and prolactin represent the main hormones motivating parental behaviour, as they increase attraction, contact and protectiveness towards young (Rilling and Young, 2014). In birds, prolactin is also involved in the expression of parental behaviour, such as egg incubation, chick-brooding or chick-provisioning, and is also probably involved in alloparental behaviour (Angelier et al., 2016). Therefore, oxytocin and prolactin, directly acting on the central nervous system of parents, appear to be primarily related to their intrinsic motivation to provide parental care. However, the parental motivation triggered by these hormones needs to be weighted by the amount of resources individuals can invest into parental care. Stress hormones (cortisol and corticosterone) appear to assume this role, as they regulate resource

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allocation between self-maintenance and reproduction (Wingfield and Sapolsky, 2003). For instance, high cortisol levels in female rhesus macaques (*Macaca mulatta*) increase the probability of rejecting their young, and can annihilate the positive maternal effects associated with high oxytocin levels (Maestripieri et al., 2009). In birds, even though low corticosterone levels promote parental care, high corticosterone levels induce a decline in prolactin levels, so that high corticosterone levels coupled with low prolactin levels lead parents to decrease nest attendance and ultimately desert their nest (Angelier et al., 2009; Criscuolo et al., 2005; Spée et al., 2010). Such negative effects of stress hormones on oxytocin and prolactin may explain why stress hormones are typically low and unresponsive to perturbations when parental care needs to be provided to offspring, while the opposite is true at the onset of breeding when energy needs to be mobilized to promote reproduction (Krause et al., 2015, 2016). Social facilitation of parental care could then be triggered in species breeding in groups if the hormonal status of an individual (thereafter, focal individual) is modulated by its exposure to the reproductive behaviour of conspecifics. In that case, focal individuals exposed to the reproductive behaviour of conspecifics would be expected to exhibit increased oxytocin and prolactin levels but low and constant levels of stress hormones, which may allow them to enhance their current reproductive performance. Prioritizing reproduction, however, is expected to decrease resource allocation to self-maintenance, which could be assessed through the measurement of physiological markers mediating homeostasis balance. For instance, reproduction may lead to a deficit in antioxidant defences, thereby increasing the risk of exposure to high levels of oxidative damage (Alonso-Álvarez et al., 2004). This shift in the oxidative balance of reproductive individuals is therefore thought to reflect how reproducing individuals prioritize reproduction relative to self-maintenance (Beaulieu et al., 2015). Thus, social facilitation of parental care is likely to be mediated not only by hormonal levels, but also by variation in oxidative status (i.e. low antioxidant defences and high oxidative damage).

The social conditions experienced by reproducing individuals have to be considered in view of the environmental conditions under which reproduction occurs. Indeed, environmental conditions can alter reproductive behaviour (Winkler et al., 2002), presumably because they determine the overall level of resources to allocate between reproduction and self-maintenance. Accordingly, environmental conditions can alter the afore-mentioned physiological markers mediating reproductive behaviours (Angelier et al., 2016; Beaulieu and Costantini, 2014; Wingfield, 2013). Reproductive behaviour is therefore likely to depend on the interaction between environmental conditions and social stimulation. As favourable environmental conditions allow parents to maximize their investment into reproduction, the effects of social stimulation on parental investment are likely to be weak under such conditions. In contrast, under poor environmental conditions, parental investment should be far from its upper limit, so that it could still be enhanced by social stimulation. Under the assumption that social stimulation still occurs despite poor environmental conditions and that high parental investment enhances reproductive success, an evolutionary role for social facilitation may be to buffer the negative impact of environmental conditions on parental investment. Alternatively, reproduction failure is likely to be precipitated under extremely poor environmental conditions that reduce not only resource availability but also social stimulation, thereby preventing the occurrence of social facilitation of reproduction.

Here, we examined whether the exposure of focal individuals to parental interactions performed by conspecifics altered physiological mediators of parental care (hormonal levels, oxidative status). We conducted our study in a colonial Antarctic seabird, the Adélie penguin (*Pygoscelis adeliae*), in two years characterized by different environmental conditions: the first year (2006–07) was characterized by an early sea-ice retreat before summer compared with the second year (2007–08). This resulted in more favourable conditions when penguins reproduced in summer 2006–07, as proxies of food availability were

enhanced (Beaulieu et al., 2010a). Importantly, we have already shown in Adélie penguins that low prolactin levels and high corticosterone levels deteriorate behavioural traits involved in parental care (e.g. incubation commitment, foraging behaviour) (Cottin et al., 2014; Spée et al., 2010; Thierry et al., 2013), and that antioxidant defences appear to be involved in self-maintenance mechanisms during reproduction (Beaulieu et al., 2011). Therefore, if social facilitation of parental care occurs in this species, we expect high exposure to parental interactions to be related to elevated prolactin levels, to low corticosterone levels, and to reduced antioxidant defences (and possibly to high oxidative damage). We also expect the effects of social stimulation on physiological mediators of parental care to be exacerbated during the second year, when environmental conditions were less favourable.

2. Methods

2.1. Fieldwork

Our study was conducted in Dumont d'Urville, Antarctica (66°40'S, 140°01'E) and was approved by the Ethic Committee of the French Polar Institute Paul-Emile Victor, as part of the Program 137. In austral summers 2006–07 and 2007–08, 92 and 96 penguins, respectively, were selected within a colony of ca. 150 m² and containing a total of >500 individuals (see picture in Supplementary material 1). A few days before egg laying (early November), the birds were individually identified with a symbol painted on their chest with waterproof Nyanzol-D, and with a pseudo passive transponder (31.2 × 3.8 mm, 0.8 g, Texas Instruments TIRIS, Dallas, TX, U.S.A.) implanted subcutaneously. Sex was determined *a posteriori* by using a combination of parameters including cloacal inspection, copulatory position and incubation routine (Kerry et al., 1993).

In Adélie penguins, after egg hatching (mid- to late December), one parent stays on the nest to provide protection to its offspring, while the other forages at sea to bring food back to the nest. Throughout the brooding stage, males and females regularly switch parental duties during nest relief ceremonies, when one parent comes back from the sea while the other one is about to leave the nest to forage at sea. In our study, during the early brooding stage (late December to early January), the colony was observed from a distance (ca. 20 m) every hour each day to monitor the nest relief ceremonies of identified birds that were still rearing chicks (n = 84 in 2006–07 and n = 90 in 2007–08). The time of nest relief was recorded. Among these identified birds, 94 individuals (n = 47 in both seasons) were captured once and bled immediately after being relieved by their partner (i.e. after they took part in their own nest relief ceremony). We captured focal penguins after they were relieved by their partner to avoid capturing them while they were still brooding their young chicks on the nest. Blood was collected from the wing vein with a heparinized syringe. After centrifugation, plasma samples were stored at –20 °C. Because the capture and the restraint constitute an acute stress that may influence physiological markers in blood (Angelier et al., 2013), we minimized the stress of penguins by covering their head with a hood, and by collecting blood as quickly as possible (mean ± SE = 267 ± 7 s).

2.2. Social stimulation

The number of nest relief ceremonies involving identified penguins and occurring within the hour preceding blood sampling was used as an index of social stimulation received by focal penguins from other active parents on the colony. During nest relief ceremonies, both partners typically stand and wave their necks back and forth while uttering a loud cackling call (Müller-Schwarze and Müller-Schwarze, 1980). Given the small size of the colony (ca. 150 m²), we assumed that these loud mutual displays associated with nest relief ceremonies were audible by all penguins breeding on the colony, irrespective of the location of their nest within the colony (see

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