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Active territory defence at a low energy cost in a colonial seabird

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Aggressive behaviour associated with the defence of a territory is thought to impose substantial energy costs and thus to represent a trade-off with other energy-demanding activities. The energy costs of aggressive behaviours, however, have rarely been estimated in the wild, and the overall contribution of territorial defence to daily energy expenditure has never been determined. We studied the activity budget of breeding king penguins, *Aptenodytes patagonicus*, equipped with heart rate data loggers to estimate the energy costs associated with territory defence in this colonial bird exhibiting very high rates of agonistic interactions. We also assessed whether threat displays imposed lower energy costs than attacks with body contact. During territorial defence (i.e. threats and physical attacks combined), energy expenditure averaged 1.27 times resting metabolic rate. Defence accounted for 13% of the daily time budget and contributed to 2.7% of the total daily energy expenditure. Interactions with body contact cost three times more than threat displays, but accounted for only 16% of the aggressive behaviours recorded. Neither did body mass, body size, penguin sex or breeding stage affect the cost of aggressiveness. Our results are consistent with previous research reporting that fighting imposes significant metabolic costs. However, we found that aggressive behaviour in king penguins was not an expensive activity compared to the total energy budget. Because king penguins go without food and are sleep deprived while breeding, they may have developed behavioural strategies (e.g. lower rates of attacks with body contact) allowing them to defend their territory efficiently at a low energy cost.

In many animal species, individuals perform aggressive behaviours to gain access to limited resources, such as food, territories or mates, which can improve their fitness (Cutts et al. 1999; Hagelin 2002; Logue & Gammon 2004). Usually, however, individuals will limit their use of aggressive behaviours because they often incur short-term costs in terms of time, energy demands or risk of injuries (Hack 1997; Neat et al. 1998; but see Riechert 1988), and these proximate costs can result in fundamental long-term fitness costs (Hagelin 2002; Langkilde et al. 2005). They may also increase predation risk as a result of reduced vigilance during fights (Jakobsson et al. 1995; Brick 1998). Nevertheless, the benefits of defending a resource are generally higher than the costs associated with aggressive behaviours, so that agonistic interactions among individuals are common (Maynard Smith 1982).

Based on trade-offs between expected benefits and costs of fighting, different strategies and decision rules have evolved for resolving conflicts (Maynard Smith & Parker 1976; Enquist & Leimar 1983). As physical aggression is associated with a greater risk of injury than threat displays (Clutton-Brock et al. 1979), most animals typically assess the fighting ability and motivation of their opponent before escalating into a fight with body contact (Payne 1998; Jonart et al. 2007). Animals may therefore assess correlates of resource-holding power (RHP), a measure of the probability of winning an escalated contest (Parker 1974; Maynard Smith & Parker 1976). Resource-holding power is largely determined by individual characteristics such as body size and condition (Marden & Rollins 1994; reviewed in Huntingford & Turner 1987). In addition to RHP, fighting success may also depend on the individual's motivation to fight (Elwood et al. 1998; reviewed in Enquist & Leimar 1987), which in turn depends on its willingness to expend energy or to risk injuries (Enquist & Leimar 1987). Such motivation may be estimated by determining whether the individual is the initiator or the receiver in a fight (Arnott & Elwood 2007; Briffa & Sneddon 2007).

Although aggressive behaviours are expected to impose substantial energy costs (Parker 1974; Riechert 1988), only a few

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empirical studies have attempted to quantify these costs (Smith & Taylor 1993), and these were all performed in laboratory conditions (e.g. Hack 1997; Neat et al. 1998; Briffa & Elwood 2004). Previous studies estimated the energy costs of aggressive behaviours by measuring contest duration (Smith & Taylor 1993; Morrell et al. 2005) or by monitoring physiological changes, such as increases in lactate and energy expenditure or reductions in energy stores (Rovero et al. 2000; Briffa & Elwood 2004; DeCarvalho et al. 2004). An alternative and nonphysiologically invasive approach to estimating the energy costs of various behaviours is the monitoring of heart rate (HR), but calibration issues still limit the application of this method (Butler et al. 2004).

In free-living animals, a direct estimate of the energy cost of specific aggressive behaviours coupled with the contribution of these costs to the overall energy budget has never been performed. This is a major gap in our understanding of the behavioural strategies used by animals for territorial defence under natural conditions, because only knowledge of these costs can provide information on how energy constraints may have shaped behavioural interactions among individuals of various species. Achieving such a goal requires the simultaneous determination of the energy costs associated with the various aggressive behaviours of the study species, and of the time spent performing these behaviours. Up to now, this has proved challenging, but the use of a validated indirect method to estimate the cost of activities on a short timescale, for example heart rate recording (Butler et al. 2004), in an easily accessible and observable species would offer such an opportunity.

King penguins, *Aptenodytes patagonicus*, are highly territorial seabirds that breed in dense colonies and exhibit high rates of aggression, as pairs vigorously defend a small territory of about 0.5 m^2 (average rate of 100 interactions/bird per h, Côté 2000). Given that king penguins face severe energy constraints while breeding ashore because they fast during extended periods (up to 30 days, Groscolas & Robin 2001) while sleep deprived (Dewasmes et al. 2001), our study aimed at answering the following question: how might an animal sustain high rates of aggressive behaviour in a context of energy limitation? To quantify the energy costs of aggressive behaviours in free-living breeding king penguins, we first assessed time spent in agonistic interactions using behavioural observations. Then, we used HR variations during agonistic interactions, and equations relating energy expenditure (EE) to HR in freely breeding king penguins (Groscolas et al. 2010), to estimate the energy cost of overall and specific interactions. Notably, we evaluated the energy costs of threat displays and of attacks with physical contact, expecting physical contact to be more costly than threat displays because of corresponding higher physical activity. We also determined whether the energy cost of aggressive behaviours differed between fight initiators and fight receivers, or was affected by sex, body mass, body size and breeding stage. Finally, we assessed the contribution of aggressive behaviours to daily energy expenditure (DEE), expecting that territory defence would contribute to a significant proportion of DEE because of the elevated rate of agonistic interactions.

METHODS

Animals

We conducted this study on Possession Island (Crozet Archipelago 46°25′S, 51°52′E) over three breeding seasons between 2003 and 2007. We monitored king penguins in a subcolony of ca. 3500 pairs in the colony of La Baie du Marin. A total of 381 birds (211 males and 170 females) were flipper-banded from November to March, that is, throughout the incubation and early chick-brooding periods. During the incubation (ca. 53 days) and chick-brooding (ca. 30 days) stages, females and males alternate between periods of fasting on land and foraging at sea (Weimerskirch et al. 1992). Incubation shifts average 15 days and brooding shifts 8 days (Weimerskirch et al. 1992). As males always perform the first incubation shift, we easily sexed birds from observations of breeding behaviour. We checked marked birds twice daily to determine the laying date as well as the onset of each incubation and brooding shift.

Behavioural Observations

In king penguins, aggressive behaviours for territory defence include threat displays (no physical contact) and attacks with body contact. Threat displays consist of beak pointing (no vocalization, beak closed, body stretched out) and gaping (pointing but with bill open and vocalizing, body stretched out), whereas attacks with body contact consist of pecking and flipper blows (Côté 2000).

Scan sampling

From November 2006 to March 2007, the average proportion of time spent in territory defence by breeding penguins was estimated using scan sampling (Altmann 1974). Scans were performed every 15 days on random unmarked ($N = 88$) or marked male ($N = 101$) and female ($N = 81$) king penguins. Most individuals were scanned only once but some were scanned up to three times, each time at a different incubating or brooding shift. During each scan, we considered 30 of these birds and counted the birds engaged in aggressive behaviours. Scans were performed every 5 min, for at least 6 h consecutively. The scans totalled 63 h of observations. Individuals observed during scans were located at least 4 m apart to maximize independence of their behaviour relative to their neighbours. We balanced observations during all hours of daylight, from 0600 to 2000 hours, that is, approximately 7% of scans for each hour.

Video recording

Video recording was used to compare the time spent in aggressive behaviours between day and night. In January 2004, we recorded 30 marked birds (18 males and 12 females) on video. Videoed birds were located within a 6 m diameter zone under the field (8 × 20 m) of a fixed video camera and at 3–7 m from the edge of the colony. The video camera was set at 3 m height and coupled with infrared lighting to observe individuals 24 h/day. We recorded the behaviours of birds continuously at the frequency of three images/s, using a Panasonic (model TL750) video recorder. A preliminary study confirmed that behavioural time budgets from video recordings were equivalent to visual focal observations. For example, 20 focal observations (Altmann 1974; Côté 2000) performed both visually in the field and using video recordings led to estimated proportions of time spent in aggressive behaviours that were not significantly different (visual: 18.6 ± 3.5%; video: 17.5 ± 3.3%; paired Wilcoxon signed-ranks test: $V = 61$, $P = 0.11$). To estimate time spent in aggressive behaviours day and night, the 24 h video recordings of five individuals (three males and two females selected at random) were divided into 15 min consecutive focal observations (i.e. 96 focal observations per bird and 480 focal observations in total) and the proportion of time spent in aggressive behaviours was calculated for diurnal and nocturnal focal observations. Since video recording was performed on birds previously equipped with HR loggers, a first estimate of the global energy cost of aggressive behaviours was obtained from these birds, based on HR increase during episodes of aggressive interactions (see below).

Visual focal observations

We carried out visual focal observations to compare the frequency rates of threat displays versus attacks with body contact.