



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.

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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 m² (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. Videod 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: $18.6 \pm 3.5\%$; video: $17.5 \pm 3.3\%$; 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.

Between November 2004 (laying date) and March 2005 (chick-brooding period), we performed 550 focal observations, each of 15 min, in the field (two to seven per individual; [Altmann 1974](#); [Côté 2000](#)) to record the behaviour of 169 marked penguins (92 males and 77 females). Body mass and body size of these birds were determined and used as indexes of RHP. Birds were hand-caught in the colony and transported to a nearby shelter. They were weighed on an electric platform scale (± 10 g), in the natural incubating position. Their flipper length was measured (with a ruler ± 1 mm) as an index of body size. Because displacing the birds was risky (i.e. potential egg loss and thus breeding failure), only birds that remained calm when handled were weighed (100 of 169 birds). We conducted observations from 0600 to 2000 hours at a distance of 10–250 m, using binoculars and spotting scopes when necessary to minimize disturbance. During each focal observation, we timed aggressive interactions and also other mutually exclusive behaviours such as resting and comfort behaviour. When a bird was engaged in an aggressive interaction (which occurred for 488 of the 550 focal observations), we recorded the number of different aggressive behaviours to estimate frequency rates of interactions with and without body contact. Since visual focal observations were performed on penguins previously equipped with HR loggers they allowed us (1) to obtain a second estimate of the global cost of aggressive behaviours from a large number of birds, (2) to determine the energy cost of threats versus attacks, (3) to test for the potential effects of sex, breeding stage, body mass and size on these costs, and (4) to calculate the contribution of territory defence to the daily energy budget of breeding king penguins (see below).

Heart Rate Recording

When manipulated for HR logger equipment, weighing and body size measurement, incubating or brooding birds were hand-caught while standing on their territory. Equipped birds were located in a subcolony where penguins have been habituated to human presence for the last 50 years. Indeed, the study colony is close to a permanent station and scientific installations are present in its close vicinity (ca. 50 m). A current study shows that incubating penguins at this location only become vigilant (slight head movements) and initiate displacement (slight leg movements) when closely approached by humans (at 8–10 and 1–2 m, respectively; R. Groscolas & V. A. Viblanc, unpublished data). Thus, when approached for capture, incubating or brooding birds did not try to flee, so that their agitation and that of their neighbours was limited.

We recorded the HR of birds with an externally mounted data logger (Polar, model S810, Polar Electro, <http://www.polar.fi>) adapted for use on king penguins ([Groscolas et al. 2010](#)). The system included two units: a sensor-transmitter (30–40 g) and a receiver/logger (a recording watch, 30 g). The HR logger package weighed $<1\%$ of adult body mass. Heart rate transmitters were attached in a dorsal, midline position with Tesa tape wrapped around several layers of feathers. In this position they did not hinder the movements of birds. Electrodes made from gold-plated safety needles were placed subcutaneously and separated by 25 cm. One electrode was placed at the height of the wing pit and the second one just above the tail. Electrodes were disinfected with iodine (Betadine) and alcoholic antiseptic solutions and inserted under the skin in the subcutaneous fat layer (at approximately 5 mm depth, and over a length of 1 cm). Safety needles were secured to prevent their retraction. We never observed birds trying to remove electrodes or HR loggers, nor did we observe any adverse effects of equipment on birds' health or behaviour. Further details on this method and how it accurately estimates HR of king penguins are described in [Groscolas et al. \(2010\)](#). We equipped

birds with loggers 1 or 2 days after the beginning of an incubation shift or a brooding shift, and removed loggers 1 or 2 days before the end of the average duration of the corresponding shift to avoid losing them. We therefore obtained HR values from birds fasting for 1–14 days (an average of 1 week). HR was recorded either at a fine scale (5 s intervals, videoed birds), but for no more than 45 h given the storage capacity of the HR logger, or at a larger scale (1 min intervals, field focal observations) allowing up to 20 days of continuous recording. The advantage of 5 s recording was the very fine resolution allowing a close matching of HR and behavioural changes, whereas the advantage of 1 min recording was to collect a large number of HR–behaviour data throughout the whole incubation and brooding shifts.

Matching Aggressive Behaviour with HR Records

Videoed birds

From seven randomly selected birds (five males at shift 1 of incubation and two females at shift 2) of the 30 birds fitted with HR loggers and videorecorded, we selected 36 episodes during which birds exclusively performed continuous aggressive behaviours (3–10 episodes per individual, during the day or night). Selection was at random regarding the type of aggressive interactions so that data were considered representative of average aggressive behaviour. The selection of sufficiently long episodes was difficult and time consuming because aggressive behaviours were frequently interrupted by other behaviours, such as comfort behaviour. In addition, episodes of aggressive behaviour had to be preceded and followed by resting periods lasting over 1 min (on average 2.4 ± 0.6 and 1.3 ± 0.2 min for the pre- and postaggression resting durations, respectively; see [Fig. 1a](#)), which also proved difficult to obtain. Such resting periods were required to calculate accurately the energy cost of aggressive behaviours, that is, energy spent in excess of

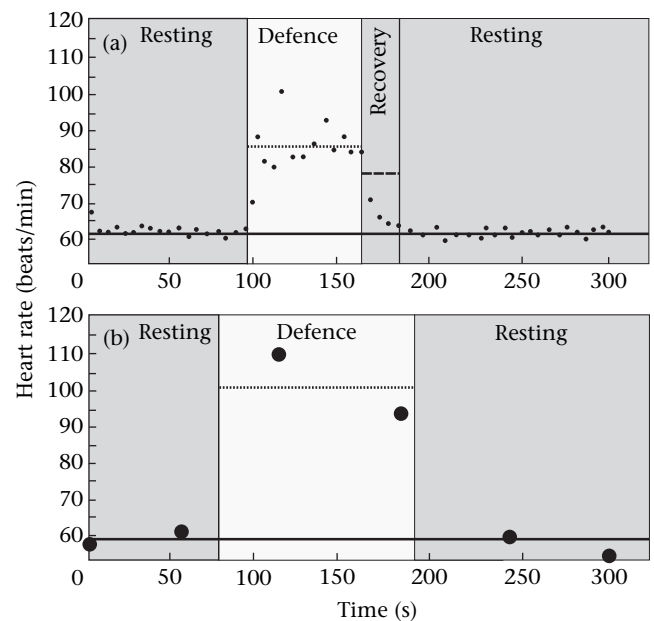


Figure 1. Example of a continuous record of heart rate (HR, beats/min) showing the increase in HR during an episode of territory defence in king penguins. Recording was at the sampling rate of one HR value (a) per 5 s (videoed birds) or (b) per 1 min (focal observations). Shaded areas indicate the resting periods before and after the episode of defence. In (a) a recovery period is shown, which could not be accurately timed in focally observed birds in (b). The continuous horizontal line shows resting HR whereas horizontal dotted and dashed lines show average HR during territory defence and recovery period, respectively.

resting metabolic rate (RMR; see below). These difficulties explain why the selected episodes were not equally distributed over individuals. The rate of aggressive behaviours (number/min, threats and body contacts together) was calculated for each episode.

Visual focal observations

For birds whose HR was measured every 1 min, we divided each of the 550 focal observations into 15 episodes of 1 min. For each 1 min episode, we assigned the HR value measured at its end to territory defence only if this behaviour occupied at least half of the time (i.e. >30 s) of the 1 min preceding HR measurement. For periods of continuous territory defence lasting over 1 min, we assigned to this behaviour the corresponding average HR. In addition, only episodes assigned as territory defence and preceded and followed by at least one 1 min episode assigned as resting (see Fig. 1b) were considered. In total, we obtained 589 1 min episodes of aggressive behaviours that met our criteria, of which 345 episodes were obtained for individuals of known body mass and size. These episodes were obtained from 269 focal observations among the 550 focal observations initially performed, and from the 169 individuals used for focal observations (two to four episodes/individual). The resting HR associated with each of these episodes was the average of pre- and postaggression resting HR. We further redefined 1 min episodes associated with aggressive behaviours during 15 min focal observations by discriminating when birds performed only threat displays or only attacks with body contact. In addition, for these two types of behaviours we discriminated whether the focal bird was the initiator or the receiver of the interaction. We discarded all 1 min episodes when both behaviours occurred. A total of 481 episodes were thus selected, of which 127 were attacks (58 as initiator and 69 as receiver) and 354 episodes were threats (170 as initiator and 184 as receiver). Among the 481 episodes, we obtained 279 observations for which both birds' body mass and the type of behaviour were known (72 observations, 63 birds for physical attacks and 207 observations, 93 birds for threat interactions).

Estimating the Energy Costs of Aggressive Behaviours

Videod birds

Energy costs of aggressive behaviours were calculated from the corresponding increase in HR (Fig. 1a), according to the method described by Smith & Taylor (1993). This method was also used by Rovero et al. (2000) to estimate the energy cost of fighting in shore crabs, *Carcinus maenas*. All HR calculations were done using the Polar ProTrainer software (<http://www.polar.fi>). We estimated resting HR by averaging pre- and postaggression resting HR. Fighting HR was the mean HR during aggressive behaviours and recovery HR was the mean HR during the recovery phase, that is, from the end of the aggressive behaviour to the time needed for HR to recover to resting levels. Excess HR during aggressive behaviours was calculated as [(fighting HR – resting HR) × fight duration]/resting HR (Smith & Taylor 1993). This excess corresponded to the time that would be required for the number of heart beats in excess during fighting to occur at the resting HR level (Rovero et al. 2000). The same calculation was performed for the recovery phase, using recovery HR, and the total excess in time due to a fighting episode was the sum of excesses during aggression and recovery. The energy cost of an aggressive episode (kJ) was calculated as: excess in time (min) × RMR (kJ/min). Dividing the cost of the episode by its duration (min) and then multiplying by 60 yielded energy cost in kJ/h. RMR was estimated from resting HR using equation 1a in Groscolas et al. (2010): $EE \text{ (J/min)} = -387 + 36.4 \times \text{HR (beats/min)}$ ($F_{1,133} = 19.33$, $R^2 = 0.85$, $P < 0.0001$). This equation was obtained from freely incubating male and

female king penguins (no sex difference) fasting for a duration comparable to that of birds in the present study and having similar breeding status and level of physical activity. Such prerequisites are required for validly estimating EE from HR (Butler et al. 2004). A validation test performed by Groscolas et al. (2010) showed that EE predicted from HR using the above equation did not differ significantly from measured EE.

Visual focal observations

We used a similar procedure for calculating energy costs in birds subjected to visual focal observations except that we could not include the recovery phase because of the large time resolution for HR measurements (Fig. 1b). We estimated resting HR from HR values during the resting episodes preceding and following episodes of aggressive behaviours. Fighting HR was the corresponding HR value for 'extracted' aggressive behaviour episodes. Fight duration was the number of minutes spent in defence.

We determined the contribution of the energy cost of territory defence to total DEE of breeding king penguins from the 169 birds used for focal observations. Total DEE of each bird was calculated from its average daily HR as calculated over the whole recording period (1 week on average) and using the same equation as above. The daily energy cost of territory defence was calculated as the average energy cost of aggressive behaviours (kJ/h) × average time (h) spent in aggressive behaviours daily, as determined by scan sampling.

Ethical Note

We placed a hood over the bird's head immediately after capture and throughout handling to keep it calm. After weighing, we quickly returned it to the colony. Manipulations lasted between 5 and 10 min and during this time we placed the bird's egg or chick in an incubator. This procedure never resulted in egg or chick abandonment. As a result of the handling, most penguins developed a tachycardia (up to 165 beats/min on average) from which they usually recovered within 15 min following release. We removed flipper bands from all banded birds before the winter, as they are known to affect survival negatively at that time of year (Gauthier-Clerc et al. 2004). Capture and tagging procedures were approved by the Ethical Committee of the Institut Polaire Français – Paul-Emile Victor. Authorization to enter the colony and to manipulate birds was obtained from Terres Australes et Antarctiques Françaises. The experiments comply with the current laws of France.

Statistical Analyses

We estimated the proportion of time spent in aggressive behaviours from scan samples. We performed all analyses using linear mixed models (LMMs with a compound symmetry structure; Littell et al. 2006), including bird identity as a random term to control for replicate observations on the same individual. Normality of residuals was assessed using the Shapiro–Wilk normality test and visual inspection of the residuals indicated no violation of assumptions of homoscedasticity. When sex was considered, bird identity was nested in sex, as birds cannot change sex. We included body size (as indexed by flipper length) and body mass as covariates in the models, as they may affect energy costs. We performed all statistical analyses with the SAS (SAS Institute, Cary, N.C., U.S.A.; version 9.1) and R (<http://www.r-project.org/>; version 2.10.1) statistical software. For each LMM, the number of observations (n) used and the number of birds (N) concerned are reported. We report all values as means ± 1 SE, and the alpha level was set at 0.05 for all statistical procedures.

RESULTS

Time Spent in Territory Defence

From diurnal scan sampling, we determined that aggressive behaviours contributed to $13.1 \pm 2.0\%$ of the time budget of breeding king penguins. From the estimates of the time spent in aggressive behaviours in the five videotaped birds that were observed for 24 h, we determined that the birds devoted a similar proportion of their time budget to aggressive behaviours during the day ($15.7 \pm 1.0\%$, $n = 280$) and at night ($14.6 \pm 1.1\%$, $n = 200$), that is, a day/night factor was not significant when included in an LMM controlling for repeated measurements by individual identity ($F_{1,474} = 0.75$, $P = 0.38$, $n = 480$, $N = 5$). Thus, time spent in aggressive behaviours obtained from diurnal scan sampling was used to estimate the total daily energy cost of territory defence.

Average Cost of Aggressive Behaviours

Videod birds

The average duration of the 36 selected episodes of aggressive behaviour was 1.9 ± 0.4 min (0.3–9.8 min). The average time needed for HR to recover initial levels (recovery phase) averaged 0.24 ± 0.03 min (0–2.6 min). HR increased during each episode of aggressive behaviour, on average from 57.5 ± 1.4 beats/min at rest to 73.3 ± 1.8 beats/min during aggressive behaviour ($n = 36$, $N = 7$). The corresponding RMR and EE were 1.83 ± 0.05 and 2.33 ± 0.06 kJ/min, respectively, indicating that during aggressive behaviour EE was on average 1.27 times higher than RMR. The total excess of EE due to an aggressive episode was 0.97 ± 0.04 kJ, of which $6 \pm 2\%$ was for the recovery phase. This yielded an average energy cost of aggressive behaviour of 0.50 ± 0.04 kJ/min or 29.8 ± 2.4 kJ/h ($n = 36$). After controlling for the fact that this estimate was obtained from repeated measures (3–10 episodes) over seven birds, that is, by running an LMM in which only the random effect was included, we found that the average energy cost of aggressive behaviour (i.e. the estimated intercept) was highly significant (LMM: $F_{1,29} = 151$, $P < 0.001$, $n = 36$, $N = 7$) and identical to that reported above. Moreover, the hourly energy cost calculated from each episode was positively related to the rate of aggressive behaviours (number/min, threats and body contact together) during the episode (LMM: $F_{1,28} = 22.60$, $P < 0.001$, $n = 36$, $N = 7$), but was not influenced by sex (males = 30.6 ± 3.1 kJ/h; females = 27.6 ± 2.8 kJ/h; LMM: $F_{1,5} = 0.25$, $P = 0.64$, $n = 36$, $N = 7$) or by the duration of the aggressive encounters (LMM: $F_{1,28} = 0.25$, $P = 0.61$, $n = 36$, $N = 7$).

Visual focal observations

The duration of episodes associated with aggressive behaviours averaged 1.7 ± 0.2 min ($n = 589$). Heart rate during these episodes (71.5 ± 1.4 beats/min, $n = 589$) was higher (LMM: $F_{1,1008} = 979.48$, $P < 0.001$, $n = 1178$, $N = 169$) than during the associated resting episodes (56.7 ± 1.2 beats/min, $n = 589$). Applying the same equations as above to these HR data and taking into account the duration of aggressive behaviours during focal observations, we estimated the average energy cost of aggressive behaviours at 27.2 ± 1.4 kJ/h ($n = 589$). This value was not significantly different from the 29.8 kJ/h estimate obtained from videoed birds (LMM: $F_{1,449} = 0.16$, $P = 0.69$, $n = 625$, $N = 176$). In addition, neither body mass (LMM: $F_{1,244} = 2.07$, $P = 0.15$, $n = 345$, $N = 100$) nor body size (LMM: $F_{1,244} = 0.43$, $P = 0.51$, $n = 345$, $N = 100$) of birds affected the hourly energy cost of aggressive behaviours. Finally, neither sex (LMM: $F_{1,167} = 0.66$, $P = 0.42$, $n = 589$, $N = 169$) nor shift (LMM: $F_{6,415} = 0.58$, $P = 0.74$, $n = 589$, $N = 169$) had a significant effect on the hourly energy cost of aggressive behaviours, even when we only

considered individuals for which both body mass and body size were known and when these variables were considered in the model (LMM with body mass: sex: $F_{1,97} = 1.58$, $P = 0.21$, $n = 345$, $N = 100$; shift: $F_{6,239} = 0.52$, $P = 0.97$, $n = 345$, $N = 100$). Running separate LMMs with body size and the residuals of a regression between body mass and body size yielded similar results.

Cost and Rate of Aggressive Behaviours

From data obtained during focal observations, after discriminating when birds performed only threat displays or attacks with body contact, we found that the energy cost of threat displays (19 ± 1 kJ/h, $n = 354$; Fig. 2) was more than three times lower than that of attacks with body contact (61 ± 3 kJ/h, $n = 127$; Fig. 2; LMM: $F_{1,177} = 2978.13$, $P < 0.001$, $n = 279$, $N = 100$ when controlling for body mass as a covariate in the model). Energy expenditure during attacks with body contact averaged 171 kJ/h, that is, $1.56 \times$ RMR. During threat displays, it averaged 129 kJ/h, that is, $1.17 \times$ RMR. Threat displays, however, occurred five times more frequently than attacks with body contact (81 ± 4 versus 16 ± 1 behaviours recorded/h; LMM: $F_{1,318} = 178.15$, $P < 0.001$, $n = 488$, $N = 169$). The energy cost of threat displays did not vary between initiators and receivers (LMM: $F_{1,112} = 0.16$, $P = 0.72$, $n = 207$, $N = 93$; Fig. 2), but attacks with body contact tended to impose higher energy costs on initiators than receivers, although the difference was not significant at the 0.05 alpha level (LMM: $F_{1,7} = 4.21$, $P = 0.07$, $n = 72$, $N = 63$). Whereas most of the birds (approximately 80%) mainly performed threat displays (70–100% of their aggressive behaviours), approximately 20% performed a mix of aggressive behaviours including 50% of threat displays and 50% of physical attacks.

Contribution of Territory Defence to DEE

Using the hourly energy cost of aggressive behaviours that included the recovery phase for HR, that is, 29.8 kJ/h (95% confidence interval, CI = 25.1–34.5 kJ/h for videoed birds), and the average time spent daily in aggressive behaviour, that is, 13.1% or 3.14 h, we found that on average king penguins spent 94 kJ/day (95% CI = 79.3–108.7 kJ/h) for territory defence. This cost contributed to 2.7% (95% CI = 2.3–3.1%) of the total DEE (3454 ± 180 kJ/day, $n = 169$).

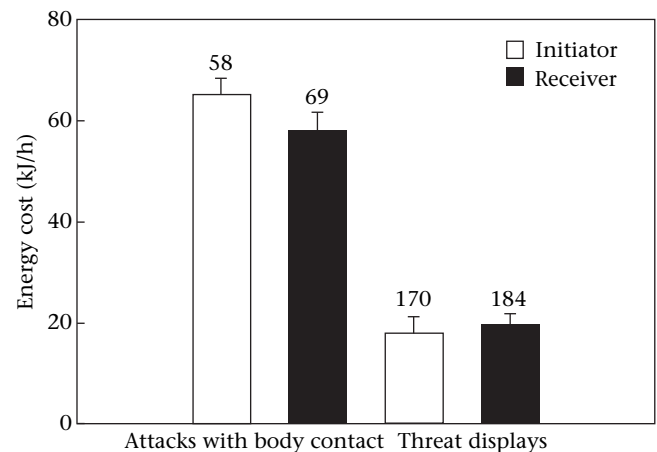


Figure 2. Energy costs of attacks with body contact (pecking and flipper blows) and threat displays (beak pointing and gaping) for receivers and initiators of agonistic encounters, in king penguins breeding on the Crozet Archipelago. The numbers of 1 min episodes where only threats or only attacks with body contacts were observed are given above the bars.

DISCUSSION

Time Spent in Aggressive Behaviours

We determined that king penguins spent 13% of their time in territory defence, which is comparable to, albeit slightly lower than, the 20% found in previous studies (Challet et al. 1994; Côté 2000). However, we are confident that our estimation is accurate, because scan sampling used in our study is a more relevant method to estimate activity budgets of animals (Altmann 1974) as opposed to the focal sampling used in previous studies (Challet et al. 1994; Côté 2000). Moreover, we determined that vigilance accounted for 7% of the total activity budget of king penguins (V. M. Viera, R. Groscolas & S. D. Côté, unpublished data), but this behaviour was not listed in the behavioural repertoire of previous studies. Vigilance may have been partly included in territory defence by previous authors (Challet et al. 1994).

The high level of aggressiveness observed in king penguins is likely to be related to their breeding pattern and constraints, that is, colonial breeding, no nest building and limited access to suitable breeding locations. To reproduce successfully, king penguins must acquire and maintain a territory, and competition for good-quality territories is high (Côté 2000). Central territories offer the eggs or chicks better protection from avian predators and from frequent flooding than territories located at the edge of the colony (Côté 2000; Viera et al. 2006). During brooding, the rate of pecking and flipper blows is higher in central than in peripheral birds (Côté 2000). Thus, high aggressiveness may contribute to acquiring and maintaining a central territory, which would at least indirectly improve breeding success (Côté 2000; Descamps et al. 2009). On the other hand, high rates of aggressive behaviours involve risks that may cause injuries and reduce future reproductive success (Montgomerie & Weatherhead 1988; Laidre 2007). In king penguins, pecking is the main behaviour involving high costs in terms of risk of injury, notably when directed at the eyes. Moreover, harassment by neighbours during breeding may lead to the desertion of the territory by one partner, and therefore jeopardize the success of the current breeding attempt. Indeed, king penguins do not build a nest but incubate their progeny on their feet so that when a parent deserts its territory, the egg or chick is lost.

Aggressive Behaviour Imposes an Energy Cost

Our estimates of energy costs were based on the measurement of daily and resting HR, on the increase in HR during episodes of territory defence, and on the use of an equation relating energy expenditure to HR in undisturbed breeding king penguins. The HR of resting birds was far below the maximum HR observed in king penguins, usually when stressed, around 250 beats/min. Thus, the increase in HR during aggressive interactions could not be constrained (limited) by the fact that HR at rest was close to its maximum sustainable level, and thus could not be underestimated. On the other hand, the possibility that this increase could not be entirely the result of the increase in physical activity associated with aggressive behaviours cannot be discarded. Actually, a part of the increase could be related to an emotional or motivational component associated with aggressive interactions. This 'additional HR', that is, an HR increase beyond that associated with increased energy expenditure, has, for instance, been observed in humans and is used as an indicator of emotional activation or arousal (Stromme et al. 1978; Wilhelm & Roth 1998). If this effect occurs in king penguins, our estimates of the energy cost of aggressiveness would be overestimated, suggesting that the overall energy cost of territory defence in king penguin is actually far lower than what may be expected (see below).

The two methods we used to estimate the average hourly cost of aggressive behaviours yielded similar results (29.8 kJ/h versus 27.2 kJ/h) and revealed that neither bird sex nor breeding season affected these costs. Thus, aggressive motivation (and therefore HR increase) did not seem to differ at different breeding stages, and defending a chick did not seem to represent a greater investment than defending an egg. The slight underestimation in birds used for focal observations probably resulted from the constraint imposed by the HR sampling rate (one value/min) that precluded us from taking into account the energy cost corresponding to the HR recovery phase. Correcting for this underestimation by considering that 6% of the energy cost of aggressive behaviours corresponded to the recovery phase (see Results for videoed birds) would yield an energy cost of fighting of 28.9 kJ/h, which represents a difference of only 3% compared to the value obtained from videoed birds. Our results also showed that the average HR obtained during both resting and aggressive behaviours differed by only 2% between videoed and focally observed birds. These findings support the view that by recording HR at a sampling rate of one value/min and by pooling information from a large number of individuals, we can obtain accurate estimates of energy costs of activities in free-living animals on a long-term basis and without major disturbance.

Overall, our results are consistent with other published studies that reported EE increases during aggressive behaviours in invertebrates or fishes (Smith & Taylor 1993; Hack 1997; Neat et al. 1998; Rovero et al. 2000; DeCarvalho et al. 2004). However, the average energy cost we determined, a 1.27-fold RMR, was lower than the range observed in other animal models: for instance, \dot{V}_{O_2} during fights ranged from 1.3 to 4.8 (mean = 2.8) times \dot{V}_{O_2} at rest in the house cricket, *Acheta domesticus* L. (Hack 1997), 3.9 times RMR in a cichlid fish *Neolamprologus pulcher* (Grantner & Taborsky 1998), and twice as high as RMR in shore crabs (Rovero et al. 2000). These differences may have occurred because the latter costs were determined for fighting animals (attacks with body contact) whereas the average cost estimated in king penguins was for aggressive interactions involving mostly threat displays. However, even the cost of attacks with body contact seems lower in king penguins ($1.57 \times \text{RMR}$) than in previously studied species. Nevertheless, the possibility that fights in king penguins may impose energy costs as high as for the other species mentioned above should not be discarded. In the study colony, this could occasionally happen during periods of flooding when some incubating birds have to crowd on restricted unsubmerged areas. In this case, birds are observed to fight intensively for prolonged periods of time, sometimes up to the moment when they have to abandon their breeding territory and egg because they are exhausted. Throughout our study, we did not have the opportunity to record HR during such periods of intense fighting.

Intensity of Behaviours, Energy Costs and Fighting Strategies

We found that the energy costs of aggressive behaviours depended on their intensity, that is, lower costs for threats than for interactions with body contact. Because attacks with body contact are more costly, birds should perform threats to save energy, as predicted by theory on animal conflicts (Maynard Smith & Parker 1976). However, we found that whereas the majority of birds in our study actually devoted more time to threat displays, a significant number of penguins (20%) none the less performed attacks just as frequently as threats. It would be informative to correlate further each tactic with the RHP of individuals, and with their breeding success. Numerous studies have shown that in territorial defence, threat and display postures have a number of advantages over fights. Such advantages include lower energetic costs (Brown 1975; Geist 1981), reduced risk of injuries (Brown 1975; Maynard

Smith 1982; Huntingford & Turner 1987), and the opportunity to assess the opponent's fighting abilities (Maynard Smith 1982; Enquist & Leimar 1983). Birds in better condition should perform aggressive behaviours for longer or at higher rates than birds in poor condition (Smith & Taylor 1993; Briffa & Elwood 2004). However, we did not find such a pattern in king penguins, as neither body mass nor body size influenced the time spent in aggressive behaviours or the energy costs of such behaviours. Moreover, we found that the energy costs of interactions with body contact during fights tended to be higher for initiators than for receivers. The intensity of the attack by the initiator has been shown to be a key predictor of success at winning the fight and is thought to act as a signal advertising the capacity to bear high costs and/or risk associated with dangerous behaviours (Briffa et al. 1998; Briffa & Elwood 2000). In line with this, Wascher et al. (2009) found a higher HR increase in individuals actively attacking conspecifics compared to individuals being attacked by others in greylag geese, *Anser anser*, although the energy equivalent was unknown. They suggested that the amount of physical activity involved in interactions was likely to be the same for both opponents, but the motivational states of the two individuals were different as also shown in previous studies (Sgoifo et al. 2001; Wascher et al. 2008). The risk of injuries and/or the depletion of energy reserves could, however, also be involved in the decision whether or not to initiate a fight. It is difficult to explain, however, why we did not observe the same trend for threats. A possible explanation may result from limitations in detecting significant differences with our 1 min interval recordings. The individual performing a threat needs to convince the receiver of both its ability and its willingness to fight and there is an inherent risk of threatening an individual who might be willing to fight back (reviewed in Számadó 2008). Számadó (2008) suggested that proximity risk is the major factor promoting the honest use of threat displays, but in the specific context of a colony, proximity may have maintained high frequency of threats without imposing different costs on the two opponents.

Cost of Territory Defence and DEE

We found that aggressive behaviours contributed to 2.7% of total DEE, that is, imposed low energy costs on breeding king penguins. Ultimately, the influence of energy expenditure on the evolution of fighting strategies depends on their consequences for survival and reproduction. Territory defence is an important component of the reproductive allocation of the parents and involves an obvious trade-off: the time and energy devoted to protecting both offspring and territory cannot be allocated to other activities enhancing offspring survival (Montgomerie & Weatherhead 1988). A trade-off between the energy devoted to aggressive behaviours and that allocated to parental care has been well documented in birds (Ketterson et al. 1992; Tuttle 2002), so that the more aggressive males during intrasexual competition generally allocate less to parental care, which may negatively impact offspring survival (Stoehr & Hill 2000). During the breeding season, king penguins fast for prolonged periods and, when their body mass decreases beyond a certain critical threshold, they may abandon their egg or chick (Groscolas & Robin 2001). Expensive activities could therefore critically deplete energy stores and force an individual to abandon its breeding territory to go and forage at sea. A conflict between the energy allocated to reproduction and that allocated strictly to territory defence is thus likely to occur during critical periods of energy demand, notably at the end of an incubation or brooding shift after several days of fasting. Aggressive behaviours of low energy cost may then have been selected by natural selection, enabling king penguins to defend their territory and egg (or offspring) efficiently during reproduction and yet save energy

throughout the long-term fast they face, thus delaying the critical moment of egg or offspring abandonment (Robin et al. 2001; Groscolas et al. 2008).

To conclude, we found that energy costs of aggressive behaviours represented a small proportion of the DEE of breeding king penguins. This finding supports the view that these birds manage to save energy in a context of fasting and sleep deprivation by resorting to the least energetically costly behaviour (i.e. threats) when defending their territory. Overall, we have shown that highly aggressive animals can devote a large proportion of time to defending their territory without jeopardizing their energy status.

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