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## Seasonal variations in the behavioural thermoregulation of roosting Humboldt penguins (*Spheniscus humboldti*) in north-central Chile

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**Abstract** We examined the thermoregulatory behaviour (TRB) of roosting Humboldt penguins (*Spheniscus humboldti*) in north central Chile during summer and winter, when ambient temperatures ( $T_a$ ) are most extreme. Each body posture was considered to represent a particular TRB, which was ranked in a sequence that reflected different degrees of thermal load and was assigned an arbitrary thermoregulatory score. During summer, birds exhibited eight different TRBs, mainly oriented to heat dissipation, and experienced a wide range of  $T_a$  (from 14 to 31°C), occasionally above their thermoneutral zone (TNZ, from 2 to 30°C), this being evident by observations of extreme thermoregulatory responses such as panting. In winter, birds exhibited only three TRBs, mainly oriented to heat retention, and experienced a smaller range of  $T_a$  (from 11 to 18°C), always within the TNZ, even at night. The components of behavioural responses increased directly with the heat load which explains the broader behavioural repertoire observed in summer. Since penguins are primarily adapted in morphology and physiology to cope with low water temperatures, our results suggest that behavioural thermoregulation may be important in the maintenance of the thermal balance in Humboldt penguins while on land.

**Keywords** Behavioural thermoregulation · Humboldt Penguin · Seasonal changes · *Spheniscus humboldti* · Thermoneutral zone

### Introduction

Endotherms respond morphologically, physiologically and behaviourally to their thermal environment in order to achieve thermal homeostasis. The first two responses include aspects such as body size and form, thermal insulation, blood flow, vascular arrangements and metabolism. Behavioural responses, on the other hand, involve changes in body posture or the selection of a thermally favourable microhabitat, and are comparatively rapid, less costly and more flexible than the former. In birds, behaviour plays a major role in this regard, often allowing them to save or dissipate energy, conserve water and reduce thermal stress (e.g. Lustick 1984; Davenport 1992; Dawson and Whittow 2000).

Penguins appear to be primarily adapted to low water temperatures through efficient morphological and physiological mechanisms, although this would seem disadvantageous when the birds are on land and exposed to high ambient temperatures (see Williams 1995). It is thus likely that penguins rely to a large degree on behaviour for thermoregulation, this being particularly pertinent in *Spheniscus* penguins which live in temperate and tropical regions (e.g. Galapagos, Peru-Chile, southern Africa) with cold upwelled waters, but hot terrestrial habitats (Boersma 1975; Frost et al. 1976; Luna-Jorquera et al. 1997). In temperate regions, where seasons are marked, differential behavioural responses during the warm and cold seasons may be expected and, by observation of these, it should be possible to obtain a measure of the thermal milieu experienced by the birds.

The Humboldt penguin (*Spheniscus humboldti*) occurs in Peru and Chile in the south-eastern Pacific over a 4,500-km coastline from 5 to 42°S (Williams 1995). In its north and central range, birds breed twice a year with

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well-defined events in winter and summer, when climatic conditions are most extreme (Paredes et al. 2002; Simeone et al. 2002). We hypothesise that these conditions are likely to expose penguins to different thermal environments and thus generate differential behavioural responses to balance the birds' thermoregulatory demands. In this paper, we aim: (1) to describe the components of thermoregulatory behaviours of Humboldt penguins when on land during winter and summer, and (2) to use these behaviours to assess the thermal environment experienced by the birds.

## Methods

### Study area

Observations during summer were carried out at Pájaros Island (29°35'S, 71°33'W), north-central Chile, between 12 and 19 December 2001 and between 4 and 8 January 2002 (total: 13 days). This 124-ha surface area island is located 21 km offshore and supports a breeding population of ca. 600 pairs of Humboldt penguins (Simeone et al. 2003). During winter we attempted to continue the study on this island, but abnormal heavy rainfall resulted in a pronounced absence of birds. We therefore moved to Chañaral Island (29°01'S, 71°34'W), 65 km north of Pájaros Island, where we conducted our observations between 10 and 18 July 2002 (total: 9 days). Chañaral has a 572-ha surface area, is located 6.3 km from the mainland and supports a breeding population of ca. 7,000 pairs of Humboldt penguins among other seabirds (Simeone et al. 2003). Although observations were made at two different colonies, we consider it unlikely that the responses of the birds differ since climatic regimes at the two sites are very similar (Table 1) and both are influenced by similar oceanographic conditions including water temperature and marine productivity (Fonseca and Fariás 1987; Rutllant and Montecino 2002).

### Observational methods

Observations on roosting Humboldt Penguins were made through 10x42 binoculars from a vantage point. The birds formed discrete groups on rock platforms directly adjacent to the sea and, depending on the time of day, the size of the groups varied between 3 and 63 birds during summer and between 2 and 51 during winter. The body posture of every individual present in the group was recorded every 2 h using instantaneous scan sampling (Altmann 1974). In this method, the group is scanned and the behaviour of each bird recorded at the instant it is first seen. The scanning of the

group and the registration of behaviours normally took less than 3 min. Observations were only conducted during the daylight periods (i.e. from 0800 to 2000 hours in summer and from 0800 to 1800 hours in winter).

We considered the extent to which each body posture represented a particular thermoregulatory behaviour (TRB). As no simultaneous determinations of TRBs and oxygen consumption were conducted, it was not possible to assign energy units to each TRB. Consequently, each component of TRB was ranked into a sequence that reflected different degrees of thermal load and was subsequently assigned an arbitrary thermoregulatory score (Fig. 1). In this score-assigning process we relied mostly on literature dealing with mechanisms of behavioural thermoregulation in penguins and how certain body parts such as the flippers, feet, and bare facial patches were exposed or covered, since these can have a major role in penguin thermoregulation through changes in blood circulation (e.g. Drent and Stonehouse 1971; Le Maho et al. 1976; Despin et al. 1978; Lustick 1984; Stahel and Nicol 1988; Luna-Jorquera 1996; Wilson et al. 1998). Shivering (heat production) and panting (heat loss) are physiological responses applied by birds when environmental conditions exceed the behavioural and other physiological capacities to maintain a normothermic body temperature and their onset indicates the end of sequences of behavioural thermoregulation and thus the beginning of thermal stress (Bartholomew and Dawson 1979; Lustick 1984). Luna-Jorquera (1996) observed that in Humboldt penguins these responses are observed only at temperatures below and above the thermoneutral zone (TNZ). Thus, shivering and panting represented the limit scores of our system. Resting (i.e. standing with the flippers against the sides of the body) is a frequent posture adopted by Humboldt penguins both within and outside the TNZ (Luna-Jorquera 1996) and we considered this likely to represent a "neutral" TRB (Fig. 1).

To characterise the total behavioural thermoregulatory response of the roosting birds at any particular time, we calculated a thermoregulatory index (TRI, see Bartholomew and Dawson 1979) as follows:

$$TRI = \sum TRBS_i n_i / N$$

where  $TRBS_i$  is the score assigned to a specific TRB,  $n_i$  is the number of individuals exhibiting that TRB and  $N$  is the total number of penguins observed at that particular time. With this procedure, TRI values ranged from -2.0 (all birds shivering) to 2.0 (all birds panting). Positive values were associated with heat loss, negative values with heat retention or production.

Ambient temperature ( $T_a$ ) near the penguin roosting sites was simultaneously recorded using a data-logger (LTD 100, Lotek Marine Technologies, Canada), placed 1 m above the ground. The unit recorded temperature at 20-min intervals with an accuracy of 0.1°C. Before parametric or non-parametric tests were made, data were tested for normality with a Kolmogorov-Smirnov test ( $\alpha = 0.05$ ). For comparing the mean occurrences of behaviours (in Fig. 1), data were previously arcsine transformed as recommended for proportional observations (Zar 1999).

**Table 1** Average climatic conditions at the two study areas in north central Chile (source: FAO 1985)

	Summer (January)		Winter (July)	
	Pájaros	Chañaral	Pájaros	Chañaral
Daily temperature (°C)	18.5	19.6	11.6	12.9
Daily max. temperature (°C)	22.6	23.7	15.8	16.7
Daily min. temperature (°C)	14.9	16.3	8.2	9.9
Rainfall (mm)	0	0	18	6
Total radiation (J cm <sup>-2</sup> day <sup>-1</sup> )	2,083	2,167	806	945
Wind speed (m s <sup>-1</sup> )	1.4	1.5	1.4	1.5

## Results

We identified eight TRBs during summer and three during winter (Fig. 1). Mean percentages of penguins lying with feet covered and flippers folded (Fig. 1a) were significantly higher in winter than in summer (*t*-test,  $P < 0.05$  for all hours). Mean percentages of birds standing with the flippers folded (i.e. resting, Fig. 1b) were significantly higher in summer than in winter (*t*-test,  $P < 0.05$  for all hours) and, during summer, this behaviour showed highest occurrences early in the morning and late afternoon. Lying with the beak pointing upwards (i.e. exposing bare facial patches,

**Fig. 1** Mean percent of roosting Humboldt penguins (*Spheniscus humboldti*) exhibiting different postures over the day during summer and winter. Numbers in parenthesis refer to the thermoregulatory scores (see Methods)

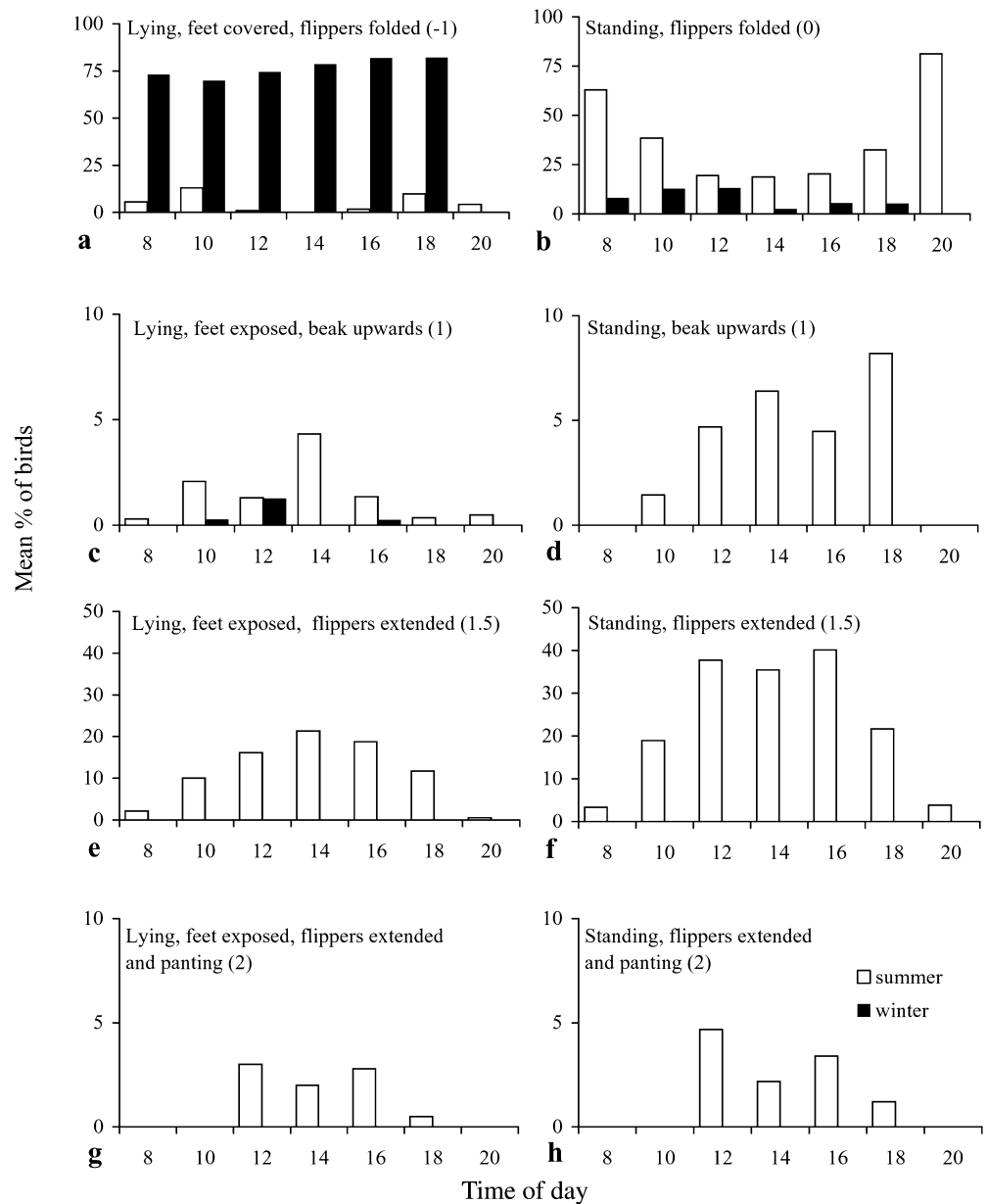


Fig. 1c) was recorded in low numbers (<5% of the time) both in summer and winter. The remaining five behaviours were observed only in summer. Standing and lying with the flippers extended (Figs. 1e, f) had peaks around midday following an approximately normal distribution. Birds standing with the beak pointing upwards (Fig. 1d) and panting (both lying and standing, Figs. 1g, h) occurred at low numbers (<10%) and their onset normally occurred around midday coinciding with the highest  $T_a$  of the day (Fig. 2a).

The highest TRI value (1.33) during summer was recorded on 12 December at 14 h, whereas the lowest (-0.06) was recorded on 13 December at 20 h. Daily fluctuations in mean TRI during summer (Fig. 2b) followed a pattern similar to that of  $T_a$  (Fig. 2a) with highest values around midday and lowest in the early morning and late afternoon. During winter, the highest TRI value

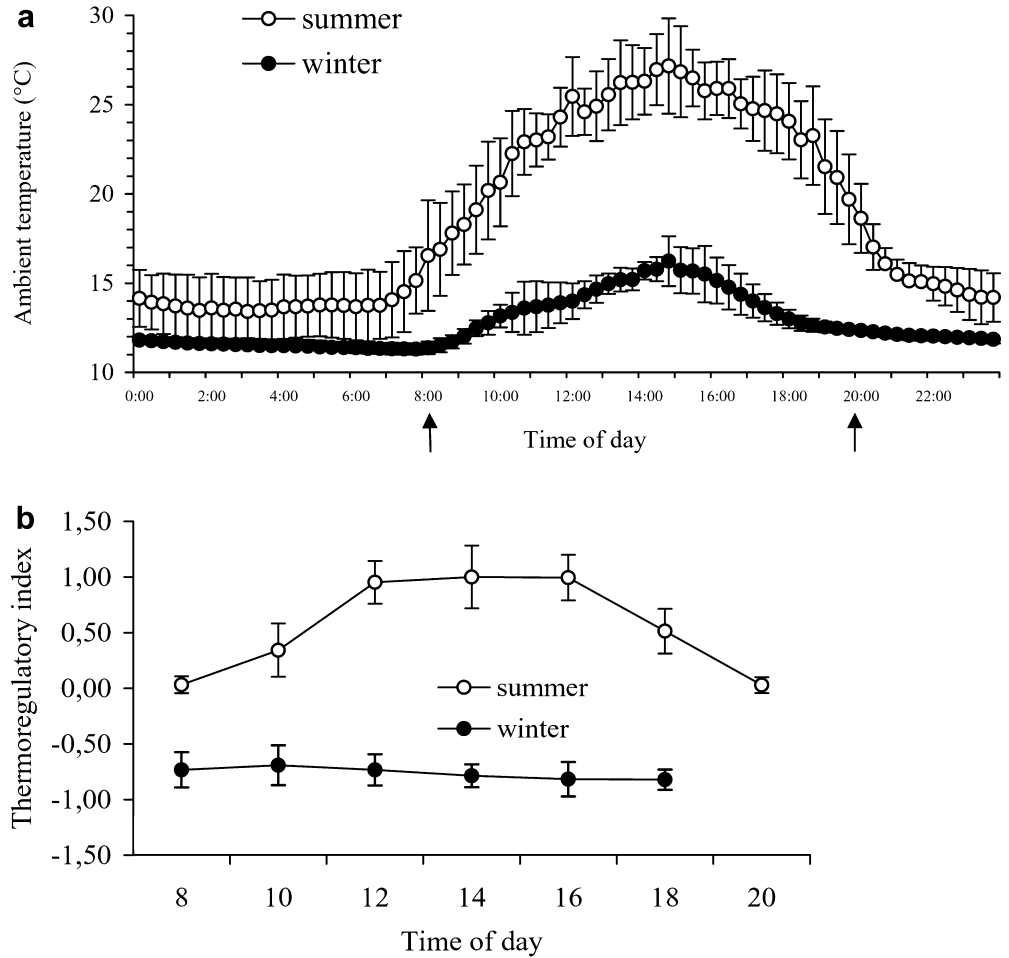
(-0.43) was recorded on 15 July at 16 h, while the lowest (-1.00) was recorded on 12 July at 10 h. Daily fluctuations in mean TRI during winter (Fig. 2b) showed no apparent relation with  $T_a$  (Fig. 2a). Both mean summer and winter TRI were found to differ significantly over all hours (Mann-Whitney  $U$ -test,  $P < 0.01$ ).

During summer, increasing TRI values were significantly correlated with increases in  $T_a$  ( $r = 0.84$ ,  $P < 0.01$ ,  $n = 52$ , Fig. 3). During winter, no significant correlation between the two variables was observed ( $r = -0.25$ , n.s.,  $n = 30$ , Fig. 3).

## Discussion

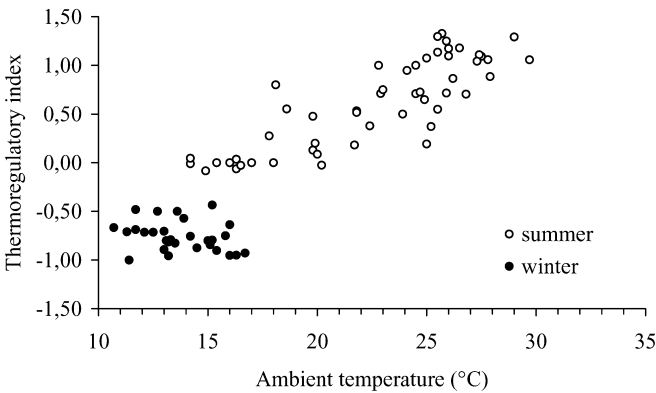
The components of behavioural responses increase directly with the heat load (e.g. Bartholomew and Dawson

**Fig. 2** Daily fluctuations ( $\mu \pm SD$ ) of **a** ambient temperatures near the roosting sites and **b** thermoregulatory index of roosting Humboldt penguins. The space between the *two arrows* marks the period when observations were made



1979), which explains the greater repertoire during summer of thermoregulatory behaviours observed in roosting penguins than in winter (eight vs three); in the former, birds coped with a greater range and higher  $T_a$  (see Table 2). Correspondingly, TRI values were highest and correlated well with  $T_a$  during summer, but not in winter. Probably, the range of  $T_a$  during winter is so reduced that birds need little variability in thermoregulatory behaviour to cope with it.

During winter, birds were seen most of the time lying with the feet under the body and flippers folded. This is a common posture adopted by penguins that helps retain heat by reducing the surface area available for heat loss via radiation both from flippers and feet (e.g. Le Maho et al. 1976; Despin et al. 1978; Wilson et al. 1998). Despite careful observation, extreme mechanisms of thermogenesis such as shivering (see Dawson and Whittow 2000 and references therein), were not observed during winter, which suggests that birds did not have to cope with critically low temperatures. As the TNZ of the Humboldt Penguin lies between 2 and 30°C (Drent and Stonehouse 1971; Luna-Jorquera 1996), it is thus possible to say that during winter birds remained well within



**Fig. 3** Relationship between ambient temperature and thermoregulatory index of roosting Humboldt penguins

**Table 2** Summary of the ambient temperatures (°C) experienced during the day by Humboldt penguins during the periods of observation

	Summer	Winter
Mean temperature	23.2	14.1
Mean max. temperature (range)	28.7 (26.4–31.4)	16.6 (15.2–18.4)
Mean min. temperature (range)	16.1 (14.2–20.6)	11.4 (10.7–11.7)
Temperature range	17.2	7.7

their TNZ (see Table 2). Even at night, when no observations were conducted,  $T_a$  rarely dropped below 10°C (see Fig. 2a).

Moving the flippers away from the body or stretching the neck so as to expose the bare facial patches helps to reduce the heat load via radiation and, if there is wind, this process can be enhanced by convective heat loss produced by the circulation of air (Lustick 1984; Williams 1995; Dawson and Whittow 2000). Prone birds can expose their feet and thus increase the dissipation of heat (Wilson et al. 1998). Standing or lying with the flippers extended and exposing the bare facial patches are postures particularly important in regulating the heat budget of *Spheniscus* penguins under heat stress (e.g. Boersma 1975; Frost et al. 1976; Luna-Jorquera 1996). Panting, an extreme mechanism of respiratory evaporative cooling in penguins (e.g. Baudinette et al. 1986; Chappell and Souza 1988; Stahel and Nicol 1988), was observed only in summer and normally occurs only when penguins are exposed to  $T_a$  above the upper critical temperature (i.e.  $> 30^\circ\text{C}$ ; Luna-Jorquera 1996). Although particularly effective, panting may also be energetically more expensive owing to the concomitant increased respiratory frequency and water loss (Lustick 1984; Chappell and Souza 1988).

Variability in our study may arise through our inability to quantify other factors influencing temperature perceived by the birds such as solar radiation, ground temperature and wind speed (Bartholomew and Dawson 1979; Chappell et al. 1990; Luna-Jorquera 1996). Increased solar radiation and low wind velocity, for instance, may produce a downward shift in the upper end of the TNZ, resulting in birds showing extreme thermoregulatory behaviours (e.g. panting) even at  $T_a$  within the TNZ (e.g. Lustick et al. 1978; Chappell et al. 1990). On the basis of our measurements of  $T_a$  alone, however, we can approach a measure of energy expenditure using the regression model proposed by Luna-Jorquera (1996) for calculating the resting metabolic rate (RMR) above the TNZ ( $\text{RMR} = 0.35 T_a - 6.57$ ). According to this author, resting Humboldt penguins have a mean energy expenditure of  $3.77 \text{ W kg}^{-1}$  within the TNZ. Penguins at  $31.4^\circ\text{C}$  (the maximum  $T_a$  recorded in summer) should increase their energy expenditure to ca.  $1.2 \times \text{RMR}$ . In his study at the colony on Pan de Azúcar Island ( $26^\circ\text{S}$ ), Luna-Jorquera (1996) recorded maximum  $T_a$  of  $34^\circ\text{C}$ , where panting was frequent among penguins; in such a thermal scenario, birds would incur an energy expenditure of  $1.4 \times \text{RMR}$ . These figures are likely to be underestimates of the energy expenditure, as they fail to take into account other environmental factors such as solar radiation, which is higher in northern Chile (FAO 1985), which would further increase the periods of thermal stress where Humboldt penguins would have to incur elevated thermoregulatory costs.

Although we have emphasised behavioural responses, physiological and morphological responses are also likely to be involved. Some birds undergo an

acclimatisation in body temperature and metabolic rate in response to seasonal changes in climatic factors, being thus able to cope more effectively with high summer and low winter temperatures (Dawson and Whittow 2000; Ellis and Gabrielsen 2002 and references therein). Plumage, an anatomical feature, should also be important in certain seasonal adjustments as it accounts for ca. 80% of the body's insulation in Humboldt penguins (Drent and Stonehouse 1971). During summer, birds have old feathers that will be replaced during the moult in February (Simeone et al. 2002). At this stage, feathers probably do not have all their insulative properties (Lustick 1984; Davenport 1992) and birds may require other mechanisms to compensate for this deficiency (e.g. behaviour). Birds in winter, on the other hand, have a new plumage with unimpaired insulative properties. Moulting Humboldt penguins at Pan de Azúcar Island were observed to have significantly higher TRI values than non-moulting birds (Luna-Jorquera 1996). The better insulation of birds in winter could help further to explain the reduced behavioural repertoire observed in this season.

We are aware of the arbitrary nature of our score-assigning process, but after consulting the literature, we consider the sequence of thermoregulatory behaviours to be valid, although it is unlikely that it represents absolute quantities of energy expenditure. We have attempted to employ body posture, at least in a basic sense, to derive the degree of thermal load experienced by penguins and thus suggest its use as a simple field tool.

Our behavioural approach has been simplistic. The considerable distributional range of the Humboldt penguin, in contrast to our local and reduced data, makes it difficult to generalise about thermoregulatory strategies and it is conceivable that latitudinal variations may occur. Our data, nevertheless, suggest that Humboldt penguins do not face cold stress during winter. During summer, however, penguins experienced high  $T_a$  with occasional elevated heat loads and therefore displayed a behavioural repertoire mainly directed towards heat dissipation. This endorses the belief that Humboldt penguins are primarily adapted in morphology and physiology to cope with a cool environment and that these adaptations may result in "over-insulated" birds when they are in a hot terrestrial environment (Drent and Stonehouse 1971; Luna-Jorquera et al. 1997). This also validates the importance of behaviour in the maintenance of the species' thermal balance on land.

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