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PHYSIOLOGICAL CONDITION IN MAGELLANIC PENGUINS: DOES IT MATTER IF YOU HAVE TO WALK A LONG WAY TO YOUR NEST?

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Abstract. Colony edges, as opposed to interiors, are often considered less advantageous nesting places in colonial species. For temperate-breeding penguins, inland colony edges should be less desirable than other edges, as there are added costs of walking farther inland, and ambient temperatures are higher. During settlement and incubation, we compared body condition and baseline and stress-induced levels of the hormone corticosterone in male Magellanic Penguins (*Spheniscus magellanicus*) nesting on the sea edge of a colony with those nesting on the inland edge, >800 m from shore. Body condition in both groups was significantly lower during settlement than during incubation, but was similar in both groups within breeding stages. Corticosterone levels were similar between breeding stages and for groups within each breeding stage. While body condition can vary over time, penguins appear to be well buffered to physiological extremes, as they do not show modification of corticosterone levels with variations in nesting conditions.

Key words: corticosterone, energetic costs of nesting, Magellanic Penguin, penguin physiology, *Spheniscus magellanicus*.

Condiciones Fisiológicas en el Pinguino *Spheniscus magellanicus*: ¿Tiene Importancia Caminar una Larga Distancia al Nido?

Resumen. En especies coloniales, los bordes de la colonia son generalmente considerados como lugares menos ventajosos para el establecimiento de nidos. Para los pingüinos que crían en climas templados, los bordes de las colonias orientados tierra adentro deben ser menos deseables que otros bordes, ya que se suman los costos adicionales de caminar una distancia mayor desde la orilla y debido a que las temperaturas ambientes allí son más elevadas. Durante el establecimiento y la incubación, comparamos las condiciones corporales y los niveles de referencia e inducidos por estrés de la hormona corticosterona en los machos de *Spheniscus magellanicus* que anidaban en el borde de la colonia adyacente al mar con los que anidaban sobre el borde que mira hacia el interior, a más de 800 m

desde la orilla. La condición corporal en los dos grupos fue significativamente menor durante el establecimiento que durante la incubación, pero fue similar en los dos grupos durante las etapas de crianza. Los niveles de corticosterona fueron similares para ambas etapas de crianza y para los dos grupos durante cada etapa de crianza. Aunque la condición corporal puede variar en el tiempo, los pingüinos parecen amortiguar bien los extremos fisiológicos, ya que no muestran modificación de los niveles de corticosterona con las variaciones en las condiciones de nidificación.

Animals suffer physiological consequences for living in marginal habitats (Wingfield 1994). For example, individuals in more extreme environments such as deserts or poor wintering habitat may experience elevated baseline levels of glucocorticosteroids (in birds, corticosterone; Wingfield et al. 1992, Marra and Holberton 1998). These elevated baseline levels of corticosterone are important for the maintenance of homeostatic energy balance in suboptimal conditions (Dallman et al. 1993). Baseline levels of corticosterone also fluctuate on predictable (e.g., daily) cycles (Breuner et al. 1999) or during life-history changes such as migration or molt (Ramenofsky et al. 1995, Romero et al. 1997, Deviche et al. 2000). In addition to its baseline, homeostatic functions, corticosterone also increases rapidly in times of acute, unexpected stress, and mobilizes the additional energy needed to survive during unexpected perturbations (Wingfield and Ramenofsky 1999, Sapolsky et al. 2000). Furthermore, physiological condition of individuals also can affect corticosterone levels. Indeed, birds in very poor body condition (e.g., after extensive fasts or very poor calorie diets; Cherel, Robin, Walch, et al. 1988, Hood et al. 1998, Kitaysky et al. 1999) have higher corticosterone titers. Importantly, however, it appears that corticosterone and body condition do not relate in a linear fashion, and it appears that only when animals are in extremely poor condition do hormone levels start to rise (e.g., PHASE III, Cherel, Robin, and LeMaho 1988).

For colony-nesting birds, much attention has focused on nest-site selection and the reproductive benefits gained by position in a colony (Aebischer and Coulson 1990, Brunton 1997, Massaro et al. 2001). However, little attention has focused on the physiological costs suffered by individuals nesting in different locations in colonies. Nests on colony edges are generally of lower quality, and parents nesting there have

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lower reproductive success (Tenaza 1971, Kharitonov and Siegel-Causey 1988, Regehr et al. 1998). For flying birds, regardless of colony size, the costs of returning to edge nests are likely similar among individuals. In contrast, penguins must walk from the ocean to their nests. Walking is energetically costly for penguins (Pinshow et al. 1977, Dewasmes et al. 1980, Griffin and Kram 2000); therefore birds nesting on the inland edge must expend more energy to reach their nest sites. Additionally, for temperate-breeding penguin species, inland-nesting birds may suffer additional physiological costs due to increased ambient temperatures far from the sea. Indeed, in temperate-breeding species such as African Penguins (*Spheniscus demersus*; Frost et al. 1976), Galápagos Penguins (*Spheniscus mendiculus*; Boersma 1974), and Magellanic Penguins (*Spheniscus magellanicus*; Stokes and Boersma 2000), adults and chicks often overheat and die.

Magellanic Penguins live along the southern Atlantic and Pacific coasts of South America (Williams 1995). The largest colony of this species is located at Punta Tombo, Argentina (Gandini et al. 1996), where birds nest from within meters of the high-tide line to 1 km inland (Boswall and MacIver 1975). During settlement, male penguins establish and defend nest sites, and although they may return to the ocean to drink, they fast for upwards of 30–40 days (Yorio and Boersma 1994, Hood et al. 1998). After females lay eggs, males go to sea to feed and return 15–30 days later to relieve their mate and continue incubating the eggs (Yorio and Boersma 1994). At Punta Tombo, penguins nesting inland have lower reproductive success than penguins nesting in other areas (Gochfeld 1980, Frere et al. 1992, Stokes and Boersma 1998), partly because of the increased temperatures of inland habitat (Stokes and Boersma 1998). However, predation pressure does not appear to contribute to the lower reproductive success inland, as predation pressure is the highest in the densest areas of the colony (Stokes and Boersma 2000). Despite the potential benefits of lower nest densities and decreased fighting for penguins nesting at the colony's inland edge (Stokes and Boersma 2000), males have to walk farther, are subjected to higher ambient temperatures, and likely have a lower probability of attracting a mate. Indeed, nest quality and reproductive success are higher in areas of the colony where penguins can build thermally insulated burrows, unlike the nests on the edges of the colony, which typically are located below bushes (Stokes and Boersma 1991). This suite of negative characteristics of inland-edge nests suggests that the physiologic costs of nesting inland may be greater for penguins choosing to settle there.

We examined the differences in body condition and corticosterone levels between Magellanic Penguins that were nesting on the sea edge or inland edge of the colony at Punta Tombo. We expected both groups would be in poorer body condition and have higher corticosterone levels during settlement than upon return from their preincubation foraging trip. During the energetically demanding settlement stage, we expected inland-edge penguins to have higher plasma corticosterone and be in poorer body condition than shore-

edge birds, due to the added negative costs of nesting inland. However, we expected both shore-edge and inland-edge penguins to have similar body condition and hormone levels just after returning from the preincubation foraging trip, when energetic losses from the previous settlement period had been fully replenished.

METHODS

We compared the physiological condition and circulating corticosterone levels in Magellanic Penguins nesting within 20 m of the colony edge nearest the water ("shore edge") to those nesting on the landward side ("inland edge") of the Punta Tombo penguin colony, Chubut, Argentina (44°02'S, 62°11'W) during the breeding season of 1999–2000. Inland nests were a minimum of 800 m from the sea, as measured by walking a straight line from the nest to the high-tide line. We used only males in this study to control for differences between the sexes in chronology associated with foraging and incubating schedules early in the breeding season. We sampled penguins in both areas during two breeding stages: (1) settlement, when males were fasting in their nest, waiting for females to return to the colony; and (2) incubation, when males had just returned from the long, preincubation foraging trip. We sampled 10 penguins in each area during each breeding stage. No penguin was sampled twice. During settlement, we captured lone males by searching nests along the shore and inland edges of the colony. These males were chosen 2–3 weeks after the initial return of males to the Punta Tombo colony in 1999. During incubation, we selected nests with females on eggs, checked them daily, and captured the males on the day they returned from foraging to relieve the female.

We took a blood sample within 3 min of capture to measure levels of corticosterone in plasma. As circulating corticosterone does not increase significantly until 3 min after disturbance in most animals (Wingfield et al. 1982), this sample represented the baseline or constituent level of corticosterone in the plasma, prior to the capture stress. Birds were held for 30 min, and sequential blood samples collected at 10 and 30 min after initial disturbance, to measure increases in corticosterone in response to the capture. We collected blood samples (75–150 μ L) into heparinized microcapillary tubes after puncture of the interdigital (foot-web) vein. Samples were held on ice in the field and were later centrifuged to separate plasma. Plasma samples were subsequently frozen at -10°C until transferred to the laboratory for analysis. We measured corticosterone in plasma samples following a modified direct radioimmunoassay format (Wingfield and Farner 1975), without chromatography, as described in Wingfield et al. (1992).

During restraint, we weighed each bird with a spring balance (to the nearest 100 g) and measured bill length, bill depth, flipper length, and foot length using a dial calipers (to the nearest 0.01 cm) or ruler (to the nearest 0.1 cm). Body size was calculated as $0.899(\text{bill length}) + 0.924(\text{bill depth}) + 0.867(\text{flipper length}) + 0.907(\text{foot length})$. Coefficients were component scores from a principal components analysis of standardized morphological measurements for this species (from Hood et al. 1998). Body condition was deter-

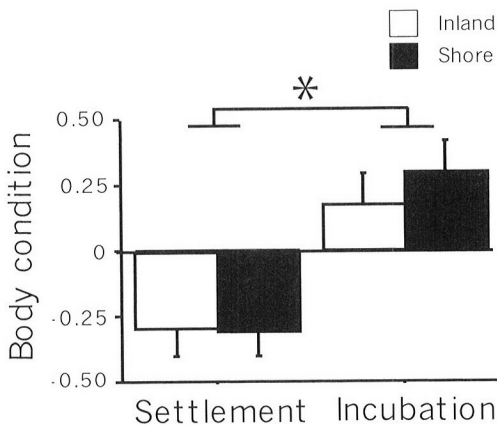


FIGURE 1. Body condition (mean ± SE) of male Magellanic Penguins nesting on the inland edge and shore edge of a colony at Punta Tombo, Argentina, during two stages of the breeding season (settlement and incubation). There were no differences in body condition within breeding stages, but body condition for penguins was significantly lower during settlement. Body condition is an index derived from principal components analysis of four body measurements. Sample size = 10 individuals for each area during each breeding stage. * $P < 0.05$ from a two-factor ANOVA.

mined using the residuals of a regression between body size and mass (Hood et al. 1998). Negative residuals indicated a bird was in poor condition for its size, and positive residuals indicated a bird was in good body condition.

STATISTICAL ANALYSIS

We tested for differences in body size and baseline levels of corticosterone in penguins between breeding stages and different edges of the colony using a two-way ANOVA with breeding stage and location as fixed factors. To quantify how penguin corticosterone levels responded to the stress series protocol, we integrated the corticosterone data from baseline to 30 min using the arithmetic trapezoidal rule (i.e., we calculated the area under the curve; Breuner et al. 1999, Picard-Hagen et al. 2001). The integrated value provided a measure of total corticosterone secreted during the capture-stress challenge, while encompassing the preexisting levels of circulating corticosterone prior to disturbance. Integrated corticosterone levels were compared with two-way ANOVA and Fisher's PLSD. We log-transformed corticosterone data prior to analysis to satisfy assumptions of non-normality and heterogeneity of variance. We used $\alpha = 0.05$ and the StatView computer program (SAS Institute 1998) for all statistical analyses.

RESULTS

Males in both shore-edge and inland-edge nests were in better body condition when they returned from their preincubation foraging trip than they were during settlement ($F_{1,36} = 24.6$; $P < 0.001$; Fig. 1). Body condition was similar for sea-edge and inland-edge nesters

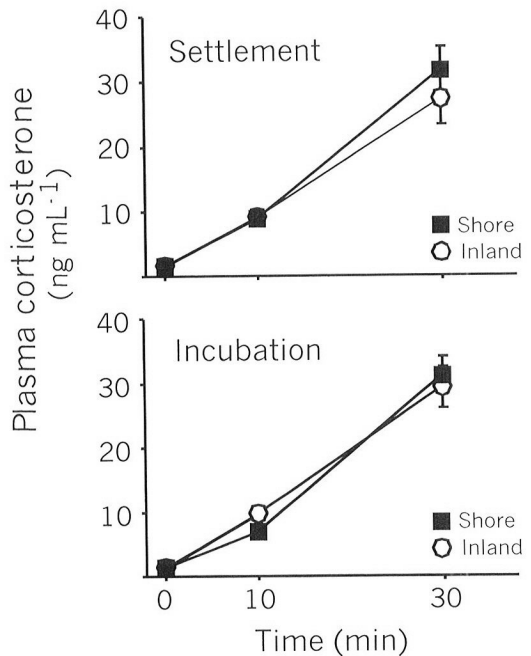


FIGURE 2. Patterns of corticosterone increase for Magellanic Penguin males subjected to a capture stress protocol. Penguins nested on either the inland edge or shore edge of the colony at Punta Tombo, Argentina, and were sampled during two stages (settlement and incubation) of the 1999–2000 breeding season.

within each breeding stage ($F_{1,36} = 0.2$; $P = 0.63$; Fig. 1). There was no interaction between treatments ($F_{1,36} = 0.4$; $P = 0.51$).

Baseline corticosterone levels were similar between settlement and incubation stages ($F_{1,36} = 2.8$; $P = 0.11$; Fig. 2), and shore-edge and inland-edge penguins had similar baseline corticosterone levels ($F_{1,36} < 0.1$; $P = 0.91$; Fig. 2). There was no interaction between treatments ($F_{1,36} = 0.8$, $P = 0.38$). The amount of corticosterone secreted during capture and handling (i.e., integrated corticosterone) was similar between breeding stages ($F_{1,36} < 0.1$; $P = 0.91$; Fig. 2) and areas ($F_{1,36} = 0.1$, $P = 0.75$; Fig. 2). There was no interaction between location and breeding stage ($F_{1,36} = 0.6$, $P = 0.46$). Finally, there was no significant correlation between body condition and either baseline corticosterone or integrated corticosterone for shore-edge or inland-edge penguins during either breeding stage (Table 1).

DISCUSSION

As predicted, body condition was lower in settling penguins compared to birds returning from foraging. Settling males were fasting while waiting for females to return to the colony, whereas males returning from the preincubation foraging trip had replenished energy stores in order to incubate eggs. These differences in body condition between the two breeding stages, how-

TABLE 1. There were no correlations between body condition and baseline or integrated levels of corticosterone for male Magellanic Penguins living inland or along the shore at a colony at Punta Tombo, Argentina. Ten male penguins were measured at each location and each breeding stage; no penguins were measured twice.

Location Breeding stage	Baseline corticosterone		Integrated corticosterone	
	r^2	P	r^2	P
Inland				
Settlement	0.04	0.60	<0.001	0.97
Incubation	0.15	0.27	0.001	0.94
Shore				
Settlement	<0.001	0.97	0.001	0.92
Incubation	0.44	0.56	0.004	0.86

ever, were not reflected in the baseline or stress-induced levels of plasma corticosterone.

While males during settlement had been ashore fasting long enough for their overall body condition to worsen significantly, plasma corticosterone levels were the same as in incubating birds. Furthermore, across all animals, there was no correlation between body condition and plasma corticosterone levels. Hood et al. (1998) showed that for Magellanic Penguins, baseline corticosterone did not increase in fasting males or females up to 14 days after food deprivation, but did increase in females fasting for over 19 days. Similarly, for both sexes, stress-induced corticosterone (after 25 min of capture) showed only a slight increasing trend as the fast progressed (Hood et al. 1998). It therefore appears that Magellanic Penguins do not incorporate the energetic benefits of increased corticosterone (e.g., increased energy mobilization, Wingfield 1994) until they are in extremely poor condition. Thus, the male Magellanic Penguins that we sampled during the settlement period had apparently not yet spent enough time ashore to reach an extreme level of physiological compromise that would elicit changes in corticosterone profiles. That significant increases in corticosterone levels do not occur until severe physiological compromise is not surprising. Both King Penguins (*Aptenodytes patagonicus*) and Emperor Penguins (*Aptenodytes forsteri*) withstand periods of extended fasting while raising young (Cherel, Robin, and LeMaho 1988, Cherel, Robin, Walch, et al. 1988, Cherel et al. 1994), with corticosterone levels only increasing very late (35–40 days) into the fast (Cherel, Robin, Walch, et al. 1988). Indeed, it appears that other physiological cofactors (e.g., protein breakdown as measured by uric acid, Jenni et al. 2000) directly relate to how and when glucocorticosteroid levels change in physiologically compromised individuals. Recently, McEwen and Wingfield (2003) proposed that it is not until animals reach a point of “allostatic overload,” that is, until they surpass their normal capacity to physiologically adapt to perturbations, that certain corrective mechanisms such as corticosterone levels will change.

We found no differences in body condition between shore-edge and inland-edge nesting penguins, nor were baseline corticosterone or patterns of corticosterone change different. We expected these similarities between shore-edge and inland-edge males for birds returning from foraging. Both groups would be equally likely to return energetically prepared for incubation. However, we did not expect to find that settling shore-edge and inland-edge males also had similar body condition and corticosterone levels. Costs during the long period of settlement for inland-edge nesters (i.e., higher heat index, higher transit costs, lower likelihood of attracting mates) were predicted to cause an increased energetic demand as compared to birds nesting directly along the shoreline. However, for shore-edge nesting penguins, factors such as increased penguin density and the concomitant increases in fighting at the nest site (Stokes and Boersma 2000) may decrease the physiologic benefits of nesting close to the ocean.

The most notable difference between shore-edge and inland-edge nest sites was the added minimum of 800 m that inland-edge penguins walked to get to their nests. We hypothesized that walking this distance would be energetically costly for a penguin nesting inland. However, we found that corticosterone levels and body condition were similar for both groups during both periods. Various authors have shown that the waddling of penguins is energetically demanding as compared to the gait of other birds (Pinshow et al. 1977, Griffin and Kram 2000). Such costs may be primarily due to the evolutionary constraints imposed on flightless species adapted to both aquatic and terrestrial environments (Fish and Baudinette 1999, Fish et al. 2001). Our data suggest that walking >800 m to inland-edge nests must be a minor physiological cost. However, during both the periods we chose to examine, the males had made only one recent trip to the nest. Perhaps a more appropriate period to measure any added physiological cost of nesting on the inland edge of the colony would be during chick rearing. During this period, ambient temperatures are higher (up to 35°C, Stokes and Boersma 1998), and adults make multiple trips back and forth to feed young. Thus, adults experience increased thermal constraints, higher energetic output from multiple transits, and an increased energetic demand from their chicks. None of these were present during either the settlement or incubation periods that we examined.

To our knowledge, our study is the first to examine whether nesting in different areas of a colony affects body condition and corticosterone levels in birds. Other authors have used corticosterone assessment to examine the energetic consequences of nesting in different environments (e.g., desert vs. moderate climates, Wingfield et al. 1992) or the effects of human disturbances such as recreational vehicles (Creel et al. 2002) or tourism (Romero and Wikelski 2002, Walker 2003). That both body condition and corticosterone levels were similar between shore- and inland-nesting birds suggests that Magellanic Penguins are relatively robust to variations in nesting conditions within their breeding colony. Previous studies quantifying the costs of nesting in different areas of the colony focused primarily on differences in reproductive success (Parrish

1995, Massaro et al. 2001). However, measuring how an individual's physiology may be compromised during reproduction is also important. While reproductive output may be equal within a season, animals with a higher energetic output may suffer subsequent negative consequences such as lowered future reproductive success or even decreased longevity (Cody 1966, Drent and Daan 1980). Such potential consequences are not measurable by assessment of within-season reproductive output alone.

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