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THE ADRENOCORTICAL RESPONSE TO STRESS IN INCUBATING MAGELLANIC PENGUINS (*SPHENISCUS MAGELLANICUS*)

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ABSTRACT.—Circulating levels of glucocorticoids increase rapidly in response to capture and handling in many vertebrate species, which is indicative of the sensitivity of the hypothalamo-pituitary-adrenal axis to a variety of acutely stressful events. We measured circulating levels of corticosterone at capture and after 25 min of handling and restraint in free-living Magellanic Penguins (*Spheniscus magellanicus*) during their first two long incubation turns. Initial levels of corticosterone were higher for males than for females; however, levels of corticosterone after 25 min of handling and restraint increased throughout incubation and were higher for females than for males. These 25-min levels of corticosterone were negatively correlated with body mass and body condition. Initial levels of circulating corticosterone, however, were not associated with mass and did not change during the fast, except for an increase among three females that had been incubating the longest. The higher 25-min corticosterone levels for females may be due to their lower body mass and longer fast during incubation. Magellanic Penguins appear to be more responsive to stress as fasting proceeds, suggesting that disturbances should be minimized when penguins have depleted fat stores.
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MAGELLANIC PENGUINS (*Spheniscus magellanicus*), like many other members of the family Spheniscidae, fast for long periods during breeding and molting. Males fast for about three weeks, beginning with their arrival at the colony and lasting through nest defense, courtship, and egg laying. Females fast for an average of 31 days, extending their fast from arrival at the colony through the first long incubation turn (Yorio and Boersma 1994). Males and females take turns incubating during the approximately 40-day incubation period (Boersma et al. 1990). The female usually takes the first and longest incubation turn (ca. 13 to 19 days), followed by the male for 11 to 17 days (Yorio and Boersma 1994). Subsequently, pair members exchange nest attendance more frequently.

In most avian species, fasting or food deprivation is physiologically stressful, but for Magellanic Penguins fasts are part of their life history and are not stressful. Nonetheless, fasting may become physiologically stressful when fasts are unusually long or when individuals have insufficient fat reserves. One way penguins can maintain homeostasis through fasting is through modulation of glucocorticosteroid levels in their blood. For example, King Penguins (*Aptenodytes patagonicus*) maintain baseline levels of corticosterone until the very end of fasting, when levels rise abruptly (Cherel et al. 1988).

The release of glucocorticoids in birds (primarily corticosterone; Holmes and Phillips 1976) is important in the regulation of facultative behavior and physiology (i.e. maintaining glucose levels) during environmental stress (Wingfield 1994). Glucocorticoids promote gluconeogenesis, especially the breakdown of protein reserves in muscles (Harvey et al. 1984). The energy released from protein breakdown may be used immediately or stored as fat (Gray et al. 1990, Wingfield and Silverin 1986). Many birds exhibit higher levels of corticosterone during inclement weather when foraging is more difficult (Wingfield 1984, 1988; Smith et al. 1994). This release of corticosterone may be particularly important in altering behavior patterns during stress because corticosterone is associated with increased food-searching behavior during food deprivation and with suppression of reproductive behavior without influencing sex steroid levels (Astheimer et al. 1992, Wingfield 1994).

In birds, many different acute physiological and psychological stressors induce the hypothalamic-pituitary-adrenal (HPA) axis to release corticosterone (Siegel 1980, Harvey et al.

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1984). Corticosterone increases dramatically in response to the acute stress of capture and handling by humans in many species (see Wingfield 1994), including Magellanic Penguins (G. Fowler unpubl. data), King Penguins, and Gentoo Penguins (*Pygoscelis papua;* Holberton et al. 1996). The magnitude of this increase in corticosterone from human handling is indicative of the sensitivity of the HPA axis to stressful events (Wingfield 1994). This stress response differs dramatically between individuals in different geographic locations and breeding seasons, and appears to have an ecological basis (Schwabl 1995, Wingfield et al. 1995). The magnitude of the adrenocortical response to stress appears to be modulated according to individual characteristics, including genetic factors (Schwabl 1995), body mass or condition (Smith et al. 1994, Wingfield 1994, Wingfield et al. 1994, Schwabl 1995), geographic location (Wilson and Wingfield 1994), stage of breeding, and degree of parental care (O'Reilly 1995, Wingfield et al. 1995).

We measured circulating levels of corticosterone immediately after capture (i.e. initial level) and after 25 min of handling during the first two long incubation turns of male and female Magellanic Penguins. We predicted that corticosterone levels would increase throughout fasting as the body condition of penguins deteriorated.

METHODS

Nest monitoring and blood collection.—At Punta Tombo Provincial Reserve, Chubut, Argentina (44°02'S, 65°11'W), we followed 56 nests and determined egg-laying dates, day of desertion (if appropriate), date of the male return to relieve the female, and date of the subsequent return of the female to relieve the male.

Blood samples were taken from females 1 day (n = 8), 8 days (n = 8), 14 days (n = 9), and 19 days (n = 3) after the second egg was laid. Males were sampled 1 day (n = 8), 8 days (n = 8), and 14 or 15 days (n = 8) after they returned to relieve their mates. No penguins were sampled more than once, and all were bled in the afternoon between 1200 and 1700 standard local time.

Two blood samples were taken from each bird, one within 3 min of when the bird noticed the observer ("initial" sample), and one after 24 to 27 min of capture and handling. Corticosterone can increase immediately (Le Maho et al. 1992), and birds sampled 2 to 3 min after capture had significantly higher corticosterone levels ($\bar{x}$ = 3.52 ± SD of 1.51 ng/mL, n = 22) than those sampled within 2 min of capture ($\bar{x}$ = 2.61 ± 1.09 ng/mL, n = 31; t = −2.41, df = 36, P = 0.021). Although many birds were sampled after 2 min of handling, the sex ratio of sampled birds was approximately equal, and samples were taken throughout the study period. Therefore, we treated all first samples the same in the analyses, even though they were not always at baseline levels. Corticosterone levels increase appreciably after 25 min of capture and restraint and are used as indicators of response to stress. Because the second sample always was taken after a specific period of time, this measure allowed us to determine how quickly corticosterone levels rise. Between the two blood samples, penguins were weighed, measured (length of foot, flipper and bill, and bill depth), and marked with a numbered stainless steel tag on the web of the left foot.

The brachial vein in the penguin's flipper was punctured with a 21-gauge needle and the blood collected into heparinized capillary tubes. Whole blood was stored on ice until evening, when it was centrifuged and the plasma was extracted. Plasma was stored at −20°C until it was transported on dry ice to the United States, where it was kept frozen until analysis.

Radioimmunoassay of corticosterone.—Plasma levels of corticosterone were measured by a direct radioimmunoassay (see Wingfield and Farner 1975, Wingfield et al. 1992). To avoid variability among assays, all samples were included in the same assay. Variability within assays (variation between duplicate samples) was 8.4%.

Twenty μL of plasma was allowed to equilibrate overnight with 2,000 cpm tritiated corticosterone (recoveries). Corticosterone was extracted in 4-mL redistilled dichloromethane added to each sample. Extracts were aspirated with Pasteur pipettes and evaporated under nitrogen. After evaporation of dichloromethane, samples were dissolved in a buffer and allowed to equilibrate overnight at 4°C. Aliquots (200 μL) of samples were transferred to duplicate test tubes for radioimmunoassay. In addition, a 100-μL aliquot was placed in a vial for determination of percentage recovery of the initial 2,000 cpm. This recovery value was used to adjust final assayed concentrations of corticosterone. A standard curve was set up over the range of 2 to 500 pg. Samples were allowed to equilibrate overnight after addition of equal (100 μL) amounts of labeled corticosterone and antiserum. Dextran-coated charcoal (0.5 mL) was added 12 min prior to centrifugation to separate bound and free fractions. Supernatants were decanted into scintillation vials and counted after addition of 4.5 mL of scintillation fluid.

Statistics.—A two-way ANOVA, excluding the three females that were sampled after incubating 19 days (i.e. the longest incubation turns), was performed on corticosterone levels and body condition.

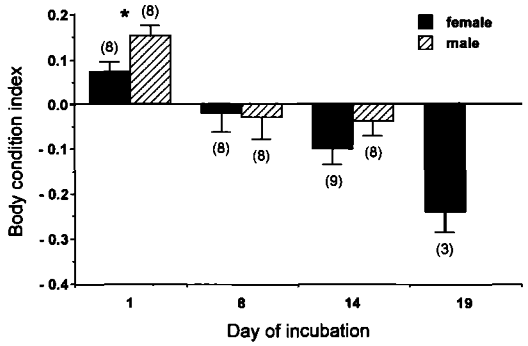

FIG. 1. Body condition ($\bar{x} \pm$ SE; sample size in parentheses) of male and female Magellanic Penguins on day 1, 8, 14, and 19 of incubation. Males were not sampled on day 19. The body condition index represents the difference between the actual and expected mass based upon size measurements (see Methods). The asterisk indicates that body condition on day 1 was significantly higher than on other days (Tukey test, $P < 0.002$).

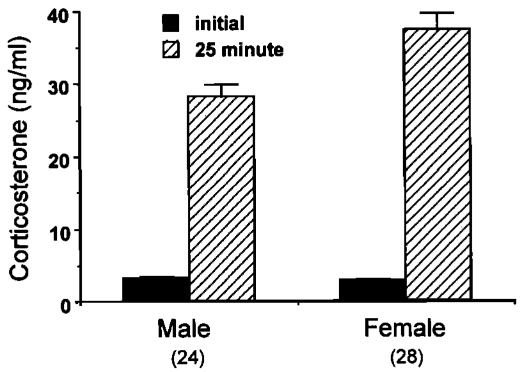

FIG. 2. Adrenocortical response to stress ($\bar{x} \pm$ SE; sample size in parentheses) by male and female Magellanic Penguins sampled initially and after 25 min of handling.

Factors were sex of the individual and the amount of time spent incubating. The Tukey posthoc test was used to evaluate differences between incubation days. Variables appeared to be normal; thus Pearson's correlation analysis was performed and reported for all correlations. Although the results are not reported here, Spearman rank correlations performed on the same variables yielded no change in statistical significance.

The percent increase in corticosterone was calculated for each individual by dividing the difference between the 25-min corticosterone level and the initial corticosterone level by the initial corticosterone level, and multiplying by 100.

To derive the body condition of each penguin, it was necessary to remove the influence of body size on the mass of each bird. To derive body size, the first factor was extracted from a principal components analysis of four variables (bill length, bill width, flipper length, and foot length). The first factor explained 81% of the variance, and the loading for each measurement was above 0.86. This first factor was an index of body size. The residuals of a regression between body size and mass (mass = 3.68 + 0.66 $\times$ size; $r^2 = 0.64$) were divided by the actual mass. This standardized residual represents body condition.

RESULTS

Incubation length and desertion.—The mean length of the first incubation turn (female) was 18.8 $\pm$ 4.0 days (n = 56),and the second turn (male) was 17.1 $\pm$ 4.7 days (n = 34). Desertions occurred in nine nests; eight of the desertions were by females. The exact fasting length for individual females was unknown, however, because females began fasting before they laid eggs (nests were not checked before egg laying), and they did not leave the nest until after the first incubation turn. The length of the male fast was known because males took the second incubation turn, and the date of male relief was known.

Body condition declined during incubation for both sexes ($F = 13.6$, df = 2 and 48, $P < 0.0001$) but did not differ significantly between sexes ($F = 2.49$, df = 1 and 48, $P = 0.12$; Fig. 1).

Adrenocortical response to handling throughout incubation.—Corticosterone levels increased significantly after 25 min of handling ($t = -18.8$, df = 104, $P < 0.001$; Fig. 2). The secretion of corticosterone exhibited no apparent pattern related to time of day (Fig. 3).

Initial corticosterone levels were significantly higher for males than females ($F = 6.33$, df = 1 and 48, $P < 0.02$) and were not influenced by amount of time spent incubating ($F = 0.26$, df = 2 and 48, $P > 0.05$; Fig. 4). In contrast, 25-min corticosterone levels increased significantly throughout incubation ($F = 3.67$, df = 2 and 48, $P < 0.05$) and were higher in females than in males ($F = 6.36$, df = 1 and 48, $P < 0.02$; Fig. 5). The adrenocortical response to stress (measured as the percent increase in corticosterone from initial to 25-min levels) was higher for females than males ($F = 11.48$, df = 1 and 48, $P < 0.002$) and showed a strong trend toward increasing during incubation ($F = 3.12$, df = 2 and 48, $P = 0.054$; Fig. 6).

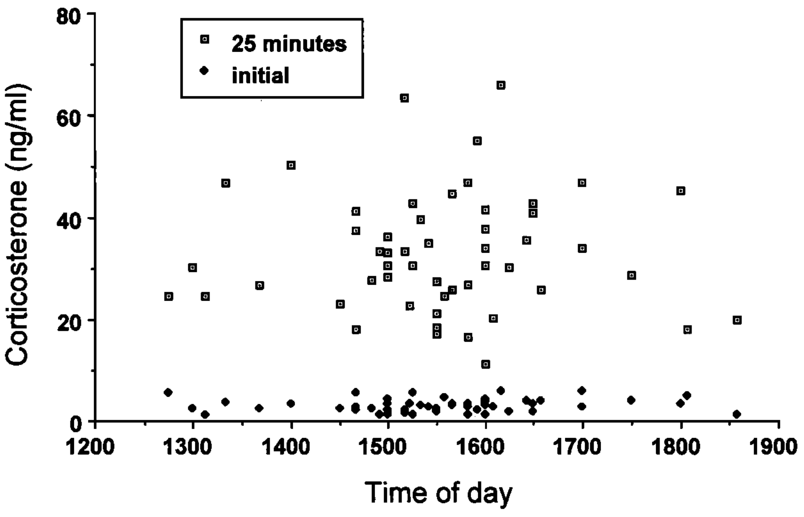

FIG. 3. Initial and 25-min levels of corticosterone versus time of day for all Magellanic Penguins sampled (n = 53).

Response to stress in relation to body mass and condition.—Increases in 25-min corticosterone levels and the percent increase in corticosterone over time may be a result of increasing corticosterone with decreasing body condition, which declines during incubation (Fig. 1). In males and females grouped together, the 25-min level of corticosterone was significantly negatively correlated with body mass (Table 1, Fig. 7) and body condition (Table 1).

Separate analyses of males and females showed correlations between 25-min corticosterone levels and body mass. The correlation of body mass and 25-min corticosterone levels was stronger in females than in males; however, male and female correlation coefficients were similar ($P > 0.05$; see Table 1).

As for body condition, males alone showed no significant correlation between body condition and 25-min corticosterone levels, whereas females did (Table 1). This correlation among females, however, was strongly influenced by the three females who had incubated for 19 days. When these females were excluded from analysis, the relationship between body condition and 25-min corticosterone level was not significant for females ($r = -0.363$, $n = 26$, $P = 0.07$). This was the only grouping, however, in

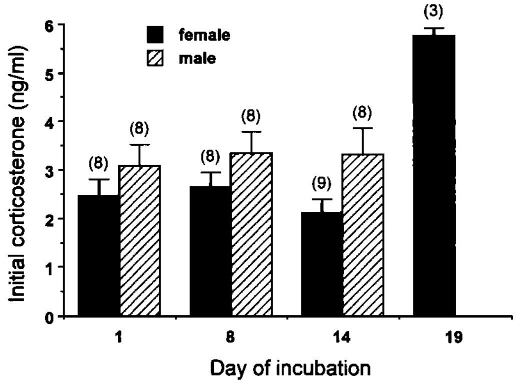

FIG. 4. Initial corticosterone levels ($\bar{x} \pm$ SE; sample size in parentheses) in male and female Magellanic Penguins on day 1, 8, 14, and 19 of incubation.

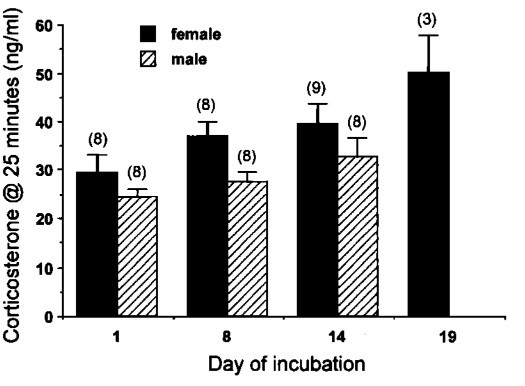

FIG. 5. 25-min corticosterone levels ($\bar{x} \pm$ SE; sample size in parentheses) in male and female Magellanic Penguins on day 1, 8, 14, and 19 of incubation.

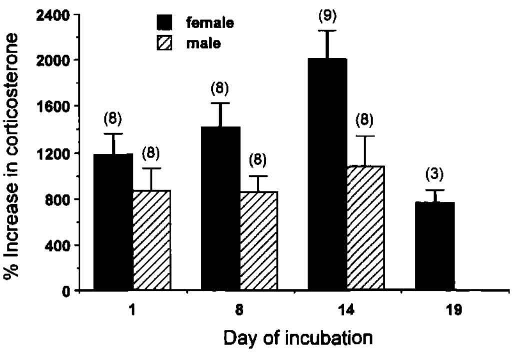

FIG. 6. Percent increase in corticosterone levels ($\bar{x}$ ± SE; sample size in parentheses) in male and female Magellanic Penguins on day 1, 8, 14, and 19 of incubation.

which these three anomalous females changed the statistical significance of the correlation.

DISCUSSION

Adrenocortical response to stress during incubation.—The circulating level of corticosterone increased significantly in response to capture and handling (Fig. 2). This response to an apparent stressor is typical of that exhibited by many species (Holmes and Phillips 1976, Wingfield 1994). Holberton et al. (1996) documented an increase in corticosterone in non-fasting King Penguins and Gentoo Penguins. Before our study, however, there were no reports of variation in the adrenocortical response of fasting penguins.

Corticosterone and fasting.—We hypothesized that the stress response would increase during incubation because birds are fasting. Profiles of corticosterone levels in some long-lived seabirds with long incubation periods provide one basis for that expectation, although the studies document initial levels of corticosterone only. As incubation progresses and body condition declines due to fasting, circulating corticosterone increases in *Diomedea* albatrosses (Hector and Harvey 1986). During fasting (ca. 50 days), normal circulating levels of corticosterone in King Penguins initially decreased, stayed at low levels during the middle of the fast, and increased at the end (Cherel et al. 1988). This period at the end of the fast also was characterized by an increased rate of loss of body mass and a high concentration of uric acid in the blood, indicating that individuals were mobilizing protein reserves. In those two studies, however, the response to acute stress (an indicator of sensitivity to stress) was not examined.

The penguins in our study had higher initial levels of circulating corticosterone only after extended fasting, in this case after 19 days of incubation (Fig. 4). This is similar to the results for the final stage of fasting in King Penguins (Cherel et al. 1988). The 25-min corticosterone levels, in contrast, increased as the fast lengthened and penguins lost mass (Fig. 5). This indicates that while the initial level of corticosterone may only increase dramatically when penguins have been fasting for unusually long periods, the response to stress may increase before that late stage. These results also indicate that declining body mass and condition are important factors in the adrenocortical response.

Corticosterone and declining body mass.—Although initial levels of circulating corticosterone were not related to either mass or condition, the 25-min levels increased with decreas-

TABLE 1. Pearson correlations between corticosterone levels and body mass and condition in Magellanic Penguins (n = 29 females, 24 males).

	Body mass		Body condition	
Variable	r	P	r	P
Basal corticosterone in all subjects	−0.026	0.85	−0.167	0.23
Basal corticosterone in females	−0.287	0.13	−0.265	0.17
Basal corticosterone in males	−0.209	0.33	−0.181	0.40
Maximum corticosterone in all subjects	−0.573	0.0001	−0.450	0.0007
Maximum corticosterone in females	−0.590	0.001	−0.490	0.007
Maximum corticosterone in males	−0.450	0.03	−0.212	0.32
% increase in corticosterone in all subjects	−0.347	0.01	−0.237	0.09
% increase in corticosterone in females	−0.124	0.52	−0.245	0.20
% increase in corticosterone in males	0.045	0.83	0.004	0.99

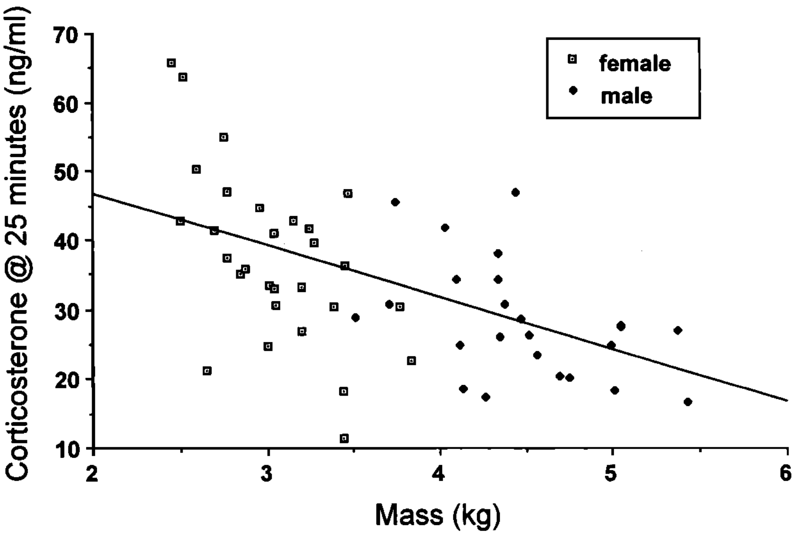

FIG. 7. 25-min corticosterone levels versus body mass for all male and female Magellanic Penguins sampled ($r = -0.573$, $n = 53$, $P < 0.001$).

ing mass and body condition for males and females combined (Table 1). This is not surprising, in light of the importance of glucocorticoids in gluconeogenesis when fat stores are depleted (Harvey et al. 1984). Indeed, for Common Diving-Petrels (*Pelecanoides urinatrix*), another high-latitude species, body condition and maximum corticosterone are negatively correlated (Smith et al. 1994). Nevertheless, not all studies of bird populations have found this relationship between mass and corticosterone. For example, among arctic-breeding shorebirds, maximum corticosterone was not correlated with body mass or condition in any stage of breeding, except among males during spring migration (O'Reilly 1995).

Our data are consistent with the suggestion by Wingfield et al. (1994) that maximum corticosterone may increase with decreasing mass only when individuals do not have substantial fat stores. For example, in a high-latitude population of Common Redpolls (*Carduelis flammea*), body mass and maximum corticosterone levels were negatively correlated during the breeding season but not during winter (when the birds have more fat). In White-throated Sparrows (*Zonotrichia albicollis*), body mass and corticosterone were correlated in fasted birds but not in birds fed *ad libitum* (Schwabl 1995). For Magellanic and King penguins, the physiological response to stress may be dampened when individuals are heavy at the beginning of a fast, and only when fat stores are low do they begin to show an increasing response.

Male-female differences.—Females fast for an average of 15 days (during courtship and egg laying) before beginning to incubate (Yorio and Boersma 1994). Therefore, it is not surprising that females incubating for the same length of time as males tended to be in poorer body condition (Fig. 1). In addition, female incubation was unusually long during this study: the mean incubation turn for females (18.8 days; $n = 56$) was longer than those reported for incubation periods from 1983 to 1989, which ranged from 13 to 16 days (Yorio and Boersma 1994). Females exhibited a more pronounced adrenocortical response to stress throughout the incubation turn, and the female stress response was more highly correlated with body mass and condition, supporting the hypothesis that the relationship between corticosterone and mass is more important among birds whose fat stores are more depleted. It appears that males and females differ in their adrenocortical response to stress during incubation, perhaps because: (1) in general, females weigh less than males; and (2) incubating females have fasted for longer periods than have incubating males.

Differences between the sexes in the sensitivity of the HPA axis cannot be attributed solely to differences in mass and body condition. In Magellanic Penguins, corticosterone levels were significantly higher in oiled than non-oiled females, whereas oiled and non-oiled males had similar initial levels (although females had a sharper drop in body mass in response to oil; Fowler et al. 1995). Females may have a lower response to stress during the reproductive phase (Wingfield 1988, Wingfield et al. 1992). Among arctic bird species during incubation, the sex that is responsible for most of the parental care has a lower adrenocortical response (O'Reilly 1995, Wingfield et al. 1995).

In addition, social and behavioral factors may play a role. In this study, males had higher initial levels of corticosterone than females (except for females at day 19). This may be because males generally are more vigilant in defending a nest site, and they may have to fight more frequently to defend the nest site from other males. It is unknown, however, how long after a fight corticosterone remains elevated, or how frequent challenges must be in order to result in prolonged high levels of corticosterone.

Implications for behavior and conservation.—It appears that psychological perception based on previous experience and environmental conditions, as well as behavior, influence the sensitivity of the HPA axis to an external, stressful stimulus (Harvey et al. 1984). We know that this may apply to the acclimation of Magellanic Penguins to humans, because penguins that live in areas with more frequent human contact have a lower adrenocortical response to an observer standing near the nest (G. Fowler unpubl. data). This corresponds to the behavior of penguins in these high-contact areas, which show alert and aggressive behavior at shorter distances from observers than penguins with less human contact (Yorio and Boersma 1992). Therefore, the modulation of the adrenocortical response to stress in Magellanic Penguins may depend on previous exposure to the stimulus as well as on body mass and condition, which decline during fasting periods.

What are the potential effects of this modulation? In the short term, elevated levels of corticosterone are associated with increased foraging behavior (Astheimer et al. 1992), activation of migratory behavior (Silverin et al. 1989, Wingfield et al. 1990), and decreased reproductive behavior (Silverin 1986, Wingfield and Silverin 1986, Harvey and Hall 1990). High levels of corticosterone may increase the likelihood of nest desertion in incubating Magellanic Penguins, which would be consistent with these effects. Indeed, penguins may have an "alarm signal" that induces feeding at the end of a fast (Le Maho et al. 1988, Robin et al. 1989). If that is the case, then individuals with low body mass should be the most susceptible to nest desertion.

Other studies of Magellanic Penguins support the link between body mass and desertion. Yorio and Boersma (1994) found that body condition was the most important factor in explaining desertion, rather than length of the fast or delay of the returning mate. In addition, reproductive success throughout the colony is lower when the mean mass of males and females is low at the beginning of the breeding season (Boersma et al. 1990). Because the sensitivity to stress is associated with body mass, the disturbance of penguins that have been fasting is more likely to cause desertion or other disruptive behavior than when they are heavier.

The effects of stressful stimuli on reproductive behavior are related to body mass, past experience, and psychological factors. In Magellanic Penguins, individual body mass and condition are important in the adrenocortical response to stress (this study), in predicting reproductive success (Boersma et al. 1990), and in influencing the likelihood of nest desertion (Yorio and Boersma 1994).

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