

formed by the Yellow-legged Gull which commonly prey on nests of Audouin's Gull, especially in sub-colonies with low densities (Oro and Martínez 1994, González-Solís et al. 1995). However, Clode (1993) suggested that seabird aggregations have evolved to utilize a dispersed and unpredictable food supply; as such, she stated that colonial nesting leads to increased vulnerability to predation, rather than being a strategy selected to combat it.

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## THE CORTICOSTERONE STRESS RESPONSE IN GENTOO AND KING PENGUINS DURING THE NON-FASTING PERIOD<sup>1</sup>

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*Key words: stress; corticosterone; penguin; glucocorticoid; Gentoo Penguins; King Penguins.*

Penguins rely primarily on stored fat reserves as an energy source during fasting periods, such as molt or incubation, often for weeks or months (Watson et al. 1971, Chérel et al. 1988a, 1988b, Williams et al. 1992).

During the final phase of fasting, when fat stores are depleted and food is not available, they begin mobilizing protein reserves as an energy source (Chérel et al. 1988a, 1988b). These energy reserves are derived primarily from skeletal muscle through the process of gluconeogenesis promoted by the adrenal glucocorticoid, corticosterone. Corticosterone secretion is under the control of adrenocorticotropin hormone (ACTH) released by the anterior pituitary which, in turn, is under the control of corticotropin releasing factor (CRF) from the hypothalamus (Holmes and Phillips 1976, Siegel 1980, Harvey et al. 1984). Corticosterone may be released rapidly into the bloodstream in response

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to a variety of stressors to help an individual through periods of increased energy demand. In most bird species, the pattern of acute corticosterone secretion in response to the stress of capture and handling is typically characterized by relatively low plasma hormone concentrations at the time of capture that often reach maximal levels 30–60 min later (Dawson and Howe 1983, Wingfield et al. 1992, 1994a, 1994b, Smith et al. 1994, Holberton et al. 1996). The profile of acute corticosterone secretion is considered an indicator of hypothalamic-hypophyseal-adrenal (HPA) axis sensitivity and is a common paradigm for assessing an individual's endocrine response to stress. Many studies have found that the activity of the HPA axis may vary with environmental conditions (Wingfield et al. 1983, Smith et al. 1994), energetic demand (Wingfield et al. 1994a) and activities throughout the annual cycle such as migration and parental care (Astheimer et al. 1994, Wingfield 1994, Ramenofsky et al. 1995, Holberton et al. 1996). Indeed, Cherel et al. (1988b) have shown that King Penguins (*Aptenodytes patagonicus*) suppress corticosterone secretion during fasting until the latter stage when fat reserves have been depleted and protein reserves must be mobilized.

Although the corticosterone stress response has been well documented in a wide variety of bird taxa, including many species of passerines (Dawson and Howe 1983, Schwabl et al. 1991, Wingfield et al. 1992, 1994a, 1994b, 1995, Astheimer et al. 1994, Holberton et al. 1996), shorebirds (O'Reilly and Wingfield 1995, Ramenofsky et al. 1995), gallinaceous birds (Wingfield et al. 1995), and several species of seabirds (Holberton and Wingfield 1994, unpubl. data, Smith et al. 1994), it was not known if penguins also exhibited a stress response during the non-fasting period when they would be most likely to show it. As part of a larger study on the ecology and endocrinology of seabirds wintering in the southern oceans, we captured and sampled two species of penguins during the non-fasting season to determine if they, like other species, exhibit the acute corticosterone stress response to capture and handling.

## METHODS

This study was conducted aboard the NSF Research Vessel/Ice Breaker Nathaniel B. Palmer during the winter months of May and June 1993, in the waters off of South Georgia, U.K. (55°S, 37°W), approximately 2,000 km E of Cape Horn. These latitudes are characterized by high winds and rough seas throughout most of the year. The island comprises mountains and glaciers with tall tussock grass bordering its rocky shoreline.

We were forced to restrict our sampling to relatively calm days as rough seas made going ashore to collect blood samples difficult. We followed the blood collection protocol described in Wingfield et al. (1992) for the collection of repeated blood samples from individual birds during restraint after capture. On both sampling days, we recruited many of the ship's crew and other scientists to help catch and restrain the birds while two people collected blood samples. In all cases used in the analyses, the initial sample, which best represents the pre-disturbance plasma value, was collected within 3 min after initial disturbance and capture. To develop a profile of corticosterone secretion

in response to capture and handling stress, we collected subsequent samples at 5, 10 and 30 min after capture. We omitted the 60 min sample on both days due to approaching bad weather. Each blood sample (50–100  $\mu$ l) was collected in a heparinized capillary tube after puncture of a small vein in the foot with a 21 ga needle and kept cool until centrifuged back on board the ship. The plasma was then collected with a 50  $\mu$ l Hamilton syringe and kept frozen in microcentrifuge tubes until assayed for corticosterone by radioimmunoassay (as described in Wingfield et al. 1992). Body mass and wing length were recorded for King Penguins only and no attempt was made to determine the sex of any of the birds. All animals were released immediately after the final sampling.

Care was taken to avoid contact with all birds, although viewed from afar, until equipment and materials were ready. At midday on 9 June, ten Gentoo Penguins (*Pygoscelis papua*) in adult plumage were quickly herded and captured as a group by hand or with fish nets on the shores of Annenkov Island on the west coast of South Georgia. Average wind speed during the morning ranged from 29–38 km/hr with swells of 2–3 m. By midday, the time of capture, wind speed had declined to less than 6 km/hr resulting in calm seas. Dry air temperatures ranged from 2.1–3.8°C during the day and skies were mostly clear with 10% cloud cover. The previous 24 hours had been characterized by a snowstorm with 89–102 km/hr winds, average dry air temperatures of –0.9°C and swells of 4–6 m.

Similarly, at midday on 22 June, seven adult King Penguins were corralled together and captured by hand along the shores of Salisbury Plain, Bay of Isles, on the northeast coast of South Georgia. Morning wind speed ranged from 29–40 km/hr with 1–2 m high swells with temperatures between 0.7–2.5°C accompanied by snow and freezing rain. The previous day was stormy with winds up to 80 km/hr, temperatures between –1.2 and 1.2°C and 3–4 m swells.

In some species, corticosterone secretion has been found to be suppressed during parental care (Holberton and Wingfield, unpubl. data, O'Reilly, unpubl. data). Although most King penguins cease feeding young during winter (Watson et al. 1971), we observed several instances of chick feeding by adult birds in the Salisbury Plain colony. To avoid any possible confounding effects that parental care may have on the stress response of these individuals, we selected birds that we believed were not actively feeding young. To do this, we only captured individuals that loitered on land along the shoreline for almost an hour instead of returning immediately to the colony upon coming ashore. In this way we assumed that these individuals were non-breeders or were not actively caring for young at the time of our sampling. Gentoo Penguins had completed their breeding activity at the time of sampling. Neither species showed signs of molt at the time of capture.

We used a one-way, repeated measures analysis of variance (ANOVA, Sokal and Rohlf 1981) to look for the expression of the stress response, that is, a significant change in plasma corticosterone concentration with handling time, for each species. In King Penguins we also looked for relationships between corticosterone levels and energetic condition (Wingfield et al. 1994a, 1994b, 1995). We used StatView SE+ software for all

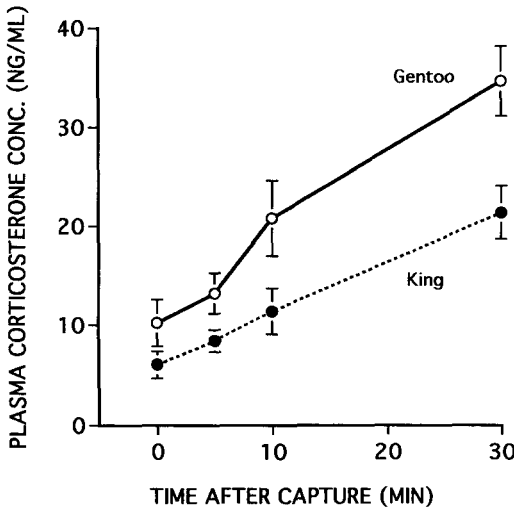


FIGURE 1. The change in mean  $\pm$  SE plasma corticosterone levels in response to capture stress in non-fasting Gentoo ( $n = 6$ , open circles) and King ( $n = 5$ , solid circles) Penguins during the 1993 Austral winter at South Georgia, U.K.

analyses and included data only from individuals from which we were able to quickly collect a complete series of plasma samples. Values listed are means  $\pm$  SE.

## RESULTS

Both species exhibited a corticosterone stress response, i.e., a significant increase in corticosterone with time after capture (Fig. 1). Gentoos showed an initial mean plasma concentration of  $10.22 \pm 2.34$  ng/ml of corticosterone at the time of capture that increased significantly to  $34.67 \pm 3.51$  ng/ml 30 min later ( $n = 6$ , one-way repeated measures ANOVA,  $F_{3,23} = 21.4$ ,  $P < 0.001$ ). The initial value of corticosterone concentration for King Penguins was  $6.03 \pm 1.37$  ng/ml that increased significantly to  $21.40 \pm 2.69$  ng/ml after 30 min ( $n = 5$ , one-way repeated measures ANOVA,  $F_{3,19} = 19.8$ ,  $P < 0.001$ ). Although the initial values of corticosterone did not differ between the two species (Mann-Whitney  $U$ -test, two-tailed,  $P > 0.05$ ), Gentoo Penguins showed significantly higher levels of corticosterone at 30 min after capture (Mann-Whitney  $U$ -test, two-tailed,  $P < 0.05$ ).

In King Penguins, there was no correlation between energetic condition, corrected for body size and expressed as  $\text{kg}/\text{wing length}^3$ , and corticosterone levels at the time of capture or 30 min (initial corticosterone:  $r_s = 0.300$ ,  $P = 0.55$ ; 30 min corticosterone:  $r_s = 0.00$ ,  $P = 1.00$ ,  $n = 5$ , Fig. 2).

## DISCUSSION

When sampled during the non-fasting period, Gentoo and King Penguins show an acute corticosterone response to capture stress similar to that observed in many other bird taxa. The initial and maximal values of corticosterone measured in these penguins fall well within the range reported in a growing number of stud-

ies on a wide variety of other bird species (Schwabl et al. 1991, Wingfield et al. 1992, 1994a, 1994b, 1995, Smith et al. 1994, Ramenofsky et al. 1995, Holberton et al. 1996). The basic pattern of the acute corticosterone stress response appears, therefore, to be well-conserved across disparate taxa of birds.

Modulation of the stress response has been reported for some species during parental care (K. O'Reilly, unpubl. data; Holberton and Wingfield, unpubl. data) and during migration (Holberton et al. 1996). In migrants, the suppression is believed to be a means by which skeletal muscle needed for migratory flight is protected from corticosterone's catabolic activity (Holberton et al. 1996). The data from this study, in conjunction with those from Cherel et al. (1988a, 1988b), suggest that penguins also show the ability to modulate the secretion of corticosterone by suppressing the hormone when protein sparing is most desired (Stage II of fasting as described by Cherel et al. 1988b).

Suppression of corticosterone release during fasting in penguins appears not to be influenced by absolute values in body mass. Although we assumed by their behavior along the shoreline and their apparent better physiological condition compared to those feeding chicks (pers. observ.) that our sampled King Penguins were not actively fasting or feeding young at the time of capture, they weighed less on average ( $\bar{x} = 12.93 \pm 0.47$  kg) at this time, the end of the breeding season, than King Penguins on the Isles Crozet (Cherel et al. 1988a, 1988) at the beginning of the pre-nuptial molt ( $\bar{x} = 18.27 \pm 0.34$  kg) and just prior to the onset of breeding ( $\bar{x} = 14.79 \pm 0.14$  kg). In fact, the average body mass of our birds falls within the range of values for fasting Kings well into the protein-sparing stage when corticosterone is significantly suppressed (Phase II, Cherel et al. 1988a, 1988b). In spite of this, our birds did not suppress corticosterone expression at these relatively low masses. One might conclude, therefore, that although corticosterone secretion may be influ-

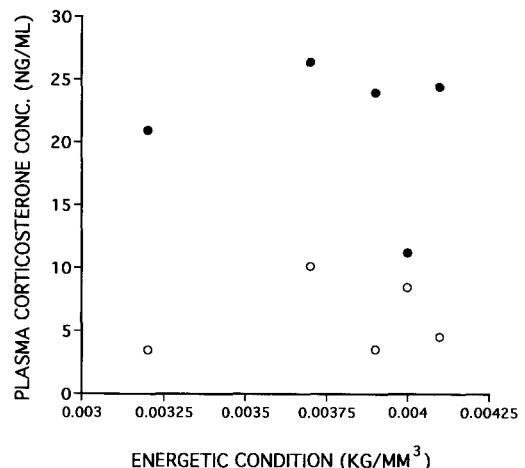


FIGURE 2. Plasma corticosterone levels within 3 min of capture (open circles) and 30 min later (solid circles) as a function of energetic condition (body mass  $\times$  wing length $^{-3}$ ) for individual non-fasting King Penguins.

enced by exogenous factors such as weather or food availability, the pattern of its release may also be under some endogenous control as a function of the annual cycle (Cockrem 1990, Holberton and Able 1992, Asheimer et al. 1994).

The amount of fat or energy reserves has been associated with the strength of the stress response in some species. Birds with greater fat reserves that are less likely to be affected by adverse conditions often show a reduced response to stress (Wingfield et al. 1994a, 1994b, 1995). In this study we failed to find such a correlation between energetic condition and initial or highest corticosterone concentration in our non-fasting King Penguins but our sample sizes may have been too small to detect such a relationship. Although both days of sampling were relatively calm, the previous 24 hours for each day were stormy. It is unknown if penguins respond by maintaining elevated corticosterone levels during storms as gliding and soaring seabirds appear to do (Holberton and Wingfield 1994, unpubl. data, Smith et al. 1994) but any effects that this weather may have on the penguins' stress response during such conditions does not appear to last after conditions ameliorate. Although the corticosterone stress response thus far appears to be well-conserved across diverse avian taxa, variations in its expression may reflect seasonal changes within the annual cycle and differences in species ecology and natural history.

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## USING ARTIFICIAL FOOD PATCHES TO EVALUATE HABITAT QUALITY FOR GRANIVOROUS BIRDS: AN APPLICATION OF FORAGING THEORY<sup>1</sup>

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*Key words:* foraging behavior; predation; supplementation; giving-up density; Northern Bobwhites; *Colinus virginianus*.

The distribution of food and predators plays an important part in spatial behavior and population dynamics of animals in natural habitats (Stephens and Krebs 1986). However, estimating food availability or predation risk within different habitat types remains a formidable task in ecological studies, largely due to difficulties associated with evaluating habitats "through the eyes" of the organism. Recently, empirical tests of theoretical patch foraging models have been used to assess the relative values of habitats in field experiments (Brown and Alkon 1990, Kotler et al. 1991, 1994, Kohlmann and Risenhoover 1994). Assuming animals favor those resources or habitats providing the greatest net utility, rate-maximizing foragers should abandon a patch when the sum of all foraging costs equals foraging gains incurred in the patch. Because the relationship between harvest rate and resource density in depletable patches is normally asymptotic (i.e., functional response, Holling 1959), the relationship between foraging gains and foraging costs also is nonlinear. As resource density declines, each additional food item becomes more costly to harvest until the net benefit of exploiting a patch is zero and the animal abandons the patch. The harvest rate at this point is termed the "quitting harvest rate" which is functionally linked to the density of resources remaining in the patch or "giving-up-density" (GUD; Brown 1988). Thus, GUD should represent the resource density within a patch at which foraging gains equal foraging costs. Foraging cost in Brown's (1988) model is a cumulative term formalized as:

$$C_i + P_i + MOC_i \quad (1)$$

where  $C_i$  is the energetic cost of exploiting the patch,  $P_i$  is the specific cost of predation in a patch, and  $MOC_i$  represents the patch specific "missed opportunity cost" (Brown 1988, Brown and Alkon 1990, Brown 1992). All these terms can be expressed in energy as the common currency (Caraco 1979, Stephens and Krebs 1986).

Theoretically, it should be possible to assess foraging costs in natural habitats by creating artificial patches containing a known density of resources and by measuring the GUDs in these patches after animals abandon them. This approach is based on the assumption that the forager balances its harvest rate in the artificial patch with habitat specific foraging costs, thus effectively treating the artificial patch as part of the natural environment. Hence, evaluation of habitat-specific elements of the cost function may be possible either by comparing GUDs among habitats and speculating on the effects of structural or physical differences on foraging costs imposed on the animal (Brown 1988, Abramsky et al. 1990, Brown and Alkon 1990, Brown et al. 1992a, 1992b), or by experimental manipulation of foraging costs (Kotler et al. 1991, 1992).

Here we report on two controlled experiments designed to evaluate the effects of different foraging costs (food abundance and cover from predation) on patch-use patterns of a granivorous bird, the Northern Bobwhite (*Colinus virginianus*). In the first experiment, we tested the hypothesis that exploitation of artificial patches by foraging Bobwhites was related to the availability of resources in the environment. We predicted Bobwhites would abandon artificial food patches at higher food density in rich, supplemented, environments compared to environments where resources were scarce. We also anticipated that GUDs in artificial patches should reflect the amount of augmented food available. In the second experiment, we tested the hypothesis that habitat structure and predation risk perceived by Bobwhites explained foraging decisions. Assuming that Bobwhites are capable of assessing habitat specific risk of predation, which may depend on the

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