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Long-Term Unpredictable Foraging Conditions and Physiological Stress Response in Mountain Chickadees (*Poecile gambeli*)

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Birds respond to short-term deterioration in foraging conditions by increasing their plasma level of corticosterone but the physiological effects of long-term deterioration in food supplies are not well known. In resident passerine birds that winter in temperate climates, such as the mountain chickadee (*Poecile gambeli*), the food supply may be limited and unpredictable over long periods of time. Whether the long-term limited and unpredictable food supply has an effect on (a) baseline levels of corticosterone and (b) the adrenocortical stress response to a standardized acute stress of handling and restraint in mountain chickadees was assessed. For a period of 94 days, one group of chickadees was maintained on limited and unpredictable food (food-restricted) and the other group was maintained on an *ad libitum* food supply. The food-restricted birds had significantly higher baseline levels of corticosterone than those maintained on *ad libitum* food. All birds responded to the acute stressor by an increasing secretion of corticosterone but there were no differences between the treatment groups in their stress response. There was a significant effect of sex on the stress response, with females reaching higher levels of corticosterone and responding at a faster rate than males. These results suggest that permanent resident birds wintering in harsh environments may have elevated levels of corticosterone on a long-term basis. Whereas other factors, such as day length and ambient temperature, may contribute to energetic hardship during the winter, the results showed that limited and unpredictable food alone can trigger significant changes in baseline levels of plasma corticosterone. The potential costs and benefits of long-term increased corticosterone levels in resident food-caching birds are discussed.

Key Words: corticosterone; unpredictable food; food-caching birds; mountain chickadee; stress response.

During the winter, many resident bird species have to cope with harsh environmental conditions characterized by low ambient temperatures, a limited and unpredictable food supply, and only a few hours of daylight in which to replenish the energy reserves that are essential for surviving the long, cold winter nights. These conditions occur for a couple of months at moderate latitudes but may last many months of the year in some areas, such as Alaska or northern Siberia. Birds have evolved several behavioral and physiological mechanisms facilitating their survival under these harsh conditions. All birds increase their fat reserves during the winter and some species also create numerous external food caches (see Witter and Cuthill, 1993; Pravosudov and Grubb, 1997a). It has been shown experimentally that many conditions associated with the winter season (day length, unpredictable food supply, ambient temperature) cause birds to increase their fat reserves and the number of food caches (Ekman and Hake, 1990; Bednekoff *et al.*, 1994; Pravosudov

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and Grubb, 1997a,b) but the physiological mechanisms of this energy management are not well understood.

It has been suggested that one of the proximate mechanisms regulating energy management in wintering birds could be related to plasma levels of corticosterone (Rohwer and Wingfield, 1981; Schwabl *et al.*, 1985, 1988; Astheimer *et al.*, 1992; Rogers *et al.*,1993; Wingfield *et al.*, 1998). Most of the research to date suggests that increases in corticosterone occur on a short-term basis, as a result of inclement weather such as snowstorms and sudden decreases in ambient temperature (Rogers *et al.*, 1993; Wingfield *et al.*, 1998). Short-term food deprivation elicits elevated levels of corticosterone in migratory and / or nonresident birds (Harvey *et al.*, 1984; Astheimer *et al.*, 1992). Wingfield *et al.* (1998) referred to these short-term increases in corticosterone levels and associated changes in behavior as "emergency life history stages" in which a response to a sudden change in environmental conditions might interrupt the normal life history cycle and redirect behavior and physiology toward survival. In particular, increased levels of corticosterone might facilitate foraging behavior and trigger irruptive migration and mobilization of stored energy reserves to fuel increased locomotory activities. During the winter, however, "survival emergency" may last for many months while the resident birds devote most of their time to foraging (Pravosudov, 1985). For permanent residents, such as food-caching parids, food may be limited and / or unpredictable for a long period of time during the winter; however, these species do not show eruptive migration in response to food shortages (Pravosudov, 1985). Furthermore, an increased secretion of corticosterone during the winter was previously documented in resident parids (Silverin, 1998), but experimentally increased levels of corticosterone did not trigger irruptive migration (Silverin, 1997). This raises the question of whether permanent resident birds respond to prolonged conditions of limited and unpredictable foraging by an increased secretion of corticosterone or whether the observed elevation in corticosterone during the winter is directly related to foraging conditions. Prolonged, elevated levels of corticosterone resulting from long-term stress have been suggested to cause muscular atrophy, structural damage to the brain, and cognitive impairments (McEwen and Sapolsky, 1995; Sapolsky, 1996). It is not clear, however, if relatively small long-term increases in baseline levels of corticosterone similar to ones reported in Silverin (1998) have the same negative consequences.

During the winter, in addition to limited and unpredictable food supply, other factors, such as day length and ambient temperature, make birds' survival energetically challenging. It is important to know if each one of these factors may affect birds' adrenocortical response to stress separately or if all these factors have to be combined to have an effect. This study tested whether long-term unpredictable food conditions alone can affect baseline corticosterone levels as well as adrenocortical responses to acute stress in a permanent resident food-caching passerine, mountain chickadee *(Poecile gambeli)*.

MATERIALS AND METHODS

Adrenocortical responses to long-term unpredictable foraging conditions were examined in wild-caught mountain chickadees (*P. gambeli*). Twenty-four mountain chickadees were caught during November 1999 near the Sage Hen area of Tahoe National Forest in northern California using mist nets near the feeders and decoy birds. After capture, all birds were transported to the laboratory and placed individually in wire-mesh cages (60 × 42 × 60 cm). After 1 week in captivity, the birds were randomly assigned to two groups, with 12 birds (3 females and 9 males) in each group. All birds were maintained on a 8:16-h light: dark cycle corresponding to the shortest day length in the area at a constant temperature of 20°C and fed with a mixture of shelled sunflower seeds, crushed peanuts, and mealworms. One group was maintained on *ad libitum* food and the other group was given a limited and unpredictable food schedule (food-restricted). Birds on the food-restricted schedule were given three or four 20-min intervals of unlimited access to food per day, resulting in either 60 or 80 min of access to food per day. Each day, we randomly determined whether birds received three of four 20-min feeding intervals, which we randomly distributed within each day. Birds in both treatment groups received the same amount of human disturbance. Every time food had to be added or removed from the cages of one treatment, birds in the other treatment were disturbed similarly. Both groups were maintained in the same room, separated only by a small observation chamber; thus, all birds experienced exactly the same physical parameters of the room with the exception of different feeding schedules. As a result, any changes expressed by the birds in either group could be attributed only to different feeding treatments.

Birds were maintained on their feeding schedules for 94 days, from December 21, 1999, to March 23, 2000. Sixty days from the beginning of the experiment, all birds were also subjected to several spatial memory tests (Pravosudov and Clayton, 2001). Four blood samples were collected from a wing vein during March 24–27, 2000. The first sample was collected within 3 min of entering the cage, the second sample at 5 min, the third sample at 20 min, and the fourth sample was collected at 50 min after entering the cage. This is standard procedure for testing adrenocortical stress response in small birds with a body mass of less than 15 g (Wingfield *et al.*, 1995). The total amount of blood collected during the stress series did not exceed 1.5% of bird body mass, which should not cause an additional physiological stress to birds. All chickadees were held in cloth bags between sample collections. We used samples collected within 3 min of entering the cage to determine a baseline level of corticosterone because it has been shown that corticosterone levels usually do not start to elevate until 3 min after capture (Wingfield *et al.*, 1982; Kitaysky *et al.*, 1999). In this study the corticosterone levels did not increase significantly in response to handling within an interval of 0–3 min after capture (regression analysis of corticosterone concentration on time since entering the cage, $F(1,19) = 3.14$, $P = 0.092$). Blood was collected at the same time of day for both treatments. Blood was collected into heparinized capillary tubes and then emptied into 0.3-ml vials which were kept on ice. All samples were centrifuged within 2 h of blood collection, and the collected plasma samples were frozen at −20°C and then shipped in dry ice to the University of Washington for radioimmunoassay analyses (Wingfield and Farner, 1975; Wingfield *et al.*, 1992).

We measured concentrations of corticosterone after extraction of 5- to 20-μl samples in dichloromethane. Recovery values of the extraction averaged 80.77% (range 74.5–93.2%). To avoid an interassay variation we analyzed all samples during a single assay. The intra-assay variance was 8% and the sensitivity of the analysis was 7.8 pg/ml.

After collecting blood samples, all birds were killed for further analyses and their sex was determined by dissection. We also measured wing length and body mass prior to blood collection. The fatness index was used to assess the body condition of individual birds, and it was calculated as a ratio of body mass to wing length cubed (Pravosudov and Grubb, 1997b). Previous studies demonstrated that the fatness index is a good indicator of overall fat reserves in birds (for more discussion on the fatness index see Pravosudov and Grubb, 1997b).

An ANCOVA was used to compare baseline levels of corticosterone between the two treatment groups and to assess any potential sex differences. We used time since entering the cage until the first bleeding as a covariate when comparing baseline levels of corticosterone because the time of first blood collection varied from 2 to 3 min between the birds. A repeated-measures ANCOVA (PROC MIXED; SAS Institute, 1994) compared the entire stress response, including all four samples taken within 50 min of entering the cage. All assumptions of statistical tests were upheld and the significance level was set at 0.05.

RESULTS

The baseline levels of corticosterone were significantly higher in food-restricted birds than in birds maintained on *ad libitum* food (ANCOVA, $F(1,16) = 6.69$, $P = 0.019$, Fig. 1), but there were no significant differences between males and females (ANOVA, $F(1,16) = 1.27$, $P = 0.28$). A sex by treatment interaction was not significant ($P > 0.9$) and it was dropped from the final analysis. There were no statistically significant differences between the treatments in time of collecting blood for baseline levels of corticosterone since entering the cage ($t = 0.50$, $df = 20$, $P = 0.62$).

There were no statistically significant differences between the two treatment groups in the adrenocortical response to a standardized acute stress protocol (repeated-measures ANOVA, $F(1,19) = 0.92$, $P = 0.35$, Fig. 2). Birds significantly increased their levels of corticosterone during the stress protocol (repeated-measures ANOVA, Time effect, $F(3,55) = 15.70$, $P <$

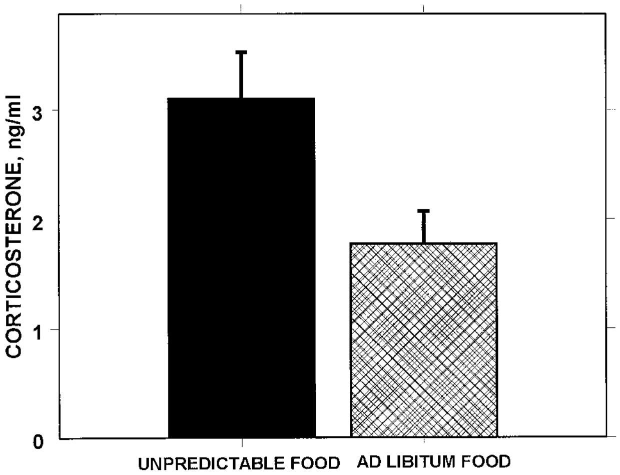

FIG. 1. Baseline levels of corticosterone (mean and SE) in mountain chickadees maintained on a food-restricted schedule (food-restricted birds, solid bar) and in mountain chickadees maintained on *ad libitum* food schedule (hatched bar).

0.001, Fig. 2). Independent contrasts analysis showed that there were no significant differences between 3 and 5 min after entering the cage ($P = 0.26$), but corticosterone levels were significantly higher at 20 min after entering the cage ($P < 0.001$, Fig. 2). Corticosterone concentration was not significantly different between 20 and 50 min after entering the cage ($P = 0.18$). Thus, the highest levels of corticosterone were reached at 20 min after entering the cage but treatments did not statistically differ in their rates of corticosterone change over time (repeated-measures ANOVA, treatment × time interaction, $F(3{,}55) = 0.25$, $P = 0.86$, Fig. 2). There were significant sex differences, however, in the adrenocortical response to stress, with females reaching higher levels of corticosterone than males (repeated-measures ANOVA, $F(1{,}19) = 9.39$, $P = 0.046$, Fig. 2). Females also showed higher rates of increase in the level of corticosterone than males (repeated-measures ANOVA, time × sex interaction, $F(3{,}55) = 2.72$, $P = 0.05$, Fig. 2). Males and females in the two treatment groups responded to the stress differently (repeated-measures ANOVA, treatment × sex interaction, $F(1{,}19) = 4.52$, $P = 0.047$, Fig. 2). Females in the food-restricted group had significantly higher mean levels of corticosterone during the entire stress response than males ($P < 0.05$), whereas there was no significant differences between males in females in the *ad libitum* food group ($P > 0.05$). An interaction between sex, time, and treatment was not statistically significant ($F(3{,}52) = 0.47$, $P = 0.71$).

At the beginning of the experiments, there were no differences between the two treatment groups in either body size (wing length, ANOVA, $F(1{,}20) = 0.32$, $P = 0.59$) or body mass (ANOVA, $F(1{,}20) = 0.003$, $P = 0.96$) but females were significantly smaller (wing length, ANOVA, $F(1{,}20) = 4.86$, $P = 0.04$) and lighter (ANOVA, $F(1{,}20) = 14.45$, $P = 0.001$) than males. A repeated-measures ANOVA showed that birds significantly increased their body mass during the experiment ($F(1{,}21) = 12.89$, $P < 0.01$) but there was no significant difference between the two experimental groups ($F(1{,}21) = 0.29$, $P = 0.59$), and an interaction between time and treatment was also not significant ($F(1{,}21) = 0.96$, $P = 0.34$). Separate analyses, however, indicated that whereas food-restricted birds increased their mass significantly over the course of the experiment (Paired t test, $df = 10$, $t = -4.25$, $P = 0.002$), a mass increase in the *ad libitum* food group was not significant (Paired t test, $df = 11$, $t = -1.59$, $P = 0.14$). There were no statistically significant effects of either body mass or body condition measured as the fatness index on adrenocortical response to stress (repeated-measures ANCOVA,

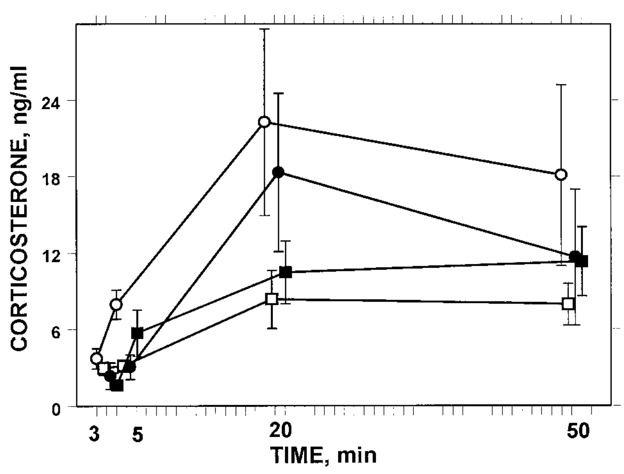

FIG. 2. Adrenocortical response to stress (mean and SE) in male and female mountain chickadees maintained on a food-restricted schedule and on an *ad libitum* food schedule at 0–3, 5, 20, and 50 min after entering the cage; circles, females; squares, males; open symbols, food-restricted treatment; filled symbols, *ad libitum* food treatment. The data points were slightly spaced out for better viewing of the results because the values were very similar.

body mass, $F(1,17) = 0.36$, $P = 0.55$; fatness index, $F(1,17) = 0.50$, $P = 0.48$).

DISCUSSION

These results show that mountain chickadees maintained on a short-day photoperiod respond to a long-term limited and unpredictable food supply by increasing baseline circulating levels of corticosterone. However, there were no differences in the adrenocortical response to a standardized acute stress of capture and restraint between food-restricted and control groups. Males and females responded differently to the acute stressor, with females reaching higher levels of corticosterone and more rapidly than males.

These results suggest that birds wintering in temperate climates with harsh winters may have elevated baseline levels of circulating corticosterone over long periods of time as opposed to only short-term elevations caused by limited and unpredictable food supply. Certainly other factors, such as day length and ambient temperature, could also contribute to the harshness of the environment during the winter. Our study, however, kept temperature and day length constant and as a result we were able to isolate the effect of limited and unpredictable food. Considering that elevated levels of corticosterone appear to be responsible for increased feeding activity and/or increased fat stores (Silverin, 1985; Wingfield and Silverin, 1986; Gray *et al.*, 1990; Astheimer *et al.*, 1992), our findings are not surprising. Numerous studies have demonstrated that, although fat reserves in birds might fluctuate during the winter in correspondence with short-term environmental stress caused by factors such as snowstorms, birds have heightened fat reserves during the entire winter (see Witter and Cuthill, 1993; Pravosudov and Grubb, 1997a). Whereas many factors can cause birds to increase their fat reserves during the winter (Witter and Cuthill, 1993; Pravosudov and Grubb, 1997a), limited and unpredictable food supply has been shown to independently affect fattening strategies in birds (Ekman and Hake, 1990; Pravosudov and Grubb, 1997b). Feeding rates in parids during the winter are also much higher than those during the rest of the year (e.g., Pravosudov, 1985). Our experiment also demonstrates that food-restricted birds increased their mass significantly over the course of the experiment while maintaining increased levels of corticosterone.

This study demonstrates that limited and unpredictable food supply affects baseline levels of corticosterone independently of other factors. It would be important to find out, however, if other factors associated with winter conditions, i.e., ambient temperature and day length, can trigger similar responses.

Mountain chickadees, like many other parids, cache food during the winter (Haftorn, 1974, personal observation). In food-caching birds, it has been demonstrated that unpredictable food conditions result in increased caching rates (Hurly, 1992; Pravosudov and Grubb, 1997b). It is possible that an increase in caching rate may also be mediated by elevated levels of corticosterone and increased levels of corticosterone may also have an effect on memory for food caches. For instance, there are some indications that a short-term elevation in corticosterone may result in a better memory for caches in mountain chickadees (Saldanha *et al.*, 2000). During the spatial memory tests, it has been found that birds maintained on a limited and unpredictable food supply were more accurate in cache retrieval and they performed better on spatial memory tests than birds maintained on an *ad libitum* food supply (Pravosudov and Clayton, 2001). It is possible that the better spatial memory performance of food-restricted birds was facilitated by the elevated baseline levels of corticosterone demonstrated in this study.

It has been reported that in some species increased levels of corticosterone might initiate an irruptive migration to more favorable areas (Wingfield *et al.*, 1998). It does not appear, however, to occur in resident food-caching parids, which have been known not to move in the middle of the winter even if conditions are extremely harsh (Pravosudov, 1985; Silverin, 1997). In food-caching willow tits (*Parus montanus*), increased levels of corticosterone stimulated dispersal behavior of juveniles but not adults during the autumn, but increased levels of corticosterone did not cause either juvenile or adult birds to leave their territories during the winter (Silverin, 1997). In wintering food-caching birds, instead of triggering irruptive migration, increased corticosterone levels might mediate an entire suite of adaptive energy management behaviors, including gaining extra fat reserves, creating more food caches, and facilitating more accurate memory about the locations of their caches. Thus, the moderate elevation of baseline levels of corticosterone may actually increase the birds' probability of survival during harsh winter conditions.

Although food-restricted birds have significantly elevated baseline levels of corticosterone, those levels are lower than the maximal levels of corticosterone achieved by the birds during the acute stress protocol, suggesting that there may be a threshold below which increased levels of corticosterone enhance survival and above which deleterious effects are produced over the long term. The recorded changes in baseline corticosterone could have been within the range normally found in wild birds so that birds were able to compensate for food shortages by, for example, eating more and/or being more efficient in extracting food energy (Wingfield *et al.*, 1997). If so, slightly increased levels of corticosterone might be an "anti-stress mechanism" facilitating behaviors directed toward maximizing the probability of survival during energetically demanding conditions.

The results of this study also show significant differences between sexes in the adrenocortical response to a standardized acute stressor. It is not clear why female mountain chickadees have a stronger stress response during the winter. A study of wintering dark-eyed juncos (*Junco hyemalis*), for example, did not find any differences between males and females (Rogers *et al.*, 1993). It is also interesting that the difference between males and females in our study was not related to their mass or condition index, although females were lighter than males. From studies of other free-ranging parids, it is known that females usually carry more fat reserves than males (Gosler, 1996; Pravosudov *et al.*, 1999) and that these differences are thought to be a result of social dominance. In winter flocks, female parids always assume a subordinate position and thus they might be more vulnerable when an energetic emergency appears (Pravosudov *et al.*, 1999). It is possible that females have a stronger adrenocortical stress response so that their behavior can be redirected toward energy saving and accumulation at a faster rate than that of dominant males, who always have a priority of access to all available food resources.

One concern about the results of this study is that plasma corticosterone was measured only once at the end of the experiment. It is possible that the concentration of corticosterone changed with time during the experiment and that the birds adjusted their corticosterone levels to existing conditions. However, because there was a significant difference in baseline levels of corticosterone between the treatments at the end of the experiment, we believe that the birds indeed differed for a long period of time. If anything, such differences could have been larger during the beginning of the experiment. There is no reason to think that there were no differences between the treatments in baseline concentration of corticosterone during most of the experiment and that then such differences would suddenly appear during the last few days. Birds experienced the same conditions for duration of the entire experiment, so the differences were clearly caused by the treatment.

Another concern is that all birds experienced some stress because of captivity. However, both groups had identical disturbance because every time we removed or added food to the birds maintained on a limited and unpredictable food schedule, we provided a similar disturbance to the birds on *ad libitum* food. There were also no significant differences between the groups in the time needed to capture them inside the cage to collect blood samples for baseline levels of corticosterone. Even if all the birds experienced stress levels higher than natural, we found that our treatment had an additional significant effect on baseline levels of corticosterone. It is not likely, however, that captivity resulted in constantly elevated levels of corticosterone because baseline and stress-induced levels of corticosterone in hand-raised mountain chickadees (Pravosudov *et al.*, unpublished) were very similar to values observed in this study.

In conclusion, it is suggested that increases in corticosterone secretion are not limited to short-term deterioration of environmental conditions but can occur over long periods of time. It is possible that some moderate increases in baseline corticosterone levels may not be deleterious for birds, but instead highly beneficial, by mediating behaviors directed toward survival over long periods of time. Local foraging conditions do not appear to affect the adrenocortical stress response, which suggests that this response may be regulated seasonally. Elevated levels of corticosterone can result in increased feeding rates and increased fat reserves in all birds, but noncaching birds may have to respond by leaving their territories for more favorable areas, whereas food-caching resident passerines can respond by improving their spatial memory for food caches. More direct studies are needed to ascertain the role of corticosterone in food-caching behavior, and memory for caches in particular, as well as more generally for understanding the costs of long-term elevated levels of corticosterone in birds.

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