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Seasonal Changes of the Adrenocortical Response to Stress in Birds of the Sonoran Desert

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ABSTRACT Many avian species of the North American Sonoran desert, e.g., the black-throated sparrow, *Amphispiza bilineata,* cactus wren, *Campylorhynchus brunneicapillus,* and curve-billed thrasher, *Toxostoma curvirostre,* can potentially breed from March/April to August. It is possible that, at least in summer, intense heat and aridity may have inhibitory effects on breeding by precipitating a stress response. Stress typically results in a rise in secretion of adrenocorticosteroid hormones that then inhibit reproduction by suppressing release of gonadal hormones. However, we found that plasma levels of corticosterone were not higher during summer, compared with winter, even in 1989 when summer temperatures were higher than normal. In June 1990, temperatures were also above normal and soared to the highest level recorded in Arizona (50°C). Plasma levels of corticosterone during June were high in black-throated sparrows, but less so in two other species (Abert's towhee, *Pipilo aberti,* and Inca dove, *Scardafella inca*) found in more shady riparian and suburban habitat with constant access to water. The adrenocortical response to stress (as measured by the rate of corticosterone increase following capture) was reduced in the hottest summer months in black-throated sparrows, cactus wrens, and curve-billed thrashers, but less so in Abert's towhee an Inca dove. These data suggest that at least some birds breeding in the open desert with restricted access to water are able to suppress the classical adrenocortical response to stress. The response is then reactivated in winter after breeding has ceased. It is possible that this stress modulation may allow breeding to continue despite severe heat. Analysis of plasma from these species indicated that the apparent modulation of the adrenocortical response to stress was not an artifact of reduced affinity or capacity of corticosterone binding proteins.

A wide spectrum of stressor stimuli are known to increase secretion of corticosterone in birds (e.g., Harvey et al., '84). This response is a result of enhanced released of corticotropin releasing factor and adrenocorticotropic hormone in a manner similar to those responses induced by stress in all groups of gnathostome vertebrates studied to date (e.g., Greenberg and Wingfield, '87). It is generally accepted that stress-induced increases in secretion of adrenocortical hormones such as corticosterone are an integral part of the process of acclimation to the stress. Effects of elevated circulating levels of corticosterone include mobilization of energy stores (gluconeogenesis), suppression of reproduction, and, in severe cases, immunoincompetance (e.g., Harvey et al., '84; Axelrod and Reisine, '84).

Female white-crowned sparrows, *Zonotrichia leucophrys gambelii,* may be able to suppress the acute adrenocortical response to stress (e.g., capture and handling) during the breeding season (Wingfield et al., '82; Wingfield, '88). This is in contrast to other species such as the European starling, *Sturnus vulgaris,* that maintain a marked adrenocortical response to stress when breeding (Dawson and Howe, '83). Why such modulation of the acute response to stress occurs remains obscure, but it has been suggested (Wingfield, '88) that it may be found in species adapted to severe environments, or with very short breeding seasons. This "resistance" to acute stress may be adaptive in environments in which the potential for disruption of breeding is great. Given the well-known deleterious effects of stress-induced elevations of corticosterone on reproductive function, a reduced sensitivity to stress in summer may allow the progression of reproductive activities despite potentially severe climatic conditions (Wingfield, '88).

To test the hypothesis that species breeding in severe climates (and thus potentially stressful during reproduction) show resistance to acute stressor stimuli, we investigated the adrenocortical response to stress in five avian species of the Sonoran des-

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ert of Arizona. Two species occur mainly in riparian habitat with water and shade always accessible. We predicted that these species would show no modulation of the stress response since they inhabit a relatively benign habitat and thus responsiveness to acute stress may be indicative of environmental conditions to which individuals should respond by inhibiting reproduction accordingly. Three species are found mainly in desert scrub and are not dependent upon the immediate presence of water. These latter species thus live in more severe habitat and resistance to acute stress may be a mechanism that allows successful reproduction. Many birds of the Sonoran desert breed when conditions can be most severe (summer) and even unpredictable, whereas in most other habitats species breed when conditions are most benign.

MATERIALS AND METHODS

Birds, field sites, and collection of samples

Two species found commonly in riparian habitat (and also suburban gardens) were studied: Inca dove, *Scardafella inca,* and Abert's towhee, *Pipilo aberti.* Three species studied were captured primarily in the lower Sonoran zone of the Arizona desert: black-throated sparrow, *Amphispiza bilineata,* cactus wren, *Campylorhynchus brunneicapillus,* and curve-billed thrasher, *Toxostoma curvirostre.* All were captured in Potter traps baited with seeds, or in Japanese mist nets after luring birds to the nets by playing tape-recorded songs of the respective species. Previous investigations have shown that responses to playback of tape-recorded song do not affect plasma levels of corticosterone, and baseline levels of corticosterone are similar in birds captured in nets and traps (Wingfield, '85). Study sites were distributed throughout the lower Sonoran zone within Arizona in Phoenix, Mesa, Usery Mountains, Pinal Parkway near Oracle Junction, Santa Rita Experimental Range (University of Arizona) near Continental, and near Wilcox.

Most birds were caught in the morning hours (06.00–12.00), but some were captured later in the day in order to assess the effect of diurnal rhythms on corticosterone levels (see results). Blood samples were collected from a wing vein into heparinized micro-capillary tubes after puncture with a 26 gauge needle. Tubes were sealed at one end with molding clay and stored on ice until centrifuged (usually within 2–5 hours). Plasma was stored at −20°C and later transported on dry ice to the Department of Zoology, University of Washington in Seattle.

The stress response and collection of samples

It was important that all birds be stressed in the same way so that any responses would be comparable. We make the assumption that capture and handling is equally stressful to all the wild species studied. Although this cannot be proven we feel that the response to capture stress is probably a good indication of the responsiveness of the hypothalamo-hypophysial-adrenocortical axis to acute stressors in general. This "capture stress" paradigm was used for all individuals of all species. We regard this as a standard way of stressing all birds equally regardless of age, sex, and physiological state. All birds were held in cloth bags in shade while serial blood samples were collected as follows: immediately after capture (usually within 1–2 minutes) a single capillary tube full of blood (approximately 40 μl) was collected and additional single capillary tubes of blood were collected at 5, 10, 30, and 60 minutes after capture. Measurement of corticosterone concentrations in samples at each time point provided a direct assessment of the effects of capture stress on the rate of increase in corticosterone levels that can be compared across seasons and with gender. After sampling, sex was determined by presence of a brood patch or cloacal protuberance. If neither method was reliable, and in the non-breeding season, unilateral laparotomy was performed to confirm sex. These data also gave an indication of the reproductive state of each individual.

One series of samples was collected in December 1988 and January 1989 when no birds were breeding, and when gonads were regressed or just beginning to recrudesce. A second series was collected in July and August 1989, followed by a further set of samples collected in June 1990, without serial repeats on the same individual, in order to measure corticosterone binding proteins (see below), and to provide more samples of baseline corticosterone concentrations in hot summer months. At these times birds were known to be actively breeding and territorial or were known to have large developed gonads indicative of readiness to breed.

Radioimmunoassay of corticosterone

The assay procedure was a modification (without chromatography) of the methods described by Wingfield and Farner ('75) and Ball and Wingfield ('87). All plasma samples (ranging in volume from 5–30 μl) were equilibrated with 2,000 cpm of tritiated corticosterone (New England Nuclear) and 0.3 ml of distilled water for at least 2 hours (usually overnight at 4°C). They were then extracted in 5 ml of freshly redistilled dichloromethane. The

organic phase was aspirated and dried under a stream of nitrogen at 40°C. Dried extracts were reconstituted in 0.55 ml of phosphate-buffered saline and 200 μl aliquots taken to duplicate assay tubes and 100 μl to a scintillation vial (with 4.5 ml of scintillation fluid, 4 g Omnifluor, New England Nuclear, in 1 liter of toluene). The cpm of tritium in this vial for each sample provided an estimate of percent recovery following extraction.

The radioimmunoassay utilized an antibody to corticosterone (B21-42, Endocrine Sciences, Tarzana, CA). Of the steroids likely to be encountered in avain blood, progesterone showed 57.8% cross reaction with the antibody. However, progesterone has a low extraction in dichloromethane, and corticosterone is the main steroid assayed in this system. Reconstituted extracts were incubated with 100 μl of antibody (diluted 1/100 from each vial) and 100 μl of tritiated corticosterone (approximately 10,000 cpm) overnight at 4°C. Separation of bound and free cpm was achieved by addition of 0.5 ml of dextran coated charcoal for 10 minutes at 4°C. All samples were then promptly centrifuged at 2,000 rpm for 10 minutes at 4°C in a Beckmann TJ-6 refrigerated centrifuge. Supernatants (containing bound cpm) were decanted into scintillation vials, 4.5 ml of scintillation cocktail added, and equilibrated for 4 hours or overnight before counting in a Beckmann LS3500 system (for 10 min or 2% accuracy).

With each assay, 2 solvent blanks and a standard sample (containing 1,000 pg of corticosterone) were taken through the entire assay procedure as a check on reliability criteria. Accuracy of measurement for the standard sample was 96.3%, interassay coefficient of variation was 8.8% (n = 8 assays), and other reliability criteria were within limits described in detail by Wingfield and Farner ('75).

Protein-binding studies

The radioimmunoassay for corticosterone provides a measure of both free hormone (the biologically active form) and that bound to plasma binding proteins (CBP; e.g., Wingfield et al., '84). If the level of CBP falls dramatically, then it is possible that the ratio of biologically active corticosterone could increase despite no apparent change in total plasma concentration. Thus it is necessary to assess levels of CBP in relation to potential modulation of the adrenocortical response to stress. The affinity and capacity of CBP were determined by the methods of Wingfield et al. ('84). Plasmsa samples from 6 black-throated sparrows (pooled to give 3 samples for analysis), 1 cactus wren, 3 curve-billed thrashers, 16 Abert's towhees, and 14 Inca doves were treated with 1 ml each of dextran coated charcoal (5 × the concentration used in the corticosterone assay—6.25 g charcoal, Norit A, and 0.625 g Dextran T-70) suspended in phosphate-buffered saline (500 ml). The mixture was incubated at room temperature for approximately 2 hours. Endogenous steroids were adsorbed to the charcoal that formed a pellet during centrifugation leaving the supernatant essentially free of steroid hormones.

The binding of corticosterone by proteins in the steroid-free plasma was assessed as follows: plasma was diluted to 2% in phosphate buffered saline with 2% gelatin (PBSG). Samples from individuals were pooled within species to ensure enough diluted plasma for at least 6 duplicates for Scatchard analysis. Duplicate 0.5 ml aliquots of diluted plasma and were incubated with increasing quantities of unlabelled corticosterone (0.078 to 10 ng) and a constant amount (ca. 10,000 cpm) of tritiated corticosterone for at least 2 hours at 4°C. Bound and free moieties were separated by the charcoal adsorbtion method as described for the corticosterone radioimmunoassay. Bound activity was then counted to 2% accuracy in a Beckmann LS 3500 system as described above. For each duplicate the bound/unbound ratio could then be calculated and, since the total mass of steroid hormone added to each duplicate was known, the bound/unbound ratio could then be used to calculate the total mass of hormone bound (Scatchard, '49). The slope of a line fitted to a plot of bound/unbound ratio versus total hormone bound (by the method of least squares) is the association constant (*Ka*) and its reciprocal is the dissociation constant (*Kd*). All binding affinities are expressed as *Kd* in mol/liter. The intersection of the line with the abscissa is the binding capacity in mol/liter. All lines fitted to these curves were corrected for non-specific binding as suggested by Chamness and McGuire ('75).

Statistics

The plasma samples used for measurement of corticosterone concentration provide two kinds of data: baseline levels under prevailing field conditions among individuals, and change in corticosterone level within an individual in response to capture stress. Changes in corticosterone within individuals in response to capture stress were analyzed by a two-factor, repeated measures ANOVA to compare the responses among seasons and sexes. The corticosterone level measured in each individual within 1 or 2 minutes of capture was our best estimate of the baseline sample for a bird unstressed by our handling procedure. We used these baseline values

for each individual to assess the effect of time of day, season, sex, and temperature (using temperature data for the Tucson area from the National Climatic Data Center, Asheville, North Carolina). Comparisons of baseline values among sexes and seasons were made by Mann Whitney U tests or by Fisher's Protected Least Squares Difference tests (PLSD) after an ANOVA.

Comparisons of binding affinity and capacity across species and sex were made by ANOVA followed by post hoc comparisons of pairs by Fisher's PLSD test.

RESULTS

Adrenocortical responses to capture stress in riparian species

In male and female Inca doves there were highly significant increases in plasma levels of corticosterone following capture and handling in both winter and summer (Fig. 1; $F = 18.052$, $df = 3$, $P < 0.001$, and $F = 33.09$, $df = 3$, $P < 0.001$, respectively; two-factor ANOVAs for repeated measures).

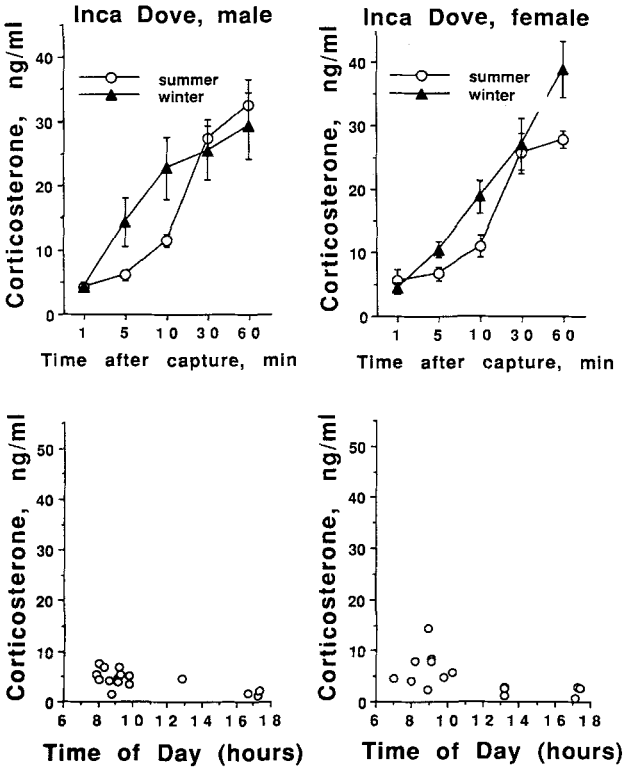

Fig. 1. Changes in plasma levels of corticosterone (mean ± SE) following capture and handling in male Inca doves (top left panel) and in relation to time of day (bottom left panel). Similar data for female Inca doves are given in right hand panels. N = 9 for summer and 7 for winter (males) and N = 7 for summer and 8 for winter (females).

There was a suggestion that the response to stress may have been lower in summer than in winter. This was not significant for males, but was for females (Fig. 1; $F = 3.136$, $df = 3$, $P = 0.087$; $F = 6.595$, $df = 3$, $P = 0.016$, respectively). There were no differences in responses between the sexes in either winter or summer ($F = 0.971$, $df = 4$, $P = 0.438$; $F = 0.26$, $df = 4$, $P = 0.901$, respectively). Ideally, a separate subset of samples should also have been collected immediately after capture at different times of day. Plasma levels of corticosterone in these samples would have controlled for changes owing to time of day and none-stressful events. Under field conditions it is impossible to obtain sufficient control samples (i.e., baseline samples from the same individual at each time point) since the very act of capture and handling is stressful. To circumvent this we plotted the corticosterone level in the first sample collected from each bird (i.e., closest to the basal, unstressed level) with time of day. These data provide an assessment that diurnal rhythms in basal, unstressed, levels of corticosterone do not explain possible changes in the rate of corticosterone increase following application of a stressor. Further, each bird contributes as its own control.

Note that these baseline corticosterone levels during the day (i.e., levels in samples taken immediately after capture) were below those generated during capture stress (Fig. 1, lower panels).

The responses of circulating corticosterone to capture stress were also highly significant in male and female Abert's towhees (Fig. 2; $F = 63.02$, $df = 3$, $P < 0.001$, and $F = 33.64$, $df = 3$, $P < 0.001$, respectively), and these changes were not influenced by diurnal fluctuations in baseline levels (Fig. 2, lower panels). In males there was no difference in the response to stress with season, but there was a marked and significant decrease in the response of corticosterone to capture stress during the breeding season (summer) in females (Fig. 2; $F = 0.14$, $df = 3$, $P = 0.71$; $F = 15.57$, $df = 3$, $P < 0.001$, respectively). In fact, the seasonal change in response to acute stress in females resulted in a slightly higher response than males in winter ($F = 4.9$, $df = 4$, $P = 0.0069$) and a retarded response in summer ($F = 14.96$, $df = 4$, $P < 0.001$).

Adrenocortical responses to capture stress in desert birds

In black-throated sparrows there were marked increases in corticosterone following capture (Fig. 3; $F = 14.2$, $df = 3$, $P < 0.001$) that were not affected by diurnal changes in baseline levels (Fig. 3, lower panel). Note, however, that the rate of increase of

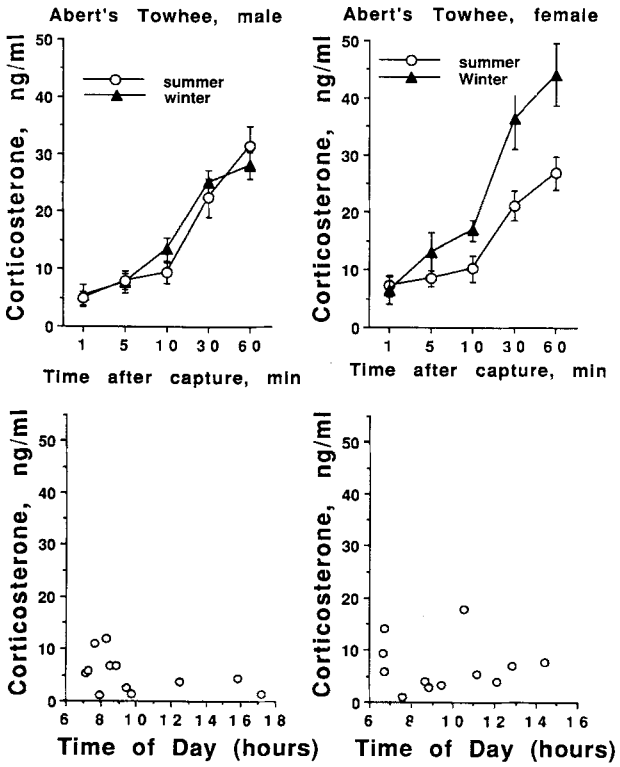

Fig. 2. Changes in plasma levels of corticosterone (mean ± SE) following capture and handling in male Abert's towhees (top left panel) and in relation to time of day (bottom left panel). Similar data for female Abert's towhees are given in the right hand panels. N = 8 for summer and 5 for winter (males) and N = 6 for summer and 6 for winter (females).

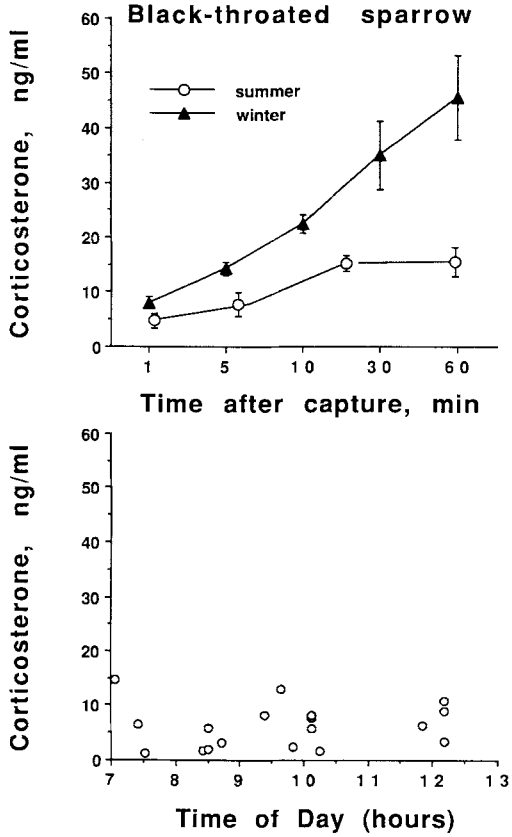

Fig. 3. Changes in plasma levels of corticosterone (mean ± SE) following capture and handling in black-throated sparrows (top panel) and in relation to time of day (bottom panel). N = 10 for summer and 9 for winter.

corticosterone levels in summer was considerably lower than in winter ($F = 5.66$, $df = 3$, $P < 0.0035$). Similarly for the cactus wren and curve-billed thrasher, there were significant increases in circulating corticosterone following capture in winter and summer (Figs. 4 and 5; $F = 30.34$, $df = 4$, $P < 0.001$, and $F = 12.47$, $df = 4$, $P < 0.001$, respectively) that were independent of any significant diurnal changes (Figs. 4 and 5, lower panels). Reduced rates of corticosterone increases in summer were marked in both species (Figs. 4 and 5; $F = 3.68$, $df = 4$, $P < 0.0163$, and $F = 4.1$, $df = 4$, $P < 0.0138$, respectively, for cactus wren and curve-billed thrasher). There were no obvious differences in response of corticosterone levels to stress by sex and thus data were lumped within species to increase sample size.

Baseline corticosterone levels in relation to season and ambient temperature

Baseline concentration of corticosterone (i.e., immediately after capture) did not change with season in Inca doves, Abert's towhees, or cactus wrens (see Table 1). However, there were slight but significant decreases in plasma levels of corticosterone in black-throated sparrows and curve-billed thrashers (Table 1). For three species we have enough data from two summers to analyze them separately by year and to compare them with winter baseline values collected when the average maximum temperature reaches only about 17°C. In 1989 we collected samples between 22 July and 6 August following one of the hottest periods (July) on record. For instance, in Tucson the July maximum temperature was 40.2°C (average maximum is 36.9°C) and exceeded the average maximum temperature on all but three days—often by as much as 5°C. The plasma samples in 1990 were collected between 17 and 27 June when the mean maximum temperature in Tucson was over 44°C and reached 50°C in Phoenix where Inca doves and Abert's towhees were sampled.

Despite these unusually high summer temperatures, there was no elevation of baseline corticosterone levels in Inca doves in either summer 1989 or 1990 compared with winter, and these values were much lower than peak levels measured

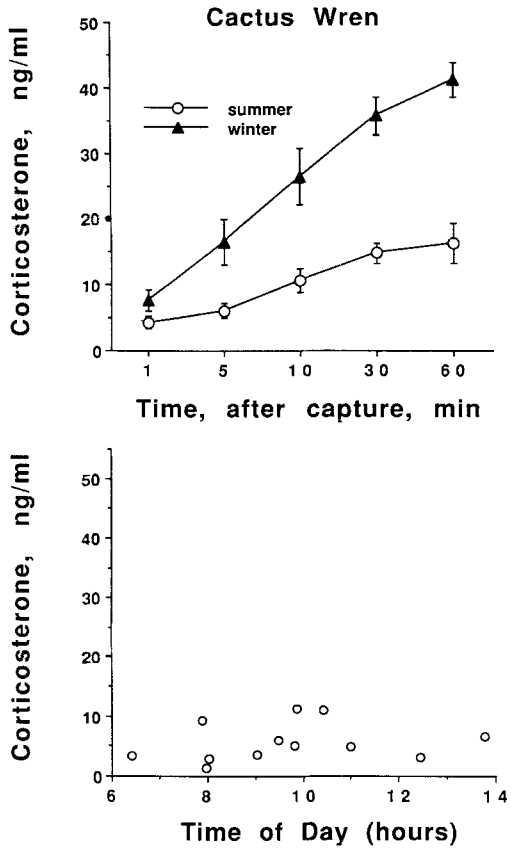

Fig. 4. Changes in plasma levels of corticosterone (mean ± SE) following capture and handling in cactus wrens (top panel) and in relation to time of day (bottom panel). N = 10 for summer and 5 for winter.

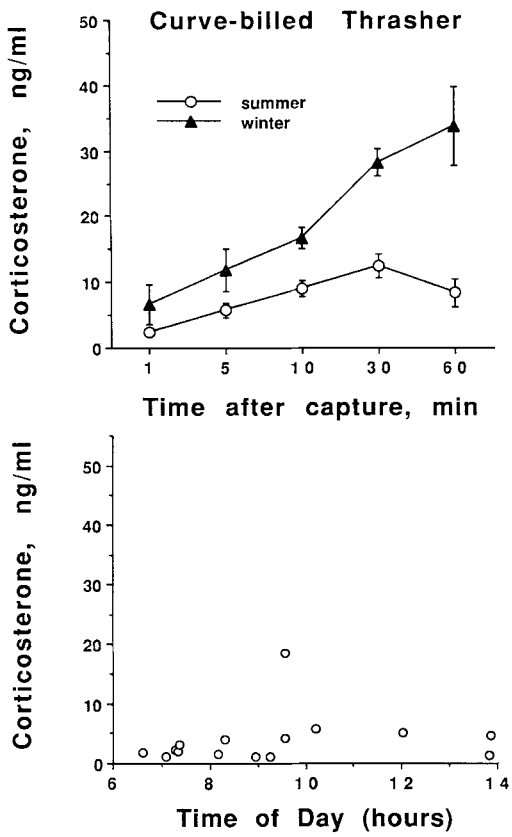

Fig. 5. Changes in plasma levels of corticosterone (mean ± SE) following capture and handling in curve-billed thrashers (top panel) and in relation to time of day (bottom panel). N = 10 for summer and 5 for winter.

during capture stress (Fig. 6, top panel; $F = 66.17$, $df = 3, P < 0.001$; comparisons of summer 1989 and 1990 with winter not significant by Fisher's PLSD test). There were also no differences between males and females ($F = 0.55$, $df = 3, P = 0.656$).

In Abert's towhees, baseline corticosterone levels were below capture stress levels in winter and both summers (Fig. 6, middle panel; $F = 12.91$, $df = 3, P < 0.001$, and $F = 21.68$, $df = 3, P < 0.001$ for males and females, respectively). Although within sexes there were no differences in baseline corticosterone between winter and summer 1989, males ($P < 0.05$, Fisher's PLSD test), but not females, had a significantly elevated corticosterone level during the intense heat of June 1990. However, this was still less than those levels resulting from capture stress ($P < 0.05$, Fisher's PLSD test). A two-factor ANOVA comparing season and sex revealed that there were no differences in baseline levels of corticosterone in males and females (Fig. 6; $F = 2.72$, $df = 3, P = 0.068$).

In black-throated sparrows, corticosterone levels immediately after capture were similar in winter and summer 1989 and below capture stress levels (Fig. 6, lower panel; $F = 8.14$, $df = 3, P = 0.004$). However, corticosterone titers were elevated in June 1990 ($P < 0.05$, Fisher's PLSD test) to levels comparable with those generated by capture stress.

Corticosterone-binding proteins

Examples of Scatchard plots with total binding curves and inhibition curves corrected for nonspecific binding are presented for riparian species in Figure 7 and for desert birds in Figure 8. Note that in all cases specific binding was prominent, indicating the presence of a high affinity corticosterone-binding protein in each species.

Comparisons of the affinity of corticosterone binding showed no differences among species (at least for black-throated sparrow, curve-billed thrasher, male and female Inca doves, and Abert's towhees; Table 2; single-factor ANOVA, $F = 2.12$, $df = 5, P = 0.09$). However, capacity of the binding protein did vary

TABLE 1. Baseline plasma levels of corticosterone (ng/ml) in Sonoran desert birds sampled in winter and summer

Species	Winter level mean ± SE	Summer level mean ± SE	Mann-Whitney U-test
Inca dove (male)	4.27 ± .69 N = 7	4.27 ± .72 N = 9	U = 34, NS
Inca dove (female)	4.34 ± .94 N = 8	5.58 ± 1.71 N = 7	U = 31, NS
Abert's towhee (male)	5.30 ± 1.87 N = 5	4.83 ± 1.16 N = 8	U = 22, NS
Abert's towhee (female)	6.48 ± 2.34 N = 6	7.22 ± 1.81 N = 6	U = 23, NS
Black-throated sparrow	7.93 ± 1.04 N = 8	4.73 ± 1.34 N = 10	U = 62, $P < 0.05$
Cactus wren	7.58 ± 1.60 N = 5	4.30 ± .96 N = 7	U = 28, NS
Curve-billed thrasher	6.68 ± 3.04 N = 5	2.40 ± .50 N = 10	U = 39, $P = 0.05$

N = sample size; NS = not significant.

among taxa (Table 2; F = 5.36, df = 5, $P = 0.0012$). Corticosterone binding capacity was similar in plasma from black-throated sparrows, curve-billed thrashers, and male and female Abert's towhees, but was significantly higher in male and female Inca Doves ($P < 0.05$ in all cases, Fisher's PLSD tests). In each species the capacity of corticosterone binding was not exceeded by the maximal plasma level of corticosterone generated by capture stress. This suggests that at all times the protein binding capacity for corticosterone was not a major factor when interpreting the responses of circulating corticosterone to capture stress. There was insufficient plasma from cactus wrens to make comparisons of corticosterone binding affinity and capacity.

DISCUSSION

The data presented here for birds of the Sonoran desert support the hypothesis that avian species breeding in severe habitats, in which the potential for environmental stress is great, may suppress the adrenocortical response to acute stress. All three species that inhabit the desert and were not dependent upon the immediate presence of water showed marked resistance to capture stress in summer. Two species of riparian habitats showed only slight resistance to stress (with the possible exception of female Abert's towhees). It was possible that the decreased response of corticosterone to stress in summer could have been a result of greatly reduced binding protein levels. For example, if at one season the maximum plasma level of corticosterone generated was much less than at other times, and if the binding protein content was greatly reduced, then the "free" (= biologically active) level may actually not have changed. However, CBPs with high affinity were found in all species studied (see also Wingfield et al., '84 for greater species diversity). Moreover, the binding capacities for corticosterone in black-throated sparrows, curve-billed thrashers, and Abert's towhees were identical, although lower than in Inca doves. Binding capacities for corticosterone were similar to, or in excess of, the maximum plasma levels of corticosterone generated by capture stress. It is possible that there still may be changes in CBP levels with season, but they are unlikely to make a major impact on the observed adrenocortical responses to stress.

In domesticated species such as the chicken and turkey, it is well known that high ambient temperature can result in elevated levels of corticosterone (e.g., Siegel, '80; Harvey et al., '84). Furthermore, drought is often accompanied by high ambient temperatures in semi-arid and arid environments and may also result in elevated secretion of corticosterone in bobwhite quail, *Colinus virginianus* (Cain and Lien, '85). Thus any apparent reduced adrenal response to acute stress could indicate either that the birds were maximally stressed at the onset of the experiment, or that they responded more rapidly before the first blood sample could be drawn. In these investigations, baseline levels of corticosterone (i.e., just after capture) were similar in all species both in summer and winter (Fig. 6). These data suggest that even those species living under the harshest conditions in the Sonoran desert were not stressed. Only during the record high temperatures of June 1990 were corticosterone levels elevated in some birds indicating they may be stressed by unusual heat. The possibility that corticosterone levels increased rapidly before the first sample could be collected is unlikely because some samples were collected within 30–90 seconds and the values at 30 seconds were not noticeably lower than those at

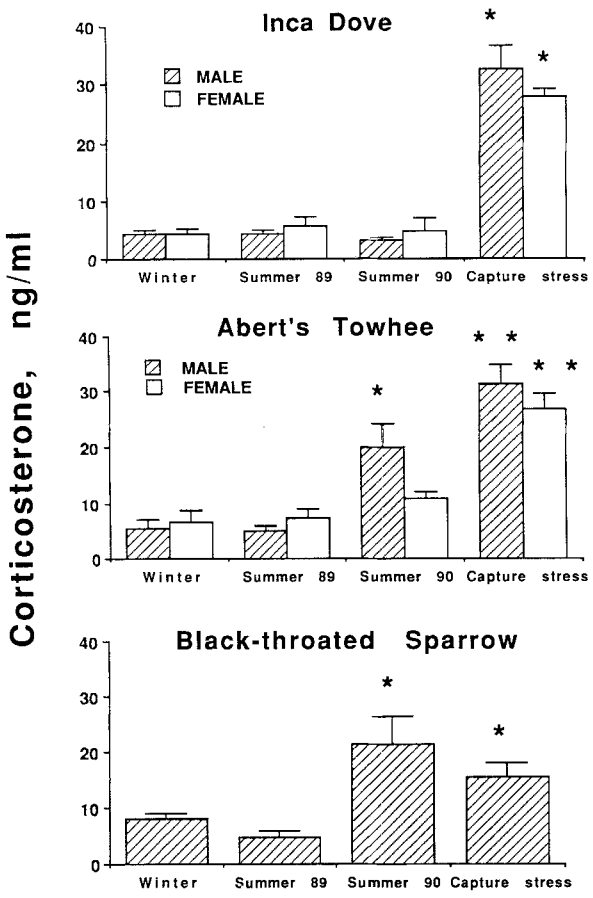

Fig. 6. Plasma levels of corticosterone (mean ± SE) in relation to season, ambient temperature, and one hour capture stress in Inca doves (upper panel, N = 7,8; 9,7; 8,5; and 9,7 for males, females in winter; summer 1989; summer 1990; and capture stress, respectively); Abert's towhees (middle panel, N = 5,6; 8,6; 10,10; and 7,6 for males, females in winter; summer 1989; summer 1990; and capture stress, respectively); and black-throated sparrows (lower panel, N = 8, 10, 6 and 10 for winter, summer 1989, summer 1990, and capture stress, respectively). *indicates significantly different from all of rest; ** indicates capture stress significantly higher than summer 1990 (see text for details).

90 seconds. The data indicate that the resistance to stress-induced rises of corticosterone in summer was not due to the fact that the birds were stressed to begin with, but rather represents a change in responsiveness of some component of the hypothalamo-hypophysial-adrenal axis with season and, at least in the Abert's towhee, with sex. Some birds (male Abert's towhee and black-throated sparrow) showed elevated baseline corticosterone levels during unusually intense heat, which suggests that under chronically unfavorable conditions the stress response is activated but to a reduced level (at least in black-throated sparrows). Our data address only development of stress-resistance to acute stimuli. Whether even more chronic stress could result in a greater response (similar to winter) remains to be seen.

Resistance of the hypothalamo-hypophysial-adrenal axis to acute stress has been documented in other species. Female white-crowned sparrows show only a slight increase of corticosterone to capture stress during the breeding season, and although males show a marked response, the elevation is delayed by 20 minutes compared with winter (Wingfield et al., '82). In feral California quail, *Callipora californicus,* depletion of ascorbic acid content of adrenocortical tissue (a measure of corticosterone release) was only slight in response to cold and caging, which elicit marked responses in domestic fowl (Flickinger, '59). However, it is not clear whether this response varies with season in California quail. In neonate chickens and laying hens, plasma levels of corticosterone do not increase in response to handling and restraint suggesting that there may be variations in stress responsiveness with development and reproductive condition in domesticated species also (Newcomer, '59; Freeman and Manning, '79; Freeman and Flack, '80; Etches, '76).

Seasonal, dimorphic, and developmental changes in responsiveness to acute stress are noteworthy, but their adaptive significance requires further

TABLE 2. Species comparison of affinity and capacity of corticosterone-binding proteins in blood of Sonoran desert birds[1]

Species	Affinity (Kd) in picomoles/liter	Capacity in nanomoles/liter
Inca dove (male), N = 7	5.37 ± 0.52	32.21 ± 9.35
Inca dove (female), N = 7	5.60 ± 0.53	18.79 ± 1.73
Abert's towhee (male), N = 8	7.87 ± 0.97	9.44 ± 1.11
Abert's towhee (female), N = 8	7.70 ± 0.86	7.45 ± 0.90
Black-throated sparrow (male), N = 3	4.24 ± 1.59	4.43 ± 1.73
Curve-billed thrasher (male), N = 3	5.69 ± 2.32	4.61 ± 1.60

[1]ANOVA for Kd, F = 2.124, total df = 35, P = 0.09. Anova for capacity, F = 5.359, total df = 35, P = 0.0012.

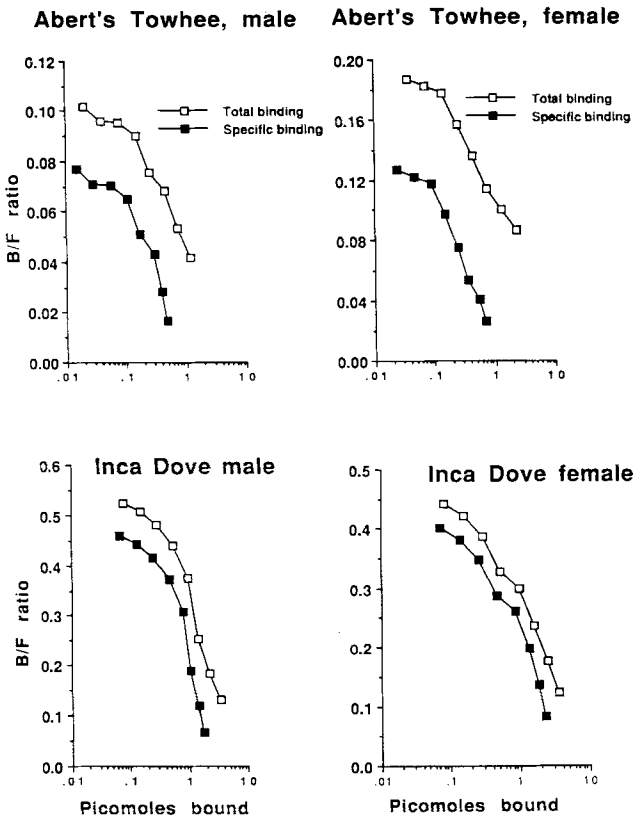

Fig. 7. Examples of Scatchard plots of corticosterone binding in the plasma of riparian birds.

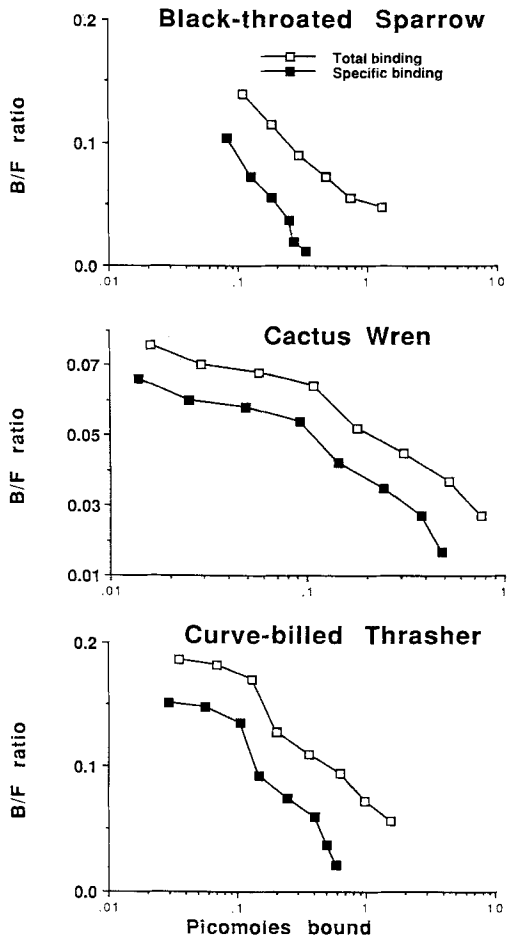

Fig. 8. Examples of Scatchard plots of corticosterone binding in the plasma of desert birds.

experimentation. Reduced adrenal response to acute stress when breeding may allow reproduction to proceed despite potentially severe and disruptive environmental conditions (Wingfield, '88). This could be highly adaptive given the capacity of elevated corticosterone levels to disrupt reproductive function (see Greenberg and Wingfield, '87; Wingfield, '88), although it is also possible that reduced sensitivity to acute stress may be related to more general desert conditions in summer and not breeding per se. The mechanisms underlying modulation of this stress response remain, however, completely unknown. In the white-crowned sparrow, adrenocortical tissue shows histological signs of regression as the breeding progresses (Lorenzen and Farner, '64), providing a possible basis for reduced responsiveness to stress, at least in females (Wingfield, '88). Modulation at the levels of the anterior pituitary and hypothalamus, such as increased sensitivity to negative feedback from corticosterone, or even higher in the central nervous system, is also possible.

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