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CORTICOSTERONE RESPONSES IN WILD BIRDS: THE IMPORTANCE OF RAPID INITIAL SAMPLING

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Abstract. Corticosterone concentrations in birds usually rise in response to capture and handling, and it is often assumed that this change is predictable. We tested this assumption by leaving Gambel's White-crowned Sparrows (*Zonotrichia leucophrys gambelii*), House Sparrows (*Passer domesticus*), and Lapland Longspurs (*Calcarius lapponicus*) in nets or traps for 15 min following capture and comparing their corticosterone response over the next 60 min with birds removed immediately. White-crowned Sparrows and House Sparrows left in mist nets for 15 min and then bled had significantly elevated corticosterone concentrations compared to controls that were immediately removed from the net and bled. Corticosterone concentrations over the next 45 min of handling and restraint were similar between groups. In another experiment, White-crowned Sparrows and Lapland Longspurs were captured using seed-baited Potter traps. The corticosterone response of White-crowned Sparrows left in the trap for 15 min did not differ from White-crowned Sparrows removed immediately. Leaving Lapland Longspurs in the trap had no effect in the initial 10 min of handling and restraint, but at 30 and 60 min these birds had significantly lower corticosterone concentrations than longspurs removed immediately from the trap. These data indicate that failing to immediately remove birds from nets or traps can alter the corticosterone response to subsequent stressful stimuli in unpredictable ways. This result emphasizes that the elapsed time from capture is a critical variable in assessing stress responses in free-living birds.

Key words: corticosterone, glucocorticoids, stress, techniques, wild birds.

Respuestas de los Niveles de Corticosterona en Aves Silvestres: La Importancia de un Muestreo Inicial Inmediato

Resumen. Las concentraciones de corticosterona en las aves usualmente aumentan en respuesta a la captura y manipulación, y muchas veces se supone que estos cambios son predecibles. Pusimos a prueba esta suposición reteniendo individuos de las especies *Zonotrichia leucophrys gambelii*, *Passer domesticus* y *Calcarius lapponicus* en redes o trampas durante los 15 minutos subsecuentes a la captura y comparamos sus respuestas en los niveles de corticosterona durante los siguientes 60 minutos con las de individuos removidos inmediatamente de las trampas y redes. Las muestras de sangre de *Z. l. gambelii* y *P. domesticus* que fueron obtenidas después de 15 minutos de retención en las redes tuvieron niveles de corticosterona significativamente más altos que las de los individuos control obtenidas inmediatamente después de la captura. Durante los 45 minutos siguientes de manipulación y captura, las concentraciones de corticosterona fueron similares entre los dos grupos. En otro experimento, *Z. l. gambelii* y *C. lapponicus* fueron capturados mediante trampas ''Potter'' cebadas con semillas. La respuesta en los niveles de corticosterona de *Z. l. gambelii* no fue diferente entre individuos retenidos en las trampas por 15 minutos e individuos removidos inmediatamente. Para individuos de *C. lapponicus* retenidos en las trampas no hubo un efecto durante los 10 minutos iniciales de manipulación y captura, pero a los 30 y 60 minutos estas aves tuvieron concentraciones significativamente menores que los individuos removidos inmediatamente. Estos resultados indican que al no remover inmediatamente a las aves de las redes o trampas, las respuestas en los niveles de corticosterona a estímulos estresantes pueden verse alteradas de una manera impredecible. Estos resultados enfatizan que en aves silvestres, el lapso de tiempo desde la captura es una variable crítica en la determinación de las respuestas al estrés.

INTRODUCTION

Many studies have recently focused on stress as a marker for an animal's well-being in its natural habitat (Wingfield et al. 1997). Since one of the hallmarks of stress in birds is the release of corticosterone, a member of the glucocorticoid family of steroid hormones (Norris 1997), there has been an interest in analyzing corticosterone concentrations in free-living birds. There are difficulties, however, in capturing and taking blood samples from wild birds. Many capture tech-

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niques are labor intensive, and it is difficult to capture birds and quickly take blood samples. Unfortunately, speed is of the essence when studying corticosterone responses to stress, because corticosterone concentrations quickly rise in response to capture and handling (Wingfield et al. 1997). Interpreting an animal's response to stress, however, requires knowledge of the baseline concentrations of corticosterone (assumed to reflect pre-stress hormonal levels, Wingfield and Romero 2001), in part because concentrations vary seasonally (Romero et al. 1997). For a variety of avian species, samples taken less than 2–3 min after capture are known to provide reliable baseline, unstressed corticosterone concentrations (Schoech et al. 1999).

Due to the difficulty in collecting samples, however, it is often tempting to infer baseline corticosterone concentrations when samples taken in under 3 min are unobtainable. An *a priori* assumption common to the literature is that failure to collect baseline corticosterone concentrations is irrelevant to the subsequent stress response. Samples collected later than 3 min after capture are assumed to accurately reflect normal stress-induced concentrations, and these may even be used to extrapolate baseline concentrations. Laboratory studies, however, indicate that prior stressful stimuli (e.g., capture) can have unpredictable effects on the stress response to subsequent stressful stimuli (e.g., handling; Dallman et al. 1992). Unfortunately, there has never been a systematic study analyzing the effects of capture on the subsequent corticosterone response to the stress of handling in wild birds.

The present study compared corticosterone responses between birds that were immediately removed from either mist nets or traps with those left in the nets or traps for 15 min. Two different capture methods were used on three different species: White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) trapped both with mist nets and seed-baited Potter traps; House Sparrows (*Passer domesticus*) trapped with mist nets; and Lapland Longspurs (*Calcarius lapponicus*) trapped with seed-baited Potter traps. Two different capture protocols on three different species were used to test the generality of the *a priori* assumption. The results explicitly tested whether birds respond normally to the stress of handling and restraint after a period of time in a mist net or trap, and whether inferring baseline concentrations from samples collected more than 3 min after capture is justified.

METHODS

Wild White-crowned Sparrows were captured on their wintering grounds 17–31 March 2001, in Albuquerque, New Mexico (35°0′N, 106°45′W). Wild Lapland Longspurs were captured on their breeding grounds on the Arctic tundra near the Toolik Lake field station, approximately 250 km south of Prudhoe Bay, Alaska (68°30′N, 149°30′W). All longspurs were trapped between 29 May and 1 June 1997. Although longspurs were captured during a brief mild storm, adverse weather has not been found to influence corticosterone release in this species during this time of year (Romero et al. 2000). Wild House Sparrows were captured 18–20 December 1999 in Albuquerque, New Mexico. Since neither White-crowned Sparrows (Romero et al. 1997), Lapland Longspurs (Astheimer et al. 1995, Romero et al. 1998), nor House Sparrows (L. M. Romero, unpubl. data) show sexual differences in corticosterone concentrations at these times of year, males and females were combined for analysis. All experiments were conducted in accord with AALAC guidelines and approved by the Tufts University Institutional Animal Care and Use Committee.

CAPTURE AND SAMPLING TECHNIQUES

Sixteen White-crowned Sparrows and 16 Lapland Longspurs were captured in seed-baited Potter traps. Control birds (n = 9 for each species) were removed immediately from the traps and a blood sample was taken within 2 min of the trap being sprung. The remaining birds were left in the trap for 15 min, after which a blood sample was taken within 2 min of removing the bird from the trap. Assignment of birds to control and treatment groups was random for each species.

Eighteen White-crowned Sparrows and 25 House Sparrows were captured in mist nets as they came to forage at suburban bird feeders. Control birds (n = 9 and 12, respectively) were immediately removed from the mist net and a blood sample was taken within 3 min of the bird hitting the net. The remaining birds were left suspended in the mist net for 15 min, after which a blood sample was taken within 3 min of approaching the net.

Once the initial blood sample was taken, all birds were placed in opaque cloth bags for a period of restraint. Lapland Longspurs were then removed and blood samples taken at 5, 10, 30, and 60 min post-capture, whereas White-crowned Sparrows and House Sparrows were removed and blood samples taken at 15, 30, and 45 min post-capture. Birds were replaced in the cloth bags between bleeds. Blood samples were taken by pricking the alar vein with a hypodermic needle and collecting approximately 60 μL upwelling blood in heparinized microhematocrit tubes. We used cotton to stanch blood flow between samples. Once all samples were taken, birds were provided a U.S. Fish and Wildlife Service aluminum leg band (to prevent resampling), and released.

SAMPLE PROCESSING AND ANALYSIS

Blood samples were stored on ice for up to 12 hr, at which time they were centrifuged at approximately 400 *g*. The plasma then was removed, stored at −20°C, and transported to Tufts University for analysis. Corticosterone concentrations were measured by radioimmunoassay after extraction with dichloromethane as previously described (Wingfield et al. 1992). Samples from each species were analyzed in a single assay, and the intra-assay variability was less than 8% for each.

Differences in corticosterone concentrations between treatments and between bleed times were analyzed by repeated measures ANOVA using Statview (Statview 1999) with $P < 0.05$ interpreted as significant. Values reported are means ± SE.

RESULTS

Both White-crowned Sparrows and Lapland Longspurs were briefly startled by the closing Potter trap door. After trying to escape for a minute or so, they usually resumed feeding and tried to escape only periodically throughout the 15-min containment period. White-crowned Sparrows immediately removed from traps and those left for 15 min both increased their plasma corticosterone concentrations over the 45 min of handling and restraint (Fig. 1; $F_{3,42} = 29.3$, $P < 0.001$). Furthermore, leaving the birds in the traps for 15 min had no effect on the subsequent corticosterone response ($F_{1,14} = 0.9$, $P = 0.37$ for overall treatment effect; $F_{3,42} = 0.8$, $P = 0.53$ for the treatment × corticosterone increase interaction). Lapland Longspurs also increased their corticosterone concentrations over the 60 min of handling and restraint (Fig. 1; $F_{4,56} = 10.2$, $P < 0.001$). Like White-crowned Sparrows, the response was nearly identical for the first 10 min in both groups so that there was no overall treatment effect ($F_{1,14} = 0.7$, $P = 0.42$). In contrast to White-crowned Sparrows, however, longspurs left in the trap for 15 min had lower corticosterone concentrations than controls at 30 and 60 min, as evidenced by a significant interaction effect between treatment and the increase of corticosterone over time ($F_{4,56} = 3.5$, $P < 0.02$).

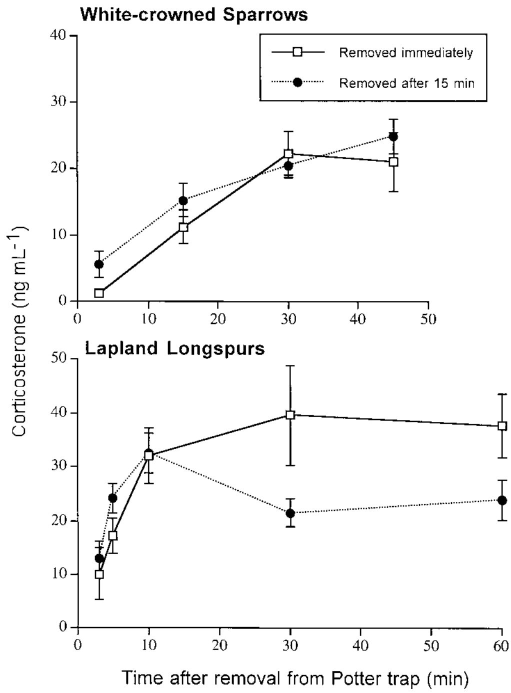

FIGURE 1. Corticosterone response to capture and handling in White-crowned Sparrows and Lapland Longspurs. Birds were either removed immediately from seed-baited Potter traps ($n = 9$ for each species) or left in the trap for 15 min before removal ($n = 7$ for each species).

Both White-crowned Sparrows and House Sparrows generally struggled throughout the 15 min they remained in the net. This was reflected in elevated corticosterone concentrations in the initial sample for both species (Fig. 2). In both species, birds bled immediately and those left in the net increased their corticosterone concentrations during the period of handling and restraint ($F_{3,48} = 14.0$, $P < 0.001$ for White-crowned

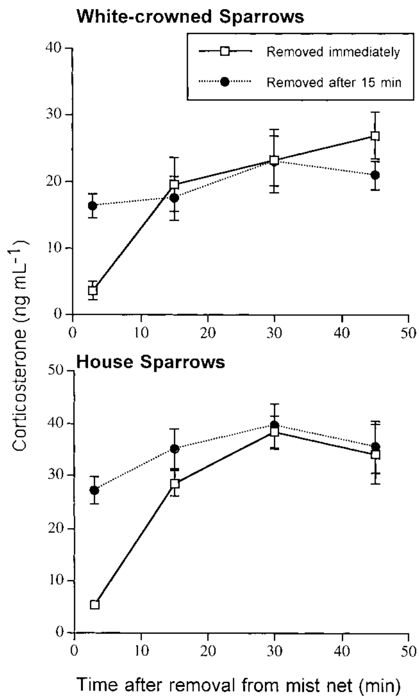

FIGURE 2. Corticosterone response to capture and handling in White-crowned Sparrows and House Sparrows. Birds were either removed immediately from mist nets (n = 9 and 12 for White-crowned Sparrows and House Sparrows, respectively) or left entangled in the net for 15 min before removal (n = 9 and 13 for White-crowned Sparrows and House Sparrows, respectively).

Sparrows, and $F_{3,69} = 21.7$, $P < 0.001$ for House Sparrows). White-crowned Sparrows and House Sparrows bled immediately upon capture had lower initial corticosterone concentrations than birds left in the net (treatment × corticosterone increase interaction: $F_{3,48} = 5.6$ and $F_{3,69} = 5.4$, respectively, both $P < 0.003$; mean difference = 12.7 and 21.0 ng mL^{-1}, respectively; Fisher's PLSD, both $P < 0.001$). This difference nearly resulted in an overall treatment effect for House Sparrows ($F_{1,23} = 3.9$, $P = 0.06$) but not for White-crowned Sparrows ($F_{1,16} = 0.12$, $P = 0.75$).

For White-crowned Sparrows, the capture method made no difference to the corticosterone response when birds were removed immediately upon capture ($F_{1,16} = 1.5$, $P = 0.24$ for overall treatment effect; $F_{3,48} = 0.9$, $P = 0.43$ for treatment × corticosterone increase interaction).

DISCUSSION

Waiting more than 3 min to remove a bird from either a mist net or a Potter trap had a large impact on the corticosterone response to the stress of capture and handling in the three species we studied. The effect, however, was not equivalent for the three species. Several studies have shown that corticosterone concentrations begin to rise within a few minutes of capture. Wingfield et al. (1982) showed that samples from White-crowned Sparrows taken 3–4 min after capture with mist nets are elevated compared to samples taken <2 min after capture, and Dawson and Howe (1983) report that European Starling (*Sturnus vulgaris*) corticosterone concentrations begin to rise 1.5–2 min after capture with mist nets. Furthermore, Schoech et al. (1999) showed that, although Dark-Eyed Junco (*Junco hyemalis*) corticosterone concentrations do not begin to rise until 3 min after capture with mist nets, when juncos are given testosterone implants, corticosterone concentrations become elevated after about 2 min. This suggests that the physiological state of the animal can alter the speed at which corticosterone is released after initiation of a stressful stimulus. Samples taken within 3 min of capture, therefore, will likely reflect unstressed corticosterone concentrations, but evidence suggests that corticosterone concentrations from samples collected near the end of that time frame could already be slightly elevated.

The studies cited above highlight the importance of collecting blood samples very quickly after capture when assessing unstressed corticosterone concentrations in free-living birds. However, the assumption has always been that if collection of the initial blood sample is delayed, further samples will still accurately reflect the normal stress-induced corticosterone response. This assumption clearly holds for both White-crowned Sparrows and House Sparrows left in mist nets, which mirrors results obtained by leaving juvenile Willow Tits (*Parus montanus*) in mist nets for varying periods (Silverin et al. 1989). The most important result from the present study, however, is that leaving birds in mist nets or Potter traps alters corticosterone release in a manner that is not consistent across species or capture techniques. In contrast to results with mist nets, leaving White-crowned Sparrows in Potter traps for 15 min had no effect on corticosterone release. Surprisingly, however, leaving Lapland Longspurs in Potter traps for 15 min did not alter the initial corticosterone response to handling and restraint, yet significantly altered the response over time. Consequently, if the capture time were unknown for Lapland Longspurs, a corticosterone sample taken 30–60 min after removal from the trap would not necessarily accurately reflect the normal stress response. Furthermore, the lack of consistency between the responses of Lapland Longspurs, House Sparrows, and White-crowned Sparrows indicates that one cannot simply assume that one can extrapolate baseline from stress-induced corticosterone concentrations.

One question arising from this study is why being captured in a Potter trap did not induce an immediate rise in corticosterone concentrations. One potential answer is that birds are only mildly stressed by capture in Potter traps. It has long been known that different stressful stimuli elicit different corticosterone responses (Sapolsky et al. 2000), and that the basis for these differences lies in the functioning of the hypothalamic-pituitary-adrenal (HPA) axis (Antoni 1986, Romero and Sapolsky 1996). For example, increases in the degree of novelty of a novel situation presented to rats (e.g., being put into progressively different types of new cages) results in graded corticosterone responses (Hennessy et al. 1979). This graded response is controlled by different levels of adrenocorticotropin (ACTH) secretion driven by different levels of ACTH-releasing hormones secreted by the hypothalamus (Romero et al. 1995b). Levine et al. (1989) proposed that the perception of a psychological stimulus (such as capture, as compared to a physical stimulus such as an injury) being stressful is required for a corticosterone response. The present data suggest, therefore, that if birds regulate corticosterone release similarly to rats, they perceive capture in a Potter trap as being only mildly stressful, requiring a very low to nonexistent immediate corticosterone response.

However, the differences in responses to Potter traps between White-crowned Sparrows and Lapland Longspurs precludes making differences in perception the only explanation. Both species respond normally in the first 10–15 min after being removed from the trap, which suggests that both species have equivalent perceptions as to the stressfulness of Potter traps. And yet, Lapland Longspurs left for 15 min had significantly lower corticosterone concentrations at 30 min compared to controls. The way in which Potter traps are used might explain this response. In laboratory rats, food consumption can result in rapid (<5 min) inhibition of plasma corticosterone levels (Levine and Coover 1976, Romero et al. 1995a) by a mechanism that is not entirely understood. Birds in this study fed extensively during their 15 min in the trap. If birds also inhibit corticosterone release when eating, the stress of being in a trap might be ameliorated by food consumption. It should be kept in mind that all birds in this study elevated corticosterone release in response to handling and restraint. In the experimental birds, therefore, the increase in corticosterone over time was an integrated response of both the 15 min of delayed removal from the mist net or trap, and the response to handling and restraint. Multiple and sequential stressors, however, are known to interact in sometimes unpredictable ways to alter HPA function, either by inhibiting corticosterone release via negative feedback (Dallman et al. 1992, Schwabl 1995) or by augmenting corticosterone release via facilitation (Dallman et al. 1992). Thus, for Lapland Longspurs, even though the Potter trap altered neither initial blood concentrations of corticosterone nor the response in the first 10 min, inhibition of corticosterone concentrations during feeding may have altered HPA function (perhaps by regulating ACTH release) such that the HPA axis was incapable of reacting as strongly to the subsequent stressors of handling and restraint.

If this mechanism explains the inhibition of corticosterone release in Lapland Longspurs, why did White-crowned Sparrows not show a similar response? A possible explanation is that 15 min of ingesting seed might reduce the perceived stressfulness of handling and restraint if the bird has not acquired the energetic reserves to cope with the stressful stimulus. The Lapland Longspurs captured for this study had just completed their spring migration, they presumably had little energy reserves, and they were captured during a mild storm. White-crowned Sparrows, on the other hand, were captured during a period of pre-migratory hyperphagia (King and Farner 1959), and may have had abundant energy reserves. This difference in physiological states (akin to changes in HPA function after testosterone implantation, Schoech et al. 1999) could explain the disparate responses in these two species. These possibilities remain to be tested.

Regardless of mechanism, these data clearly show that how quickly birds are removed from mist nets or Potter traps has a profound impact on the resultant corticosterone response to stress. The consequences of not immediately collecting the initial sample differed by both trapping technique and by species, indicating that capture does not result in consistent and reproducible increases in corticosterone concentrations. As with all studies of stress, extreme care must be taken to ensure that the stressful stimuli under study are not confounded with other concurrent or subsequent stimuli. This is especially true for free-living animals, where an underlying assumption of all such studies is that the animals are unstressed prior to capture (or at least all stressed in a consistent manner). Although field researchers can never be sure that the animal under study was not, for example, chased by a predator prior to capture, the current study indicates that the *a priori* assumption of all animals being equivalently stressed only has a hope of being correct if the animal is bled immediately after capture. Since collecting blood samples within minutes of capture is often difficult under field conditions, researchers often will assume that the remaining stress response continues normally, and will occasionally rely upon this assumption to use regression to extrapolate initial corticosterone levels. The present data indicate that without detailed knowledge of the effects of the specific trapping technique on the targeted species, such analyses are risky at best.

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