

ENDOCRINE RESPONSE OF CAPTIVE MALE BROWN-HEADED COWBIRDS TO INTRASEXUAL SOCIAL CUES¹

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Abstract. The hormonal response to a spectrum of intrasexual social stimuli was studied in captive Brown-headed Cowbirds (*Molothrus ater*). Males were housed in individual cages in one of four conditions: (1) in a semicircle with other males (= visual + vocal stimuli), (2) in acoustic chambers with visual access to a devoiced companion (= visual stimuli only), (3) in chambers in which a tutor tape was played daily (= vocal stimuli only), and (4) in acoustic chambers with no other input (neither visual nor social stimuli). Blood samples were taken at 2-week intervals throughout the spring and early summer and assayed for testosterone. The results indicate that the greatest increase in testosterone was in the birds receiving visual plus vocal stimuli and in those receiving only visual stimuli; males receiving only vocal stimuli had a muted endocrine response, and those receiving no social stimulation exhibited the briefest response. The relatively small response to vocal stimulation is consistent with the absence of a behavioral response to simulated territorial intrusions (i.e., song playbacks) that has been shown in previous studies in male cowbirds.

Key words: *Social stimulation; endocrine response; testosterone; Brown-headed Cowbird; Molothrus ater.*

INTRODUCTION

Birds exhibit marked changes in behavior when they begin to breed in spring. These changes are initiated by changes in circulating levels of pituitary and gonadal hormones which, in turn, are stimulated by the vernal increase in daylength. However, in order for the full complement of physiological and behavioral changes to be expressed, additional cues must be perceived (Wingfield 1983, Wingfield and Moore 1987).

One set of cues that is known to affect endocrine secretions in individual birds, and has received much attention, is the behavior of opposite-sex conspecifics. For instance, the presence of males can stimulate ovarian development in females (Lehrman et al. 1961), as can exposing females to male vocalizations (Hinde and Steel 1978). Exposure to male songs also can affect the speed with which females build nests (Kroodma 1976). Similarly, females can affect hormonal responses and gonadal development in males. Male birds exposed to females exhibit elevated levels of the gonadal steroid hormone testosterone (T)

(Feder et al. 1977, O'Connell et al. 1981, Dufty and Wingfield 1986a), and these levels may be further influenced by the degree of receptiveness of the female (Moore 1982, 1983).

Much less is known about the effects of intrasexual interactions on hormone secretion. No change in T levels was found in male Ringed Turtle-Doves (*Streptopelia risoria*) that were presented with another male (Feder et al. 1977). However, several correlational studies have shown that circulating levels of T in male birds increase during periods when aggressive interactions over territories and/or mates occur (e.g., Wingfield and Farner 1978a, 1978b; Silverin and Wingfield 1982; Wingfield 1984a). Further, Ramenofsky (1984) showed that plasma T levels correlated with aggression in Japanese quail (*Coturnix coturnix*) during the establishment of dominance rank. Likewise, Hegner and Wingfield (1987) found that dominance rank and circulating T levels were positively correlated during flock formation in House Sparrows (*Passer domesticus*), and Wingfield (1984b, 1985) noted that Song Sparrows (*Melospiza melodia*) exhibited elevated T levels when challenged by a simulated intruder or by a neighbor.

Thus, much evidence suggests that intrasexual

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interactions do stimulate T secretion. However, except for a study on Song Sparrows that examined acute hormonal responses to intrasexual social stimulation (Wingfield and Wada 1989), little experimental work has been done to determine what aspects of male-male social interactions facilitate the rise in T described above. Are visual cues important? Do vocal stimuli have a role? Or are both sets of cues required to elicit a hormonal response? We investigated these questions using captive male Brown-headed Cowbirds (*Molothrus ater*).

Cowbirds are highly interactive birds. Males are not territorial (Darley 1982, Dufty 1982), yet their social interactions (songs and visual displays) are used to establish and maintain a dominance hierarchy. Male song, in particular, has received much attention for its role in social interactions (e.g., West and King 1980, Rothstein et al. 1988). Males must be able to sing to attain dominance rank (Dufty 1986), and subtle differences between songs correlates with mating success and may reflect a bird's rank (West et al. 1981). Male cowbirds often display (a deep bow with wings spread) at the time a song is given. Indeed, it is not unusual to see four or more males in a tree, singing and displaying within a few feet of each other. Hence, cowbirds are excellent subjects for an investigation of the effects of visual and auditory cues on endocrine responses.

METHODS

This experiment was conducted using captive birds housed at The Rockefeller University Field Research Center in Millbrook, New York (42°N). Male cowbirds were captured in the fall in Potter traps baited with seed. The birds were assigned to one of four groups: (1) Isolate Males: birds ($n = 6$) housed singly in cages in acoustic chambers with neither visual nor acoustical access to other males; (2) Grouped Males: birds ($n = 5$) housed singly in cages placed end-to-end in a semicircle, with approximately 10 cm between cages; the chord length between the end cages was approximately 1.5 m. Thus, these birds had visual and acoustical (but not physical) access to all other males in the group; (3) Isolate/Tutored Males: birds ($n = 5$) housed in the same manner as the Isolate Males, except that tape recordings of male cowbird songs were broadcast daily into each chamber. The 2-hr tape consisted of four different song types recorded in captivity at a distance

of less than 1 m from a single dominant male. Songs were presented every morning at a rate of six songs/minute from 6 March to 24 June. Hence, these birds had auditory but not visual stimulation; (4) Males with Devocalized Companions: birds ($n = 5$) also housed in the same manner as the Isolate Males, except that each had a temporarily devocalized male cowbird as a companion, beginning 1 March. Pairs were separated by a wire screen across the middle of the cage that allowed visual but not physical interactions. Devocalizations were performed by puncturing the interclavicular air sac (Smith 1977) and were repeated at 10- to 15-day intervals to avoid the reestablishment of singing behavior. Thus, the experimental males in this group had visual but not auditory stimulation. All groups were housed in identical 27 × 30 × 52 cm cages and were maintained on natural daylengths.

No attempt was made to quantify the singing and display rates of the Grouped Males and Males with Devocalized Companions. Nonetheless, casual observations indicated that males in both groups interacted with each other. In the case of devocalized males, this included agonistic 'bill-up' displays and intention movements consistent with singing (which were aborted).

Blood samples (ca. 500 μ l whole blood) were taken from the brachial vein at approximately 2-week intervals. The plasma was removed and stored at -20°C until assayed. Testosterone was measured by radioimmunoassay (RIA) after partial purification of plasma on a diatomaceous earth: glycol microcolumn. Interassay variation was less than 14%, intra-assay variation was less than 10%, and water blanks measured less than 4.5 pg of testosterone. For further details on RIA procedures see Wingfield and Farner (1975) and Dufty and Wingfield (1986b).

Four separate repeated-measures analyses of variance (General Linear Models Procedure, SAS 1985) on log-transformed data were conducted to assess the effects of the presence or absence of vocalizations (i.e., Grouped Males vs. Males with Devocalized Companions; Isolate Males vs. Isolate/Tutored Males) and presence or absence of companions (Isolate Males vs. Males with Devocalized Companions; Grouped Males vs. Isolate/Tutored Males).

In addition, the peak values of T were compared among groups using Tukey's a posteriori multiple comparison test (Means Procedure, SAS 1985). Means within groups were compared us-

ing the Tukey-Kramer test for unplanned comparisons (Sokal and Rohlf 1981). Although analyses were conducted on the transformed data, the untransformed data are presented in the figures to facilitate comparison with other studies.

RESULTS

Repeated-measures ANOVAs showed that the presence of a companion had a strong effect on plasma T levels (Table 1; Fig. 1). This occurred both with and without the accompaniment of song. That is, Males with Devocalized Companions had significantly higher T secretion than did Isolate Males, and Grouped Males had higher T levels than did Isolate/Tutored Males. A significant effect of time on T levels was also noted in both comparisons, indicating the stimulatory effect of lengthening photoperiod on hormone secretion. Further, a significant interaction between companionship and time indicated that companionship affected the pattern of T secretion over time. In each case, the group with companions showed prolonged elevated plasma T levels compared to the isolates.

The effect of vocalizations was less clear-cut. Neither comparison examining this cue produced a significant main effect of sound (Table 2), although the Isolate Male vs. Isolate/Tutored Male comparison was very close to significance ($P < 0.0643$). This particular comparison did result in a significant interaction between time and sound, indicating a difference in the pattern of T secretion in the two groups: Isolate Males exhibited a brief but significant rise in plasma T levels in late February/early March, which declined by mid-April (Fig. 1A). However, Isolate/Tutored Males did not show a comparable rise in plasma T until mid-March, but these titers were maintained until late May (Fig. 1B). Thus, it appears that song may have acted to maintain the photoperiodically induced rise in plasma T levels in Isolate/Tutored Males.

Conversely, song had neither a significant main effect nor a significant interaction with time when the patterns of T secretion of Grouped Males and Males with Devocalized Companions were compared. However, time did have a significant effect. Grouped Males (Fig. 1C) produced significant increases in T during the earliest stages of the experiment, and values continued to rise until early May. This was followed by a decline to moderate levels that were maintained until mid-June, when a final decline to basal levels (July)

TABLE 1. The effect of the presence or absence of a companion on plasma testosterone levels in male Brown-headed Cowbirds, analyzed by repeated-measures analysis of variance.

Source	df	MS	F	P
A. Isolate Males compared to Males with a Devocalized Companion.				
Companion	1	19.78	5.86	0.03585
Error	9	3.38		
Time	7	5.07	10.66	0.0001
Time × companion	7	5.04	10.59	0.0001
Error	63	0.48		
B. Isolate/Tutored Males compared to Grouped Males.				
Companion	1	3.00	5.48	0.0474
Error	8	0.55		
Time	9	6.92	17.66	0.0001
Time × companion	9	1.78	4.56	0.0001
Error	72	0.39		

began. Males with Devocalized Companions (Fig. 1D) also produced an early-season rise in plasma T that was maintained at maximal levels throughout April and May; these values declined throughout June.

Although all four groups exhibited significant changes over time in T secretion (Tukey-Kramer test; Fig. 1A–D), it is apparent that differences occurred among them in the amplitude of the maximal values of circulating T (Fig. 2). The following comparisons of maximum T values were significant at the 0.05 level (Tukey's a posteriori test): Grouped Males > Isolate/Tutored Males, Isolate Males; Males with Devocalized Companions > Isolate/Tutored Males, Isolate Males. No other comparisons were significant.

DISCUSSION

Most experimental investigations of social influences on avian physiological responses have focused on the effects of intersexual stimulation. Although intrasexual interactions also are thought to stimulate hormonal responses, the specific features that promote these responses are poorly understood. The present results shed light on how intrasexual social cues help to determine the pattern of T secretion in male cowbirds. The results indicate a strong effect of visual cues on testosterone secretion, and a much smaller effect of vocal cues. This was somewhat unexpected, given the prominent role played by vocalizations in

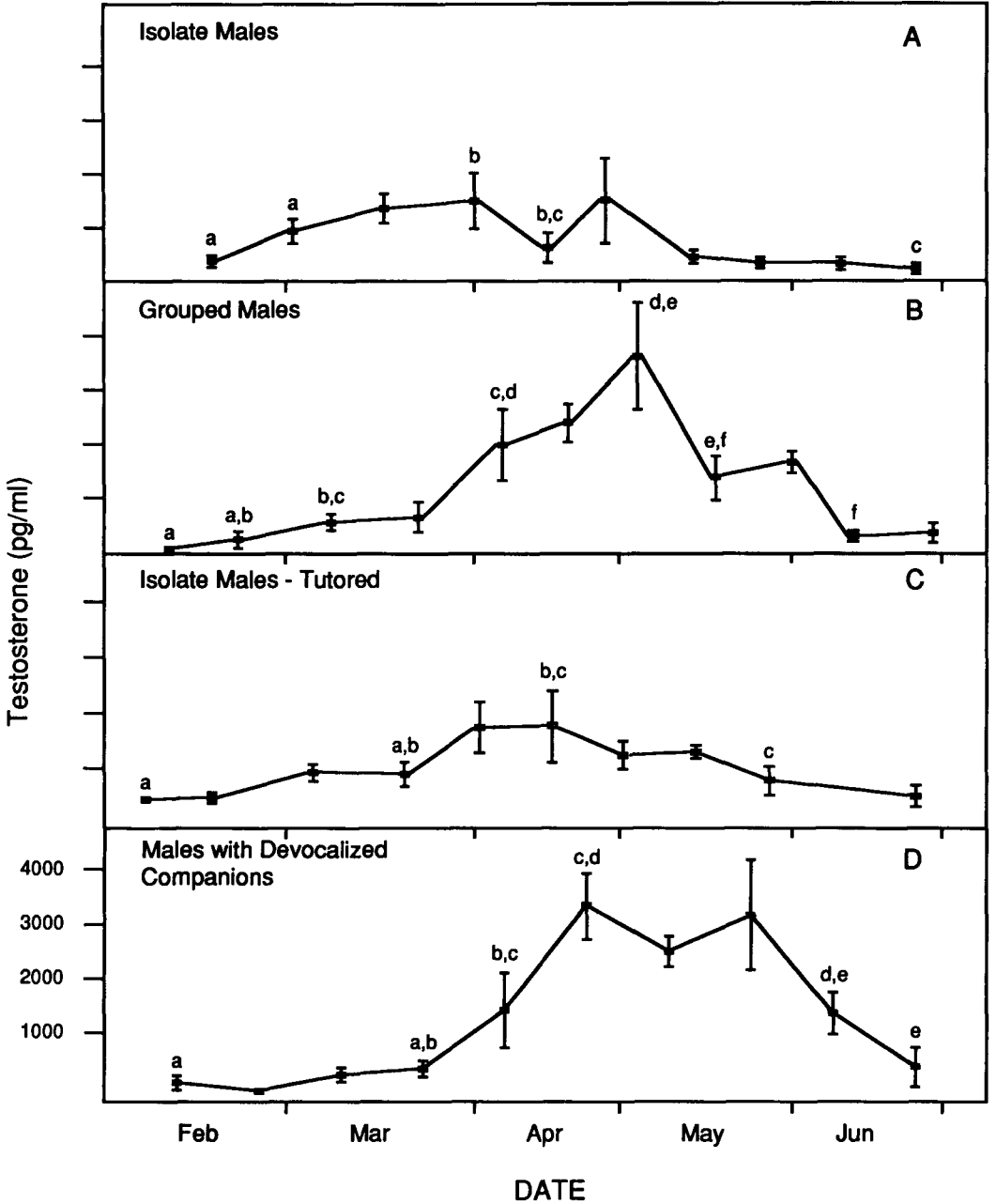


FIGURE 1. Temporal pattern ($\bar{x} \pm SE$) of testosterone secretion in male Brown-headed Cowbirds housed (A) in acoustic and visual isolation (Isolate Males); (B) singly in cages, with both visual and acoustical access to other male cowbirds (Grouped Males); (C) in visual isolation and played tape recordings of male cowbird songs (Isolate/Tutored Males); and (D) with a devocalized companion male cowbird that provided visual, but not acoustic, stimuli (Males with Devocalized Companions). Within each panel, means with the same letter are significantly different at $P < 0.05$ (Tukey-Kramer test for unplanned comparisons).

intrasexual and intersexual interactions in this species (West and King 1980, King et al. 1981, West et al. 1981, Dufty 1986).

A small but significant increase in plasma T occurred in the absence of all social input, probably due to the stimulating effect of lengthening photoperiod (e.g., Farmer and Follett 1979, Follett 1984). But this was a transient rise, which quickly declined toward basal levels in the absence of additional stimuli. When vocal stimulation alone was provided, the peak levels of T secretion were not changed, but these levels were maintained for several weeks longer than in Isolate Males, indicating that vocal cues can affect the pattern of T secretion in the absence of visual stimuli. Vocal activity is known to be an important component of social behavior among male cowbirds, for males singing inappropriate songs may be killed (West and King 1980), and nonsinging males do not attain dominant rank (Dufty 1986).

In an earlier study (Dufty and Wingfield 1986a) we also maintained a group of males in visual but not acoustic isolation. These birds exhibited a much more pronounced endocrine response than did Isolate/Tutored Males of the present study. However, the difference possibly may be explained by procedural differences between the two investigations. In the former study a total of nine birds was housed in a large chamber; therefore, each male heard eight other birds singing throughout the day, as opposed to a 2-hr tutor tape in the present study. Thus, the amount of acoustic stimulation was undoubtedly greater in the earlier investigation, and may have contributed to the more accentuated changes in plasma T levels. In addition, the photoperiod changed abruptly from 8L:16D to 16L:8D in Dufty and Wingfield (1986a), whereas it reflected the natural changes in daylength in the present study. The rapid change from short to long days may have resulted in a more pronounced photoperiodic effect.

The present findings are also consistent with the pattern of events proposed by Wingfield and Moore (1987) and Wingfield et al. (1987) to account for development of avian reproductive competency in the spring. According to this model, initial predictive information (i.e., lengthening photoperiod) triggers endocrine secretions and gonadal development. However, additional cues, such as social interactions pro-

TABLE 2. The effect of the presence or absence of auditory stimulation on plasma testosterone levels in male Brown-headed Cowbirds, analyzed by repeated-measures analysis of variance.

Source	df	MS	F	P
A. Isolate Males compared to Isolate/Tutored Males.				
Vocalizations	1	10.82	4.44	0.0643
Error	9	2.44		
Time	8	2.26	6.19	0.0001
Time × vocalizations	8	1.25	3.43	0.0021
Error	72	0.36		
B. Grouped Males compared to Males with Devocalized Companions.				
Vocalizations	1	0.15	0.09	0.7668
Error	8	1.57		
Time	9	14.33	26.62	0.0001
Time × vocalizations	9	0.52	0.97	0.4683
Error	72	0.54		

vided by conspecifics, can elevate T further, especially in situations of elevated aggression. Whereas earlier studies focused on the stimulatory effect of male vocalizations on the reproductive physiology of females (see Introduction), the above results indicate that intrasexual stimulation also occurs.

In contrast to the Isolate and Isolate/Tutored Males, Grouped Males and Males with Devocalized Companions exhibited T profiles that, in general, are similar to those of free-living male cowbirds (Dufty and Wingfield 1986b). Interestingly, Grouped Males showed an increase in T secretion in the very first samples (early February), whereas Males with Devocalized Companions did not produce a similar increase until several weeks after the companion was introduced (i.e., late March). The pattern of T decline, except for an earlier initial drop in the Grouped Males, was similar in both sets of birds. These results suggest that the combination of visual and vocal cues is more effective in initiating elevated T secretion than are visual cues alone, although both types of stimulation result in similarly high levels of T.

An investigation of the response of Song Sparrows to acute exposure to social stimuli produced generally similar results. Wingfield and Wada (1989) found that neither auditory nor visual

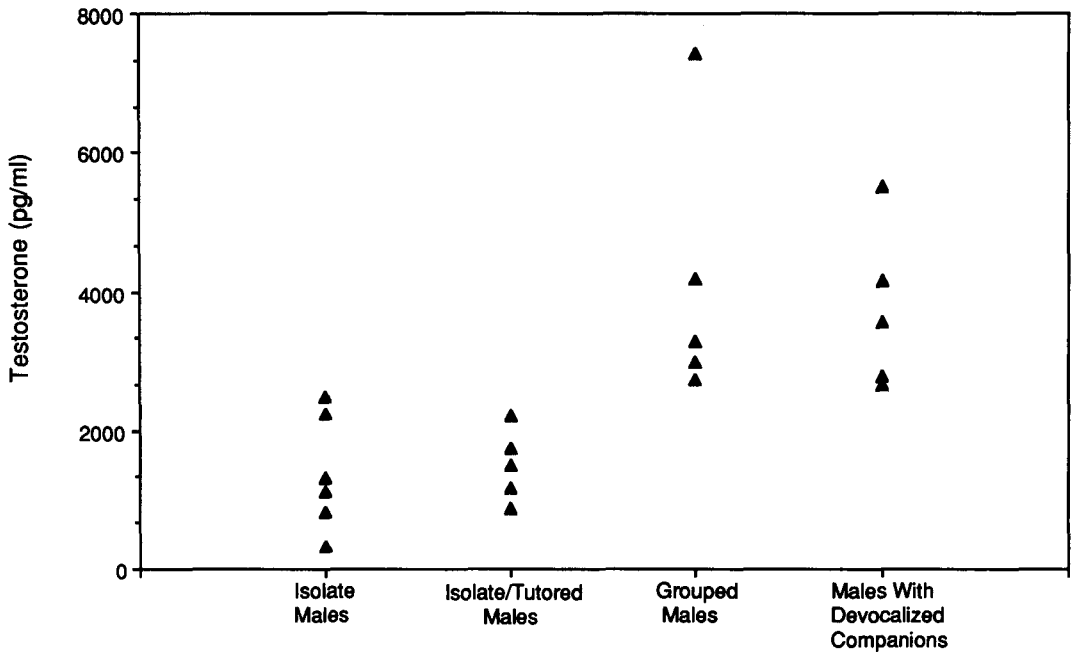


FIGURE 2. Peak testosterone levels for individual males in each housing regime. For significance values see text.

stimulation alone produced as great an increase in T as did a combination of these stimuli.

The apparent similarity in hormonal responses to acoustic stimulation in cowbirds and Song Sparrows is surprising, given the behavioral differences exhibited by these two species in response to conspecific songs: Song Sparrows possess all-purpose territories that they defend aggressively against conspecific males (Nice 1943), and they respond quickly to conspecific vocal stimulation (e.g., Wingfield 1985). The interesting absence of an accompanying hormonal response to acoustic stimulation may reflect reproductive and energetic costs of maintaining high plasma T levels. Elevated T levels are not compatible with parental care (e.g., Silverin 1980; Wingfield 1984a, 1984b), and, as a result, Song Sparrows may have been selected to reduce androgen titers to maintenance levels after egg laying, unless strongly challenged (i.e., visual plus vocal cues). Further, there are energetic demands in maintaining elevated T levels (Hännslér and Prinzing 1979, Högstadt 1987). Thus, it may be beneficial to produce additional T only when a challenger is visually verified, given that such increases in androgen secretion can occur within minutes (Wingfield and Wada 1989).

On the other hand, nonterritorial male cowbirds frequently hear conspecifics singing in their ranges. However, unlike the sparrows, cowbirds do not perceive such vocalizations as threatening, and conspecific singing rarely elicits an overt response by males (Dufty 1982, Rothstein et al. 1988).

When free-living cowbirds do sing to each other, it is usually over very short distances, often less than a meter (Friedmann 1929, pers. observ.). In the present case, a conspecific male cowbird in close proximity, whether singing (Grouped Males) or not (Devocalized Companions), is likely to be interpreted as a direct challenge, and will produce a more intense hormonal response than will vocal stimulation alone. Indeed, important acoustic parameters of their songs degrade with distances of only 3 m (King et al. 1981), and it would be interesting to determine whether male cowbirds housed more than 3 m apart exhibit similar hormonal responses.

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