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SHORT COMMUNICATIONS

The effects of exogenous testosterone on male Northern Mockingbirds during the breeding season.—The challenge hypothesis (Wingfield et al. 1990) states that a positive correlation between plasma testosterone (T) and aggression occurs only under conditions of social instability, that is, when access to resources is being persistently challenged in contests over territory borders or position in a dominance hierarchy. Sizeable increases in plasma T levels above a relatively low breeding-season baseline are produced by intermale aggression and female sexual activity, while male parental care is associated with lower T levels. The hypothesis accounts for fluctuations in breeding-season levels of plasma T in numerous temperate avian species (Wingfield et al. 1990).

Northern Mockingbirds (*Mimus polyglottos polyglottos*) in the southeastern United States aggressively defend all-purpose territories year-round against conspecific intruders and male T levels fluctuate substantially across the breeding season (Logan and Wingfield 1995). However, recent work has failed to establish a connection between heightened aggression and elevations in plasma T in mockingbirds. Specifically, Logan and Carlin (1991) showed that exogenous T administered in autumn stimulated reproductive behavior such as song, mate acquisition, and nest building. Territorial behavior, however, was either unaffected or inhibited, even though territorial interactions normally peak in autumn in mockingbirds. When mockingbirds were trapped periodically for blood samples during the breeding season, mated males' T levels peaked during early nest building and remained low later in the season despite continued maintenance of the territory and the female. Unmated males defending spring territories showed T levels below the peak seen in mated males (Logan and Wingfield 1995). These data raise the possibility that T may not be related to intermale aggression during the breeding season in mockingbirds. The purpose of this study was to examine experimentally the impact of exogenous T on breeding-season territorial aggression in male mockingbirds. If the challenge hypothesis applies, the frequency of territorial aggression should increase in T-implanted males, and consequently, neighbors of T-implanted males should show elevated plasma levels of T.

Methods.—Using the procedures described in Logan and Carlin (1991), four color-banded male mockingbirds residing on campus at the University of North Carolina at Greensboro were implanted with sealed 20 mm lengths of Silastic tubing packed with crystalline T (T-implanted birds) between 10 March and 1 July 1992. Four color-banded control males holding territories on campus similarly were implanted with empty implants (C-implanted birds) between 27 February and 14 April of the same year. Prior work indicates that the T implants elevate plasma T levels to approximately 10.3 ± 4.9 ng/ml (Logan and Carlin 1991). In each group there were three unmated and one mated bird, each bird having one to three territorial neighbors. When captured and implanted, the T-implanted mated bird had a nest with one egg, and the C-implanted mated bird had just acquired a mate.

A mean of 12 (range 6–20) 15-min focal-animal behavior samples were taken on each of the C-implanted birds and T-implanted birds from mid-March through mid-July. Behavior sampling typically began several days after implantation. In addition, a mean of seven (range 2–16) 15-min samples were also taken on each of 10 unimplanted, color-banded males whose territories bordered those of the implanted birds. Those birds whose territories bordered a T-implanted bird will be referred to as "T neighbors" (N = 5); territories of "C neighbors" (N = 5) bordered the territory of a C-implanted bird. Upon capture, 300–400 μl of blood was collected from C neighbors and T neighbors. Plasma steroid hormone concentrations were determined via radioimmunoassay at the University of Washington according to the methods of Wingfield and Farner (1975).

We tested whether aggression levels were influenced by T implants by comparing conspecific territorial chases and the production of "hew" calls in T- versus C-implanted birds. In the neighbors of implanted birds, we examined whether territory size decreased due to the expansion of the territory owned by the neighboring implanted bird. Territory size, which was measured for most birds, was assessed using the method described by Odum and Kuenzler (1955). Other measures included overall activity levels and time spent in song. Song was not included as a measure of territorial aggression because previous studies have suggested that male mockingbirds use song primarily for mate attraction (Logan and Carlin 1991, Merritt 1985). Time-out time was recorded when all visual and acoustical contact with the focal bird was lost. The mean ratio of time-out time to total time sampled was 0.162 for T-implanted birds, 0.120 for C-implanted birds, 0.148 for T neighbors, and 0.117 for C neighbors (Kruskal-Wallis $H = 1$, $P > 0.30$)

Nonparametric statistics were used in all analyses. Each individual bird's mean across focal samples was used to calculate the group means. Two-tailed tests were used unless the experimental hypothesis specified a particular direction for between-group differences, in which case a one-tailed test was used.

Results.—T-implanted birds were not greater than C-implanted birds in the average number of territorial chases per 15 min. The mean ± SE average number of territorial chases per 15 min was 0.047 ± 0.05 for T-implanted birds and 0.104 ± 0.036 for C-implanted birds (one-tailed Mann-Whitney $U = 5$, $P > 0.20$). Also, T-implanted birds were not greater than C-implanted birds in the percentage of 15-min samples during which one or more territorial chases were recorded. The mean ± SE was 4.69 ± 4.7% for T-implanted birds and 8.15 ± 3.59% for C-implanted birds (one-tailed $U = 5$, $P > 0.20$). Further, T-implanted birds did not produce more "hew" calls than C-implanted birds. The mean ± SE number of "hews" per min of time-in time was 0.047 ± 0.031 "hews" for T-implanted birds and 0.026 ± 0.022 hews for C-implanted birds (one-tailed $U = 6$, $P > 0.30$). T-implanted birds differed from C-implanted birds in territory size. Mean ± SE territory size was 1.48 ± 0.18 ha for N = 4 T-implanted birds and 0.503 ± 0.17 ha for N = 3 C-implanted birds (two-tailed $U = 0$, $P = 0.056$; territory size data were not available for the mated C-implanted bird). Similar effects of T on spatial behavior have been reported in Dark-eyed Juncos (*Junco hyemalis,* Chandler et al. 1994). However, none of the T-implanted birds annexed part or all of another bird's territory. That is, the territory gains of T-implanted birds did not come at the expense of neighbors. Rather, T-implanted birds expanded their territories into adjacent unoccupied areas, stopping when they reached a defended area. Subsequently they used both the older and newly acquired space. In contrast, one C-implanted bird had a large, unoccupied, and apparently suitable area adjacent to his territory which he was never observed using. Another C-implanted bird, apparently shifting his territory, was consistently seen in an area west of that which he occupied in the previous sample, but was never seen using the area from which he expanded.

Because exogenous testosterone increases song in the fall in this species, it was predicted that T-implanted birds would sing more than C-implanted birds in the spring as well. Initial comparisons showed no differences between groups in the amount of song produced per 15 min. However, because increases in song produced by exogenous T in autumn can be inhibited by the presence of a female, song production was reanalyzed after eliminating the mated male from each group. Unmated T-implanted birds sang more than unmated C-implanted birds: the mean ± SE number of 15-sec intervals with song per 15 min was 24.34 ± 1.65 for the three T-implanted birds and 8.44 ± 3.0 for the three C-implanted birds (one-tailed $U = 0$, $P = 0.05$).

T also increased overall activity levels. For each bird, the total number of perch changes across all samples was divided by the total number of minutes of time-in time. The mean ± SE number of perch changes per min of time-in time was 0.640 ± 0.093 for T-implanted birds and 0.351 ± 0.063 for C-implanted birds (two-tailed $U = 0$, $P = 0.014$).

The challenge hypothesis predicts that neighbors of T-implanted birds (T neighbors) would have higher levels of plasma T than neighbors of C-implanted birds (C neighbors) if the T-implanted birds were aggressively challenging their neighbors. Two T neighbors were trapped; their plasma T titres equalled 1.19 ng/ml and 0.91 ng/ml. To increase the sample size for the comparison group, four neighbors of unimplanted males were combined with three neighbors of C-implanted males; the mean ± SE plasma T titres in these seven birds was 1.06 ± 0.24 ng/ml. T neighbors were not greater than C neighbors (one-tailed $U = 6$, $P > 0.30$).

Using those birds for which territory size data were available, three T neighbors did not differ in territory size from four C neighbors (two-tailed $U = 3$, $P > 0.20$). Using all birds, T neighbors ($N = 5$) did not differ from C neighbors ($N = 5$) in the percentage of 15-min samples with territorial chases (two-tailed $U = 11$, $P > 0.30$), mean number of territorial chases per 15 min (two-tailed $U = 10$, $P > 0.30$), mean time in song (two-tailed $U = 6$, $P > 0.20$), or average activity levels (two-tailed $U = 12$, $P > 0.30$). T neighbors differed from C neighbors in the production of hew calls per 15 min in that T neighbors produced more hew calls (two-tailed $U = 1$, $P = 0.02$). However, hew calls are used in a variety of aggressive contexts, including nest defense against predators (Breitwisch 1988). Four of five T neighbors had eggs or young during sampling, whereas only one of five C neighbors had eggs or young. Thus, this result may be due to phase in the breeding cycle rather than T-induced aggression in implanted birds.

Discussion.—T implants are known to enhance territorial aggression in several avian species. For example, male Red-winged Blackbirds (*Agelaius phoeniceus*) show enhanced territorial aggressiveness following T implantation (Beletsky et al. 1990). The impact of T was apparent in the behavior of the T-implanted mockingbirds: they were more active and increased their territory size, and unmated males sang more than controls. However, the measured aggressive behaviors were not affected by T implants, and the changed behavior in the T-implanted birds appeared to have no impact, hormonal or behavioral, on their neighbors.

It is possible that the results reported here are due to the small sample sizes used. However, in other species of birds, exogenous T has had large effects on the behavior of other species. For example, T implants induced polygyny in normally monogamous White-crowned Sparrows (*Zonotrichia leucophrys*), and T-implanted birds' territory sizes averaged more than twice that of controls (Wingfield 1984). In Red-winged Blackbirds (*Agelaius phoeniceus*), T implants more than doubled both the mean frequency of attacks and the song rate (Searcy and Wingfield 1980). In mockingbirds, the effects of T on other behaviors were large enough to be detected, in most cases, with sample sizes of three. Therefore, it is unlikely that the lack of relationship between T and territorial aggression in mockingbirds resulted solely from the small sample sizes.

If most territorial chases occur as a result of intruders entering the territory and being chased out, then the lack of differences in territorial aggression found here may reflect a lack of a difference in intruder pressure on T-versus C-implanted birds; that is, it is possible that the groups did not differ in territorial chase rate because they did not differ in the rate of intrusions onto their territories. However, if exogenous T did elevate aggressive behavior, it is likely that T-implanted birds would have initiated aggressive interactions with their neighbors, which would have resulted in between-group differences in territorial interaction frequency.

Researchers have found that T in breeding birds fails to produce conspecific aggression in two different circumstances. First, many tropical species show either very low levels of T during periods of territorial activity or greatly reduced fluctuations in T compared to temperate species (see summary in Levin and Wingfield 1992), though a greater sensitivity to T in tropical species has not been ruled out. The current range of the Northern mockingbird and other *Mimus* species extends into the tropical zone, and bird counts and anecdotal evidence have charted a northward expansion of the Northern mockingbird (Derrickson and Breitwisch 1992). It is therefore possible that the relationship between T and behavior in *M. polyglottos* was influenced by tropical conditions at some point in the species' phylogeny. Thus, the results presented here could be viewed as consistent with current data on T levels in tropical avian species, to which the challenge hypothesis does not apply.

Second, it appears that the effects of T on aggressive behavior can be dampened under highly stable social conditions, such as being housed with familiar individuals (Archawaranon et al. 1991) or perennial territoriality (Wingfield and Hahn 1994). Levin and Wingfield (1992) have argued that the association between T and territorial aggression seen in several temperate migratory species may be extremely metabolically costly in temperate species that defend territories year-round. Wingfield and Hahn (1994) found that simulated territorial intrusions produced a significant increase in plasma T in migratory White-crowned Sparrows, but no significant plasma T increase in sedentary Song Sparrows (*Melospiza melodia*), despite strong behavioral reactions in both species. Though some effects of T may be present early in the season in Song Sparrows, particularly in high-density populations, they suggest that aggressive behaviors that are T-dependent in migratory species may not require high T levels in species or populations that defend territories year-round. As most mockingbird populations in the southeast are perennially territorial, this metabolic constraint may apply. Specifically, it may be too energetically costly for mockingbirds to link aggressive behavior to the production of hormones when the aggressive maintenance of a territory is required year-round. Also, perennial territoriality may lead to stable social conditions (due to familiarity with neighbors) which, despite hormonal state, inhibit or fail to stimulate aggressive behavior (Archawaranon et al. 1991). Thus, the combination of perennial territoriality and social inertia may account for the ineffectiveness of T in altering spring territorial aggression in mockingbirds.

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MICHAEL J. JUSTICE AND CHERYL A. LOGAN, *Dept. of Psychology, Univ. of North Carolina at Greensboro, Greensboro, North Carolina 27412-5001.* *Received 6 Aug. 1994, accepted 15 Feb. 1995.*

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Effects of food supplementation and predator simulation on nuthatches and parids within mixed-species flocks.—Although many ornithologists have studied mixed-species flocks, few have examined spatial positioning of birds within flocks. Flocks, here defined as three or more birds that move together as a group, vary from loose associations of individuals separated by tens of meters to tight clusters of birds only centimeters apart. Variations in spacing are interesting because they may either enhance or reduce the benefits that birds acquire by flocking. For example, birds that are farther apart may have more difficulty acquiring information about food or predators from each other but may have reduced costs due to fewer aggressive interactions. Thus, spacing within flocks may reflect a balance between attractive and repulsive forces between flock members (Emlen 1952). Distances between flock members are likely to change over time scales of minutes or hours as attractive and repulsive forces vary with changes in flock size and composition (Caraco and Bayham 1982, Pearson 1989), energy reserves of flock members, or environmental factors such as habitat structure, food availability, and predation pressure (Grzybowski 1983, Prescott 1987, Pearson 1991). In this paper I examine spacing among Brown-headed Nuthatches (*Sitta pusilla*), Carolina Chickadees (*Parus carolinensis*), and Tufted Titmice (*P. bicolor*) within heterospecific flocks. The basic goal was to determine whether distances between birds varied either as food availability varied or as apparent threat of predation