The Role of the White Wing Patch In Communication Among Northern Mockingbirds

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Introduction

The wing patch of Northern Mockingbirds (*Mimus polyglottos*) is formed from white on the primaries and on a row of greater primary coverts. The tips of the primaries, the lesser coverts, and the secondaries, all of which border the wing patch, are grayish-black. Because the white patch stands in sharp contrast to the gray-black surrounding it, the wing patch could be relatively visible even at fair distances in poor light. Such patches could potentially transmit information over long distances in the openness of typical mockingbird habitat.

In other avian species, such patches of color are known to be used by males as intrasexual "status" signals - that is, signals of ability to win in a contest over resources. Many are signals of age-sex class, which is often associated with dominance (Fugle *et al.* 1984; Holberton *et al.* 1989; Jackson *et al.* 1988; Ketterson 1979; Parsons & Baptista 1980; Rohwer 1977, 1978; Watt 1986a, b). Status signals operating within age-sex classes have been found in Red-winged Blackbirds (*Agelaius phoeniceus*: Smith 1972; Peek 1972; Hansen & Rohwer 1986; Røskaft & Rohwer 1987; Eckert & Weatherhead 1987), House Sparrows (*Passer domesticus*: Møller 1987a, b; Møller & Erritzoe 1988), Least Auklets (*Aethia pusilla*: Jones 1990), Great Tits (*Parus major*: Järvi & Bakken 1984), Yellow Warblers (*Dendroica petechia*: Studd & Robertson 1985), and Eurasian Siskins (*Carduelis spinus*: Senar *et al.* 1993).

Mockingbirds, which exhibit aggressive territoriality year-round, could benefit from an effective, long-distance visual signal of presence and/or competent defense. Such a signal could supplement or alleviate singing and calling, reduce the frequency of territorial intrusions, and help settle contests by display in lieu of escalated combat. The behavior of mockingbirds supports this reasoning. Intrasexual territorial chases without physical contact are observed as often as once per hour during daily active times in the breeding season, but escalated fighting with physical contact is extremely rare by comparison (M. Justice, unpublished data). This suggests that many aggressive interactions are settled with signals, thereby avoiding escalation to physical contact. Because chases necessarily involve exposure of the wing patch, mockingbirds could make use of its signal value in this context. Indeed, exposure of the wing patch occurs during bouts of singing (in flight displays) and occurs year-round, while singing does not.

Presumably, the ability of male mockingbirds to defend their territory is a highly variable trait. If the wing patch corresponds to status, it too will be highly variable. Justice & Justice (1998) quantified various parameters of the wing patches of 34 male mockingbirds. They found considerable variability in the size of the wing patch. Most of the size variability was in its "length" from the wrist to its edge on primaries 1-4. The "width" of the wing patch (due more to the amount of white on primaries 5-10), the whiteness of the patch, and the white-gray contrast with the surrounding feathers have also been measured. These were all found to be considerably less variable (Justice & Justice 1998; M. Justice, unpublished data).

If male mockingbirds use wing patch size as a reliable signal of competence in territorial defense, then two predictions can be made. First, the frequency and intensity of territorial contests should negatively correlate with wing patch size. Mockingbirds with large wing patches will be recognized as better defenders, and conspecifics will avoid conflicts with them. Second, manipulating the size of the wing patch should influence the frequency and intensity of contests. Specifically, decreasing its size may allow for bolder conspecific intrusions into the territory, resulting in more, or more intense, territorial interactions. Further, eradicating the wing patch entirely should lead to aggressive interactions even more frequent and extreme.

Methods

Samples for these studies were taken from a population of wild mockingbirds residing on the 72ha suburban residential campus of The University of North Carolina at Greensboro (36°N 79°W). The campus is in a piedmont in southeastern North America. It supports approximately 60-70 individual mockingbirds, the majority of which were color banded for this study. Federal and state permits and IACUC approval were obtained prior to trapping and data collection. Wooden, 25cm-square "platforms," attached atop 1.6m posts, were built, and one was placed in every mockingbird territory on campus to serve as a feeding and trapping station. For feeding, two tablespoons of a peanut butter/cornmeal mix were placed on each platform twice per week. For trapping, 18cm-cube treadle traps were placed in randomly selected territories and baited with the peanut butter/cornmeal mix.

Adult mockingbirds cannot be definitively sexed by external morphology. Upon trapping an unbanded mockingbird, the likelihood of its being male was assessed using wing patch size (see Justice & Justice 1998). Upon trapping a banded mockingbird, records of prior sex-specific behavior were typically available. Upon capture of a male (or likely male), the bird was first banded (if necessary), then wing patch size and wing length were measured as described in Justice & Justice (1998), and finally its wing patch size was manipulated experimentally as described below.

A dark gray, nontoxic ink was applied to the dorsal and ventral surfaces of both wings. Using stratified random assignment, three groups were formed, and ink was applied to each group differently. In the "reduced" group, the ink reduced the size of the wing patch by covering all of the white area on the primaries beyond the distal edge of the greater coverts. This produced birds with wing patches smaller than ever naturally observed and also manipulated the "length" of the wing patch. In the "covered" group, the ink completely eliminated the wing patch by covering all the white on the primaries and greater coverts. The control group included both sham and non-sham controls. Sham controls had their wing patches left intact, but the gray area on the primaries was inked. Non-sham controls were banded and measured but no ink applied. The ink was dried by gently separating and blowing on the feathers, and the bird was released after approximately 20 minutes handling time. The ink wore off sufficiently to reveal the original wing patch after about one to three weeks, but some ink usually remained until the next molt.

Focal-animal sampling (Altmann 1974) of behavior began at least one day following capture and was completed before the ink began to fade. The total sample time was divided into 15-second bins, and the occurrence and/or frequency of various behaviors was recorded as having occurred in a particular bin. No blinds were used because this population is routinely exposed to the close presence of humans. All samples were taken during the birds' most active times (0700 - 1130hr and 1600 - 1900hr). Perch locations were recorded in the field on a small-scale map of the campus so that subjects' territory boundaries were known.

"Chases" of an intruder were scored when the territory resident flew in the direction of a conspecific intruder. Four types of chases were distinguished and numbered higher as the severity of the interaction increased:

Type 1 - The intruder left without offering any resistance, that is, the intruder's flight path remained pointing away from the center of the resident's territory;

Type 2 - The intruder offered some resistance before leaving, such as flying back toward the center of the resident's territory or perching within the resident's territory;

Type 3 - There was physical contact involved, but it occurred near the territory border; and

Type 4 - There was physical contact in or near the center of the resident's territory.

The duration of chases was also measured. Time began when the birds involved were within 5m of one another and ended when the resident ceased to chase. The observer also recorded when the focal animal sang. Lastly, if all visual and acoustical contact with the bird was lost for more than 15s, this was scored as "time-out time." The remaining sampling time will be referred to as "time-in time."

For the behavioral measures, each individual bird's mean across samples was calculated. These individual means were averaged to obtain group means. Parametric statistics were used wherever the data met the assumptions. Sample sizes vary because not all measures were available for all birds. Because sample sizes were generally small, indices of the strength of the relationship between the independent and dependent variable were computed for most inferential statistics.

Results

A total of 24 male mockingbirds were sampled for this study. Six non-sham controls were not different from three sham controls on any of the dependent measures (two-tailed Mann-Whitney U statistics, all p values > 0.25), and thus these were combined into one larger control group for all subsequent analyses. There were nine control birds, nine reduced birds, and six covered birds. Mean ± SD hours of time-in time for the control birds was 4.8 ± 1.52, for the reduced birds was 2.9 ± 0.52, and for the covered birds was 2.6 ± 0.75. There was no difference between the groups in the percentage of sampling time that was time-in time (Kruskal-Wallis H = 2.796, n = 24, p = 0.25; overall mean = 86.4%). Wing lengths (as defined in Justice & Justice 1998) were compared between groups, and the differences were small: mean ± SE wing lengths for control birds was 112.3 ± 1.53, for reduced birds was 110.8 ± 1.46, and for covered birds was 111.5 ± 1.60 (H = 0.16, n = 24, p = 0.92).

Mean ± SE number of chases per hour of time-in time for control birds was 0.50 ± 0.225, for reduced birds was 0.41 ± 0.208, and for covered birds was 1.78 ± 0.418 (H = 8.363, n = 24, p = 0.015, $\epsilon_R = 0.55$; Fig. 1). Post-hoc protected rank-sum tests provided evidence that covered birds had more chases per hour than both reduced (z = 2.59, one-tailed p = 0.005) and control birds (z = 2.36, one-tailed p = 0.009). The average duration of chases did not differ between the three groups. The mean ± SE average duration (in seconds) for control birds (n = 9) was 7.1 ± 2.71, for reduced birds (n = 9) was 4.7 ± 1.98, and for covered birds (n = 3) was 17.4 ± 11.44 (H = 1.882, n = 21, p = 0.55). The average intensity score of chases also did not differ across the three groups. The mean average intensity score for control birds (n = 5) was 1.39 (range 1.00 - 1.67), for reduced birds (n = 4) was 1.55 (range 1.00 - 2.00), and for covered birds (n = 4) was 1.67 (range 1.00 - 2.00) (H = 1.118, n = 13, p = 0.57). Note that, in keeping with other results, the proportion of birds involved in chases was highest in the covered group (5/6) and about equal for reduced (4/9) and control (5/9) birds.

Song production did not differ across the three groups. Mean ± SE bins with song per bins of sampling time for control birds (n = 9) was 0.18 ± 0.056, for reduced birds (n = 9) was 0.25 ± 0.081, and for covered birds (n = 6) was 0.21 ± 0.074 (H = 0.151, n = 24, p = 0.93). Thus there is no evidence for changes in song output as a result of the manipulation.

Mating status and breeding phase are known to influence many aspects of mockingbird behavior (Logan 1983, 1988, 1994; Breitwisch *et al.* 1986; Breitwisch & Whitesides 1987). Four of the reduced birds were unmated, and all other birds in the study were mated. In order to control for breeding phase, the analyses were rerun using only mated birds in the nest building phase of the breeding cycle. Sampling time in other phases was too small to permit individual analyses.

Using only mated birds in the nest-building phase affected one result: The average duration of the territorial interactions was in the predicted direction and statistically significant. Mean ± SE average duration of chases (in seconds) for control birds (n = 4) was 0.4 ± 0.42, for reduced birds (n = 3) was 11.5 ± 1.92, and for covered birds (n = 3) was 17.3 ± 11.44 (H = 6.876, n = 10, p < 0.01, $\epsilon_R = 0.83$; Fig. 2). Post-hoc comparisons showed covered birds had longer chases than control birds (z = 2.12, p = 0.017). Two other measures with sufficient sample sizes for testing were unchanged by controlling for mating status and breeding phase. First, number of chases per hour of time-in time was still different between the groups: mean ± SE for control birds (n = 4) was 0.13 ± 0.128, for reduced birds (n = 3) was 0.83 ± 0.447, and for covered birds (n = 3) was 1.88 ±

0.195 (H = 6.168, n = 10, p < 0.046). Second, number of bins with song per bins of sampling time was still not different between the groups: mean ± SE for control birds (n = 4) was 0.31 ± 0.073, for reduced birds (n = 3) was 0.24 ± 0.013, and for covered birds (n = 3) was 0.31 ± 0.120 (H = 0.164, n = 10, p = 0.921).

Using only control birds, wing patch size was not significantly negatively correlated (one-tailed p values above 0.05) with number of chases per hour of time-in time (Spearman's rho = 0.458, n = 9), average intensity score of chases (rho = - 0.616, n = 5), or average duration of chases (rho = 0.390, n = 9). Controlling for breeding phase (by only using data for one phase) did not change the results of the correlational analyses. Thus, territorial interactions were not inversely related to wing patch size in control birds.

An important addition to these results comes from casual observations of the resident female, which could often be readily seen for a large proportion of the sampling time. Field notes on the females' behavior were taken, particularly if the behaviors seemed out of the ordinary. These notes, although anecdotal, suggest the possibility that reducing or covering the males' wing patches had a disruptive effect on the maintenance of the pair bond. For example, one of the covered males could not evict another male that would regularly enter the territory and interact with the resident female. Another covered male lost his territory and his female to a neighboring male. Three of the experimental males' females were seen leaving the territory and interacting with the neighboring male, which in turn led to chases between the males involved. Such episodes are extremely infrequent among unmanipulated birds.

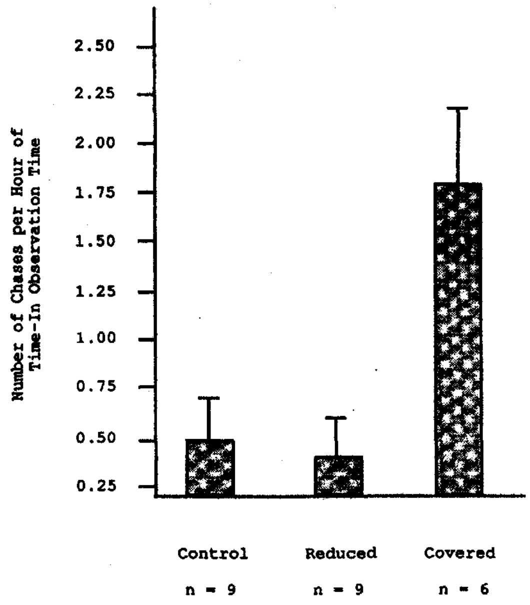

Figure 1. Both unmated and mated males in all breeding phases were used here. Error bars are one SE.

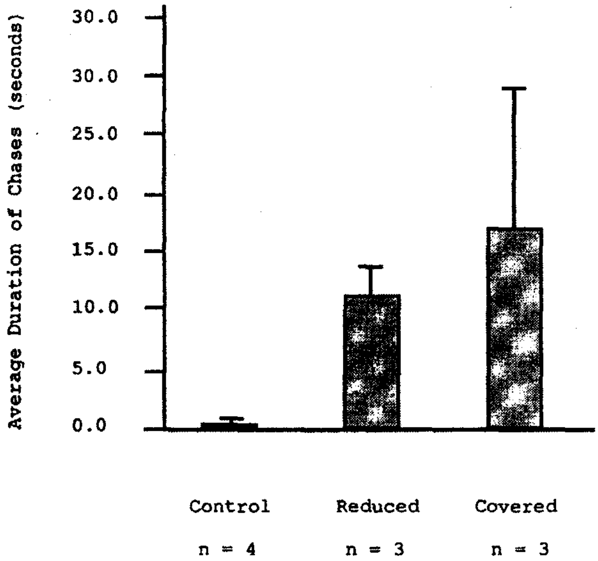

Figure 2. Only mated birds in the nest building phase were used here. Error bars are one SE.

Discussion

The above results showed that –

1) covering the wing patch produced statistically significant increases in territorial interactions;
2) reducing wing patch size produced insignificant increases in measures of territorial interactions (apparent when mating status and breeding phase is controlled)that were not statistically significant;
3) paradoxically, wing patch size is not inversely related to territorial interactions in unmanipulated birds; and
4) manipulating the wing patch may have adversely affected the pair bond.

There are now three alternative (but not mutually exclusive) explanations of wing patch function that need to be considered.

Explanation 1: Larger wing patch size is a signal of greater ability to defend the territory. This explains why covering the wing patch increased territorial interactions: The manipulation removed an important signal for territory defense. This explanation, however, would require that reducing the wing patch also produces significant increases in territorial interactions; yet the observed changes, although in this direction, are not significant. If the effect size of reducing the wing patch is smaller than that of covering the wing patch, then perhaps this result was not significant because of sample size. Also, this explanation requires that territorial interactions would be negatively correlated with wing patch size in control birds. The observed results are either not significant or in the opposite direction. In sum, then, there is only weak evidence supporting this explanation.

Explanation 2: The presence of a wing patch is a species recognition marker. Some close relatives of Northern Mockingbirds do not have wing patches, so Northern Mockingbirds may have evolved a wing patch for species recognition. Conspicuous signals for species recognition could be beneficial to mockingbirds in two ways: 1) while investigating potential territories, a signal could indicate an occupied area; and 2) once the territory is established, species markers should lower the frequency of territorial behaviors misdirected at heterospecifics.

If potential intruders can use the wing patch to tell that an area is being defended by a conspecific, then the pattern of results seen here can be interpreted in the following way. Covering the wing patch led to territorial interactions because potential intruders did not receive a signal that the area is being defended by a conspecific. Reducing the wing patches did not dramatically increase territorial interactions because a signal of species was still present. Territorial interactions did not increase as wing patch size decreased in unmanipulated birds because all unmanipulated birds had intact signals for species identification.

Explanation 3: Females use the size of the male's wing patch as a signal of the male's quality. Covering or reducing the wing patch causes pair maintenance problems because the males' low quality is being signaled to their mates. These pair maintenance problems may have been caused by the manipulation itself or by the consequent increase in male-male agonistic interactions. This explanation, however, was prompted by anecdotal observations. Systematic observations of the females' behavior and delineation of the communicative role of the wing patch in females are needed.

No one of the above explanations stands out as entirely better able to explain the entire set of data presented here. These three explanations are certainly not mutually exclusive, however. Indeed, they could be considered complementary. The presence (versus absence) of the wing patch may be a cue to species recognition. The size of the male's wing patch may signal both males and females. The male-to-male signal may serve territory formation and defense, while the male-to-female signal may serve mate acquisition and retention.

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