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THE ROLE OF THE WHITE WING PATCH IN COMMUNICATION AMONG NORTHERN MOCKINGBIRDS

by

Michael J. Justice

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Dissertation Advisor

UMI Number: 9632141

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APPROVAL PAGE

This dissertation has been approved by the following committee of the Faculty of The Graduate School at The University of North Carolina at Greensboro.

Dissertation Advisor Cheryl A. Logan

Committee Members D. R. Soderquist

John J Seta

Robert E. Gatten

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Date of Acceptance by Committee

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Date of Final Oral Examination

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Northern Mockingbirds (*Mimus polyglottos*) have large white patches on dark gray wings. Previous research has shown that the size of such plumage "badges" may function as a status signal, which allows individuals to evaluate the fighting ability of conspecifics without actually initiating combat. The present research was undertaken to test the hypothesis that male mockingbirds' wing patches are status signals. To this end, male mockingbirds were captured and their wing patches were experimentally enlarged, reduced, or covered. If wing patches are status signals, then reducing and covering the wing patch should increase the frequency and intensity of territorial intrusions and chases, while increasing wing patch size should have the opposite effect. Covering the wing patch did increase territorial chases, but neither reducing nor enlarging the wing patch had an effect on territorial chases. These results suggest that the wing patch may simply be a cue to species recognition, but do not refute the possibility that the wing patch is a status signal.

During data collection, several anecdotal observations suggested that altering patch size could disrupt the pair bond: the female investigated other males, which sometimes lead to fights between the males involved. Further evaluation of this hypothesis showed that males had larger wing patches

than females, unmated males had smaller wing patches than mated males, and males with larger wing patches responded more intensely to a potential nest predator. All of these results are consistent with a possible female preference for males with larger wing patches. Thus, an intersexual choice hypothesis is considered as an alternative interpretation of the data.

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This dissertation is dedicated to Dr. Robert Kunzendorf and to the memory of Leo Gallant, both of whom were invaluable friends and mentors.

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CHAPTER I

INTRODUCTION

Game Theory and Status Signalling in Aves

Many animals use displays to settle contests over resources rather than escalating to overt fighting. Since neither contestant risks injury or death when displays are used, early ethologists interpreted this as behaving for the good of the species (Eibl-Eibesfeldt 1961). Later, Maynard Smith and Price (1973) used mathematical modelling based on game theory to demonstrate the potential advantages for the individual when displays are used, assuming the only difference between the contestants is in the tactics used in the agonistic situation (i.e., escalate versus display). In such contests, game theory models predict that a behavioral polymorphism in the population is generally the outcome, that is, two or more different tactics are used, and no one tactic can successfully spread throughout the population to the exclusion of the others. Parker (1974) later applied game theory modelling to the case of contests in which individuals are asymmetric in Resource Holding Potential (RHP), defined as the ability to win fights in defense of resources. Together, Maynard Smith and Parker (1976) demonstrated mathematically that settling animal contests on the basis of RHP asymmetries between the contestants rather than escalated fighting would be an evolutionary stable strategy. In addition to RHP, Maynard Smith & Parker (1976) named two other types of asymmetries: 1) asymmetries in the gain from acquiring and/or retaining possession of the resources being contested (which here will be called perceived resource value or PRV), which result in asymmetries in motivation to acquire and retain such resources and 2) uncorrelated asymmetries (also called arbitrary decision rules), which are any arbitrary asymmetries that can be identified and used when fighting is costly and contestants are equal in RHP and PRV (presumably a rare situation: Maynard Smith & Parker 1976). Given the limitations of mathematical modelling, this research prompted empirical investigation into the nature of animal signals and their use in settling agonistic contests.

Investigations into the nature of avian PRV signals are relatively rare. Individuals with higher motivation to acquire or defend a food resource tend to win dominance interactions; this has been shown in House Sparrows (*Passer domesticus*; Andersson & Ahlund 1991), Great Tits (*Parus major*; Lemel & Wallin 1993), Fulmars (*Fulmaris glacialis*; Enquist et al. 1985), Black-chinned Hummingbirds (*Archilochus alexandri*; Ewald 1985), Bald Eagles (Hansen 1986), a species of starling

(Kacelnik, a personal communication cited in Enquist & Leimar 1987), Bluethroats (*Luscinia svecica;* Lindstrom et al. 1990) and American Goldfinches (*Carduelis tristus;* Popp 1987). Although hunger transiently affects dominance status, it is typical that overt fighting and potentially injurious behaviors increase as PRV increases (Enquist & Leimar 1987), which suggests that signals are ignored when PRV is high (Grafen 1987). However, some of these interactions were won through threat posturing, resisting displacement, or chasing, suggesting that some species may use signals of PRV to settle some contests. In the only systematic study of avian PRV signals being used to settle contests, Enquist et al. (1985) showed that the type of display used by Fulmars competing for food was dependent upon PRV; further, many contests were settled simply by the exchange of display behaviors.

In contrast to signals of PRV, the form and use of avian RHP signals (often referred to as "status signals") have been investigated in several species. Rohwer (1977, 1978) found that those Harris' Sparrows (*Zonotrichia querula*) with more extensive black coloration on the head and throat were dominant in winter flocks. He proposed that "bib" size was a signal of status by which wintering flocks of Harris' sparrows were settling disputes over resources. It later became apparent that in Harris' sparrows the bib plumage was only signalling age-sex class, which correlated with dominance; within age-sex classes, bib size did not predict relative dominance (Jackson et al. 1988; Watt 1986a). This is also the case in White-crowned Sparrows (*Zonotrichia leucophrys*): crown color and crown contrast signal age and sex class. True subordinates painted to resemble dominants achieved high social status, but crown variability within age and sex classes did not operate as status signals (Fugle et al. 1984; Parsons & Baptista 1980; Watt 1986b). Ketterson (1979) showed that plumage characteristics of Dark-eyed Juncos (*Junco hyemalis*) indicate age and sex class and therefore dominance. Later, Holberton et al. (1989) found that if the subordinate within a pair of female or immature juncos is manipulated to resemble an adult male, the change in plumage will allow the subordinate to become dominant.

The largest body of evidence for avian color patterns being used as reliable badges of status within age and sex classes is the studies of Red-winged Blackbirds (*Agelaius phoeniceus*). Early work showed that blackening the red epaulettes usually resulted in the loss of the territory due to increased intrusion pressure (Smith 1972; Peek 1972). Later, in a sample of 14 captive adult males, the Spearman's rho for the correlation between greatest length of red on the epaulettes and won/lost ratio in agonistic encounters was 0.444 (Searcy 1979); although this was reported as not statistically significant, the associated p value of 0.06 (one-tailed test, my analysis) suggests this may be a Type II error, given the sample size. An actual relationship has since been further supported. Hansen & Rohwer (1986) showed that territory owners displayed the most aggression toward simulated intruders whose epaulettes had been experimentally enlarged, which may have made them appear to be more of a threat. Also, when males arrive at the breeding site, they avoid simulated intruders with normal epaulettes and avoid to a greater degree simulated intruders with experimentally-enlarged epaulettes (Røskaft & Rohwer 1987). Finally, Eckert & Weatherhead (1987a) showed that dominance rank among adult males increases with epaulette size.

Signals of status that operate within age and sex classes have also been found in other species. In House Sparrows (*Passer domesticus*), Møller (1987a, 1987b) showed that variation in the area of black on the throat signals dominance, although birds with larger badges were not all of the same age class, size, or condition. Further, house sparrows with larger testes had larger badges (Møller & Erritzoe 1988), suggesting that these badges may contain information about aggressive motivation or reproductive potential, since testes produce both sperm and testosterone. The lightness of the ventrum of Least Auklets (*Aethia pusilla*) indicates status within age classes: lighter birds defeated darker birds in encounters, and light-colored mounts were approached less closely than dark ones (Jones 1990). The width of the breast stripe in Great Tits (*Parus major*) increases with dominance and operates within age and sex classes (Järvi & Bakken 1984). During simulated territorial intrusions in Yellow Warblers (*Dendroica petechia*), the intensity of the aggressive response from residents was a function of both the amount of brown streaking on the breast of the simulated intruder and the amount of brown streaking on the resident (Studd & Robertson 1985). Most recently, variation in the size of the black bib in male Eurasian Siskins (*Carduelis spinus*) was found to be a reliable badge of status used to settle contests over artificial feeding resources (Senar et al. 1993).

Status Signals in Northern Mockingbirds

A. Natural History

1. General Appearance. Northern Mockingbirds (*Mimus polyglottos*) are medium-sized (40 - 60g; 23 - 28cm) oscines. Relative to other oscines, they are slender and have a long tail. The crown, nape, back, and rump are grayish, while the breast, flanks, and belly are whitish. The beak and legs are black. The wings are darker gray with a white patch across the primaries and two white wing bars across the greater secondary coverts. The tail is dark gray centrally with the outermost retrices white.

2. Classification. Northern Mockingbirds are typically placed in the Mimidae family with catbirds, thrashers, and other mockingbirds (American Ornithologists' Union 1983; Ridgway 1907). Classically, the Mimidae are considered to be most closely related to either the thrushes (Turdidae) or the wrens (Troglodytidae), but a recent reclassification of Aves based on interspecific DNA - DNA hybridization has suggested that mockingbirds and starlings (Sturnidae) are closest relatives (Sibley & Ahlquist 1984).

3. Range, Habitat, and Territories. The genus Mimus (approximately 30 species) is restricted to the New World tropics with the exception of the study species, which is temperate. The nominate subspecies breeds in eastern North America from southern Canada south to the Caribbean and Mexico. Northern Mockingbirds are generally believed to be year-round residents throughout their range, although the northernmost populations may be partially migratory (American Ornithologists' Union 1983). Bird counts and anecdotal evidence have charted 1) a northward expansion of *M. polyglottos'* range from about 38°N to about 45°N in the past 100 years (Stiles 1982), and 2) an increase in their numbers in North and South Carolina from the 1940s to the 1960s followed by a decrease from the 1960s to the 1980s (H. Hendrickson, personal communication, 1994).

Northern mockingbirds defend year-round territories in residential areas, city parks, farmlands, and open country. These territories, about one hectare in area, are all-purpose: they provide all food (arthropods when available and fruit year-round), water, shelter, nesting materials (sticks and grasses), and nest sites (bushes, tangled vines, and low trees). In the study population, territories are typically bordered by small patches of woods, or up to four neighboring mockingbird territories. Territories are aggressively defended against conspecifics; detected intruders are typically chased out of the territory quickly. Although territorial interactions occur frequently, escalated fighting with physical contact is rarely observed.

4. Behavioral Cycles. Daily, mockingbirds at the study site are most active in the morning (approximately 0700 to 1200hr) and are again active in late afternoon (approximately 1530 to 1930hr). Annually, they are very active during the spring breeding season, which at the study site begins in late February/early March and lasts through early July. At this time, mated pairs may attempt as many as 6 - 8 overlapping broods, building a new open cup nest for each brood, and typically fledging only one or two of these attempted broods.

It appears the male initiates nesting by building a base of twigs in dense foliage from 1 - 15m above ground; the female lines the base with grasses. Females incubate 2 - 4 eggs for about twelve days, after which both sexes feed the nestlings. Upon fledging, the male provides most parental care while the female incubates the next clutch (Zaias & Breitwisch 1989, 1990). After the breeding season, mockingbirds are very inactive for about 6 - 8 weeks while they molt. At the study site they are active again in September and October, when yearlings are attempting to establish territories and mate acquisition may occur. Territorial fights peak during autumn (Laskey 1936), after which mockingbirds are relatively inactive until the beginning of the breeding season.

5. *Breeding System.* Most mockingbirds appear to be socially monogamous; however, the frequency of extrapair copulations and conspecific nest parasitism has not been assessed. In the study population, about 10 - 20% of males are unmated at any one time (personal observation); this along with the scarcity of unmated females during the breeding season indicates a male-biased sex ratio. Other populations have been found to be male-biased as well (Breitwisch 1989).

B. RHP and PRV in Northern Mockingbirds

If a territorial resident has a conspecific territorial neighbor, and this neighbor does not impose a cost on intrusions into its territory, then the resident can increase its fitness relative to its neighbor's by using its neighbor's resources to supplement its own. However, in reality the neighbor will most likely defend its resources and thus present a cost to a potential intruder. Costs to an intruder will vary with the RHP and PRV of the territory defender. For the same benefits, an intruder should invade the territory with the least potential cost, that is, the territory defended by the individual with the relatively lowest RHP and lowest PRV. Shutler & Weatherhead (1991) suggest that this occurs in the red-winged blackbirds' social system: nonterritorial "floaters" attempting to usurp space test several owners to detect the one least able to defend its territory (see also Freeman 1987).

If mockingbirds are signalling their RHP and/or PRV in any manner, then this information should affect the intensity and frequency of territorial interactions. Those with high RHP and/or high PRV will have relatively fewer territorial interactions than those with low RHP and/or low PRV, because other mockingbirds can detect the signals and respond according to the risks of an agonistic interaction with a particular opponent.

C. Potential Roles for the Wing Patch

1. Description. Northern Mockingbirds have ten primary flight feathers, each one being dark gray at the distal tip and white otherwise (Figures 1 and 2). Over the primaries, there are three partially-overlapping rows of coverts; a row of white coverts overlaps the white portion of the primary feathers. The wing patch comprises the white in the primary feathers along with the white greater primary coverts. Viewed ventrally, the wing patch is still evident, but it is obscured near the wrist by light gray underprimary coverts and the contrast with the surrounding gray is reduced due to the generally lighter gray on the underside of the feathers.

2. The Wing Patch as a Signal of Resource Holding Potential (RHP). RHP is defined as the ability to win fights in defense of resources. Thus, for mockingbirds, RHP is defined as the ability to win fights with conspecifics in order to maintain exclusive access to the resources being contested. Because RHP should vary continuously across individuals within an age/sex class, a signal of RHP should vary in the same way (Rohwer 1982). This rules out the shape, hue, contrast, and location of the wing patch as potential signals of RHP and/or PRV because these parameters vary little or not at all across adult males (Ridgway 1907, Forbush 1929, personal observations). However, some preliminary evidence suggests that wing patch size is variable across males (Michener 1953; personal observation). If wing patch size does show considerable variation across males, then it is a plausible indicator of RHP.

3. The Wing Patch as a Signal of Perceived Resource Value (PRV). PRV is defined for mockingbirds as the bird's perceived gain resulting from the acquisition or retention of the resources being contested. For any given resource, the information in the signal reflecting PRV must change as resource value changes. Wing patch size can only be changed during the annual molt, and even then it typically only changes slightly (Michener 1953). Given this, it seems wing patch size is not well suited to signal PRV, which should change much more rapidly than RHP (Lindstrom et al. 1990). However, frequency of exposure of the wing patches, which can be adjusted rapidly, is well suited to signal PRV. As the resources on the territory improve or their value increases (and therefore PRV increases), residents' activity levels may rise. Such an increase in activity levels would force the increased exposure of the wing patches. This increase might act as a signal of PRV to other mockingbirds and decrease territorial interactions.

General Predictions

Given that 1) Northern Mockingbirds engage in interference competition for resources, 2) escalated fighting is rarely observed in mockingbirds, despite frequent territorial intrusions 3) game theory models predict that mockingbirds should settle contests on the basis of detected asymmetries in RHP or PRV, 4) other avian species use conspicuous plumage characters as signals of status in place of escalated fighting to settle some contests, and 5) certain features of the wing patch appear to be suitable for signals of RHP and / or PRV, it can be predicted that 1) Northern Mockingbirds signal their RHP and their PRV, 2) their wing patches are used as signals of RHP and/or PRV, and 3) this information is used to settle contests, thereby avoiding escalated fighting.

If mockingbirds use RHP and/or PRV signals to settle contests, then the frequency and intensity of territorial contests should be negatively correlated with RHP and/or PRV. If wing patch size signals RHP, then 1) wing patch size will vary across males, 2) the frequency and intensity of contests should negatively correlate with wing patch size and 3) manipulating the size of the wing patch should influence the frequency and intensity of contests. If frequency of exposure of the wing patch signals PRV, then 1) frequency of exposure should increase as PRV increases, and 2) manipulating the frequency of wing patch exposure should affect the frequency and intensity of territorial contests. It will be assumed that frequency of exposure varies sufficiently across males to allow its use as a signal of varying PRV.

CHAPTER II

METHODS AND RESULTS

Subjects

Samples for these studies were taken from a population of wild mockingbirds residing on the 72 ha suburban residential campus of The University of North Carolina at Greensboro (36°N 79°W). The campus is situated in a piedmont in southeastern North America. It supports approximately 60 - 70 individual mockingbirds, the majority of which have been color banded.

Trapping and Sampling

Data were collected during the breeding seasons of 1993, 1994, and 1995. Mockingbirds were trapped under federal and state licenses in 18 x 18 x 18 cm treadle traps that were placed on platforms elevated 1.6m off the ground. A peanut butter/cornmeal mix was used as bait and as a food source (twice per week, one tablespoon was placed on the platform in the absence of a trap). Adult mockingbirds cannot be reliably sexed by external morphology and therefore at the time of trapping sex was either unknown or known from records of prior behavior, depending on whether the bird was banded at the time of capture. Upon capture, the bird was first banded (if necessary), then measured, and finally manipulated experimentally (if being performed).

Measures of behavior employed focal-animal sampling (Altmann 1974) using 8-power binoculars. Any behavioral sampling of birds that were trapped and measured began at least one day following capture. The total sample time was divided into 15-second bins, and the occurrence and/or frequency of each behavior 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. The behaviors recorded during focal-animal samples were

1) Perch changes, defined as flights that result in at least a 2m change in position.
2) Chasing a intruder: this was defined as flying in the same direction as a conspecific intruder. Five types of chases were distinguished:

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

Type 2 - The intruder offers 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 is physical contact involved, but no clear winner emerges because the interaction takes place near the territory border

Type 4 - There is physical contact coupled with chasing from the territory; the resident is the clear winner because the intruder is chased out

Type 5 - The resident makes an attempt to evict the intruder, but ultimately concedes.

3) Duration of chases. For chases, time began when the birds involved got within 5m of one another and ended when the resident ceased to chase.
4) The production of song.
5) The exchange of hew calls between the male and female within a pair.
6) Time-out time, defined as the number of 15-second bins in which all visual and acoustical contact with the bird was lost. The remaining time will be referred to as "time-in time."

All references to "territorial interactions" refer to the measures of chase frequency, duration, and intensity. Where appropriate, each individual bird's mean across samples was used to calculate group means.

For most birds, the location of all perches and territorial interactions were marked on a small-scale map of the territory and numbered consecutively. "Flight paths" were later generated by connecting the sequential perch positions with straight lines. Flight paths that were extraordinarily different from linear were recorded in the field. Territory size was measured as the area bounded by the flight paths connecting the locations of perches and territorial interactions (Figure 3) after cumulating these across all sampling time (in all cases, at least 1.5 hours of time-in time had been accumulated). This area was traced using an electronic planimeter (Los Angeles Scientific Instruments Company Model No. 42P with the medium arm setting), and the output (square inches on the map) was transformed to hectares of actual territory size.

Statistical Analyses

Parametric statistics were used wherever the data met the assumptions. For most significant statistical results presented, a corresponding measure of the strength of the relationship between the independent and dependent variable is also presented. All statistical computations were performed either by hand or using Systat v5.0 for Microsoft Windows on an AST PC with an Intel 486sx/25MHz microprocessor.

Study 1: Does Wing Patch Size Vary Across Males?

A. Introduction

As stated earlier, a signal of RHP should, like RHP itself, vary continuously across male mockingbirds (Rohwer 1982). A series of figures in Michener (1953) suggests that mockingbird wing patch size is variable. However, the variability was not quantified and the data were collected from a different population of mockingbird (*M. p. leucopterus*) which is known to have larger wing patches (Rigdway 1907, Sprunt 1964, personal observation). Thus the present study was undertaken to quantify the variation in mockingbird wing patch size. Wing patch size is a plausible indicator of RHP only if it shows considerable variation across males.

B. Methods

1. Measures. Wing patch size was measured from the ventral surface of the left wing's primary flight feathers, without flattening their natural curvature. The measure was taken in the field using dial-type Vernier calipers calibrated to 0.01mm.

Each of the ten primaries is white by the wrist and dark grey distally (Figure 2). Ventrally, the wing patch is comprised of all the white on the primaries except some near the wrist that is covered by very light gray underwing coverts. Dorsally, the white near the wrist is obscured by dark gray coverts; the wing patch is comprised of a row of white primary coverts and the white on the primaries that extends beyond the coverts. On each individual primary, the border between the white and gray is often irregular and sometimes blurred (Michener 1953; personal observation). The amount of white on an individual feather was measured as the length of the chord from the outer edge of the carpus to the most distal point on the shaft where a line drawn perpendicular to the shaft across either the inner or outer vane did not intersect any gray area (Figure 2). Wing patch size was computed as the sum of these lengths across all ten primaries. Occasionally, primary #10 did not have any white extending beyond the underwing coverts; in these instances the amount of white was the chord of the distance from the wrist to the distal edge of the underwing coverts.

2. Precision of the Wing Patch Size Measure. Because fourteen birds were captured more than once and re-measured by the same experimenter, precision of the measures could be assessed by examining the difference scores on pairs of measures of the same variable. Ten birds were measured only twice, but the other four were measured more than twice. For these four a single pair of measurements taken between successive molts was selected for the assessment of precision because wing patch size and shape can vary slightly across the molt (Michener 1953).

Two analyses were performed on the resulting 14 paired sets of measures. First, the amount of white measured on each of the ten primaries at the first measurement was subtracted from the amount of white measured on that primary at the second measurement. For the n = 140 difference scores, mode = 0.20mm, median = 1.00mm, mean = 1.49mm, SEM = 0.12mm, minimum = 0.00mm, and maximum = 7.30mm. Because the typical length of white on a primary is about 50.0mm, the median difference represents a 2% error, which is in the range of acceptability suggested by Sokal & Rohlf (1981). Second, the first measures of the amount of white on each of the ten primaries were correlated with the corresponding second measures of the amount of white on the same feathers for each of the 14 birds measured twice or more (yielding N = 140 pairs of measures). The ranking of feathers based on the first measure of amount of white was highly positively correlated with the ranking based on the second measures (Spearman's rho = 0.959, N = 140, r^2 = 0.92).

C. Results

1. Male Wing Patch Size. Mean ± SE wing patch size (in mm) for known males (n = 34) was 546.7 ± 4.7 (range 479.5 - 597.1). A Kolmogorov-Smirnoff one-sample test for normality indicated that wing patch size was normally distributed within males (n = 34, p = 0.08). Descriptive statistics on the amount of white on each of the ten primary flight feathers are presented in Table I. All primaries showed variability in the amount of white. However, primaries 1, 2, 3, and 4 were considerably more variable than the others (pairwise F tests, all p values < 0.001). When the wing is extended, the variability in the white on these four feathers would largely affect how long the wing patch appears as it extends from the 10th primary toward the secondaries (Figure 1). Variability in the other primaries, which was considerably lower, would largely affect how wide the wing patch looks from the proximal edge of the white coverts to the distal edge of the wing patch on the primaries.

2. Other Results. Mean ± SE wing patch size for both sexes combined (n = 74) was 517.5 ± 4.9 (range 442.5 - 597.1), and for known females (n = 29) was 486.0 ± 5.0 (range 442.5 - 564.8). Kolmogorov-Smirnoff one-sample tests for normality indicated that wing patch size was also normally distributed with both sexes combined (n = 74, p = 0.372) as well as within females (n = 29, p = 0.525). The variance in wing patch size was the same for both sexes ($F = 1.04$, df = 33, 28, $p > 0.20$). Males' wing patch sizes were significantly larger than females' ($t = 8.76$, df = 61, two-tailed $p < 0.001$, $r^2 = 0.557$; Figure 4). For each of the ten primaries, the length of white was significantly longer in males (t tests, all two-tailed p values < 0.001). Table I shows that males' larger wing patches are due largely to having more white on primaries 1, 2, 3, and 4.

As in other reports (Ridgway 1907; Derrickson and Breitwisch 1992), average wing length was longer in males, with considerable overlap across the sexes. Mean ± SE wing length (in mm) for known males ($n = 36$) was 111.8 ± 0.65 (range 103.3 - 119.7) and for known females ($n = 33$) was 104.8 ± 0.66 (range 97.7 - 110.9) ($t = 7.563$, df = 67, two-tailed $p < 0.001$, $r^2 = 0.461$). Wing length for both sexes combined ($n = 81$) was 108.4 ± 0.57 (range 97.7 -119.7).

Wing length and wing patch size were correlated within males (Pearson's $r = 0.576$, $n = 34$, $p < 0.001$), within females ($r = 0.586$, $n = 29$, $p < 0.001$), and with both sexes combined ($r = 0.814$, $n = 74$, $p < 0.001$). Territory size did not correlate with either wing patch size ($r = - 0.317$, $n = 7$, $p = 0.488$) or wing length ($r = 0.074$, $n = 7$, $p = 0.875$).

D. Conclusions

Wing patch size in male mockingbirds is highly variable, particularly the "length" of the wing patch, which changes with the amount of white on primaries 1, 2, 3, and 4. Within males, the range of wing patch sizes (largest minus smallest) was 117.6mm. On the first four primaries, where the largest differences were found, there was 20 - 30mm difference between the longest and shortest amounts of white. This is over one-third of the average length of these feathers. Thus, there is likely to be sufficient variability in wing patch size for it to act as a signal of RHP, which is expected to vary continuously across males.

The significant correlation between wing patch size and wing length indicates that there is likely to be a relationship between these two variables in the population. This raises the possibility that the information contained in wing length is redundant with the information contained in wing patch size. However, the strength of the relationship in the population cannot be determined from a significant correlation. Further, the sample correlations are not very high; in fact, only 33% of the variation in males' wing patch size is explained by variation in wing length. Therefore, it is unlikely that another mockingbird could get the same amount and type of information contained in wing patch size from an assessment of wing length.

The sexual dimorphism in wing patch size may be due to a greater role for males in territorial defense, although this has not been systematically studied. It is also possible that wing patch size is used in female choice of mates. This latter explanation would also address the lack of a correlation between wing patch size and territory size: wing patch size would be unrelated to territory size because it is involved in male-female signalling for mate choice rather than male-male signalling for territory defense. Alternatively, wing patch size may indeed be related to territory quality, but it may be that in mockingbirds territory quality is independent of territory size.

Study 2: Are Territorial Interactions Affected by RHP or PRV?

A. Introduction

Given that 1) mockingbirds engage in interference competition for resources, 2) escalated fighting is rarely observed in Northern Mockingbirds 3) other avian species settle contests without escalated fighting by signalling their dominance status or motivation, 4) game theory models predict that contestants should settle contests on the basis of detected asymmetries in RHP and PRV, and 5) the riskiness of intrusion onto a particular territory should affect the frequency and intensity of intrusions onto that territory, it can be predicted that mockingbirds signal both their RHP and PRV, and the presence of this information affects the rate and/or intensity of agonistic interactions.

B. Methods

In order to determine whether mockingbirds signal their RHP, the measures of territorial interactions were each correlated with a measure of RHP. Because the ability of an individual to win in agonistic encounters defines RHP, there are numerous potential measures of RHP, including size, agility, strength, intelligence, experience, extent of morphological "weapons" such as claws, and physical condition. However, larger body size has been found to be related to success in intrasexual conspecific agonistic encounters in many species from diverse taxa (see Archer 1988 for a review) including Aves (Richner 1989), and it has been used as a measure of RHP in Aves (Jackson et al. 1988). Thus, wing length, a commonly used measure of avian body size, was used in these analyses. Wing length was measured as the chord of the wing from the anterior edge of the wrist to the tip of the longest primary, without flattening the natural curvature of the feather (Baldwin et al. 1931).

In order to determine whether mockingbirds are signalling their PRV, measures of territorial interactions were compared within-subjects between a high-PRV phase of the breeding cycle and a low-PRV phase. In determining which phases to use for this study, the following two assumptions were made: 1) resident mockingbirds are familiar with the resources present on their territory, and 2) the value of these resources fluctuates with phase of the nesting cycle, other things being equal. For example, the relative value of a fixed density of food is probably greater during the period when offspring are being fed than during the periods when offspring are not present. Similarly, for a mated male, the value of defending the territory against male intruders is probably greater just prior to egg - laying than at other times when extrapair copulations obtained by the intruders are much less likely to result in fertilized gametes.

Given these assumptions, territorial interactions were compared (within subjects) between the nestbuilding and incubation phases of the breeding cycle. Thus, the value of food should be constant because, with no dependent offspring present, food use by the male should be approximately the same during nestbuilding and incubation. In contrast, female fertility and the risk of extrapair copulations should be highest during nestbuilding, as she prepares to lay eggs, and low during incubation. Thus, males should be more motivated to defend the territory and the fertile female (that is, have higher PRV) during the nestbuilding phase compared to the incubation phase. Specifically, territorial interactions were compared between 1) the days on which male nestbuilding or female egg-laying was observed (nest building phase) and 2) the days during which the female was observed to be incubating (incubation phase). If PRV is higher during nest building and is signalled, then the frequency and intensity of territorial interactions should be lower during nest building.

Because mockingbirds are multibrooded, there is a possibility that nestbuilding will take place while fledglings from the prior brood are still on the territory. Because the presence of fledglings may affect the motivation to defend food, samples from such pairs were only used if the fledglings were present in both the nestbuilding and incubation phases or if the fledglings were present during nestbuilding samples but not during incubation samples. Either of these situations should produce higher PRV in the nest building period.

Territorial interactions were scored as described above. Because the aggressiveness of the chases increases from Type 1 to Type 4, these types of chases were used to compute an average intensity of the interactions for each bird. Type 5 interactions could reasonably be placed at either end of this scale because the resident loses badly but with little or no overt aggression. Thus, type 5 interactions were not averaged into this measure.

C. Results

1. RHP Was Not Related to Territorial Interactions. Ten birds whose wing lengths were known were available for this study. Nine were sampled during both the nest building and incubation phases of their breeding cycle; one was sampled only during the nestbuilding phase. Mean ± SD hours of time-in time for these ten birds was 4.8 ± 1.44. There was no evidence for a relationship between wing length and chases per hour of time-in time (Spearman's rho = - 0.031, p > 0.45).

Birds defending larger territories (with longer perimeters) could have more neighboring territories bordering their own and perhaps a more difficult time defending the territory against intruders. Thus, the number of chases per hour of time-in time was corrected for territory size by dividing chases per hour of time - in time by the number of hectares of territory area for nine birds for which territory size was available. There was also no evidence for a relationship between wing length and chases per hour of time-in time per hectare of territory area (rho = 0.034, p > 0.25). Average chase duration was also not related to wing length (rho = - 0.129, n = 10, p > 0.20). Average intensity measures were available for six birds; average intensity score was also not related to wing length (rho = - 0.232, p > 0.25). These results did not change when breeding phase was better controlled by using only samples taken in the nest building period. Thus, there is no evidence to support the predicted negative relationship between body size (as measured by wing length) and territorial interactions.

2. PRV Was Not Related to Territorial Interactions. Seven birds were sampled during both the nestbuilding and incubation phases of their breeding cycle. Mean ± SD time-in time for nestbuilding was 2.1 ± 0.66 hours per bird and for incubation was 2.9 ± 0.65 hours per bird. Mean ± SE number of chases per hour of time-in time was 0.71 ± 0.204 during the nestbuilding period and 0.76 ± 0.381 during the incubation phase; there was no difference between the phases (mean difference = - 0.044, SD of the differences = 0.712, t = -0.164, df = 6, two-tailed p > 0.50; Figure 5). Mean ± SE number of chases per hour of time-in time per hectare of territory area was 0.90 ± 0.234 during nestbuilding and 1.00 ± 0.498 during incubation; again, there was also no between-phase difference (n = 6 birds for which territory size was available, mean difference = 0.05, SD of the differences = 0.975, t = 0.126, df = 5, two-tailed p > 0.45). Thus, there was no evidence to support the predicted higher frequency and intensity of territorial interactions during the incubation phase, when PRV is expected to be lower.

D. Conclusions

These data do not provide any evidence to suggest that mockingbirds are signalling their RHP or PRV. Wing length, as a measure of RHP, was not negatively correlated with territorial interactions, as would be expected if mockingbirds were signalling their RHP. Further, territorial interactions did not increase with decreasing PRV (assumed to fluctuate with nesting phase), as expected if mockingbirds were signalling their PRV.

There are at least two other possible explanations for the lack of evidence for signals of RHP and PRV. First, the conclusions from the data may be Type II errors due to the small sample sizes used. Second, it is possible that the dependent measures of RHP and PRV are invalid. Although body size is related to success in agonistic encounters in numerous species (Archer 1988), this does not necessarily mean it is a valid indicator of RHP in mockingbirds. Given that extended fights with physical contact are rarely observed in this species, and that during chases the birds often match each other's movements, perhaps agility may have better measured RHP in mockingbirds. Likewise, there may not actually be a true shift in PRV from the nest building to the incubation phase. Perhaps another, unanticipated set of variables is affecting true PRV such that it is actually remaining rather constant across the two measured breeding phases. One possibility is the threat of usurpation: it may be the case that any resources or areas that are not well-defended may be annexed by neighboring males. Thus, the signalled level of defense may not change across the breeding season, keeping territorial interactions at a fairly constant level. Given these possibilities, these data can not conclusively demonstrate a complete lack of signals of RHP and PRV in mockingbirds.

Study 3: Are Territorial Interactions Affected by the Wing Patch?

A. Introduction

Considering that 1) the wing patch is conspicuous, 2) conspicuous plumage markings are signals of status in other avian species, and 3) characteristics of the wing patch (variability in size and frequency of exposure) match the requirements for signals of RHP or PRV, then it is possible that the wing patch is used as a signal of either RHP, PRV, or both. If wing patch size signals RHP, then 1) wing patch size will be negatively correlated with the measures of territorial interactions in unmanipulated birds, 2) covering or reducing the wing patch will result in disruption of the signalling and consequent increases in territorial interactions, and 3) enlarging the wing patch will decrease territorial interactions. If frequency of exposure of the wing patch signals PRV, then 1) territorial interactions should decrease as frequency of exposure increases in unmanipulated birds, 2) covering the wing patch will increase territorial interactions, and 3) reducing or enlarging wing patch size will not affect territorial interactions because these manipulations do not affect the frequency of wing patch exposure.

B. Methods

1. Manipulation of the Wing Patch. Traps were placed in randomly-selected territories. Upon capture of a male, the wing patch was either 1) reduced both dorsally and ventrally by dyeing over all of the white area on the primaries beyond the distal edge of the greater coverts using a dark grey nontoxic marker ("reduced"), 2) enlarged both dorsally and ventrally by extending the white 15mm further down the primaries using a nontoxic white paint pen ("enlarged"), 3) left the same size as a control, with the gray area on the primaries dyed gray with a nontoxic marker ("control"), or 4) completely eliminated by dyeing over all the white on the primaries and greater coverts with a dark gray nontoxic marker ("covered"). The first manipulation reduced the size of the wing patch to smaller than ever naturally observed, the second made the wing patch larger than ever naturally observed, and both manipulated the "length" of the wing patch, which was shown in Study 1 to be a highly variable aspect of the wing patch. The dye wears off sufficiently to reveal the original wing patch after about one to three weeks, but some dye remains until the next molt (personal observation).

2. Other Measures. Amount of song produced was measured because mockingbirds may compensate for ineffective visual defense of the territory with enhanced vocal defense of the territory. Because time-out time involves a loss of acoustic contact with the focal animal by definition, the number of bins in which song was recorded was divided by total bins of sampling time, rather than by total bins of time-in time, for the measure of song production.

The measure of frequency of exposure of the wing patch was the number of perch changes per minute of time-in time. Because the rate of wing patch exposure within each flight may vary with flight speed, flight duration, flight direction, wind speed, and numerous other variables, the relative proportions of the various circumstances in which flights take place must be assumed to be approximately equal across all subjects, although this has not been verified systematically.

C. Results

1. Absence of the Wing Patch Affects Territorial Interaction Frequency. A total of 18 birds were captured, dyed, and sampled for this study. In addition, 6 birds that were captured but not dyed were available for controls, as they did not differ from the sham controls (two-tailed Mann-Whitney U statistics, all p values > 0.25). Sampling times for each group by breeding phase are presented in Table II.

On seven occasions a bird was recaptured, at which time it underwent a manipulation different from the previous capture. For the analyses, birds appropriate to two groups were placed in the group to which they were chronologically first assigned. This would eliminate the possibility that having been in one condition would affect responses under a second condition. Conveniently, this arrangement placed all birds except one in the group in which they had the most sampling time.

Nine birds in the control group ("control" males) were compared to nine birds with reduced wing patches ("reduced" males) and six birds with covered wing patches ("covered" males). Three birds with enlarged wing patches were analyzed separately (see below). Four reduced birds were unmated; all other birds were mated. 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. Thus there was a large difference between the control group and the experimental groups in the amount of time-in time (Kruskal-Wallis H = 2.796, n = 24, p = 0.004; control birds vs reduced birds: rank-sum z = 2.79, p = 0.004; control birds vs covered birds: z = 2.82, p = 0.002). Behavioral measures were corrected for the amount of time-in time to control for this.

Although there is no evidence that wing length affects territorial interactions (Study 2), to eliminate any such possibility, wing lengths were compared between groups and the differences were not significant: 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, ε = 0.55; Figure 6). Planned, post-hoc, one-tailed, orthogonal, protected rank-sum tests provided evidence that covered birds were different from reduced and control birds (z = 2.59, p = 0.005 and z = 2.36, p = 0.009, respectively). No other significant post-hoc between-group differences were found.

Although territory size measures were not available for all birds, the above analysis was rerun after correcting the dependent measure by territory size. Mean ± SE chases per hour of time-in time per hectare of territory area for control birds (n = 8) was 0.66 ± .300, for reduced birds (n = 9) was 0.85 ± 1.302, and for covered birds (n = 4) was 2.45 ± 0.573 (H = 5.784, n = 21, p = 0.05, ε = 0.46). Post-hoc analyses again revealed only that covered birds were different from both reduced and control birds (z = 1.85, p = 0.03 and z = 2.38, p = 0.009, respectively). Although it appears the results do not change when corrected for territory size, it should be noted that there were important between-group differences in the amount of area that was added to the estimate of territory size from the penultimate to the last focal-animal sample. Specifically, mean ± SE (range) percentage of total measured territory area that was added in the last sample was 4.04 ± 2.5 (0.00 - 16.27) for the control birds, 6.98 ± 0.7 (0.00 - 16.62) for the reduced birds, and 31.65 ± 7.1 (12.71 - 46.56) for the covered birds. Thus, while it seems that the amount of area being added with each successive sample was asymptoting in the reduced and control groups, further samples on the covered birds may have led to larger estimates of territory size for this group. In turn, larger estimates of territory size would produce smaller estimates of chases per hour of time-in time per hectare of territory area, which would run counter to the observed between-group differences. Thus, it is uncertain whether the present results do indeed change when corrected for territory size.

The mean ± SE percentage of bins spent in chases for control birds (n = 9) was 0.16 ± 0.078, for reduced birds (n = 9) was 0.12 ± 0.079, and for covered birds (n = 4) was 0.86 ± 0.520 (H = 3.01, n = 22, p = 0.22). The average duration of chases did not differ across the three groups, although duration scores were not available for some birds. 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. However, only those birds that were involved in chases could have intensity scores, thus reducing the sample size. The mean average intensity score for control birds (n = 5) was 1.39 (range 1 - 1.67), for reduced birds (n = 4) was 1.55 (range 1 - 2), and for covered birds (n = 4) was 1.67 (range 1 - 2) (H = 1.118, n = 13, p = 0.57).

Lastly, 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). In order to control for possible influences of the presence of a mate, the analyses were rerun using only mated birds, and in order to control for breeding phase, the analyses were rerun using only mated birds in the nest building phase of the breeding cycle. Other phases could not be examined individually because of the greatly reduced sample sizes for other breeding phases.

The results did not change when controlling for mating status by removing the four unmated birds from the reduced group. For the mated birds in the reduced group (n = 5), mean ± SE chases per hour of time-in time was 0.73 ± 0.312 ($H = 6.573$, $n = 20$, $p = 0.037$, $\varepsilon = 0.52$). As in the above tests, the sample results are in the predicted direction, and post-hoc tests again showed only that covered birds were different from both reduced and control groups. Mean ± SE percentage of bins spent in chases was 0.22 ± 0.131 ($H = 2.575$, $n = 18$, $p = 0.284$), and mean ± SE average duration of chases (in seconds) was 8.5 ± 2.48 ($H = 1.124$, $n = 17$, $p = 0.570$). Because none of the unmated reduced birds was involved in a territorial interaction, data on average intensity score of chases are unchanged from above. Lastly, mean ± SE bins with song per bins of sampling time was 0.14 ± 0.059 ($H = 0.500$, $n = 20$, $p = 0.78$).

Using only mated birds in the nest building phase in order to control for breeding phase affected two results: both the average duration of the territorial interactions and the percentage of bins spent in chases were 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, $p < 0.01$; Figure 7). Covered birds were different from control birds (z = 2.12, p = 0.017), but no other significant between-group differences were detected post - hoc. Mean ± SE percentage of bins spent in chases for control birds (n = 4) was 0.006 ± 0.01, for reduced birds (n = 3) was 0.313 ± 0.21, and for covered birds (n = 3) was 1.141 ± 0.61 (H = 7.621, n = 10, $p < 0.01$; Figure 8). Post-hoc analyses showed that the control group was significantly different from both the covered and reduced groups (z = 2.12, p = 0.017 for both differences); there was a strong trend for covered birds to be greater than reduced birds: z = 1.53, p = 0.063.

Two other measures with sufficient sample sizes for testing were unchanged by controlling for breeding phase. First, mean ± SE number of chases per hour of time-in time 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, mean ± SE bins with song per bins of sampling time for control birds (n = 4) was 0.31 ± 0.073 (which is somewhat higher than that reported in Logan [1994] for a larger sample of unmanipulated birds in the nest-building phase), 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).

2. Enlarging the Wing Patch Does Not Affect Territorial Interactions. Three unmated males were captured and their wing patches were enlarged. However, two of these had previously been captured and had their wing patches reduced. They were then assigned to the reduced group, which left only one bird in the enlarged wing patch group for the above analyses. To address this, the one enlarged bird was removed from the above ANOVAs and all birds with enlarged wing patches were compared to the control group in separate analyses. Because all of the control birds were mated and all of the enlarged birds were unmated, mating status is a possible confound for each of these results.

Mean ± SE number of chases per hour of time-in time for control birds (n = 10) was 0.49 ± 0.202 and for enlarged birds (n = 3) was 0.81 ± 0.473 (Mann-Whitney U = 11.5, two-tailed p = 0.55; Figure 9). Mean ± SE number of chases per hour of time-in time per hectare of territory area for control birds (n = 9) was 0.62 ± 0.267 and for enlarged birds (n = 2) was 1.71 ± 1.707 (U = 7.5, two-tailed p = 0.72). Mean ± SE average duration of chases (in seconds) for control birds (n = 10) was 7.62 ± 2.478 and for enlarged birds (n = 3) was 11.35 ± 7.378 (U = 12.5, two-tailed p = 0.67). Mean ± SE average intensity score for control birds (n = 6) was 1.44 ± 0.102 and for enlarged birds (n = 2) was 2.75 ± 0.250 (U = 0, two-tailed p = 0.072). Lastly, mean ± SE bins of song per bins of sampling time for control birds (n = 10) was 0.18 ± 0.050 and for enlarged birds (n = 3) was 0.23 ± 0.192 (U = 17, two-tailed p = 0.74). Thus, there is no evidence to support the predicted lessening of the frequency and intensity of territorial interactions among males with enlarged wing patches.

3. Wing Patch Size and Exposure Rate Are Not Negatively Correlated with Territorial Interactions in Unmanipulated Birds. Ten unmanipulated birds were available for these analyses, although not all measures were available for all subjects. The mean ± SD time-in time for these 10 birds was 4.8 ± 1.44 hours. 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), number of chases per hour of time-in time per hectare of territory area (rho = 0.107, n = 7), average intensity score of chases (rho = - 0.616, n = 5), or average duration of chases (rho = 0.390, n = 9). Similarly, perch change frequency was not significantly negatively correlated with number of chases per hour of time-in time (rho = 0.644, n = 10), number of chases per hour of time-in time per hectare of territory area (rho = 0.780, n = 9), average duration of chases (rho = - 0.143, n = 7), or average intensity score of chases (rho = - 0.714, n = 6). Controlling for breeding phase (by only using data for one phase) did not change any of the results. Thus, while experimentally covering (and possibly reducing) the wing patch affected territorial interactions, territorial interactions were not inversely related to wing patch size and frequency of exposure in unmanipulated birds.

D. Conclusions

The above results showed 1) no evidence that either wing patch size or frequency of wing patch exposure is inversely related to territorial interactions within unmanipulated birds, and 2) no evidence that experimentally enlarging the wing patch affects territorial interactions. However, 3) experimentally covering the wing patch increased territorial interactions.

In terms of the status signalling hypothesis, these results are inconclusive. Increased territorial interactions resulting from covering the wing patch suggests that the wing patch may function as a status signal. However, data from Study 2 do not provide evidence that either RHP or PRV are being signalled in any way. Further, even if the apparent lack of signals for RHP and PRV is explained by questioning the validity of the measures or adequacy of the sample sizes involved, the status signalling hypothesis would predict 1) wing patch size would correlate negatively with territorial interactions within unmanipulated birds and 2) enlarging the wing patch should lower territorial interactions. Study 3 showed no evidence to support these predicted relationships, but these results were obtained from small sample sizes.

One alternative explanation for the above results is that the presence of the wing patch is a cue for species recognition in Northern Mockingbirds. On this view, after the wing patch was covered, other mockingbirds did not receive any signal that the area was being defended by a conspecific. They entered the area and were chased out (by the resident with covered patches) in what were scored as territorial interactions. One potential problem with this interpretation is that several other potential cues to species recognition remained intact, such as song, calls, body shape, and other plumage characters such as gray-white dorsoventral contrast, tail stripes, and the two white wing bars across the greater secondary coverts. Male Red-winged Blackbirds (*Agelaius phoeniceus*) can distinguish a mount of a Brewer's blackbird (*Euphagus cyanocephalus*), which is all black, from a mount of a Red-winged Blackbird with blackened epaulettes, which was also entirely black (Hansen & Rohwer 1986). Thus, Red-winged Blackbirds could discern conspecifics from Brewer's Blackbirds based solely on morphological contours and proportions. If male Northern Mockingbirds have similar capabilities, they should have recognized the manipulated males as conspecifics.

CHAPTER III

FEMALE CHOICE BY WING PATCH SIZE

Introduction

A. Observation of Pair Maintenance Problems

During focal-animal behavior sampling of mated males that had been dyed, the behavior of the female could often be readily observed for a large proportion of the sampling time. Field notes on the females' behavior were taken, particularly if her behaviors seemed out of the ordinary. In five cases, field notes on female behavior were available for a period during which her mate was dyed and a period during which her mate was not dyed. These notes suggest the possibility that reducing or covering the males' wing patches had a disruptive effect on the maintenance of the pair bond, which will be termed a pair maintenance problem. Pair maintenance problems generally involved females interacting with males who were not their mate or highly unusual problems with territory defense that suggest the resident female may have been soliciting other males. For example, one of the covered males could not evict another male that would regularly enter the territory and interact with the resident female. Abridged field notes describing the pair maintenance problems are reproduced in Appendix A.

Manipulating plumage patterns has had mixed effects on mate attraction and pair bonds of other species. Color marking is known to disrupt the pair bond of captive Mourning Doves (*Zenaida macroura;* Frankel & Baskett 1963), although this resulted from an extreme color manipulation. In contrast, attraction of females was not hindered by obscuring the black face mask of male Common Yellowthroats (*Geothlypis trichas;* Lewis 1972, described in Butcher & Rohwer 1989) or by bleaching the black coloration to orange in male Bullock's Orioles (*Icterus galbula bullockii*, now *Icterus bullockii;* Butcher 1984, described in Butcher & Rohwer 1989). Data from two studies of Red-winged Blackbirds (*Agelaius phoeniceus*) are equivocal. In one study, fully blackening the red epaulettes of male Red-winged Blackbirds did not prevent the attraction of females, although harem size was not compared to controls (Smith 1972), whereas a second study reported that the same manipulation apparently prevented mate attraction (Peek 1972). Thus the present anecdotal data from mockingbirds are not closely paralleled by any published systematic studies.

Three anecdotal incidents described in Appendix B also suggest the importance of the wing patch in female choice. These involve three unmated birds with enlarged wing patches, and they seem to suggest that enlarging the wing patches prompted visits by females. However, for these observations there is no appropriate control group available and thus the rate of occurrence of these events among normal unmated males is unknown.

If pair maintenance problems do result from covering or reducing the wing patch, as suggested by these field notes, then an alternative explanation for the data presented above can be offered. Specifically, male wing patch size may be signal of male quality on dimensions that are relevant to female mate choice, and thus reducing or covering the wing patch prompts the female to investigate other males. In turn, this leads to territorial fights among the competing males. This hypothesis also explains the anecdotal evidence from enlarging the wing patch: females are approaching the highly attractive large wing patch.

To examine this interpretation, evidence that females prefer males with larger wing patches is needed. Further, this hypothesis would be supported if a basis for such choice can be elucidated, namely a relationship between wing patch size and some aspect of the male that is important to successful reproduction. The purpose of the following studies was to find such evidence 1) in data already collected, 2) in the examination of several new dependent measures added for this study, and 3) through the execution of one new study specifically designed for this purpose.

B. The Role of Color in Mate Choice

When females use plumage patterns in mate choice, males are selected for the extent of the development of their colors. There are numerous avian examples of female preferences for a particular male plumage coloration (Least Auklets *Aethia pusilla*: Jones & Montgomerie 1991; Ring-necked Pheasants *Phasianus colchicus*: Mateos & Carranza 1995; Village Weaverbirds *Ploceus cucullatus*: Collias et al. 1979; Great Snipe *Gallinago media*: Hoglund et al. 1990; American Redstarts *Setophaga ruticilla*: Lemon et al. 1992, Proctor-Gray & Holmes 1981; Darwin's Medium Ground Finches *Geospiza tinnunculus* and Cactus Finches *Geospiza scandens*: Price 1984; Pied Flycatchers *Ficedula hypoleuca*: Jarvi et al. 1987a, Lifjeld & Slagsvold 1988, Slagsvold & Dale 1994; Indigo Buntings *Passerina cyanea*: Payne 1982; Red Jungle Fowl *Gallus gallus*: Zuk et al. 1992; Parasitic Jaegers *Stercorarius parasiticus*: O'Donald 1959; Mallards *Anas platyrhynchos*: Holmberg et al. 1989, Weidmann 1990; Satin Bowerbirds *Ptilonorhynchus violaceus*: Borgia & Collis 1989; Orchard Orioles *Icterus spurius*: Enstrom 1993; White-throated Sparrows *Zonotrichia albicollis*: Kopachena & Falls 1993; Great Tits *Parus major*: Norris 1990a). Such female choice may spur the evolutionary development of both the males' color pattern itself and congruent display behaviors.

Four hypotheses have attempted to explain the observed female preferences for particular male color patterns. Of these, the runaway sexual selection hypothesis (Fisher 1930) is the only one that does not try to explain the expenditure of time and energy for female choice in terms of fitness benefits for the choosy female. Rather, the particular feature of the males's plumage that females prefer is arbitrary, that is, females select those males with the most extreme development of an arbitrarily selected feature that does not necessarily provide fitness benefits to the female or her offspring. Heritability of the feature itself in males and heritability of the preference in females together result in a runaway process which amplifies the feature until other selection pressures counter the effect (Fisher 1930, Kirkpatrick 1982, Harvey and Arnold 1982).

If males vary in the level of their contribution to the viability and quality of the offspring, females should devote some amount of time and energy to an attempt to select the best male. The remaining hypotheses address this by relating female choice for color patterns to benefits for herself or her offspring.

The second hypothesis is that females may be selecting males based on plumage characters that are genetically linked to "good genes," which presumably upon expression in the offspring contribute to the development of traits that increase the fitness of the offspring (Zahavi 1975; Hamilton

& Zuk 1982). If plumage color signals genetic quality, females can provide their offspring with high-quality genetic material by selecting the appropriately colored male. A third and related hypothesis is that color patterns may indicate genotype. Specifically, there may be particular genetic loci at which heterozygosity or homozygosity is beneficial; color patches may indicate genotype at these loci and allow for assortative or disassortative mating (Butcher & Rohwer 1989). Also, color patterns that indicate genotype may also be used to avoid extreme inbreeding or outbreeding (Bateson 1983; Butcher & Rohwer 1989).

While the first three hypotheses suggest female choice for attributes that affect the fitness of the offspring, a fourth hypothesis suggests that females may choose those male traits that provide direct fitness benefits to the female. Male plumage has been shown to correlate with male traits that could provide proximate benefits for the female (testes size: Møller & Erritzoe 1988; parental quality: Sundberg & Larsson 1994; age: Ralph & Pearson 1971; nest defense effort: Eckert & Weatherhead 1987b; age, size, and territory quality: Jarvi et al. 1987a; sexual behavior: Møller 1990). In species with high levels of paternal care, variation in male parental care increases variation in reproductive success (Price 1984) and therefore females are likely to benefit by selecting males that provide the best care (Lyon et al. 1987, Sasvari 1986, Mock & Fujioka 1990; Hoelzer 1989). Further, an accurate signal of the quality of paternal care would reduce the amount of time and energy committed to mate selection, allowing the redistribution of these resources toward actual reproduction (Slagsvold et al. 1988).

Female choice for a particular color pattern and a relationship between the color pattern and paternal care have been suggested in several species. In House Finches (*Carpodacus mexicanus*), a species whose red coloration is dependent on dietary intake of carotenoids during the molt, Hill (1990, 1991) showed that females paired more quickly and frequently with males artificially brightened by food supplements or dyes. Further, the naturally brightest males had the highest frequency of feeding the mate and offspring. Norris (1990a) provided evidence that female great tits (*Parus major*) preferred males with the widest black breast stripe, and later (1990b) showed that males with wider stripes showed higher nest attentiveness and fledged heavier offspring, which tend to survive better in this species. In Pied Flycatchers (*Ficedula hypoleuca*), females initially preferred to settle with black males over brown males, and the likelihood of mate retention after a nest loss was higher for blacker males; nestlings of black males have a larger body weight on average than those of brown males (Lifjeld & Slagsvold 1988; Jarvi et al. 1987a). Within a small Galapagos population of Darwin's Medium Ground Finches (*Geospiza fortis*), females preferred the blackest males, which were also the oldest males.

Correlations between extent of adult plumage and 1) nestling mass at eight days, 2) fledgling success, and 3) proportion of the fledglings fed by the male (which prompts laying of a second brood if high) were all positive but small and nonsignificant (Price 1984). Lastly, captive female European Kestrels (*Falco tinnunculus*) preferred to approach the brighter male of a pair; in the wild, brighter males spent more time hunting and their mates produced more offspring (Palokangas et al. 1994).

C. Intersexual Choice Based on Wing Patch Size in Mockingbirds

Some data already presented suggest female choice mechanisms may be operating on male mockingbirds' wing patch size. First, males have larger wing patches (from Study 1), which may result from long-term female choice. Second, the wing patch is often displayed during song via the jump display, and the bulk of the data on mockingbird song indicates that song functions in mate attraction (see review in Derrickson & Breitwisch 1992). Third, anecdotal evidence (see the Appendices) suggests that mated males with reduced or covered wing patches suffered pair maintenance problems, while unmated males with enlarged wing patches were visited by females.

Available data can be used to assess two hypotheses consistent with the use of wing patch size in mate choice by female mockingbirds. First, if females prefer larger wing patches, those males left unmated should have smaller wing patches than mated males (Study 4). Second, if males with reduced or covered wing patches are having pair maintenance problems, this may be reflected by changes in intersexual interactions within the mated pair (Study 5).

Methods and Results

A. Study 4: Unmated versus Mated Males' Wing Patch Sizes

To determine mating status, an observer spent 5 - 15 minutes in each territory three times per week throughout the breeding season. Individual males were considered mated if on at least 80% of these visits a second bird was sighted in the territory and remained there for the duration of the visit without being chased out by the resident male. If no second bird was detected in at least 80% of the visits, the bird was considered unmated. Ambiguous cases were rare; in virtually all cases there was other supporting evidence for the determination of mating status, such as the presence of active nests and offspring in the mated birds' territories. If mating status changed during the breeding season, the bird was not used in this analysis.

Mean ± SE wing patch size for mated males ($n = 16$) was 558.74 ± 6.89 (range 522.9 - 597.1) and for unmated males ($n = 5$) was 528.02 ± 10.22 (range 499.9 - 559.0); this difference was significant ($t = 2.25$, $df = 19$, two-tailed $p < 0.05$, $r_{PB} = 0.46$; Figure 10).

Because it is possible that the smallest wing patches generally belong to the youngest males, these data could be confounded by age. Thus, females may not be selecting males on the basis of wing patch size, but on other, perhaps behavioral, signals of age, which happen to correlate with wing patch size. Because adult-plumaged mockingbirds cannot be reliably aged either in the field or in the hand, the effect of age cannot be assessed.

B. Study 5: Changes in Intersexual Interactions as a Result of Dyeing

For many of the birds in the dyeing study, the exchange of hews was the only aspect of within-pair intersexual interactions that was recorded. After some observations of pair maintenance problems, 13 measures of within-pair male-female interactions were added. Sample sizes are small for these added variables, however, because 1) the variables were added mid-study and 2) levels of intersexual interactions, including females' response to their mates' auditory signals, fluctuate across breeding phases (Logan 1994; Donaghey & Logan

1995), necessitating the use of a common breeding phase and the elimination of birds sampled exclusively in other phases.

The following measures were added to assess the effect of the dyeing manipulation on within-pair intersexual interactions. For these measures, an "encounter" is defined as a mated pair perched within 3m of each other and a "follow" is defined as one bird flying in the same direction as the mate flew within three 15-second bins of the mate's take-off.

1) The number of encounters per hour of time-in time.
2) The number of times the male approached the female to within 3m per hour of time-in time.
3) The number of times the female approached the male to within 3m per hour of time-in time.
4) The number of 15-second bins spent within 1m of each other divided by the total number of bins of time-in time.
5) The number of 15-second bins spent within 1 - 3m of each other divided by the total number of bins of time-in time.
6) The number of 15-second bins spent within 3m of each other divided by the total number of bins of time-in time.
7) The average number of 15-second bins spent in an encounter.
8) The number of times the male departed (ending the encounter) per hour of time-in time.

9) The number of times the female departed (ending the encounter) per hour of time-in time.
10) The number of follows per hour of time-in time.
11) The number of male-follows-female per hour of time-in time.
12) The number of female-follows-male per hour of time-in time.
13) The percentage of interactions accompanied by hew exchanges.

Considering those birds for which these new measures were available, more sampling time was available for the "nestlings present" phase than other breeding phases. During this phase, both the male and female are engaged in feeding and defending the nestlings. For most of these added variables it is difficult to make predictions about the direction of the change that the manipulation may cause. However, if females use wing patch size in mate choice, females should ignore or avoid males with small wing patches. Thus, if a male's wing patches are experimentally reduced or covered, then 1) female approaches should decrease, 2) female departures should increase, 3) encounter duration should decrease, and 4) female-follows-male should decrease.

The exchange of hews was also recorded for a considerable number of birds in the nest building phase, and thus this variable is examined for this phase as well. Hew exchanges are relatively low during nest building and high when nestlings are present (Logan 1994) and thus changes in this variable due to the manipulation will be more easily detected in one direction, even though changes in either direction would be of interest.

The results of the nonparametric ANOVAs are presented in Table III. Despite the small sample size, results for the control group are very similar to those reported in Logan (1994) for a larger sample of unmanipulated pairs. No statistically significant group differences were found. The results do not change if the reduced and covered birds are combined into a "manipulated" group and compared to controls using Mann-Whitney U statistics. Thus, there is no evidence to suggest that the experimental manipulations changed male-female interactions.

C. Study 6: The Relationship between Nest Defense and Wing Patch Size in Males

Because male mockingbirds contribute extensively to the care of the offspring, females may select males according to their level of paternal care. As discussed above, a signal of paternal quality would economize the selection process (Slagsvold et al. 1988). To this end, wing patch size was compared between males that scored high versus low on a measure of paternal care, the response to a potential nest predator. The American Crow (*Corvus brachyrhynchos*) was chosen as a predator model because it is known to be a predator of mockingbird eggs and nestlings, but is not known to prey upon adult mockingbirds (Derrickson & Breitwisch 1992). Thus, the response to a crow should reflect entirely nest defense and not be influenced by a requirement for self defense.

A crow specimen was mounted in a perching posture and fastened atop a 1m stand made of 4cm x 8cm wood. Having covered the crow with a bag, two observers entered the territory and placed the stand in the open approximately 8m from a point on the ground directly beneath the nest. All nests were between 1.5 and 4m from the ground, and thus the linear distance from the crow to the nest was at least 8.1m but not more than 8.9m. Although the observers did not use blinds, at the study site mockingbirds rarely respond to humans as potential nest predators when they are more than 10m away from the nest (personal observation), presumably because of the frequency of passersby on the campus. The crow was uncovered and the observers moved to about 15m from the nest. Responses were recorded for 45 seconds; this was immediately repeated three more times, with the crow moved 2m closer to the nest each time. Because the response of other species may influence the focal animal's response, the number of heterospecifics that approached the mount within 3m or produced alarm calls during the presentation was recorded. In addition, four different responses of the resident male mockingbird were recorded: 1) number of "hew" vocalizations, 2) number of "chat" vocalizations, 3) number of swoops, defined as U-shaped flight patterns that troughed within 2m of the mount, and 4) number of wing flashes (Sutton 1946, Allen 1947, Brackbill 1951, Eifrig 1948).

After the four presentations, the nest was examined to ensure that the nestlings were still present. Close visual inspection of the nest was sometimes possible, and in most other cases nests could at least be reached by hand or inspected with a long-handled mirror. Based on the number of eggs present during the incubation period (which places an upper limit on the possible number of nestlings), and inspections of the nest during the nestling period, all nests used for this study (n = 14) had two or three nestlings, although in many cases the exact number could not be determined. About one-half of the nests used were tracked closely enough to determine exact post-hatching ages of the nestlings; in other cases, the nestlings' ages could be approximated through visual inspection. Based on these observations, all nestling ages during testing were known to be between one and five days post-hatching.

On numerous occasions a score of zero was recorded for a particular response at one of the four crow positions. Further, the total number of all responses summed across all four crow positions, called a total response score, had many scores of zero. Thus, correlating the responses to wing patch size is inappropriate because the correlation coefficient would be inflated (Siegel 1956), increasing the risk of a Type I error. However, an examination of the raw data revealed that the subjects could easily be separated into two groups based on intensity of response and speed of response. Six birds that each had a total response score of zero, and one bird with a total response score of one, were placed in a "low response" group while seven others were placed in a "high response" group (mean ± SD number of responses in this group was 28.14 ± 17.60, range 9 - 62). A "quick response" group was formed from six birds that initially responded to the crow during the first 45s (when the crow was 8m away). Eight birds that initially responded during the second, third, or fourth presentation or did not respond at all were placed in a "slow response" group.

The number of heterospecifics responding was not significantly different between high and low responders. Mean ± SE of number of heterospecifics responding with low responders was 0.71 ± 0.756 (range 0 - 2) and with high responders was 0.29 ± 0.488 (range 0 - 1) ($U = 16.5$, two-tailed $p = 0.244$). The number of heterospecifics responding was also not different between quick and slow responders. Mean ± SE of number of heterospecifics responding with quick responders was 0.50 ± 0.548 (range 0 - 1) and with slow responders was 0.50 ± 0.756 (range 0 - 2) ($U = 22.5$, two-tailed $p = 0.83$). Thus there is no evidence to suggest that the level of response from heterospecifics should be controlled in further analyses.

Assessment of wing patch size in these birds indicated that mean ± SE wing patch size for the high response group was 570.0 ± 8.24, and for the low response group was 534.2 ± 12.61 ($t = 2.376$, $df = 12$, two-tailed $p < 0.05$, $r^2 = 0.32$; Figure 11). Exact nestling ages were known for seven of the nests used. Among the high response birds were two nests with one-day-old nestlings, one nest with two-day-old nestlings, and one nest with three-day-old nestlings. Among the low response birds was one nest with one-day-old nestlings and two nests with five-day-old nestlings. However, because the exact nestling ages for the other nests were not known, it does remain possible that both 1) nest defense varies across nestling ages and 2) the two groups were biased toward different nestling ages.

There was no difference in wing patch size between quick and slow responders: mean ± SE wing patch size for quick responders was 555.8 ± 25.02, and for slow responders was 549.3 ± 39.17 ($t = 0.355$, $df = 12$, two-tailed $p = 0.729$).

Results presented earlier showed a fairly high positive correlation between wing patch size and wing length (Study 1). Interestingly, however, there was no significant difference in wing length between high and low responders despite the difference in wing patch size between these two groups. Mean ± SE wing length for high responders was 111.5 ± 0.60 and for low responders was 113.8 ± 1.68 ($t = 1.313$, df = 12, two-tailed $p = 0.214$, $r^2 = 0.13$). Indeed, when considered from the perspective of the information available to the female in a pre-breeding assessment of a male, 32% of the variability in the level of response to a potential nest predator (high or low) is explained by wing patch size, compared to only 13% for wing length. Further, the sample results for wing patch size and wing length are in the opposite direction.

As with wing patch size, there was no difference in wing length between quick and slow responders. Mean ± SE wing patch size for quick responders was 112.8 ± 1.83 and for slow responders was 112.5 ± 0.97 ($t = 0.142$, df = 12, two-tailed $p = 0.89$).

Birds in the high response group had larger wing patches than birds in the low response group. This might provide a basis for a female preference for males with larger wing patches: selecting a male with large wing patches increases the chances of selecting a male with a high response to a potential nest predator. This information was not available from a direct assessment of wing length.

Conclusions

These studies were undertaken to examine the possibility that female mockingbirds use wing patch size in mate choice.

Consistent with this hypothesis, mated males had larger wing patches than unmated males. However, the potential age confound calls these data into question, and thus they should only cautiously be interpreted as supportive of the hypothesis. There was no evidence to suggest that the experimental manipulations changed any of the measured male-female interactions. These negative results are surprising given the anecdotal observations of pair maintenance problems in the reduced and covered males. If reducing or covering the wing patch reduces or removes a stimulus that is attractive to females, it would not be surprising to see large effects on many of the recorded intersexual interactions. However, it is possible that many other male-female signals remained intact and this reduced the impact of manipulating the wing patch.

The nest defense study, while not directly addressing the male quality hypothesis, demonstrates the presence of a potential basis for a female preference for males with larger wing patches. Because males that had a high response to a potential nest predator had larger wing patches than males with a very low response or no response, females may use patch size to assess an important dimension of male parental care. Selecting a male with large wing patches would increase the level of nest defense provided for the offspring, which in turn would increase the female's fitness because the offspring are more likely to survive (Breitwisch 1988). The existence of a female preference for larger wing patches is rendered more plausible given a positive relationship between wing patch size and the level of a behavior that may increase offspring survivorship.

CHAPTER IV

GENERAL DISCUSSION

The Status Signalling Hypothesis

As detailed in the Introduction, mockingbirds could certainly benefit from signals of status, which allow for the resolution of contests over resources without escalation to overt aggression. Indeed, these signals probably exist, given that territorial intrusions and chases are observed frequently but escalated fights only rarely. However, the bulk of the evidence indicates that the white wing patch does not serve a status signalling function.

Although covering the wing patch increased territorial interactions (Study 3), this is the only result that is in line with the hypothesis that the wing patch is used as a status signal. In order to view the other results as consistent with this hypothesis, they would each have to be considered either Type II errors or otherwise invalid. Specifically, one would have to conclude that both the lack of a correlation between wing length and territorial interactions and the lack of a difference in territorial interactions between the nest building and incubation phases (Study 2) resulted from either a small sample size or a mismeasure of true RHP and true PRV. Likewise, small sample sizes would be blamed for the failure to gain support for the predictions that 1) wing patch size would negatively correlate with territorial interactions in unmanipulated birds (Study 3), 2) frequency of exposure of the wing patch would negatively correlate with territorial interactions in unmanipulated birds, and 3) enlarging the wing patch would lower territorial interactions (Study 3). The remaining results are not directly addressed by this hypothesis. Though these possibilities cannot be ruled out, it is probably worthwhile to seek alternative explanations.

One alternative is that, for male mockingbirds, wing patch size is a status signal, but RHP is determined by the male's overall level of territorial aggression (Studd & Robertson 1985) rather than body size. That is, the size of the wing patch is positively correlated with the likelihood of an aggressive response to a territorial intrusion and the intensity of such a response. Note that wing patch size would not signal minute-to-minute changes in aggressive motivation; rather it signals a pervasive, general level of aggression used in territorial defense from conspecific intruders. With this system, variability in males' wing patch sizes reflects variability in their territorial defense strategy. Those males with larger wing patches and higher territorial aggression are able to defend high quality territories but must deal with increased intrusion pressure from conspecifics attempting to access the resources available on the territory. Conversely, those males with smaller wing patches and lower territorial aggression have poorer territories but reduced competition. This will be called the "aggressive motivation" hypothesis, after Studd & Robertson (1985).

Before addressing the present results, it should be recognized that this hypothesis makes assumptions which, although reasonable for mockingbirds given what is known of their natural history, have not actually been confirmed for mockingbirds. First, it assumes that there is variability in overall levels of territorial aggression. Second, it assumes that those birds with the highest levels of territorial aggression are defending the highest quality territories. Third, it assumes that intrusion pressure from conspecifics positively correlates with territory quality.

Given these assumptions, this hypothesis would address the results in the following way. There was no evidence of a signal for RHP (Study 2) because RHP was mismeasured: RHP is more strongly related to levels of territorial aggression than to body size. Also, Study 2 did not show evidence for a signal of PRV because level of territorial aggression remained relatively constant across the nest building and incubation phases, which kept territorial interactions fairly constant despite any changes in PRV that may have been occurring.

Covering or reducing the wing patch leads to territorial interactions (Study 3) because this results in a bird that is defending a higher quality territory than his plumage badge indicates he is able to defend; thus males intrude into the territory and possibly initiate the pair maintenance problems. There was no correlation between wing patch size and territorial intrusions in unmanipulated birds (Study 3) because those with smaller patches have poorer territories that have fewer incentives for intrusions (and presumably fewer intrusions), while those with large patches have much to attract intruders but their signals of high aggressive motivation function to deter intruders. Thus, levels of territorial interactions remain relatively constant across various wing patch sizes. Unmated males have smaller wing patches than mated males (Study 4) because those males with the smallest patches cannot adequately defend sufficient resources for reproduction and, further, this lack of resources hinders their ability to attract a female. The covering and reducing manipulations did not affect intersexual interactions (Study 5) because the wing patch signal is primarily directed at other males; females do not make use of the information and thus intrapair interactions are not affected by manipulating the signal. Responses to the mounted crow (Study 6) can be considered anti-predator aggression rather than territorial aggression; because there is no a *priori* reason to suspect that levels of anti-predator aggression are necessarily related to levels of territorial aggression in this species, these results do not really speak to the hypothesis. Similarly, male-female differences in wing patch size (Study 1) would not be directly addressed by this hypothesis.

There are some difficulties in interpreting the present results with the aggressive motivation hypothesis. First, this hypothesis would predict that enlarging the wing patch should lower territorial interactions, which was not observed. However, the comparison was confounded (see Study 3), and the sample sizes used ($n = 10$ control and $n = 3$ enlarged) make a Type II error a reasonable possibility. Second, it seems unlikely that females would not use available information about the male's level of territorial aggression, especially if the signalled value changed dramatically. If females do use this information, then the manipulations should have produced changes in intersexual interactions.

Future tests of this hypothesis should begin by demonstrating that the assumptions outlined above actually hold for mockingbirds, and that wing patch size actually correlates with territorial aggressive motivation. Experimental studies could then evaluate how territorial interactions change with changes in the signal and changes in the resources being defended. Also, it becomes more difficult to assess the status signalling hypothesis when there is little information about the status of the intruders. Status signalling hypothesis predicts that intruders would have a higher status than the territory defender. However, due to the swerving flight patterns and fleeting nature of most territorial interactions between mockingbirds, it is difficult to quantify the relative status of the intruders compared to the territory defenders. Lacking quantification of intruders' wing patch sizes, it remains unknown how the results may have been affected by the status of each subjects' contingent of intruders.

The Species Recognition Hypothesis

Given that 1) mockingbirds defend all-purpose territories year round, 2) intruders onto the territory are aggressively chased, 3) there are other avian species that are similar to mockingbirds in size, body contours, and/or color, and 4) mockingbirds typically do not defend heterospecific territories (Derrickson and Breitwisch 1992), conspicuous signals of species recognition could be beneficial to mockingbirds because 1) they would allow for fewer aggressive interactions with conspecifics while investigating areas for territory establishment and 2) would lower the frequency of aggressive interactions with heterospecifics misidentified as conspecifics. The species recognition hypothesis predicts that males use the presence of a wing patch to signal species identity to other males such that potential intruders can detect that an area is being defended by a conspecific. The pattern of results seen here can be addressed by this hypothesis in the following way.

Covering the wing patch leads to territorial interactions (Study 3) because potential intruders do not receive a signal that the area is being defended by a conspecific. Reducing the wing patches did not dramatically increase territorial interactions (Study 3) because a signal of species was still present, although reduced. Enlarging the wing patch did not decrease territorial interactions (Study 3) because merely the presence of the wing patch signals specific identity; size of the signal is not related to this function. Territorial interactions did not increase as wing patch size decreased in unmanipulated birds (Study 3) because all unmanipulated birds had intact signals for species identification.

The remaining results are not addressed by the species recognition hypothesis. Specifically, although no evidence for a signal of RHP or PRV was found (Study 2), this hypothesis predicts that the wing patch is signalling something other than RHP and PRV. This hypothesis also states that it is only the presence of the wing patch that is important for species recognition, and thus predictions are not made about the effects of increasing exposure of the wing patch on territorial interactions (Study 3). Unmated males may have smaller patches than mated males (Study 4), but all males can be recognized as Northern Mockingbirds because they all have wing patches present. In other words, it is the presence versus absence of the wing patch that signals species, although variability in other aspects of the patch may contain additional information. Lastly, the responses to the mounted crow (Study 6) would not be a test of the species recognition hypothesis as described above. Future studies could examine the several potential recipients of a signal for mockingbird species identity. For example, females may use the same signal as males, as suggested above. Closely related heterospecifics would also be expected to respond in predictable ways to the presence of a wing patch on a bird that has the other characteristics of a Mimid. Also, given the pugnacity of mockingbird nest defense, predators of eggs and nestlings may also respond in predictable ways to the presence of a wing patch if they are able to associate wing patches with competent and aggressive nest defense.

The Male Quality Hypothesis

There has been some controversy over the extent to which sexual selection is operating in mockingbirds (Howard 1974; Derrickson & Breitwisch 1992). There is a male-biased sex ratio in this species (1.1:1 for one measured population [Breitwisch 1989] and likely to be higher in the study population [personal observation; C. Logan, personal communication, 1995]). Therefore, most or all females are able to choose from among two or more males. Further, female choice in mockingbirds has been inferred through observations of mate switching (Logan 1991) and sequential polyandry (Fulk et al. 1987). However, it is believed that sexual selection often results in a more extreme sexual dimorphism in plumage pattern than is observed in mockingbirds. Also, males provide extensive paternal care in this species (Sprunt 1964, Breitwisch 1988); assuming that there is variability across males in the quality of paternal care provided (there is some evidence for this from Study 6), there may be competition among females for access to those males that provide the best care. Such female-female competition for the best males may, to some extent, offset the effects of male-male competition for access to females. If this is the case, the effects of long-term sexual selection on males may not be as evident in mockingbirds as they are in species that provide less paternal care.

The male quality hypothesis predicts that wing patch size is positively related to male quality and thus is used by females in mate selection. The extent to which this hypothesis explains the present data set is interesting given the conflicting thoughts on sexual selection in this species. Therefore, the results will be reviewed in light of this hypothesis.

The observation that male wing patch size is greater than female wing patch size (Study 1) is predicted by the male quality hypothesis: long-term female choice for larger wing patches would produce a sexual dimorphism in wing patch size. By covering or reducing the wing patch (Study 3), the male is signalling his very low quality, which may prompt the female to investigate nearby males. In turn, this leads to aggressive encounters between the competing males that are scored as territorial interactions. The male quality hypothesis is congruent with the anecdotal evidence that enlarging the wing patch prompted investigations by females: females should be attracted to wing patches that signal high male quality. If wing patch size is a signal of male quality, then males with smaller wing patches are more likely to be left unmated. This is the result observed in Study 4. Even if it is truly the case that unmated males are generally younger, if age affects *both* wing patch size *and* quality as a mate (perhaps through experience), then wing patch size would still be signalling at least one aspect of male quality. Lastly, results from the crow study suggest a basis for the use of the wing patch in female mate selection. Because a male's level of nest defense is positively related to his wing patch size, wing patch size could be used as a signal of at least one aspect of paternal quality (aggressive defense of the offspring). Thus it may affect the process of mate selection in females, especially given the high levels of parental care that males provide. The variance in level of nest defense unexplained by wing patch size may be related to other aspects of paternal care or to various facets of overall quality.

The remaining results are not addressed by the male quality hypothesis. Although no evidence for a signal of RHP or PRV was found (Study 2), this hypothesis predicts that the wing patch is signalling something other than RHP and PRV. Also, under this hypothesis, territorial interactions are not necessarily affected by changes in exposure of the wing patch or increases in its size (natural or experimental).

There are two problems with using the male quality hypothesis to explain the present results. First, why did females stay with mates that had been reduced or covered? It may be that females ultimately retain the manipulated male as a mate because 1) most other males encountered are already mated and, except in rare cases of extremely high quality males, full commitment from a lower quality male may be better than half commitment from a higher quality male (who would be made bigamous if the female mated with him), 2) neighboring females resist investigation into their mates, and/or 3) the wing patch is only a part of an array of cues for overall male quality, and the effect of the manipulation is offset by other cues signalling male quality. A corollary to this last suggestion would be that the wing patch is used in the early stages of mate acquisition, such as the initial attraction of a mate, but becomes progressively less important as other, possibly more accurate assessments of male quality are made by the female.

Second, intersexual interactions should be measurably altered if the female is receiving a signal that her mate is of poor quality. This would be especially true if the female adjusts her behavior, such as increasing parental care in an attempting to compensate for the male's poor quality or even searching for a more suitable mate. Although this hypothesis has difficulty in explaining the lack of an effect of the dyeing manipulation on intersexual interactions, there are, however, reasons to question whether the male quality hypothesis should be considered weakened based on this result. First, the sample sizes are very small and thus the risk of a Type II error is large. If the effects of the manipulation are smaller than expected, they may not be detectable with the sample sizes used. There are some large between-group differences in sample means which, should they become significant at a larger sample size, would conform with the male quality hypothesis. However, each of these is subject to interpretation and there are certainly many other sample results that would not be so compatible should they be statistically significant. Second, only one phase of the breeding cycle, the "nestlings present" phase, is analyzed in depth. Logan (1994) has shown that, when nestlings are present, female approaches are low relative to males, female departures are high relative to males, and female follows are low relative to the nest building period. Thus, changes due to the manipulation may be hampered by floor or ceiling effects. Also, females may be much less likely to leave when offspring are present. Analyses from other breeding phases may have generated different results. Third, if the females' only major response to the manipulation is investigating other males, and this response occurs infrequently, then these occasions may not greatly affect overall rates of the recorded aspects of intersexual interactions. Lastly, there are many aspects of intrapair interactions that were not measured, such as orientation when perched together, closeness of following, direction and frequency of flights with regard to the mates position and orientation, et cetera. It is possible that effects of the manipulation could turn up in subtle aspects of intrapair communication that are not easily observed or measured. Indeed, it is difficult to imagine the existence of a pair maintenance problem that is not accompanied by at least a some changes in intrapair interactions. Given these concerns and the potentially useful role these results could play in evaluating the male quality hypothesis, it is probably best to await confirmation of the present results from a more thorough investigation before considering the male quality hypothesis in light of this outcome.

Other future investigations could attempt to establish that females would actually choose males with larger wing patches given a choice. This could be accomplished with laboratory choice experiments, or in the field with artificially enlarged wing patches and controls. Also, a large amount of variation in wing patch size was not explained by level of nest defense. It would be important to know if other aspects of paternal care, such as quality of food provisioning or nest construction, are being signalled by the wing patch. This could be done by quantifying male traits and correlating them with wing patch size.

The Sex Recognition Hypothesis

Given that mockingbirds appear to be otherwise sexually monomorphic, the sex difference in wing patch size (Study 1) may be an important cue in sex recognition. This hypothesis can explain two other results presented. First, several nonsignificant trends and one significant difference in Study 3 suggest that reducing the wing patch may lead to an increase in territorial interactions. Because reducing the wing patch gives the male a female-sized wing patch, other males may then respond to the reduced wing patch with approach (as they would a genuine female). Presumably this would elicit an aggressive territorial response from the reduced male, which would be scored as a territorial interaction. Second, mated males have larger wing patches than unmated males (Study 4) because those males with the smallest wing patches can be mistaken for females. Because females are intrasexually territorial, males with small patches may actually elicit aggression from females, which obviously would hamper the ability to acquire a mate.

There are some problems with the sex recognition hypothesis. First, the results of Study 1 indicated that there was a great deal of overlap between the sexes in wing patch size. If 1) males with patches in the females' size range are less able to breed than males with larger patches, and 2) wing patch size is heritable, then selection processes should have eliminated most of the overlap in wing patch size. Second, most of the results in Study 3 indicated that the covering manipulation led to more territorial interactions than the reduced manipulation. The sex recognition hypothesis would predict that reducing the wing patch should have the greatest consequences. Third, according to the sex recognition hypothesis, a reduction in male wing patch size should produce drastic changes in intersexual interactions. This was not found in Study 5, but problems with the data set have been discussed above.

Final Notes and Recommendations

All three interpretations have their merits and drawbacks in terms of results that are explained, not addressed, or explained only by questioning the methods involved. Given what is already known about mockingbirds, no one hypothesis stands out as entirely better able to interpret the entire set of data presented here. The aggressive motivation hypothesis certainly has the most untested assumptions. Most of these are reasonable, but they still should be tested to ensure that they apply to mockingbirds. The species recognition hypothesis is adequate to explain several results, but because this hypothesis only deals with the presence of the wing patch, several other results are not directly addressed by this hypothesis. Further, the nature of the wing patch and the pattern of results presented here suggest that the wing patch may contain information in addition to species recognition. For example, wing patch size is continuously variable, and experimentally reducing the size of it may increase territorial interactions. This suggests that, although its presence may signal species identity, size of the wing patch may provide additional information. Thus, although the data support the use of the wing patch as a signal of species identity, it is inadvisable to consider this the sole function of the wing patch. The male quality hypothesis is also capable of explaining several results while not addressing other results. One advantage of this hypothesis is that it explains results that one or both of the other hypotheses either do not address or have difficulty explaining. For example, it is the only hypothesis that directly addresses and explains the sexual dimorphism in wing patch size, and it is most compatible with the anecdotal evidence that females investigate males with larger wing patches. Also, data from the crow presentations, which showed more aggressive nest defense from males with larger wing patches, provide a basis for female choice for larger wing patches.

It should be noted that the status signalling, species recognition, and male quality hypotheses are certainly not mutually exclusive; rather, they could be considered complementary. The presence (versus absence) of the wing patch may be a cue to species recognition, while males use the size of the wing patch to signal their aggressive motivation to *both* other males (for territory defense) and to females (for mate acquisition and reproduction).

Moving beyond the wing patch, many other features of the mockingbirds color pattern have not been investigated to discern their function. The gray-white dorsoventral contrast has been addressed (Justice 1995), but the white wing bars, white tail stripes, black featherless areas, brown iris, and black eye line all remain uninvestigated, despite a plethora of hypotheses that predict their functions.

The study of mockingbirds, and particularly sexual selection in mockingbirds, has been dominated by an interest in their acoustical communication because of their elaborate songs. The present research indicates that mockingbirds also have a well-developed system of visual signals as well, which should be considered in future studies of their life history and their system of intraspecific communication.

BIBLIOGRAPHY

Allen, F. H. (1947) The mockingbird's wing-flashing. Wilson Bulletin 59: 71-73.

Altmann, J. (1974) Observational study of behavior: sampling methods. Behaviour 49:227-267.

American Ornithologists' Union (1983) Check-list of North American Birds, 6th Edition. American ornithologists' Union: Washington, D.C.

Andersson, S., & Ahlund, M. (1991) Hunger affects dominance among strangers in house sparrows. Animal Behaviour 41: 895-897.

Archer, J. (1988) The Behavioral Biology of Aggression. New York, NY: Cambridge University Press.

Baldwin, S. P., Oberholser, H. C., & Worley, L. G. (1931) Measurements of birds. Scientific Publications of the Cleveland Museum of Natural History 2:1-126.

Balph, M. H., Balph, D. F., & Romesburg, H. C. (1979) Social status signaling in winter flocking birds: an examination of a current hypothesis. The Auk 96: 78-93.

Bateson, P. (1983) Optimal outbreeding. pp. 257-277 *In* Mate Choice (P. Bateson, ed.). Cambridge: Cambridge University Press.

Borgia, G. & Collis, K. (1989) Female choice for parasite-free male satin bowerbirds and the evolution of bright male plumage. Behavioral Ecology and Sociobiology 25: 445-453.

Brackbill, H. (1951) Wing-flashing by male mockingbirds. Wilson Bulletin 63:204-206.

Breiehagen, T., & Sætre, G. (1992) Territorial defence and plumage colour in pied flycatchers, *Ficedula hypoleuca*. Animal Behaviour 44: 987-989.

Breitwisch, R. (1988) Sex differences in defence of eggs and nestlings by Northern Mockingbirds, *Mimus polyglottos*. Animal Behaviour 36: 62-72.

Breitwisch, R. (1989) Mortality patterns, sex ratios, and parental investment in monogamous birds. Current Ornithology 6: 1-50.

Breitwisch, R. & Whitesides, G. H. (1987) Directionality of singing and nonsinging behavior of mated and unmated Northern Mockingbirds, *Mimus polyglottos*. Animal Behaviour 35: 331-339.

Breitwisch, R., Diaz, M., Gottlieb, N., Lee, R., Zaias, J. (1986) Defense of fall territories by mated and unmated Northern Mockingbirds in southern Florida. Journal of Field Ornithology 57: 16-21.

Burtt, E. H. (1979) The behavioral significance of color. New York, NY: Garland STPM Press.

Burtt, E. H. (1986) An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood warblers. Ornithological Monographs 38:1-126.

Butcher, G. S. (1984) Sexual color dimorphism in orioles (the Genus *Icterus*): Tests of communication hypotheses. Ph.D. Dissertation: University of Washington-Seattle.

Butcher, G. S., & Rohwer, S. (1989) The evolution of conspicuous and distinctive coloration for communication in birds. Current Ornithology 6: 51-108.

Chen, D., Collins, J. S., & Goldsmith, T. H. (1984) The ultraviolet receptor of bird retinas. Science 225:337-340.

Collias, E. C., Collias, N. E., Jacobs, C. H., McAlary, F., & Fujimoto, J. T. (1979) Experimental evidence for facilitation of pair formation by bright color in weaverbirds. Condor 81: 91-93.

Derrickson, K. C., and Breitwisch, R. 1992. Northern Mockingbird. *In* The Birds of North America. No. 7. *Edited by* A. Poole, P. Stettenheim, and F. Gill. The American Ornithologists' Union, Washington, D.C..

Donaghey, B. & Logan, C. A. (1995) Individual recognition by song in free-living male and female Northern Mockingbirds. Unpublished manuscript.

Drickamer, L. C. & Vessey, S. H. (1986) Animal Behavior: Concepts, Processes, & Methods. Belmont, CA: Wadsworth.

Dugatkin, L. A., & Biederman, L. (1991) Balancing asymmetries in resource holding power and resource value in the pumpkinseed sunfish. Animal Behaviour 42: 691-692.

Dusenbery, D. B. (1992) Sensory Ecology. New York, NY: W. H. Freeman and Company.

Eckert, C. G. & Weatherhead, P. J. (1987a) Owners, floaters, and competitive asymmetries among territorial red-winged blackbirds. Animal Behaviour 35: 1317-1323.

Eckert, C. G. & Weatherhead, P. J. (1987b) Male characteristics, parental care and the study of mate choice in the red-winged blackbird (Agelaius phoeniceus). Behavioral Ecology and Sociobiology 20: 35-42.

Eibl-Eibesfeldt, I. (1961) The fighting behavior of animals. Scientific American 205: 112-122.

Eifrig, E. W. G. (1948) Wing-flashing of the mockingbird once more. The Florida Naturalist 21: 75-76.

Enquist, M., & Leimar, O. (1987) Evolution of fighting behavior: the effect of variation in resource value. Journal of Theoretical Biology 127: 187-205.

Enquist, M., Plane, E., & Roed, J. (1985) Aggressive communication in fulmars (*Fulmaris glacialis*) competing for food. Animal Behaviour 33: 1007-1020.

Enstrom, D. A. (1993) Female choice for age-specific plumage in the orchard oriole: implications for delayed plumage maturation. Animal Behaviour 45: 435-442.

Evans, M. R., & Hatchwell, B. J. (1992) An experimental study of male adornment in the scarlet-tufted malachite sunbird: I. The role of pectoral tufts in territory defence. Behavioral Ecology and Sociobiology 29: 413-419.

Ewald, P. W. (1985) Influence of asymmetries in resource quality and age on aggression and dominance in black-chinned hummingbirds. Animal Behaviour 33: 705-719.

Fisher, R. A. (1930) The genetical theory of natural selection. Oxford: Clarendon.

Forbush, E. H. (1929) Birds of Massachusetts and other northeastern states, Part III. Norwood, MA: Norwood Press.

Frankel, A. I, & Baskett, T. S. (1963) Color marking disrupts pair bonds of captive mourning doves. Journal of Wildlife Management 27: 124-127.

Freeman, S. (1987) Male red-winged blackbirds (*Agelaius phoeniceus*) assess the RHP of neighbors by watching contests. Behavioral Ecology and Sociobiology 21: 307-311.

Fugle, G. N., & Rothstein, S. I. (1987) Experiments of the control of deceptive signals of status in white-crowned sparrows. The Auk 104: 188-197.

Fugle, G. N., Rothstein, S. I., Osenberg, C. W., & McGinley, M. A. (1984) Signals of status in wintering white-crowned sparrows, *Zonotrichia leucophrys gambelli.* Animal Behaviour 32: 86-93.

Fulk, K. R., Logan, C. A., & Hyatt, L. E. (1987) Polyandry in a female Northern Mockingbird. Wilson Bulletin 99: 286-288.

Geist, V. (1966) The evolution of horn-like organs. Behaviour 27: 175-214.

Goodenough, J., McGuire, B., & Wallace, R. (1993) Perspectives on Animal Behavior. New York, NY: John Wiley & Sons.

Grafen, A. (1987) The logic of divisively asymmetric contests: respect for ownership and the desperado effect. Animal Behaviour 35: 462-467.

Hailman, J. P. (1977) Optical Signals: Animal Communication and Light. Bloomington, IN: Indiana University Press.

Halliday, T. R., & Slater, P. J. B. (1983) Communication. New York, NY: W. H. Freeman and Company.

Hamilton, W. D. & Zuk, M. (1982) Heritable true fitness and bright birds: a role for parasites? Science 218: 384-387.

Hansen, A. J. (1986) Fighting behavior in Bald Eagles: a test of game theory. Ecology 67: 787-799.

Hansen, A. J., & Rohwer, S. (1986) Coverable badges and resource defense in birds. Animal Behaviour 34: 69-76.

Harvey, P. H. & Arnold, S. J. (1982) Female mate choice and runaway sexual selection. Nature 297: 533-534.

Hill, G. E. (1990) Female House Finches prefer colorful males: Sexual selection for a condition-dependent trait. Animal Behaviour 40: 563-572.

Hill, G. E. (1991) Plumage coloration is a sexually selected indicator of male quality. Nature 350: 337-339.

Hoelzer, G. A. (1989) The good parent process of sexual selection. Animal Behaviour 38: 1067-1078.

Hoglund, J., Eriksson, M., & Lindell, L. E. (1990) Females of the lek-breeding great snipe, *Gallinago media*, prefer males with white tails. Animal Behaviour 40: 23-32.

Holberton, R. L., Able, K. P., & Wingfield, J. C. (1989) Status signalling in dark-eyed juncos, *Junco hyemalis*: plumage manipulations and hormonal correlates of dominance. Animal Behaviour 37: 681-689.

Holmberg, K., Edsman, L., & Klint, T. (1989) Female mate preferences and male attributes in mallard ducks *Anas platyrhynchos*. Animal Behaviour 38: 1-7.

Howard, R. D. (1974) The influence of sexual selection and interspecific competition on mockingbird song (*Mimus polyglottos*). Evolution 28: 428-438.

Huhta, E., & Alatalo, R. V. (1993) Plumage colour and male-male interactions in the pied flycatcher. Animal Behaviour 45: 511-518.

Jackson, W. M., Rohwer, S., & Winnegrad, R. L. (1988) Status signaling is absent within and-and-sex classes of Harris' sparrows. The Auk 105: 424-427.

Janetos, A. C. (1980) Strategies of female mate choice: A theoretical analysis. Behavioral Ecology and Sociobiology 7: 107-112.

Jarvi, T., & Bakken, M. (1984) The function of the variation in the breast stripe of the great tit (*Parus major*). Animal Behaviour 32: 590-596.

Jarvi, T., Roskaft, E., Bakken, M., & Zumsteg, B. (1987a) Evolution of variation in male secondary sexual characteristics: A test of eight hypotheses applied to pied flycatchers. Behavioral Ecology and Sociobiology 20: 161-169.

Jarvi, T., Walso, O., & Bakken, M. (1987b) Status signalling by *Parus major*: an experiment in deception. Ethology 76: 334-342.

Jones, I. L. (1990) Plumage variability functions for status signalling in least auklets. Animal Behaviour 39: 967-75.

Jones, I. L., & Montgomerie, R. (1991) Mating and remating of least auklets (*Aethia pusilla*) relative to ornamental traits. Behavioral Ecology 2: 249-257.

Justice, M. (1995) Countershading and the tendency of male Northern Mockingbirds to orient toward the sun while singing. Submitted.

Keeley, E. R., & Grant, J. W. A. (1993) Asymmetries in the expected value of food do not predict the outcome of contests between convict cichlids. Animal Behaviour 45: 1035-1037.

Kendall, M., & Gibbons, J. D. (1990) Rank Correlation Methods. Oxford University Press: New York.

Ketterson, E. D. (1979) Status signaling in dark-eyed juncos. The Auk 96: 94-99.

Keys, G. C., & Rothstein, S. I. (1991) Benefits and costs of dominance and subordinance in white-crowned sparrows and the paradox of status signalling. Animal Behaviour 42: 899-912.

Kirkpatrick, M. (1982) Sexual selection and the evolution of female choice. Evolution 36: 1-12.

Kopechena, J. G., & Falls, B. J. (1993) Aggressive performance as a behavioral correlate of plumage polymorphism in the white-throated sparrow (*Zonotrichia albicollis*). Behaviour 124: 249-266.

Laskey, A. R. (1933) A territory and mating study of mockingbirds. Migrant 4: 29-35.

Laskey, A. R. (1935) Mockingbird life history studies. The Auk 52: 370-381.

Laskey, A. R. (1936) Fall and winter behavior of mockingbirds. Wilson Bulletin 48: 241-255.

Lemel, J., & Wallin, K. (1993) Status signalling, motivational condition and dominance: an experimental study in the great tit, *Parus major* L.. Animal Behaviour 45: 549-558.

Lemon, R. E., Weary, D. M., & Norris, K. J. (1992) Male morphology and behavior correlate with reproductive success in the American redstart (*Setophaga ruticilla*). Behavioral Ecology and Sociobiology 29: 399-403.

Lewis, D. M. (1972) Importance of face-mask in sexual recognition and territorial behavior in the yellowthroat. Jack-pine Warbler 50: 98-109.

Lifjeld, J. T., & Slagsvold, T. (1988) Mate fidelity of renesting pied flycatchers *Ficedula hypoleuca* in relation to characteristics of the pair mates. Behavioral Ecology and Sociobiology 22: 117-123.

Lindstrom, A., Hasselquist, D., Bensch, S., & Grahn, M. (1990) Asymmetric contests over resources for survival and migration: a field experiment with bluethroats. Animal Behaviour 40: 453-461.

Logan, C. A. (1983) Reproductively dependent song cyclicity in mated male mockingbirds (*Mimus polyglottos*). The Auk 100: 404-413.

Logan, C. A. (1988) Breeding context and response to song playback in mockingbirds (*Mimus polyglottos*). Journal of Comparative Psychology 102: 136-145.

Logan, C. A. (1991) Mate switching and mate choice in female Northern Mockingbirds: facultative monogamy. Wilson Bulletin 103: 277-281.

Logan, C. A. (1994) Fluctuations in intra-pair calling across breeding phases in Northern Mockingbirds (*Mimus polyglottos*). Behaviour 130: 123-141.

Lyon, B. E., Montgomerie, R. D., & Hamilton, L. D. (1987) Male parental care and monogamy in the snow bunting. Behavioral Ecology and Sociobiology 20: 377-382.

Lythgoe, J. N. (1979) The Ecology of Vision. Oxford: Clarendon Press.

Marler, P. (1955) Studies of fighting in chaffinches. (2) The effect on dominance relations of disguising females as males. British Journal of Animal Behaviour 3: 137-146.

Mateos, C. & Carranza, J. (1995) Female choice for morphological features of male ring-necked pheasants. Animal Behaviour 49: 737-748.

Maynard Smith, J. & Parker, G. A. (1976) The logic of asymmetric contests. Animal Behaviour 24: 159-175.

Maynard Smith, J. & Price, G. R. (1973) The logic of animal conflict. Nature 246: 15-18.

Metz, K. J., & Weatherhead, P. J. (1992) Seeing red: uncovering coverable badges in red-winged blackbirds. Animal Behaviour 43: 223-229.

Michener, J. R. (1953) Molt and variations in plumage pattern of mockingbirds at Pasadena, California. The Condor 55: 75-89.

Michener, H., & Michener, J. R. (1935) Mockingbirds, their territories, and individualities. The Condor 37: 97-140.

Mock, D. W., & Fujioka, M. (1990) Monogamy and long-term pair bonding in vertebrates. Trends in Ecology and Evolution 44: 39-43.

Møller, A. P. (1987a) Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signalling. Animal Behaviour 35: 1637-1644.

Møller, A. P. (1987b) Social control of deception among status signalling house sparrows *Passer domesticus*. Behavioral Ecology and Sociobiology 20: 307-311.

Møller, A. P. (1990) Sexual behavior is related to badge size in the house sparrow *Passer domesticus*. Behavioral Ecology and Sociobiology 27: 23-29.

Møller, A. P., & Erritzoe, J. (1988) Badge, body and testes size in House sparrows *Passer domesticus*. Ornis Scandinavia 19: 72-73.

Norris, K. J. (1990a) Female choice and the evolution of the conspicuous plumage coloration of monogamous male great tits. Behavioral Ecology and Sociobiology 26: 129-138.

Norris, K. J. (1990b) Female choice and the quality of parental care in the great tit *Parus major*. Behavioral Ecology and Sociobiology 27: 275-281.

O'Donald, P. (1959) Possibility of assortative mating in the Arctic skua. Nature 183: 1210.

Odum, E. P., & Kuenzler, E. J. (1955) Measurements of territory and home range size in birds. The Auk 72:128-137.

Palokangas, P., Korpimaki, E., Hakkarainen, H., Huhta, E., Tolonen, P., & Alatalo, R. V. (1994) Female kestrels gain reproductive success by choosing brightly ornamented males. Animal Behaviour 47: 443-448.

Parker, G. A. (1974) Assessment strategy and the evolution of fighting behavior. Journal of Theoretical Biology 47: 223-243.

Parsons, J., & Baptista, L. F. (1980) Crown color and dominance in the white-crowned sparrow. The Auk 97: 807-815.

Payne, R. B. (1982) Ecological consequences of song matching: breeding success and intraspecific mimicry in Indigo Buntings. Ecology 63: 401-411.

Peek, F. W. (1972) An experimental study of the territorial function of vocal and visual display in the male Red-winged blackbird (*Agelaius phoeniceus*). Animal Behaviour 20: 112-118.

Platt, J. R. (1964) Strong Inference. Science 146: 347-353.

Popp, J. W. (1987) Resource value and dominance among American goldfinches. Bird Behavior 7: 73-77.

Price, T. D. (1984) Sexual selection on body size, territory and plumage variables in a population of Darwin's finches. Evolution 38: 327-341.

Proctor-Gray, E., & Holmes, R. T. (1981) Adaptive significance of delayed attainment of plumage in male American redstarts: tests of two hypotheses. Evolution 35: 742-751.

Ralph, C. J., & Pearson, C. A. (1971) Correlation of age, size of territory, plumage, and breeding success in white-crowned sparrows. The Condor 73: 77-80.

Richner, H. (1989) Phenotypic correlates of dominance in carrion crows and their effects on access to food. Animal Behaviour 38: 606-612.

Ridgway, R. (1907) Family Mimidae. *In* The birds of North and Middle America, Part IV. United States National Museum Bulletin #50.

Roskaft, E., Jarvi, T., Bakken, M., Bech, C., & Reinersten, E. (1986) The relationship between social status and resting metabolic rate in great tits (Parus major) and pied flycatchers (Ficedula hypoleuca). Animal Behaviour 34: 838-842.

Roskaft, E., & Rohwer, S. (1987) An experimental study of the function of the red epaulettes and the black body colour of male red-winged blackbirds. Animal Behaviour 35: 1070-1077.

Rohwer, S. (1977) Status signaling in Harris' sparrows: some experiments in deception. Behaviour 61: 107-129.

Rohwer, S. (1978) Reply to Shields on avian winter plumage variability. Evolution 32: 670-673.

Rohwer, S. (1982) The evolution of reliable and unreliable badges of fighting ability. American Zoologist 22: 531-546.

Rohwer, S. (1985a) The social significance of avian winter plumage variability. Evolution 29: 593-610.

Rohwer, S. (1985b) Dyed birds achieve higher social status than controls in Harris' sparrows. Animal Behaviour 33: 1325-1331.

Rohwer, S., & Ewald, P. W. (1981) The cost of dominance and advantage of subordination in a badge signaling system. Evolution 35: 441-454.

Rohwer, S., & Rohwer, F. C. (1978) Status signalling in Harris' sparrows: experimental deceptions achieved. Animal Behaviour 26: 1012-1022.

Rohwer, S., & Roskaft, E. (1989) Results of dyeing male yellow-headed blackbirds solid black: implications for the arbitrary identity badge hypothesis. Behavioral Ecology and Sociobiology 25: 39-48.

Sasvari, L. (1986) Reproductive effort of widowed birds. Journal of Animal Ecology 55: 553-564.

Searcy, W. A. (1979) Morphological correlates of dominance in captive male red-winged blackbirds. Condor 81: 417-420.

Senar, J. C., Camerino, M., Copete, J. L., & Metcalfe, N. B. (1993) Variation in black bib of the Eurasian Siskin (*Carduelis spinus*) and its role as a reliable badge of dominance. The Auk 110: 924-927.

Shields, W. M. (1977) The social significance of avian winter plumage variability: a comment. Evolution 31: 905-907.

Shutler, D., & Weatherhead, P.J. (1991) Owner and floater red-winged blackbirds: determinants of status. Behavioral Ecology and Sociobiology 28: 235-241.

Sibley, C. G., & Ahlquist, J. E. (1984) The relationships of the starlings (Sturnidae: Sturnini) and the mockingbirds (Sturnidae: Mimini). The Auk 101: 230-243.

Siegel, S. (1956) Nonparametric statistics for the behavioral sciences. New York: McGraw Hill.

Slagsvold, T., & Dale, S. (1994) Why do female pied flycatchers mate with already mated males: deception or restricted mate sampling? Behavioral Ecology and Sociobiology 34: 239-250.

Slagsvold, T., Lifjeld, J. T., Stenmark, G., & Breiehagen, T. (1988) On the cost of searching for a mate in female pied flycatchers *Ficedula hypoleuca*. Animal Behaviour 36: 433-442.

Slotow, R., Alcock, J., & Rothstein, S. I. (1993) Social status signalling in white-crowned sparrows: an experimental test of the social control hypothesis. Animal Behaviour 46: 977-989.

Smith, D. G. (1972) The role of the epaulets in the red-winged blackbird (*Agelaius phoeniceus*) social system. Behaviour 41: 251-268.

Sokal, R.R. and Rohlf, F.J. 1981. Biometry, 2nd Edition. New York, NY: W. H. Freeman and Company.

Sprunt, Jr., A. (1964) Eastern Mockingbird. *In* Life Histories of North American nuthatches, wrens, thrashers, and their allies. (A. C. Bent, Ed.) New York: Dover.

Stiles, E. W. (1982) Expansions of mockingbird and multiflora rose in the northeastern Unites States and Canada. American Birds 36: 358-364.

Studd, M. V., & Robertson, R. J. (1985) Evidence for reliable badges of status in territorial yellow warblers (*Dendroica petechia*). Animal Behaviour 33: 1102-1113.

Sundberg, J., & Larsson, C. (1994) Male coloration as an indicator of parental quality in the yellowhammer, *Emberiza citrinella*. Animal Behaviour 48: 885-892.

Sutton, G. M. (1946) Wing-flashing in the mockingbird. The Wilson Bulletin 58: 206-209.

Watt, D. J. (1986a) Relationship of plumage variability, size, and sex to social dominance in Harris' sparrows. Animal Behaviour 34: 16-27.

Watt, D. J. (1986b) A comparative study of status signalling in sparrows (genus *Zonotrichia*). Animal Behaviour 34: 1-15.

Watt, D. J., Ralph, C. J., & Atkinson, C. T. (1984) The role of plumage polymorphism in dominance relationships of the white-throated sparrow. The Auk 101: 110-120.

Weidmann, U. (1990) Plumage quality and mate choice in mallards (*Anas platyrhynchos*). Behaviour 115: 127-141.

Whitfield, D. P. (1986) Plumage variability and territoriality in breeding turnstone *Arenia interpres*: status signalling or individual recognition. Animal Behaviour 34: 1471-1482.

Whitfield, D. P. (1988) The social significance of plumage variability in wintering turnstone *Arenia interpres*. Animal Behaviour 36: 408-415.

Wilson, J. D. (1992) A re-assessment of the significance of status signalling in populations of wild great tits, *Parus major*. Animal Behaviour 43: 999-1009.

Zahavi, A. (1975) Mate selection - a selection for a handicap. Journal of Theoretical Biology 53: 205-214.

Zaias, J. & Breitwisch, R. (1989) Intra-pair cooperation, fledgling care, and renesting by Northern Mockingbirds. Ethology 80: 94-110.

Zaias, J. & Breitwisch, R. (1990) Molt-breeding overlap in Northern Mockingbirds. The Auk 107: 414-416.

Zucker, N. (1994) A dual status-signalling system: a matter of redundancy or differing roles. Animal Behaviour 47: 15-22.

Zuk, M., Ligon, J. D., & Thornhill, R. (1992) Effects of experimental manipulation of male secondary sex characters on female mate preference in red jungle fowl. Animal Behaviour 44: 999-1006.

APPENDIX A

FIELD NOTES ON THE BEHAVIOR OF FEMALES THAT WERE MATED TO MALES WITH REDUCED OR COVERED WING PATCHES

Of nine mated males with covered wing patches, five had pair maintenance problems:

1) 21 May 1995, 9:05AM, Male-focal sample, Nestlings present. Upon arrival in the territory, the resident male was producing hew and chat calls. He flew over to the female and perched within 1m of her. Although actively hopping about, he remained within 3m of her. A third mockingbird was perched near the center of the territory about 8m from the pair. The resident male swooped at the third bird and returned to the vicinity of the female, hewing almost continually, but the third bird did not move. After eight minutes of this, the third bird left the territory. The resident male continued to produce hew calls. During the next twenty minutes, a third mockingbird was twice observed flying through the territory, unbothered by the residents.

22 May 1995, 8:25AM, Female-focal sample, Nestlings present. At the outset of the sample the resident male was perched within 1m of the female for four minutes, after which he left to forage. When she moved from her perch he followed her. He was out of sight for about a minute when the female was observed approaching a third bird, which was perched in the territory, to within 1m. At this point the resident male was again detected because he began producing hew and chat vocalizations; he was perched over 16m away from the female and the third bird and did not approach them. After about thirty seconds the third bird left the territory. About 35 minutes later the resident female was seen leaving the territory in the same direction as the intruder left. Two other mockingbirds and the focal female were found in a neighboring territory, although the female did not interact with either of these birds during the few minutes she was observed there.

2) 23 March 1995, 7:55AM, Male-focal sample, Pre-nestbuilding. The during the first 40 minutes there were some brief periods of song production by the resident male and countersong from a neighboring male (who was the former mate of the resident female, now unmated). Eventually the resident male chased this neighbor for 39s, but because the chase occurred near the border between the two territories, it was difficult to be certain in whose territory the chase occurred.

Four minutes later a similar 16s chase took place. After this chase, the resident male sang 7 minutes until a clear intrusion by this second male and a consequent 38s, Type 2 chase. Song resumed for about 3 minutes until a second clear intrusion. This time, the resident male made no attempt to evict the intruder; rather, he produced hew calls until the intruder left, 47s later.

3) 17 April 1995, 10:30 AM, Male-focal sample, Nestbuilding phase. At the very beginning of the sample the male was observed displacing the female from her perch on the corner of a building. They exchanged hew calls on his arrival, and the female immediately dropped straight down into some thick shrubbery at the corner of the building. The resident male produced some hew calls over the next minute or so, after which the resident female and the neighboring male were seen leaving the shrubs. The resident male chased the intruder to the territory border, where they had a 49s boundary dance (Laskey 1933, 1935, 1936) and a couple of brief chases. Over the next 27 minutes the resident male was observed following the female twice, carrying a twig, and producing about four minutes of song.

4) 28 March 1995, 5:00PM, Male-focal sample, Nestbuilding phase. There were brief periods of song for the first 14 minutes. The resident male then flew to the

territory border, where the female and a third bird were already involved in short chases of each other. The resident male spent 19s chasing the third bird out of the territory; the third bird did offer some mild resistance. [The third bird was probably a male given the nature of the response of the resident male.]

5) 7 June 1993, 9:45 AM, Male-focal sample, Nestlings present. While the focal male was being banded, measured, and dyed, a second male entered the territory and began to sing. The original resident, upon release with covered wing patches, immediately chased the intruder. An extremely long (well over 20 minutes) and very physical fight followed, ending with the eviction of the manipulated animal from his territory. The second bird took up residence and mated with the resident female. The new resident was trapped a few days later and his wing patches were covered. The original resident was again detected about two weeks later, defending a territory adjacent to his old one; the dye had faded almost completely. The original resident was involved in several territorial chases with the new resident (whose wing patches were now covered). Soon thereafter, the female was detected with her original mate in his new territory.

Of five mated males with reduced wing patches, three had pair maintenance problems:

1) 6 June 1995, 8:30AM, Male-focal sample, Nestlings present. During this sample the female flew out of the resident male's territory and into an area that was known to be occupied and defended by a bigamous male. She stayed there for at least one minute. Her mate did not pursue her into the neighboring territory.

2) 13 March 1995, 9:30AM, Male-focal sample, Nestbuilding phase. During the first 8 minutes of this sample the male sang and picked up a twig, which he soon dropped. In the 9th minute the female flew into the neighbor's territory. The male pursued her into the neighbor's territory and was chased out in 20s. He flew back into his territory, produced 4 chat calls and a few notes of song, and again went into the neighbor's territory after the female. This time he was chased out in 13s. He intruded into the neighbor's territory three more times, each intrusion resulting in a chase, and was ultimately successful in chasing the female back into his territory. Immediately after she returned he sang almost continuously for 18 minutes. No further incident of this nature was noted while the male was dyed, but a few days after the dye wore off, the female abandoned this male and her eggs

in favor of a different neighbor, who had until that time been unmated and singing loudly and frequently.

3) 16 June 1995, 7:45AM, 2 Observers, Concurrent Male- and Female-focal samples, Nestlings present. The female was observed leaving the territory and briefly chasing a bird; this bird followed her back into the territory. This bird perched in the territory, produced some hews, and continued along its path until it left the territory. It was never chased by the resident male. Over the next 30 minutes, the resident male followed and interacted with the female five times. A third bird then flew through the territory, but neither of the residents responded to it.

20 June 1995, 7:42AM, Male-focal sample, Fledglings present. The female was observed perching in the territory within 3m of a bird that was not her mate. Neither she nor the resident male chased it.

20 June 1995, 6:45PM, Male-focal sample, Fledglings present. Twice during this 30-minute sample, a third bird entered the territory and perched for a few moments before being chased out by the resident male.

Of five mated control males (3 sham dyed and 2 not dyed) that were observed only as control birds (unlike those mentioned above which were observed both as manipulated and control), only 1 had a pair maintenance problem:

6 June 1995, 10:38AM, Male-focal sample, Fledglings present. A few minutes into this sample, the resident male chased out a male intruder (identified by bands), and just a few minutes later was chasing out a different male intruder (identified by bands). The female was involved in this second interaction, which ended with both males perching near the border of their territories. The female perched much closer to the intruder than she was to her mate, but ultimately returned to her old territory. A third intruder, identified by bands as different from the first two, was chased out about 30 minutes later; again, the female was briefly involved with chasing the intruder with short flights, vocalizations, and nearby perches.

27 June 1995, 5:45PM, Male-focal sample, Incubation phase. The resident male was involved in 6 territorial chases in this 60-minute sample. During two of them, the female vocalized and also perched and flew in the vicinity of the chase. The female was again detected later in the sample as her mate flew into an adjacent territory and chased the female from that area back into his territory.

28 June 1995, 9:11AM, Male-focal sample, Incubation phase. The resident male was observed flying into a neighboring territory. When he arrived, the female was observed to already be in the neighbor's territory, perched close to the neighboring male. The males engaged in a long

chase (73s). During the chase the actions of the female could not be observed.

APPENDIX B

FIELD NOTES ON MALES WITH ENLARGED WING PATCHES

The following events were recorded while observing three of the unmated males with enlarged wing patches:

1) 21 May 1995, 8:25AM. About five minutes into the sample, a mockingbird was seen flying through the territory; it did not elicit any territorial aggression from the focal animal, which began to sing about one minute later. He sang for two minutes and then flew into the lower branches of a tree in his territory, where he perched within 3m of a second bird. After he sang for about 75s, the second bird left the territory. [Given the focal animal's behavior, the bird he perched near while singing was almost certainly a female.]

2) 8 June 1995, 7:10AM. While searching the territory for the male with enlarged wing patches, the neighboring female (identified by bands) was found in his territory. She was on the side of the territory directly opposite from where her own territory borders that of the focal animal. She

perched in the focal animal's territory five times in as many minutes while en route to her own territory. The focal animal, once detected, was observed following her at considerable distance, but he eventually approached the female to within 3m. They remained perched this close together for about 45 seconds when she flew back into her own territory. The focal animal tried to follow her but was met at the territory border by the female's mate (identified by bands). A 39s chase involving physical contact ensued, which resulted in each male flying back into his own territory.

3) 20 May 1995, 10:30AM. The focal animal was first detected on the ground. He walked along the ground a short distance, wing flashed, and walked another short distance. He then picked up a twig and flew to a nearby perch with it. He held the twig for about 40 seconds and then dropped it. He wing flashed two more times, changed perch, and began singing. [Picking up twigs suggests the possibility that a female had recently been in the area and the male was stimulated to nest build.]

Table I. Descriptive statistics on amount of white on each of the ten primary flight feathers. Min, Max, M, and SE are all in mm.

Primary	Group	*n*	Min	Max	M	SE	CV
#10	Both	70	30.0	39.5	33.97	0.27	0.067
	Males	32	30.6	39.5	35.23	0.35	0.057
	Females	27	30.4	38.0	32.62	0.33	0.052
#9	Both	71	39.4	55.2	46.05	0.35	0.065
	Males	32	44.9	55.2	48.07	0.40	0.047
	Females	28	39.4	49.4	44.11	0.50	0.050
#8	Both	71	42.7	53.2	48.14	0.30	0.052
	Males	32	46.6	53.2	49.64	0.28	0.031
	Females	28	42.7	51.4	46.26	0.38	0.043
#7	Both	71	42.8	56.8	49.82	0.38	0.064
	Males	32	47.3	56.6	51.63	0.42	0.046
	Females	28	42.8	52.8	47.79	0.44	0.048
#6	Both	71	41.2	57.9	51.05	0.42	0.069
	Males	32	41.5	57.9	52.97	0.55	0.058
	Females	28	44.3	55.3	49.12	0.46	0.050
#5	Both	71	40.5	59.0	50.14	0.42	0.070
	Males	32	49.3	59.0	52.33	0.45	0.049
	Females	28	42.0	53.5	47.95	0.49	0.054
#4	Both	71	39.2	65.0	50.16	0.64	0.108
	Males	32	47.6	65.0	53.87	0.80	0.084
	Females	28	39.2	50.7	46.18	0.47	0.054
#3	Both	71	42.2	78.0	59.14	1.14	0.162
	Males	32	54.7	78.0	66.00	1.08	0.093
	Females	28	42.5	72.6	52.27	1.30	0.132
#2	Both	71	47.6	78.2	64.81	0.85	0.111
	Males	32	57.5	78.2	69.91	0.81	0.065
	Females	28	47.6	72.9	59.35	0.97	0.086
#1	Both	71	47.6	77.7	64.81	0.77	0.100
	Males	32	59.3	77.7	69.44	0.75	0.061
	Females	28	47.6	69.9	59.97	0.89	0.078

Table II. Hours of time-in time for the birds used in Study 3. The top line is mean (SD); the bottom line is the number of birds in that group that had sampling time in that phase. Several birds had sampling time across multiple phases.

	Group		
Stage	Control	Reduced	Covered
Nest Building	2.6 (0.87) n = 5	2.6 (0.36) n = 3	2.6 (0.92) n = 4
Incubation	3.0 (0.75) n = 5	0.0 (N/A) n = 0	1.8 (N/A) n = 1
Nestlings Present	2.9 (N/A) n = 1	3.6 (N/A) n = 1	0.0 (N/A) n = 0
Fledglings Present/Nest Building	2.7 (1.02) n = 4	1.9 (N/A) n = 1	1.6 (0.28) n = 2

Table III. ANOVAs on the intersexual interaction variables. The top line is the mean ± SE for the group and the second line is the sample size. Under the ANOVA column is the value of the Kruskal-Wallis H and the associated probability. All results are for the "Nestlings present" phase except where indicated.

Variable	Control	Reduced	Covered	ANOVA
Hew exchanges per time-in hours	3.2 ± 0.95 n = 4	0.8 ± 0.44 n = 3	0.0 n = 1	H = 3.54 p = 0.17
Hew exchanges per time-in hours (Nest building)	1.8 ± 0.39 n = 3	0.4 ± 0.37 n = 3	1.4 n = 4	H = 4.30 p = 0.12
Male approaches per hour of time-in time	1.2 ± 0.24 n = 4	1.8 ± 0.26 n = 2	1.1 n = 1	H = 2.41 p = 0.30
Female approaches per hour of time-in time	1.5 ± 0.42 n = 4	0.6 ± 0.29 n = 2	1.7 n = 1	H = 2.41 p = 0.30
Male departures per hour of time-in time	1.4 ± 0.35 n = 4	1.0 ± 0.27 n = 2	0.5 n = 1	H = 2.41 p = 0.30
Female departures per hour of time-in time	1.4 ± 0.26 n = 4	1.5 ± 0.24 n = 2	2.2 n = 1	H = 2.46 p = 0.29
Total follows per hour of time-in time	0.3 ± 0.17 n = 4	0.5 ± 0.51 n = 2	0.6 n = 1	H = 0.58 p = 0.75

Table III. (Continued)

Variable	Control	Reduced	Covered	ANOVA
Male follows female per hour of time-in time	0.1 ± 0.05 n = 4	0.5 ± 0.51 n = 2	0.6 n = 1	H = 2.14 p = 0.34
Female follows male per hour of time-in time	0.2 ± 0.10 n = 4	0.0 n = 2	0.0 n = 1	H = 1.75 p = 0.42
Bins within 1m of each other / total bins of time-in time	0.014 ± 0.004 n = 4	0.016 ± 0.012 n = 2	0.018 n = 1	H = 0.00 p > 0.90
Bins within 1-3m of each other / total bins of time-in time	0.015 ± 0.004 n = 4	0.016 ± 0.005 n = 2	0.016 n = 1	H = 0.29 p = 0.87
Bins within 3m of each other / total bins of time-in time	0.029 ± 0.006 n = 4	0.034 ± 0.007 n = 2	0.034 n = 1	H = 0.54 p = 0.77
Bins within 3m of each other / total number of encounters	2.4 ± 0.26 n = 4	3.4 ± 0.76 n = 2	3.0 n = 1	H = 2.58 p = 0.28
Encounters per hour of time-in time	3.1 ± 0.75 n = 4	2.4 ± 0.03 n = 2	2.7 n = 1	H = 1.39 p = 0.50
Percentage of interactions with hew exchanges	38.13 ± 8.4 n = 4	35.00 ± 15.0 n = 2	12.50 n = 1	H = 2.25 p = 0.33

FIGURE CAPTIONS

Figure 1. Dorsal aspect of the mockingbirds' wing patch. The individual primaries are numbered.

Figure 2. An individual primary flight feather. The measurement of the amount of white is indicated on the left.

Figure 3. Schematic diagram of events recorded in the field, flight paths generated (thin lines) and the perimeter traced by the planimeter (thick polygon). P = Perch locations, TI = Territorial Interaction location. Both measures were numbered consecutively in the field.

Figure 4. Histogram comparing mean ± SE wing patch size between males and females.

Figure 5. Histogram comparing mean ± SE number of chases per hour of time-in time between the nestbuilding phase and the incubation phase.

Figure 6. Histogram comparing mean ± SE number of chases per hour of time-in time between control birds, reduced birds, and covered birds. Both mated and mated males in all breeding phases were used here.

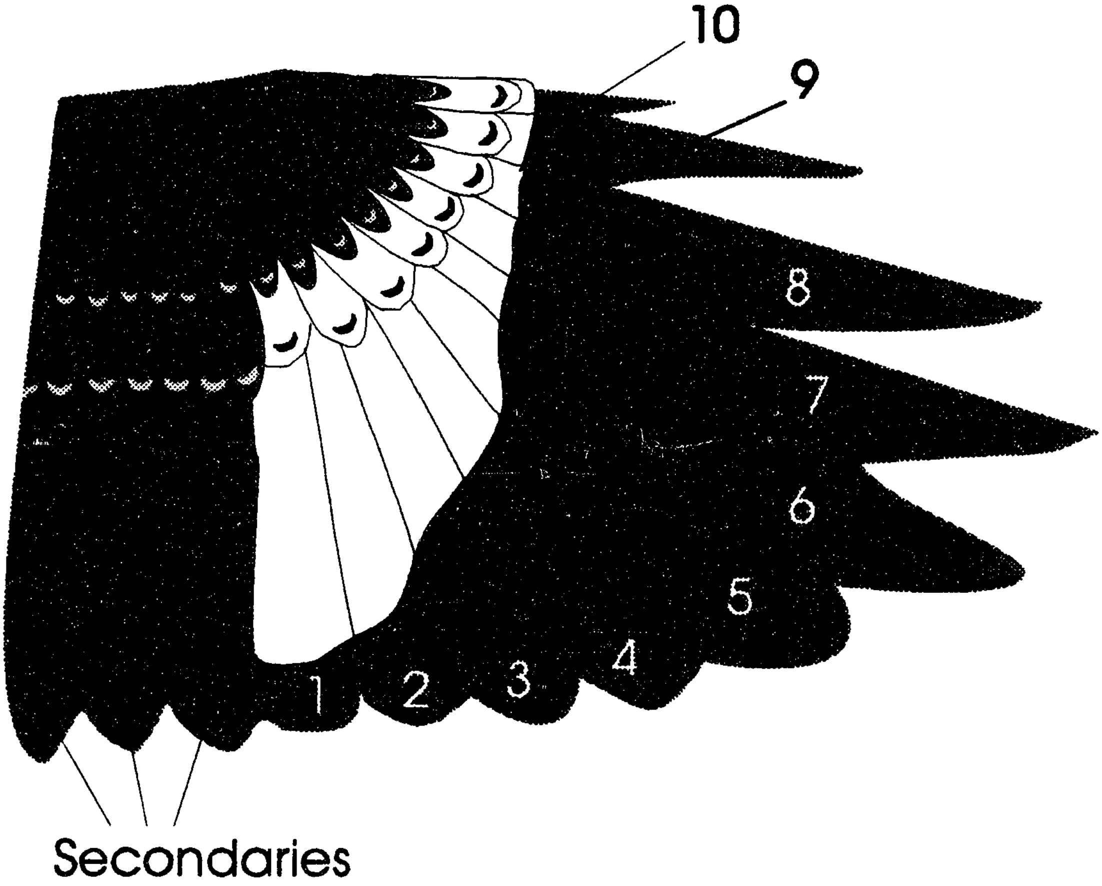
Figure 7. Histogram of mean ± SE average duration of chases (in seconds) for control birds, reduced birds, and covered birds Only mated birds in the nest building phase were used here.

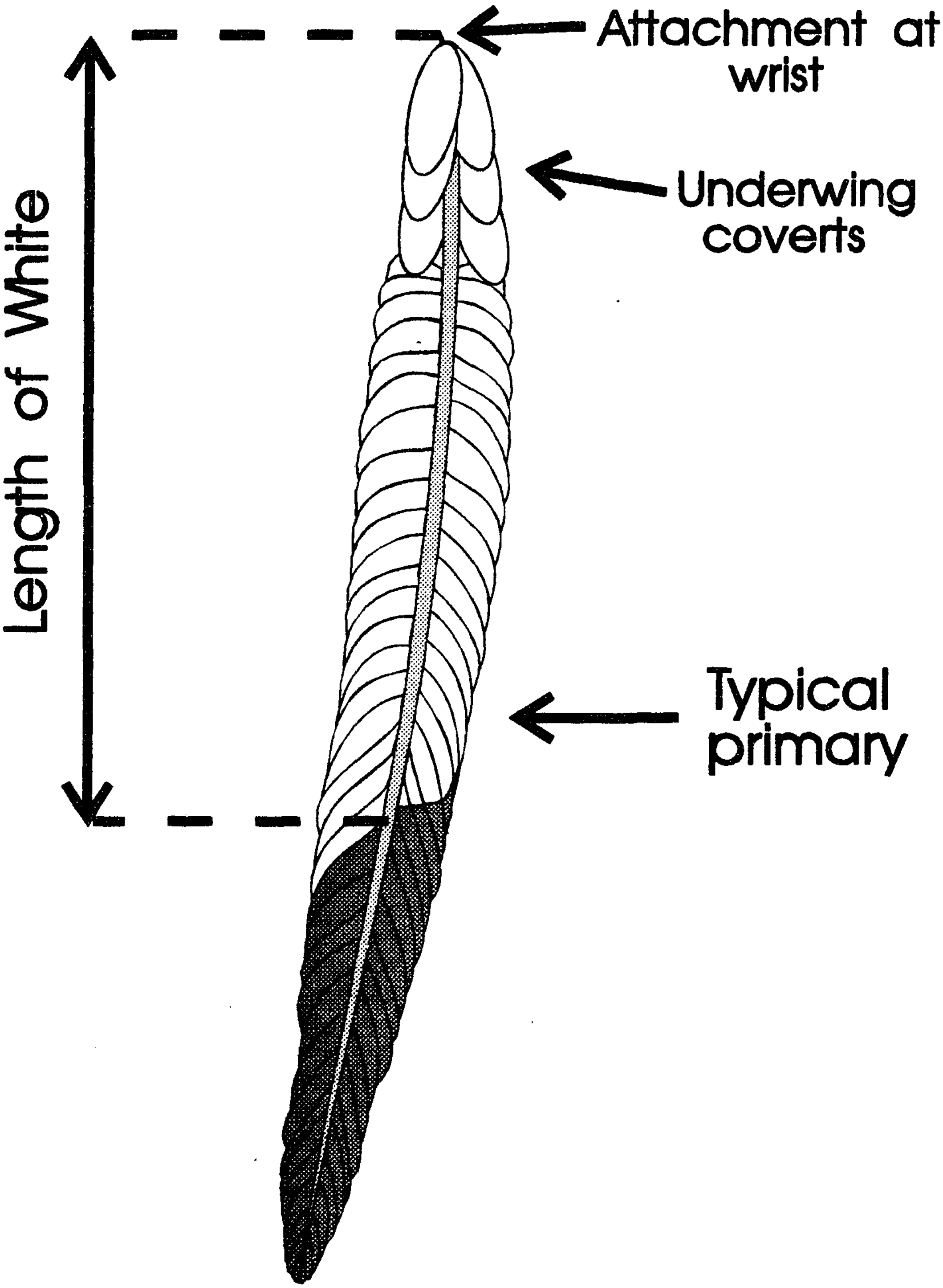
Figure 8. Histogram comparing mean ± SE percentage of bins spent in chases between control birds, reduced birds, and covered birds. Only mated birds in the nest building phase were used here.

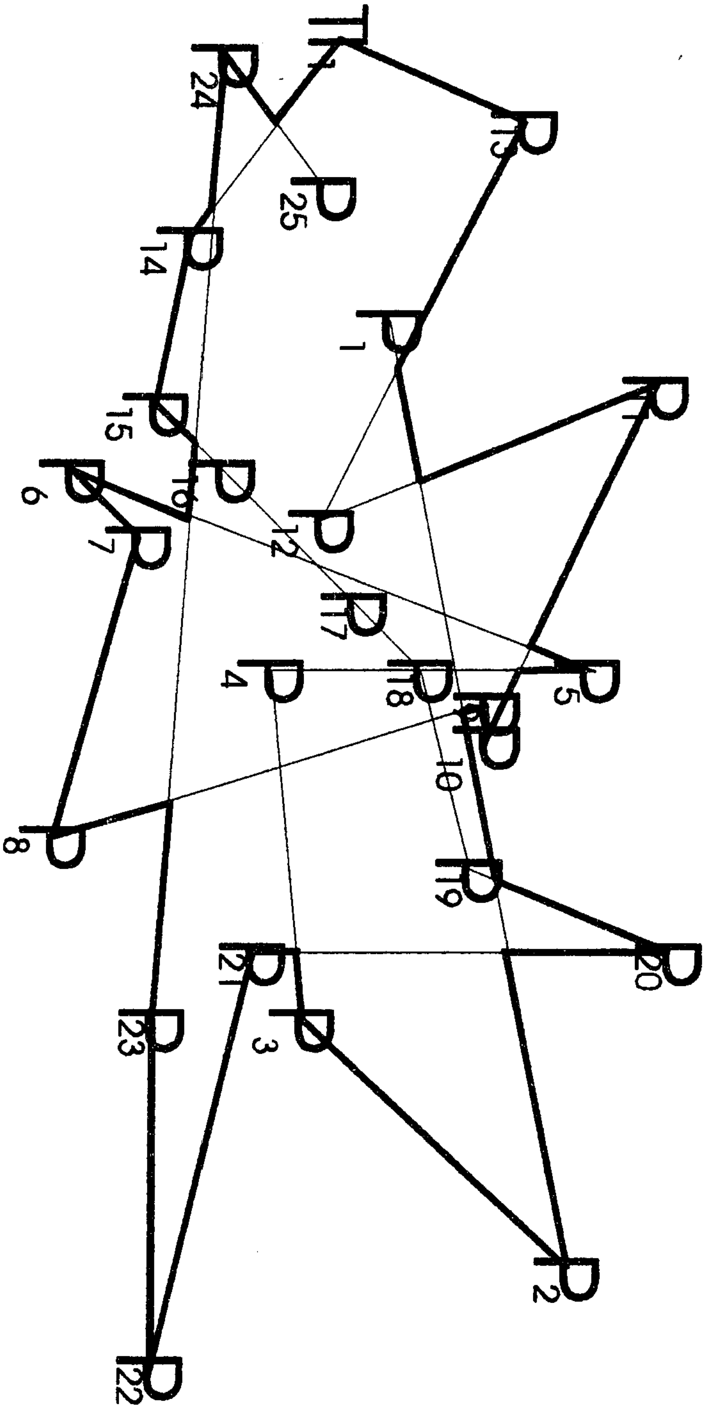
Figure 9. Histogram comparing mean ± SE number of chases per hour of time-in time between control birds and enlarged birds.

Figure 10. Histogram comparing mean ± SE wing patch size (in mm) between mated males and unmated males.

Figure 11. Histogram comparing mean ± SE wing patch size (in mm) between birds in the high response group and birds in the low response group.


10
9
8
7
6
5
4
3
2
1
Secondaries


Attachment at wrist
Underwing coverts
Typical primary
Length of White


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
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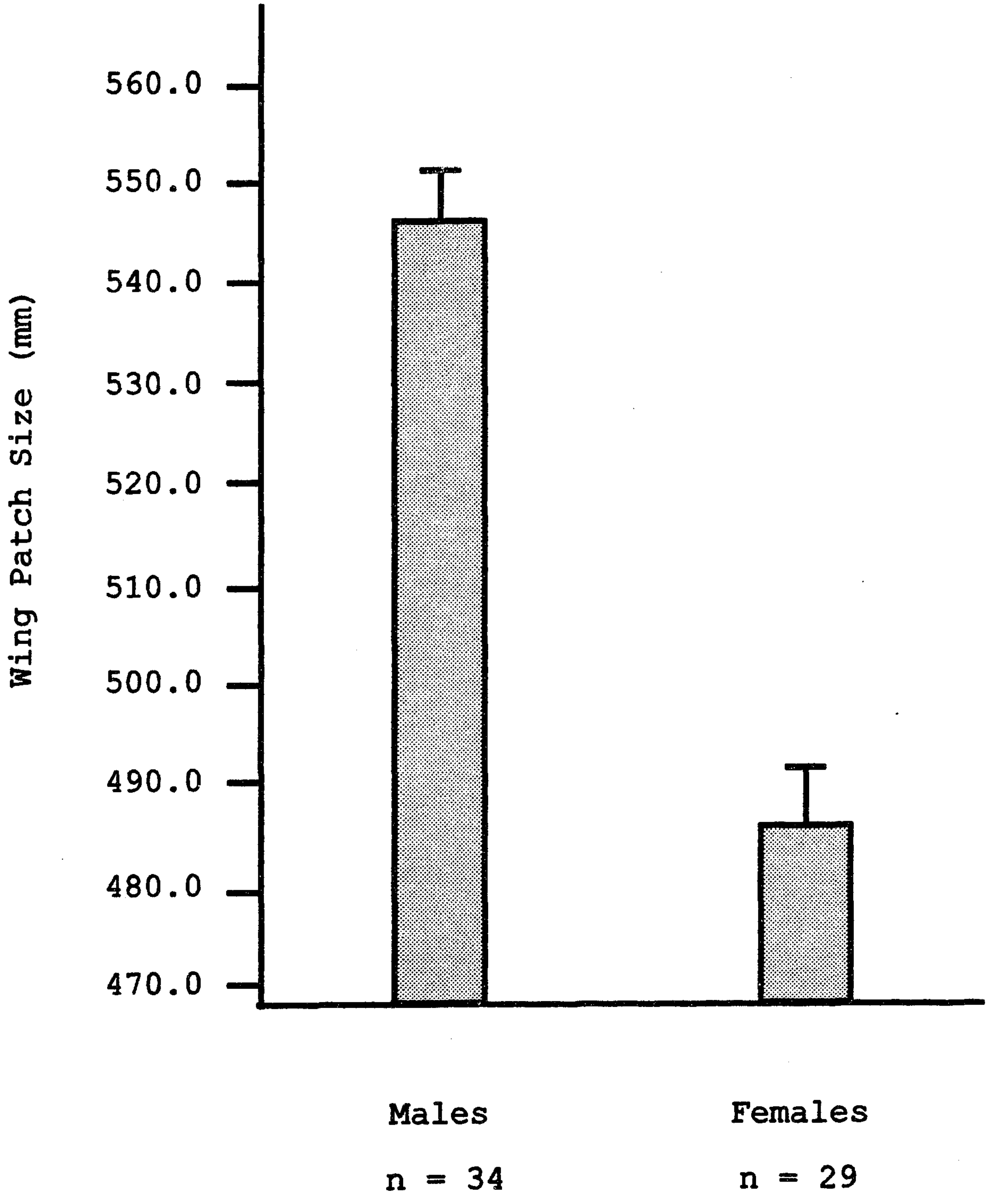
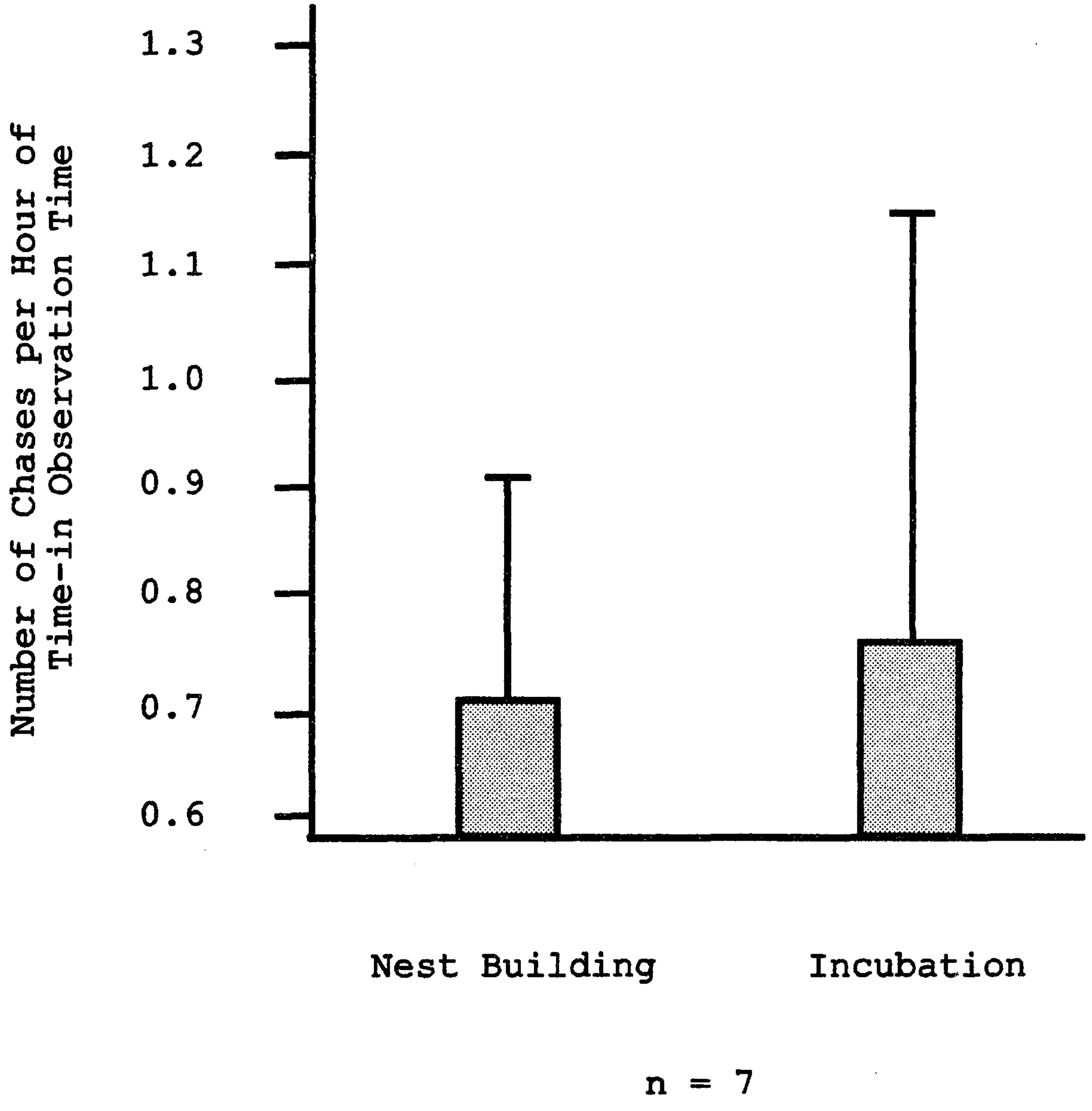
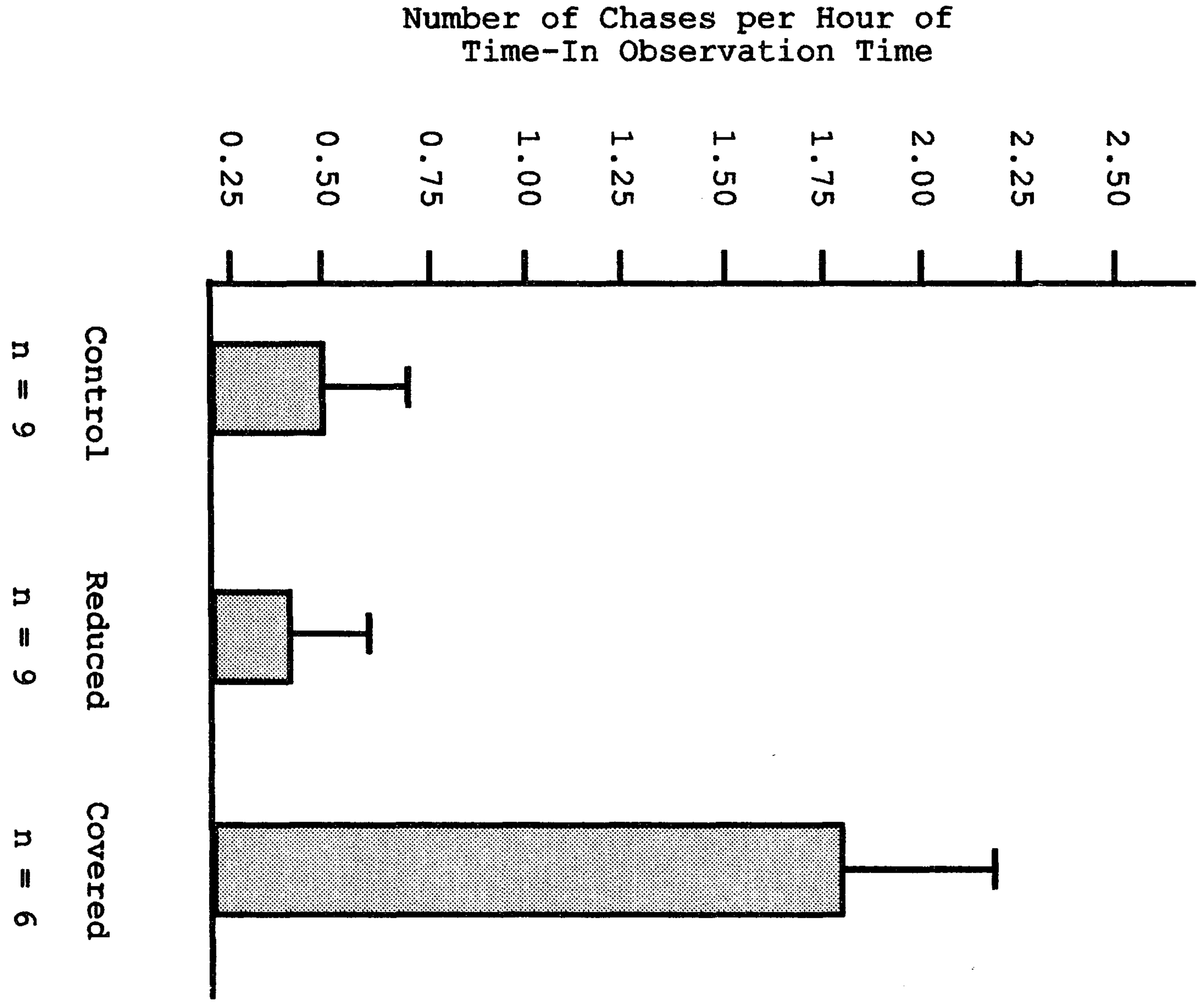
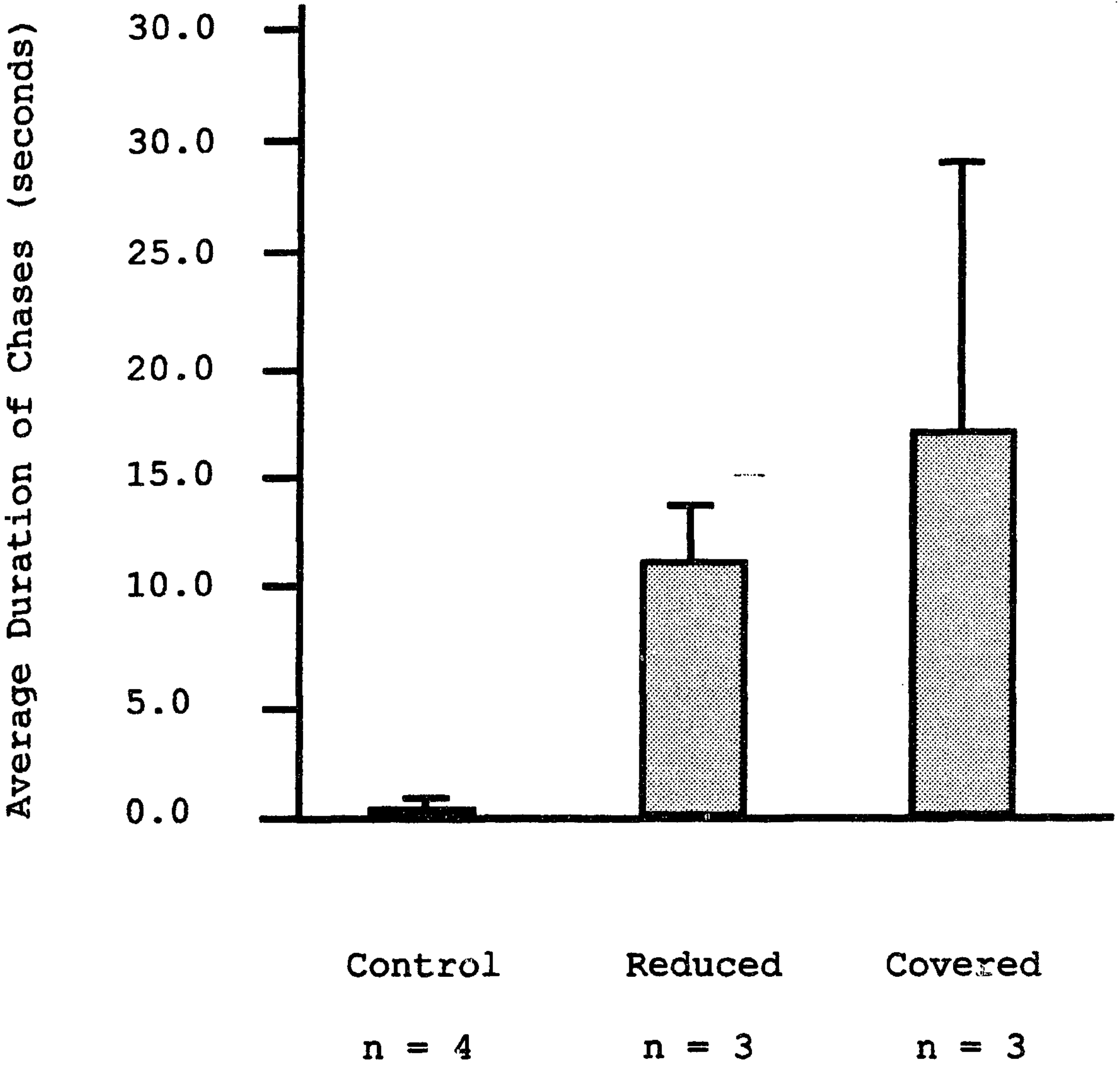
19
20
21
22
23
24
25

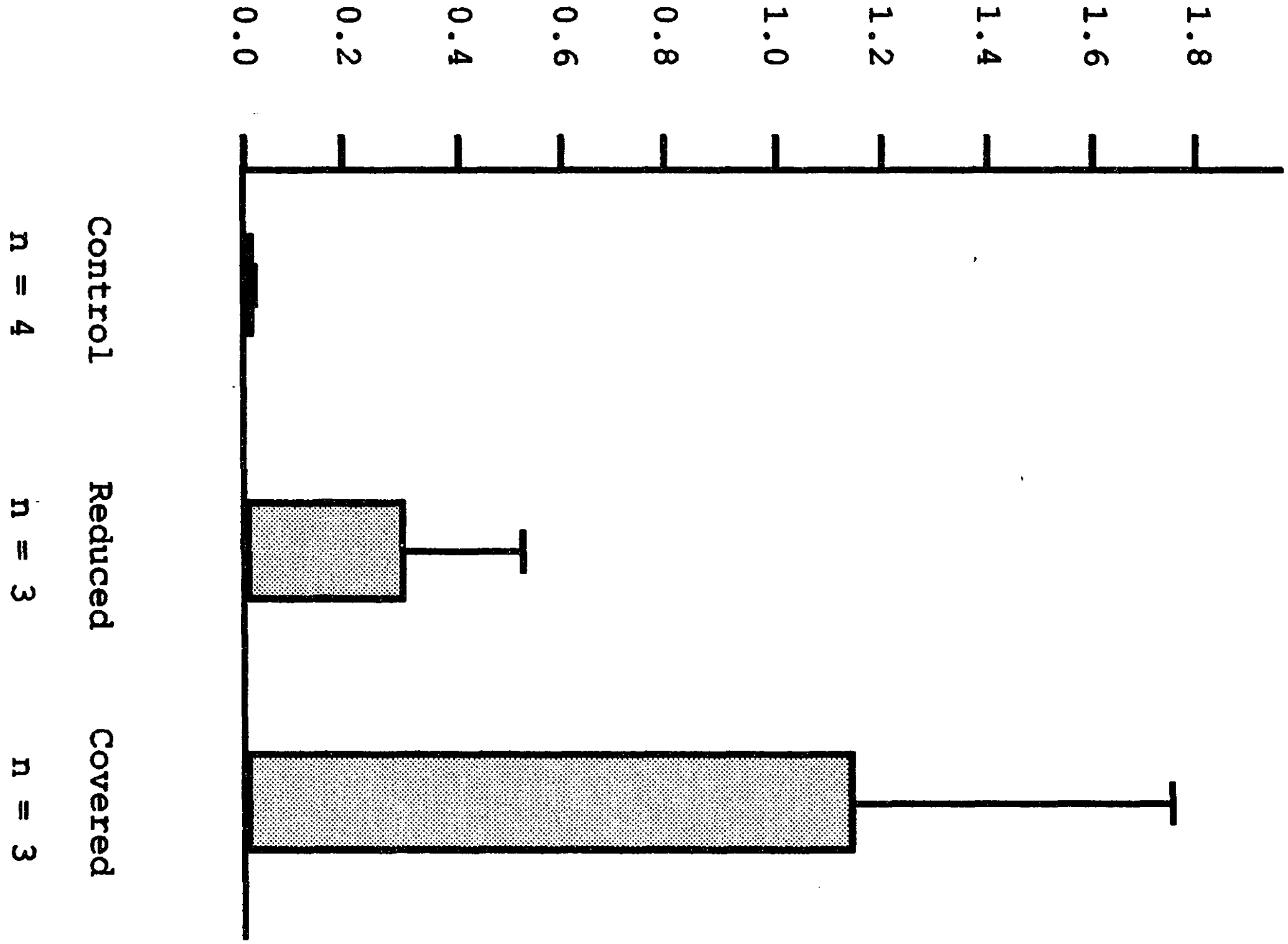

Wing Patch Size (mm)
560.0
550.0
540.0
530.0
520.0
510.0
500.0
490.0
480.0
470.0
Males
n = 34
Females
n = 29

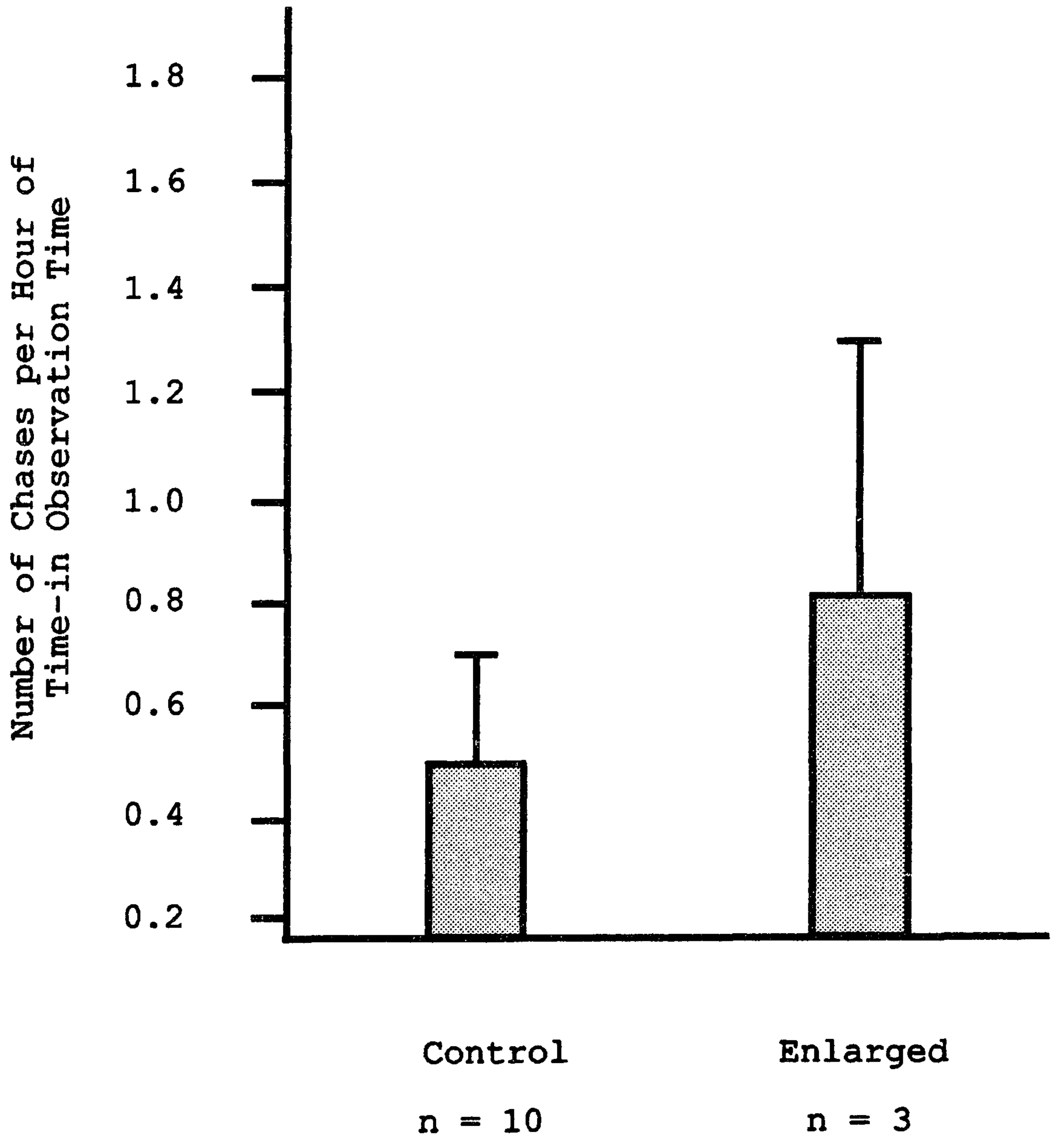

Number of Chases per Hour of
Time-in Observation Time
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
Nest Building
Incubation
n = 7

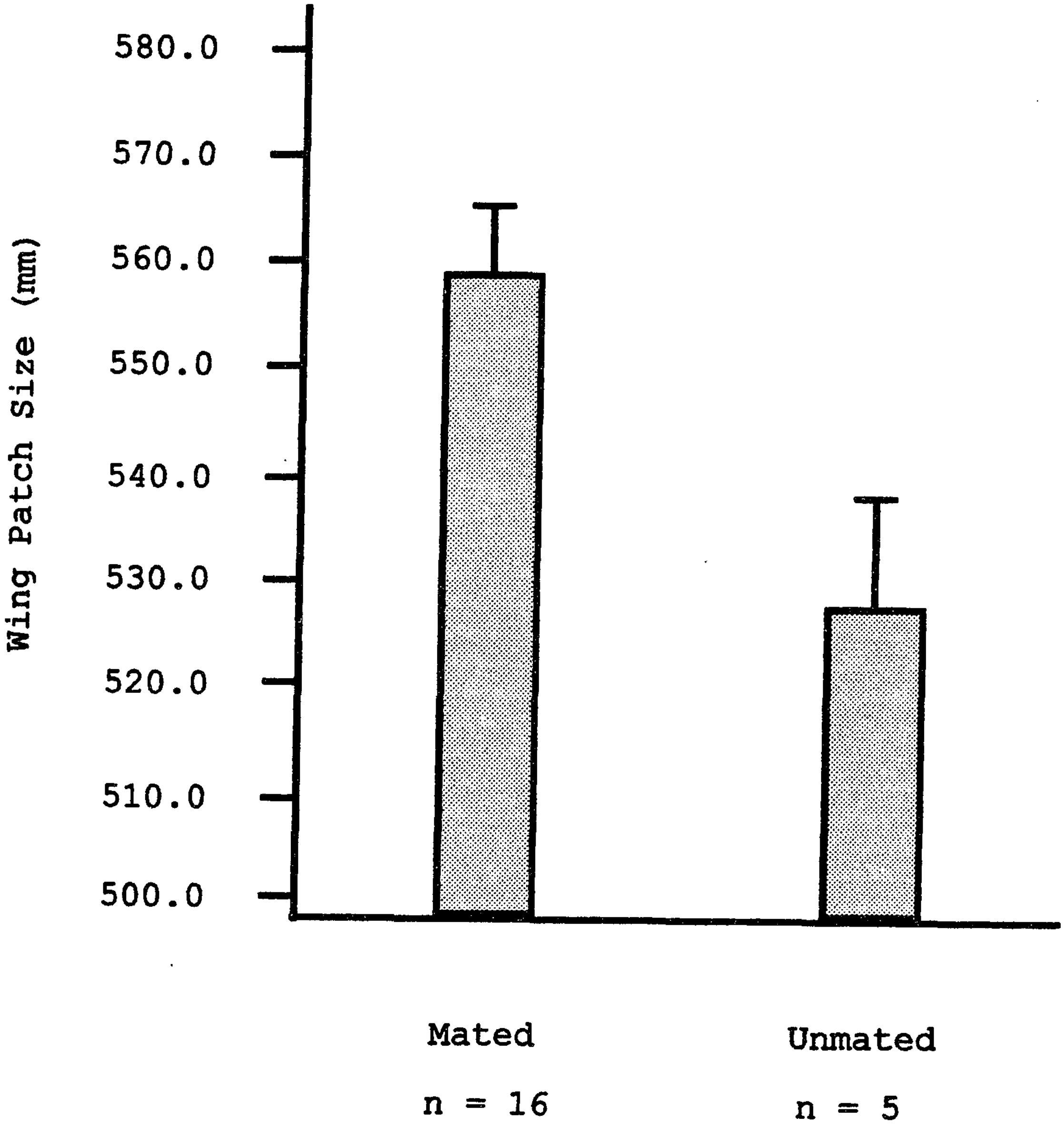

Number of Chases per Hour of Time-In Observation Time
0.25
0.50
0.75
1.00
1.25
1.50
1.75
2.00
2.25
2.50
Control
n = 9
Reduced
n = 9
Covered
n = 6

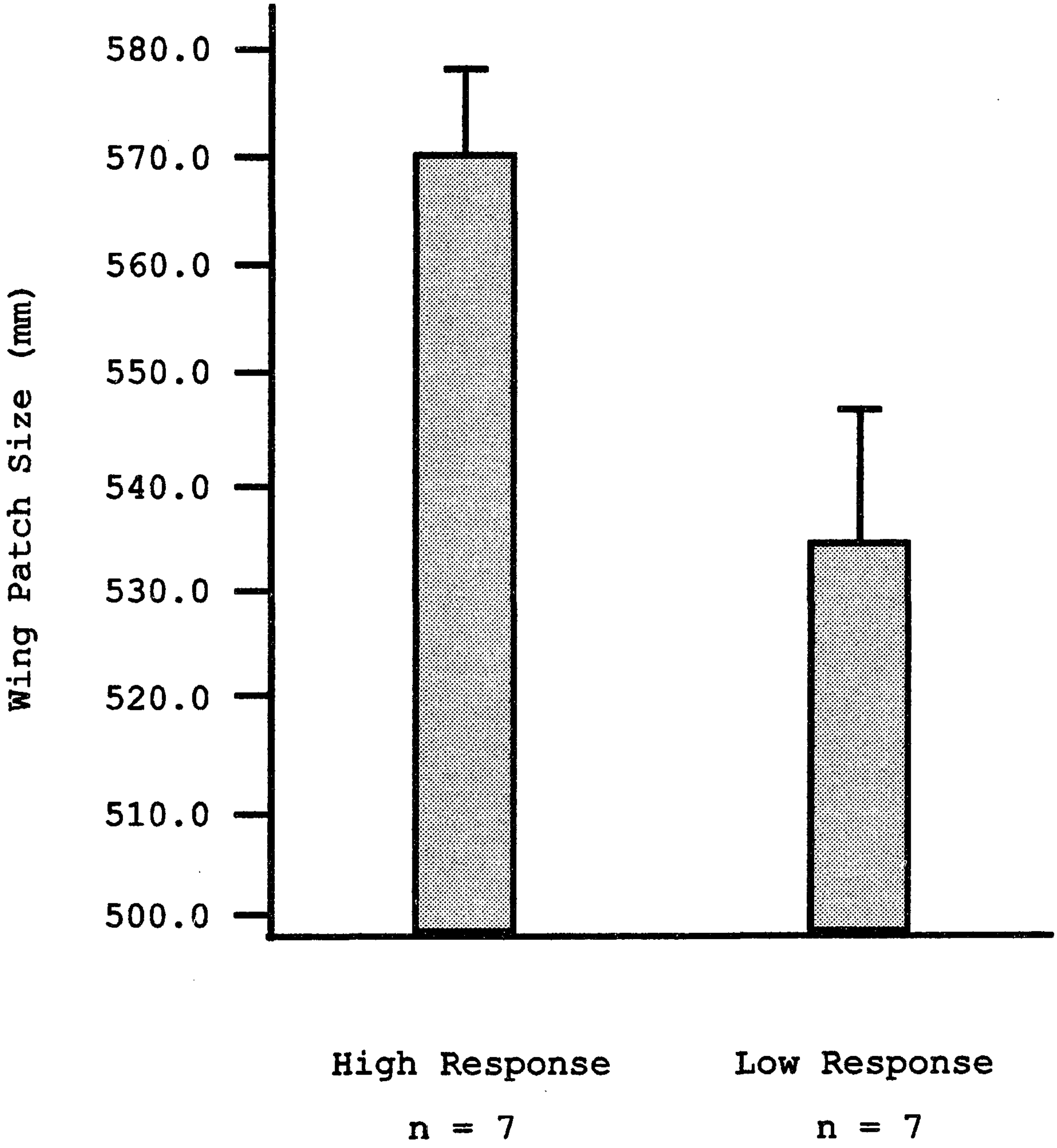

Average Duration of Chases (seconds)
30.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
Control
n = 4
Reduced
n = 3
Covered
n = 3

Percentage of Time-in Sampling
Bins Spent in Chases




Number of Chases per Hour of
Time-in Observation Time
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
Control
n = 10
Enlarged
n = 3


580.0
570.0
560.0
550.0
540.0
530.0
520.0
510.0
500.0
Wing Patch Size (mm)
Mated
n = 16
Unmated
n = 5


Wing Patch Size (mm)
580.0
570.0
560.0
550.0
540.0
530.0
520.0
510.0
500.0
High Response
n = 7
Low Response
n = 7