

# Experimental analyses of intra- and intersexual competition in red-winged blackbirds

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The roles of intra- and intersexual selection in determining harem size for many polygynous birds have proved difficult to separate. We designed experiments to feed only one sex to distinguish between intra- and intersexual selection in polygynous red-winged blackbirds. We then tested whether choices made by females benefit females. Our experiments were conducted on a number of different marshes, so we could evaluate whether females were choosing males within marshes or whether they are choosing their breeding situation primarily by making choices between different marshes. Females choosing between marshes strongly preferred marshes with males that had supplemental food and experimentally increased display rates. At the marsh level, some male displays were predictors of larger harem size and of greater nesting success. But while female choice was very strong among marshes, we detected only weak female preference for individual male traits within marshes. These results suggest that problems of scale probably affect studies of mate choice in avian breeding systems in ways that, to the best of our knowledge, have not previously been investigated by behavioral ecologists. *Key words:* *Agelaius phoeniceus*, female preference, mate choice, red-winged blackbirds, sexual selection. [*Behav Ecol* 8:524–533 (1997)]

In resource-based breeding systems, females simultaneously acquire males and the resources males defend. Thus it is difficult to assess the degree to which females base their choice of a breeding situation on male quality versus the quality of the resources that the male controls. Even when experiments successfully tease apart the effects that male attributes versus male resources have on female choice, interesting questions remain. When females choose resources, what specific resources are being chosen, and how do these resources affect reproductive success? When females choose males, what is the importance of male investment versus male genetic quality?

Red-winged blackbirds, *Agelaius phoeniceus* (hereafter "redwings"), have long been a model for the study of such questions. Most studies agree that territory quality influences female mate choice in redwings, but the role of male quality still generates considerable debate (reviewed in Searcy and Yasukawa, 1995). Two studies indicate that supplemental feeding increases harem sizes in redwings (Ewald and Rohwer, 1982; Wimberger, 1988). In each experiment, both sexes were fed, so neither distinguished whether females were responding to increased male displays or whether females were responding to the extra food.

In an earlier study, we used feeders that fed either males or females, but not both, to investigate the effects of sexual selection on the evolution of male body size and found that, under certain experimental conditions, male redwings with longer wings and tails and greater rates of several displays had larger harems (Rohwer et al., 1996). Yet such correlations cannot tell us if females directly prefer certain males or if those males have an advantage in male–male competition and therefore win larger territories, indirectly leading to larger harems.

In the present study, we used these same feeders to investigate the effects of male display and the effects of food (and, indirectly, territory quality) on harem size in redwings. Because our experiments were conducted on a number of different marshes, we were also able to evaluate whether females choose among males within marshes or whether they choose their breeding situation primarily by making choices between different marshes.

Mating systems are partly determined by local sex ratios (Davies 1992; Emlen and Vehrencamp, 1983; Rowley, 1981); therefore, we designed our feeding experiments to minimize effects on the numbers of males per marsh. We installed feeders after males had established territories and placed just one centrally located feeder on each fed territory. Occasionally new males inserted themselves, but changes in male density were unusual because the feeders were easily defended. Because our experiments had little effect on male densities, the harem size changes we found were caused almost entirely by changes in the number of females settling on a marsh. In another study in which more than 10 feeders were installed per original territory, the density of both males and females tripled, resulting in no change in harem size (Ewald and Rohwer, 1982).

We arranged our experimental feeders in five different treatments: (1) all males at a marsh were fed (contiguously fed); (2) alternate males at a marsh were fed (discontiguously fed); (3) alternate males at the same marshes were unfed (discontiguously not fed); (4) neither males nor females at a marsh were fed (controls); and (5) all males at a marsh were given female feeders (female fed). By contrasting these treatments, we addressed the following four questions about female choice and its consequences for female fitness:

1. What are the relative importances of agonistic (= intra-) and epigamic (= inter-) sexual selection on harem size? To examine this question, we attempted to assess the effects of territorial expansion on harem size. When all males were fed (contiguously fed), we expected that no expansion of territories could occur, but display rates could increase. When every other male was fed (discontiguously fed), we expected that the fed males could both increase their displays and expand their territories at the expense of their neighboring unfed males, who would be placed at an energetic disadvantage.

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If the position of territory boundaries was dependent on food availability, feeding alternate males should enable them to expand the sizes of their territories. In this case, we envisioned three possible outcomes with regard to harem sizes: (1) If females settled independent of male display rates, discontinuously fed males would have larger harem sizes than contiguously fed males, and contiguously fed harem sizes would be no larger than controls. (2) Alternatively, if display rates alone were the critical factor, discontinuously fed and contiguously fed harem sizes would not differ, and both would be greater than unfed controls. (3) But if both display rates and territory expansion played additive roles, harem sizes would be greatest for discontinuously fed males, intermediate for contiguously fed males, and lowest for controls.

However, if territory defense were independent of food availability, then feeding alternate males would have no effect on territory sizes. In this case, if contiguously fed and discontinuously fed had equal harem sizes and both were larger than controls, this would support the hypothesis that females preferred males with increased displays. (But it would not rule out effects of male–male competition on harem size through mechanisms other than display rates.)

2. Do females choose high male display rates, greater food availability, or both in choosing their breeding situation? We used female-only feeders to address this question. We compared harem sizes where only females were fed (extra food for females, display rates not expected to be significantly higher than for control males) to harem sizes where only males were fed (no extra food for females, display rates expected to be higher for males); we also compared both of these feeding treatments to controls, where neither sex was fed. If food was the most important cue for females, we would expect larger harems at female-fed marshes. If male display rates were a more important cue, we would expect larger harem sizes at male-fed marshes. Feeding males might make more natural food available for females if males with feeders spent less time foraging on their territory. To test this, we compared the time that males with and without feeders spent foraging on natural foods.

3. If male display affects harem size, are the effects of male display expressed at the level of marshes, or among males within marshes? To address this question, we compared results obtained by contrasting marshes receiving different treatments with results obtained by contrasting differences among males within marshes. We also compared males within marshes that received different treatments.

4. Does female choice directly benefit female fitness? If male display behavior is correlated with other male attributes affecting breeding performance, females could use displays to select a partner likely to offer them their direct material benefits (Greig-Smith, 1982; Searcy, 1979). Females, for example, might choose males whose displays suggest that they would provide effective parental care (Halliday, 1978; Trivers, 1972). Males rarely feed chicks in this population (Beletsky and Orrians, 1990), but male vigilance deters nest predation. If male vigilance affects nest success, if males differ in their vigilance, and if certain male displays provide reliable cues of vigilance behavior, then females should prefer males with those displays (see Yasukawa et al., 1992). If male vigilance were not energetically constrained or if it had no effects on nest success, then fed males and controls should not differ in the probability of success of nests on their territories.

## METHODS

### Natural history

All field work was done along the Winchester Wasteway in Grant County, Washington, USA (47°1' N, 119°5' W). The

study site is on a wind-swept plateau in the Columbia River basin of eastern Washington. From previous studies at this site, we knew that the amount of food available on red-winged blackbird breeding territories in early spring profoundly affects the time males spend on their territories, the number of females attracted to the territory, and the timing of female nesting (Ewald and Rohwer, 1982; Wimberger, 1988).

Male red-winged blackbirds in Washington typically have harems of three to eight females (Orrians, 1980). Males in this population rarely feed young (Beletsky and Orrians, 1990), but they do mob nest predators such as black-billed magpies, *Pica pica*, and northern harriers, *Circus cyaneus*. Starvation of nestlings was a factor in nest success, but not as important as predation.

### Territories

We trapped all territory-holding males on the marshes with decoy traps and color-banded them with unique combinations of anodized aluminum bands. We mapped male territories by setting up a 10 m × 10 m grid system of flagged poles and then mapping marsh vegetation with reference to this grid. Territories were mapped by locating song display sites and boundary dispute sites of males to within 1 m on the map. We mapped each male's territory from three to five times during the breeding season, and more often if territory takeovers were observed. When boundaries changed, nests were assigned to males using the appropriate map.

### Time budgets

For each male each year, we did from 5 to 15 early-morning time budgets, which consisted of a continuous 30-min record of male activity (except in 1988, when time budgets lasted 15 min). Observers sat quietly at least 20 m from the territory in the uplands and waited until the male had stopped alarm calling at their approach before beginning the time budget. Time budgets were taken only during the morning activity hours, when display rates were at their highest and all territorial males were present on the marsh. Since activity rates are highest shortly after dawn and then decrease, we controlled for time-of-day differences by rotating the time of each male's time budgets, so that all males had an equivalent set of 30-min intervals throughout the early morning hours. We stopped taking time budgets each year after the majority of females had settled on territories and male display rates had declined.

We used four behavior variables in the analyses: the song rate (number of songs divided by time in s spent on the territory during the time budget); rate of display flights (slow, flapping flights over the territory divided by time in s spent on territory); time in s spent perched vigilantly, either high in the cattails or on some other exposed perch; and total time in seconds on the territory. For each variable, we calculated each male's mean value from all his time budgets.

### Determining harem size

We checked marshes for nests every 4 days. First egg date was calculated by subtracting the number of eggs in the nest, less one, from the date on which the nest was found. After nests were found, we assigned them to male territories by comparing nest location to the most recent male territory maps. When nests were near the boundary of two males' territories, we rechecked their ownership by mapping boundary disputes to see which male guarded the nest. We measured harem size as the maximum number of simultaneously nesting females on the territory (Searcy, 1979; Yasukawa, 1981).

We defined the probability of nest survival on a male's territory as the number of nests on the territory that fledged at least one young, divided by the total number of nests that were completed on that territory.

### Feeders

We installed feeders in the last week of February and the first week of March, after males had settled but before most females had arrived. Feeders provided sunflower seeds and were designed to feed one or the other of the two sexes, but not both (see Rohwer et al., 1996, for design). The feeders exploited the size differences of male and female redwings. Male feeders opened when a male landed on the perch, but did not open when a female landed on the perch. Female feeders consisted of a tray enclosed in a wire mesh that enabled females but not males to pass through. Female feeders were distributed so that all original territory-holding males on the treatment marshes were given female feeders. In no cases did we feed both males and females at a marsh or on a territory. Several females could feed simultaneously at the enclosed tray, facilitating learning by later females and eliminating queuing for access to the feeder in large harems.

Feeder checks (one person watching from three to five feeders for several hours and recording when each bird used the feeders) were carried out several times each week to make certain that the proper birds were using the feeders assigned to them and that others were not stealing food from the feeders. Each fed male had a single feeder, so even in the discontinuous-fed treatment, males had little trouble preventing intruders from stealing food.

### Marshes

Nine marshes scattered over several square miles were included in this study. Marshes were sufficiently separated from each other to prevent birds from stealing food between marshes. We chose marshes that were similar in size, number of redwing territories, water depth, and dominant vegetation. We included only marshes without nesting yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, to eliminate problems of interspecific territoriality. All marshes were separated from the Winchester Wasteway, thus eliminating marshes with carp, *Cyprinus carpio*, which decrease numbers of emergent insects (Orlans, 1980). This also removed effects of egg destruction by marsh wrens, *Cistothorus palustris*, since they mainly settle in marshes adjoining the wasteway in our study area. Although we chose marshes to be as similar as possible, there was still variation in water depth, vegetation cover, nest success, predation rates, and harem sizes. Predation rates, success rates, starvation rates, and first egg dates also varied between years. Treatments were rotated through the marshes from year to year (see Table 4), but because of the large number of treatments involved, we could not replicate all treatments in each marsh.

### Statistics

To avoid pseudoreplication in cases where our treatments were blocked by marsh, we computed means for the males from a single marsh in a single year and treated these means as our units of analysis. We did not pool data from different years when a marsh had the same treatment in different years because year effects were sometimes strong and would be masked by pooling across different years. Means were used in all of our analyses comparing control males (where neither sex was fed), contiguously fed males (where males were fed in a contiguous block on a marsh), and females fed (where

females were fed in a contiguous block of male territories on a marsh). In 1986–1988 we also had discontinuously unfed and discontinuously fed males interspersed on single marshes to determine whether fed males were able to expand their territories at the expense of unfed neighbors. We treated individual males as units for analysis in this comparison because marsh effects cannot be responsible for differences when treatments are systematically interspersed within marshes.

Treating means as data points eliminated pseudoreplication but also made it impossible to look for effects of differences among males on mate choice. To overcome this problem we analyzed our data by calculating deviations from the mean within each group, separated by marsh, treatment, and year. For example, for a male that received a feeder in 1988 at the marsh "Dead Cow," we calculated the deviation of his harem size from the mean harem size for fed males at Dead Cow that year. With this technique, data from different years, marshes, and treatments could be combined. If there were differences in variances for harem size among marshes, the deviations would be larger for marshes with larger variances, thus skewing results. Variances, however, were homogenous across all marshes ( $F$  max tests,  $p \gg .05$ ). Interaction effects between marshes, years, and treatments would be hidden by this deviation method, but detecting possible interaction effects would require many more years of data.

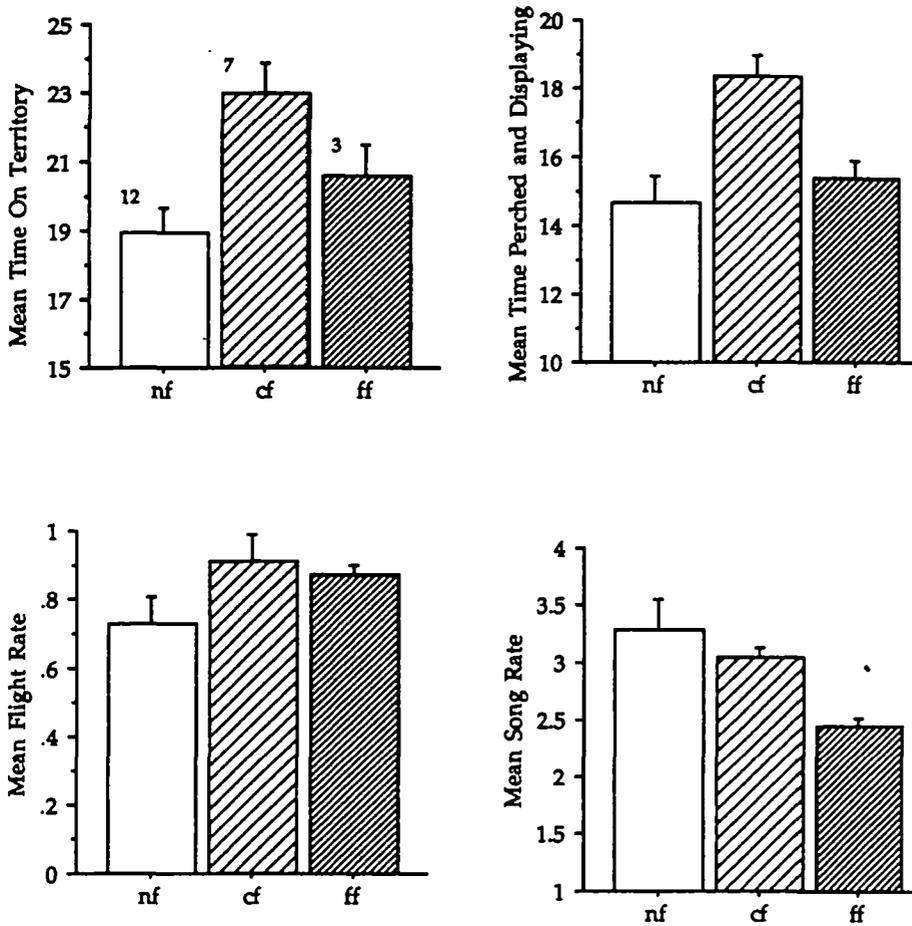
Some of our analyses used of multiple behavioral variables to evaluate the effects of male behavior on mate choice by females. Where this was the case the single hypothesis that male behavior affects female choice is being tested repeatedly using different behavioral variables. We used sequential Bonferroni tests to eliminate problems of multiple comparisons (Rice, 1989). In our tables we present individual  $p$  values, but we report tablewide significance levels in the text, based on sequential Bonferroni corrections.

## RESULTS

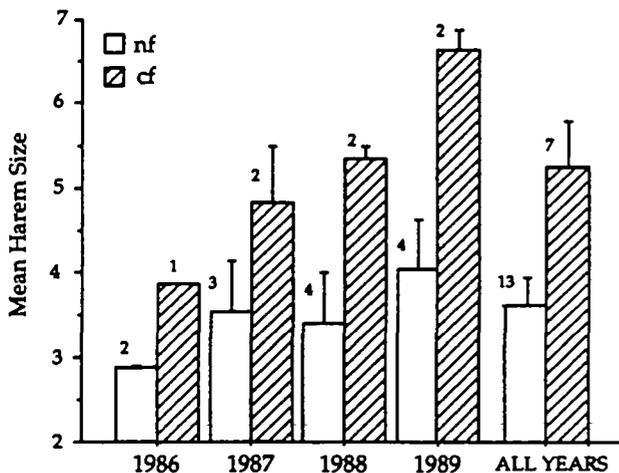
### Display rates, treatments, and harem size

If male display rates are energetically constrained, we predicted that supplemental feeding should increase the display rates of contiguously fed males over control males. With marshes as the level of analysis, as explained above, we found that feeding males produced significant changes in the time they spent on their territories and in the time they spent perched in full view and displaying (Figure 1). Both of these tests are also significant at the tablewide level when the critical  $\alpha$  is adjusted by the appropriate number of comparisons ( $k = 4$ ; Rice, 1989). Males whose females were fed were not different from controls. Song rates and flight rates, computed as numbers per time on territory, were not affected by feeding either males or females (Figure 1).

None of the contiguously fed males lost their territories, so there was never a mean expansion of territory size in this treatment. Some suffered a slight reduction in the size of their territories because of insertions by additional males that apparently were attracted to these marshes by the high level of activity at them. If females preferred males with increased display rates, even in the absence of territory expansion, we predicted that harem sizes of contiguously-fed males would be larger than control males. Figure 2 shows that contiguously fed males had significantly larger harem sizes than unfed males ( $p = .005$ ). Although mean harem sizes tend to increase from 1986 to 1989, neither the year effect ( $p = .105$ ), nor the year-by-treatment interaction ( $p = .67$ ) was significant in a two-factor ANOVA. Combining the means for all years (which largely eliminates marsh effects because treatments were rotated through marshes), fed males had 1.8 females more than



**Figure 1**  
Mean behaviors of control males (nf) versus contiguously fed males (cf) and males with female-only feeders (ff). Marshes are the level of analysis; bars are SEs. ANOVA; all years combined.  $N = 12$  marshes for nf; 7 marshes for cf, and 3 marshes for ff. Mean time on territory in minutes:  $F_{2,19} = 6.1$ ,  $p = .009$ , control versus male-fed differences significant. Mean time perched and displaying in minutes:  $F_{2,19} = 6.0$ ,  $p = .01$ , control versus male-fed differences significant; song rate  $F_{2,19} = 0.219$ ,  $p = .22$ ; flight rate  $F_{2,19} = 1.65$ ,  $p = .26$ .



**Figure 2**  
Mean harem sizes of control (nf) versus contiguously fed (cf) males. Analysis is at the level of marshes, not males; bars are SEs. Treatment effects are significant in a two-factor ANOVA: treatment  $df = 1$ ,  $F = 12.15$ ,  $p = .0045$ ; year  $df = 3$ ,  $F = 2.545$ ,  $p = .11$ ; interaction  $df = 3$ ,  $F = 3.0$ ,  $p = .67$ . When years are combined, harem size differences remain significant (Mann Whitney  $Z = -2.895$ ;  $p = .0038$ ).

unfed males, an increase of 51% in average harem size (Figure 2). When males are used as the unit of analysis, fed males had 2.1 more females than controls, giving a 64% increase in average harem size. We use the more conservative figure of 51% for the remainder of this paper.

#### Display and male-male competition

To evaluate the effect of possible changes in territory size on male mating success, we compared harem sizes of contiguously fed and discontinuously fed males. As explained above, for this comparison we treated individual males as units for analysis because marsh effects cannot be responsible for differences when treatments are systematically interspersed within marshes. Contiguously fed and discontinuously fed males did not differ significantly in any behavior (Table 1), and both spent significantly more time on their territories and more of this time perched vigilantly than controls (compare Table 1 and Figure 1).

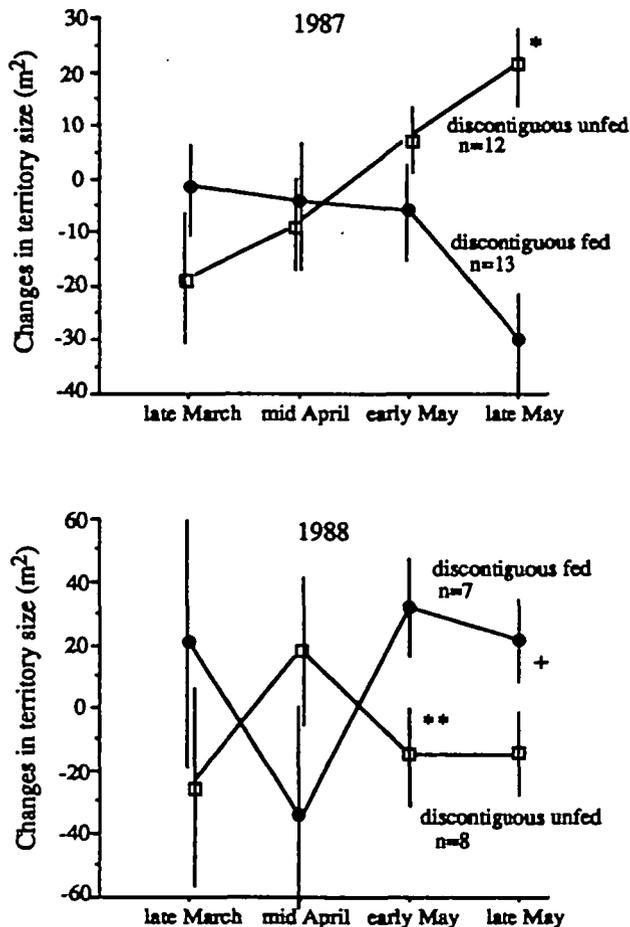
To examine whether discontinuously fed males expanded their territories, we measured territory size in 1987 and 1988. Figure 3 shows changes in territory size for discontinuously fed and discontinuously unfed males between successive territory mappings (mean territory sizes were well over 200 m<sup>2</sup>). Because a few additional males inserted and established territories after the first mapping in early March, territory sizes

**Table 1**  
Mean ( $\pm$  SE) display behavior of contiguously fed (CF) versus discontinuously fed (DF) males

Behavior	CF (n = 45)	DF (n = 27)	Z	p
Song rate (display/min on territory)	3.0 $\pm$ 0.1	3.1 $\pm$ 0.2	-0.352	.7
Flight rate (display/min on territory)	0.95 $\pm$ 0.063	0.93 $\pm$ 0.05	-0.262	.8
Time vigilant (min)	18.15 $\pm$ 0.53	18.49 $\pm$ 0.49	-0.343	.7
Time on territory (min)	22.17 $\pm$ 0.54	22.49 $\pm$ 0.66	-0.273	.8

Comparisons are Mann-Whitney tests.

of the original males might decrease (negative changes) in subsequent mappings. In 1987, discontinuously fed males did not increase territory sizes, and discontinuously unfed males did not lose territory size, opposite to our prediction. In 1988, territory size did not change significantly for fed and unfed males until early May, after the peak of nest initiation. These changes were small, however, and probably insufficient to have much effect on harem size because they occurred after peak nest initiation. In sum, our prediction that discontinuously fed males would expand their territories was not supported; in one year the size of their territories increased



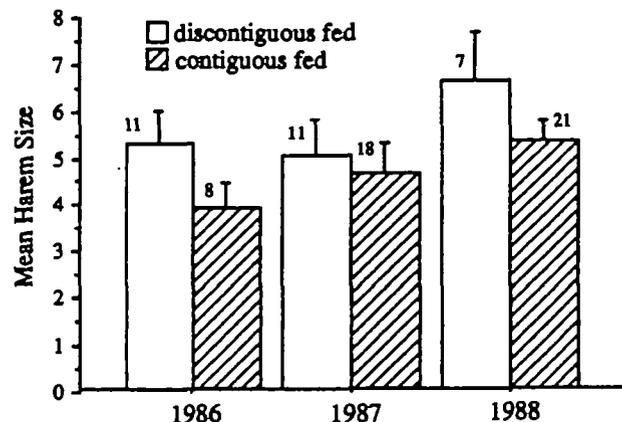
**Figure 3**  
Changes in territory size ( $m^2$ ) for discontinuously fed and discontinuously unfed males in consecutive mapping periods. Two-tailed *t* tests; + $p < .1$ ; \* $p < .05$ ; \*\* $p < .01$ .

slightly, but in the other year it decreased. Although discontinuously fed males had slightly greater harem sizes than contiguously fed males in each year, in no year was this difference significant (Figure 4). The most reliable summary comes from combining years because treatments were rotated through marshes to minimize marsh effects. Combining all three years, discontinuously fed males obtained 0.7 females/male more than contiguously-fed males, a 14.5% increase, which is not significant (Mann-Whitney  $Z = -1.0$ ,  $p = .3$ ).

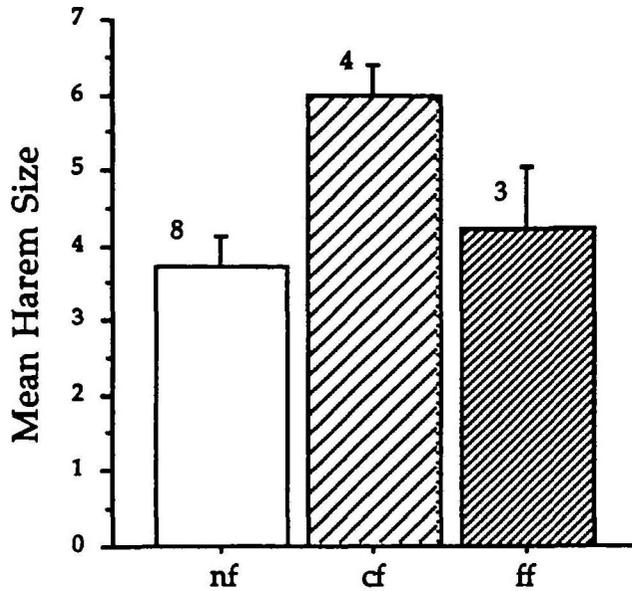
#### Food and females.

We used female-only feeders to test whether females preferred greater activity of males or greater food availability for themselves. As Figure 5 shows, harem sizes were unaffected by feeding females in 1988 and 1989, the 2 years in which we had functioning female feeders ( $p = .470$ ; Fisher's Protected Least Significant Difference). In these same 2 years, contiguously fed males had harem sizes that were significantly higher than both unfed control males ( $p = .005$ ; Fisher's PLSD) and than males on female-fed territories ( $p = .049$ ; Fisher's PLSD; Figure 5). These results suggest that the time males spend on territories may be a more important criterion than food when females are choosing mates or marshes.

Alternatively, territories with male-only feeders might have more food available for females if males with feeders spent less time taking natural foods on their territories. To test this, we compared the amount of time contiguously fed and control males spent foraging on their territory. In the early morning (0500-0700 h), fed and control males spent an equal



**Figure 4**  
Mean harem sizes of contiguously fed versus discontinuously fed males; bars are SEs. In no year do harem sizes show a significant difference (two-tailed Mann-Whitney tests; 1986  $Z = -1.36$ ,  $p = .17$ ; 1987  $Z = -0.5$ ,  $p = .6$ ; 1988  $Z = -1.1$ ,  $p = .3$ ).



**Figure 5**  
Mean harem sizes for 1988 and 1989 combined at control (cf), contiguously fed (cf), and female-fed (ff) marshes; bars are SEs. When years are grouped, the harem sizes differences are significant (ANOVA,  $F_{2,12} = 5.505$ ,  $p = .02$ ; nf versus cf significant at  $p = .006$ ). When year effects are isolated in a two-way ANOVA, both treatment and year effects are significant (treatment  $F_{2,12} = 7.157$ ,  $p = .014$ ; year  $F_{1,12} = 5.811$ ,  $p = .039$ ; treatment-year  $F_{2,12} = 0.681$ ,  $p = .53$ )

amount of time on the territory down in the cattails, where they were presumably foraging (11.4% for fed males versus 11.9% for control males; Mann Whitney tests,  $p > .5$  in all 4 years; when years combined,  $Z = -0.112$ ,  $p = .9$ ). During the midday, fed males spent most of their time on the territory, including foraging on their territory but not at their feeder. Control males, in contrast, were away from the territory most of the day, foraging at considerable distances from the territory. For example, in 1988 fed males spent 95% of their time on the territory during midday spot checks, whereas control males spent only 20% of their time on the territory (Rohwer et al., 1996). Thus, feeding males might actually have reduced the amount of food on or near the territory for females, rather than increasing it.

#### Choices within and among marshes

In an attempt to determine whether females were choosing among males within marshes on the basis of normal variation among males in their displays, we tested for correlations between displays and harem sizes using deviations of individual males from their marsh means. The use of deviations enabled us to pool males from all of the different control and treatment groups for this analysis, since we already knew that feeding has strongly positive effects on the time males spend on their territories and on the time they spend vigilantly perched. Males that spent more time vigilantly perched came close to having significantly larger harems (Table 2). This relationship is significant individually, but just misses tablewise significance ( $k = 4$ ; critical  $\alpha = .012$ ).

When treatment effects are examined by pooling males and treating marshes as units of analysis, females were strongly attracted to marshes where male feeding increased the time that males spent on their marshes (Figures 1, 2). Likewise, when all 272 males were combined, regardless of marsh or

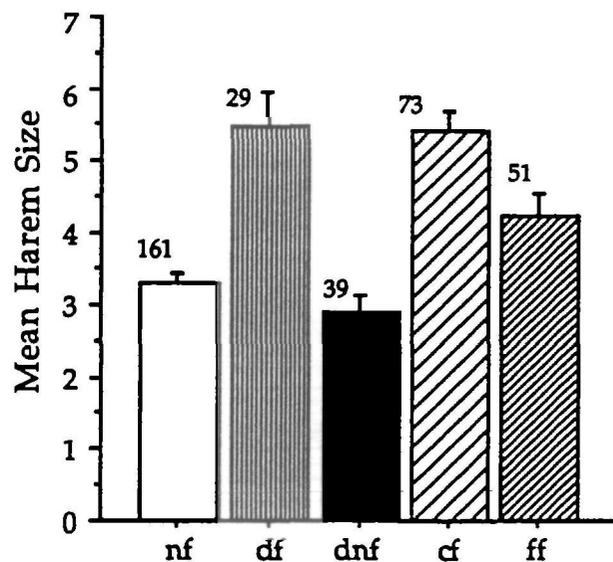
**Table 2**

Correlations between harem size deviations and behavior deviations and between harem sizes and male displays (two-tailed Spearman rank correlations)

Behavior	$\rho$	$p$	$n$
Correlations between behavior deviations and harem size deviations: within-marsh comparisons			
Song rate	+0.056	ns	267
Flight rate	+0.113	.06	268
Time vigilant	+0.145	.02	268
Time on territory	+0.048	ns	268
Correlations between behavior and harem size: all males			
Song rate	+0.004	ns	271
Flight rate	+0.266	.0001	272
Time vigilant	+0.299	.0001	272
Time on territory	+0.252	.0001	272

treatment, in a correlation of behavior versus harem size, males that displayed more and spent more time on their territory were much more likely to have larger harems (Table 2). But within marshes, the time that males spent on their territories was only weakly correlated with the time that they were vigilantly perched and with their harem sizes (Table 2). These results suggest that females are making their primary choices at the marsh level, not within marshes.

If marsh-level choices were the only significant choice females made, we would expect the harem sizes of discontinuously unfed males to be as large as discontinuously fed males, and significantly larger than the harem sizes of control males, since discontinuously unfed males are nesting at marshes where the general level of display has been significantly increased by feeders at alternative territories. This is not what we found: overall, mean harem sizes of discontinuously unfed males were much smaller than their neighboring discontin-



**Figure 6**  
Harem sizes by treatments; males as the unit of analysis; all year combined; bars are SEs. ANOVA,  $F_{4,348} = 20.95$ ,  $p < .0001$ . Fisher's PLSD tests show that two comparisons are not significantly different: discontinuously fed (df) versus contiguously fed (cf), and control (nf) versus discontinuously not fed (dnf). All others are significant at  $p < .005$ .

**Table 3**  
Mean ( $\pm$ SE) display behavior of discontinuously fed (DF) versus discontinuously not fed (DNF) males (years combined)

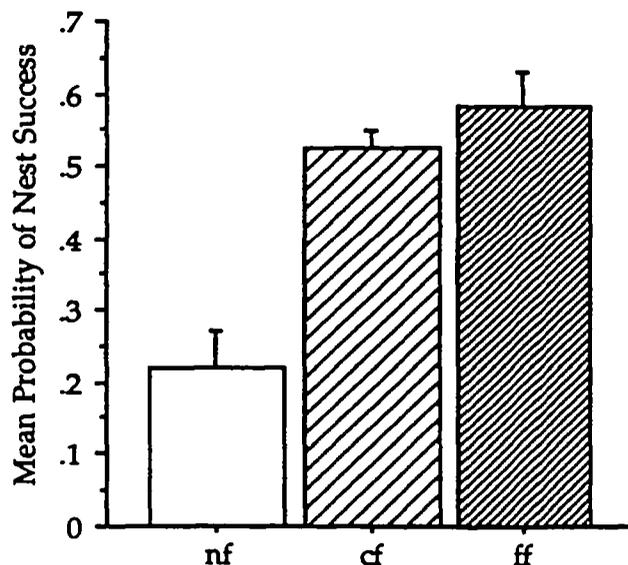
Behavior	DF (n = 27)	DNF (n = 38)	Z	p
Time vigilant (min)	18.2 $\pm$ 0.5	13.4 $\pm$ 0.8	-4.62	<.0001
Time on territory (min)	22.2 $\pm$ 0.5	17.4 $\pm$ 0.9	-3.7	.0002
Song rate (display/min on territory)	3.0 $\pm$ 0.1	3.0 $\pm$ 0.2	-0.13	.9
Flight rate (display/min on territory)	0.95 $\pm$ 0.06	0.67 $\pm$ 0.05	-3.3	.0009

uously fed males, and even slightly smaller than harems of control males (Figure 6).

When analyzed within marshes where the fed and unfed males were interspersed (the discontinuous treatment), mean harem sizes were always larger for the males with food. Eight different marshes received this treatment during 1986–1988; mean harem size for the discontinuously fed males was 5.46, while that for discontinuously unfed males was 3.21 (paired  $t = 6.06$ ;  $df = 7$ ;  $p = .0005$ ). These results suggest that females also make choices within marshes, when differences between neighboring males are greatly exaggerated by supplemental feeding. Indeed, feeding every other male did not lead to territory expansion, but it did lead to fed males being present and flying significantly more than their unfed neighbors (Table 3).

#### Material benefits to females: differences in nest success

The probability of nests surviving at a marsh varied greatly with treatment (Figure 7). In a two-factor ANOVA involving treatment and year, treatment effects were highly significant ( $F_{1,15} = 16.6$ ;  $p = .0013$ ), but year effects ( $F_{1,15} = .03$ ;  $p = .87$ ) and year-by-treatment interactions ( $F_{4,15} = .54$ ;  $p = .82$ ) were not. As Table 4 shows, in the absence of feeding, the probability of nest survival varied from 1% (at Reprieve marsh, in



**Figure 7**  
The mean probability of nest success, at control (nf), contiguously male fed (cf), and female fed (ff) territories; bars are SEs. Two-factor ANOVA: treatment  $F_{1,15} = 16.6$ ;  $p = .0013$ ; year:  $F_{1,15} = 0.03$ ;  $p = .87$ ; year-by-treatment interactions:  $F_{4,15} = 0.54$ ;  $p = .82$ .

1989) to 73% (at 1–10 marsh in 1987). With feeding of males, the probability of nest survival ranged from 22% (at 1–10 in 1987), to 71% (at Dead Cow in 1987). In seven cases out of nine cases, at marshes where some males were fed and others were not fed in a single year (here we include Rest Area marsh, 1989), the fed territories had a higher success (not significantly different than expected by chance, one-tailed binomial distribution  $p = .09$ ).

Overall, the probability of nest success at marshes where males were contiguously fed was 2.45 times that at control marshes with no feeders at all; the probability of nest success at marshes where females were fed was similarly increased, being 2.70 times higher than that at marshes with no feeders (Figure 7). These results show that the increased presence of males on a marsh strongly influences nesting success. Differences between male and female feeding were not significant (Fisher's PLSD  $p = .62$ ), suggesting that females are as effective as males at increasing nest success. Recall that feeding females did not significantly influence the amount of time that males spent on their territories or their rates of display (Figure 1).

Were females using the behavior of males early in the season to choose territories within marshes where nesting success would be high? To test for this we looked for correlations between probability of nest success and male behaviors during female settlement. We controlled for the effects of feeding in this analysis by comparing behavior deviations with deviations in the probability of nest success. For all of the treatments combined, none of these correlations is significant (Table 5). We also looked at this prediction using just the unfed controls, again using deviations to correct for differences among marshes (Table 5). Again, none of the correlations is significant at the tablewide level, despite the fact that in this analysis the time males spent perched vigilantly had an individual  $p$  value of .04.

#### DISCUSSION

The key to this work was our invention of sex-specific feeders that allowed us to feed male or female red-winged blackbirds on their territories without simultaneously feeding both sexes. With these feeders we have explored the importance of intra- versus inter-sexual selection in determining male harem sizes, the role of food versus male display in attracting females, and the degree to which females make choices among marshes compared to choices among males within marshes.

#### Inter- versus intrasexual competition

Our results indicate that increased male presence at a marsh attracts more females to that marsh, leading to larger harems. This effect occurs in the absence of changes in territory size; contiguously fed males (whose territories did not expand) had harems that were 51% larger than the harems of control

**Table 4**  
Probability of a nest surviving, by marsh, treatment, and year

Marsh	1986		1987		1988			1989		
	MF	NF	MF	NF	MF	NF	FF	MF	NF	FF
Mars	0.55	0.57	—	—	—	0.04	—	—	—	0.63
Dead Cow	—	0.24	0.71	0.54	0.56	—	—	—	0.22	—
1-10	0.52	—	0.22	0.73	—	0.06	—	—	0.51	—
86	0.42	0.46	—	0.55	0.64	—	—	0.27	—	—
Reprive	—	0.44	0.47	—	0.62	0.54	—	—	0.01	—
Peters	—	—	—	0.11	—	—	0.48	—	—	0.59
Skeleton	0.37	0.52	0.57	—	—	0.19	—	—	0.05	—
Beda	—	—	—	0.27	0.31	0.11	—	0.58	—	—
Rest Area	—	—	0.31	0.25	—	0.28	—	0.6	0.52	—

Male feeders, MF; no feeders, NF; males with female feeders, FF. For 1986–1988, marshes with values both for MF and NF were used for the discontinuous feeding treatment; thus, MF are discontinuously fed males and NF are discontinuously not fed males. This is not true for Rest Area in 1989, when the MF and NF territories were contiguous blocks on opposite halves of the marsh because we did not have enough feeders to feed all the males on this marsh. We excluded the 1989 data from Rest Area from marsh level analyses, but included them in the individual analyses as contiguously fed and not fed males.

males. We expected discontinuously fed males to expand their territories at the expense of discontinuously unfed neighbors, but they did not. However, although they did not expand their territories, they did have larger harems than their unfed neighbors within the marsh. Thus, both discontinuously fed and contiguously fed males had larger harems than unfed males. These results support the hypothesis that females prefer males that display more, but they do not rule out effects of male–male competition on harem size. Males fight hard to gain territories on these marshes.

#### Food versus display in female choice

Harems were significantly larger at territories with male-only feeders than at territories with female-only feeders (Figure 5). This result supports the hypothesis that females chose territories on the basis of male presence and also suggests that the presence of displaying males is a more important criterion for female choice than supplemental food. Although this result was completely unanticipated, in retrospect it is less surprising: differences in harem sizes are largely generated by late-settling females whose nesting is not constrained by early

spring food shortages but whose success is limited by predation (Langston et al., 1990). As nest success on marshes where males were fed was more than twice that on control marshes (Figure 7), the increased presence of males caused by feeding should be an important criterion for mate choice in later settling females. Late-settling females may also have been responding to the reduced number of nest failures on territories where males were fed. For yellow-headed blackbirds, early nest failures strongly deter later female settlement (Gori et al., 1996).

Our least conclusive result is that feeding females failed to increase harem size. It took us 2 years to learn how to make female feeders that excluded males. In 1988, feeding females did not increase harem sizes; indeed, the mean harem size for female fed males was only 2.7, while that for control males was 5.4 (means of marsh means). In 1989, however, feeding females increased harem sizes somewhat; males whose females were fed had a mean harem size of 5.0, while controls had 4.0 (means of marsh means). At one marsh (Peters), mean harem size went from 2.7 in the first year of feeding to 5.4 in the second; additional years might have led to additional increases as the number of females familiar with the feeders increased.

Our low harem sizes for the first year of female feeding contrasts sharply with earlier results from open trays (Ewald and Rohwer, 1982; Wimberger, 1988). Two factors may explain this drop. First, females cannot learn about the artificial food before settling on the territory by watching the male feed; thus our female-only feeders are most likely to affect female settlement only for returning females that learned to use the feeders in the previous year. Second, in the first year of female feeding, the earliest female to settle on a territory is likely to be the first to learn to exploit the feeder. Females are energy limited in early spring, and primary females behave aggressively to later arrivals (Langston et al., 1990), so providing females with food that they must learn to exploit creates asymmetries favoring early residents. The energetic costs of excluding other females should be low for primary females with access to supplemental food, and unsettled females should undervalue the territory since they have not yet learned about the supplemental food.

#### Benefits of choice to females

A striking result of this study is that females are clearly making strong and adaptive choices concerning their breeding situa-

**Table 5**  
Spearman rank correlations between male behaviors and the probability of nest success

Behavior	$\rho$	$\hat{p}$	$n$
Correlations between behavior deviations and probability of survival deviations: all treatments			
Song rate	+0.07	ns	267
Flight rate	-0.03	ns	268
Time vigilant	+0.05	ns	268
Time on	+0.03	ns	268
Alarm calls	-0.060	ns	268
Correlations between behavior deviations and probability of success deviations: controls only			
Song rate	-0.027	ns	92
Flight rate	+0.058	ns	92
Time vigilant	+0.211	.04	92
Time on	+0.144	ns	92
Alarm calls	-0.060	ns	92

tion at the level of treatments. Where males were fed, harems were considerably larger, and feeding males greatly increased nest success. These results suggest that females choose marshes by criteria that enable them to considerably enhance the probability of fledging young. Male vigilance is implied as a causal factor because fed males spent much more time on their territories than unfed controls. Marshes where females were fed had higher nesting success; although we did not quantify female behavior, it is likely that feeding females reduced the time they spent away from their territories foraging. On average, nesting success on marshes where either males or females were fed was more than 2.5 times higher than on control marshes (Figure 7).

Interestingly, however, females did not seem to make choices among males within marshes on the basis of normal intermale variation (i.e., when differences between treatments were statistically removed). When male displays were measured as marsh deviations, they were uncorrelated with a parallel set of marsh deviations in harem sizes. Similarly, we found no correlations between marsh deviations in male display and deviations in nesting success by territory. This was not the case when fed and unfed males were interspersed within marshes. In the discontinuous treatment, feeding strongly affected harem size, suggesting that females respond only to extreme differences among males within marshes. Interestingly, no increase in nest success was associated with the preference females showed for discontinuously fed males within marshes. Thus, choice between marshes seems to be more important to female fitness than choices between males within marshes.

Although greater male presence is associated with an increase in male harem size, we cannot be certain that the increased vigilance from males that spent more time on their territories drove the increase in harem size. Some other effect of having provided food to males could be driving the differences in harem sizes or nesting success. One possibility is that females simply prefer to nest near other females to dilute the effects of predation. This interpretation seems rather unlikely. Feeding males increased harem sizes only 51% and feeding females scarcely increased harem sizes at all; yet, both of these treatments increased the survival of nests by more than 250%. Other studies have also addressed the roles of male vigilance and predator dilution in reducing nest predation. Searcy and Yasukawa (1995) review both experimental and observational studies suggesting that vigilance and nest defense have positive influences on nesting success (see also Picman et al., 1988; Weatherhead, 1990; Yasukawa et al. 1992). They also review studies that are consistent with predator dilution, active defense, or both (see Picman et al., 1988; Ritschel, 1985). In sum, evidence from at least three other studies support male vigilance and nest defense as forces reducing nest predation in redwings.

The presence and abundance of predators that males can defeat probably vary greatly from marsh to marsh, but it would be difficult to adjust male display and female choice to conditions at individual marshes. Thus results are likely to vary among studies. Yasukawa et al. (1987) found that males with more intensive nest defense had larger harems but that these males did not have greater nesting success. Ritschel (1985) demonstrated that nest defense by male redwings did reduce marsh wren losses and that females preferred those males. Magpies are important nest predators in our study area (Beletsky and Orians, 1991), and mobbing behavior of males often deters magpies. While the effectiveness of males at deterring magpie predation may reliably be signaled to females by the amount of time that males are present on their territories, the amount of time that a male is present on his territory is unlikely to have any significant effect on the number of nests taken by nocturnal predators.

The possibility that female choice is normally exercised most strongly at the marsh level helps resolve how females may avoid being deceived by males with unusually high display rates. That females might be attracted strongly to marshes where many males are present and displaying for much of the day seems reasonable because many predators that attack redwing nests are mobbed communally by both males and females. When northern harriers or magpies approach a redwing marsh, they are usually attacked by multiple males; there is also much neighbor involvement in the mobbing of predators that have landed on a particular territory. For harriers, owls, and magpies, any redwing nest on marshes of the size we studied is a potential target for predation (Beletsky and Orians, 1991), and we found no increase in nest survival when females chose fed over unfed males within marshes. In contrast, our data suggest that females have much to gain by choosing marshes where many males are present throughout the day.

### Interaction effects

These feeding experiments were designed to address problems of male body size evolution, so we do not have the final treatment group needed for a complete analysis of the effects of food and displays on female choice—open trays that provisioned both sexes. Feeding both sexes would resolve whether there is a significant interaction between feeding females and increasing male displays. If feeding both sexes yielded a significantly greater increase in harem size than the summed increase caused by feeding males and females separately, it would imply that females value reinforcing information involving both food and displays more than information on either effect alone.

Experiments done a decade before these single-sex feeding experiments indicate that feeding both sexes does not have a greater effect on harem size than feeding either sex. In 1977, Ewald and Rohwer (1982) provided open trays on two marshes within this study area. Both males and females used the food, and harem sizes on fed territories increased by 38%. Wimberger (1988) repeated this open tray experiment in 1981, using an improved design to minimize marsh effects. At one marsh, harem sizes on fed territories increased by 38%; at another marsh they increased by 11%. None of these increases exceeds the average 51% increase that we achieved by feeding only males. While these indirect comparisons are only preliminary, they suggest that feeding both sexes is no more effective than feeding males alone. Again, display seems important to females in choosing their breeding situation at the level of marshes.

Searcy and Yasukawa (1995) criticized both of these early studies because the feeding treatments were blocked into separate marshes or in separate halves of marshes, rather than interspersed. While interspersed may be the correct theoretical design, it does not work because females take food from feeders on neighboring territories.

### Problems of scale

Past studies of redwings attempting to distinguish between female choice of male traits and female choice of territories have often had ambiguous results (reviewed in Searcy and Yasukawa, 1995). This may be because most studies looking for evidence of female choice have focused primarily on choices among males on individual marshes. In this study we monitored the harem size and reproductive success of individual males on six to nine marshes every year for 4 years. The contrast in the results of our analyses of choice between

and within marshes suggests that studies of female choice may be plagued by problems of scale.

The lack of correlations between male display and either harem size or nest survival within marshes suggests the possibility that isolated male feeders (e.g., one per marsh) might have virtually no effect on the harem size or nesting success of the fed male. If this is true, it would appear that males have been placed in an interesting bind by the way in which selection has molded choice in females. Having a relatively high rate of display within his own marsh might accomplish no more for that particular male than it would for his neighbors. But fighting his way onto a marsh with active males should mean a lot to an individual male, both with regard to the size of his harem and to the success of his nests. If this is true, females cannot be fooled by males that display a lot when prospecting females visit their territories because females seem mainly to be interested in the level of activity at the lake (presumably on a density basis) or in the success of earlier nests. Displaying at a high rate has measurable costs to males. In another study, we show that males that display more, either because their females were fed or because their neighbors were fed, were more likely to die between seasons than males that were fed and also had high rates of display (Rohwer et al., 1996). The body condition of fed males was considerably higher than it was for all other groups of males in the study.

In conclusion, females seem to be much more strongly attracted to marshes with high levels of activity than to individual males within marshes. This result suggests that males can gain much by fighting their way on to a hot marsh, but little by advertising to be the best male in that marsh. In early spring, as females arrive, one often sees groups of females settle on a marsh for a short while, only to leave without having visited individual territories, moving on to a neighboring marsh. These flocks of females may be making choices among marshes. Given the enormous variation in nesting success among marshes, choosing a marsh may be far more important to a female's reproductive success than choosing among males within a marsh.

We were surprised that female choice was so strong at the level of marshes and that we could detect female preference within marshes only by greatly exaggerating differences in male behaviors that apparently have strong effects at the marsh level. This lack of significance associated with normal intermale variation within marshes suggests that ecological problems of scale are probably affecting studies of mate choice in avian breeding systems in ways that, to the best of our knowledge, have not previously been investigated by behavioral ecologists.

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