

Basal song rate variation in male red-winged blackbirds: sound and fury signifying nothing?

Male red-winged blackbirds (*Agelaius phoeniceus*) vary substantially in how much they sing. We tested whether song rate reflected the male's quality, the quality of his territory, or his frequency of interaction with potential competitors. Song rate declined with the seasonal decline in nest initiations, suggesting that song is used to attract females. However, males with higher song rates did not obtain larger harems. This suggests that females do not use male song rate to assess either male quality or territory quality. If song rate signals male quality to male rivals, and if territory owners are of higher quality than floaters, then owners' song rates should be higher than those of floaters. However, when we removed territory owners temporarily, the song rate of their floater replacements was similar to that of the original owners. Finally, a male's song rate was not affected by how frequently he chased intruders, or by the proximity or number of neighbors he had. In short, the only information that basal song rate of red-winged blackbirds appears to provide to conspecifics is that the territory is occupied. In simulated territory takeover attempts, however, song rate was significantly higher than the basal rate. Thus, more may be revealed by the singer in these situations. [*Behav Ecol* 1991;2:123-132]

During the breeding season, male birds display to attract mates or repulse rivals or both. For some species, more vigorous displays reap greater reproductive return (e.g., Duncan and Bird, 1989; Pruett-Jones and Pruett-Jones, 1990; Vehrencamp et al., 1989). Song is a common component of passerine display. Both mate attraction and rival repulsion functions for passerine song have been vividly illustrated when males have had their singing ability surgically muted (McDonald, 1989; Peek, 1972; Smith, 1972, 1976, 1979). Muted males have difficulty acquiring and holding territories or mates. When the effects of the surgical muting are temporary, males are able to regain territories or mates once their voices return. Song rate varies less in natural populations than in muting experiments. However, in natural populations, greater singing vigor has been associated with better parental care (Grieg-Smith, 1982), higher male quality (Reid, 1987), and more rapid mate attraction (Alatalo et al., 1990; Reid and Weatherhead, 1990). Despite the ease of measuring song rate, it has received less attention than more elaborate aspects of song (Alatalo et al., 1990). In this paper, we examine both potential causes and consequences of song rate variation in red-winged blackbirds (*Agelaius phoeniceus*).

The red-winged blackbird is a common North American passerine that breeds polygynously over much of its range (Eckert and Weatherhead, 1987b; Orians and Christman, 1968). The species breeds in various habitats ranging from cattail (*Typha* sp.) marshes where nest density is high, to upland fields where nest density is low (Eckert and Weatherhead, 1987b). Breeding sites are nonetheless limited; some males defend no territories, some defend territories that attract no females, and some defend territories with multiple females (Orians, 1980). These facts, and the fact that females breed exclusively with territory owners (Gibbs et al., 1990; Monnett et al., 1984; Searcy, 1979a), lead to intense competition and selection for territory ownership. The red-winged blackbird territorial system is thus characterized by pronounced variation in male success, territory quality, and intrusion rates. We focus on these three variables in testing hypotheses to explain variation in song rate. In essence, we are asking what information conspecifics can obtain from song rates.

The first hypothesis we consider is the resource-holding potential (RHP) hypothesis. RHP is usually viewed as the total of an individual's fighting abilities, which often depend on size or strength. It has been assumed that better fighters obtain better or more re-

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sources (Darwin, 1871; Parker, 1974). Thus, this hypothesis predicts that male red-winged blackbirds with high RHP will control larger harems than individuals with low RHP. Non-territorial "floaters" that have been unable to capture a territory will have the lowest RHP. If song rate is indicative of a male's RHP, then males with higher song rates should have larger harems than males with lower song rates. Furthermore, territory "owners" should sing at higher rates than their replacements, i.e., males that were previously floaters. Thus, if RHP affects song rate, conspecifics could determine a territory occupant's quality by monitoring his song rate.

The second hypothesis we consider is the territory-value hypothesis. According to this hypothesis, male song rate reflects the value of the territory being defended and is independent of male quality. Radesäter and Jakobsson (1989) found that, in their population of male willow warblers (*Phylloscopus trochilus*), there was no competition for territory vacancies, and all replacing males sang at rates indicative of the territory's potential for attracting females. Hence, males on poor-quality territories sang at lower rates than males on high-quality territories, regardless of the males' status. If the territory-value hypothesis applies to red-winged blackbirds, it predicts an association between higher song rates and larger harems. However, in contrast to the RHP hypothesis, the territory-value hypothesis predicts that the song rate of replacements should be similar to that of owners. If the territory-value hypothesis holds, conspecifics that monitored song rate would obtain information about the quality of a territory rather than about the occupant. For willow warblers, song rate may be an honest signal of food availability on the territory. However, in situations where males are able to obtain food from outside their territories, song rate may no longer honestly reflect the abundance of food on a territory.

The final hypothesis we consider is the interaction hypothesis. In red-winged blackbirds, neighbors and floaters frequently intrude on territories (Metz and Weatherhead, 1991; Peek, 1971). Because singing aids in repulsing intruders (see above), more frequent singing may be used to counter more frequent intrusions. If, on the other hand, singing functions to repel intruders before they actually intrude, then intrusions will be less frequent on territories defended by males with greater song rates. This hypothesis proposes that the frequency of interactions between males determines song rate. If interaction frequency is a function of male quality or territory value (e.g., Arcese, 1987; McNair, 1987; Norton et al., 1982), this hypothesis will

not be mutually exclusive of the previous two hypotheses.

We determined harem size and used several indexes of the frequency of interactions between competing males to test whether song rate revealed information about these factors. We used removal experiments to test whether song rates of owner and replacement red-winged blackbirds were indicative of RHP, territory value, or both.

MATERIALS AND METHODS

Our study area was in southeastern Ontario near the Queen's University Biological Station (45°37' N, 76°13' W). The territories in our population of red-winged blackbirds were irregularly spaced along the sides of approximately 30 km of highway. We used most of these territories in both years of the study.

All analyses were performed on a micro-computer version of the Statistical Package for the Social Sciences (Nie, 1988). All means reported are ± 1 SD.

Song rate

We observed territory occupants from inside a vehicle parked 20 to 30 m from the territory. We determined song rates (number of songs per minute) while the male occupant was visible and within hearing range. Ninety-four percent of our observation periods ($N = 1850$) were 5 min. We only included observation periods for which the male was visible and within hearing range a minimum of 10% of the time ($N = 1011$). We also did not include assessments where males gave alarm calls in response to our presence; this generally did not occur until females were feeding nestlings. We visited each territory repeatedly (mean = 6.5 ± 3.9 visits per year) to determine the occupant's song rate. In most cases, territories were visited in systematic order (i.e., starting one territory beyond the one we had last observed in the previous visit to the field), but we made more visits to territories where we had performed removals. Observations were made between 0500 and 1000 h and between 1800 and 2030 h from early April to mid-July in both years.

Breeding activity

We tested whether males with higher song rates attracted larger harems. Harem size was defined as the maximum number of simultaneously "active" nests (having one or more eggs or nestlings) on a territory. Red-winged blackbirds have conspicuous nests, and we are confident that we found all nests on the territories that we used in this analysis.

We removed some males before their females began nesting (see below). To determine whether this affected the harem size on the territory when the final occupant was present, we tested if a territory's harem size in years when owners were removed was different from years when owners were not. We also performed removal experiments in 1988 and determined harem sizes on many of the same territories used in the present analysis. Thus, we included data from 1988 (and all possible pairs of years) for this test. Harem size decreased between years in 8 of 47 cases where owners were removed, and in 13 of 45 cases where no removals were performed in either year ($\chi^2 = 1.23$, $p = .27$). Because this indicates that our removal experiments had no effect on a territory's ultimate harem size, in testing the territory-value hypothesis all males taken from a particular territory were assigned the ultimate harem size that their territory supported.

In temperate-breeding birds, breeding opportunities occur less often as the breeding season progresses. If males defend territories to entice females to breed, a decline in female availability will cause a concomitant decline in territory value. We estimated the seasonal decline in territory value for our population by counting nest initiations (date when first egg was laid) as the breeding season progressed. We searched territories for nests every 3–7 days from the day the first nest was built until the last day we monitored song rates. We found the great majority of nests at the egg stage or earlier. We estimated the initiation date of each nest by backdating, based on an incubation period of 11 days and a nestling phase of 10 days (Nero, 1956). With experience, we could visually age nestlings to within a day.

Owners and floaters

We performed removal experiments to compare the song rates of owners and their floater replacements. We assessed a territory occupant's song rate before capturing and removing him. Owners were captured and removed using playback, stuffed male decoys, and traps (Smith, 1972) or mist nets. Owners were housed in aviaries until we completed removal experiments on their territory. Owners were usually replaced within a day. We then measured the song rates of replacements. On some territories, we removed the replacement and repeated the procedure. We continued to remove birds until no replacements occurred or until a replacement was too unresponsive to be captured. The most birds removed from any one territory was seven. Removals were performed until 13 and 25 June in 1989 and 1990, respectively.

We termed the first replacement a "shallow floater." Males that replaced shallow floaters and all subsequent replacements were referred to as "deep floaters." On average, in 1989, we obtained song rates of individual owners 4.8 times, shallow floaters 3.4 times, and deep floaters 2.7 times. In 1990, the same values were, respectively, 3.6, 3.6, and 5.4 times.

We had to be certain that replacements had previously been floaters, since we would otherwise have compared song rates of owners to owners. Prior to removing a territory owner, we mapped the territory boundaries of neighbors, and, in some cases, we also banded neighbors. After removing a territory occupant, we ascertained whether the replacement was banded or whether he also occupied a neighboring site simultaneously. The spacing of many of our territories (see below) also reduced the chances that neighbors would replace the males we removed. If a neighbor did claim a vacancy, we excluded that male from our analyses.

Male–male interactions

If songs are used to repulse rivals, song rates may be higher where chases occur more frequently. While monitoring song rates, we recorded all instances where owners chased neighbors or floaters. From these data, we computed chases per hour for each territory.

Males from neighboring territories may display to each other without actually becoming involved in chases. We thus tested whether song rates were affected by the distance between territories or by the number of neighbors. Most of our territories were separated from neighbors by areas of habitat unsuitable for breeding (i.e., plowed fields or forest). Each "isolated" territory was occupied by one male, and each was centered on patches of cattail approximately 25 to 250 m² in size. Some isolated territories were close enough that neighbors came in contact with each other. However, it was rare that a male was able to defend the perimeter of two isolated territories. "Contiguous" territories were on cattail marshes that were subdivided into 10 or more territories. Contiguous territories ranged in size from 200 to 1000 m². Vacancies created by removal experiments on contiguous territories were more likely to be annexed by neighbors than was the case on isolated territories. As a further index of the frequency of interactions between males, we counted the number of neighbors surrounding each territory. Here again, we compared the song rates of males according to the number of neighbors they had.

Finally, we tested the effects of simulated

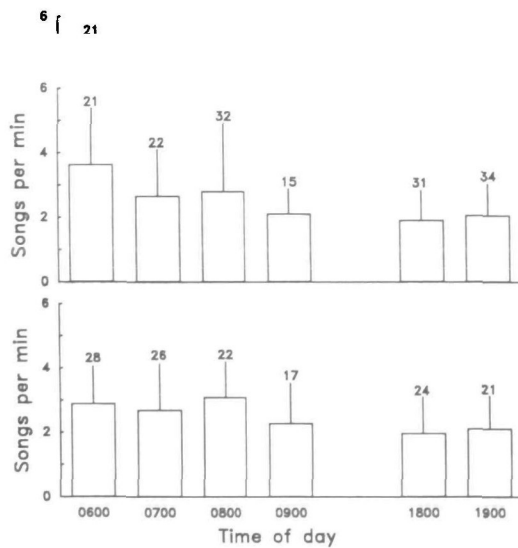


Figure 1
Song rates for owners relative to the hour of the day in 1989 (top) and 1990 (bottom). Sample sizes are given above the vertical lines that indicate standard deviations.

dom sing when they arrive in a territory (Orlans and Christman, 1968; Røskaft and Rohwer, 1987). A singing male in a territory is either an owner or a male attempting to take over. The aggressive reactions of owners to takeovers is presumably what we exploit with our capture methods. To test whether song rates increased during takeovers, we compared an occupant's song rate from 5 min before a playback experiment with the song rate during 5 min of playback. Playback experiments involved placing a stuffed, male red-winged blackbird in the center of a territory. A cassette player suspended below the decoy played territorial song at a rate of 3.5 songs per minute. Songs had been taped from a single male that occupied a territory on a marsh outside of the study area. Song rates of territory occupants were monitored for the first 5 min after the male detected the decoy (i.e., once the occupant oriented or moved toward the source of the playback).

RESULTS

Between years, changes occurred in many of the individual males sampled, harem sizes on specific territories, quality of individual territories, pairing dates, etc. Because such changes make these data partially independent, we treat each year separately in our tests.

We could not simultaneously test the relationship between all of our variables and song rate because the resulting design had sample sizes ranging from 1 to 15 in individual cells, and this weakens the multiway analysis of variance (Tabachnick and Fidell, 1989). Instead, we ran separate tests on the importance of each variable. In many cases, we subdivided our data for additional tests. This approach required that we divide our experimentwise error rate by the number of tests. Thus, when we tested for a relationship between song rate

and a variable in eight nonindependent tests, we could only reject the null hypothesis of no differences between groups when $p \leq .006$.

Song rate

For various reasons, we had more sampling periods for some days than for others. To weight each day equally and to remove within-day variation, we computed an average song rate for each day. Based on owners only, daily average song rate declined as the breeding season progressed (for 1989, $r = -.34$, $p = .005$, $N = 66$ days; for 1990, $r = -.48$, $p < .001$, $N = 60$ days). Our removal experiments were done in a way that required us to obtain more owner song rates early in the season and more floater replacement song rates late in the season. In comparing song rates, we controlled for potential seasonal biases by computing a regression of owner song rate against Julian date. We then adjusted song rates of both owners and replacements to reflect the middle of the season (15 May or Julian date 135) by using the slope (m) from the owner regression as follows:

$$\text{adjusted rate} = \text{actual rate} - m(\text{day} - 135).$$

After adjusting for seasonal effects, we found that song rate still varied among owners from hour to hour (Figure 1; ANOVA for 1989, $F = 4.94$, $p < .001$; for 1990, $F = 3.34$, $p = .007$). To avoid any potential biases from time of day effects, we readjusted song rates of both owners and replacements as follows:

$$\text{readjusted rate} = \frac{\text{mean rate for hour}}{\text{mean rate for all hours}} \times \text{adjusted rate}.$$

Finally, we determined whether a bird's increased energy requirements in cold weather resulted in a concomitant decrease in song rate (e.g., Reid and Weatherhead, 1990). We found that, after having controlled for season and time of day, song rate was not affected by temperature (for 1989, $r = -.06$, $p = .26$, $N = 123$ hourly temperature averages; for 1990, $r = .02$, $p = .41$, $N = 105$). Except where indicated, we only used song rates adjusted for season and time of day.

The average song rate of individual males still varied after these adjustments (Figure 2). Some males consistently sang at low rates (e.g., one owner had a mean rate of 1.3 songs per minute, range 0.1–3.9, $N = 11$), whereas others consistently sang at high rates (e.g., another owner had a mean rate of 3.6 songs per minute, range 1.8–5.5, $N = 9$). We tested whether male quality, territory quality, or the

frequency of male-male interactions could explain the remaining variation.

Breeding activity

We used average song rates for males that had been recorded more than once. We first tested whether males with higher song rates attracted larger harems. Harem sizes ranged from 0 to 5 in 1989 ($N = 76$ territories, mean 1.3 ± 0.9 females) and from 0 to 4 in 1990 ($N = 63$, mean 1.6 ± 1.0). In neither year was song rate correlated with harem size (Figure 3). The results were similar when we used owners only (Figure 3). Because most females arrived a few weeks before nesting began, we repeated the analyses to determine whether females used male song rate as a cue for choosing nest sites. To make this determination, we considered song rate before the date the population's first egg was laid. Again, we found no relationship between male song rate and ultimate harem size in either year, whether we tested using all males or owners only (Figure 3).

Early nesters have greater reproductive success in many bird species (reviewed in Price et al., 1988). Thus, we tested whether females laid eggs earlier on territories where males (owners only) sang at higher rates. We found no support for the prediction; the date the first egg was laid on a territory was not related to owner song rate in 1989 ($r = -.12$, $p = .16$, $N = 67$ males) or 1990 ($r = .11$, $p = .20$, $N = 56$). The relationship was also not significant using only song rates from the period before egg laying (for 1989, $r = .02$, $p = .45$, $N = 47$; for 1990, $r = -.13$, $p = .23$, $N = 38$).

A male red-winged blackbird in a low-density population can be more certain of his paternity in the nests on his territory (Gibbs et al., 1990). We tested whether the relationship between breeding activity and song rate was more reliable among males from territories in low-density habitats that had no neighbors. Again, all results were nonsignificant (data not shown). Thus, extrapair fertilizations were probably not confounding the relationship between nesting activity and male song rate.

Nesting in both years peaked between 15 and 20 May (Figure 4). Song rate (without making adjustments) was negatively correlated with cumulative nest initiations in 1989 (Figure 4; $r = -.52$, $p < .001$) and 1990 ($r = -.38$, $p = .004$). This suggests that males sang at a rate that was related to the likelihood that they would attract an additional female.

Owners and floaters

In 1989, we used 20 territories for removal experiments from which we obtained song rate

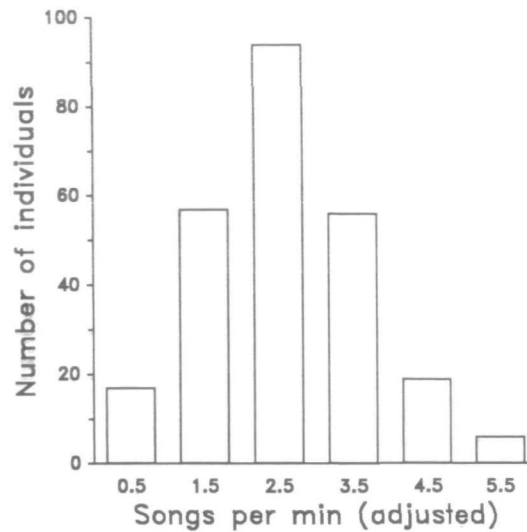
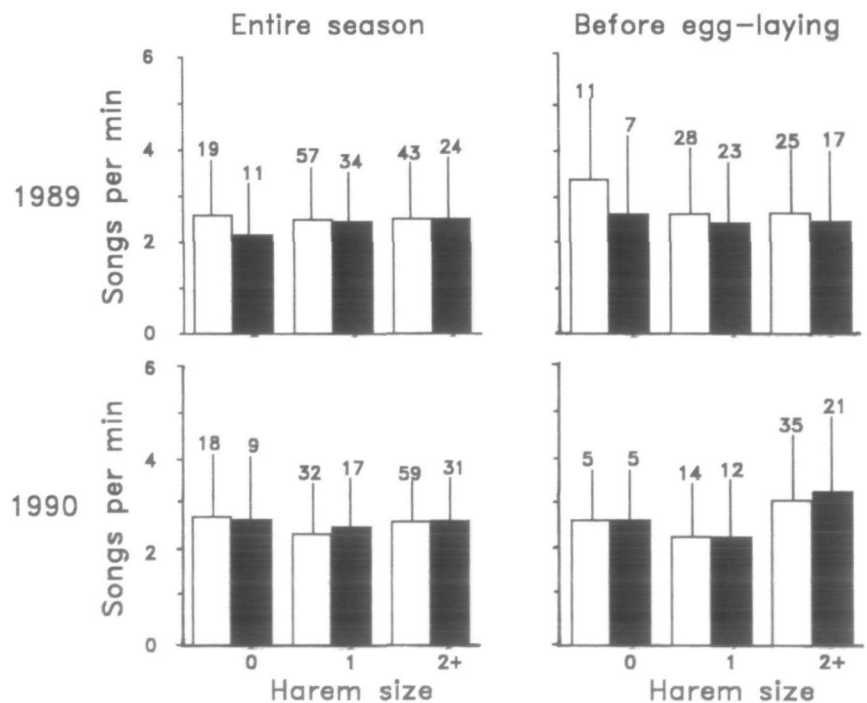


Figure 2
Variation in average song rates for individual males ($N = 249$) after correcting for seasonal and time-of-day effects.

data for both owners and floater replacements. We also had two territories where the owner disappeared without our intervention. In 1990, the equivalent values were 27 removal experiments and two territories where the owners disappeared naturally. In total, we obtained song rates for 142 owners (including owners from territories where no removal experiments were performed), 47 shallow floaters, and 42 deep floaters.

To avoid pseudoreplication, we averaged song rates for individuals we had observed more than once. Comparisons of song rates of owners and floater replacements revealed no significant differences (Figure 5; ANOVA for 1989, $F = 0.13$, $p = .88$; for 1990, $F =$

Figure 3
Song rate of males sampled on a territory combined over the whole season and before egg laying only. Song rates of different males from the same territories are treated as separate values. Blank bars are data for all males; solid bars are data for owners only. No significant relationships between harem size and song rate were detected (eight separate ANOVAs, all p values $> .15$).



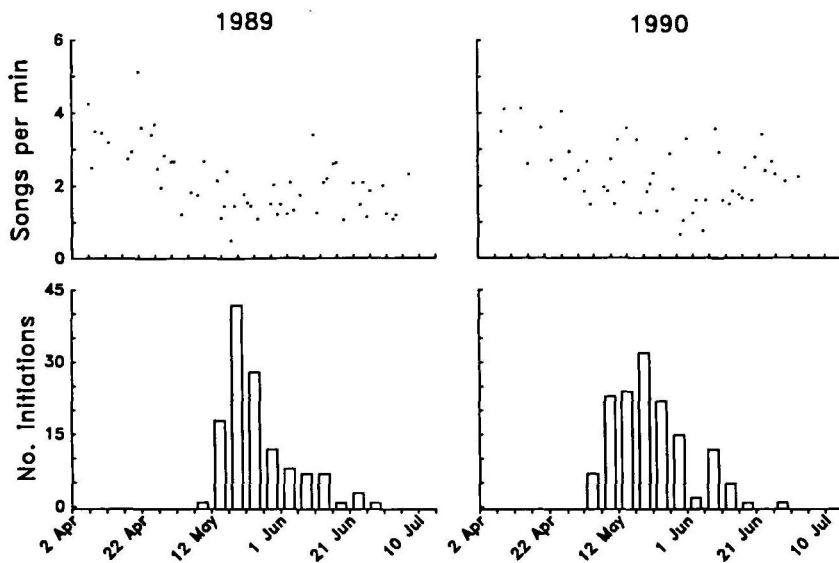


Figure 4
Daily average song rates (owners only) versus nest initiations for the whole population ($N = 125$ nests for 1989, $N = 141$ for 1990). Intervals are 5 days.

0.15, $p = .86$). We then compared the song rates of owners and shallow floater replacements on a territory-by-territory basis. In the 2 years, 21 shallow replacements had song rates greater than the owners they replaced, and 18 had song rates less than the owners they replaced (paired t test, $t = -1.33$, $p = .19$). Similarly, 11 deep replacements sang at higher rates than owners, and 8 sang at lower rates ($t = -1.04$, $p = .31$). Thus, in neither of our tests did song rate betray any difference in the RHP of owners and floaters.

Male floater red-winged blackbirds compete most intensely shortly after vacancies appear (Peek, 1971). We tested whether song rate declined with the duration of a floater replacement's tenure. In both years, floater song rate did decline the longer the floater had been on the territory (for 1989, $r = -.12$, $p = .08$, $N = 146$ individual song rates; for 1990, $r = -.27$, $p < .001$, $N = 179$). This

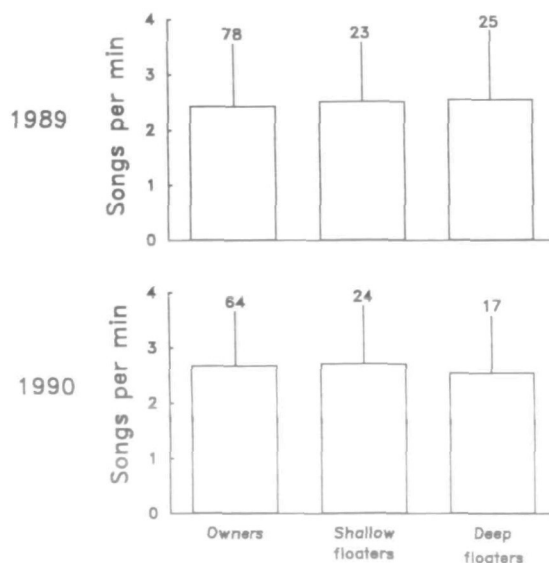


Figure 5
Song rates of owners, shallow floaters, and deep floaters. See text for explanation of designations.

suggests that, if anything, song rate is negatively correlated with male experience. It also suggests that, if contests for territory ownership are most intense shortly after vacancies appear (Peek, 1971), song rate should be related to the frequency of male-male interactions.

Male-male interactions

We first tested whether song rates were higher during chases. We did not include data from territories adjoining forested areas because we could not reliably monitor chases in these situations. Chases were observed in 60 of 534 observation periods in 1989, and in 91 of 453 observation periods in 1990. Song rates during observation periods in which chases occurred were not significantly different from observation periods in which they did not occur (Table 1). These findings were the same when we considered owners only (Table 1). We then compared song rates on territories where we observed at least one chase during the breeding season with song rates on territories where chases were never observed. To control for differences in the number of observation periods on different territories, we averaged song rate for each territory. We found no difference in song rate on territories where chases occurred versus where they did not occur, whether we considered all males or owners only (Table 2). Thus, we have no evidence that the frequency of chases affects song rate, or vice versa.

We then examined the effects of proximity to neighbors. We observed 58 isolated and 27 contiguous territories in 1989 and 49 isolated and 21 contiguous territories in 1990. We again used mean song rate observations for individual males for this test. In neither year did song rate differ between isolated and contiguous habitats, whether we included all males or just owners (Table 3).

As an additional index of the potential for interaction with other males, we counted the number of territories that shared boundaries with each territory and tested whether this affected song rate. In neither year was song rate affected by the number of neighbors a male had (Figure 6; ANOVA for 1989, $F = 1.68$, $p = .19$; for 1990, $F = 1.28$, $p = .28$). This result was unchanged if owners alone were considered.

Finally, we considered the reaction of owners to simulated takeovers. When we placed stuffed decoys on territories and played recordings of territorial song, the song rates of territory occupants increased by 20% (unadjusted song rates, data pooled for 1989 and 1990; before playback, mean songs per min = 2.96 ± 1.7 ; during playback, mean = 3.53

± 1.6 , paired *t* test, $t = -3.31$, $p < .001$). Together with the other results for male-male interactions, these data indicate that male song rate does not change in response to passive interactions, but increases dramatically when an interaction becomes more threatening.

DISCUSSION

We found no evidence that song rate was an index of RHP. Owners with large harems sang at rates similar to males with small harems, and owners sang at rates similar to floater replacements. Several other studies have also failed to find evidence that measures of RHP relate to reproductive success for adult male red-winged blackbirds (Beletsky and Orians, 1989; Eckert and Weatherhead, 1987a,b,d; Shutler and Weatherhead, 1991). The differences between successful and unsuccessful territory claimants in this system remain elusive, and chance may play an important role (Eckert and Weatherhead, 1987b).

There was little evidence that song rate was related to territory value. Males did sing less as the seasonal reproductive value of the territory declined, as has been shown for several other avian species (reviewed in Welty, 1982). Because floater replacements sang at rates similar to owners, all males could have adjusted their song rate to reflect the value of the territory they had claimed. However, the crucial evidence needed to support the territory-value hypothesis was a relationship between a male's harem size (which was our measure of territory value) and his song rate. Because we did not find this relationship, we cannot conclude that the relative value of a male red-winged blackbird's territory influences his song rate.

The absence of a relationship between song rate and territory value in our population contrasts with evidence from food supplementation experiments. With additional food, males of many species, including red-winged blackbirds, increase their song rate (e.g., Gottlan-

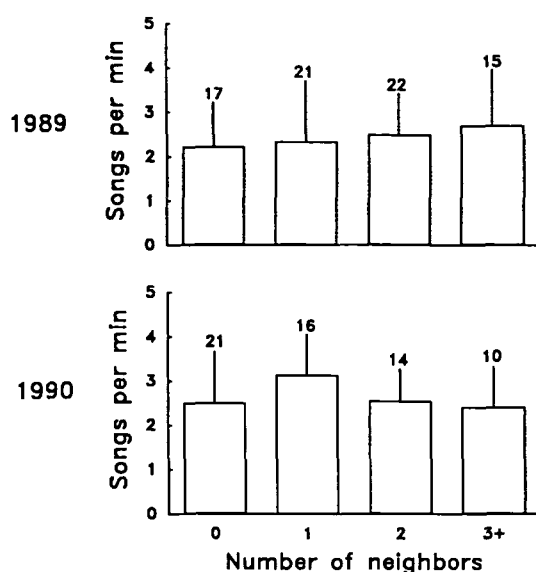


Figure 6
Owner song rates relative to the number of neighbors associated with the territory.

der, 1987; Searcy, 1979b), suggesting that song rate is an honest signal of territory quality. Females may use this signal because red-winged blackbird territories with additional food attract larger harems (Ewald and Rohwer, 1982), and females on these territories breed earlier (Wimberger, 1988).

However, food supplementation may cause greater variation in song rate than occurs in natural situations, which may be a partial explanation for our negative results. Yasukawa et al. (1987) also found no relationship between male display intensity and harem size in experiments where food was not supplemented. An additional factor that would explain why we found no relationship between song rate and harem size is that males in our population frequently forage off the territory, which would decrease any correlation between food abundance on the territory and song rate (Ydenberg, 1984). Thus, our results and those of Yasukawa et al. (1987) suggest that food availability in natural situations does not vary enough to affect song rate in a way that affects female settlement patterns.

Table 1
Effect of male-male chases on song rates

Song rate for	Observation periods with chases	Observation periods without chases	<i>t</i>	<i>p</i>
1989				
All males	2.5 \pm 1.6 (474)	2.6 \pm 1.3 (60)	-0.64	.53
Owners only	2.4 \pm 1.6 (318)	2.6 \pm 1.5 (39)	-0.76	.45
1990				
All males	2.6 \pm 1.5 (362)	2.4 \pm 1.4 (91)	0.94	.35
Owners only	2.6 \pm 1.4 (186)	2.4 \pm 1.2 (44)	0.85	.40

The data were compared using *t* tests. Means \pm SD of song rates are indicated. The numbers of observation periods are given in parentheses.

Table 2**Effects on song rates of defending territories that were susceptible to chases**

Song rate for	Territories where chases were seen	Territories where chases were not seen	<i>t</i>	<i>p</i>
1989				
All males	2.4 ± 1.2 (73)	2.6 ± 0.8 (40)	-1.10	.28
Owners only	2.3 ± 1.3 (48)	2.6 ± 0.8 (26)	-1.02	.24
1990				
All males	2.6 ± 1.1 (59)	2.6 ± 0.8 (52)	-0.11	.91
Owners only	2.6 ± 1.1 (34)	2.8 ± 0.8 (29)	-0.67	.50

Data were compared using *t* tests. Means ± SD of song rates are indicated. The numbers of territories associated with each category are given in parentheses.

We also found little support for the hypothesis that the frequency of male-male interactions was related to song rate. If greater display rates signal better quality resources, floaters may preferentially intrude on territories where display rates are high because usurpation of these territories will produce greater payoffs for the victor (Tamm, 1985). On the other hand, males that display more may be more formidable foes and worth avoiding. Unless these factors balance each other, a relationship between intrusion rate and display rate would result. We found no such relationship, indicating that song rate conveyed no useful information to floaters. Song rate was also not affected by the likelihood of interaction with neighbors. However, intense simulated male-male interactions did cause an increase in song rate. During simulated intrusion, territorial males infected with blood parasites are less aggressive than unparasitized males (Weatherhead, 1990). Although song rate may be important in this latter context, we cannot evaluate how important increased song rate would be to preventing actual takeovers.

We have thus far ignored the possibility that other aspects of red-winged blackbird song are better correlated with the variables we measured. The only other aspect of red-winged blackbird song that has received any attention is repertoire size. Repertoire size has been

shown to be correlated with male age, breeding experience, and harem size (Yasukawa et al., 1980; but see Smith and Reid, 1979). Repertoires may be more important in female choice than in male-male interactions because males present their repertoire more rapidly in the presence of females than in the presence of males (Searcy and Yasukawa, 1990; Smith and Reid, 1979). However, repertoires are more effective at repelling male intruders than is repetition of a single song (Yasukawa, 1981). Whether repertoires serve a female attraction or a rival repulsion function, these data are consistent with an RHP function for repertoire size. However, we cannot separate out the effects of territory quality because we do not know whether males use larger repertoires to signal the quality of their territories independent of their age or experience. Nonetheless, it appears that red-winged blackbird repertoires convey more information than song rate in most situations.

An inconsistency between the repertoire data and our data is Yasukawa's (1981) finding that males with larger repertoires [and hence more experience (Yasukawa et al., 1980)] sing at faster rates (but see Smith and Reid, 1979). Our data suggest that song rate was unrelated to experience, and thus faster song rates were probably not associated with larger repertoires. However, our song rate data for inexperienced males were obtained from males

Table 3**The effects of neighbor proximity on song rates**

Song rate for	Isolated	Contiguous	<i>t</i>	<i>p</i>
1989				
All males	2.5 ± 1.1 (85)	2.5 ± 1.1 (33)	-0.25	.80
Owners only	2.3 ± 1.1 (53)	2.6 ± 1.2 (25)	0.93	.36
1990				
All males	2.7 ± 1.0 (88)	2.4 ± 0.9 (24)	1.04	.30
Owners only	2.8 ± 1.0 (46)	2.4 ± 0.8 (18)	1.53	.13

Data were compared using *t* tests. Means ± SD of song rates are indicated. The numbers of males sampled are given in parentheses.

that had just taken over territories, whereas Yasukawa's (1981) inexperienced males had been in his study area for 1 year or more. Because we found that recent replacements elevate their song rates for a brief period during territory establishment (see also Peek, 1971), we have overestimated their long-term song rates. The important issue, however, is whether song rate is an honest signal. Because recent replacements sang at the same rate as more established owners, this argues against the possibility that higher song rate is an honest signal of male quality. In fact, just the opposite is suggested, because floater replacement song rate declined with time of tenure.

In general, despite much variation, the basal song rate of red-winged blackbirds appears to indicate only that a territory is occupied. We conclude that prospecting females that monitored a male's song rate would gain little information about the quality of the male or the quality of his territory. Similarly, competing males would gain little information from monitoring other males' song rates. Other studies have also found that red-winged blackbird display rates are weak predictors of nest defense or provisioning rate (Eckert and Weatherhead, 1987c; Yasukawa et al., 1987). If there is information to be gained from displays, it probably comes either during territory takeovers (Weatherhead, 1990) or from sources other than song rate. Alternatively, the variation among males in song rate is insignificant in most situations (Rohwer, 1982) and may be worth evaluating only when food resources limit males' abilities to display (Radesäter and Jakobsson, 1989; Reid and Weatherhead, 1990).

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