

## TERRITORY ESTABLISHMENT IN RED-WINGED BLACKBIRDS: IMPORTANCE OF AGGRESSIVE BEHAVIOR AND EXPERIENCE

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In this paper I assess the importance of aggression in acquisition of initial breeding territory by male Red-winged Blackbirds (*Agelaius phoeniceus*). The ability to acquire territory is expected to depend upon that portion of male quality determined primarily by intrasexual selection.

Darwin (1859, 1871) formulated the theory of sexual selection to account for certain apparent exceptions to his concept of natural selection, but evolutionary biologists now realize that sexual selection is a special case of individual selection relating to the evolutionary implications of competitive mating. Most zoologists agree with Darwin that sexual selection has two phases: intrasexual, usually in the form of competition between males; and intersexual or epigamic, usually in the form of female choice of a mate (Selander 1972, Emlen 1973, Brown 1975, Wilson 1975, but see also Mayr 1972). In practice it is difficult to separate the effects of non-sexual and sexual selection (Mayr 1972) and to distinguish between intra- and intersexual selection (Selander 1972). While the conceptual distinctions have been valuable, these difficulties have limited advances in the study of sexual selection.

In a polygynous territorial species such as the Red-winged Blackbird, males control access to mates by defending resources essential to females (Emlen and Oring 1977) and control of a territory is necessary for male reproductive success. Several features of Red-winged Blackbird reproductive ecology support the view that acquisition of initial breeding territory is mediated primarily through the intrasexual phase of sexual selection. Male Red-winged Blackbirds return to the breeding grounds approximately three weeks before females (Orians 1961, Case and Hewitt 1963) and attempt to establish territories. Returning males with prior reproductive experience are extremely faithful to their previous territories (Nero 1956, Case and Hewitt 1963), and re-establishment occurs with little difficulty (Nero 1956, pers. observ.). Fidelity to territory and the relative ease of re-establishment indicate that intrasexual selection is

most intense when males attempt to acquire their initial territories. Competition between males occurs primarily among birds in fully adult plumage, that is, birds who are at least two years old. The existence of considerable competition for territories is indicated by: rapid replacement following removal (Orians 1961); high conspecific male trespass rates (Peek 1971); and defense of suboptimal areas (Orians 1961, Case and Hewitt 1963, Robertson 1972, 1973).

Male Red-winged Blackbirds establish territories by taking over unoccupied areas, intruding between occupied areas and expanding, or displacing established residents (Nero 1956). As defined here, males are "successful" when they possess suitable nesting sites and are not displaced by other males prior to the onset of nesting by females (regardless of whether they acquire females themselves). In contrast, males who are unsuccessful: (1) take possession of areas lacking suitable nesting sites; (2) are displaced from or desert suitable areas prior to the onset of nesting; or (3) take possession of suitable areas but only as replacements of successful males whose mates have completed their nesting cycles.

I studied the aggressive tendencies of male Red-winged Blackbirds attempting to establish initial breeding territories. My hypothesis that aggression determines the outcome of competition for initial territories was tested by comparing the sizes, ages, behaviors and time budgets of successful and unsuccessful males that lacked prior reproductive experience on my study area.

I assessed the aggressive tendencies of these birds by using the relation between male Red-winged Blackbird behavior and aggression, as determined from my previous experiments with conspecific song playback and male-mount presentation within the territory (Yasukawa 1978). Aggressiveness is taken to be the tendency to approach, spend time near, and attack the mount. I had found these to be positively correlated with rate of more intense Song Spread display (the Song Spread is the most common territorial display given by the male; Nero 1956, Orians and Christman 1968), with

mean Song Spread intensity, and with proportion of time allocated to singing and defending the territory (Yasukawa 1978). The rate of less intense Song Spread display and the proportion of time spent foraging on the territory were negatively correlated with Red-winged Blackbird aggressive tendencies.

## STUDY AREA AND METHODS

I analyzed data collected from a population of Red-winged Blackbirds at Yellowwood Lake (Yellowwood State Forest) in Brown County, Indiana. The birds inhabited a marsh at the north end of this small (54 ha) man-made lake. Cattail (*Typha latifolia*), bulrush (*Scirpus validus*) and bur reed (*Sparganium eurycarpum*) were the dominant emergents of the marsh. About one-half of the territories adjoined a frequently-mowed camping area. The remaining territories and the campgrounds were surrounded by mixed deciduous forest interspersed with large planted stands of pines, including red (*Pinus resinosa*), Virginia (*P. virginiana*) and Scotch pine (*P. sylvestris*). Willows (*Salix* spp.) and planted bald cypress (*Taxodium distichum*) were common at the marsh-forest and marsh-campground edges.

Data had been gathered on this population during the six years prior to my study (W. H. Barnard and V. Nolan, unpubl. data); 54 males (color- and U.S. Fish and Wildlife Service-banded) with no known breeding experience at the study area formed the sample. Of these, 37 were successful and 17 were unsuccessful. All were at least two years old and in the definitive plumage.

To minimize confounding factors arising from intersexual interactions, analysis was limited to observations conducted prior to each male's first interactions with a female. I conducted 15-min observations of individuals daily in 1974, 1975 and 1976 between sunrise and 10:00 h. A random-number table was used to determine the order in which males were observed. Data from the three years were pooled. Behavior and time-budget variables (see below) were registered by hand on a flow chart marked in one-second intervals. A stopwatch and shorthand system allowed both time and duration of activities to be recorded. Observations were aided by binoculars and a spotting scope. My presence, 10 to 20 m distant, did not seem to affect the birds' behavior.

Terminology for display and behavior follows Orians and Christman (1968). The Song Spread was divided into four intensity categories (incipient, low, medium and high) based on the degree of wing extension (Peek 1972, Yasukawa 1978). A rate per minute for each category and a mean intensity were calculated for each male, as were rates of Flight Song, total songs, alarm calls, and trespass. A trespass occurred when a conspecific male perched within the subject male's territory for at least one second. The date each male was first sighted on the study area was noted and expressed relatively; the arrival of the first male of the year being treated as day 1 of that year. Also determined were the proportion of time spent on the territory and, within time on territory, the proportions of time spent singing and defending (including silent periods of alert perching), preening, resting (inactivity exceeding 30 s), foraging, and flying about the territory.

Flattened wing length (Palmer 1976) was used to estimate body size. Geographic variation in Red-winged Blackbird wing length was found to be highly correlated with geographic variation in cube root of

body weight (Power 1969). Exact ages were known for males captured previously as yearlings. Ages of males first captured in the definitive (as opposed to yearling) plumage were unknown, and a minimum age of two years was assumed.

Differences between successful and unsuccessful males were tested using *t*-tests and Mann Whitney *U*-tests (two-tailed). Statistical significance was accepted at the 0.05 level. The angular transformation was applied to time-budget variables (proportions) and the natural log transformation was applied to wing length (Sokal and Rohlf 1969). Untransformed data and 95% confidence intervals (CI) of the means are presented where appropriate.

## RESULTS

Evidence consistent with the hypothesized importance of aggression would be the following. When compared with unsuccessful males, successful males would: (1) perform Song Spreads of higher intensities at faster rates; (2) perform Song Spreads of lower intensities at slower rates; (3) produce a Song Spread of higher mean intensity; (4) allocate more time for singing and defending the territory; and (5) spend less time foraging on the territory. These predicted differences between the two groups of males were not fulfilled and the data offer no support for the aggression hypothesis.

I found the following: (1) Successful males performed medium intensity Song Spreads at a significantly slower rate than did unsuccessful males (Table 1). (2) Successful males performed incipient (least intense) Song Spreads at a significantly faster rate than did unsuccessful males (Table 1). (3) Successful males tended to produce a Song Spread of lower mean intensity than did unsuccessful males. This difference was near statistical significance ( $P < 0.08$ ; Table 1). (4) Successful males spent less time singing and defending the territory than did unsuccessful males; however, this difference was not statistically significant ( $P > 0.2$ ; Fig. 1). (5) Successful males spent significantly more time foraging on territory than did unsuccessful males (Fig. 1).

These results cannot be explained by differences in duration of observation time. Mean lengths of time the 37 successful and 17 unsuccessful males spent on territory during observation periods were  $86.8 \text{ min} \pm 4.71 \text{ (S.E.)}$  and  $96.2 \pm 5.40 \text{ min}$ , respectively; these periods did not differ significantly ( $t = -0.336$ ,  $P > 0.7$ ). Nor can the results be explained by differences in total song rate, trespass rate, date first sighted (Table 1), size (mean wing length for successful males = 126.7 mm, 95% CI 125.8–127.6 mm; unsuccessful males = 126.0 mm, 95% CI 124.4–127.5 mm;  $t = 0.90$ ,  $P > 0.3$ ),

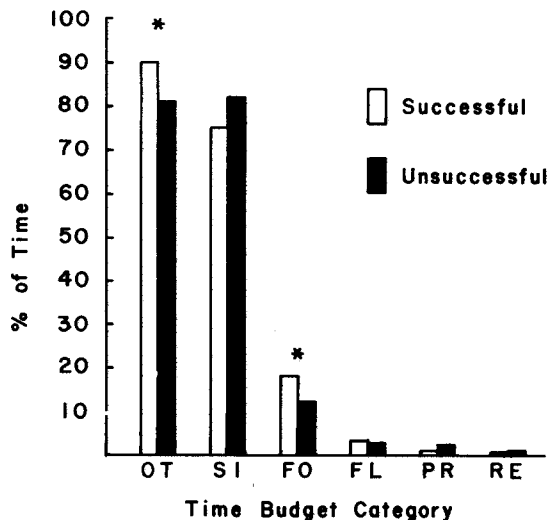


FIGURE 1. Comparison of time budgets of successful and unsuccessful male Red-winged Blackbirds expressed as percentage of total time spent on territory (OT), and percentages of time on territory spent singing and defending (SI), foraging (FO), flying (FL), preening (PR) and resting (RE). The *t*-tests are based on angular transformations of proportions of time in each category. Significant differences between the two groups (denoted by an asterisk) occurred in proportion of total time spent on territory ( $t = 2.09$ ,  $P < 0.05$ ) and proportion of time on territory spent foraging ( $t = 2.02$ ,  $P < 0.05$ ).

or age (median minimum age for successful males = 2.4 yr; unsuccessful males = 2.3 yr; Mann-Whitney  $U = 320$ ,  $P > 0.9$ ).

Successful males also spent significantly more time on territory than did unsuccessful males (Fig. 1). While it is difficult to account for this difference, because data are lacking on territorial food density and male activity while away from territory, it is unlikely that differences in food resources or energy requirements are responsible for this result. All males foraged on at least part

of their territories, and all but four unsuccessful males defended areas that fell within territories of successful males in other years or other parts of the same breeding season. The two groups of males did not differ significantly in size or age, and total foraging times seem similar. Much of the time male Red-winged Blackbirds spend away from territory is allocated to foraging (Orians 1961). If we assume that all time off territory was spent foraging, then the percentages of total time spent foraging by the two groups were quite similar: successful males = 26.3%, unsuccessful males = 28.9%. However, it is also possible that a portion of time away from territory was used to explore and assess other potential territories (Martin 1974, Nolan 1978).

As success in initial territory establishment does not appear to be related to aggressive tendencies, successful males must possess some other advantages in encounters with other males. Observations made at times other than the 15-min periods described above indicate that prior experience (excluding breeding experience at the study area, since all observed males lacked such experience) can affect the location and success of attempted territory establishment. In comparison with unsuccessful males, a significantly greater proportion of successful males had been captured at the study area in years prior to those analyzed in this paper (Table 2). Assuming equal probabilities of capture, this suggests that successful males had greater opportunities to acquire experience at the study area in earlier years. However, since five unsuccessful males had also been previously captured, mere prior presence at the study area does not seem to have been sufficient to produce success. Twelve of the previously captured success-

TABLE 1. Comparison of behavior of successful and unsuccessful male Red-winged Blackbirds.<sup>a</sup>

Male behaviors	Successful (N = 37) $\bar{x} \pm SE$	Unsuccessful (N = 17) $\bar{x} \pm SE$	<i>t</i>
Incipient Song Spread rate <sup>b</sup>	2.00 ± .187	1.35 ± .204	2.10*
Low intensity Song Spread rate	1.67 ± .149	1.97 ± .221	-1.14
Medium intensity Song Spread rate	0.514 ± .0776	0.817 ± .134	-2.08*
High intensity Song Spread rate	0.132 ± .0358	0.301 ± .0730	-0.90
Mean Song Spread intensity <sup>c</sup>	0.749 ± .0603	0.945 ± .0871	-1.83
Flight Song rate	0.128 ± .0156	0.116 ± .0276	0.40
Total song rate	4.44 ± .194	4.45 ± .252	-0.01
Alarm rate	0.268 ± .0515	0.156 ± .0551	1.31
Bill-up rate <sup>d</sup>	0.285 ± .0792	0.272 ± .0854	0.11
Trespass rate	0.0886 ± .0109	0.0826 ± .0135	0.32
Date first sighted on territory <sup>e</sup>	33.2 ± 3.73	34.4 ± 7.01	-0.17

<sup>a</sup> Significant differences between the two groups denoted by an asterisk,  $P < 0.05$ .

<sup>b</sup> Rate = number per minute.

<sup>c</sup> Song Spread intensity categories based on degree of wing extension.

<sup>d</sup> Sample sizes are 28 successful and 13 unsuccessful.

<sup>e</sup> Date expressed relatively; arrival of first male determines day 1.

ful males had first been caught as year-old birds one year before establishment, and seven successful males briefly defended their eventual territories late in the previous breeding season after the original owners had disappeared. Experience before success gained by yearling males combined with late-season territorial behavior could be advantageous in encounters between males in subsequent breeding seasons.

## DISCUSSION

Aggressive behavior appears to be an important element of initial territory establishment in many birds. Social hierarchies in lekking grouse such as the Greater Prairie Chicken (*Tympanuchus cupido*) are the result of differential social aggressiveness among the participating males. Robel (1972) asserted that selection for aggressiveness has resulted from the reproductive advantage accruing to high-ranking males. Aggressive behavior was apparently important in successive territorial shifts toward central status on leks of male Black Grouse (*Lyrurus tetrrix*; Kruijt et al. 1972). Aggressiveness of territorial male Red Grouse (*Lagopus l. scoticus*) toward neighbors was correlated with territory size (Watson and Miller 1971), and testosterone propionate implantations indicated that aggressiveness was important in territory acquisition and expansion (Watson and Moss 1971).

My results do not support the hypothesized importance of aggression but rather indicate that non-breeding experience acquired a year or more before successful territory establishment may produce delayed benefits. These benefits may take the form of a relatively long-term site-specific advantage in intrasexual encounters and a reduction in the overt aggression necessary for success at the site of the experience.

Experience can produce long-term effects, a finding that is indicated by data on several aspects of avian behavior. First, and most closely related to my results, location-specific experience may be an important determinant of success in territory establishment in other species. Young, non-territorial, male Carolina Wrens (*Thryothorus ludovicianus*) often trespass and behave cryptically within territories of breeding males. These young males can eventually take over the territories trespassed upon when vacancies occur (Eugene Morton, pers. comm.). A more complex form of male territory acquisition has evolved in a Costa Rican population of the Rufous-collared Sparrow (*Zonotrichia capensis*). Nonbreed-

TABLE 2. Comparison of previous captures of successful and unsuccessful male Red-winged Blackbirds.<sup>a</sup>

	Captured <sup>b</sup>	Not captured
Successful	23	14
Unsuccessful	5	12

<sup>a</sup>  $\chi^2 = 4.97$ ,  $P < 0.03$ .

<sup>b</sup> Captured in any year prior to year of observation.

ing males restrict their movements to a few occupied breeding territories and establish linear dominance hierarchies within these, but do not reproduce. When a breeding male dies, the vacancy is quickly filled by the dominant, formerly non-breeding, male. Experience within a territory seems necessary for its successful acquisition (Smith 1978). Observations and experiments have shown that location-specific experience with females is important in determining the site on which male Black Grouse attempt to acquire territories, and in reinforcing fidelity of experienced males to their established territories (Kruijt et al. 1972).

Experience shortly after leaving the nest appears to help determine the area and territory selected for first breeding in the Reed Warbler (*Acrocephalus scirpaceus*) and the Sedge Warbler (*A. schoenobaenus*; Catchpole 1972). Possibly related to this apparent link between youthful experience and choice of territory is evidence that winter dominance rank and breeding-season territoriality are associated in Field Sparrows (*Spizella pusilla*) and Carolina Chickadees (*Parus carolinensis*). Male Field Sparrows in winter flocks were dominant over their associates when these flocks foraged on breeding territories of such males (Fretwell 1968). Further, first-year male chickadees with high rank in winter flocks acquired initial breeding territories within the flock's home ranges (Dixon 1963).

Experience can also affect the amount and result of a male's overt aggression, as suggested by experimental studies of grouse behavior. Removal of male Sharp-tailed Grouse (*Pedioecetes phasianellus*) holding central territories on a lek resulted in an orderly, relatively predictable progression of centripetal movements without associated changes in levels of aggression (Rippin and Boag 1974). Increases in individual aggressiveness induced by implantation of testosterone propionate were not sufficient to change the previously established status of male Sharp-tailed Grouse on a stable lek (Trobec and Oring 1972). Finally, simulation of ritualized combat based on game the-

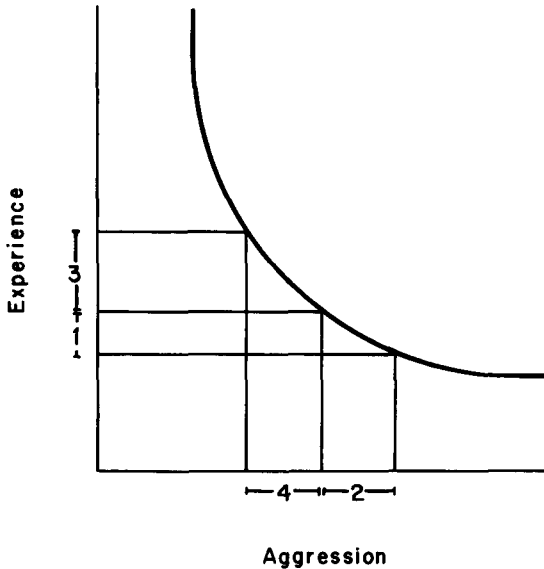


FIGURE 2. Graphic model of the relation between experience and aggressive tendencies. The curve represents the minimum levels of experience and aggressive tendencies necessary for successful territory establishment and defense. (1) Experience gained prior to initial territory establishment by male Red-winged Blackbirds results in (2) a decrease in aggressive tendencies exhibited during establishment. (3) Experience gained after initial establishment results in (4) a further decrease in aggressive tendencies exhibited during re-establishment in the second territorial year.

ory indicates that a previously established asymmetry can determine the outcome of a contest regardless of actual fighting abilities (Maynard Smith 1974).

The foregoing evidence indicates that experience prior to acquiring a territory can be beneficial. The advantages apparently held by experienced males could result from: (1) dominating competitors while holding late-season territories; (2) acquiring knowledge of specific areas; or (3) establishing asymmetries (*sensu* Maynard Smith) important in later confrontations. This suggests that the late-season occupation of deserted territories by male Red-winged Blackbirds is adaptive despite the low probability of acquiring a mate at that time. The immediate cost of this territorial behavior, especially when it is performed by year-old males in yearling plumage, seems relatively low. Territorial defense by male Red-winged Blackbirds decreases as the breeding season advances (Peek 1971), and territorial males frequently tolerate trespasses by yearling males (Nero 1956). Further, experimental presentations to territorial Red-winged Blackbirds indicate that the yearling plumage reduces the probability of attack by territory owners (Rohwer 1978).

Year-old males that more closely resembled females were attacked less often than were darker yearlings.

The level of aggressiveness exhibited by successful males may be related to the mode by which they established their territories. Of the 37 successful individuals studied, 11 acquired territories of males that had failed to return to the study area in spring, presumably having died during the non-breeding season; seven acquired territories of males that had returned in spring but had unexpectedly disappeared, probably having died during the breeding season; 11 acquired territories that had apparently been deserted by other reproductively inexperienced males, since most of the latter birds were sighted on the study area after leaving their territories (see below); seven inserted themselves at boundaries of early-established territories and acquired portions of these; and one displaced an old, reproductively experienced male, driving him away with repeated attacks. The 29 males that occupied vacant areas showed little initial overt aggression, as might be expected since they were not resisted. Males that obtained territories by insertion performed a behavior called "challenging" (Nero 1956), in which they elicited chase by territory owners. The seven challengers were successful simply by withstanding limited attacks by territorial males rather than by their overpowering or conspicuous aggressiveness. Thus territory establishment under circumstances normally accompanied by fighting (Nero's category 3) occurred only once in 37 cases.

The apparently lower aggressive tendencies and greater experience of successful male Red-winged Blackbirds suggests a relation between levels of overt aggression and amount or quality of experience. Such a hypothesized relation is shown in Figure 2. As the level of experience increases, the minimum amount of overt aggression necessary for successful competition (for territories, mates, food, etc.) decreases. This graphical model predicts that Red-winged Blackbird males returning to defend territories established in previous years behave less aggressively than males establishing and defending their initial territories.

Lack of experience could explain the 11 cases of apparent abandonment of territories by males that had first attempted to acquire these sites. Variability of the Song Spread display (Orians and Christman 1968) and the apparent relation between intensity of this display and aggressive tendencies of

displayers (Yasukawa 1978) suggest the existence of an evolutionarily stable signaling system in which undetected cheating is rare (Rohwer 1977). Unsuccessful males who desert could have been cheaters, i.e., birds feigning higher aggression by performing inflated displays. If these speculations are correct, then lack of experience forced these males to cheat but they deserted their territories when confronted by more experienced males. The apparent difference in aggressive tendencies between successful and unsuccessful males could, therefore, result from inflated signals produced by cheaters. This alternate interpretation underscores the eclectic and elusive nature of aggression (see Wilson 1975). Future study of the effects of experience should help to determine its important variables and its relationship to aggression, territory establishment, and sexual selection.

#### SUMMARY

The importance of aggression in initial territory establishment was investigated by comparing sizes, ages, behaviors and time budgets of two groups of male Red-winged Blackbirds. Fifty-four males believed to be seeking their first breeding territories were classed as successful or unsuccessful and predictions, based on the hypothesized importance of aggression, were tested. Results did not support a hypothesis that predicts that successful males are more overtly aggressive than unsuccessful males.

Successful males relied on less intense display and spent more time foraging while on territory than did unsuccessful males. These results were contrary to those predicted by the aggression hypothesis and could not be explained by between-group differences in length of observation, singing frequency, trespass rate, age or size. In addition, successful males spent a greater proportion of time on territory than did unsuccessful males.

I suggest that experience gained prior to attempted establishment is important. A greater proportion of successful (than unsuccessful) males was captured at the study area at least one year before they gained territories and mates. Experience may help territory acquisition while reducing overt aggression. A potential function for late-season territorial behavior and territoriality of yearling males is thus indicated.

#### ACKNOWLEDGMENTS

It is my pleasure to acknowledge the assistance of Val Nolan Jr., J. Merritt Emlen, Cindy B. Patterson, Wil-

liam H. Barnard, William A. Searcy, Donald E. Kroodsmma, Jared Verner, and an anonymous reviewer. The Indiana Department of Natural Resources and the staff at Yellowwood State Forest allowed use of the study area. This research was conducted in partial fulfillment of the requirements for the Ph.D. in the Department of Zoology, Indiana University, and was funded in part by Grants-in-Aid of Research from Indiana University and Sigma Xi.

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