

TERRITORIAL BEHAVIOR OF A BLACKBIRD: MECHANISMS OF SITE-DEPENDENT DOMINANCE

by

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(With 7 Figures)

(Acc. 16-X-1979)

INTRODUCTION

The evolution and ecology of territoriality have received extended treatment in recent decades. In comparison, there has been little attention to the behavioral mechanisms of territoriality. What controls the behavioral reactions of individuals to produce the social relationship called territoriality?

The essential social relationship of territoriality, and the best criterion for its definition, is site-dependent dominance (EMLEN, 1957; MARLER & HAMILTON, 1966; WILLIS, 1967). Other features of territorial behavior are less general. In particular, the relationship between each individual's area of dominance and the area it uses, and consequently the extent of overlap in the areas used by neighboring territorial residents, vary markedly among species (WASER & WILEY, 1979). Exclusive occupation of an area represents an extreme case, in which undisturbed access to limiting resources is a major ecological consequence of territorial behavior (PITELKA, 1959). Yet even without exclusive occupancy, dominant individuals in an area often have priority in access to resources (BROWN, 1963; WILLIS, 1967). The definition of a territory as a defended area can refer either to an area of dominance or an exclusive area. This definition ignores the possibility that avoidance as well as aggression might contribute to site-dependent dominance.

In this paper, we consider two kinds of behavioral mechanisms that could generate site-dependent dominance (WASER & WILEY, 1979). First,

1) In the course of this study, we received invaluable guidance from B. THOMAS and P. SCHWARTZ in Venezuela, F. C. LEHMANN in Colombia, and F. FEEKES in Surinam. Our studies at Fundo Pecuario Masaguaral in Venezuela were made possible by the foresight and dedication of T. BLOHM, who maintains this ranch as a wildlife reserve. Financial support came from Sigma Xi and the National Institute of Mental Health (MH22316).

a resident's agonistic tendencies might vary with the location of an encounter, so that an individual's dominance (the relationship between its aggressive or avoidance tendencies and those of neighbors or intruders) would also change with location. It is important to note that the aggressive *tendency* of an individual is the probability or intensity of aggression in standardized situations. *Frequencies* of aggression depend both upon an individual's tendencies and its opportunities for aggression, in the form of encounters with opponents. An individual's tendency to perform aggression in standardized situations as a function of location constitutes an aggression field, where "field," as in physics, means a function of spatial coordinates (WILEY, 1973; WASER & WILEY, 1979).

A second mechanism of site-dependent dominance is suggested by the observation that territorial aggression in some species develops as an extension of an individual distance (CONDER, 1949; MARLER, 1956a, b). At the same time, individuals develop site fidelity by restricting their activities to a limited area (MARLER, 1956a). A combination of site fidelity and defense of an individual distance, together with some avoidance of neighbors, could generate a pattern of largely exclusive territories without site-dependent aggressive tendencies. With this mechanism, interactions with intruders would occur most frequently in localities frequented by the resident, yet the resident's aggressive tendencies as a function of an opponent's proximity would remain the same at all locations. The relationships of neighbors at boundaries or within zones of overlap would lack any consistent association with location.

Thus the behavioral mechanisms that generate territoriality could include variation in a resident's aggressiveness with distance from an opponent or variation in a resident's aggressiveness with the opponent's absolute location. Both might contribute in various proportions to the spacing behavior of different species under natural circumstances.

Some evidence that a territorial resident is more aggressive in the center of its territory than in the periphery has come from comparisons of the frequencies of aggression by residents on territories of different sizes (HUXLEY, 1934; van den ASSEM, 1967). With smaller territories, however, interactions with neighbors might well occur more frequently, regardless of any change in aggressive tendencies in any one interaction.

Other evidence for changes in a resident's aggressiveness at different locations within a territory comes from reactions to intruders as a function of the intruder's location (van IERSEL, 1958; SYMONS, 1965; BLACK, 1971; BURGER & BEER, 1975). However, only one such study has considered the effects of the intruder's distance from the resident as well as

its absolute location within the territory. In that study, the aggressiveness of territorial black-headed gulls *Larus ridibundus* varied primarily with the intruder's distance from the resident rather than the intruder's absolute location within the territory (PATTERSON, 1965).

The best available evidence that a territorial resident's aggressive tendencies are lower in the periphery than in the center of its territory comes from playbacks of taperecorded songs to passerine birds (DHONT, 1966; ICKES & FICKEN, 1970; FALLS & BROOKS, 1975). In using this technique to investigate variation in aggressive tendencies with location, one must control for possible effects of the resident's distance from the speaker. If a resident spends more time near the center of its territory than in equal areas of the periphery, a playback in the center would more likely be near the resident male than a playback in the periphery. ICKES & FICKEN (1970), by controlling the distance between the speaker and resident redstarts *Setophaga ruticilla*, while varying the locations of the speaker within territories, have demonstrated that a male is most aggressive near the center of his territory.

An individual's aggressiveness toward intruders could vary with location for at least two reasons. First, individuals might have more aggressively in encounters at locations with which they have acquired some familiarity (NICE, 1941; WASER & WILEY, 1979). In laboratory situations, prior residence in a cage is a major determinant of dominance there. If similar effects hold under field conditions, an individual's aggressive tendencies would vary with the amount of time that an individual had recently spent at or near the site of an encounter with an opponent. The spatial and temporal parameters of familiarity with a locality would probably prove difficult to specify. Nevertheless, effects of familiarity on aggressiveness should yield a correlation between the distribution of an individual's time at different locations and its aggressiveness there. In addition, an individual's aggressiveness at a location would presumably influence its chances of winning encounters there and consequently its tendencies to return to that location. The effects of previous experience in agonistic encounters at a site and those of familiarity with the site would both tend to generate a correlation between an individual's use of a location and its aggressiveness there (BLACK & WILEY, 1977; WASER & WILEY, 1979).

In this report, we compare the use of space by yellow-hooded blackbirds *Agelaius icterocephalus* and their aggressive tendencies toward established neighbors and transitory intruders. We show that a territorial male in this species uses the central portion of its territory more intensive-

ly than the periphery; yet its tendencies for aggression toward intruders vary little within its territorial boundaries. On the other hand, the dynamics of changes in boundaries between neighbors suggest that use of an area is a prerequisite for its defense.

PROCEDURES

Study sites.

We studied territorial behavior of yellow-hooded blackbirds at three localities in northern South America, all in herbaceous marshes where males held territories within which females nested. In this species, males build nests within their territories and use them to attract females (WILEY & WILEY, in press). In 1971, we worked from 20 June to 8 August in Trinidad on the eastern edge of the Caroni Swamp, 8.5 km SE of Port-of-Spain. In 1973, we observed territorial males from 21 June to 23 July in Surinam, 11 km NE of Paramaribo. At both of these sites, the marshes occupied abandoned rice fields and supported diverse emergent vegetation that included several species of grasses and sedges. In 1974, we continued this work from 12 October to 21 October in Venezuela, 42 km S of Calabozo, Guarico, in the llanos bajos. Here blackbirds nested in emergent vegetation that grew in vast areas of seasonally flooded savanna. The nesting blackbirds established territories in dense stands of *Thalia geniculata*, 1-2 m in height above water, adjacent to expanses of the wild rice *Oryza perennis*. Further information about the nesting habitat and seasonality at these locations is presented elsewhere (WILEY & WILEY, in press).

In 1971, we focused on four males with contiguous territories, which we could observe from a dike that extended into the marsh. In 1973 and 1974, we constructed wooden platforms within marshes in order to observe activity within territories. In 1973 we focused on two adjacent territories but collected some additional information about a third. In 1974, we focused on three contiguous territories. In all locations the observed males held territories in vegetation typical for the area. At each site, we could easily recognize the males by their individually distinctive songs.

Sampling activities within territories.

We recorded the activities of only the territorial resident (1971) or of all yellow-hooded blackbirds (1973, 1974) within a focal territory for periods of 45-60 min and also recorded signals from an interval timer. We thus recorded both the frequencies of brief behavioral events and, by means of the interval timer, estimated the proportions of time spent by individuals in different behavioral states (see ALTMANN, 1974). At each site we prepared a detailed map that permitted us to locate an individual within each focal territory with a maximum error of one meter.

In 1971 and 1974, the intensively studied territories were observed in rotation on successive days between 0600 and 0930. During late morning and the afternoon, territorial activity subsided considerably. In 1973, in order to document daily changes in males' behavior, we observed each territory at the same time each day, one beginning between 0615 and 0630, the other an hour later.

Maps of activities.

We constructed maps of the spatial distributions of the frequencies of behavioral events, such as songs, and, for 1973 and 1974, maps of the spatial distributions of an individual's time in behavioral states, such as perched in exposed situations. From each map we determined the center of the spatial distribution by calculating a vector mean (analogous to a center of gravity).

Presentation of the spatial distribution of territorial activities has had no consistent treatment. The total area within a convex polygon circumscribed around the mapped

positions depends on sample size (for instance, ODUM & KUENZLER, 1958), just as the range of values in samples from any univariate probability distribution depends on sample size. Distributions of animals' activities in natural environments only rarely have radial symmetry, so that a single measure of dispersion around the vector mean, such as a standard deviation, fails to reveal the effects of asymmetrically distributed neighbors or focal positions within an individual's activity field.

To circumvent both of these difficulties in characterizing the two-dimensional variation in an animal's activities, we have employed a new measure: the area of a specified percentage of the observed spatial distribution closest to the vector mean. We have selected 68% and 95%, by analogy with the percentiles for one and two standard deviations around the mean of a normal distribution. The "68% area" thus is the smallest convex hull that encloses 68% of the observed distribution closest to the vector mean. This "percentile area", a two-dimensional percentile, will not vary systematically with sample size (for the use of percentiles and quantiles in nonparametric statistics, see HOLLANDER & WOLFE, 1973). We employed vector means as the foci of these percentile areas, rather than vector medians, because the location of the latter depend on the orientation of the axes selected.

RESULTS

Territorial advertisement.

Activities related to the defense of a territory are conveniently divided into advertisement and reactions to intruders. Advertising activities of birds, either acoustic or visual displays, broadcast a long-range signal, usually detectable beyond the territorial boundaries. They are produced, often without a noticeable triggering stimulus, when the resident is present on its territory and prepared to challenge intruders. Male yellow-hooded blackbirds had three sorts of advertising behavior. The most conspicuous but infrequent were song flights: the male climbs with rapidly beating wings at a steep angle to 5-15 m above ground. He begins to sing just before reaching the apex, where he sets his wings, fully spread and angled about 30° below horizontal, and then sails downward while he finishes his song. During the stiff-winged glide, he holds his head back on his shoulders, so the beak points upward as he sings. Less conspicuous but much more frequent was singing from a perch atop the emergent vegetation. Males lifted their beaks and spread their wings to varying degrees during each song. Each male had 5-10 song patterns. Simply perching atop the emergent vegetation provided a conspicuous visual signal even while the male remained silent. These three forms of behavior, conspicuous perching, song, and song flight, produced the principal signals that would notify other birds of the male's presence on his territory.

In addition to these activities, males spent much of their time more or less concealed in the vegetation while they searched for food or nest material. Males were also inconspicuous during activities at nests, including building the nests and courting females, because the nests were

well concealed in dense emergent vegetation. Even when a male sang at a nest in the presence of a female, the song carried much less well than when the male perched atop the vegetation.

Males also took brief absences from their territories, presumably in order to feed at locations 100-500 m away. During this time they of course had no opportunity for surveillance of their territories. Absences rarely lasted longer than 10 min. Males averaged from 69-99% of their time on their territories between 6:00 and 9:00 in the morning (Table 1).

Males perched conspicuously 19-52 times per hour on average; the mean duration of these periods averaged 0.5-1.2 min (Table 1). Overall

TABLE 1

Territorial advertisement (conspicuous perching, songs, and song flights) by male yellow-hooded blackbirds

Male	Observation periods* (N)	Perched conspicuously		Songs while perched conspicuously		Song flights/hr	% Time on territory
		% Time	Instances/hr	Mean duration (min)	Number/hr		
1971 - 1	8		35.8(13.1)**		40.7(33.2)	1.47	94.8
1971 - 3	9		27.3(11.3)		40.2(6.4)	1.37	79.5
1971 - 7	11		33.7(14.5)		31.3(14.6)	1.02	91.5
1973 - P	16	54.2(10.4)	28.9(9.1)	1.13	47.4(18.6)	1.62	91.1
1973 - E	13	21.1(15.3)	19.1(8.7)	0.66	40.5(23.7)	2.12	10.6(3.9)
1974 - C	5	62.0(9.8)	30.7(14.7)	1.21	77.3(21.6)	2.52	6.6(6.2)
1974 - B	4	59.4(2.1)	42.7(14.6)	0.83	44.7(28.1)	1.04	8.7(3.9)
1974 - D	3	39.7(12.0)	52.0(13.8)	0.46	60.9(14.6)	1.17	5.7(2.5)

*Observation periods lasted 60 (1971 and 1973) or 45 (1974) minutes between 0630 and 0930, with starting times permuted among individuals each year. **Mean (standard deviation).

males averaged 21-62% of their time perched conspicuously. The locations in which neighboring males perched conspicuously overlapped only slightly. The 68% areas of neighboring males usually did not overlap (Figs 1 and 2).

The total time perched conspicuously was even more concentrated near the center of a male's territory than the frequency of conspicuous perching. For three males studied in 1974, the 68% areas for total time perched conspicuously amounted to 11-68% of the corresponding areas for frequencies of conspicuous perching (Table 2, Fig. 2). Consequently, a male remained perched at any one location for briefer periods when farther from his center of activity. Even within a male's 68% area, certain perches were used far more often than others.

Males sang from conspicuous locations 31-77 times per hour on

average (Table 1). For each period of conspicuous perching, males averaged 1.0-2.5 songs. Songs per time perched conspicuously did not change systematically with distance from the center of a male's activity. Consequently, the spatial distribution of a male's songs closely matched the distribution of his time perched conspicuously (Table 2, Fig. 2).

Like the distributions of songs and time perched conspicuously, song flights were strongly concentrated near the center of a male's territory.

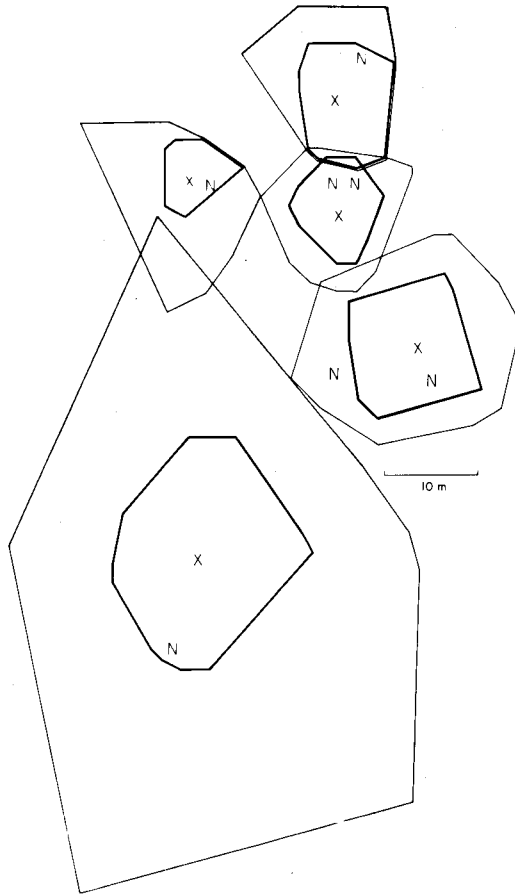


Fig. 1. Advertisement activity fields of five territorial males in Trinidad: percentile areas for locations of songs during conspicuous perching. For each male, the outer polygon includes 95% and the inner polygon 68% of the locations of songs nearest the vector mean. X, vector mean of the locations of songs. N, locations of nests constructed by males. Other males held territories in all directions from these five. Males observed for one-hour periods on four (top left) to 12 (second from top on right) days.

For several males in 1971, we plotted the paths of song flights. In each case, song flights were far more likely to cross the center of the male's territory than more peripheral areas (Fig. 3).

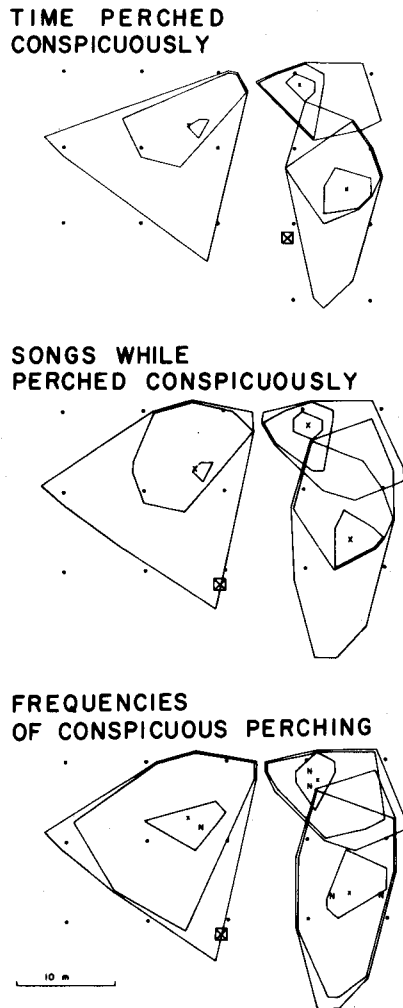


Fig. 2. Advertisement activity fields of three territorial males in Venezuela: percentile areas for three measures of advertising activities. For each male, the outer polygon includes 100%, the middle polygon 95%, and the inner polygon 68% of the distributions nearest the vector mean for time perched conspicuously (X). Small dots, grid markers; small box, observation platform; N, nests constructed by males (bottom diagram only). Other males held territories in all directions except east (right). Males observed for 45-min periods on three to five days each.

TABLE 2

Areas included within the 68% and 95% areas for three measures of territorial advertisement: time perched conspicuously, songs while perched conspicuously, and frequency of conspicuous perching

Percentile area	Male	Measure for which areas are computed (m ²)		
		Time perched conspicuously	Songs	Frequency of conspicuous perching
68%	C	2.0	2.0	19.0
	D	6.0	5.0	14.0
	B	17.0	18.5	25.0
95%	C	84.5	65.5	190.5
	D	31.0	29.5	78.5
	B	82.0	62.5	155.0

See Fig. 2 for maps of these distributions.

Reactions to intruders.

Although neighboring males rarely trespassed on each other's territories, intruding strangers were not infrequent. Many were immature males, which retained brown patches in the yellow hood. No male with these signs of immaturity, presumably in his first year of life, ever established a territory in our study areas (WILEY & WILEY, in press). Many males with fully adult plumage also seemed to have no territories. These males, which wandered aimlessly from location to location, perched in our study areas until challenged by the residents and then moved away. Territorial males, even during their absences from their territories, never showed such lackadaisical behavior; they flew from their territories directly to feeding grounds and returned directly to their territories. Intruders in some cases were attracted by females, particularly ones that had chosen a nest but not yet begun incubation. These females, for a period of several days, tended to perch alone near their nests or to gather material for the nest lining. Although intruding males sometimes approached these females, usually intruders had no discernible object to their movements. When more than one intruder visited a territory, they often tended to land near each other, often within one meter, perhaps an expression of the flocking response of nonbreeding birds.

Did intruders tend to avoid proximity to resident males? Our evidence on this point is inconsistent. In one territory studied intensively in 1973, intruders clearly approached, rather than avoided, the resident male perched conspicuously (Table 3). Also intruders tended to alight more often

near the center of the territory when the resident perched conspicuously than when he was concealed in vegetation or absent from his territory. Since the resident tended to perch most often near the center of his territory, the attraction of intruders to the resident could explain this result. At this locality, intruding males also tended to land near each other, so their general attraction for other males seemed to explain their tendencies to approach the resident.

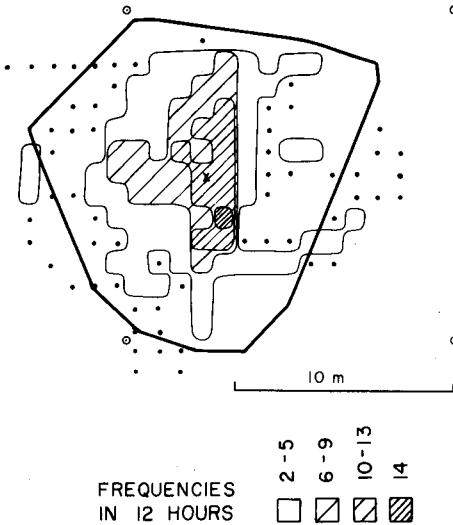


Fig. 3. Distribution of song flights by one territorial male in Trinidad. Heavy polygon, 68% area for songs during conspicuous perching (see Fig. 1, second from top on right). X, vector mean of songs during conspicuous perching. Small circles, grid markers. Contours show frequencies with which the male crossed each one-meter quadrat in song flight; small dots indicate quadrats crossed only once.

In 1974, in three territories observed intensively, intruders seldom alighted near the centers of territories, regardless of whether the resident perched conspicuously or was concealed in vegetation (Table 4). There was a statistically significant tendency for intruders to perch near the center of a territory more often during the resident's absence than during his presence. However, the behavior of intruders during absences of the resident did not match their behavior when the resident was concealed in vegetation. In this study area, intruders evidently largely ignored or perhaps weakly avoided conspicuously perched residents.

A resident reacted promptly to intruding males that approached females within his territory, provided the resident was perched with a view of his territory. The resident usually peremptorily supplanted or chased away the intruder.

In the absence of nearby females, the residents' reaction to an intruder varied widely. In some instances, the resident made no detectable

TABLE 3

Association between intruders' distances from a resident's center of activity and the resident's conspicuousness

Distance from center of activity (m)	Resident		
	absent	perched conspicuously	concealed in vegetation
≤ 3	0	18	3
> 3	4*	14	12**

Distance from resident (m)	Resident		
	absent	perched conspicuously	concealed in vegetation
≤ 3	—	13	0
> 3	—	18	10***

Data from territory P in 1973; instances excluded when intruder interacted with females or males other than resident.

* $X^2 = 4.50$, $N = 36$, d.f. = 1, $P < .05$; ** $X^2 = 5.43$, $N = 47$, d.f. = 1, $P < .05$; *** $X^2 = 6.14$, $N = 41$, d.f. = 1, $P < .05$.

TABLE 4

Association between intruders' distances from a resident's center of activity and the resident's conspicuousness

Distance from center of activity (m)	Resident		
	absent	perched conspicuously	concealed in vegetation
≤ 3	5	3	3
< 3	3*	12	9**

Data from territories B, C and D in 1974; instances excluded when intruder interacted with females or males other than resident.

* $X^2 = 4.15$, $N = 23$, d.f. = 1, $P < .05$; ** $X^2 = 0.10$, $N = 27$, d.f. = 1, N.S.

response; he simply continued singing at intervals from his perch. Often the resident approached and landed 1-2 m away without supplanting him. If the intruder did not leave within 10-30 s, usually the resident supplanted or chased him.

After approaching an intruder, the resident usually began bill-up/down displays and resumed singing. During bill-up/down displays, residents often took lateral orientations to the intruder. The downward movements of the beak were usually weak and infrequent in comparison to displays addressed to neighbors at boundaries; in some encounters with intruders, residents completely omitted the downward components

from their bill-up/down displays. The intruder usually perched tensely, with little movement, its feathers sleeked, when the resident approached. Usually the intruder faced away from the resident or took a lateral orientation with its beak turned away. Sometimes when flying to approach an intruder, the resident performed a distinctive bouncing flight with periodic bursts of rapid flapping while holding his beak steeply upward, evidently an attempt to perform bill-up movements in flight.

An intruder's location within a territory had no consistent effect on the resident's reaction. To study the possible effects of an intruder's location, we considered only instances in which both the intruder and the resident perched conspicuously in the territory and no other individuals interacted with them. Assuming that the intruder's tendencies remained the same at different locations within a resident's territory, we expected that the resident would more often engage in overt aggression toward intruders (supplant or chase them) when the intruder's location evoked a stronger aggressive response from the resident.

We considered two ways that the location of an intruder might influence the resident's aggression. Either (1) the distance of the intruder from the center of the territory or (2) the distance of the intruder from the resident himself might influence the resident's reactions. For each intruder meeting the above conditions ($N = 32$ in territory P in 1973; $N = 21$ in territories B, C, and D in 1974), we estimated to the closest meter the distance of the intruder from the resident at the time of the intruder's arrival and the intruder's distance from the center of the territory as determined by the vector mean of the resident's time perched conspicuously. All intruders were within the 95% area of the resident's positions while perched conspicuously.

In neither year was a resident more likely to show overt aggression toward intruders near its own position in comparison to intruders farther away; nor toward intruders near the center of the territory in comparison to intruders farther from the center (Tables 5 and 6). Although these tables divide the intruders' distances from the resident or the territorial center at greater or less than 8 or 9 m, the results are similar when other distances are used. In both years, about a third of the instances involved intruders close to the boundary of the territory; intruders in these positions, provided they are within the resident's boundary, evoked reactions similar to those directed at intruders well within the boundary. Note that in both years many intrusions near the territorial center or near the resident evoked no overt aggression. The similarity of the residents' reactions to intruders in different locations is emphasized when the kinds of

TABLE 5

A resident's reactions to intruders in relation to the intruders' locations when both intruder and resident perched conspicuously

Intruder's distance from resident's center of activity (m)	Agression* by resident	
	present	absent
≤9	11	10
<9	7	3**

Intruder's distance from resident at time of arrival (m)		
	≤9	16
<9	3	3***

Data from territory P in 1973; instances excluded when intruder interacted with individuals other than the resident and when either resident or intruder was concealed in vegetation.

*Supplantation or chase; ** $X^2 = 0.86$, N.S.; *** $X^2 = 0.27$, N.S.

TABLE 6

Residents' reactions to intruders in relation to the intruders' locations when both intruder and resident perched conspicuously

Intruder's distance from resident's center of activity (m)		
	present	absent
<8	7	8
≥8	1	5**

Intruder's distance from resident at time of arrival (m)		
	<8	6
≥8	2	6***

Data from territories B, C and D in 1974; instances excluded when intruder interacted with females or males other than resident and when either resident or intruder was concealed in vegetation.

*Supplantation or chase; ** $X^2 = 1.64$, N.S.; *** $X^2 = 0.94$, N.S.

reactions by a resident are compared for intruders at different locations (Fig. 4).

Although our limited data are not sufficient to rule out relatively small effects of the intruders' locations, at least in four territories in two study

areas the locations of intruders with respect to the territorial center or the resident himself had little effect on the resident's reactions. Once within a territory, regardless of the details of their locations, intruders received roughly the same treatment from the resident.

Interactions of neighbors.

Neighbors regularly approached each other at their mutual boundaries and performed bill-up/down displays, which were in general more intense than those directed at intruders. Sometimes the movements of the beak were clean jerks upward or downward and then back to the resting

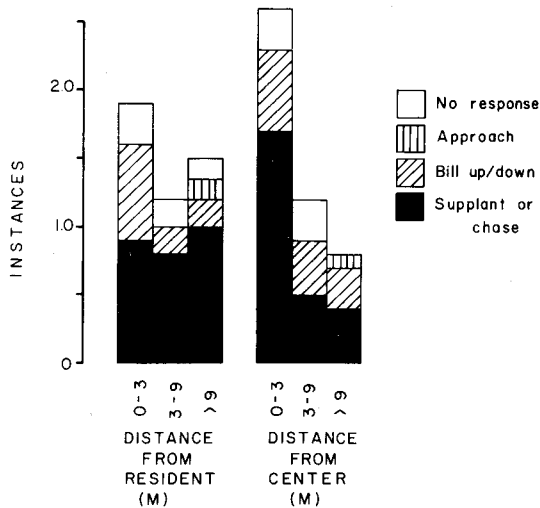


Fig. 4. Reactions to intruders by a territorial resident in Surinam, according to the distance of the intruder from the resident and from the territorial center (the vector mean of the resident's locations of singing while perched conspicuously).

position slightly above horizontal. At other times the movements consisted of longer excursions upward or downward with irregular, tense, jerking movements at the top or bottom. In extreme cases the beak reached positions past vertical either upward or downward. Sometimes upward and downward movements alternated quickly, about 1 cycle per second, but usually the upward movements were more frequent or more prolonged than the downward ones. Occasionally a bird interrupted its downward movements to wipe its beak stiffly on the perch. Both birds interrupted their bill-up/down displays to sing at intervals.

Usually neighbors perched 1-2 m apart and oriented away from each

other or sideways. Sometimes a bird turned to face its neighbor as the neighbor moved away from the encounter. Yet there seemed to be no clear relationship between a bird's orientation in an encounter and its tendency to move away. If a bird began to encroach too far into its neighbor's territory, the neighbor hopped and crept through the emergent vegetation toward the encroaching bird, who usually withdrew. Occasionally a bird that had intruded slightly too far was supplanted by its neighbor. Usually these encounters ended with both birds returning toward the centers of their territories. Males approaching or leaving boundary encounters often used the distinctive bouncing flight (see above). On three occasions, we observed males approach their boundaries and perform bill-up/down displays even though the neighbor was 10 m or more away inside its own territory.

Neighbors, except on rare occasions, avoided intrusions into each other's territories. During our observations of individual territories, we observed a territorial male enter a neighbor's territory on 24 occasions. Ten of these instances occurred while the neighbor was absent. On 12 occasions, the intruding male approached a female; once the intruder supplanted a non-territorial male that had landed in its neighbor's territory; and once a male chased a female cowbird from the neighbor's territory. Territorial males crossed boundaries to chase female cowbirds regularly in a successful nesting colony in Venezuela, in which the males' territories were much smaller than those studied intensively elsewhere (WILEY & WILEY, in press). Otherwise the most frequent occasion for trespassing involved approaching females in a neighbor's territory during an absence of the neighbor.

Changes during the male's breeding cycle.

At two stages in the male's breeding cycle, males changed their territorial behavior. A major change occurred when a male began to feed nestlings. A male substantially reduced defense of its territory while actively feeding young. Males at this time sang less frequently, even while perched in their territories, and less consistently expelled intruding males. For instance, male 8 in 1971, while actively feeding nestlings during the latter half of the nestling period, on three occasions approached intruding males but left them before expelling them from his territory. Male 1 in 1971, after feeding nestlings at a successful nest in his territory, began a period of about three weeks of desultory singing before he finally began a new nest and resumed actively courting females. In the successful nesting colony in Venezuela in 1974, males feeding nestlings also

devoted noticeably less time to territorial activities. They sang less frequently and were less attentive to intruders.

A second, more transient change in the territorial male's behavior occurred during the 2 to 4-day period after a female had selected a nest. During this period the female perched near the nest for long periods, intermittently collected fine grasses for nest lining usually within the male's territory, and took long absences on feeding grounds. Particularly toward the end of this period, as egg laying began, she often responded to the male's approaches by performing a solicitation display, with quivering wings and a high-pitched vocalization. During these days the territorial male focused his activities around the female's nest. Once a female began collecting nest lining, the male largely ceased his own collection of nest material. During her long absences, the male was less active in singing and approaching other females than during the days before he had acquired a committed female. He recognized his new mate's arrival from a distance and often greeted her with spectacular song flights. During her periods near the nest, the male rarely moved far away. Thus during these few days, a territorial male visited the peripheral areas of his territory less frequently than during the much longer periods when he had no committed female and spent much of his time building a nest.

Changes in boundaries.

The boundaries of territories shifted in three circumstances; when vacancies occurred following the disappearance of a territorial male; when newcomers squeezed into the interstices between existing territories; and following shifts in the territorial male's activity fields as a consequence of changes in the locations of their nests under construction. Changes in boundaries revealed the importance of the use of an area before it is defended and the effects of changes in a males' behaviour during a nesting cycle.

The reoccupation of vacancies revealed that use of an area preceded its defense. In 1971 male 7 took advantage of a series of three vacancies in the area south and east of male 3's territory. First, between 30 June and 6 July, males 6 and 7 established new territories in an area vacated by the disappearance of male 2 south of male 3's territory. On 19 July, male 6 disappeared; on the following day male 7 restricted his activities predominantly to his usual territory. In the ensuing few days, however, he extended his activities into the area previously occupied by male 6. Although male 3 visited the former territory of male 6 on several occa-

sions, from the start male 7 spent more time there and eventually occupied almost all of the vacated area.

By 24 July male 5 had disappeared, vacating an area east of male 3's territory and north of male 7. Although male 7 visited most of the area vacated by male 5, he remained most active in his previous area, where he constructed two nests (Fig. 5). Although male 3 visited the vacated area, his activities also remained concentrated in his usual area. Consequently male 5's former territory remained largely unused for about ten

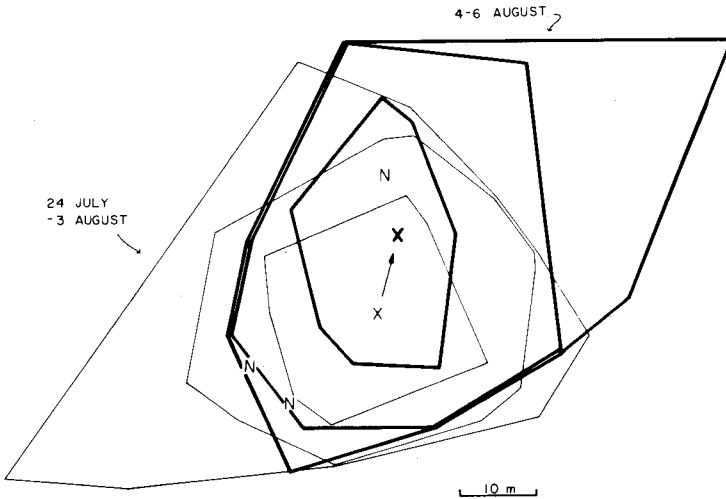


Fig. 5. Change in the activity area of Male 7 in Trinidad to occupy a vacancy left by the disappearance of a neighboring male. For each group of dates, the outer polygon encloses 100%, the middle polygon 95%, and the inner polygon 68% of locations of singing while perched conspicuously. X, vector means of these two distributions (arrow indicates the direction of shift). N, nest constructed by the male; the two in the lower left were built during the first group of dates, the one in the upper center during the second group of dates.

days. By 4 August, male 7 had begun a new nest in the area vacated by male 5 and had shifted his activities into this area (Fig. 5). During this entire period, while male 7 moved his territory first to the west and then to the north around the boundaries of male 3's territory, he defended the areas that he used. As he extended his activities into a vacated area, his defense of the area became more consistent. During the same period male 3 successfully attracted females to his nests in his usual area adjacent to the vacancies occupied by male 7. Although male 3 visited the vacancies, male 7 extended his use of each vacancy first and eventually defended it.

with bill-up/down displays 10 m east of P's former southwestern nest. Male N began to construct a nest at this location. Finally by 13 July, male N had completely occupied the southwestern portions of P's territory and supplanted P once in this area. After male P's second female began incubating he once again shifted his activities southward, but he was not able to reclaim the southwestern portions of his territory.

The neighbor thus extended his activities into the southwestern portion of male P's territory during a period when male P made little use of this area. The neighbor gradually increased his defense of the area as he in-

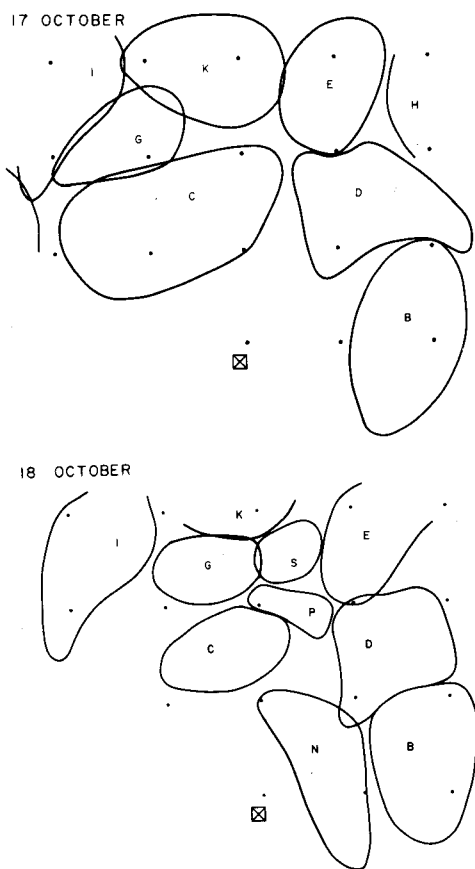


Fig. 7. Areas used by territorial males on two successive mornings in Venezuela to show establishment of new males in the interstices of areas used by previously established males. Lines enclose the entire areas used during three hours each morning. Small dots, grid markers; box, observation platform.

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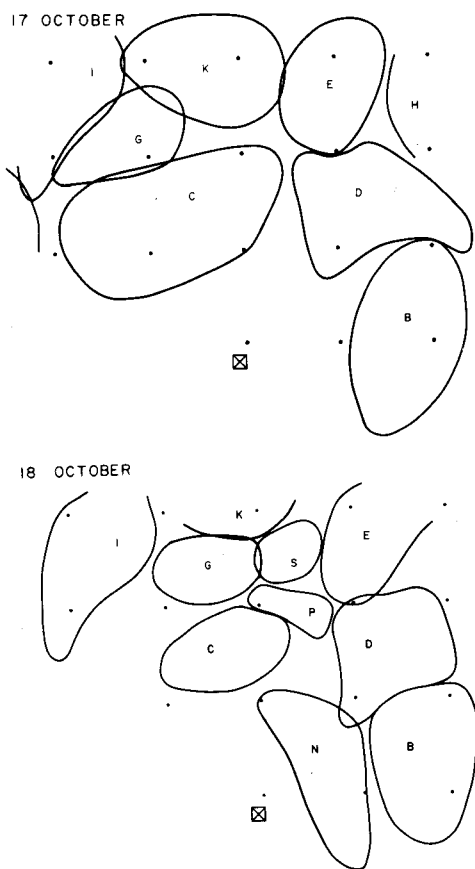


Fig. 7. Areas used by territorial males on two successive mornings in Venezuela to show establishment of new males in the interstices of areas used by previously established males. Lines enclose the entire areas used during three hours each morning. Small dots, grid markers; box, observation platform.

creased his use of it; male P lost the area as his neighbor came to use it more than he did.

Instances of newcomers establishing themselves in the interstices of existing territories again suggest the importance of occupying an area before adequate defense begins. In Venezuela we observed the progressive establishment of territories in our intensive study area over a period of 10 days. In some cases newcomers managed to occupy relatively lightly used areas between the territories of previously established males. For instance, male N occupied a territory between males C, D, and B with relatively little resistance (Fig. 7). This area consisted primarily of low vegetation, not optimal for nesting. Male P, on the other hand carved out a small territory after repeated interactions with male C at a time when the latter had acquired a female committed to a nest. Evidently at successful colonies in the Venezuelan llanos, this pattern of rapid occupation of territories by insertion of newcomers into interstices of previously existing territories eventually results in the small, densely packed territories characteristic of successful colonies in this area (WILEY & WILEY, in press).

DISCUSSION

Territorial displays.

The displays used by yellow-hooded blackbirds in territorial defense closely resemble those of other marsh-nesting blackbirds (NERO 1956, 1963; ORIANS & CHRISTMAN, 1968). Singing from exposed perches is the primary form of territorial advertisement of both the red-winged blackbird *Agelaius phoeniceus* and the yellow-headed blackbird *Xanthocephalus xanthocephalus* of North America. Singing male yellow-hooded blackbirds perform a song-spread display similar to that of red-winged blackbirds, without the peculiarities of yellow-heads. Song flights high above a male's territory are also characteristic of red-winged blackbirds. During encounters with intruding males, the red-winged blackbird normally only raises its bill, although bill-wiping, which involves lowering the bill, also occurs frequently in agonistic situations (NERO, 1963). In contrast, *Xanthocephalus* normally lowers its bill during agonistic encounters and only on rare occasions raises it. The yellow-hooded blackbird's pattern of alternating between jerking movements upward and downward combines elements of both of these North American species. Bouncing flight, in which the bird periodically raises its beak, is a regular agonistic display of *Xanthocephalus*, particularly when approaching

territorial intruders, but almost never occurs in red-winged blackbirds (NERO, 1963; ORIAN & CHRISTMAN, 1968), just the opposite of the situation in perched displays. In this respect, the yellow-hooded blackbirds resemble *Xanthocephalus*. Territorial defense in all of these species involves displays with strong visual as well as acoustic signals. Plumage patterns, however, have surprisingly little correspondence to the actions that compose the displays of these species.

Activity fields of territorial males.

Few studies of birds have considered differential use of areas within individuals' territories, although studies of other vertebrates have often focused on this point (see WASER & WILEY, 1979; BLACK & WILEY, 1977). The distribution of an individual's time or activities as a function of location constitutes an activity field. "Field", just as in the term aggression field, means a function of spatial coordinates (WASER & WILEY, 1979). A territorial tree sparrow *Spizella arborea* uses the central area of its territory more than the periphery (WEEDEN, 1965), a common pattern for many species. In studies of territorial ovenbirds *Seiurus aurocapillus*, ZACH & FALLS (1979) found that the singing positions of a male have greater central clustering than its foraging locations. In contrast, pairs of titi monkeys *Callicebus moloch* use loud calls primarily around the peripheries of their territories, so that the locations of loud calls, which serve for communication between neighboring pairs, lack central clustering (ROBINSON, 1979).

A territorial yellow-hooded blackbird concentrates its advertisement displays in the center of its territory, but no more so than its other activities. The number of songs per unit time remains approximately the same throughout a male's territory; a male sings more near the center of its territory because it spends more time there. A male tends not to remain in any one place as long when perched in the periphery in comparison to near the center of its territory. The small territories and the vegetation of approximately uniform height permit a territorial male to survey most of its territory from a perch at the center.

Males focus their activities strongly around a nest once a female selects it and before she begins egg-laying and incubation. During this period, peripheral areas of the male's territory are visited less frequently, and some peripheral areas distant from the nest go largely ignored for this 3 to 4-day period. Similar contractions in territory size during the mate's egg laying occur in other passerines (STEFANSKI, 1967; ROOT, 1969), and an analogous phenomenon occurs in the parental phase of the breeding cycle of male sticklebacks (Black, 1971).

Spatial variation in aggressive tendencies.

Aggression toward intruders by territorial yellow-hooded blackbirds fits neither of the patterns recorded for other territorial species. Agonistic reactions to intruders do not vary strongly either with the intruder's location within the territory or its distance from the resident male. Although our data are insufficient to eliminate small effects of either sort, there are no major differences in a resident's reactions to intruders regardless of location, provided the intruders are within the resident's territorial boundary. Most but definitely not all, intruders are promptly confronted by the resident regardless of the intruder's location.

As a result, the amount of time that an established resident spends in different portions of its territory does not correlate with its agonistic tendencies toward intruders there. If familiarity with the site of an encounter or previous experience in encounters at a site influences a male's agonistic tendencies there, one would expect a correlation point by point between an individual's activity and aggression fields. Instead, at least within its territorial boundaries, a male yellow-hooded blackbird's aggression field is relatively flat, while its activity field decreases away from the center.

Because the territories of male yellow-hooded blackbirds are relatively small, a male could obtain some visual familiarity with all portions of its territory even from perches near the center. Perhaps this experience is enough to make reactions to strange intruders about the same anywhere in the territory. It remains possible that both an intruder's proximity and the resident's detailed familiarity with the locations of encounters would prove to be more important during the early stages of territory establishment. If so, the relatively flat aggression fields of territorial yellow-hooded blackbirds would develop gradually.

Aggression between neighbors, in contrast to aggression toward intruders, suggests that a male's previous use of the immediate area of an encounter does influence its agonistic behavior there. Changes in boundaries between neighbors involved a decrease in the use of the contested area by its original owner and an increase in the use of the area by the new owner before the outcome of agonistic encounters in this area reversed.

Although many previous studies have reported that new territories are often established in the interstices of existing territories (HOWARD, 1920; SNOW, 1956; DHONDT, 1972) or that males adjust their activities and even territorial boundaries in accordance with the locations of their mates' nests (KENDEIGH, 1941; NICE, 1943; NERO & EMLLEN, 1951; MARLER,

1956a; FICKEN, 1962; STEFANSKI, 1967), these studies have not considered the relationship between activity and aggression fields during these changes. Such changes in territorial boundaries provide clear information about the relationship between an individual's use of an area and its dominance there over intruders or neighbors.

Our observations of boundary changes are consistent with the hypothesis that the aggressive tendency of a male toward a neighbor at a particular location is an increasing function of the amount of time that the male has recently spent in the immediate vicinity, in other words his immediate familiarity with the location. This hypothesis leads to a prediction that the dominance between neighboring males should reverse where the values of the activity fields of the two males cross. In addition, it predicts that a new male could establish himself in the interstices between existing territories when he could remain in this area long enough to have spent more time there than the neighboring residents.

SUMMARY

The behavioral mechanisms that produce territoriality require that a resident's agonistic tendencies vary with the locations of encounters with opponents or with the distance between the resident and an opponent. Variation in agonistic tendencies with location could result from increased aggressiveness in familiar locations. Only a few field studies have previously documented variation in aggressive tendencies either with the location of an encounter or the distance of an opponent.

In this study, we measured the spatial distributions of advertising activities in the territories of male yellow-hooded blackbirds *Agelaius icterocephalus* and related these distributions to aggressive tendencies of the residents. Advertising and agonistic activities resembled those of other marsh-nesting blackbirds in the genera *Agelaius* and *Xanthocephalus*. To portray the spatial distributions of activities, we determined convex hulls for the 95% and 68% of instances or seconds of an activity closest to the vector mean of the distribution. A territorial male's time perched conspicuously, instances of conspicuous perching, songs and song flights were concentrated near the center of his territory. In spite of this uneven distribution of a male's time and advertising activities within his territory, a male's aggressive tendencies toward intruders did not vary clearly either with the intruder's location or distance from the resident, provided only that the intruder was within the resident's boundaries.

Interactions with neighbors suggested that use of an area is a prerequisite for its defense. Changes in boundaries and establishment of new territories revealed that a male's use of an area increased before aggression toward neighboring residents began. Changes in a resident's territorial boundaries often resulted from changes in the spatial distribution of residents' activities as a result of localizing activities around nests of egg-laying females or changes in the locations of nests under construction. These observations suggest that predominance in use of an area leads to dominance in defense of that area.

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RÉSUMÉ

Les mécanismes comportementaux effectuant la territorialité exigent que les tendances agonistiques d'un résident varient avec le lieu de rencontre d'un opposant ou avec la distance entre le résident et l'opposant. La variation spatiale des tendances agonistiques peut résulter en une augmentation de l'agressivité en des endroits familiers. Peu de recherches ont examiné les tendances agressives d'un résident territorial en relation à la fois avec le lieu d'une rencontre et avec la distance de l'opposant.

Les distributions spatiales des activités des mâles territoriaux d'*Agelaius icterocephalus* (Icteridae, Aves) sont comparées avec les tendances agressives des mâles. Les actions agonistiques ainsi que celles du signalement du territoire ressemblent à celles des autres espèces d'*Agelaius* et de *Xanthocephalus*. Pour montrer les distributions spatiales des activités, nous avons déterminé les coques convexes pour les 95% et les 68% des occurrences, ou des secondes d'une activité, les plus proches du vecteur moyen de la distribution. Pour un mâle territorial, le temps qu'il se perche visiblement, les cas de se percher visiblement, les chants et les chants en vol convergent près du centre du territoire. Néanmoins, les tendances agressives d'un résident vers des opposants ne varient pas d'une façon évidente ni avec le lieu de l'opposant ni avec sa distance du résident, pourvu que l'opposant soit entre les limites territoriales du résident.

Les rencontres des voisins territoriaux suggèrent qu'il est nécessaire de séjourner à un certain endroit antérieurement à la défense de cet endroit. Les changements des limites du territoire et l'établissement de territoires nouveaux ont révélé que les séjours d'un mâle à un certain endroit se prolongent avant que s'établisse l'agression contre les résidents voisins. Changements des limites du territoire d'un résident ont résulté de changements de la distribution spatiale des activités du résident suite à des restrictions des activités près d'un nid d'une femelle en ponte ou de changements des endroits de nids en construction. Ces observations suggèrent que la prédominance en l'usage d'un endroit mène à la dominance et à la défense de cet endroit.