TERRITORIAL RELATIONSHIPS OF BLUE-WINGED WARBLERS, GOLDEN-WINGED WARBLERS, AND THEIR HYBRIDS

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TERRITORIAL relationships of congeners are of special interest to ecological and evolutionary theory (e.g., Orians and Willson, 1964; Hamilton, 1962), although such systems in hybridizing forms have been the subject of very few studies. The Blue-winged Warbler (*Vermivora pinus*) and the Golden-winged Warbler (*V. chrysoptera*) have recently come into contact in the northeastern and north central United States and hybridize (Short, 1963); they provide a good opportunity for a study of territorial relationships of two species and their hybrids.

The purpose of this paper is to describe intraspecific territorial relationships, those of two hybrids, of hybrids and a parental species, and interspecific ones. From this study we determine the role of visual and vocal releasers in eliciting territorial behavior. Although these have been the subject of numerous experimental studies using both visual (e.g., Noble and Vogt, 1935) and vocal releasers (e.g., Dilger, 1956; Lanyon, 1963; Gill and Lanyon, 1964), few such studies have used observations on natural encounters. Finally, the role of the territorial system in the speciation of this complex is discussed.

METHODS

Territorial behavior was studied in a colony consisting of both species and Brewster's hybrids at Varna (Tompkins Co.), New York in May and June, 1961, May through August of 1962, and May, 1963 and 1966. Additional observations of male Blue-wings, a Brewster's hybrid, and a Lawrence's hybrid were made near Thurmont (Frederick Co.), Maryland in May 1964.

Notes were taken on all agonistic interactions. In addition, territories were roughly mapped by observing the positions of males for at least two days and usually over a period of several weeks.

THE BIRDS

The two species differ primarily in size and color of wing bars, back and breast color, and face pattern. Hybrids show varying degrees of intermediacy. The plumage colors of the birds we studied are indicated in Table 2. Short (1963) showed that many birds that appear "pure" in the field actually show introgression from the other species. However, for the purpose of this study, Blue-wing and Golden-wing refer to birds that looked typical of that species in the field.

The primary song of the Blue-wing is a *bee* followed by a long *buzz*, that of the Golden-wing a *zee* followed by a variable number of short *bee* notes (Ficken and Ficken, 1967). Each individual hybrid that we studied consistently gave the song of one or the other parental species. A secondary song, similar in both species, consists of a trill followed by a *buzz*.

OBSERVATIONS

General aspects of territorial behavior.—Resident male Blue-wings arrived between 6 May and 14 May in the Varna colony in 1962 and 1963. Golden-wing males arrived from 12 May to 23 May and Brewster's hybrid males from 6 May to 12 May. "Pure" males usually obtained conspecific females within a week of their arrival. Both sexes confined all their activities to the territory from the time of arrival until the young were fledged. After this time territorial boundaries broke down.

Territories usually consisted of overgrown fields with many shrubs and small trees (under 20 feet) bordered by taller deciduous trees. Size of territories varied from less than one acre to almost two acres. Small trees within the territory and trees at the edge of the territory were used as singing posts, particularly during incubation. All the nests that we found were situated at the field-woodland edge and this is the typical nest site in both species (Bent, 1953).

Vocalizations concerned with territorial defense.—Unmated males sing primary songs almost uninterruptedly as they forage. Later in the season, particularly in the Blue-wing, and following territorial encounters in both species and hybrids, the secondary song, similar in both species, is given (Ficken and Ficken, 1967). Our observations indicate that since secondary song usually only occurs after an encounter has already started, that it is not important in initiating interspecific encounters. Song is usually absent during encounters and is only resumed after a few minutes, typically when one of the encountering males has left the area. Songs given during and immediately following encounters are usually different from songs of undisturbed birds. In Golden-wings the primary song is shortened or the secondary song is given while Blue-wings usually give only secondary songs (Ficken and Ficken, 1967).

Some interactions consist solely of song exchanges. The following is an example of one such short intraspecific exchange: Blue-wing No. 1 approaches Blue-wing No. 2 to 10 feet in the boundary zone between their territories. Blue-wing No. 2 sings primary song, Blue-wing No. 1 which had been singing primary songs before No. 2's approach, changes to secondary song. No. 1 leaves. Interspecific exchanges also occurred but more rarely. For example, a Blue-wing and a Golden-wing with overlapping

territories had the following exchange while in the same tree: Blue-wing, which had been giving primary song, switches to secondary song and Golden-wing shortens primary song. Both move off, in opposite directions. Similar exchanges were noted between a Brewster's hybrid with Blue-wing song and a Brewster's hybrid with Golden-wing song.

Other types of vocalizations are uncommon during territorial encounters. A snapping sound made by contact of the mandibles occurred occasionally during chases and fights. Chip notes were sometimes given in intraspecific Blue-wing encounters. On one occasion a marsh-wren like chatter was given by a Golden-wing during a chase.

Postures and displays associated with territorial defense.—These are similar in the two species and hybrids, and the following is an inventory of such behavior.

Crown raising. Pronounced raising of the crown feathers was occasionally seen in both species immediately following an encounter. This movement was more obvious in the Golden-wing because of the conspicuous crown patch.

Soliciting. We observed three instances of male Golden-wings after repeated encounters (twice with Blue-wings, once with a Brewster's hybrid) turn away from the opponent and perform a display resembling a female soliciting copulation. Male Soliciting incorporates quivering wings, raised tail and erected crown feathers and a lowered breast (illustrated in Ficken and Ficken, 1962). The display was given by the bird that seemed to be losing the encounters and immediately followed a chase by the opponent. We never observed it in Blue-wings but Frank Gill (pers. comm.) reports a similar posture in this species; after an attack by the opponent the Blue-wing raised its tail while the wings were drooped and quivering.

Tail Spreading. This is a prominent feature of all male encounters in both species and hybrids, and the tail often seems maximally spread, exposing much white. It is often performed in flight, particularly by a bird that is being chased. It is also sometimes given by a perched bird immediately after an encounter.

Chases. Chases are of common occurrence during territorial encounters, one bird usually flying at the other bird, which flees while the first bird continues pursuing it.

Supplanting. One bird flies at the other, the other leaves, and the first bird lands in the second's original position.

Flying past. This was only observed in encounters between two Brewster's hybrid males. One bird flew past the other, landing about ten feet away. The second bird then engaged in this behavior, and some encounters of 20 minutes duration consisted mainly of this behavior.

TABLE 1
A COMPARISON OF INTERSPECIFIC AND INTRASPECIFIC ENCOUNTERS

	Both males unmated	One male mated	Both males mated	No. encounters without fights	No. encounters with fights	Duration (S = < 5 min., M = 5–20 min., L = > 20 min.)
Interspecific	0	5	5	4	6	S 4
						M 4
						L 2
Intraspecific	6	3	1	10	0	S 3
						M 4
						L 2

Fighting. Fighting involves actual contact of the two birds, rather than the sham fights seen in the American Redstart (*Setophaga ruticilla*) (Ficken, 1962).

Comparison of interspecific and intraspecific encounters.—Territorial encounters were most frequent and intense before nest building; during incubation only occasional chases were seen. The following are extracts from our field notes of intraspecific and interspecific encounters:

17 May 1962. Varna, N.Y. Golden-wing male chases Blue-wing male which had approached to within 30 feet. Both females are in the immediate area. Blue-wing male flies off with tail widely spread. Two minutes later he chases the Golden-wing male. Males separate and stay 75 feet apart for several minutes. Then male Blue-wing chases male Golden-wing. Golden-wing raises crown feathers markedly after being chased. He lands in the same tree as the Blue-wing but faces away from him . . . . Blue-wing male flies after Golden-wing male. They perch briefly 20 feet apart and then they fight. Blue-wing male flies off.

11 May 1962. Varna, N.Y. Two Blue-wings, both unmated, have adjacent territories. One male chases the other. Harsh chips are heard in flight. White in tails of both birds is very prominent during chases. Chases continue for several minutes over the same small area. During the chases one is usually about a foot behind the other. They land 20 feet apart and harsh chips are heard. One male then leaves the encounter area.

Table 1 compares intraspecific (Blue-wing vs. Blue-wing and Golden-wing vs. Golden-wing) and interspecific encounters, excluding interactions consisting solely of song exchanges. Intraspecific encounters occurred more commonly among unmated males; interspecific encounters did not take place unless one male was mated. Fights were observed only in interspecific encounters. Intraspecific encounters were usually confined to a narrow boundary zone between two territories. On the other hand, interspecific encounters took place over a much wider area. The duration of encounters was similar in both situations. The postures and displays during and after encounters were similar in interspecific and intraspecific situations.

TABLE 2

RELATIONS BETWEEN PLUMAGE, SONG, AND TERRITORIAL BEHAVIOR
(BW = Blue-wing, GW = Golden-wing)

No. of cases	Birds	Song	Plumage
			OVERLAPPING TERRITORIES
5	Blue-wing vs.	BW	Yellow breast, no face or throat patch, white wing bars
	Golden-wing	GW	White breast, face and throat patch, yellow wing bars
1	Blue-wing vs.	BW	Yellow breast, no face or throat patch, white wing bars
	Lawrence's hybrid	BW	Yellow breast, face and throat patch, white wing bars
2	Golden-wing vs.	GW	White breast, face and throat patch, yellow wing bars
	Brewster's hybrid	GW	White breast, no face or throat patch, yellow wing bars
			NON-OVERLAPPING TERRITORIES
10	Blue-wing vs.	BW	Yellow breast, no face or throat patch, white wing bars
	Blue-wing	BW	Yellow breast, no face or throat patch, white wing bars
6	Golden-wing vs.	GW	White breast, face and throat patch, yellow wing bars
	Golden-wing	GW	White breast, face and throat patch, yellow wing bars
1	Brewster's hybrid	GW	White breast, no face or throat patch, yellow wing bars
	Brewster's hybrid	BW	White breast, no face or throat patch, white wing bars
1	Blue-wing vs.	BW	Yellow breast, no face or throat patch, white wing bars
	Brewster's hybrid	GW	Yellowish breast, no face or throat patch, yellow wing bars

Territorial relationships of birds similar in song and plumage.—Table 2 summarizes the territorial situation as related to the visual and vocal releasers of the birds involved. No birds with similar plumage and song had overlapping territories. Furthermore, although territories were often adjacent to a conspecific, in one case a barrier of unsuitable habitat was between the territories (Fig. 1). In this case when Golden-wing No. 2 arrived, three days after Golden-wing No. 1, he attempted to settle near Golden-wing No. 1 on the same side of the swamp, but after several short encounters he moved across the swamp and shared a territory with Blue-wing No. 3. A similar state existed between the two Blue-wings, Blue-wing No. 5 attempting to settle on part of Blue-wing No. 3's territory, but after two short encounters he also moved across the swampy area. The swamp served as a barrier, minimizing contacts between conspecifics, and except for the initial encounters, none took place subsequently except for an occasional chase.

Unfortunately, we were unable to determine the territorial relationships of two yellow-breasted Brewster's hybrid males with Blue-wing songs which were near Blue-wings. In both cases the Brewster's males were unmated and had encounters with the mated Blue-wings near the females. Other than on these occasions, their territories seemed not to overlap.

Territorial relationships of birds dissimilar in both song and plumage.—In all cases observed where a Blue-wing and a Golden-wing were near each other there was territorial overlap between them which was often extensive (Fig. 1). We have an impression of mutual avoidance of unmated males. The two males were only rarely seen together in the same tree. They were usually some distance away from each other and tended to occupy the same areas at different times as Moynihan (1963) found in different species of honeycreepers.

The only interspecific encounters observed occurred in the presence of newly arrived females. If two mated males were close at other times, no encounters resulted. There were no encounters once nest building commenced. In one case, nests of a Blue-wing and a Golden-wing pair were 75 feet apart and both species were seen frequently in the overlap area.

Territorial relationships of birds similar in plumage but dissimilar in song.—We observed territorial relations to two male Brewster's hybrids, similar in plumage but one singing Golden-wing songs and the other Blue-wing songs (Fig. 1). Male No. 1 initially wandered over a 1.5 acre field and seemed to utilize all of it although he spent more time on the upper slope while singing and foraging. Six days later (12 May) the other Brewster's hybrid arrived at the field and was seen foraging on the upper slope. Several short encounters between the two males were observed. The following day long lasting, more intense encounters were observed. By the end of the day the newer arrival, No. 2, confined his activities to the lower part of No. 1's territory. The boundary between the territories seemed quite rigid. No further encounters were observed except for one short fight when No. 2's female entered the boundary zone followed by her mate. Both males tended to avoid the boundary and never were observed crossing it.

Meyerriecks and Baird (1968) observed that a yellow-breasted Brewster's hybrid with Golden-wing songs had many boundary encounters with a Blue-wing and they maintained non-overlapping territories.

Territorial relationships of birds dissimilar in plumage but similar in song.—A male Lawrence's hybrid had a territory extensively overlapping that of a male Blue-wing (Fig. 1). Both males were mated. On three occasions they were observed within 30 feet of each other in different parts of the overlap area but they simply ignored each other.

We also observed a white-breasted Brewster's hybrid with Golden-wing songs which had extensive territorial overlap with a Golden-wing (Fig. 1). The only encounters which we observed occurred when the hybrid (at the time unmated) approached the female Golden-wing within ten feet on two occasions. Lunk (1938) also observed overlapping territories of a Golden-wing and a Brewster's hybrid.

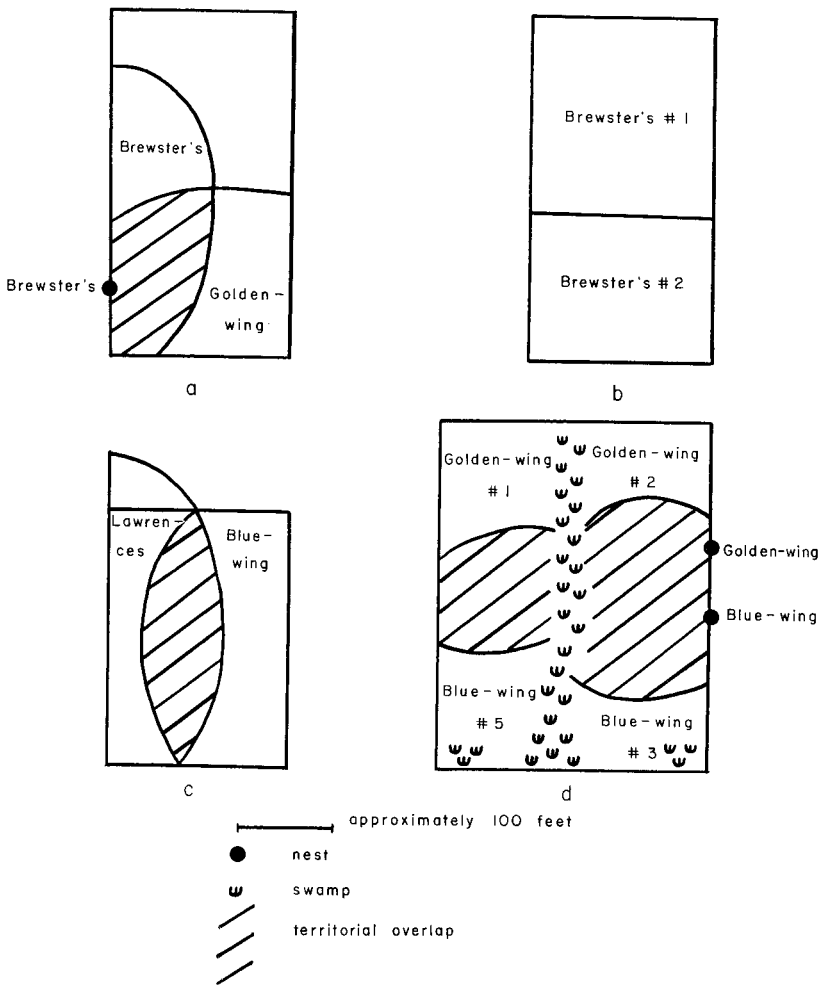

FIG. 1. Territorial relationships. Rectangles represent a field bordered by deciduous trees. a) Overlapping territories of a Brewster's hybrid and a Golden-wing. b) The same field the following year with non-overlapping territories of two Brewster's hybrids. c) Overlapping territories of a Lawrence's hybrid and a Blue-wing. d) Territories of two pairs of Blue-wings and two pairs of Golden-wings, showing overlap interspecifically and non-overlap intraspecifically.

Agonistic interactions with other warbler species.—Agonistic encounter also occurred with other warbler species. These encounters were usually of very short duration and there was no evidence of territorial exclusiveness. In all cases Blue-wings and Golden-wings were the aggressors, e.g., instigated

fights and chases. Chestnut-sided Warblers (*Dendroica pensylvanica*) and Yellowthroats (*Geothlypis trichas*) frequently had territories overlapping those of the two *Vermivora* species. Encounters between Blue-wings and Yellowthroats were more common than those of Golden-wings and Yellowthroats. On the other hand, male Golden-wings had intense encounters with male Chestnut-sided Warblers and fighting occurred in three out of six cases observed. On two of these occasions the male Golden-wing gave secondary song following these encounters, a behavior similar to that following intense intraspecific encounters. Encounters were also seen between Golden-wings and a migrant Myrtle Warbler (*D. coronata*) and between Blue-wings and migrant Nashville Warblers (*V. ruficapilla*). In summary, Blue-wings had five out of six encounters with birds of similar color, i.e., birds with yellow breasts. Golden-wings, on the other hand, had seven out of eight encounters with birds similar in color pattern (e.g., with Chestnut-sided and Myrtle Warblers, which are similar to the Golden-wing in having a yellow crown and a white breast).

DISCUSSION

Birds with similar songs and plumages have non-overlapping territories; birds with different songs and different plumages have overlapping territories. We were also fortunate in having birds which differed in only one of these features. The Brewster's hybrids with different songs but similar plumages which had non-overlapping territories point to the importance of visual releasers in species recognition. In the cases of Brewster's hybrids overlapping territories with Golden-wings and Lawrence's hybrid with a Blue-wing, the chief differences between the males involved is in facial pattern. Blue-wings and Brewster's hybrids have a black line through the eye while Golden-wings and Lawrence's hybrids have prominent face and throat patches. Thus, the principal feature involved in species recognition with regard to territorial behavior seems to be facial pattern. Facial pattern is probably of great importance in species and sexual recognition in birds (e.g., Smith, 1966). For example, Noble and Vogt (1935) showed that the face mask of the male Yellowthroat was important in sexual recognition, the male attacking a mount which he had previously responded to sexually after a face mask was pasted on.

Gill and Lanyon (1964) conducted a series of experiments on the visual and vocal basis for species discrimination in Blue-wings. In combination with playback of *V. pinus* primary song, stronger responses were elicited by *V. pinus* mounts than by mounts of *V. peregrina*, *V. chrysoptera*, *Dendroica petechia*, and *D. pensylvanica*, indicating that males were discriminating visually. Weak responses to non-conspecific mounts even in conjunction with

a playback of *V. pinus* song indicate, as do our observations, the importance of visual releasers in evoking aggression.

The territorial system of these warblers helps to explain some unusual associations between two males and a female. Some such cases are clearly "helpers" at the nest (Short, 1964) and may be temporary, e.g., occurring just during the parental period. Other associations begin earlier. For example, Campbell (1940) noted a male Lawrence's hybrid with Blue-wing songs accompanying a male Blue-wing and a female Golden-wing on 30 May. It was not known whether one or both males were mated to the female. Also, a male Brewster's hybrid was first associated with a pair of Golden-wings on 30 May. In June he accompanied the Golden-wings and young. Apparently in both cases the aggressive reactions of one male toward the other were weak. This association of two males occurs more commonly between males that have overlapping territories. It is possible that the territorial system could affect pairing relationships and even lead to polygamy in some cases.

The territorial system could increase interspecific sexual activity and hence hybridization in other ways. During intense interspecific encounters females become sexually stimulated and chances for copulation with a non-conspecific are increased. Also, males with overlapping territories sometimes approach a mated non-conspecific female on the same territory (Ficken and Ficken, 1968). Lanyon (1956) points out that territorial exclusiveness of two meadowlark species (*Sturnella magna* and *S. neglecta*) increases reproductive isolation. "Since copulations apparently occur only within the meadowlark territory, the male's defense of his territory constitutes an important check on interspecific matings across territorial boundaries."

SUMMARY

Territorial relationships of Blue-winged Warblers, Golden-winged Warblers, and their hybrids were studied. Behavior involved in territorial defense is described. Males with similar plumages and songs maintain non-overlapping territories while those with dissimilar plumages and dissimilar songs have overlapping territories. Males with dissimilar plumages but similar songs have overlapping territories while those with similar plumages but dissimilar songs maintain non-overlapping territories. It was concluded that plumage is more important than song in species recognition by males as measured by territorial behavior. Face pattern seemed the most important feature in species recognition. Overlapping interspecific territories probably increase the chances of mixed matings.

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