

COURTSHIP OF BLUE-WINGED WARBLERS, GOLDEN-WINGED WARBLERS, AND THEIR HYBRIDS

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COMPARATIVE studies of courtship of hybridizing avian species in nature have rarely been attempted with the exception of the Anatidae (e.g., Johnsgard, 1960). A rare opportunity to study birds whose courtship pattern is different than waterfowl is presented by Blue-winged Warblers (*Vermivora pinus*) and Golden-winged Warblers (*V. chrysoptera*), which commonly hybridize in their extensive area of sympatry. There is preferential conspecific mating in at least some areas of sympatry and hybrids are selected against, demonstrating the operation of reproductive isolating mechanisms (Ficken and Ficken, 1968a). Thus a study of this species complex offers an unusual chance to further the understanding of the role of courtship in the speciation process.

Courtship includes the activities of the male and female from the time of pair formation through copulation (Morris, 1956). We describe the general pattern of courtship activities and displays for conspecific pairs of both species and two pairings involving hybrids. Interspecific sexual attractions are discussed. By comparison with courtship of several other parulids, we arrive at some conclusions concerning the selective pressures which have affected courtship in these *Vermivora*. Finally, the role of courtship in reproductive isolation is discussed as are those aspects of behavior which increase interbreeding.

METHODS

Observations of both species and Brewster's hybrids were made in Varna (Tompkins Co.), New York during 1961-1963 and 1966. Daily observations took place from 0630 to 1100 E.D.T. during the courtship period. Notes were spoken into a pocket tape recorder.

During the four-year period we observed pairings in a total of 15 Blue-wings, five Golden-wings, three Brewster's hybrids mated with Golden-wings, and five Brewster's hybrids mated with Blue-wings. No interspecific pairings were observed. Detailed accounts of pairings in the colony are given elsewhere (Ficken and Ficken, 1968a). Courtship activities were studied closely in three Golden-wing pairings, five Blue-wing pairings and two pairings of male Brewster's hybrids and female Blue-wings. Both hybrids gave Blue-wing songs but they differed somewhat in coloration, one having white underparts, the other a yellow wash across the breast. By "Blue-wings" and "Golden-wings" we refer to individuals that phenotypically resembled

one or the other parental species, but it must be noted that there was introgression in this population (Short, 1962).

OBSERVATIONS

First we describe the general pattern of events in courtship and then proceed to a more detailed discussion of pair interactions and displays.

General pattern of courtship.—Males maintain a territory, usually a little over an acre, where they sing persistently before the arrival of females. Unmated males of the two species often have overlapping territories, although interspecific agonistic encounters occur during a brief period when at least one (and often both) males first become mated. After a few days these interspecific interactions cease and the birds resume territorial overlap without friction.

Females usually arrive a day or two later than males of the same species. Pair formation occurs immediately after the female's arrival. As soon as a female arrives on his territory the male spends much time following her. During this period the male approaches the female many times, apparently attracted by her call notes (*Tzips*) and she usually stays low in the undergrowth. Although both sexes are often aggressive toward each other, aggression is more marked in the male. The female initiates a bout of sexual activity by assuming the Soliciting posture; the male sometimes displays as he approaches her while she is displaying and copulation may follow.

Early arriving females wait a day or two before beginning nest building but later females may begin nest building the day of arrival. Sexual activity is most intense just prior to and during the first day of nest building. No sexual activity was observed after this time and probably did not occur since males spent much less time near their mates during later stages of nest building and females no longer gave the location call.

Pair formation.—Although we did not see the initial meeting of a pair, we made many observations of pairs early the first morning of pairing. The male spent a great deal of time approaching and chasing the female. We saw no special displays associated with early pair formation, the process being similar to that in the American Redstart (*Setophaga ruticilla*) (Ficken, 1963). Pair formation occurs very rapidly and probably involves responsiveness to color pattern and song by the female and responsiveness by the male to her visual and behavioral characteristics (Ficken and Ficken, 1968a).

Attempts at interspecific pairing.—Although no interspecific pairings occurred, we observed several situations where there were interspecific attractions. We observed a female Blue-wing which had arrived very late, approach a male Golden-wing which was mated to a Golden-wing. The Golden-wing ignored her completely but his mate gave the *Tzip* vocalization

TABLE 1
PAIRINGS ATTEMPTS BY UNMATED MALES APPROACHING FEMALES MATED TO CONSPECIFICS

Unmated male	Female	Ultimate state of unmated male
Brewster's hybrid	Blue-wing	Unmated
Brewster's hybrid	Golden-wing	Mated to Golden-wing [†]
Blue-wing	Golden-wing	Unmated
Golden-wing	Blue-wing	Mated to Golden-wing

[†] Not the same individual as the one that was approached.

indicating mild alarm and the strange female soon left. She then approached a mated male Blue-wing on the same territory; his responses were not observed but she soon left the area.

In another type of interspecific attraction, unmated males were attracted to the female of the male occupying an overlapping or adjacent territory (Table 1). These approaches were usually followed by intense encounters between the two males. In no case did the invading male "steal" the female from her mate. Berger (1958) cites an observation of three males—a Brewster's hybrid, a Blue-wing, and a Golden-wing—engaged in encounters centered on a Golden-wing female.

Agonistic and sexual interactions of the pair.—The pre-nest building period was marked by many male approaches toward the female; only rarely did the female come to the male. In many cases the male simply flew to within one foot of the female, assumed no special posture, remained a few seconds, and then flew off while the female uttered *Tzips*. This type of approach was termed non-aggressive (Table 2). In other cases the male flew directly to the female, she fled and he chased her. When she did not flee he lunged and fights often occurred. We term these approaches aggressive. Blue-wing and Golden-wing males were similar in the percentages of aggressive and non-aggressive approaches of the female (Table 2). However, the incidence of aggressive approaches was much lower in Brewster's hybrids paired with female Blue-wings. This difference between pairings involving a hybrid and conspecific ones is statistically significant using a Chi Square test ($P < 0.05$). For the purpose of this comparison sexual interactions were excluded.

Females responded to males' approaches in a variety of ways which we also categorized as non-aggressive or aggressive. Non-aggressive responses included remaining (often giving *Tzips*) and fleeing. Aggressive responses included lunges at the male, often with Bill Snaps and flying attacks directed at the oncoming male. Again both Blue-wing and Golden-wing females paired with conspecifics showed a similar pattern, females being aggressive

TABLE 2
NUMBER OF AGGRESSIVE VS. NON-AGGRESSIVE APPROACHES OF THE MATE IN
CONSPECIFIC AND HYBRID PAIRINGS (n = NUMBER OF PAIRS)

	Aggressive	Non-aggressive	Total	Per cent aggressive
<i>Male's reaction to female:</i>				
Golden-wings ($n = 3$)	8	9	17	47
Blue-wings ($n = 3$)	19	18	37	51
Brewster's hybrid and Blue-wing females ($n = 2$)	6	15	21	29
<i>Female's reaction to male:</i>				
Golden-wings ($n = 3$)	5	14	19	26
Blue-wings ($n = 3$)	10	31	41	24
Brewster's hybrid and Blue-wing females ($n = 2$)	2	17	19	11

to males during an average of 25 per cent of the male approaches. However, female Blue-wings paired with Brewster's hybrids showed a lower incidence of aggressive responses to the approach of the mate (Table 2). This difference was statistically significant using a Chi Square test ($P < 0.05$).

Females frequently uttered *Tzips* before nest building but were usually silent later on. *Tzips* were sometimes uttered when the male was away; he often then responded immediately by approaching. *Tzips* were also given in apparent response to the song of the mate, especially after he had been silent for a long time and then suddenly sang. *Tzips* were given also by the female when the male approached. This call note seems to serve several related functions: (1) it informs the male of the female's location which is important since females wander greatly around the territory the first few days, (2) it stimulates male approaches, and (3) it also may be important in cementing the pair bond. The form of the *Tzip* was identical to our ears in all birds. However, a brief series was often given by female Blue-wings, while female Golden-wings uttered it singly.

The two species and the Brewster's hybrids sometimes showed behavior indicating conflict when near the mate. Both sexes frequently Tail Spread after approaching or being approached. Tail Spreading in flight, so prominent in agonistic encounters between males (Ficken and Ficken, in press) was rare in interactions between the pair; most of the Tail Spreading was given in a stationary posture. Pivoting, in which a perched bird rotated the body without moving the feet, was often accompanied by Tail Spreading. Wing and Tail Flicking sometimes took place as well. Crown Raising, on the other hand, was seen only in the male Golden-wing when

near the female. However, since the Blue-wing does not have such a well-delineated crown patch, we possibly overlooked this display.

Males of both species performed two different flight displays near the female. In Moth Flight the male usually flew slowly with marked wing beats and the head held high. In both species this display occurred as the male flew away from his mate and usually he did not react aggressively to her afterward. Once Moth Flight preceded a copulation by a Blue-wing. In Gliding the male held the wings out rather stiffly in a long coasting flight. Gliding occurred in slightly different contexts than Moth Flight, being given more often as the male approached the female. After Gliding the male sometimes chased his mate.

Bill Dueling was observed several times in both species, occurring just after the male approached the female. She then either flew out to meet him or sometimes remained perched and they pecked at each other's bills. Occasionally they seemed to grasp bills and then fell down toward the ground still holding on. Bill Dueling was different from fighting in that it did not involve striking with the feet and was also sometimes associated with sexual activity (see p. 166).

Wing Extension was seen only twice and in a male Blue-wing. The perched bird held the wings lifted to the side and somewhat spread. On one occasion the display preceded a Hover near the female and another time Gliding.

The male performed Hovering a few inches away from the perched female. The male's breast feathers were very fluffed, the tail was spread and the bird fluttered with rapid wing beats in front of the female. It occurred once when the male approached in apparent response to female Soliciting and in two other instances was also associated with sexual activity.

The only primarily sexual display given by the female was Soliciting which is similar in form in many passerines. In the most exaggerated cases the neck was extended, the breast lowered, the tail markedly raised and the wings vibrated (high intensity Solicit). Sometimes these components were less pronounced (low intensity Solicit). In none of the seven Solicits that were seen did the birds give vocalizations accompanying the display. In both species the only copulations observed followed Soliciting. Because of its obvious importance and the variable situations in which Soliciting occurs, we give summarized accounts from our field notes on Soliciting and copulation.

Case 1.—Male Brewster's hybrid No. 1 paired with Blue-wing female, second day after pairing. Male makes many non-aggressive approaches of the female, coming to within a few feet and peering at her as she forages in the undergrowth. Female silent except when male near. Suddenly she gives a short flight, uttering *Tzips*, the male flies in from about 30 feet away and chases her. She lands and immediately gives high intensity

Solicit. Male remains within three feet for five minutes, with no special postures and makes no attempt to copulate. Shortly after Soliciting the female picks up a leaf (she has not previously been observed doing any nest building) but soon drops it.

Case 2.—Blue-wing pair No. 5, third day after pairing. Male has approached female to about one foot at least six times in the last few minutes. During one approach she briefly Solicits at low intensity, but he leaves with no attempt to copulate.

Case 3.—Golden-wing pair No. 4, first day after pairing. Female gives *Tzips* constantly. Suddenly she Solicits at low intensity, male which was off about 20 feet, immediately flies in and mounts her with much fluttering of wings while on her back.

Case 4.—Golden-wing pair No. 2, first day after pairing. Blue-wing male No. 3 moves into this Golden-wing's area. Males chase and fight and female Golden-wing approaches them. Female Solicits, male Golden-wing which had been near her, ignores her and flies back toward the male Blue-wing which remained about ten feet away. A few minutes later male Golden-wing Hovers near his female but then flies off.

Case 5.—Blue-wing pair No. 3, first day after pairing. There have been many encounters in the last half hour between this male and Golden-wing male No. 2 whose female is also in the area. During a fight of the two males, female Blue-wing Solicits at high intensity, but the male does not approach and is still engaged in encounters with the other male. Male Golden-wing chases female Blue-wing and she immediately Solicits on landing. There are no approaches by either male. After a minute or so she Solicits again and then flies off and the male Blue-wing follows her. She again lands and Solicits and the male Blue-wing approaches but does not mount. A minute later she again begins a high intensity Solicit and the male Blue-wing which was 20 feet away and still engaged in encounters with the Golden-wing male flies in, but we are unable to see if he mounts her. She continues Soliciting but both males are engaged in encounters. During one Solicit, the Golden-wing female which is nearby flies in and chases her. The Blue-wing female still Solicits and is followed by the Golden-wing female as she moves through the undergrowth in this posture. Males continue to have encounters. Blue-wing female Solicits at high intensity in presence of Golden-wing female 10 feet away, and is ignored by her. Blue-wing male comes in and chases Blue-wing female. She Solicits immediately after the chase and the Blue-wing male approaches her again, this time with Moth Flight, and they copulate. He performs a Hover in front of the female and then flies off. She shakes the feathers of her cloacal region. She resumes Soliciting, he gives a Moth Flight toward her and they Bill Duel and fall down into the undergrowth with bills held together.

From these observations it can be concluded that the male's response to a Soliciting female is variable; he may leave without attempting to mount as in Cases 1, 2, 4 and 5, or copulation may take place as in Cases 3 and 5. Male displays preceded copulation in some cases but not in others. Soliciting followed aggressive approaches by the male in Cases 1 and 5. Cases 4 and 5 occurred during interspecific encounters, and while these encounters only occupied at most a few hours of the approximately 100 during which pairs were watched closely, Soliciting was seen in females of both species and copulation in the Blue-wing. Thus it seems that direct aggressiveness by the male, or participating in and observing aggressive encounters stimulates Soliciting in both species.

There was one case of an interspecific sexual reaction (Case 5) when the female Blue-wing Solicited after being chased by the Golden-wing male. The same female also Solicited after a chase by the Golden-wing female. This indicates that Soliciting is not given exclusively in the presence of the mate but occurs when the female reaches a high degree of sexual readiness brought about by intense agonistic activity.

There were insufficient observations for detailed comparisons of the courtship behavior of the two species and hybrids. Our inventory of courtship displays is undoubtedly incomplete, since Baird (1967) noted a courtship display and courtship feeding in the Golden-wing that we did not observe, but his accounts of Gliding and Hovering in this species are similar to ours. The general pattern of sexual behavior is similar in both species as are male displays and the contexts in which the female Solicits.

DISCUSSION

Evolution of courtship behavior.—Comparative studies are a prime source of information concerning the selective pressures affecting the behavior of closely related species (Tinbergen, 1965). We have derived some ideas concerning the probable selective pressures affecting courtship in these *Vermivora* species from a knowledge of their general breeding behavior and from comparisons with other warblers, particularly the American Redstart (*Setophaga ruticilla*) as well as some *Dendroica* species (Ficken, 1963; Ficken and Ficken, 1962, 1965). The redstart is probably closely related to *Dendroica* (Parkes, 1961; Ficken and Ficken, 1965) and not very distantly related to *Vermivora*. Griscom (in Griscom and Sprunt, 1957) combines *Vermivora* and *Dendroica* in the same genus.

One difference between these *Vermivora* species and several species of *Dendroica* and *Setophaga ruticilla* is that a special vocalization accompanies Soliciting in *Dendroica* and *Setophaga* but not in *Vermivora*. The lack of a Soliciting vocalization in these *Vermivora* may be due to the fact that the female usually Solicits when the male is nearby. In *Setophaga* and *Dendroica* the female often Solicits spontaneously after a bout of nest building but the male is usually some distance away and unable to see her; her Soliciting calls are necessary to communicate sexual motivation and location to her mate. Furthermore, this difference in Soliciting is related to the difference in courtship pattern of the two groups of warblers. Males of these *Vermivora* spend a short time intensively courting the female and are near her much of the time. Hence, they are more likely to be close by when she is sexually motivated. On the other hand, courtship is more protracted in *Setophaga* and *Dendroica*, and males are often not near the female when she is sexually motivated. Soliciting vocalizations are present in many passerines and seem

to have been secondarily lost in these *Vermivora*. In the absence of direct selection for this vocalization in courtship, such vocalizations would probably be selected against because their conspicuousness would attract predators.

Female warblers give another type of vocalization, the location call, which is not confined to sexual contexts and is different in form from the Soliciting vocalization. Females of *Setophaga* and *Dendroica* continue to give location calls until the nest is built, while female *Vermivora* cease giving location calls at the onset of nest building. This difference seems correlated with the general courtship pattern of the two groups. The location calls of the female function to keep the male informed of the female's location and to stimulate his approaches. Since courtship ceases in these *Vermivora* species when nest building is under way, there is no necessity for female location calls. As in the case of Soliciting vocalization, silence in females after this time may decrease conspicuousness to predators.

We have pointed out that some differences in vocalizations are related to the general pattern of courtship in the two groups. In *Setophaga* and *Dendroica* courtship activity occurs in short bursts over a period of a week or more; in these *Vermivora* species it often occurs in one day and at the most during a three day period. The selective pressures for rapid vs. slow courtship seem impossible to determine with our present scanty knowledge of their life histories. However, it may be significant that the average arrival time of redstarts is about a week earlier than the two *Vermivora* species in the Ithaca, New York area, and the two *Vermivora* species also depart from the New York City area several weeks earlier in the fall than do *Setophaga ruticilla* and *Dendroica pensylvanica*, although *D. petechia* also leaves early (Bull, 1964). Thus the two *Vermivora* species have a shorter time available for reproduction than the other group and a more rapid courtship may be necessary for this reason. The timing of reproduction is related to many other environmental conditions, such as food supply, and is very complex. However, it seems significant that the two *Vermivora* are very specialized and restricted in their way of feeding (Ficken and Ficken, 1968*b*), even more so than *Setophaga ruticilla*, and much more so than the *Dendroica*. The late arrival and early departure of these two *Vermivora* may be related to their feeding habits.

Behavior of hybrids.—Pairings of a hybrid and a parental species are relatively frequent in the area of sympatry (Ficken and Ficken, 1968*a*). Because of the similarity of courtship of the two species, hybrids would be expected to behave in a manner similar to both parental types and courtship would be expected to be equally successful in intraspecific and hybrid matings. However, since the two species differ markedly in color and pattern and hybrids show varying degrees of intermediacy, lowered responsiveness

to visual releasers may reduce courtship success in hybrid pairings. Both sexes in the hybrid pairings which we studied were less aggressive to each other than were conspecific pairings, probably due to reduced responsiveness to the visual releasers of the mate. We also showed that female sexual behavior is often stimulated by male aggressiveness. Therefore, the courtship of hybrid pairings would be expected to be less successful than conspecific ones. Although fertility does not seem to be reduced in pairings involving a hybrid (Ficken and Ficken, 1968a), there could be a slowing of courtship with consequent deleterious effects on breeding success.

There are few detailed accounts of the behavior of avian interspecific and backcross pairs. However, in some cases the courtship of hybrids is less successful than "pures." Dilger (1960) studied the courtship of F_1 hybrids and both parental species in parrots (*Agapornis roseicollis* and *A. fischeri*). Although hybrid males possessed normal sexual vigor, hybrid females were more refractory than parental females in reaching sexual readiness as a result of male courtship. In addition, hybrids showed a partial loss of recognition of individuals of their own kind and there were more territorial violations. In F_2 ducks studied by Lorenz, the motor patterns of the displays were disrupted and occurred in unusual combinations (Dilger, 1960). If a proper sequence of courtship displays is important for copulation, these hybrids would be less successful.

In some cases interspecific pairs are as successful as conspecific ones. Hinde (1956) studied two kinds of cardueline interspecific pairs as compared to conspecific ones in captivity and found no difference in the proportion laying eggs. These interspecific matings are very rare in the wild and he concludes that specific differences in plumage and behavior are probably important in preventing interspecific pairing but do not hinder reproductive success under conditions of forced pairings.

Interspecific sexual relations in Blue-wings and Golden-wings.—Observations of unmated males approaching non-conspecific females and of unmated females approaching non-conspecific males show that there is a responsiveness to the other species. We suggest that this usually occurs when there is a threshold lowering due to a shortage of conspecific mates (Ficken and Ficken, 1968a).

We have a few observations indicating that there are opportunities for interspecific sexual behavior to occur with a bird other than the mate. This is likely to arise, although probably rarely, for several reasons: (1) Interspecific territorial encounters occur. Since females also participate, this enhances interspecific contacts between the sexes. In cases 4 and 5 (p. 166), the male of the other species was within 20 feet of the Soliciting female, although he did not approach; (2) The Soliciting female is likely to be

non-specific about the male that she copulates with since her sexual motivation is so strong. A female Solicited after being chased by a male of the other species, and also seemingly in response to a female of the other species; (3) Soliciting postures are similar in the two species so the male might be non-specific as well; (4) Both species are sexually active at the same time; and (5) Aggressive interspecific encounters increase the female's sexual motivation.

We observed a male Golden-wing watching intently and sometimes following, a female Blue-wing on his territory. At first we thought she was his mate, since his behavior was similar to males in the early courtship period. However, several hours later we found a female Brewster's hybrid with a completed nest on his territory. Subsequent observations showed that the Blue-wing female had strayed from an adjacent territory and the hybrid female was indeed the mate of the Golden-wing. Thus "pure" males, even when mated, are capable of responding to a female of the other species. However, it is possible that during pair formation each sex rapidly learns the visual and vocal characteristics of the mate and normally confines overt sexual responses to birds possessing these, even though the mating is with a hybrid or interspecific. Initial "mistakes" at pair formation could be maintained by this rapid learning mechanism. Thus the critical responsiveness occurs during pair formation and pairs once formed are not likely to break up.

Ethological isolating mechanisms involved in courtship.—Hybrids and the formation of mixed pairings are selected against during pair formation and probably during later stages of courtship as well. Interspecific pairings are probably the result of low thresholds for mating, as in the examples of unmated birds approaching non-conspecifics cited here. Differences in arrival time of the two species in some areas of sympatry also decrease chances of interspecific pairing (Ficken and Ficken, 1968a). Interspecific pairings are relatively rare compared to pairings involving hybrids, probably due to hybrid intermediacy in releasers and hybrid receptivity to both parental species. However, hybrid males are less successful in obtaining mates than "pures" of either species. A discussion of species recognition and reproductive isolating mechanisms concerned with pair formation appears elsewhere (Ficken and Ficken, 1968a).

During courtship there is a continual interaction of the members of the pair involving both behavior, including vocalizations, and visual releasers. Since in interspecific and hybrid pairings visual releasers are different from those normally responded to, courtship is probably slower and ultimately less effective. Thus species differences in receptivity may serve as an isolating mechanism.

Courtship patterns facilitating hybridization.—Although reproductive isolating mechanisms are operating in this species complex (Ficken and Ficken, 1968a) several aspects of the courtship patterns of the two species facilitate hybridization. The courtship displays and sexual reactions of the two species are similar. This similarity should facilitate the success of interspecific pairs once they are formed, although the difference in visual releasers may slow the courtship process. Compared to other parulids, courtship proceeds very rapidly in Blue-wings and Golden-wings. Such rapid courtship and the lack of intricate displays preceding copulation probably facilitate hybridization. Also, chances for hybridization would be increased where one sex, in this case the female, initiates sexual activity, rather than when there is a complex interaction of both sexes preceding copulation (e.g., Morris, 1956).

SUMMARY

Interactions between the sexes from pair formation through copulation are discussed. Courtship displays are similar in the two species. Courtship is rapid, the time from pair formation to copulation being only a day in some cases. Male aggressive displays seem to stimulate female Soliciting. Two pairs consisting of Brewster's hybrid males and female Blue-wings differed from conspecific pairings in the lower level of aggression each sex showed toward the other. It is suggested that courtship of pairs involving a hybrid is less successful than conspecific pairings. Although no interspecific pairings occurred in the study area, there were several unsuccessful attempts at interspecific pairing and weak sexual responses were directed at a non-conspecific in some cases. Isolating mechanisms are apparently operating both in pair formation and in later stages of courtship. Hybridization, on the other hand, is probably facilitated by the similarity of courtship displays in the two species, their simplicity, and the rapidity of courtship. Courtship of these two *Vermivora* species is compared with other warblers and selective pressures affecting courtship are discussed.

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