

THE SWAYING DISPLAY OF THE RED-EYED AND OTHER VIREOS

VAL NOLAN JR.

Metronome-like swaying or bowing of the head and body has been noted as a form of intraspecific display in at least five members of the genus *Vireo*. But despite its pervasiveness, the activity appears to be so rarely seen that there have been few descriptions of it and little effort has been made to interpret it generally. The purposes of this paper are to describe in detail swaying by a Red-eyed Vireo (*Vireo olivaceus*), to review the literature, and to discuss the significance of the behavior in the genus.

The kindness of Jon C. Barlow is gratefully acknowledged. Barlow, in his field work on the Bell Vireo (*Vireo bellii*), has witnessed swaying probably more than any other investigator, and correspondence with him has been of great assistance.

DESCRIPTION

The following instance of swaying by a Red-eyed Vireo occurred at Bloomington, Indiana, at 11 a.m. on April 30, 1961; the temperature was about 65° F. The first migrants of the species had returned on April 26.

Two vireos were noticed about one foot apart and 20 feet up in a leafless tree. Because of the pitch of the ground, I could observe them at eye level from a distance of less than ten yards. One bird, hereafter called A, moved first to within five inches and then to within two inches of bird B; A was then facing B and was slightly above it on the sloping branch. Immediately A began to sway slowly and rhythmically from side to side, its head describing an arc of about 120° and covering about four inches in a vertical plane. The high point of the arc was level with or a little above B's head; the low points of the arc were opposite B's flanks. It is probable that A's head and body were thrust forward at each end of the swing, that is, that they also traversed a small arc on the horizontal plane. A full swing from one side to the other was made about once a second. The head and body appeared to move together rather rigidly and the feet remained in place, so that the bowing seemed to be accomplished principally by action in the legs and pelvic region. The bill, at the top of the swing, pointed possibly 30° above the horizontal, and the plumage was probably a little sleeked. No sounds were audible.

Twenty seconds after beginning its display, A opened its bill for one second; ten seconds later, still swaying, it opened its bill wide and left it thus for 15 seconds. At about this time, it became noticeable that B, which had appeared to be motionless, was occasionally moving its head very slightly. At each such movement, the rhythm of A's swing was interrupted, although only barely perceptibly, as though the two heads were connected by a taut thread. The birds seemed tense, and I was struck by the vulnerability of each to a jab from the other.

Approximately 45 seconds after A had begun to sway, B turned away and hopped a few inches down the branch toward the trunk. Bird A stopped bowing and followed, its tail a little depressed and fanned to double its normal width at the tip. Immediately upon closing the distance between it and B to about 4 inches, A resumed swaying, but in a few seconds B again moved a little away. Several more times A approached and bowed and each time B soon turned aside. Thus for about 30 seconds there was interrupted display, the bows not so deep as before nor oriented so frontally on B. Vireo A then passed B on the branch and turned as though to confront B, which hopped to another branch, perhaps elevating the feathers of the crown briefly. B's movements seemed normal, and its behavior now suggested inattention to A. After about 30 seconds, during which the birds moved along within a few feet of each other, they left the scene.

OBSERVATIONS BY OTHERS

Vireo olivaceus.—Tyler first reported (1912:229) two observations of swaying in the Red-eyed Vireo, and in a later summary in Bent (1950: 335, 342) Tyler indicated that he had seen the behavior several more times. Only once did he record the display as occurring between two adults; on the other occasions it was performed by an adult and directed toward a full-grown young which was being fed. Tyler regarded the display to an adult as courtship of a female by a male. There were the following differences from the episode that I witnessed: The swayer's body was at a right angle to that of the passive bird, and as the head moved it swung over the upper parts of the supposed female, which crouched low, feathers fluffed. The swaying bird's feathers were noticeably sleeked. Neither vireo opened its bill, but one continually sang an unvireo-like, faint, squeaky song. (See Nolan, 1960:240, for references to similar singing by vireos.) In his summary (1950:342) of his observations of swaying directed at young, Tyler mentions the adults' sleeked plumage, states that the two birds are usually facing each other, and that the adult "gives the impression of being in a sort of trance, or . . . trying to influence the other bird in some strange way." Tyler neglects to note a point he had made earlier (1912:230), that at least one adult (on August 18) began its swaying when it was greeted, upon alighting, by the young bird's reaching out with opened bill.

An interesting case of the display was seen by Lawrence (1953:66). A male Red-eyed Vireo that arrived, simultaneously with the female, beside its nest of young was received by the female with gaping and bill snapping. To these the male responded by swinging head downward and in this position clinging to a perch. He then righted himself, at which the female thrust her bill at him; he jabbed at the female's cloacal region. When the female snapped her bill and leaned out to bite at the male, he moved away an unstated distance and began to sway, his bill open. This continued for five minutes, during which the female stood over the nest motionless. She then "suddenly . . . flew off escorted by the male." Mrs. Lawrence's interpretation was that the female had reacted toward her mate as toward a stranger because he brought no food to the nest. The male's behavior she regarded as displacement movements derived from courtship patterns and brought on "by the thwarting of his intention to inspect the young birds." However, Mrs. Lawrence did not describe, or cite references to, such behavior in courting vireos.

Vireo flavoviridis.—Skutch (*in* Bent, 1950:330) has reported swaying by an immature male Yellow-green Vireo under circumstances somewhat resembling those described by Mrs. Lawrence for the closely related *V. olivaceus*. A female feeding nestlings was followed by a full-grown immature that showed certain male characters. When the female left the nest, the stranger went to the rim, looked in, and left. The female soon returned and brooded; the young male thereupon alighted close beside the nest, faced the female, and began to sway. His mouth was open, and he uttered at first low weak notes; then he sang a disjointed but typical vireo song. The female "opened her mouth threateningly toward him," and finally flew away after several minutes, "with the young male in close pursuit." In a later account (1960:21-22) of the same episode, Skutch states that a reading of Tyler's life history of *V. olivaceus* makes it seem probable to him that the young male *V. flavoviridis* was courting the brooding female.

Vireo bellii.—Barlow (MS, Univ. Kansas) in an unpublished thesis on the Bell Vireo describes swaying as a pre- and post-coital display of the male. In that species the tail is fanned and depressed, the body plumage greatly ruffled, and the head and body moved in a vertical arc of nearly 180° and a horizontal arc of about 100°. The male faces the female with wide-open mouth and sings the courtship song, which begins at

the low point of a swing. The display, which may last as long as three minutes, elicits receptive behavior in the female; she crouches with body feathers fluffed and tail slightly raised, uttering a call note. Once a male, after two attempts to copulate with a stuffed bird, addressed the dummy from the side and swayed so that his head passed over the dummy's neck.

Barlow suggests that "[t]his ritualized behavior could conceivably be derived from hetero-preening."

Vireo solitarius.—Bent (1950:291) quoted Townsend (original not examined by me) as having twice seen male Solitary Vireos courting females. "The male puffs out his yellow flank feathers very conspicuously and bobs and bows to the female, very slim in contrast, and sings repeatedly meanwhile with many variations to his song."

Vireo gilvus.—Audubon, as quoted by Tyler in Bent (1950:363), original not examined by me, noted that during the nest building of a pair of Warbling Vireos, "they now and then stood in a stiffened attitude, balancing their body from side to side on the joint of the tarsus and toes, as on a hinge." Audubon "could not discover the import of this singular action."

DISCUSSION

It is obvious that many more observations are required before we can discuss with confidence the motivations and functions of swaying in any vireo, except possibly that in *V. bellii*; and the uncertainties are perhaps magnified when we turn to the origins of the display in the genus. The evidence does not support the oversimplified "courtship" interpretation, again except in *V. bellii*, in which the ritualized epigamic role of the behavior has been made sufficiently explicit by Barlow. Indeed, observations to date provide no adequate basis for attributing swaying exclusively to male vireos, especially in view of the virtual absence of sexual dimorphism in the genus. In the Red-eyed Vireo, on the other hand, there are positive observations that swaying occurs in situations from which sexual motivation is probably absent. In addition, there is the negative evidence of careful investigators who have not seen the display between members of the pair (see, for example, Southern, 1958, and *in litt.*, 1961).

As an hypothesis, I would suggest that swaying is primarily an appeasement display, "designed" to prevent attack without provoking escape . . . [and] produced, of course, by the usual type of hostile motivation" (Moynihan, 1955:252). Appeasement displays are often derived from hostile behavior patterns and may in fact be aggressive displays from which a few elements are absent, or reversed (Marler, 1956:45-46). Not only do a number of the situations to which vireos have responded by swaying appear to have been hostile, but also certain components of the swaying display, such as singing and gaping, indicate that the actors were hostilely motivated. Further, the position of the plumage in swaying Red-eyed and Bell vireos corresponds to plumage positions of attacking or defending birds of those species. Lawrence (1953:66) describes the flattened plumage of the female Red-eyed Vireo that defended the nest against her mate, and similar behavior is typical of incubating females approached by Blue Jays, *Cyanocitta cristata* (Lawrence, *op. cit.*: 69). I have seen the male Bell Vireo, when his territory was invaded by a second male, resort to a display in which the body feathers were much fluffed, the head and body aligned and stiffened, and the stranger presented frontally with the distended silhouette of the defender.

That hostile behavior would sometimes occur in vireos that are also sexually motivated is to be expected; "the immediate causation of many appeasement displays apparently [includes] three or more distinctly different drives," among them sexual

drive (Moynihan, *loc. cit.*). It is also not surprising if appeasement behavior has been incorporated into epigamic display in the Bell Vireo. "Appeasing ceremonies or postures may have relevance to . . . pair-formation or coition" (Armstrong, 1947:137).

Finally, two points are worth noting. First, while we have little knowledge of submissive and avoidance behavior in vireos, the reactions of the birds toward which swaying was directed suggest that they may have been responding to appeasement. Second, bowing and elevation and turning of the head have significance in the appeasement displays of many birds (Armstrong, 1947: *passim*; Marler, 1956:45). As an example the old-world jays, *Garrulus lanceolatus* and *G. glandarius*, in their "chin-up" appeasement displays move the head from side to side, although jerkily, in a manner not unlike the swaying of vireos (Goodwin, 1952:304-306).

LITERATURE CITED

- Armstrong, E. A.
1947. Bird display and behaviour (Lindsay Drummond Ltd., London).
- Bent, A. C.
1950. Life histories of North American wagtails, shrikes, vireos, and their allies. U.S. Nat. Mus. Bull. 197.
- Goodwin, D.
1952. A comparative study of the voice and some aspects of behaviour in two old-world jays. Behaviour, 4:293-316.
- Lawrence, L. de K.
1953. Nesting life and behaviour of the red-eyed vireo. Canadian Field Nat., 67:47-77.
- Marler, P.
1956. Behaviour of the chaffinch *Fringilla coelebs*. Behaviour, Suppl. 5:viii + 1-184.
- Moynihan, M.
1955. Types of hostile display. Auk, 72:247-259.
- Nolan, V., Jr.
1960. Breeding behavior of the Bell vireo in southern Indiana. Condor, 62:225-244.
- Skutch, A. F.
1960. Life histories of Central American birds. II. Pac. Coast Avif. No. 34:1-593.
- Southern, W. C.
1958. Nesting of the red-eyed vireo in the Douglas Lake region, Michigan. Jack-Pine Wabler, 36:105-130, 185-207.
- Tyler, W. M.
1912. A vireo courtship. Bird-Lore, 14:229-230.
- Indiana University, Bloomington, Indiana, December 5, 1961.*