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Interspecific Vocal Imitation in White-eyed Vireos

CURTIS S. ADKISSON AND RICHARD N. CONNER[1]
Department of Biology, Virginia Polytechnic Institute and State University,
Blacksburg, Virginia 24061 USA

The White-eyed Vireo (*Vireo griseus*) breeds in the eastern United States, eastern Mexico, and on Bermuda (A.O.U. 1957). Throughout this range it occupies forest edge or scrubby second growth habitat that follows clearing or burning (Bent 1950, James 1971, Conner and Adkisson 1975).

This species has been reported to imitate the sounds of as many as 30 bird species (Bent 1950). However, no attempts have been made to obtain spectrographic evidence of interspecific imitation. In this paper we seek to answer these questions: (1) is there good evidence of imitation? (2) if so, how does this system differ from other examples of mimicry? and (3) what kinds of sounds are the most advantageous to mimic?

We recorded White-eyed Vireos and their suspected models from 1974 to 1976 in Montgomery County, Virginia, within a 20-km radius of Blacksburg, using a Uher 4000 IC tape recorder and a Uher microphone mounted in a 61-cm diameter fiberglas parabola. We made spectrograms of all vocalizations using a Kay Elemetrics 7029A Sona-graph, using the wide-band filter.

In addition to recording singing birds when encountered, we usually stimulated each bird with playback of its own song or that of some other individual and recorded all vocalizations made thereafter for 10–15 min. The typical response to stimulation was to speed up the rate of song production, and to sing a larger portion of the song repertoire in a shorter time. The birds showed no tendency to imitate playback songs. Many territories were visited several times a season, with the assumption that the total repertoire of a given bird could be more fully sampled. However we had no marked birds and do not know that we recorded the same bird in the same place throughout the season. At least 20 individuals were recorded during this study.

The individuals recorded had many different songs, ranging from five recorded over a short span of time to at least 20 recorded over the span of several hours. Each vireo appeared to use a large but finite number of song figures, and the number of possible permutations was thus extremely large.

Certain figures in vireo song showed close similarity to the vocalizations of some common species found in or near typical vireo scrub habitat in the summer (Fig. 1). As identified by arrows, figures nearly identical to vocalizations of the Downy and Hairy woodpeckers (*Picoides pubescens* and *P. villosus*), Common Flicker (*Colaptes auratus*), Acadian Flycatcher (*Empidonax virescens*), White-breasted Nuthatch (*Sitta carolinensis*), Carolina Chickadee (*Parus carolinensis*), Carolina Wren (*Thryothorus ludovicianus*), Gray Catbird (*Dumetella carolinensis*), Wood Thrush (*Hylocichla mustelina*), Yellow-throated Vireo (*Vireo flavifrons*), Kentucky Warbler (*Oporornis formosus*), and Rufous-sided Towhee (*Pipilo erythrophthalmus*) appeared frequently in our sample. In addition, there were descending staccato call

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[1] Present address: Wildlife Habitat and Silviculture Lab., Box 7600, Stephen F. Austin State University, Nacogdoches, Texas 75962 USA.

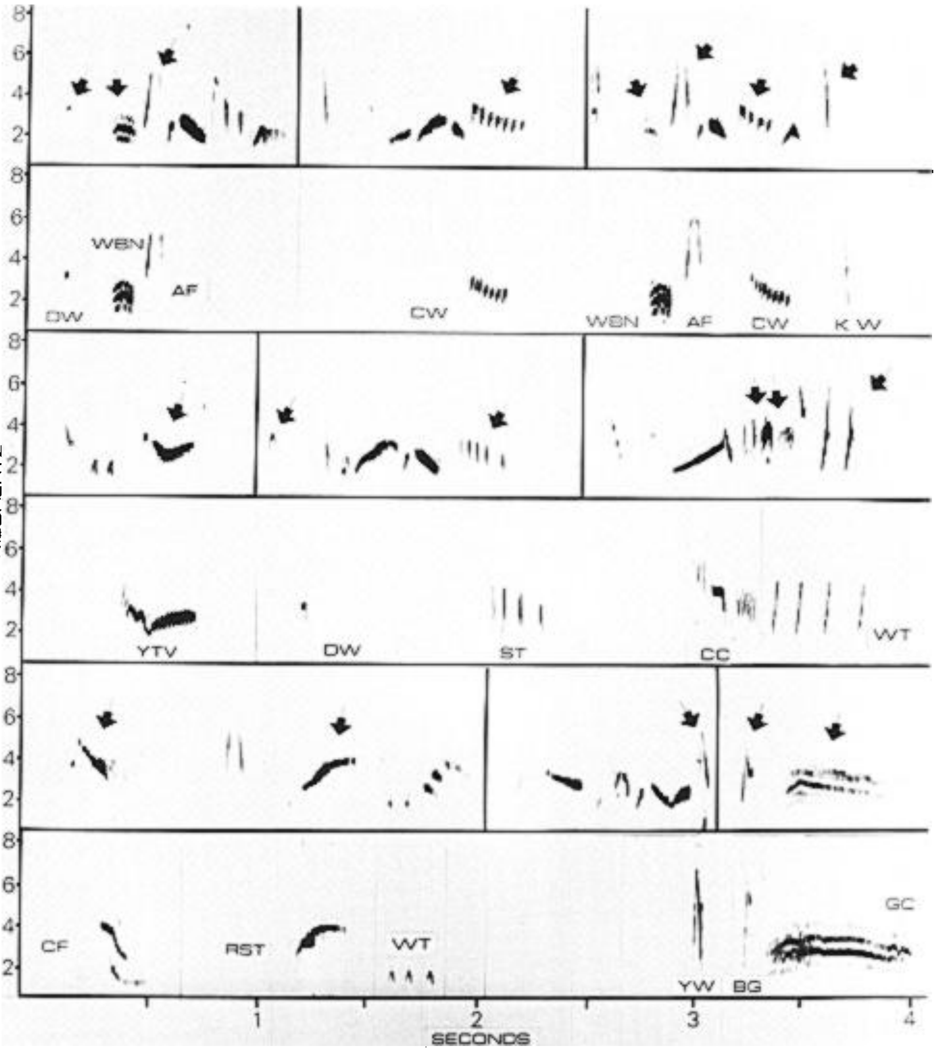

Fig. 1. Sonagrams of White-eyed Vireo songs and suspected models for imitative components. Vireo songs are on rows 1, 3, and 5. Imitative notes and note sequences are indicated by arrows. Vocalizations of suspected models appear directly beneath the appropriate vireo song component. Species codes: AF, Acadian Flycatcher; BG, Blue Grosbeak; CC, Carolina Chickadee; CF, Common Flicker; CW, Carolina Wren; DW, Downy Woodpecker; GC, Gray Catbird; KW, Kentucky Warbler; RST, Rufous-sided Towhee; ST, Summer Tanager; WBN, White-breasted Nuthatch; WT, Wood Thrush (two different calls); YTV, Yellow-throated Vireo; YW, Yellow Warbler.

notes virtually identical to those of Summer Tanagers (*Piranga rubra*), an uncommon bird locally (Murray 1974). The "quank" notes made by White-breasted Nuthatches are the most commonly heard (Bent 1948, Kilham 1972). Calls of the chickadee, thrush, flycatcher, wren, catbird, warbler, and towhee (in Fig. 1) were elicited from these birds when they mobbed a mounted Screech Owl (*Otus asio*). The calls of the three woodpeckers are apparently excitement or alarm calls (Kilham 1959, 1962, 1966; Lawrence 1966; R. N. Conner unpubl. data). The tanager call appears not to be incorporated into primary (territorial) song (C. S. Adkisson, pers. obs.), but is used in winter by both sexes to repel conspecifics (E. S. Morton, pers. comm.). As a result of the similarity of the calls of these species to certain vireo song figures, we have classed them as suspected acoustical models for the vireos. All the vocalizations of the models, with the exception of the song of the Yellow-throated Vireo, are non-territorial in nature.

The vireos in this study also included in their songs a variety of "chip" notes similar to those of several fringillid species (such as Indigo Bunting, *Passerina cyanea*; Cardinal, *Cardinalis cardinalis*; Blue Grosbeak, *Guiraca caerulea*; and Field Sparrow, *Spizella pusilla*), but these sounds are not spectrographically identical to any recorded near Blacksburg. We thus class these species as possible models for the vireos. The vireos could be exposed to such sounds, made by many species, in any season, and could be imitating some or none of them.

All the vireos recorded used imitative notes in most of their songs, with fewer than five of the more than 100 song types recorded containing no identifiable imitation. We noted considerable interindividual variation in the amount of imitation. The greatest percent imitative notes in all the songs of an individual was 78%, the lowest, 35%. Imitative notes averaged 55% in all songs. In contrast, Mockingbirds (*Mimus polyglottos*) are reported to sing mainly non-imitative songs. Wildenthal (1963, Appendix III) estimated that of all syllables sung, 18.5% in her Kansas birds and only 5% in her Florida birds were imitative. Similarly, Howard (1974) found that only two of the 14 most common syllables in Texas birds (ca. 14%) were imitative.

Without marking the birds one cannot reliably determine the extent to which neighbors share song types. In the area of our study few of the vireos recorded had neighbors audible to us, and in most of these cases it was impossible to be sure which bird we were recording on different outings. In one instance, where four neighboring males were well-separated but still within hearing distance of each other we were able to record 26 different songs over two days. Only one song type was used by all four birds, and two other song types were used, slightly modified, by three of the birds. Most of the song figures or notes were used by all four birds, but arranged in different order. One song type was sung by two birds 12 km apart in 1974, and was recorded in another locality more than 10 km from either of these localities in 1975.

We think it unlikely that chance alone could account for the close resemblance between the calls of certain native species of birds and figures in the songs of White-eyed Vireos. While one may only speculate on the origins of this kind of interspecific imitation, we hope to shed light on the problem by pointing out similarities and differences between this vireo and its relatives, and between this and other examples of imitation.

As far as we know, this species is the only vireo reported to imitate other species regularly. Reports of interspecific imitation are limited to one of a Red-eyed Vireo (*V. olivaceus*) imitating towhee songs (Borror 1961), one of a Red-eyed Vireo imitating Olive-sided Flycatcher (*Nuttalornis borealis*) songs (James 1976), and one of a Warbling Vireo (*V. gilvus*) apparently imitating Red-eyed Vireo songs (James op. cit.). While the repertoires of notes and songs of several vireo species may be large (Borror 1972, Lemon 1971), the use of the notes of other species must be very rare.

Among other passerines, many species regularly imitate the territorial songs as well as calls of other species in their own territorial songs (Marshall 1950, Robinson 1974, Thorpe 1967). In this kind of imitation it is possible that ecological competitors are excluded from the singer's territory, or at least inhibited from entering it, though we have found no evidence in support of such a theory. Howard's (1974) suggestion that Mockingbirds with the largest repertoires mate earlier and occupy better territories lends support to a theory that sexual selection has tended to produce large song repertoires.

In recent years, there have been reports of additional species capable of imitation (Robinson 1974, Snow 1974, Morton 1976, Remsen 1976), but not all these species imitate territorial songs in the context of territorial defense. Snow (1974) and Remsen (1976) reported mimicry in *Euphonia* tanagers in which the circumstances may have been territorial. Snow observed that Violaceous Euphonias (*E. violacea*) in Trinidad appeared to incorporate alarm calls of 17 other species into their songs. The screams of a mist-netted thrush were heard in the euphonia songs only after these thrushes were first handled by humans at the netting site. Remsen reported Thick-billed Euphonias imitating the calls of 25 species in Colombia, with as many as 10 different species imitated in each song. This euphonia also sang non-imitative songs, frequently in the same bout of singing as imitative songs. Some of the imitations were clearly of alarm calls. Morton (1976) noted Thick-billed Euphonias imitating in a different situation in Panama. He found them making the mobbing calls of several species of passerines while near a nest predator (cat). He speculated that by imitating the mobbing calls of several species, a euphonia could provoke mobbing in other birds and thus increase the chances of driving away the predator at small risk to itself.

Of these examples of imitation, the White-eyed Vireo most closely resembles that of the two euphonia species studied by Snow (1974) and Remsen (1976). These three species live in edge or scrub habitats, and use heterospecific alarm or mobbing calls in their territorial songs.

Recent studies have emphasized that the acoustical properties of habitats may influence the evolution of vocalizations (Emlen 1972, Morton 1975). Marshall (1950) observed that birds living on the forest floor and in dense scrub habitats in Australia are remarkable in the distance their calls carry. He suggested that the Australian "master mimics" imitate loud calls and songs in the process of making their own territorial advertisement more conspicuous. We suggest, in addition, that visibility of the imitating species may also affect the nature of the imitation. Territorial defense among open-habitat birds often involves visual as well as acoustical cues. There might be less chance of aggressive response by heterospecifics when territorial songs are imitated with the singer in full view. If these species living in dense brush habitats relied exclusively on acoustical cues for territory defense, the imitated species might respond strongly. Indeed, Robinson (1974) noted that Lyrebirds (*Menura*) imitate other birds mainly when the latter are non-territorial.

This suite of common traits among unrelated species from different regions suggests to us that imitation has often evolved as a response to selective pressures for better advertisement of territorial limits in densely vegetated habitats. Alarm and mobbing calls of many species carry well in such habitats, and it is probably more "efficient" to copy sounds already being made in that habitat by heterospecifics than to develop altogether new sounds. In this case, White-eyed Vireos may also avoid aggressive responses from song model species by imitating primarily non-territorial sounds.

A question emerging from this study is whether a vireo learns its imitations from heterospecific models or from conspecifics. If songs were learned only from the former we should find virtually no song sharing; if they were learned only from conspecifics we might find much song sharing. That our birds share barely 10% of their songs with neighbors, and also share some songs with birds several km away suggests that they may acquire their songs from fathers or neighbors, and settle elsewhere later. This cannot be shown without marking many juveniles over several seasons (Kroodsma 1974). The question of whether a vireo learns any of its repertoire from other species is not easily answered.

This species is widely-distributed, and there should be places where its syntopic, heterospecific neighbors are largely different from those in southwestern Virginia, for example, in Bermuda, the Bahamas, and coastal Mexico. Thus, the amount of geographic variation in vireo song and the extent to which calls of local birds can be matched with notes in vireo song should help clarify the sources of apparent mimicry in this unusual bird.

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Two Successive Male Eastern Bluebirds Tending the Same Nest

BENEDICT C. PINKOWSKI
245 County Line Road, Bridgeville, Pennsylvania 15017 USA

Many instances of apparently altruistic behavior have been reported for the Eastern Bluebird (*Sialia sialis*). Some of the reports involve bluebird fledglings feeding siblings of a later brood (Wetherbee 1933, Laskey 1939) or additional adult helpers at the nest (Laskey 1947, Pinkowski 1975) and may be interpretable in terms of kin selection and inclusive fitness (Hamilton 1964, Wilson 1975). There are also reports of a male bluebird feeding the offspring of an unrelated pair (Pinkowski 1976) and a male attempting to courtship-feed another male prior to the breeding season (Pinkowski 1977a); these instances, as well as others involving bluebirds feeding the young of other species (Bent 1949, Batts 1958, Carr and Goin 1965), probably represent reproductive errors. Here I describe the behavior of a male Eastern Bluebird that replaced a lost male at a nest and cared for the widowed female's offspring. I also suggest an explanation for this behavior.

On 16 May 1977 a pair of bluebirds was tending a nest containing four 6-day-old young. The nest was located in a nest box in Macomb County, Michigan, and I banded the male bluebird on 16 May. On 21 May the nest contained only two young and the resident male was missing, its territory occupied by an unbanded male new to my study area. Two young fledged on 31 May. On 21–30 May I observed the nest for 17.3 h (seven observation periods of 2–3 h each) and found that the female fed the young on 97 occasions, removed fecal sacs on 28 of her feedings, and drove off intruders such as Tree Swallows (*Iridoprocne bicolor*) 12 times. Corresponding figures for the male were 15, 4, and 2, respectively. Only one fledgling was observed on 1–13 June when, during 10 h of observations (six observation periods of 1.5–2 h each), the male fed twice and the female fed 13 times. Thus the male offered only 17 of 127 feedings (13.4%) at a time when both adults normally contribute about equally to the nutritional requirements of the young (Pinkowski 1978). However, occasionally the male fed the female and she took the food to the nestlings; two of nine female feedings observed on 21 May occurred in this fashion. Alarm notes, often in response to my presence, were only given by the female during both the nestling and the fledgling periods. The female always went to the nest box and fed the young with much less hesitancy if the male was with her than if she was alone.

The male appeared to alternate periods of courtship activity with periods of caring for the young, especially at first. Thus male feedings were erratic; five were observed in one 26-min period on 28 May but none occurred during six of the 13 entire observation periods. Courtship activities included displays about the nest box, singing, and various aerial and non-aerial displays such as "Butterfly Flight" and "Wing-waving" (Krieg 1971). These became less common as the fledgling reached independence. During the nestling period the male entered the nest box without food on 16 occasions, often as part of a display and when the female was nearby. The female did not do this, and such behavior is rarely observed in other male bluebirds at nests containing nestlings (pers. obs.). The female did not respond to these displays, nor did she behave aggressively toward the male. The male usually followed the female on her trips back and forth to the nest until fledging. After fledging the pattern was occasionally reversed as the