

RED-EYED VIREOS HAVE DIFFICULTY RECOGNIZING INDIVIDUAL NEIGHBORS' SONGS

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ABSTRACT.—I investigated recognition of individual neighbors' songs in a migratory species with large repertoires, the Red-eyed Vireo (*Vireo olivaceus*). To test for abilities to recognize individual neighbors, I measured responses to playbacks of neighbors' songs from appropriate and inappropriate boundaries in two different years. Because the responses to the two types of playbacks were not statistically different in either year, I concluded that Red-eyed Vireos have difficulty recognizing their neighbors by song. If recognition of neighbors serves to reduce energy expended in territorial defense during the breeding season, a large repertoire could be costly to male Red-eyed Vireos. Received 10 February 1992, accepted 25 November 1992.

MANY HYPOTHESES have been proposed to explain the complexity of song repertoires in passerines (e.g. Krebs 1977, Falls 1978, Krebs and Kroodsma 1980, Kroodsma 1982, Searcy and Andersson 1986, Searcy and Yasukawa 1990). Repertoires vary from only one song per individual (e.g. *Zonotrichia albicollis*; Borror and Gunn 1965) to several thousand songs per individual (e.g. *Toxostoma rufum*; Kroodsma and Parker 1977). Song by male passerines serves both to attract females and to repel or deter other males from entering a territory (Searcy and Andersson 1986). Thus, changes in the complexity of a signal can affect both intrasexual and intersexual interactions.

In several species with small to moderate song repertoires playbacks have shown that territorial males respond more aggressively to strangers' than neighbors' songs played from an appropriate boundary (see Falls 1982). Reduced response to neighbors' songs is potentially advantageous. Once boundaries are established, a male continuing to respond to neighbors singing close to shared boundaries would waste time and energy that could be spent raising young or acquiring mates.

Recognition of neighbors' songs requires that individuals have distinguishing features in their songs. Species with large repertoires have more song types that could potentially be used for discrimination of individuals. However, birds with larger repertoires present a listener with

more song types to learn. Furthermore, each song type is presented less frequently. Such a complex stimulus might be more difficult to learn to recognize.

Some studies suggest that the ability to discriminate between the songs of neighbors and strangers varies inversely with repertoire size (Kroodsma 1976, Searcy et al. 1981, Falls and d'Agincourt 1981, Falls 1982, but see Stoddard et al. 1992). For example, Eastern Meadowlarks (*Sturnella magna*), with large song repertoires (54+ songs per individual), responded almost equally to the songs of neighbors and strangers played from the appropriate boundary. Western Meadowlarks (*S. neglecta*), with smaller repertoires (5-11 songs per individual), responded more aggressively to the songs of strange birds than to neighbors' songs (Falls and d'Agincourt 1981). Presumably, the species with large repertoires had more difficulty discriminating between the songs of familiar and unfamiliar birds.

Discrimination between songs of strangers' and neighbors' demonstrates only that a subject can distinguish a familiar stimulus from an unfamiliar one. Discrimination of individual neighbors is inherently a more difficult task, as a subject must distinguish between several stimuli. Six of seven studies have successfully demonstrated abilities to recognize individual neighbors' songs (Falls and Brooks 1975, Wiley and Wiley 1977, McGregor and Avery 1986, Brindley 1991, Godard 1991, Stoddard et al. 1991; the exception, Schroeder and Wiley 1983). Except for Brindley (1991), these studies have used species with small to moderate repertoires (maximum average of 10 songs per individual). Brindley (1991) demonstrated individual rec-

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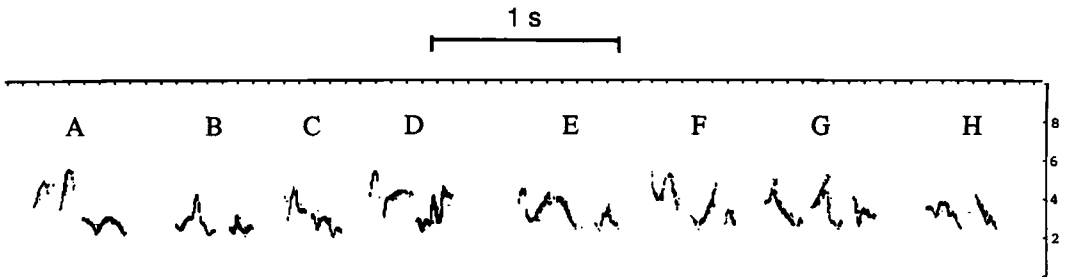


Fig. 1. Spectrograms of eight songs from two Red-eyed Vireos. (A-D) four songs from bird 4; and (E-H) four songs from bird 3. Time intervals between songs are shortened in this figure (X-axis, kHz; Y-axis, seconds).

ognition in European Robins (*Erithacus rubecula*), a year-around territorial species with a much larger repertoire (100 to 250 phrase types per individual).

Red-eyed Vireos (*Vireo olivaceus*) also sing with great complexity. Lemon (1971) found repertoire sizes of 35 and 46 for two male Red-eyed Vireos. Borror (1981) analyzed the songs of 46 Red-eyed Vireos from nine states (49 to 1,897 songs analyzed per individual). Excluding the repertoires of seven individuals singing sub-song and the one repertoire that may have actually included two recorded birds, repertoire size ranged from 12 to 79 with an average of 31.4 songs per individual. Red-eyed Vireos sing with immediate variety, each successive song usually different from the one preceding it. Unlike the year-around territorial European Robins, Red-eyed Vireos are migrants, singing on their breeding territories for only several months each year. With such a complex signal and such a brief singing period, Red-eyed Vireos make ideal subjects for a study of how abilities to recognize individuals are affected by large repertoires.

MATERIALS AND METHODS

This study was carried out at the Mason Farm Biological Reserve in Chapel Hill, North Carolina, from 1987 through 1990. The study area is a bottomland forest with a hickory-oak canopy and thick understory primarily of *Viburnum*. The area has a grid of stakes (25 to 50 m apart), which permitted accurate mapping of the territories of Red-eyed Vireos.

Repertoire sizes of Red-eyed Vireos in this population were estimated in 1987. Five banded males were recorded singing for at least 10 min on four separate occasions. I made spectrographs of 150 to 475 songs from each male from at least two recording dates in order to estimate repertoire size. Songs were analyzed with a Uniscan II real-time spectrum analyzer. I con-

sidered a continuous trace on the spectrogram a note, and intervals more than 0.3 s long were considered to be separate songs (Borror 1981). A new song type was considered to be a new note or new combination of notes sung in intervals of less than 0.3 s (Fig. 1). To estimate the size of an individual's song repertoire, I plotted the cumulative number of new song types against the number of songs sampled. An asymptote of this plot indicated the number of songs in the subject's repertoire.

In 1989 and again in 1990, the territories of 14 Red-eyed Vireos were mapped by noting locations of singing and boundary encounters. All mapped males were tape-recorded in the field with a Sony TC-D5M cassette recorder and Sennheiser K3U/ME88 ultra-directional microphone.

To test for abilities of Red-eyed Vireos to recognize the songs of individual neighbors, I played recordings of neighbors' songs to 10 male Red-eyed Vireos in 1989 and 10 males in 1990. It is likely that some of the males tested in 1989 were also used in 1990 given that I used the same study area in both years and males were not banded. Each playback tape was composed of three repetitions of a 1-min natural sequence of 30 to 40 songs recorded from a neighboring male. A minute was the maximum length of recordings with sufficiently little background noise of other birds, wind, and movement.

Each subject was presented with a recording of neighbors' songs twice, once near the boundary that the subject shared with that neighbor (neighbor test, n) and once near the boundary on the opposite side of the subject's territory (cross-neighbor test, xn). I placed the speaker 10 to 11 m inside the edge of the subject's territorial boundary. This distance represented about 10 to 20% of a typical territorial diameter in this population. A 20-m lead connected the speaker to an Amplivox amplifier connected in turn to the monitor output of a Sony TC-D5M recorder. All playbacks were standardized at 90 db 1 m away in an anechoic environment. A coin toss then determined which neighbor's song would be played first with the constraint that equal numbers of subjects received xn and n playbacks first. On the following day at approximately the same time, the same tape was played

TABLE 1. Number of songs sampled and estimated repertoire sizes of five Red-eyed Vireos.

Bird	Songs sampled	Repertoire size
1	250	46
2	475	95
3	150	31
4	300	73
5	269	51
\bar{x}	287	59

back on the opposite side of the subject's territory. In 1989, six playback tapes were used (each used either once or twice) as some males shared neighbors. In 1990, eight playback tapes were used (two twice).

To standardize the subject's behavior at the start of a presentation and to insure that it was within hearing distance, I began a playback only after the subject had been singing for at least 2 min and was 25 to 50 m from the speaker. Because the playback was intended to simulate a neighbor's singing, I also stipulated in advance that both the neighbor whose song was used for playback and the neighbor from whose boundary the songs broadcast had to be silent before playback could begin. For 3 min during the playback and for 9 min afterwards, I recorded the time singing and the number of flights by the subject, as well as the subject's total time in the vicinity of the speaker and its closest approach to the speaker. Experiments in 1989 and 1990 were similar, except that in 1989 the speaker was 2.0 to 2.5 m above the ground in a small tree, and in 1990 10 to 15 m above ground, suspended by a line.

I used Wilcoxon matched-pairs tests to compare responses to *n* and *xn* playbacks for each of the behavioral responses measured (closest approach, time to approach within 10 m, time to resume singing, time spent within 10 m of the speaker during and after the playback, and number of flights >1 m during and after playback). As these responses are correlated with each other, I used principal-components analysis as implemented in SYSTAT (Wilkinson 1989) to extract the first component from the seven responses I measured. The first component was then used in a Wilcoxon matched-pairs test to compare responses to *n* and *xn* playbacks.

RESULTS

The five Red-eyed Vireos sampled in 1987 had from 31 to 90 songs with an average of 59 songs/individual. Estimates of repertoire size for three birds (1, 2, and 3) appeared to reach an asymptote. The estimates for the other two birds (4 and 5) are probably low as cumulative songs never reached an asymptote (Table 1). Red-eyed Vireos in this population seem to have,

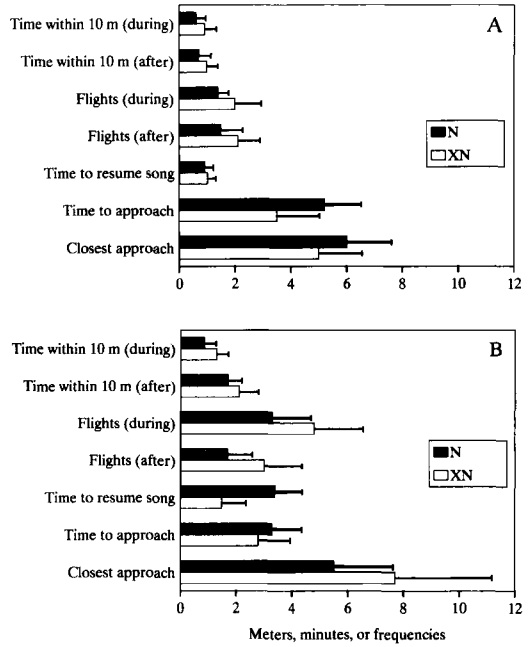


Fig. 2. (A) Bars represent mean responses of subjects to 1989 playbacks of neighbors' songs from the appropriate boundary (*n*) and from an inappropriate boundary (*xn*). Behaviors measured are: time (min) subject spent within 10 m of the speaker both during and after playback; number of flights greater than 1 m during and after playback; time (min) to resume singing; time (min) to approach within 10 m of the speaker; and closest approach to speaker (m/2). A strong response indicated by large values for first five responses and small values for remaining two responses. (B) Bars represent mean responses of subjects to 1990 *n/xn* playbacks. Responses are same as those measured in 1989. Whisker indicates SE.

on average, larger repertoires than those sampled by Borror (1981).

Responses to neighbors' songs when played from appropriate and inappropriate boundaries 2.0 to 2.5 m above the ground in 1989 indicated a tendency to respond more to *xn* than to *n* playback (Fig. 2A). Males came closer on average to the speaker, they took less time to approach the speaker, they spent more time and flew more in the vicinity of the speaker during *xn* playback, and they took longer to resume singing. However, none of these differences between *n* and *xn* playback was statistically significant (Wilcoxon matched pairs tests, all *P* > 0.05). There was also no significant difference between the first principal-component scores (Wilcoxon matched pairs test, *P* > 0.05). The

first principal component accounted for 53% of the variation with the following loadings: flights during playback (0.72); flights after playback (0.70); time within 10 m during playback (0.85); time within 10 m after playback (0.80); time to resume normal singing (0.25); time to approach to 10 m (-0.76); and closest approach (-0.85).

Red-eyed Vireos in my study area typically sing at heights greater than 8 m (Wiley and Richards 1982). Thus, in similar experiments in 1990, the speaker was placed to 10 to 15 m above ground. Again Red-eyed Vireos showed only weak, if any, recognition of individual neighbors' songs. Males approached the speaker more quickly during xn than n playback. They also spent more time and flew more in the vicinity of the speaker during xn playback. However, they came closer to the speaker during n playback and took longer to resume normal singing behavior after a n playback. Thus, five of the seven behavioral responses indicated a stronger response to xn playback and two indicated a stronger response to n playback. None of these differences was statistically significant (Wilcoxon matched pairs tests, all $P > 0.05$). A comparison of principal-component scores also revealed no statistical difference in responses to n and xn playback (Wilcoxon matched pairs test, $P > 0.05$). The first principal component accounted for 61% of the variance with the following loadings: flights during playback (0.83); flights after playback (0.65); time within 10 m during playback (0.84); time within 10 m after playback (0.79); time to resume singing (-0.55); time to approach to 10 m (-0.93); and the closest approach (-0.84).

DISCUSSION

Red-eyed Vireos evidently have difficulty discriminating the songs of individual neighbors. Though there was a suggestion of a tendency of increased response to xn playbacks when songs were broadcast at 2 to 2.5 m above ground, this difference was not significant. Even when the speaker height was raised to a more realistic singing height of 10 to 15 m in 1990, there was no significant difference in response.

These findings recall those in studies of neighbor/stranger discrimination in species with similarly large repertoires (Falls and d'Agincourt 1981). Red-eyed Vireos in my population and Eastern Meadowlarks (Falls and d'Agincourt 1981) have comparable repertoire sizes. Six of 12 measured responses in neigh-

bor/stranger discrimination studies with Eastern Meadowlarks indicated a greater response to the strangers' songs, but only one was significant (Falls and d'Agincourt 1981). All behavioral responses in 1989 and five of seven responses in 1990 indicated a greater response to xn than n , although none of the differences was significant. Reduced abilities to discriminate individual neighbors also occurs in Tufted Titmice (*Parus bicolor*), a species in which neighbors share similar versions of most of their eight to 10 song types (Schroeder and Wiley 1983). Of species without extensive song sharing, Red-eyed Vireos show the weakest discriminatory abilities of any of the species tested for individual recognition (Falls and Brooks 1975, Wiley and Wiley 1977, McGregor and Avery 1986, Brindley 1991, Godard 1991, Stoddard et al. 1991). Other than the European Robin (Brindley 1991), all of the other species had average repertoire sizes of 10 or fewer songs/individual. This evidence suggests that the increased complexity of Red-eyed Vireos' repertoire combined with their short associations makes the learning of neighbors' songs difficult.

An alternative explanation could be that neighboring Red-eyed Vireos represent a threat regardless of whether they are singing near an appropriate or inappropriate boundary. In Song Sparrows (*Melospiza melodia*) discrimination between neighbors and strangers songs was not demonstrated when songs were broadcast just inside subjects' territorial boundaries (Kroodasma 1976, Searcy et al. 1981), but was demonstrated when songs were broadcast from the neighbors' territories (Stoddard et al. 1992). Song sparrows have a significant amount of boundary instability in their territories (Stoddard et al. 1992) and, during a year of high density, one-half of the territory take-overs were shown to be carried out by neighbors (Arcese 1989). As such, Stoddard et al. (1992) concluded that the earlier studies did not demonstrate neighbor/stranger discrimination because both stimuli were perceived as relatively equal threats anywhere inside a male's territory. Red-eyed Vireos do not show the same degree of territory instability as that seen in Song Sparrows (Rice 1978a, b, pers. obs.). As such it is less likely that the very weak individual discrimination demonstrated by Red-eyed Vireos in these experiments is solely due to speaker placement.

Males that recognize their neighbors might benefit from reduced interactions with these individuals during the breeding season, thus

increasing the amount of time and energy a male could spend attracting mates and tending young. Moreover, there could be advantages to neighbor recognition from one breeding season to the next. Some studies have shown that returning songbirds have fewer and less intense interactions with neighbors from the previous year than they do with new males (Nolan 1978, Knapton 1979, Yasukawa et al. 1982, Godard 1991). Thus, the ability to recognize individual neighbors might not only enhance reproductive success within a breeding season by reducing interactions with established males, but could have an effect on reproductive success in subsequent breeding seasons (see Beletsky and Orians 1989).

Given the potential advantages to recognizing neighbors, it seems that a large repertoire might have costs for a male Red-eyed Vireo. There are many proposals for the function and evolution of repertoires (see Krebs and Kroodsma 1980, Searcy and Andersson 1986). Most are not exclusive, and the evolution of repertoires in different species might result from different selective pressures. Red-eyed Vireos do not appear to use particular songs in particular contexts as in some species (e.g. Smith et al. 1978), nor do they use songs in such a way as to simulate a dense population of conspecifics (Beau Geste effect; Krebs 1977).

Other hypotheses for the function of repertoires are more difficult to evaluate for Red-eyed Vireos. No studies to date have documented the relationship between mating success and repertoire size in this species. Perhaps the gain in attracting females via large repertoires offsets the costs of reduced recognition by neighbors. Certainly, the complexity of their singing does not seem necessary for interactions between males. Rice (1978a) played recordings of songs from strange Red-eyed Vireos in the normal singing pattern and in an abnormally simple pattern of four songs repeated for 2 min. Red-eyed Vireos responded equally to both playbacks. Because males respond to these simplified versions of conspecific song, the complexity of their song might have evolved to address females. This species offers an ideal subject to examine the effects of song on mate choice.

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LITERATURE CITED

- ARCESE, P. 1989. Territory acquisition and loss in male song sparrows. *Anim. Behav.* 37:45-55.
- BELETSKY, L., AND G. ORIANS. 1989. Familiar neighbors enhance reproductive success. *Proc. Natl. Acad. Sci. USA* 86:7933-7936.
- BRINDLEY, E. 1991. Response of European Robins to playback of song: Neighbour recognition and overlapping. *Anim. Behav.* 41:503-512.
- BORROR, D. 1981. The songs and singing behavior of the Red-eyed Vireo. *Condor* 83:217-228.
- BORROR, D., AND W. GUNN. 1965. Variation in White-throated Sparrow songs. *Auk* 82:26-47.
- FALLS, J. B. 1978. Bird song and territorial behavior. *Adv. Study Communication and Affect* 4:61-89.
- FALLS, J. B. 1982. Individual recognition by sounds in birds. Pages 237-278 in *Acoustic communication in birds* (E. Kroodsma and E. Miller, Eds.). Academic Press, New York.
- FALLS, J. B., AND R. BROOKS. 1975. Individual recognition by song in White-throated Sparrows. II. Effects of location. *Can. J. Zool.* 53:1412-1420.
- FALLS, J. B., AND L. D'AGINCOURT. 1981. A comparison of neighbor-stranger discrimination in Eastern and Western meadowlarks. *Can. J. Zool.* 59:2380-2385.
- GODARD, R. 1991. Long-term memory of individual neighbours in a migratory songbird. *Nature* 350:228-229.
- KNAPTON, R. W. 1979. Breeding ecology of the Clay-colored Sparrow. *Living Bird* 17:137-158.
- KREBS, J. 1977. The significance of song repertoires: The Beau Geste hypothesis. *Anim. Behav.* 25:475-478.
- KREBS, J., AND D. KROODSMA. 1980. Repertoires and geographical variation in bird songs. *Adv. Study Behav.* 11:143-177.
- KROODSMA, D. 1976. The effect of large song repertoires on neighbor "recognition" in male Song Sparrows. *Condor* 78:97-99.
- KROODSMA, D. 1982. Song repertoires: Problems in their definition and use. Page 125-146 in *Acoustic communication in birds* (D. Kroodsma and E. Miller, Eds.). Academic Press, New York.
- KROODSMA, D., AND L. PARKER. 1977. Vocal virtuosity in the Brown Thrasher. *Auk* 96:783-785.
- LEMON, R. 1971. Analysis of Red-eyed Vireo song. *Can. J. Zool.* 49:847-854.
- MCGREGOR, P., AND M. AVERY. 1986. The unsung songs of great tits (*Parus major*): Learning neighbor's songs for discrimination. *Behav. Ecol. Sociobiol.* 18:311-316.
- NOLAN, V. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithol. Monogr.* 26.

- RICE, J. 1978a. Behavioural interactions of interspecifically territorial vireos. I. Song discrimination and natural interactions. *Anim. Behav.* 26:527-549.
- RICE, J. 1978b. Behavioural interactions on interspecifically territorial vireos. II. Seasonal variation in response intensity. *Anim. Behav.* 26:550-561.
- SCHROEDER, D., AND R. H. WILEY. 1983. Communication with shared song themes in Tufted Titmice. *Auk* 100:414-424.
- SEARCY, W., AND M. ANDERSSON. 1986. Sexual selection and the evolution of song. *Annu. Rev. Ecol. Syst.* 17:507-533.
- SEARCY, W., P. MCARTHUR, S. PETERS, AND P. MARLER. 1981. Response of male Song and Swamp sparrows to neighbor, stranger, and self songs. *Behaviour* 77:152-163.
- SEARCY, W., AND K. YASUKAWA. 1990. Use of song repertoire in intersexual and intrasexual contexts by male Red-winged Blackbirds. *Behav. Ecol. Sociobiol.* 27:123-128.
- SMITH, W., J. PAWLKIEWICZ, AND S. SMITH. 1978. Kinds of activities associated with singing patterns of the Yellow-throated Vireo. *Anim. Behav.* 26:862-884.
- STODDARD, P., M. BEECHER, C. HORNING, AND S. E. CAMPBELL. 1991. Recognition of individual neighbors by song in the Song Sparrow, a species with song repertoires. *Behav. Ecol. Sociobiol.* 29: 211-215.
- STODDARD, P., M. BEECHER, C. HORNING, AND M. WILIS. 1992. Strong neighbor-stranger discrimination in song sparrows. *Condor* 92:1051-1056.
- WILEY, R. H., AND D. RICHARDS. 1982. Adaptations for acoustic communication in birds: Sound transmission and signal detection. Pages 131-181 in *Acoustic communication in birds* (D. Kroodsma and E. Miller, Eds.). Academic Press, New York.
- WILEY, R. H., AND M. WILEY. 1977. Recognition of neighbour's duets by Stripe-backed Wrens, *Campylorhynchus nuchalis*. *Behaviour* 62:10-34.
- WILKINSON, L. 1988. *Systat: The system for statistics*. SYSTAT, Evanston, Illinois.
- YASUKAWA, K., E. BICK, D. WAGMAN, AND P. MARLER. 1982. Playback and speaker-replacement experiments on song based neighbor, stranger, and self discrimination in male Red-winged Blackbirds. *Behav. Ecol. Sociobiol.* 10:211-215.