

## ECOLOGICAL RELATIONS AND SOCIAL INTERACTIONS OF PHILADELPHIA AND RED-EYED VIREOS

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**ABSTRACT.**—The ecological and social interactions of the interspecifically aggressive Red-eyed (*Vireo olivaceus*) and Philadelphia (*V. philadelphicus*) vireos were studied during four breeding seasons in the Hubbard Brook Experimental Forest, New Hampshire. The two species here have extensively overlapping territories but occupy different vegetational strata during most of the breeding season. The aggressiveness of the Philadelphia Vireo towards the Red-eyed Vireo varies within a breeding season, being most frequent and intense during the periods of greatest vertical overlap. The aggressiveness of Red-eyed Vireos towards Philadelphia Vireos varies between years, being most frequent and intense in years of high Red-eyed Vireo population density. In one year no aggression was apparent between the two vireos. During some aggressive encounters, the smaller, subordinate Philadelphia Vireo used what appeared to be distraction displays when Red-eyed Vireos came close to their young.

I hypothesize that resource competition may be the underlying cause of the aggression between these two ecologically similar species, largely because the most intense and frequent interspecific interactions occurred during periods of maximum overlap in foraging microhabitat. A comparison of these findings with those in another study illustrates the importance of forest height and vegetation structure in facilitating their coexistence.

The ecological and evolutionary significance of interspecific aggression in birds has been the subject of controversy in recent years (Orians and Willson 1964, Cody 1969, 1974, Murray 1971, 1976). Support for the adaptiveness of interspecific aggression (cf. Cody 1974) has come from Rice's (1978a, b, c) study of the Red-eyed (*Vireo olivaceus*) and Philadelphia (*V. philadelphicus*) vireos where they occur together in the woodlands of northeastern Ontario. In this region the two species occupy exclusive non-overlapping territories, the smaller (12 g) Philadelphia Vireo successfully defending territories against its larger (17 g) congener. Rice (1978a) considered this horizontal separation to be a form of ecological segregation, because in nearly all other respects (habitat, use of vertical strata, foraging behavior) the two species were found to be essentially identical.

In a study of the ecological relations of these same two species in a late successional forest in New England, I have observed that their territories overlap extensively and that interspecific aggression occurs at certain times during the nesting cycle. In this paper I examine the interaction of these two vireos at this site, compare the results to those of Rice (1978a, b, c) and consider reasons for the aggression between the two species.

### STUDY AREA AND METHODS

This study was conducted in the 3,076-ha Hubbard Brook Experimental Forest, West Thornton, New Hampshire. In this late successional northern hardwoods forest the canopy layer (13–27 m) is dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*) and yellow birch (*Betula alleghaniensis*) with occasional white ash (*Fraxinus americana*). The sapling layer (2–12 m) is relatively sparse (Sherry 1979) and consists primarily of beech, sugar maple and some striped maple (*A. pensylvanicum*). The shrub layer (0–2 m) is a very dense and heterogeneous mixture of hobblebush (*Viburnum alnifolium*), striped maple, mountain maple (*A. spicatum*), sugar maple and beech.

Most of my data were gathered on or near a 10-ha study plot at an elevation of 600 m. This plot is marked by a 50 m by 50 m grid, and has been the site of an intensive study of bird community dynamics and structure since 1969 (Holmes and Sturges 1975, Holmes et al. 1979a). From late May through late July during 1975–1978 I visited this plot nearly every day for a total of over 200 days and 1,200 hours. Unless otherwise stated, all observations used in this paper were made on or within 100 m of the study plot. Other sections of the forest, especially those with Philadelphia Vireos, were also visited regularly each summer. To characterize the ecological and social relations of the two species, I measured their spacing, microhabitat use, habitat selection and reproductive success, each of which is treated separately below.

*Spacing.* I mapped territories and estimated population densities of vireos on the study plot by methods similar to those of Holmes and Sturges (1975). Briefly, I made cumulative maps of all individuals heard, seen and/or captured in mist-nets and of their nest locations when known. An average of 65% of the Red-eyed Vireos (REVs) on the 10-ha plot were color-banded by

mid July of each year. A total of 57 REVs were color-banded during the 1975–1978 period. Eight Philadelphia Vireos (PVs) were color-banded during this same period, representing about 50% of the PVs seen on the 10-ha plot.

**Microhabitat use.** Each time I observed a vireo making a prey-attacking maneuver (*sensu* Eckhardt 1979), I recorded the following data: location on plot (grid coordinates), tree species, height above ground, position relative to the bole (inner, mid and outer), and substrates at which the maneuver was directed (e.g., leaf, twig, branch, bole). To estimate overlap in microhabitat use, I used the index of Holmes and Pitelka (1968).

**Habitat selection.** To characterize the composition of the canopy in areas occupied by each species, I counted and identified all trees that reached the canopy within a 20-m radius of points 50-m apart on the established census grids. Since both vireos forage primarily in the upper strata of the forest, I only counted canopy trees.

**Reproductive success.** Because of the difficulty of finding nests and because nests of both species were usually located high in the canopy, I could neither directly determine clutch sizes, nor accurately determine the total number of nests lost to predators. However, for those nests that survived to fledging, I was able to record the number of young fledged per pair. These presumably represent the outcomes of nests that were not attacked by predators, which usually take all of the eggs or young from a nest. Overall, I was able to determine the outcomes of 43 of an estimated 66 active nests of both vireos on or near the study plot. When a pair of vireos of either species fledged only one young, both parents fed it together. However, when two or more young left a nest, the adults always split up, each parent taking one or two of the fledglings and moving to a different part of the original territory. Therefore, to determine the number of young fledged from a nest from which more than one young was fledged, I located both parents, checked their color bands in order to identify them and then counted the number of young each was feeding.

## RESULTS

### ECOLOGICAL RELATIONS

**Breeding schedule.** Both species arrive at Hubbard Brook in mid May. Philadelphia Vireos arrive en masse within a period of about two days, while Red-eyed Vireos arrive over about a ten-day span (Fig. 1). PVs pair and begin nesting earlier on the average than do REVs. In 1976, for example, 9 of the 10 male PVs (including some from off the study plot in other parts of the forest) were paired by 20 May, while 12 of 14 male REVs were still unpaired on this date ( $P < .01$ ,  $\chi^2 = 13.47$ , d.f. = 1). The earliest record of a PV carrying nest material was on 24 May, while the earliest record for REVs was on 31 May. As a result, most PVs fledged earlier than REVs (Fig. 1). The first PVs to fledge were 12 days, 6 days, 9 days and 8 days ahead of the first REVs in 1975, 1976, 1977 and 1978, respectively. In Ontario, Rice (1974) also found that PVs paired earlier than REVs, yet they fledged at about the same time.

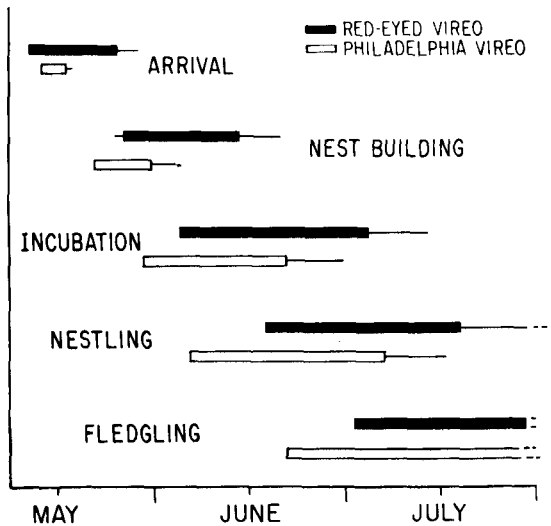


FIGURE 1. Timing of the breeding cycles of Red-eyed and Philadelphia vireos at Hubbard Brook. Thin lines indicate extreme ranges, thickened portions indicate periods of maximum activity.

**Habitat and spacing.** Each year PVs returned to the section of the study plot (Fig. 2) that they had been using at least since 1969 (R. T. Holmes, unpubl. data). Only the half of the plot that was occupied by PVs is shown in Figure 2. These preferred areas were characterized by several openings in the canopy created by treefalls, and by a high relative abundance of white ash (Table 1). PVs appeared to respond to particular habitat patches and as a consequence were irregularly distributed through this forest. In contrast, REVs occupied nearly contiguous territories throughout the forest and showed no preference for any part of the study plot, including those sections also occupied by PVs (Fig. 2).

Within their preferred patches of forest, PVs foraged over wide areas that overlapped and often included entire REV territories (Fig. 2). The extent of horizontal overlap (*sensu* Cody 1974) between the territories of the two vireos on the study plot was highest in 1975 when virtually the entire area was occupied by REVs and overlap was essentially 100%. However, in 1976, 1977 and 1978, portions of the PVs' preferred areas were not occupied by REVs and horizontal overlap was estimated at 75%, 40% and 50%, respectively (Fig. 2).

**Population densities and reproductive success.** Although sample sizes are small, the number of young fledged per pair of PVs seemed to be relatively constant from year to year (Table 2). In contrast, the number of young REVs raised by "successful" pairs

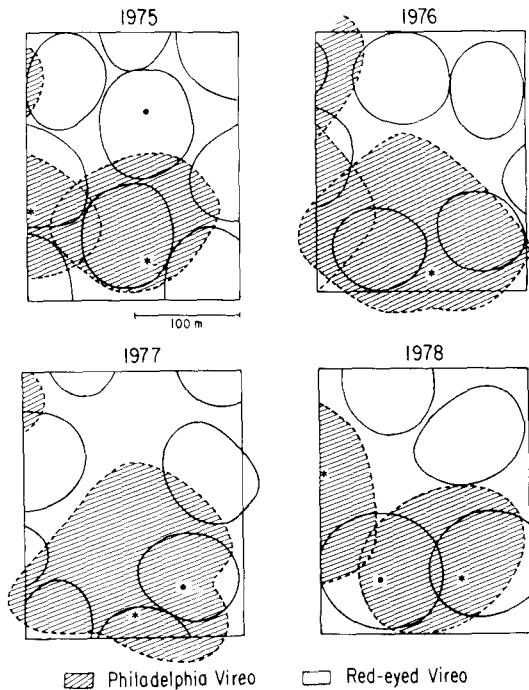


FIGURE 2. Territories of Red-eyed and Philadelphia vireos, based on cumulative maps of all sightings, banding records and locations of singing birds. Map shows half of the 10-ha study plot, an area of 200 × 250 m. Asterisks denote the locations of Philadelphia Vireo nests; black dots indicate Red-eyed Vireo nests.

(i.e., those that fledged at least one young) varied greatly between years (Table 2). Within a given season, however, the number of young fledged per pair was remarkably uniform, and was inversely related to their population density (Table 2). In 1975, when the REV population was at its peak, only one young from a presumed clutch of 3–5 (Bent 1950) was successfully fledged. The two nests that I checked in 1975 had three eggs. In 1978, when the REV population was at its lowest, each pair fledged three young. Of the 17 REV nests found from 1975–1978, four were abandoned and only one may have been robbed. No caterpillar outbreaks or other observable differences in insect abundance occurred during these contrasting years, 1975–1978 (J. C. Schultz and R. T. Holmes, pers. comm.).

**Foraging behavior.** In the context of the Hubbard Brook bird community, REV and PVs have been shown to be very similar in their foraging behavior (Holmes et al. 1979a; Holmes, in press; Robinson and Holmes, unpubl.). Both species direct about 83% of their maneuvers at leaves and both forage in outer foliage 57% of the time (Holmes et al. 1979a). The diets of both species contain relatively large proportions

TABLE 1. Tree species composition (%) of areas on the study plot occupied by breeding Philadelphia Vireos compared with areas unused by this species. Red-eyed Vireos occupied the entire plot.

Tree species	Occupied areas (18 samples)	Unoccupied areas (32 samples)	Entire study area (50 samples)
Yellow birch	36	35	35
Sugar maple	36	36	36
Beech	15	26	24
White ash	12	2	6

of caterpillars (Chapin 1925; Robinson and Holmes, unpubl.). Likewise, vireos of both species mostly hover when capturing prey (Holmes et al. 1979a).

Their foraging behavior differs strikingly, however, in one way: whereas the REV forages in tree species roughly in proportion to their occurrence, the PV markedly prefers foraging in white ash and yellow birch (Holmes and Robinson, in press). Overall, the difference between the two vireos in their use of tree species is highly significant ( $P \ll .001$ ,  $\chi^2 = 383.5$ , d.f. = 3). This difference occurs largely in the canopy, however, where the two vireos differ significantly in their use of three of the four major tree species (Table 3). In the shrub layer, where white ash and yellow birch are largely absent, the two species do not differ significantly in use of plant species ( $P > .10$ ,  $\chi^2 = 4.49$ , d.f. = 3). In the sapling/subcanopy layer, PVs forage in beech significantly more than the REV (Table 3).

**Vertical overlap.** The Red-eyed Vireo is primarily a bird of the middle canopy while the Philadelphia Vireo nests (Table 4) and does much of its foraging high in the canopy (Fig. 3). However, during the late nestling period, this vertical separation ceases as the PV expands its foraging range to include the sapling and shrub layers (Fig. 3). Then, immediately after leaving the nest, PV fledglings move from the upper canopy to the shrub layer where they remain for 2–5 days. Vertical overlap between the two species during the late nestling and early fledgling period (Table 5) was extremely large in 1976 and 1978 (no foraging data were gathered in 1977). In 1975, the year of greatest horizontal overlap (Fig. 2) and most frequent interspecific aggression (see below), the two species differed significantly in their use of the three vertical layers (Table 5). In this year PVs foraged significantly less often in the subcanopy/sapling layer than they did in 1976 ( $P < .001$ ,  $\chi^2 = 17.37$ , d.f. = 1) and in 1978 ( $P < .001$ ,  $\chi^2 = 46.25$ , d.f. = 1).

TABLE 2. Year-to-year variation in reproductive success of the two vireos and their population densities from 1975-1978.

Species	Year	Population density (individuals/10-ha plot)	Number of pairs fledging:		
			1 young	2 young	3 young
Red-eyed Vireo	1975	31.0	19	0	0
	1976	30.0	0	9	0
	1977	23.5	0	7	0
	1978	20.0	0	0	5
Philadelphia Vireo	1975	3.5	3	0	0
	1976	3.5	0	6*	0
	1977	2.0	0	4**	0
	1978	3.0	0	4**	0

\* Includes three pairs 500 m from study plot.

\*\* Includes two pairs 500 m from study plot.

In summary, for most of the breeding season, PVs forage high in yellow birch and white ash and REVs forage at mid heights in all tree species. However, during the late nestling/early fledgling period when the PV expands its vertical foraging range, the two species overlap greatly in both vertical use of the forest and in use of tree species. The extent of overlap between these two vireos varies between years, probably depending upon their population densities.

#### INTERSPECIFIC AGGRESSION

The frequency and intensity of aggressive encounters between Red-eyed and Philadelphia vireos varied between years and within seasons. "Aggressive encounters"

are defined as any contacts between individuals of each species that involve overtly aggressive acts such as attempts by one bird to supplant another, chases, or actual fights that involve physical contact. Whenever I saw such encounters, I recorded which species initiated them and whether there was physical contact.

*Between-year variation.* Almost no interspecific aggression occurred in 1977 and 1978 compared with 1975 and 1976 (Table 6). Of the eight encounters I observed in 1977 and 1978, none involved physical contact, compared with 38 of the 68 encounters seen in 1975 and 1976 ( $P < .01$ ,  $\chi^2 = 8.94$ , d.f. = 1). Although the sample size is small, the REV started significantly fewer of the encounters observed in 1977 and 1978 than in 1975 and 1976 ( $P < .05$ ,  $\chi^2 = 4.55$ , d.f. = 1). In 1978, I twice witnessed vireos of both species foraging within about 3 m of each other with no apparent conflict.

*Within-season variation.* The frequency and intensity of interspecific encounters, especially those initiated by the PV, also varied substantially between stages of the nesting cycle (Table 7). During the territorial establishment period, aggressive encounters were relatively frequent but brief and of low intensity. Only 5 of 20 encounters involved physical contact (Table 7). Typically, an individual of one species would fly up to a perched individual of the

TABLE 3. Use of tree species in foraging by Red-eyed and Philadelphia vireos in the three vertical layers during the late nestling and early fledgling periods of 1975, 1976 and 1978. N = number of trees in which at least one maneuver was observed. N total = total number of foraging maneuvers in that tree species. Percentages represent the total number of maneuvers seen in that plant species in each layer divided by the total number of maneuvers observed.

Layer	Tree species	Red-eyed Vireo	Philadelphia Vireo
Canopy	sugar maple	8.8 (%)*	4.7
	Am. beech	3.5	1.4
	yellow birch	7.8*	15.7
	white ash	1.0*	11.8
Subcanopy/ sapling	sugar maple	25.5	17.9
	Am. beech	22.5*	13.6
	yellow birch	15.2	18.7
	other	2.7	4.5
Sapling	sugar maple	3.4	1.8
	Am. beech	6.4	5.1
	striped maple	1.4	2.6
	other	1.8	2.2
	N =	564	508
	N total =	853	809

\* = different at .01 level ( $\chi^2$ ).

TABLE 4. Heights of Red-eyed and Philadelphia vireo nests on or near the study area in the years 1970-1978 (Holmes unpubl. data).

	Red-eyed Vireo	Philadelphia Vireo
N	31	14
Range (m)	2-19	12-28
$\bar{x} \pm$ S.D.	10.7 $\pm$ 5.8	24.0 $\pm$ 4.6

NESTING STAGE

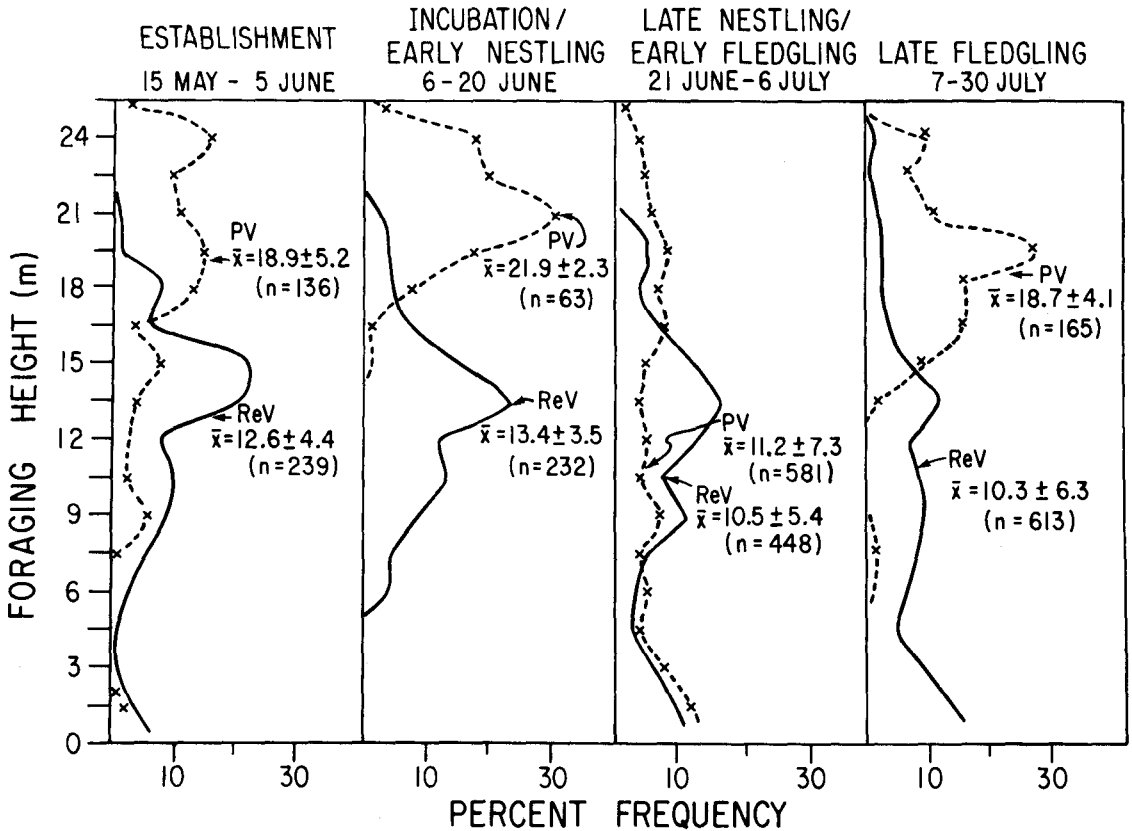


FIGURE 3. Vertical distribution of foraging maneuvers during the four major stages of the nest cycle for Red-eyed (ReV) and Philadelphia (PV) vireos in the Hubbard Brook forest, 1975-1976.

other species, supplant it and then either chase it or be chased for a short distance. In all five encounters initiated by a lone PV, the episode always ended with the PV being chased by the REV. On three occasions, however, I saw pairs of the PVs attack, supplant and chase single REV. These were the only three encounters I observed during the four years of this study that resulted in the REV being chased. By the end of May, PVs ceased starting en-

counters. Twice they did not react aggressively towards REV that were singing within a few meters of the PVs' newly completed nests. One of these nest trees was used repeatedly by a singing male REV while the PVs were incubating.

During the incubation and early nesting stages, I rarely saw Philadelphia Vireos because they remained high in the canopy (Fig. 3). Of the six aggressive encounters I observed during this period, none were ini-

TABLE 5. Percentage use of the three major vertical layers of the forest during the late nestling and early fledgling periods by foraging Philadelphia and Red-eyed vireos. Number in parentheses is the total number of prey-capturing maneuvers. Overlap of layer use calculated using index of Holmes and Pitelka (1968).

	1975		1976		1978	
	Red-eyed Vireo (287)	Philadelphia Vireo (312)	Red-eyed Vireo (290)	Philadelphia Vireo (274)	Red-eyed Vireo (276)	Philadelphia Vireo (223)
Canopy	.16*	.50	.32	.32	.17	.20
Subcanopy/sapling	.65*	.33	.58	.55	.77	.72
Shrub	.20	.17	.10	.13	.07	.09
Overlap	.66		.97		.96	

\* Species differed at .01 level ( $\chi^2$ ).

TABLE 6. Number of aggressive encounters between Red-eyed and Philadelphia vireos at Hubbard Brook during the incubation, nestling and fledgling periods, 1975–1978.

	Total # encounters	No. with physical contact	No. started by			No. observation days	No. per observation day
			Red-eyed	Philadelphia	Unknown		
1975	38	23	21	12	5	50	.76
1976	30	15	17	9	4	55	.55
1977	8	0	2	6	0	45	.18
1978	0	0	0	0	0	35	.00

tiated by PVs and only one involved physical contact. In all cases, the PVs flew away after being supplanted by REVs.

Coinciding with the abrupt expansion of the PV's vertical foraging range during the late nestling stage (see Fig. 3), there was an increase in the frequency of encounters and in the aggressiveness of PVs towards REVs (Table 7). During the late nestling stage, PVs started significantly more encounters with REVs than during the incubation/early nestling stage ( $P < .01$ ,  $\chi^2 = 6.93$ , d.f. = 1). All 33 encounters occurred within about 25 m of a PV's nest tree. Typically a PV would fly at a REV, attempt to supplant it and then be chased for at least 50 m. These chases usually carried both protagonists far from the nest tree.

The most intense and violent encounters occurred during the early fledgling period, when the PVs' fledglings were in the shrub layer. During this period PVs started conflicts only when REVs came within about 3–5 m of the PVs' fledglings. Overall, PVs began significantly fewer encounters with REVs during the early fledgling period than during the late nestling period ( $P < .05$ ,  $\chi^2 = 5.77$ , d.f. = 1). However, the proportion of fights that involved physical contact increased significantly from the late nestling to early fledgling periods ( $P < .001$ ,  $\chi^2 = 12.20$ , d.f. = 1).

Some of the encounters during the early fledgling period were extremely vigorous. In one, a pair of REVs attacked a PV that was about to feed a fledgling. The PV did

not retreat and the ensuing fight involved three minutes of violent contact, wing beating and pecking, much of which took place on the ground. At one point, the PV broke off from the fight for several seconds during which both REVs moved toward the fledgling. When the lead REV was within 1 m of the fledgling, the adult PV hovered at a leaf in front of the fledgling and quivered its wings. Both REVs then chased the PV well away from the fledgling. By the time the chase was over, the fledgling had moved to shrubs about 50 m away. James (1979) observed a Solitary Vireo (*V. solitarius*) using a nearly identical hovering maneuver when its nest was approached by a potential predator, and hypothesized that this action was a kind of distraction display. My observation is consistent with his interpretation.

In another encounter, I watched a REV attack a PV fledgling. This began when a male REV attacked a female PV who was feeding a fledgling within about 15 m of the base of the REV's nest tree. The two birds fought for about a minute, vigorously pecking and beating their wings. Afterwards, the PV flew off and resumed foraging. The REV also began to forage in the same general area, and when the PV returned to feed the fledgling, the REV attacked it again. During the ensuing fight, the REV tore several feathers from the PV's breast, after which the PV withdrew. The REV then flew up to a perch in front of the PV fledgling, spread its tail, opened its beak to reveal its bright red gape and went into a metronome-like

TABLE 7. Frequency of aggressive encounters during the major stages of the nest cycle.

Stage	Number started by			Number with physical contact	Total number encounters	Number observation days <sup>1</sup>	Encounters/observation day
	Philadelphia	Red-eyed	Unknown				
Establishment	8	10	2	5	20	20	1.0
Incubation/early nestling	0	5	1	1	6	55	0.1
Late nestling	19	11	3	12	33	25	1.3
Early fledgling	9	18	3	24	30	30	1.0
Late fledgling	0	6	1	1	7	80	0.1

<sup>1</sup> Each observation day was approximately the same duration, lasting from 07:00 to 14:00.

swaying display identical to that described by Nolan (1962) and Barlow and Rice (1977). It then hung from the perch upside down in the opposite direction underneath the fledgling, pecked it three times at the vent and flew away. During this encounter between the REV and the fledgling, the adult PV continuously preened her breast feathers as if she might have been injured. She did not return to feed the fledgling for at least three hours.

After their fledglings became more mobile, PVs seemed to stop initiating encounters. All seven fights seen during the late fledgling stage involved a REV supplanting a PV after which the latter and its young simply flew away.

#### VOCAL BEHAVIOR

A detailed treatment of the vocal behavior of these two vireos was beyond the scope of this study. However, I found some indirect evidence that the two species also interacted vocally at Hubbard Brook as they have been found to do in northeastern Ontario (Rice 1978b, c). At Hubbard Brook, Red-eyed Vireos seemed to sing their normal, species-specific song as described by Lemon (1971) and Rice (1974). For Philadelphia Vireos, however, I could distinguish four very different songs, which occurred in different contexts. Although the differences between these songs require verification by sonographic analysis, they are described here in qualitative terms since they have a bearing on the interaction between these two vireos.

1) The "non-repetitious" song of the PV sounds to me very much like that of the normal song of the REV. Each phrase of this song differs from the one preceding it. In general, it is delivered at a slower rate ( $\bar{x} = 26.1 \pm 8.6$  s.d. phrases per minute,  $N = 73$  songs of 9 individuals) than the song of the REV ( $\bar{x} = 38.6 \pm 9.9$  phrases per minute,  $N = 50$  songs of 15 individuals). I heard PVs singing this song only from areas that were unoccupied by REVs and when REVs on neighboring territories were also singing. I did not hear this song in 1975, when REVs completely overlapped PV territories. In contrast, this song was given frequently in 1977 and 1978 when REVs were absent from large areas of the plot. I heard this song primarily during the incubation/early nestling periods (Fig. 4).

2) In the "fast mixed" song, some but not all phrases are repeated several times in succession. This song is delivered at a rel-

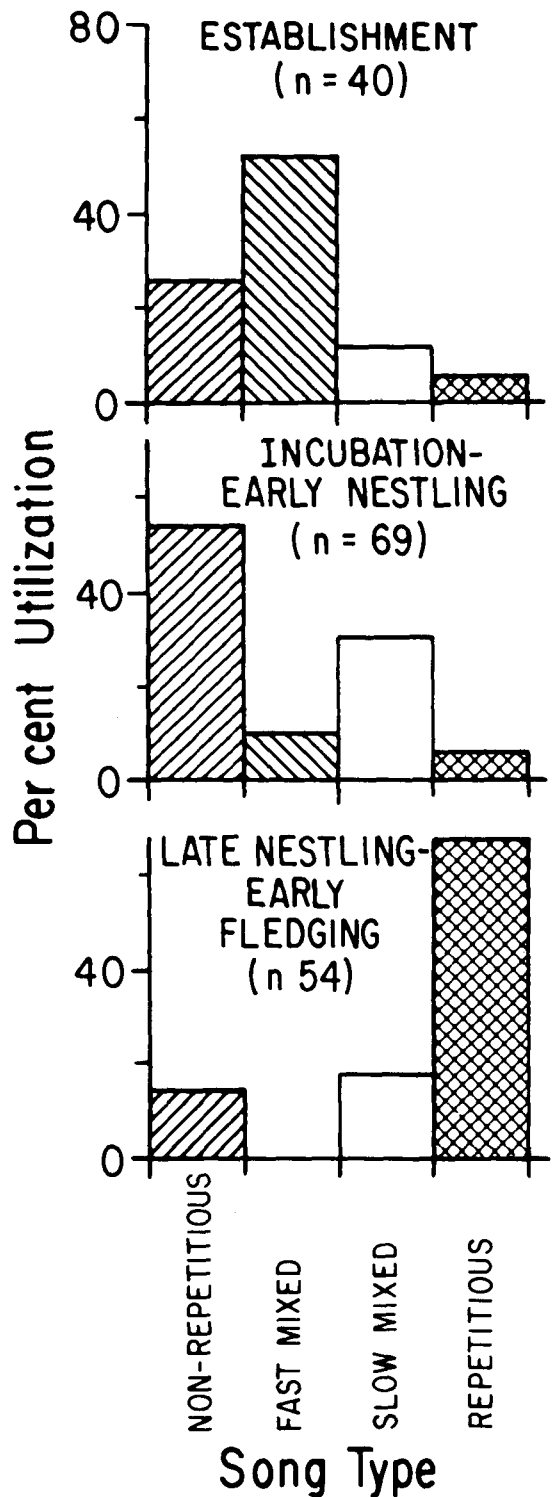


FIGURE 4. Relative use of four song types (see text) by Philadelphia Vireos at each stage of their nest cycle in 1976.

atively fast rate ( $\bar{x} = 35.0 \pm 14.3$  phrases per minute,  $N = 30$  songs of 6 individuals) and is used primarily during the territory-establishment period (Fig. 4). It was given most

frequently when other PVs were singing nearby.

3) The "slow mixed" song is characterized by its slow rate of delivery ( $\bar{x} = 11.8 \pm 3.9$  phrases per minute,  $N = 38$  songs of 7 individuals). As in the "fast mixed" song, some of the phrases are repeated several times in succession. These repeated phrases are often raspy. This song was usually given by a stationary bird from high in the canopy. I heard this song most often during the early nestling period (Fig. 4).

4) The PV's "repetitious" song, the most distinctive of all, consists of the repetition of a single, apparently identical, phrase over and over again in succession. It is delivered at about the same rate as the "slow mixed" song ( $\bar{x} = 10.2 \pm 3.5$  phrases per minute,  $N = 46$  songs of 5 individuals), usually from high in the canopy. Each of the five males I heard give this song used very different phrases in their "repetitious" songs. It is delivered primarily during the early fledgling period (Fig. 4). I did not hear this song in 1977 or 1978.

Particularly in light of Rice's (1978b, c) hypothesis that the PV mimics the song of the REV, I hypothesize that the "non-repetitious" song of the PV mimics that of the REV and is a form of interspecific territorial advertisement. This would explain why the "non-repetitious" song is generally given when REVs on neighboring territories are also singing. Likewise, it seems reasonable to hypothesize that the other three songs of the PV function intraspecifically. The "slow mixed" and "repetitious" songs, both of which are slow and involve the repetition of a single phrase many times in succession, may be designed not to attract the attention of REVs. Since I never heard a REV repeat the same phrase twice in succession, I further hypothesize that this variation in successive phrases is critical for species recognition. Rice (pers. comm.) and Barlow (pers. comm.) found that the "repetitious" song did not elicit as intense a response as the "normal" song in playback experiments. All of the above hypotheses await testing by playback experiments.

## DISCUSSION

The nature of the interactions between Red-eyed Vireos and Philadelphia Vireos at Hubbard Brook seems to be strongly affected by temporal variation in the extent of vertical and horizontal overlap between the two species (Fig. 5). In general, these birds seem to interact aggressively only during periods of high spatial overlap.

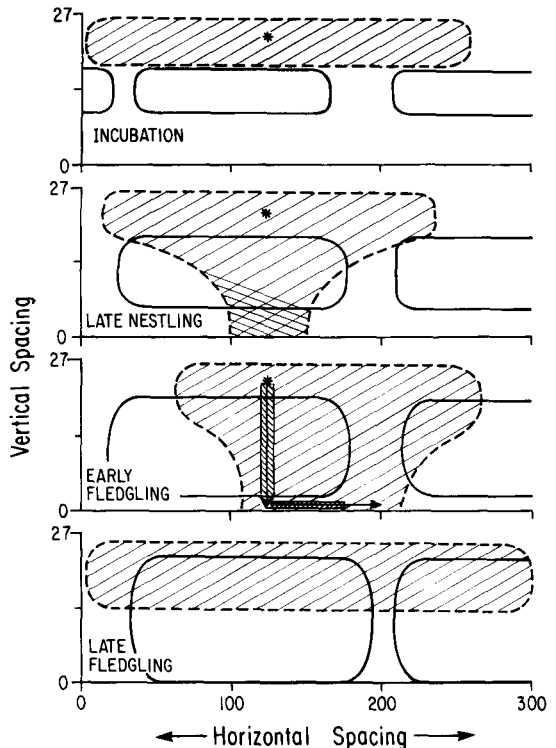


FIGURE 5. Schematic representation of a vertical cross section of the activity ranges of Red-eyed Vireos (open "territories") and Philadelphia Vireos (hatched "territories") at Hubbard Brook, based on data presented in Figures 1, 2 and 3. Cross hatching in the late nestling and early fledgling periods indicates the region actively defended by Philadelphia Vireos against Red-eyed Vireos. Asterisks denote a Philadelphia Vireo nest, and the arrow represents the route of young Philadelphia Vireos as they leave the nest. The scale is in meters.

## WHY DO THESE VIREOS CONFLICT?

Two explanations have been offered for why two species should be mutually aggressive: 1) mistaken identity (Murray 1971) and 2) resource competition (Cody 1974, Sherry 1979). Murray (1971) hypothesized that aggression between congeners is largely the result of mistaken identity and is therefore non-adaptive. Rice (1978a, b, c) described in detail the reasons why it is unlikely that mistaken identity could be responsible for the interaction between these two vireos in northeastern Ontario. In particular, he demonstrated that the Philadelphia Vireo is able to distinguish between its own song and that of the Red-eyed Vireo, although the reverse is apparently not true. At Hubbard Brook REVs may regard PVs as conspecifics and PVs may be aggressive towards REVs solely to protect their young.

As for the second possible explanation, much evidence indicates that competition, probably for food, may also be occurring. The periods of maximum overlap in forag-



ing microhabitats were also the periods of most intense and frequent interspecific aggression. Aggressive interactions were most frequent during the late nestling/early fledgling period when the two species overlapped most in their use of vertical strata and plant species. Similarly, interspecific aggression was most frequent during years of wide horizontal overlap. Given the overall similarity in the diets and foraging behavior of the two species (Holmes et al. 1979a; Holmes, in press; Robinson and Holmes, unpubl.), it is possible that the two species might be competing for the same food when foraging in the same microhabitats. There is also evidence that caterpillars in the understory, which are important in the diets of both species (Robinson and Holmes, unpubl.), are significantly reduced in abundance (by 18–63%) by avian predation at Hubbard Brook (Holmes et al. 1979b). This effect was most pronounced during late June and July. These data are highly relevant here since nearly all of the aggressive encounters between the two vireos took place in the understory at this time.

Additional, although indirect, evidence that food competition may be responsible for the REV's aggressiveness towards the PV comes from data on REV reproductive success. The observed inverse relationship between reproductive success and REV population density (Table 2) suggests that food may limit the number of young fledged per pair in years of high REV population density. It is also possible that interference between neighboring pairs of conspecifics or perhaps some between-year variation in weather or food supply could influence their reproductive success. Nevertheless, the increased aggressiveness of the REV towards the ecologically-similar PV in years of high REV population density is consistent with the possibility of food limitation.

#### WHY DO PHILADELPHIA VIREOS EXPAND THEIR VERTICAL FORAGING RANGE AT THE TIME OF FLEDGING?

The predictability with which PV fledglings move to the sapling and shrub layers after leaving the nest is difficult to explain, particularly since this brings them into direct contact with the REV. Part of the explanation may be related to the canopy-top location of the PV's nest. PVs place their nests much higher in the canopy than any other species at Hubbard Brook (Holmes unpubl. data). It may be that the food resources of the area around the nest where it is most advantageous for the adults to forage (An-

dersson 1978, Orians and Pearson 1979) become "depressed" (Charnov et al. 1976) by the end of the nest cycle. By moving their young to the shrub zone, PVs can find a fresh supply of food. Alternatively, it may be to the PVs' advantage to move their fledglings to the shrub layer because the microclimate may be more favorable than in the upper canopy. Likewise, young PVs may somehow be less vulnerable to predators in the shrub layer than in the upper canopy.

The high nest placement of the PV may be a response to the REV's aggressiveness. Rice (1974), however, also found that PVs place their nests higher in the canopy than REV's in an area where they do not overlap horizontally and Barlow (pers. comm.) has found them nesting in 5-m *Alnus* scrub in an area where REV's nest in 15-m *Populus*. This suggests that PVs may place their nests in relation to some vegetational configuration rather than in relation to REV's.

#### TEMPORAL DIFFERENCES

Philadelphia Vireos at Hubbard Brook fledge considerably earlier than Red-eyed Vireos, which may be advantageous for several reasons. First, since REV's forage mostly at mid heights, they might be less likely to discover PV fledglings in the dense shrub layer. Second, early-fledging PVs have the advantage of using the shrub layer before its food resources have been reduced by the foraging of its ecologically similar and more abundant congener and before the major period of reduction in caterpillar abundance by the bird community in general (Holmes et al. 1979b). Third, if the late nestling and early fledgling periods are when both species need the most food (Root 1967, Holmes and Sturges 1975, Holmes et al. 1978), then interspecific differences in fledging dates would separate these critical periods. Such differences in the fledging dates of one species would be selectively favored only in a forest where there was extensive horizontal overlap between the two species. It may be significant that in north-eastern Ontario where there is little horizontal overlap between the two vireos (Rice 1978a), both arrive and fledge at about the same time (Rice 1974).

#### THE EVOLUTION AND MAINTENANCE OF INTERSPECIFIC TERRITORIALITY IN HABITATS OF DIFFERENT VEGETATION STRUCTURE

Orians and Willson (1964) and Cody (1974) have hypothesized that interspecific territoriality between closely-related species

might be expected in habitats of simple vegetation structure "in which the usual options in interspecies resource division may not be exercised" (Cody 1974:216). Two species with similar foraging behavior and habitat requirements can share the resources of a habitat by defending mutually exclusive territories and thereby eliminate horizontal overlap. In more complex habitats, other forms of resource division such as vertical segregation might be possible. A comparison of my findings with Rice's (1978a) provides a test of this hypothesis. The habitats occupied by both vireos at Hubbard Brook and in Ontario differ in several major respects. The forest at Hubbard Brook is taller than that in northeastern Ontario (27 m vs. 20 m) and contains a mixture of climax (beech and sugar maple) and mid-successional (yellow birch and white ash) trees in the canopy and has an understory composed entirely of shade-tolerant climax species. These features indicate that the Hubbard Brook forest is a more complex habitat than the Ontario woodland, which was dominated by mid-successional trees such as aspen (*Populus* spp.) and birch (*Betula* spp.). As predicted in Orians and Willson's (1964) and Cody's (1974) models, the two species defend exclusive, non-overlapping territories in the simpler habitat in Ontario, while vertically dividing the more complex forest at Hubbard Brook.

It is difficult to determine whether Philadelphia Vireos forage in the upper canopy because they have been displaced by Red-eyed Vireos or because they are preadapted to the foraging conditions and vegetation structure of this layer. The PVs at Hubbard Brook are at the southern edge of their breeding range (A.O.U. Check-list 1957), and may be in atypical habitat there (Bent 1950, Barlow and Power 1970, Barlow and Rice 1977). Throughout most of its breeding range the PV is associated with mid-successional forests of aspen, birch and alder (*Alnus* spp.). The climax forest in most of these areas is spruce (*Picea* spp.) and fir (*Abies* spp.), which is not suitable habitat for these vireos. The PV's preference at Hubbard Brook for foraging in yellow birch and white ash and for nesting in areas where these trees are common may be a result of its evolutionary history of foraging in successional trees. Since these tree species are concentrated in the upper canopy at Hubbard Brook, the PV's tendency to forage in the upper canopy may therefore be a result of preadaptation and not directly a result of displacement by the REV.

#### BETWEEN-YEAR DIFFERENCES

If I had studied these two species only in 1978, I undoubtedly would have concluded that there was no interaction between them. Similarly, territory maps, nesting data and banding records for the 10-ha plot in 1970 and 1971 (R. T. Holmes unpubl. data) during a caterpillar outbreak indicate that PVs apparently did not maintain distinct territories or avoid areas with REVs. In these years PVs wandered widely and overlapped other vireos extensively. However, in 1972, the year after the caterpillar outbreak, when PV populations were at their peak densities, some evidence suggests that PVs both nested and foraged at all heights and defended small, well-defined territories against both conspecifics and REVs. At Hubbard Brook in 1972, the two vireos may have behaved much as they did in northeastern Ontario during Rice's (1978a) study.

These results show that the interaction between these two vireos is complex, varying geographically and temporally. At Hubbard Brook, whether the Philadelphia and Red-eyed vireos segregate vertically, horizontally, or not at all, may depend on the relative population densities of both species, the stage of the nest cycle, and the abundance of food.

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