

# COMPETITIVE INTERACTIONS AND ADAPTIVE STRATEGIES OF AMERICAN REDSTARTS AND LEAST FLYCATCHERS IN A NORTHERN HARDWOODS FOREST

THOMAS W. SHERRY<sup>1</sup>

*Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755 USA*

**ABSTRACT.**—Ecological interactions between American Redstarts (*Setophaga ruticilla*) and Least Flycatchers (*Empidonax minimus*) were studied in the Hubbard Brook Experimental Forest, New Hampshire, USA during three breeding seasons. These two taxonomically distinct passerines have converged on the ecological niche of "flycatching," overlapping significantly in body size, bill morphology, foraging behavior, and in patterns of habitat exploitation. They exhibit a striking amount of interspecific aggression during the breeding period. Coexistence between the two species is mediated by subtle habitat preferences and reinforced by interspecific aggression and by differences in life history characteristics. The redstart is a broad-niched, behaviorally plastic, socially subordinate habitat generalist relative to the flycatcher. It also fledges young earlier and defends larger territories. Such differences in social dominance and in niche breadths among members of an ecological guild may be important in permitting certain constellations of species to coexist and therefore important organizing features of bird community structure. *Received 10 May 1978, accepted 6 December 1978.*

THE best evidence for the existence of interspecific competition is often geographic in nature (MacArthur 1972). Dramatic intrageneric phenomena, such as abrupt species replacements, character convergence and divergence, and ecological release on environmental gradients, are emphasized (Diamond 1975, Terborgh and Weske 1975, Able and Noon 1976). The tendency for congeners to be geographically segregated means that interactions between more phylogenetically distant species (Root 1967, Morse 1975, Pearson 1975, Primack and Howe 1975) may greatly predominate in structuring local communities. The results of such interactions may be less obvious than intrageneric ones, since divergence will often be multidimensional. The present study of two ecologically similar but taxonomically distant bird species in a northern hardwoods forest was undertaken to explore their actual or potential competitive interaction and their means of ecological segregation.

The Least Flycatcher (*Empidonax minimus*, Tyrannidae) and the American Redstart (*Setophaga ruticilla*, Parulidae) are both abundant and comprise the greater part of the "flycatcher" guild in the Hubbard Brook Experimental Forest in New Hampshire (Holmes and Sturges 1975). They are both migratory, spending only 2–3 months in their north-temperate breeding grounds, which overlap extensively in the northern United States and southern Canada (A.O.U. Check-list 1957). On the breeding areas, they are very similar ecologically. They occupy mid heights in the forest and feed by hovering for insect prey on vegetative substrates. They have remarkably similar bill structures (see below), and as will be demonstrated in this study, they exhibit frequent interspecific aggression.

Plumage and vocalizations of the two species differ. The redstart is brightly patterned and sexually dimorphic in plumage, whereas the Least Flycatcher is dull-

---

<sup>1</sup> Present address: Department of Biology, University of California, Los Angeles, California 90024 USA.

colored and sexually monomorphic. Also, redstart males often take 2 yr to attain adult plumage (Ficken and Ficken 1967). The first-year males (Y) possess female-like yellow plumage and at Hubbard Brook behave differently in some respects from the adult-plumaged, red (R) males.

The field techniques of Cody (1974) were used with some modification to obtain an initial impression of the degree of ecological segregation of the two species. To explore further the observed patterns, I incorporated data on population dynamics, foraging and aggressive behavior, and habitat utilization at Hubbard Brook, as well as information from the literature. The different species-specific adaptive complexes thus revealed, and particularly the asymmetrical aggressive interference competition, are discussed in terms of the organization of the "flycatching" guild in temperate deciduous forests and in terms of community organization in general.

#### METHODS

The research was conducted in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire. Observations were made on a 10-ha plot of undisturbed, northern hardwoods forest ranging in elevation from 500 to 600 m. The slope is moderate and the aspect of the site generally southeast.

Three tree species dominate the forest canopy: beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), and yellow birch (*Betula allegheniensis* Brit.). White ash (*Fraxinus americana* L.), paper birch (*B. papyrifera* Marsh.), and red spruce (*Picea rubens* Sarg.) are also found in the canopy stratum, while the understory is comprised primarily of beech and sugar maple saplings in addition to striped and mountain maples (*A. pennsylvanicum* L. and *A. spicatum* Lam.). The herb-shrub layer contains seedlings and saplings of the major tree species, spinulose wood fern (*Dryopteris spinulosa* Fern.), hobblebush (*Viburnum alnifolium* Marsh.), and other herbaceous species. The canopy height averages 25–30 m.

The climate at Hubbard Brook is cool and moist and is characterized by a short growing season (4 months) and a 5-month snow-free period. Mean monthly temperatures during the breeding season for the bird populations range from 11°C in May to 19°C in July. Precipitation is distributed evenly throughout the year, averaging over 100 mm per month. More detailed descriptions of the study site and the Hubbard Brook Forest are given by Holmes and Sturges (1975) and Likens and Bormann (1972).

To examine the ecological interactions and relationships between redstarts and flycatchers, I collected data on their population sizes, patterns of dispersion, modes of food exploitation, and nesting ecologies. The most intensive fieldwork took place in summer 1974, with some data collected in the two preceding summers. Foraging observations are summarized as overlap indices (cf. Cody 1974). Three "component" overlaps for use of horizontal space, vertical foraging heights, and foraging mode were obtained and combined additively (cf. Yeaton and Cody 1974, May 1975). Procedures for obtaining overlap values, when they deviate from those used by Cody (1974), are detailed below.

Territorial overlap of the two species was measured during the 1-month period that territorial boundaries were stable, approximately from late May until just before the first young fledged in late June. All sightings of individuals of both species made during censusing and observations of foraging behavior were recorded cumulatively on gridded maps of the study area. Most individuals were color-marked. Territorial activity centers were obtained from these maps by enclosing observations attributable to each pair of birds and by using sites of intraspecific conflict to indicate shared boundaries. Territory maps were usually based on 10–20 observations per pair. Interspecifically shared and unshared areas were measured with a planimeter. The overlap values were calculated from the ratio of area shared by both species to the geometric mean area occupied by each species individually. This method compares favorably with that used by Cody (1974) (see Sherry 1975).

I have considered the seasonal changes in foraging patterns during four nest-cycle stages: pre-incubation, incubation, nestling, and fledgling. Foraging observations were made only on pairs of birds whose nesting status was known. In many cases the birds were color-marked, allowing positive identification of individuals and sexes. Foraging heights of observed food-getting tactics (or attempts) were estimated whenever birds of a known nest were encountered during routine traverses of the study area. Only the first height record of a foraging sequence was used in the analysis; thus each height observation is independent in a statistical sense from every other one. The height observations were assigned to the

TABLE 1. Population densities of American Redstarts and Least Flycatchers in mid-June in the Hubbard Brook Forest, 1969–1974.

	Numbers/10 ha <sup>a</sup>					
	1969	1970	1971	1972	1973	1974
<b>Redstarts</b>						
Adult (R) males	6	13	14.5	8.5	13	7.5
Second-year (Y) males				5 (2) <sup>b</sup>	0	2 (3) <sup>b</sup>
Females	6	13	14.5	13.5	13	9.5
Total	12	26	29	29	26	22
<b>Least Flycatchers</b>						
Males	13	14	21.5	23 (4) <sup>b</sup>	27 (3) <sup>b</sup>	11.5 (3) <sup>b</sup>
Females	13	14	21.5	23	27	11.5
Total	26	28	43	50	57	26

<sup>a</sup> 1969–1971 data from Holmes and Sturges (1975) in which age classes of males were not distinguished.

<sup>b</sup> Number mated plus (number unmated).

eight scaled intervals used by Cody in his tall habitats (see Fig. 2 for height intervals). Overlaps in heights at which foraging occurred were calculated using Schoener's formula (1968b: 712).

Food overlap was calculated as the product of bill overlap (to estimate food-size similarity) and feeding behavior overlap (to estimate microhabitat similarity). I used Cody's (1974) bill-overlap index. Instead of using his "sawtooth curves," I catalogued tactics into five mutually exclusive "tactic-substrate" categories (tactics *sensu* Root 1967): hawk, hover from leaf, hover from trunk or branch, glean from leaf, and glean from trunk or branch. The overlap was calculated again using Schoener's formula (1968b).

Although some differences have been found between the sexes (Sherry 1975 and in prep.), the data for all birds regardless of sex have been pooled here for analysis of overall species differences and similarities.

Differences in foliage profile densities between areas occupied were determined by the technique of MacArthur and Horn (1969). Foliage profiles were measured at six stations spaced at random along each of 20 randomly oriented sample lines located at regular intervals in the study area.

## RESULTS

The abundances of most Hubbard Brook bird species have varied considerably from year to year (Holmes and Sturges 1975). Densities of both redstarts and flycatchers have fluctuated more than two-fold between 1969 and 1974 (Table 1), mostly in synchrony, suggesting that they are influenced by similar environmental factors. The present study took place in seasons near the species' peak population densities (1973) and after a substantial decline (1974), making comparisons during this period especially instructive.

### SPACING PATTERNS AND HORIZONTAL OVERLAPS

American Redstarts and Least Flycatchers co-occurred on the study plot, but their territories were clearly not distributed at random, nor were they uniformly dispersed (Fig. 1). Adult (R) redstarts were more abundant in the northern end and the southwest corner of the study area, with fewer birds occurring in the north-central portion. Flycatchers were spread rather evenly throughout the plot in 1972 and 1973, although their territories tended to be more tightly packed in the north-central region where there were fewer redstarts. Flycatchers occurred only in the latter area in 1969 and 1970 (Holmes, unpublished data) and in 1974 (Fig. 1), years when their densities were low. The sharp boundary between areas that flycatchers and R-redstarts preferred in 1974 (Fig. 1c) and again in 1975 (Holmes, pers. comm.) occurred

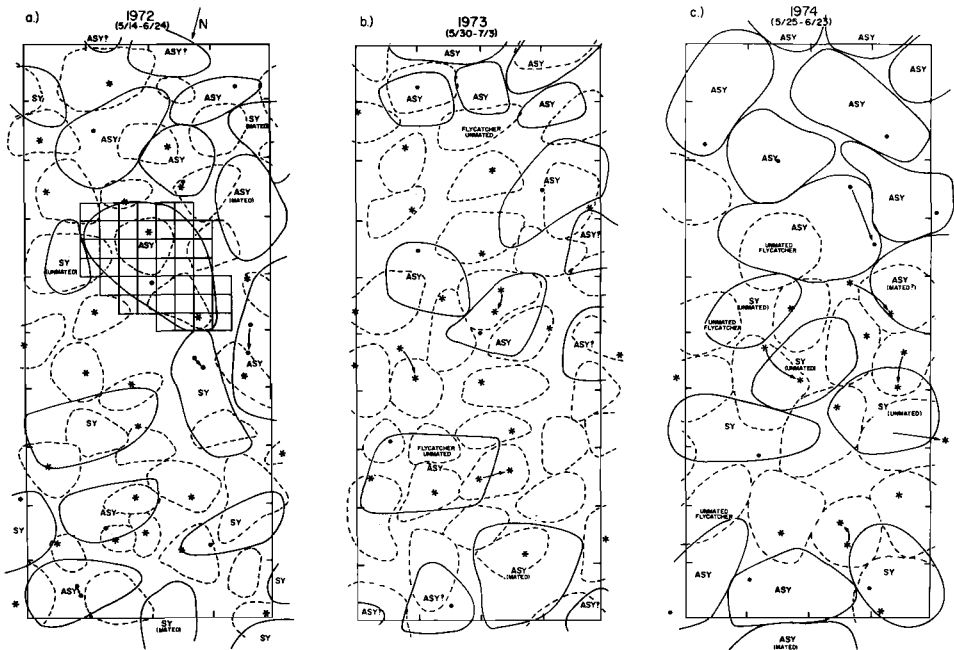


Fig. 1. Territory size and dispersion patterns for American Redstarts (solid lines) and Least Flycatchers (dashed lines) during the 1972–1974 breeding seasons in the Hubbard Brook Forest. The plumage-type of territorial redstarts, where known, is indicated (ASY = R or adult-plumaged males, SY = Y or yellow-plumaged males). Also, the breeding status, locations of nests and re-nests of redstarts (●) and Least Flycatchers (\*), and inclusive dates for periods of observations on which maps were used are included. The grid over a redstart territory in 1972 indicates the size of the 50-ft squares used by Cody (1974) to estimate horizontal overlaps.

at both the north and middle parts of the study area in the absence of any obvious habitat discontinuities (see discussion of habitat preferences below).

The Y-redstarts were variable in number from year to year, with at least seven being present in 1972, none in 1973, and five in 1974 (Table 1). The Y-redstarts were found in those parts of the study area with the fewest R-redstarts (Fig. 1a and c), possibly because of their late arrival on the study area each year and consequent exclusion from “preferred” areas by the well-established and older R-redstarts. The 1974 pattern of dispersion for all Y-redstarts and Least Flycatchers was almost precisely replicated in 1975 (Holmes, pers. comm.). The Y-redstarts, when present, therefore tended to occur in the same parts of the study area as Least Flycatchers.

As a consequence of these yearly variations in population densities of both species and the relative abundances of the two age classes of male redstarts, the values for territorial overlap between the two species varied considerably (Table 2). In 1972

TABLE 2. Horizontal overlap of territories of two age classes of American Redstarts with Least Flycatchers during breeding seasons, 1972–1974. Y = yellow-plumaged redstarts, R = red-plumaged redstarts.

Species-age combination	1972	1973	1974
Least Flycatcher-Y redstart	0.29	0.00	0.50
Least Flycatcher-R redstart	0.50	0.45	0.13
Least Flycatcher-total redstart	0.57	0.45	0.40

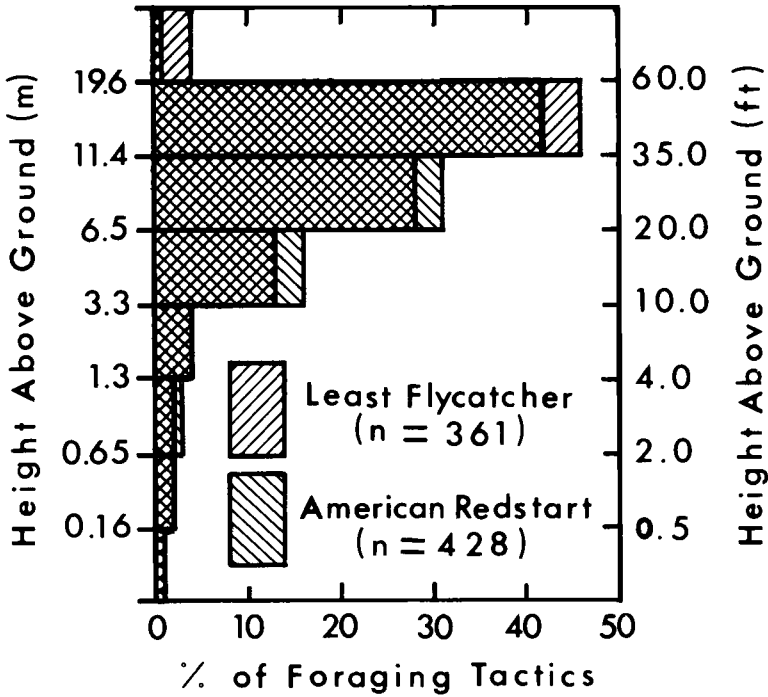


Fig. 2. Foraging-height histograms for American Redstarts and Least Flycatchers in the Hubbard Brook Forest, 1973 and 1974.

and 1973, when densities of both species were high, horizontal overlaps were highest. In 1974, the flycatchers occupied only one portion of the study area (Fig. 1), resulting in a marked decrease in horizontal overlap with R-redstarts (Table 2). In that year, however, Y-redstarts were relatively common and they overlapped the flycatchers to a much greater extent, maintaining a high overall species overlap (Table 2).

**FORAGING RELATIONSHIPS**

The overall use of heights for foraging was remarkably similar for the two species (Fig. 2). Correspondingly, the vertical overlap values were high, ranging from 0.69 to 0.84 (Table 3). Although absolute foraging heights of both species did change during the season (Sherry 1975), vertical overlap values changed relatively little (Table 3), reflecting another parallel response of both species, presumably to the same changes in food availability and demand in this seasonal environment. In all cases, the vertical overlap values exceeded the horizontal.

Even if two species forage at exactly the same horizontal locations and heights, the species may use completely different resources, depending, for example, on their abilities to catch differentially mobile or visible prey, to forage on different substrates, or to handle and swallow prey of different size or hardness. For these reasons, the index of food overlap takes into account two different kinds of indirect measures, i.e. behavioral and morphological, in an attempt to measure the two species' potential for finding and handling similar kinds of prey. The interspecific overlaps for the behavioral subcomponent of food overlap, which is based on their

use of foraging tactics and substrates from which prey are taken, ranged widely, from 0.49 to 0.81 (Table 3). The overlap values were lower in 1973 than in 1974, although 1973 sample sizes were small. The values from both years tended to be intermediate between horizontal and vertical overlaps.

It is of interest that the redstarts consistently hawked more than the taxonomic "flycatchers" (Table 3). This may be related to their rapid foraging movements and tail flash pattern, which cause insects to move and disclose their position (Ficken and Ficken 1962). Both species, however, take the majority of their insect prey from vegetation throughout the breeding season. The Least Flycatcher may take a greater percentage of its prey from vegetation than do other *Empidonax* flycatchers, but many *Empidonax* do a considerable amount of hovering (Eckhardt 1977), perhaps more than is generally recognized. Yellow-bellied Flycatchers (*E. flaviventris*) and other congeners wintering in lowland Costa Rican rain forest are also mostly hoverers (Sherry, unpublished data).

The morphological component of the food overlap is based on bill dimensions, which I consider an index to size of prey taken. The two species considered here have remarkably similar bill shapes, although the Least Flycatcher has a slightly larger bill than the redstart in all dimensions. The means (in mm  $\pm$  SE) for total culmen length, and width and depth at base, respectively, are  $9.03 \pm 0.065$ ,  $4.53 \pm 0.038$ , and  $2.94 \pm 0.024$  ( $n = 84$ ) for the American Redstart, and  $10.01 \pm 0.078$ ,  $5.83 \pm 0.044$ , and  $3.42 \pm 0.037$  ( $n = 74$ ) for the Least Flycatcher. In terms of bill length and width-to-depth ratio, the two species are more similar to each other than either is to any other Hubbard Brook species (Sherry 1975). Both have flattened, "flycatching" bills with a width-to-depth ratio of about 1.4. The bill morphological overlap, calculated from bill lengths and depths, is 0.97, suggesting that these species do not partition their food resources on the basis of prey size. This result obtains, of course, throughout the season.

Hespenheide's (1971) study relating bill length and body weight to food size distributions confirms the high food-size overlap I obtained using Cody's bill-morphological index for these small flycatching species. Hespenheide found that body weight more closely predicts food sizes than does bill length, and on the basis of a body-weight ratio of 1.17 for the redstart and Least Flycatcher (8.9 and 10.5 g, respectively—Holmes and Sturges 1975), food-size overlap should be close to unity.

#### COMPOSITE OVERLAP IN USE OF RESOURCES

Summation overlap values, combining horizontal, vertical, and food overlaps, are remarkably constant in different parts of the breeding season and between years (Table 4). Summation overlap during the incubation stage in 1974 was higher than at any other time, but it is not clear how meaningful this difference is without data spanning a number of breeding seasons. The constancy of summation overlaps results from the complementarity of component overlaps both within and between breeding seasons. When horizontal overlaps were lower in 1974 than in 1973, for example, both vertical and food overlaps were higher (Table 4). This short-term complementarity indirectly supports the hypothesis that the actions of at least one of the species impinging on the other during the period of the study.

It is clear from Table 4 that horizontal overlaps are considerably lower than any of the other components, both in 1973, when the two populations were at their greatest

TABLE 3. Height-frequency distributions and vertical overlaps (above) and substrate and foraging tactic use (below) of American Redstarts (RS) and Least Flycatchers (LF) (sex and age data pooled). Scaled height intervals were used in breeding cycle stages in 1973 and 1974.

	1973						1974					
	Nesting		Fledgling		Pre-incubation		Incubation		Nesting		Fledgling	
	RS	LF	RS	LF	RS	LF	RS	LF	RS	LF	RS	LF
<b>Foraging height intervals<sup>a</sup></b>												
>60 ft (>19.6 m)	0.03	0.07	0.00	0.00	0.03	0.18	0.01	0.03	0.00	0.00	0.00	0.01
35-60 ft (11.4-19.6 m)	0.10	0.28	0.21	0.26	0.37	0.45	0.78	0.62	0.40	0.55	0.30	0.41
20-35 ft (6.5-11.4 m)	0.31	0.16	0.29	0.21	0.33	0.18	0.16	0.31	0.38	0.37	0.25	0.32
10-20 ft (3.3-6.5 m)	0.37	0.23	0.21	0.26	0.13	0.16	0.00	0.03	0.18	0.06	0.25	0.16
4-10 ft (1.3-3.3 m)	0.10	0.10	0.21	0.05	0.04	0.02	0.03	0.00	0.01	0.01	0.05	0.07
2-4 ft (0.65-1.3 m)	0.07	0.05	0.00	0.11	0.01	0.02	0.00	0.00	0.02	0.01	0.13	0.02
6 inches-2 ft (0.16-0.65 m)	0.00	0.08	0.07	0.05	0.04	0.00	0.01	0.00	0.02	0.00	0.03	0.00
Ground-6 inches (0.00-0.16 m)	0.00	0.02	0.00	0.05	0.04	0.00	0.00	0.00	0.01	0.00	0.00	0.00
Sample size	29	60	14	19	99	51	69	61	177	89	40	81
Vertical overlap	0.69		0.74		0.80		0.84		0.78			
<b>Substrate-tactic category</b>												
Hawk	0.17 <sup>b</sup>	0.05	0.43	0.05	0.26	0.08	0.26	0.13	0.13	0.04	0.20	0.04
Hover-leaf	0.22	0.45	0.33	0.22	0.23	0.53	0.57	0.57	0.54	0.82	0.50	0.76
Hover-branch, trunk	0.13	0.50	0.24	0.72	0.23	0.33	0.07	0.28	0.21	0.14	0.17	0.19
Glean-leaf	0.26	0.00	0.00	0.00	0.19	0.00	0.05	0.02	0.05	0.00	0.07	0.01
Glean-branch, trunk		0.00	0.00	0.00	0.09	0.06	0.05	0.02	0.07	0.00	0.07	0.00
Sample size	24	52	36	18	66	35	63	58	167	80	32	70
Behavioral overlap	0.49		0.51		0.60		0.81		0.72			

<sup>a</sup> Height intervals are presented in feet with metric equivalents in parentheses.  
<sup>b</sup> Percent of maneuvers observed.

TABLE 4. Summation and component overlaps of American Redstarts and Least Flycatchers during the breeding cycle.

Overlaps	1973		1974			
	Nestling	Fledgling	Pre-incubation	Incubation	Nestling	Fledgling
Vertical	0.69	0.74	0.74	0.80	0.84	0.78
Horizontal	0.45	0.45	0.40	0.40	0.17 <sup>a</sup>	0.17 <sup>a</sup>
Composite food	0.47	0.50	0.58	0.78	0.70	0.69
Bill	0.97	0.97	0.97	0.97	0.97	0.97
Behavioral	0.49	0.52	0.60	0.80	0.72	0.72
Summation	0.54	0.56	0.57	0.66	0.57	0.55

<sup>a</sup> Low horizontal overlap values during latter half of 1974 breeding season result from departure of four unmated male Y-redstarts in the third week of June, before start of flycatcher nestling activity.

densities, and again in 1974, when both populations were considerably reduced in size. Thus horizontal spatial separation on a local scale is the most important method of ecological segregation. Two alternative mechanisms are evaluated below. Food differences (considered further in the Discussion) are of intermediate importance and vertical differences of least importance for ecological segregation.

#### HABITAT PARTITIONING

Two species that share a habitat or come into ecological contact locally may be separated horizontally by different habitat preferences or by some form of interspecific behavioral interaction. These two mechanisms are not mutually exclusive, because some kind of behavioral interaction could be an important proximate means of initiating or maintaining differential habitat preferences.

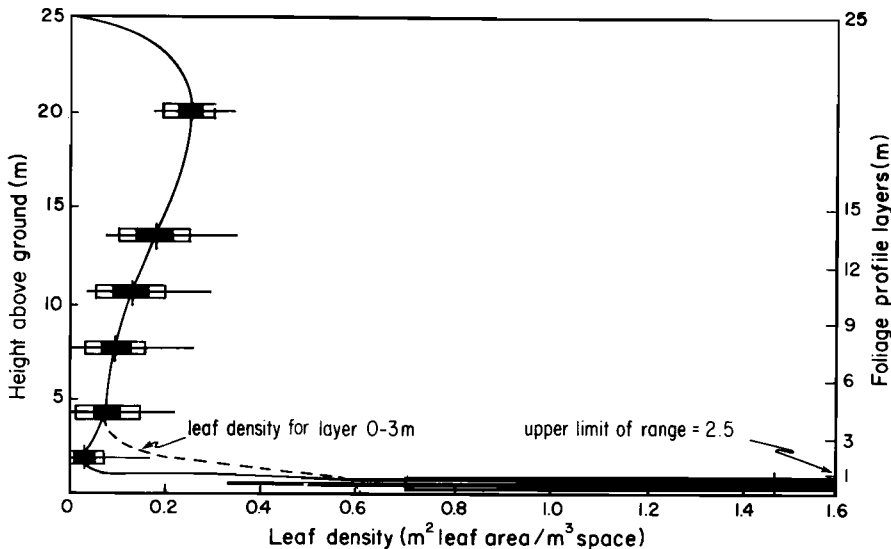


Fig. 3. Foliage density profile for entire study area. The mean, 95% confidence interval for the mean,  $\pm 1$  standard deviation, and range are indicated by vertical line, solid rectangle, open rectangle, and horizontal lines, respectively. The dashed line represents that curve estimated by treating the two lowest layers (0-3 m) as one layer. Curves are drawn by eye.



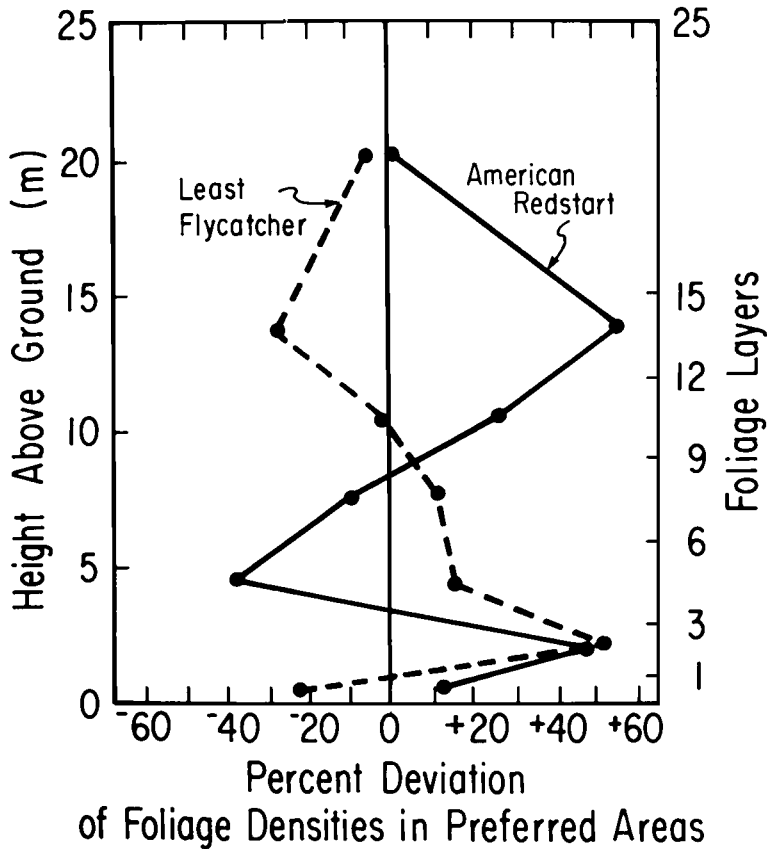


Fig. 4. Percent deviation of foliage densities in "preferred" American Redstart and Least Flycatcher habitats within the Hubbard Brook study area from actual foliage densities of the study area as a whole (Fig. 3).

*Habitat preferences.*—The study area was chosen as representative of northern hardwoods forests and for its homogeneity. Slight changes in slope and aspect do occur on the study site, especially near a small stream cutting across its northern end. One must look carefully, however, to see any systematic changes in vegetational structure associated with the topographic changes (see below). Some degree of patchiness results from tree falls, but this seems independent of other habitat characteristics.

The foliage profile for the entire study area (Fig. 3) is very similar to that of a Vermont deciduous forest used in the study of bird-species diversity by MacArthur and MacArthur (1961). Leaf densities gradually decrease from the canopy to the shrub layer and then increase dramatically where ground cover begins.

To determine if the birds perceived systematic habitat variation across the study area, comparisons were made using those seven (out of 20 total) foliage profile sample lines within each of the two species' "preferred" area (as described previously). The resulting profiles, displayed as percent deviation from the mean profile for the entire study area (Fig. 4—method after Cody 1974), show differences, especially in the foliage layers greater than 9 m. Because of considerable variability in foliage mea-

surements, however, the only foliage layer in which the two species' profiles differed significantly was at 12–15 m ( $P < 0.05$ , two-tailed  $t$ -test using equal variances).

Thus, the flycatcher occurs more frequently where the vegetation within preferred foraging heights is least dense, and the redstart vice versa (compare Figs. 2 and 4). Breckenridge (1956) found that openness (i.e. the relative absence of twigs and branches) beneath the canopy, at heights of approximately 3–9 m where most flycatchers occurred in his forest, best predicted their abundance. At Hubbard Brook, the 12–15 m layer appears to be most important to the Least Flycatcher, as most foraging (Fig. 2) and most nesting (mean = 13.7 m,  $n = 68$ ; Sherry, unpublished data) occur there. Habitat selection at Hubbard Brook is more complicated, however, than Breckenridge suggests. Flycatchers use a far broader range of heights than that occurring in this layer, the heights change significantly over the breeding season (Sherry 1975), and flycatchers do not actually prefer the least dense layers of vegetation available (compare Figs. 2 and 3). Redstarts forage extensively in this 12–15 m layer (Fig. 2), but their nesting heights are lower (mean = 5.1 m,  $n = 18$ ; Holmes, unpublished data).

Largely sympatric breeding ranges of these two species provide the potential for broad geographic interaction. The extent of co-occurrence in the same habitats on a geographic scale can be approximated from studies in the literature in which one or both species have been reported to be present in the same region. The habitat overlap or degree of syntopy can be measured with Cody's index of horizontal overlap (1974):

$$\text{overlap} = \frac{(\text{number of sites with both species})}{[(\text{number of sites with redstart}) \times (\text{number of sites with flycatcher})]^{1/2}}$$

For the redstart and Least Flycatcher, I calculated a habitat overlap of  $25/(79 \times 47)^{1/2} = 0.41$  from studies encompassing a broad geographic area including Wisconsin (Bond 1957, Beals 1960), Michigan (Hofslund, cited in MacQueen 1950), Ontario (Martin 1960), New York (Saunders 1936, Fawver 1950), Pennsylvania (Edeburn 1947), West Virginia (Fawver 1950), and New Hampshire (this study). Clearly the two species are substantially syntopic (cf. Rivas 1964) over their zone of sympatry.

Another kind of geographic evidence documents the habitat similarity of the two species. On a number of habitats used to study forest structure in Wisconsin, Bond (1957) studied how bird species responded to the habitat gradient as measured by a tree species ordination. The Least Flycatcher and redstart had very similar responses to the vegetation continuum (a gradient from disturbed xeric to mature mesic forest stands); importance values of both species peaked in the continuum midrange.

*Interspecific aggression.*—Overt aggression, which might serve to segregate two species spatially, does occur between redstarts and Least Flycatchers at Hubbard Brook (Tables 5 and 6). The values in these tables are minimal frequencies, as it is very difficult to identify both species involved in attacks, which occur quickly in areas of dense foliage. Even so, interspecific aggressive encounters were observed relatively frequently, and most involved Least Flycatcher attacks on redstarts and occasionally other species. In general, the amount of interspecific aggression appears to be roughly comparable to the amount of intraspecific aggression—given the difficulty of quantifying both types—at least after the period of territory establishment. I do not have data on interspecific strife during the arrival period in mid-May.

The data on interspecific aggression show that the flycatcher is socially dominant over other small bird species in the study area and over the redstart in particular. This aggression does not seem to be related to defense of personal space or nest site but may affect the horizontal use of space, especially by the subordinate species during the breeding period. I distinguish interspecific aggression from interspecific territoriality. The latter promotes hyper-dispersion of animals over the resource space, just as does intraspecific territoriality. Alternatively, if interspecific aggression is asymmetric, the subordinate species may have to increase the area it utilizes when it overlaps one or more individuals of the dominant species (see discussion of territory sizes and habitat utilization below). Other investigators have observed spatial separation, usually involving overt aggression between noncongeners whose territories were not mutually exclusive, among hummingbirds (Pitelka 1951), marsh wrens and blackbirds (Orians and Wilson 1964), flycatchers and sylviid warblers (Edington and Edington 1972), sylviid warblers in Mediterranean habitats (Cody and Walter 1976), flycatchers in the Rocky Mountains, USA (Eckhardt 1977), and other species (Cody 1974).

The mechanism effecting horizontal spatial separation of redstarts and Least Flycatchers is thus complex, involving both subtle differences in use of habitats and in interspecific aggression. I assume that aggression is adaptive in conferring upon the aggressor increased access to limited resources (Wilson 1971, MacArthur 1972). The occurrence of interspecific aggression between these species thus constitutes further evidence for an ongoing competition between them. Similar cases of interspecific aggression among other species have been observed to result in dominance hierarchies among presumed competitors (Morse 1976). Murray's alternative explanation (1971, 1976) for interspecific aggression involving mistaken identities cannot explain the interaction between the two species here, which represent very distinct families and which have no apparent similarities in plumage or vocalizations.

The results of this study, therefore, demonstrate that American Redstarts and Least Flycatchers are very similar ecologically during their breeding seasons. High overlaps in resource exploitation patterns do not in themselves demonstrate the existence of competition (Colwell and Futuyma 1971). However, the importance of competition is supported in this study by: 1) the complementarity of component overlaps, both seasonally and between years (Table 4); 2) abrupt spatial replacement of R-redstarts by flycatchers during the 1974 and 1975 breeding seasons (see Fig. 1c for 1974 pattern) on two parts of the study area where there were no habitat discontinuities; and 3) overt interspecific aggression that is not explainable by any known alternative hypotheses. Although I argue that competition influences access to or use of resources by at least one of the two species, the data do not fit conventional resource-partitioning models. An alternative interpretation, which, I argue, fits the data better, is developed below.

## DISCUSSION

In considering the adaptive strategies of insectivorous birds, Morse (1971b) suggested several ways in which species respond to temporal and spatial properties of their food resources and how these responses produce certain predictable patterns in their life history characteristics. The purpose of this part of the discussion is to develop the hypothesis that the action of the socially dominant Least Flycatcher affects the temporal and spatial properties of resource availability for the subordinate

TABLE 5. Aggressive interactions of American Redstarts and Least Flycatchers in the period following territory establishment and the fledging of young. The second and fourth columns contain the number of times the first and the second species (or group) initiated an encounter.

Interacting species	1973		1974	
	Number of attacks	Number initiated by first species/number initiated by second species	Number of attacks	Number initiated by first species/number initiated by second species
Redstart-redstart	2		9	
Redstart-Least Flycatcher	6	2/1	12	0/9
Redstart-other species <sup>a</sup>	0	0/0	5	0/4
Least Flycatcher-Least Flycatcher	18		21	
Least Flycatcher-other species <sup>b</sup>	4	3/0	6	6/0

<sup>a</sup> Other species: Red-eyed Vireo (*Vireo olivaceus*), Dark-eyed Junco (*Junco hyemalis*), Black-throated Blue Warbler (*Dendroica caerulescens*), and Black-throated Green Warbler (*Dendroica virens*).

<sup>b</sup> Other species: Red-eyed Vireo, Winter Wren (*Troglodytes troglodytes*), Ovenbird (*Seiurus aurocapillus*), Black-throated Blue Warbler, and Black-throated Green Warbler.

American Redstart. From the viewpoint of the subordinate species, the same environment should thus be less predictable than it would be for the dominant species, the consequence being divergence in life-history characteristics, given enough evolutionary time. Nine aspects of the life history of these two species are of particular interest here (Table 7).

The asymmetric interspecific aggression (Tables 5 and 6) was an initial clue that aspects of adaptive strategy differed. Morse (1974) found that a larger bird usually dominates a smaller, clearly the case for redstarts and Least Flycatchers. Morse (1974) also showed that socially subordinate species usually have broader niches than dominant ones (see also Miller 1967, and Colwell and Fuentes 1975) and sometimes behave more plastically because the dominant ones contribute to the unpredictability of the environment of subordinates. Niche breadths for redstarts and Least Flycatchers were compared using the eight foraging-height and five tactic-substrate categories from which overlaps were calculated. Niche breadths ( $B$ ) were calculated for the breeding stages in 1973 and 1974 using the MacArthur-Levins formula (Levins 1968):

$$B = 1 / \sum_{i=1}^n p_i^2$$

where  $n$  is the total number of categories and  $P_i$  is the proportion of observations for a species in category  $i$ . The results (Table 8) show no consistent difference

TABLE 6. Number of aggressive acts involving 6 pairs of American Redstarts observed by 6 observers during approximately 36 man-hours in the field in Hubbard Brook Forest on 2 days, 24 and 26 June 1975, during the late nestling stage.

Interacting species	Least Flycatcher or vireo aggressor	Redstart aggressor	Unknown aggressor
Redstart-redstart	0	0	4
Y redstart-Least Flycatcher	12	1	4
R redstart-Least Flycatcher	3	0	0
Redstart-Red-eyed Vireo	3	2	0

TABLE 7. Relative and absolute differences in adaptive strategies of American Redstarts and Least Flycatchers.

Characteristic	American Redstart	Least Flycatcher
Behavior	Subordinate	Dominant
Foraging niche breadth	Broader	Narrower
Foraging behavior plasticity	Greater	Lesser
Time of fledging young	Earlier (by 1 week)	Later
Bird size	Smaller (8.9 g)	Larger (10.5 g)
Territory size	Larger (0.43 ha)	Smaller (0.18 ha)
Breeding habitat breadth	Broader (approximately 2 times)	Narrower
Wintering range	Caribbean, Central and South America	Central America
Attainment of adult plumage	Delayed in males	Not delayed

between the two species in foraging-height breadth ( $P > 0.10$ , one-tailed Mann-Whitney  $U$ -test) but consistently greater "food" niche breadth for the redstart than for the flycatcher, by a factor of close to two ( $P < 0.005$ , one-tailed Mann-Whitney  $U$ -test). This broader use of tactic types and possibly substrates implies that redstarts utilize a broader range of foods.

Diet data, based on 32 redstart samples and 50 Least Flycatcher samples obtained from stomachs of collected birds and from live birds by use of an emetic (Holmes, unpublished data), support the theory of greater diet breadth of redstarts than of Least Flycatchers. Although interpretation of stomach-content data is often risky, the data are useful here to compare diets of similar-sized birds using similar insect prey. Both species take a wide variety of insect orders, suggesting high potential overlap. Diets are dominated by diptera, hymenoptera, and coleoptera (79% of 107 identifiable items taken by redstarts and 92% of 204 items taken by Least Flycatchers—in both cases in the Hubbard Brook Forest during the breeding season). The diet of redstarts is thus less dominated by these three orders. The redstart includes substantial numbers of homoptera (6%) and lepidoptera (9%) relative to the Least Flycatcher. Similarly, the redstart used significantly more lepidoptera larvae while foraging than did the Least Flycatcher (Sherry, unpublished data).

Morse (1974) states that the only unequivocal cases of subordinate species behaving more plastically than dominants derive from studies of mixed-species flocks of birds. The present study provides another example consistent with his argument. Redstarts are more plastic than flycatchers with regard to the within-season changes in foraging tactics and heights (Sherry 1975). Redstarts also show significant diurnal

TABLE 8. Niche breadths (see text for definition) for foraging behavior and foraging height categories during different breeding stages in 1973 and 1974.

Niche dimension	1973		1974			
	Nestling	Fledgling	Pre-incubation	Incubation	Nestling	Fledgling
Redstart						
Foraging behavior	4.76	2.85	4.60	2.49	2.78	3.04
Foraging height	3.86	4.52	3.72	1.57	2.96	4.25
Least flycatcher						
Foraging behavior	2.20	1.75	2.50	2.38	1.44	1.62
Foraging height	5.52	5.03	3.40	2.07	2.26	3.32

TABLE 9. Territory size statistics for Redstarts and Least Flycatchers during the breeding seasons 1972–1974.

Year	Mean area (ha) $\pm$ 1 SD	
	Redstart	Least Flycatcher
1972	0.40 $\pm$ 0.185 (n = 10)	0.14 $\pm$ 0.068 (n = 25)
1973	0.37 $\pm$ 0.189 (n = 9)	0.17 $\pm$ 0.002 (n = 24)
1974	0.54 $\pm$ 0.147 (n = 8)	0.29 $\pm$ 0.070 (n = 10)
Combined years	0.43 $\pm$ 0.185 (1.07 <sup>a</sup> )	0.18 $\pm$ 0.006 (0.45 <sup>a</sup> )

<sup>a</sup> Mean area in acres in parentheses.

variation in their use both of tactics and of foraging heights within a single habitat (Holmes et al. 1978), and their foraging tactics vary in different areas, e.g. gleaning in Maryland (Williamson 1971), more hawking than hovering in Maine (Morse 1973), and hovering in New Hampshire (this study, Table 3). Although there is less information about Least Flycatchers, they seem to employ hovering consistently in their breeding areas (Johnston 1971), suggesting that they are more stereotyped in foraging behavior than the redstart.

Therefore, the redstart, with its relatively broad niche, behavioral plasticity, and social subordinance relative to the Least Flycatcher, may differ from the flycatcher in using gaps and margins of niche space left vacant by such species as the Least Flycatcher, to the extent that such dominant species cannot efficiently monopolize all resources in an unpredictable environment. Predictions concerning other aspects of the life histories of the two species follow directly. If the size of a bird's feeding territory is related to food availability (Yeaton and Cody 1974, see also Wilson 1975 for a review of this topic), then the redstart should defend a larger territory than the Least Flycatcher, as the latter, and other dominant competitors, reduce the effective resource density of the former. Indeed, redstarts at Hubbard Brook utilized territories approximately twice the size of Least Flycatcher territories (Table 9) ( $P < 0.025$ , one-tailed significance probability,  $t$ -test assuming unequal variances;  $n = 27$  and  $59$  for redstart and Least Flycatcher, respectively), and the difference was significant all 3 years. This difference in territory sizes is especially surprising because it is opposite the result predicted from body sizes alone (see Schoener 1968a), and it is opposite that expected from the diet breadths, as the broader diet of the redstart should allow smaller territories.

Greater food-niche breadth and behavioral plasticity should preadapt a subordinate species to use effectively a greater range of habitats. Periodic, but not continual, exclusion of subordinates from the richest habitats by dominants should also promote a greater habitat breadth of subordinates, if not promoting differential habitat selection. The redstart was consistently observed in almost twice as many habitats as the Least Flycatcher (79 versus 47 in total for the redstart and Least Flycatcher, respectively) in those studies, cited above, that were used to determine habitat overlap within the sympatric range of the two species.

Cody (1974) has pointed out several cases in which related species breed at different times of year, presumably to reduce ecological overlap. Temporal resource partitioning, however, is generally considered of minimal importance in bird community structure (Ricklefs 1966). If one part of the breeding season is particularly important in terms of food availability relative to need, then the staggering of nesting activities by even a week in synchronously breeding populations could be of impor-

tance. In both 1973 and 1974 redstarts at Hubbard Brook fledged young a week earlier on average than did Least Flycatchers (Sherry, unpublished data). For a socially subordinate species, fledging young a week early could considerably reduce interference from an aggressive competitor at a critical time in the breeding cycle, or it could indicate preference for insects that appear earlier in the season. Both hypotheses could indicate underlying competition.

Finally, the behavioral subordination of the redstart at Hubbard Brook suggests a hypothesis for its delayed plumage maturation ("sexual bimaturism," Wilson 1975). Younger male (Y) redstarts often occur in less optimal habitats and breed less successfully than R-redstarts (Ficken and Ficken 1967, Morse 1973, Howe 1974). Observations from this study suggest that habitat of relatively poor quality may be just that habitat where a socially dominant competitor is found. Interference competition may constitute enough of a breeding disadvantage for Y-redstarts, which overlap Least Flycatchers more than R-redstarts, that there is selection for delaying reproduction until the chances of obtaining a more optimal territory are improved. During the nestling stage of breeding in 1975, several Y-redstart males were more harassed by flycatchers and spent more time singing and far less feeding nestlings than nearby R-redstarts (Holmes et al. 1978, Holmes and Sherry, unpublished data). Though inferential, this hypothesis is worth mentioning here, because it is novel yet consistent with other explanations of sexual bimaturism (e.g. Ficken and Ficken 1967).

The interrelatedness of adaptive strategies hypothesized above (Table 7) for the nine relative differences between redstarts and Least Flycatchers may be circumstantial. Three striking parallels in many of the same patterns in three other species complexes, however, provide support for the generality and interrelatedness of these patterns. First, the Yellow-rumped Warbler (*Dendroica coronata*) in New England forests has larger territories, larger food niche breadth, greater habitat breadth, and greater behavioral plasticity than its sympatric congeners (MacArthur 1958; Morse 1971a, 1976); it also is behaviorally subordinate to its coexisting congeners during the breeding season. Second, the two abundant flycatching species in a Welsh woodland, the European Redstart (*Phoenicurus phoenicurus*, Turdidae) and the Pied Flycatcher (*Ficedula hypoleuca*, Muscicapidae) have similar niche-exploitation patterns, involving hawking and hovering for insects at tips of foliage and use of similar heights, subtle differences in habitat preference, and considerable interspecific aggression where territories overlap. The European Redstart defends significantly larger territories and feeds nestlings at least a week earlier than did the slightly heavier Pied Flycatcher (Edington and Edington 1972). And third, among *Sylvia* warblers breeding in chaparral habitats in Sardinia there was extensive but only partial spatial separation mediated by convergent vocalizations and interspecific aggression (Cody and Walter 1976). *S. melanocephala*, furthermore, was more a habitat generalist and broad-niched species than any other syntopic congeners, and it defended significantly larger territories than did its congeners. Cody and Walter regard *S. melanocephala* as a dominant species, but why a dominant species would enlarge its territories in the presence of more specialized competitors, if dominance implies an ability to exclude competitors from shared resources, is difficult to understand, and further work on this system appears to be necessary.

The null hypothesis against which to judge the strength of these parallels in guild structure is that competition is unimportant between these species on the breeding grounds, and therefore different aspects of species' niche-exploitation strategies are independent. The findings detailed above concerning parallels in at least five or six

different aspects of life-history patterns argue strongly for some common process and against the null hypothesis. I conclude that many aspects of species' life history (Table 7) may be related in coherent patterns or species-specific strategies. This divergence in strategy within guilds is in turn related to the asymmetric interference competition of the species involved. These relationships are particularly apparent among flycatching birds, as demonstrated in the present study.

Two alternative hypotheses for the redstart-Least Flycatcher interaction are that ongoing competition leads to resource partitioning or that competition, when and if important, acts via infrequent "bottlenecks" whose occurrence is usually undetected in short-term studies (Wiens 1977). I reject the first hypothesis, as the redstart apparently has broader food, behavioral, and habitat range than the Least Flycatcher—quite a different pattern from resource partitioning. The second hypothesis is not consistent with the apparent year-to-year interaction of the species involving interference aggression at the level of individual territories. Rather, the intensity of competition varies from year to year, considering the annual variation in population sizes, distribution patterns, and component overlaps observed at Hubbard Brook. The effect of periodic "bottlenecks" cannot be evaluated from the data presented here, except to predict that a severe disturbance should differentially affect the two species, given their differences in life-history parameters.

#### THE FLYCATCHER GUILD AND COMMUNITY STRUCTURE

Hespenheide (1971) generalized from a study of birds feeding on flying insects that any homogeneous temperate habitat should contain at most two species of flycatchers (a small one and possibly a large one) and that small flycatchers should partition resources spatially, i.e. by use of different habitats. The results of this study suggest a refinement of his generalization. First, it is important to point out the variation in foraging behavior among temperate Tyrannidae (salliers, hoverers, gleaners, and pouncers that consume a range of prey sizes). Many temperate *Empidonax* flycatchers, considered by Hespenheide (1971), take more prey from vegetation than is generally recognized. Further, the redstart should certainly be considered a "flycatcher" on the basis of its behavioral and morphological similarity to the Least Flycatcher. The present study shows how two small "flycatcher" species may coexist in the same habitat, and although the separation may still be spatial, as predicted by Hespenheide, the precise nature of the spatial segregation may be complex. Other temperate forests contain similar species-pairs as that at Hubbard Brook; for example, the Welsh woodland studied by Edington and Edington (1972) noted above and the "temperate" oak forests in the highlands of Costa Rica (Sherry, pers. observation; Stiles, pers. comm.). At the latter site, the species (*Empidonax atriceps*, Tyrannidae, and *Myioborus torquatus*, Parulidae) have very similar bill morphologies and body sizes and forage to a large extent by hovering in vegetation (Sherry, unpublished data).

The differences in redstart and Least Flycatcher adaptive strategy likely facilitate syntopic coexistence in a variable environment. Similarly, MacArthur (1958) concluded that the Yellow-rumped Warbler could coexist with other foliage-gleaning parulids because of its broad-niched strategy. Thus, within a guild species may differ not only in the absolute resources used but in their patterns of resource utilization and how they fit together in a community context. If one must reduce species' competitive interactions to a set of resource-utilization curves within niche space,



it is not just the positions but the dispersion characteristics of these curves as well that are important. There is little empirical or theoretical discussion in the literature of such differences in resource-utilization strategies, even though the basic pattern of inclusive niches (Miller 1967, Morse 1974, Colwell and Fuentes 1975) is widespread.

Because species representing a range of niche breadths characterize many guilds, it is important to ask what implications this pattern has for community organization. Does the range of breadths actually facilitate coexistence of more species than would otherwise be possible? If the presence in a guild of a broad-niched species has any effect of damping fluctuations of resources available to more specialized species, this might enhance the stability of the interaction. How is the range of strategies within a guild related to the seasonality and predictability of an environment? How do these differences in strategy relate to differences in opportunism or different responses to disturbance? Diamond's (1975) treatment of island birds is notable in that the range of strategies from super-tramp to high-s species (related to increases in competitive ability) is common to all his guilds, as implied by his classification of incidence functions. I suggest that this range of strategies within guilds in unpredictable environments deserves further attention.

#### ACKNOWLEDGMENTS

For financial support I acknowledge a Mellon Foundation grant through the Dartmouth Outing Club and a National Science Foundation grant to R. T. Holmes. Fieldwork in the Hubbard Brook Forest was possible through the cooperation of R. S. Pierce and the Northeast Forest Experiment Station, Upper Darby, Pennsylvania. My ideas have benefited from discussions with S. Bennett, C. Black, J. Ebersole, R. Hutto, and J. Wright, and I thank M. L. Cody, H. A. Hespenheide, R. T. Holmes, D. H. Morse, F. G. Stiles, J. Wright, and two anonymous reviewers for many helpful suggestions on various drafts of the manuscript. Finally I thank R. T. Holmes for his support and stimulation through all stages of this study.

#### LITERATURE CITED

- ABLE, K. P., & B. R. NOON. 1976. Avian community structure along elevational gradients in the northeastern United States. *Oecologia* 26: 275-294.
- AMERICAN ORNITHOLOGISTS' UNION. 1957. Check-list of North American birds. Fifth ed. Baltimore, Maryland, American Ornithologists' Union.
- BEALS, E. W. 1960. Forest bird communities in the Apostle Islands of Wisconsin. *Wilson Bull.* 72: 156-181.
- BOND, R. R. 1957. Ecological distribution of birds in the upland forest of southern Wisconsin. *Ecol. Monogr.* 27: 351-384.
- BRECKENRIDGE, W. J. 1956. Measurements of the habitat niche of the Least Flycatcher. *Wilson Bull.* 68: 47-51.
- CODY, M. L. 1974. Competition and the structure of bird communities. Princeton, New Jersey, Princeton Univ. Press.
- , & H. WALTER. 1976. Habitat selection and interspecific interactions among Mediterranean sylviid warblers. *Oikos* 27: 210-238.
- COLWELL, R. K., & E. R. FUENTES. 1975. Experimental studies of the niche. *Ann. Rev. Ecol. Syst.* 6: 281-310.
- , & D. J. FUTUYMA. 1971. On the measurement of niche breadth and overlap. *Ecology* 52: 567-576.
- DIAMOND, J. 1975. Assembly of species communities. Pp. 342-444 *in* Ecology and evolution of communities (M. L. Cody and J. M. Diamond, Eds.). Cambridge, Massachusetts, Harvard Univ. Press.
- ECKHARDT, R. C. 1977. Optimal foraging and adaptive syndromes in a community of insectivorous birds. Unpublished Ph.D. dissertation, Ithaca, New York, Cornell University.

- EDEBURN, R. M. 1947. A study of the breeding distribution of birds in a typical upland area. Proc. West Virginia Acad. Sci. 18: 34-47.
- EDINGTON, J. M., & M. A. EDINGTON. 1972. Spatial patterns and habitat partition in the breeding birds of an upland wood. J. Anim. Ecol. 41: 331-357.
- FAWVER, B., JR. 1950. An analysis of the ecological distribution of breeding bird populations in eastern North America. Unpublished Ph.D. dissertation, Urbana, Illinois, University of Illinois.
- FICKEN, M. S., & R. W. FICKEN. 1962. The comparative ethology of the wood warblers: a review. Living Bird 1: 103-121.
- , & ———. 1967. Age-specific differences in the breeding behavior and ecology of the American Redstart. Wilson Bull. 79: 188-199.
- HESPENHEIDE, H. A. 1971. Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. Ibis 113: 59-72.
- HOLMES, R. T., T. W. SHERRY, & S. F. BENNETT. 1978. Diurnal and individual variability in the foraging behavior of American Redstarts (*Setophaga ruticilla*). Oecologia 36: 141-149.
- , & F. W. STURGES. 1975. Bird community dynamics and energetics in a northern hardwoods ecosystem. J. Anim. Ecol. 44: 175-200.
- HOWE, H. F. 1974. Age-specific differences in habitat selection by the American Redstart. Auk 91: 161-162.
- JOHNSTON, D. W. 1971. Niche relationships among some deciduous forest flycatchers. Auk 88: 796-804.
- LEVINS, R. Evolution in changing environments. Princeton, New Jersey, Princeton Univ. Press.
- LIKENS, G. E., & F. H. BORMANN. 1972. Nutrient cycling in ecosystems. Pp. 25-67 in Ecosystem structure and function (J. A. Wiens, Ed.). Corvallis, Oregon, Oregon State Univ. Press.
- MACARTHUR, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39: 599-619.
- . 1972. Geographical ecology. New York, New York, Harper & Row.
- , & H. S. HORN. 1969. Foliage profile by vertical measurements. Ecology 50: 802-804.
- , & J. W. MACARTHUR. 1961. On bird species diversity. Ecology 42: 594-600.
- MACQUEEN, R. M. 1950. Territory and song in the Least Flycatcher. Wilson Bull. 62: 195-205.
- MARTIN, N. D. 1960. An analysis of bird populations in relation to forest succession in Algonquin Provincial Park, Ontario. Ecology 41: 126-140.
- MAY, R. M. 1975. Some notes on estimating the competition matrix,  $\alpha$ . Ecology 56: 737-741.
- MILLER, R. S. 1967. Pattern and process in competition. Adv. Ecol. Res. 4: 1-74.
- MORSE, D. H. 1971a. The foraging of warblers isolated on small islands. Ecology 52: 216-228.
- . 1971b. The insectivorous bird as an adaptive strategy. Ann. Rev. Ecol. Syst. 2: 177-200.
- . 1973. The foraging of small populations of Yellow Warblers and American Redstarts. Ecology 54: 346-355.
- . 1974. Niche breadth as a function of social dominance. Amer. Natur. 108: 818-830.
- . 1975. Ecological aspects of adaptive radiation in birds. Biol. Rev. 50: 167-214.
- . 1976. Variables affecting the density and territory size of breeding spruce-woods warblers. Ecology 57: 290-301.
- MURRAY, B. G., JR. 1971. The ecological consequences of interspecific territoriality in birds. Ecology 52: 414-423.
- . 1976. A critique of interspecific territoriality and character convergence. Condor 78: 518-525.
- ORIAN, G. H., & M. F. WILLSON. 1964. Interspecific territories of birds. Ecology 45: 736-745.
- PEARSON, D. L. 1975. The relation of foliage complexity to ecological diversity of three Amazonian bird communities. Condor 77: 453-466.
- PITELKA, F. A. 1951. Ecologic overlap and interspecific strife in breeding populations of Anna and Allen hummingbirds. Ecology 32: 641-661.
- PRIMACK, R. B., & H. F. HOWE. 1975. Interference competition between a hummingbird (*Amazilia tzacatl*) and skipper butterflies (Hesperiidae). Biotropica 7: 55-58.
- RICKLEFS, R. E. 1966. The temporal component of diversity among species of birds. Evolution 20: 235-242.
- RIVAS, L. R. 1964. A reinterpretation of the concepts "sympatric" and "allopatric" with proposal of the additional terms "syntopic" and "allotopic." Syst. Zool. 13: 42-43.
- ROOT, R. B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecol. Monogr. 37: 317-350.

- SAUNDERS, A. A. 1936. Ecology of the birds of Quaker Run Valley, Allegheny State Park, New York. N.Y. State Mus. Handbook 16: 1-174.
- SCHOENER, T. W. 1968a. Sizes of feeding territories among birds. *Ecology* 49: 123-141.
- . 1968b. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49: 704-726.
- SHERRY, T. W. 1975. Foraging behavior and niche relationships of breeding American Redstarts (*Setophaga ruticilla*) and Least Flycatchers (*Empidonax minimus*): the flycatcher guild in a New England hardwoods ecosystem. Unpublished M.S. thesis, Hanover, New Hampshire, Dartmouth College.
- TERBORGH, J., & J. S. WESKE. 1975. The role of competition in the distribution of Andean birds. *Ecology* 56: 562-576.
- WILLIAMSON, P. 1971. Feeding ecology of the Red-eyed Vireo (*Vireo olivaceus*) and associated foliage-gleaning birds. *Ecol. Monogr.* 41: 129-152.
- WIENS, J. A. 1977. On competition and variable environments. *Amer. Sci.* 65: 590-597.
- WILSON, E. O. 1971. Competitive and aggressive behavior. Pp. 181-217 in *Man and beast: comparative social behavior* (J. F. Eisenberg and W. Dillon, Eds.). Washington, D.C., Smithsonian Institution Press.
- . 1975. *Sociobiology: the new synthesis*. Cambridge, Massachusetts, Belknap Press.
- YEATON, R. I., & M. L. CODY. 1974. Competitive release in island Song Sparrow populations. *Theor. Popul. Biol.* 15: 42-58.