HABITAT SELECTION BY BREEDING AMERICAN REDSTARTS IN RESPONSE TO A DOMINANT COMPETITOR, THE LEAST FLYCATCHER

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Abstract.—Through natural population changes and experimental field removals, we tested the hypothesis that Least Flycatchers (*Empidonax minimus*) restrict habitat use by socially subordinate American Redstarts (*Setophaga ruticilla*). On a 10-ha site 2-yr-and-older (ASY), but not yearling (SY), male redstarts avoided the sector occupied by flycatchers from 1975 to 1980, but preferred this sector from 1981 to 1985 when flycatchers were absent. Vegetation changed subtly on the site but could not account for the sudden shift in redstart settlement pattern. On 6 4-ha sites ASY male redstarts were most abundant in years of Least Flycatcher absence. On the 5 4-ha sites from which Least Flycatchers either disappeared independently or were removed experimentally between 1981 and 1984, redstart abundance increased on four and remained constant on the fifth; on three control areas redstart numbers declined during the same period. Least Flycatchers recolonized one removal site, and ASY redstart abundance subsequently declined. SY male redstart abundance varied inversely with that of ASY male redstarts. We conclude that flycatchers influenced the distribution of ASY male redstarts directly, and that of SY males indirectly, more than either vegetation structure or other habitat characteristics. At no spatial scale examined, however, did total redstart abundance (ASY + SY) vary inversely with that of Least Flycatchers; in fact, their total abundances correlated positively at a regional scale.

   These findings, combined with a model for asymmetric competition for mutually preferred habitat (Pimm et al. 1985, Rosenzweig 1985), illustrate how a socially dominant competitor could lead to a broadening rather than a narrowing of the habitat breadth of a subordinate species. We show that competitor species abundances need not vary inversely and that age classes may be affected differentially. This species interaction illustrates subtleties and complexities of how competition can modify avian habitat selection. *Received 2 September 1987, accepted 22 January 1988.*

Interspecific competition is widely believed to restrict the range of habitats or resources exploited by many species (e.g. Svardson 1949, Connell 1983). If each species reduces the other's abundance under different circumstances, two species should vary inversely in abundance in one habitat over time, or across an array of habitats at a particular time. Avian biologists in particular have frequently interpreted negative correlations in abundance and replacements along habitat gradients as evidence for interspecific competition (Svardson 1949, MacArthur 1972, Cody 1974, Terborgh and Weske 1975, Diamond 1978, Noon 1981, Mountainspring and Scott 1985, Grant 1986). Recent experimental studies, especially those involving the removal of individuals of one or more putatively competing species, have confirmed that interspecific competition for habitat occurs regularly in a variety of bird species (Mewaldt 1964, Davis 1973, Williams and Batzli 1979, Dhondt and Eyckerman 1980, Hogstedt 1980, Reed 1982, Garcia 1983, Alatalo et al. 1985).

   Other investigators recorded no negative correlations between densities, and concluded that species often respond independently to structural and floristic features of their environment (Wiens 1977, Rotenberry and Wiens 1980, Wiens and Rotenberry 1981, Collins et al. 1982, James and Boecklen 1984, James et al. 1984). These findings have been interpreted as evidence that species are distributed independently and are not strongly influenced by interspecific competition. The contrasting results between these two types of studies have contributed to the recent controversy concerning the relative importance of competition in structuring communities (Strong et al. 1984, Connor and Simberloff 1986).

   We examined the breeding-season interaction and habitat-use pattern of two species that appear to compete but that are positively rather

than negatively correlated in their spatial distributions. The Least Flycatcher (*Empidonax minimus*) and the American Redstart (*Setophaga ruticilla*) are locally abundant and widespread in temperate deciduous forests of North America. Although in different passerine suborders, they have converged on a "flycatcher" niche (Sherry 1979, Bennett 1980). Interspecific aggression, with the flycatcher dominating most interactions (Holmes et al. 1978, Sherry 1979, Procter-Gray and Holmes 1981); complementary distributions of the flycatcher and older male redstarts (Sherry 1979); and other ecological similarities suggested that these two species compete for habitat, and ultimately for food (Sherry 1979). An alternative explanation for the complementary spatial distribution is that they respond differentially to local vegetation. In fact, these two species do respond to vegetation gradients within their breeding habitats (Bond 1957, Sherry and Holmes 1985).

We used a combination of natural population changes and experimental removals of Least Flycatchers from multiple forest sites to test the hypothesis that Least Flycatchers, and not just vegetation characteristics, constrain the distribution of breeding American Redstarts. Then, using Rosenzweig's (1985; Pimm et al. 1985) habitat-selection model, we discuss alternative outcomes of interspecific competition. Finally, we discuss the problems of detecting competition in the field that result from the diversity of population responses to heterogeneous habitats and to each other.

STUDY AREA AND METHODS

Our studies were conducted in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire. Seven study sites (Fig. 1) were located on a south-facing slope between 400 and 600 m elevation within an approximately 6-km² section of continuous forest, which includes parts of several watersheds and stream valleys. The vegetation is primarily second-growth northern hardwoods, 70–75 yr old. American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), and occasional white ash (*Fraxinus americana*) are the dominant trees of the area, particularly on richer soils and warmer slopes. Along the relatively cool, moist stream channels and on ridges with shallower and rockier soils, yellow birch is more frequent, as are patches of red spruce (*Picea rubrum*), balsam fir (*Abies balsamea*), and eastern hemlock (*Tsuga canadensis*). The understory and shrub layers contain striped and mountain maple (*A. pensylvanicum* and *A. spicatum*), hobblebush (*Vi-*
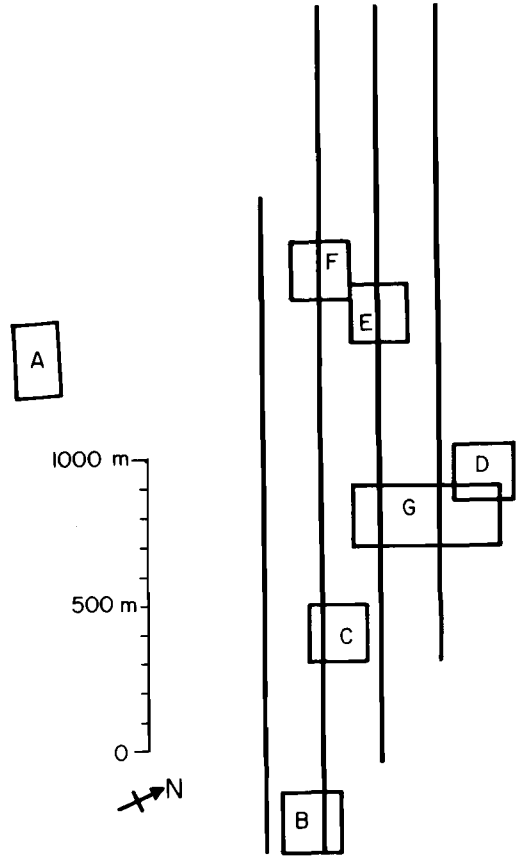

Fig. 1. Size and location of study sites in the Hubbard Brook Experimental Forest. Lines represent transects along which Sherry and Holmes (1985) quantified vegetation patterns and dispersion of the common bird species. The arrow indicates the direction of magnetic north, which is 16°10' counter-clockwise from true north.

burnum alnifolium), ferns (primarily *Dryopteris spinulosa*), various herbs, *Lycopodium* spp., and seedlings and saplings of the major tree species. Vegetation in the area covered by the four transect lines, A–D (henceforth the "transect area"; Fig. 1), and the habitat-use and dispersion patterns of the commonest bird species, were described quantitatively by Sherry and Holmes (1985). Holmes and Sturges (1975) and Holmes et al. (1986) described the avifauna of the 10-ha study site, G (Fig. 1), between 1969 and 1984, and Holmes et al. (1986) described vegetational changes on the site for the same period.

In May 1981 we selected 6 sites within continuous northern hardwoods forest and gridded them with flagging at 50-m intervals. Site A was 3.75 ha (250 × 150 m), and sites B–F were 4 ha (200 × 200 m). For convenience we refer subsequently to sites A–F as "4-

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ha sites." A seventh site, G, was the 10-ha census plot used by Holmes and Sturges (1975) and Holmes et al. (1986) in their long-term studies of bird populations at Hubbard Brook (Fig. 1).

In 1981 sites A–E each contained 6–13 Least Flycatcher territories (see Results), and most were surrounded by additional flycatcher territories. The patchy dispersion of Least Flycatcher territories at Hubbard Brook (Sherry and Holmes 1985) determined the size and location of these sites. In 1982 sites A and B were chosen as experimental sites because of their accessibility. We removed all singing male Least Flycatchers starting shortly after their arrival in mid-May, and repeated the procedure in 1983. Male removals resulted in no females settling, and experimental sites remained free of flycatchers throughout the breeding period, until 1985 (see below). We censused redstarts and flycatchers on all six 4-ha sites from 1981 through 1984, and also on site B from 1985 to 1987. Sites C–E contained both species and served as unmanipulated controls for the effects of flycatchers on redstarts over time. Site F contained only redstarts and provided a control for temporal changes in redstarts independent of any flycatcher influences. Site G also served as a control because no Least Flycatchers were present during the period 1981–1984, except for half of one male's territory in 1981 (site D, where it overlapped site G, Fig. 1). Between 1981 and 1984 we also censused redstarts in a 6-km² area of northern hardwoods forest. This transect area (Sherry and Holmes 1985) provided a third (and by far the largest) control on changes in redstart abundance and age structure. Least Flycatchers occupied only a small percentage of this area.

During the study Least Flycatchers on 3 sites (C–E) declined dramatically or disappeared altogether for reasons independent of our activities (see Holmes et al. 1986). Least Flycatchers had declined regionally since the late 1960's, based on U.S. Fish and Wildlife Service–coordinated Breeding Bird Surveys in New Hampshire ($P < 0.001$; R. A. Quinn, B. L. Noon, and S. Droege pers. comm.). This suggested some ecological factor(s) were affecting flycatcher populations over a broader geographic scale than our study area. We consider the sites from which flycatchers disappeared as additional "experimental" treatments for the effect of Least Flycatchers on redstart habitat use.

All observations were made by us and by experienced assistants. Observers rotated among sites to minimize bias. We censused during at least 4 days of clear weather per season on each of the smaller sites (the 10-ha site received more thorough coverage for all breeding birds; see Holmes et al. 1986). We concentrated our observations in the first 3 weeks of June, during the nest-building, incubation, and nestling stages of the breeding cycle.

Census methods were consistent between sites and years, but some details differed for the two species. For both species we located an individual bird, and

recorded on a map all movements within its territory until either the bird was lost from sight or its rate of using new areas declined (which usually occurred within 30 min). Simultaneously, the locations of countersinging redstarts were marked on the map. These neighbors subsequently were followed and mapped. We moved in this manner throughout the study site, generally from 0630 to 1200 EDT, during good weather. We mapped the locations and activities of males even when they extended beyond a site boundary to determine the fraction (to the nearest quarter) of each territory located on the gridded site. We found many nests, particularly of Least Flycatchers, which helped corroborate density estimates. We compiled all census and nest information for a breeding season, and estimated territory boundaries by encompassing all observations of each individual male. For redstarts we noted whether the bird was a yearling or older male (determined by plumage; see Ficken and Ficken 1967, Rohwer et al. 1983). We refer subsequently to yearling and 2-yr-and-older male redstarts, respectively, as SY (second-year) and ASY (after-second-year) males. This corresponds to "Y" and "R" males, respectively, of Sherry (1979). Because Least Flycatchers have smaller territories than redstarts and males sing intensively from a few song perches at dawn (MacQueen 1950, Sherry 1979), we obtained additional censuses of them starting at first light (about 0430 EDT). We systematically walked all interior lines in a site at a rate of approximately 50 m/6 min, using the 50-m grid as a reference, and mapped the locations of singing males, especially those heard simultaneously.

We measured foliage-density profiles on site G in 1972–1973, and again in the same locations in 1982, following the methods of MacArthur and Horn (1969) as modified by Sherry (1979). Mean foliage-density profiles were calculated from six sample lines (each of which had six sample stations; see Sherry 1979) spaced regularly throughout the area. Bird "preferences" for parts of this area were defined operationally by the number of years grid intersections (at 50-m intervals) were overlapped by, or touched a territory of a particular species or age class of birds.

RESULTS

Correlations in abundance.—Abundances of redstarts (SY and ASY males pooled) and Least Flycatchers on the 10-ha site (G) over 17 yr (1969–1985) were positively correlated ($r = 0.20$; based on data of Holmes et al. 1986, and unpubl. data). From 1972 (when we first distinguished ASY from SY redstarts on this site) to 1985, Least Flycatcher abundance was correlated positively with that of ASY males ($r = 0.33$) and negatively with that of SY males ($r = -0.19$). Although none of these correlations was statistically sig-

nificant ($P > 0.05$), these two species were positively and significantly correlated at greater spatial scales. For example, their abundances were significantly positively correlated ($r = 0.56$, $P < 0.01$) among 46 states and provinces in which at least one species occurred regularly (on roadside censuses; Robbins et al. 1986). Therefore, because of the lack of any strong negative relationship, and because of a significant positive relationship over some spatial scales, covariation in abundances of these two species is inconsistent with a traditional criterion for competition.

Natural population changes on the 10-ha site G. — Between 1975 and 1980 the number of Least Flycatcher territories on site G ranged from 7.5 to 17 ($\bar{x} = 12.6$; see Holmes et al. 1986). In 1981 only half of one territory overlapped, and from 1982 to 1985 there were no flycatchers on or adjacent to the site. We therefore considered settlement patterns of ASY and SY redstarts on this site during periods when at least 7.5 flycatcher territories were present (1975–1980) and when essentially no flycatchers were present (1981–1985).

Between 1975 and 1980 Least Flycatchers settled consistently on site G in a diagonal swath approximately 250 m wide in the northern end of the study area (Fig. 2A). This was the same area the species occupied most frequently before 1975 (Sherry 1979). ASY redstarts settled most often outside the flycatcher-occupied area (Fig. 2B). Yearling redstarts were rarely found where ASY redstarts were most common, but they occupied areas with Least Flycatchers (Fig. 2C). The same pattern was observed before 1975 (Sherry 1979). In the absence of flycatchers (1981–1985), ASY redstarts settled throughout the site, but most often in the part formerly occupied by flycatchers (Fig. 2D). If we define "preference" simply by the frequency with which an area is settled, ASY redstarts clearly preferred the same areas previously occupied by flycatchers (Fig. 2A and D). This is shown quantitatively by a positive correlation in the number of years ASY redstarts occupied the same grid intersections in 1981–1985 that flycatchers occupied in 1975–1980 ($r = 0.49, P \ll 0.01$; based on data from all 55 grid intersections in Fig. 2A and D). During 1981–1985 SY males settled most often in the southern end of the site, away from ASY redstart concentrations (Fig. 2E). The patterns strongly support the hypothesis that Least Flycatchers directly kept ASY redstarts from
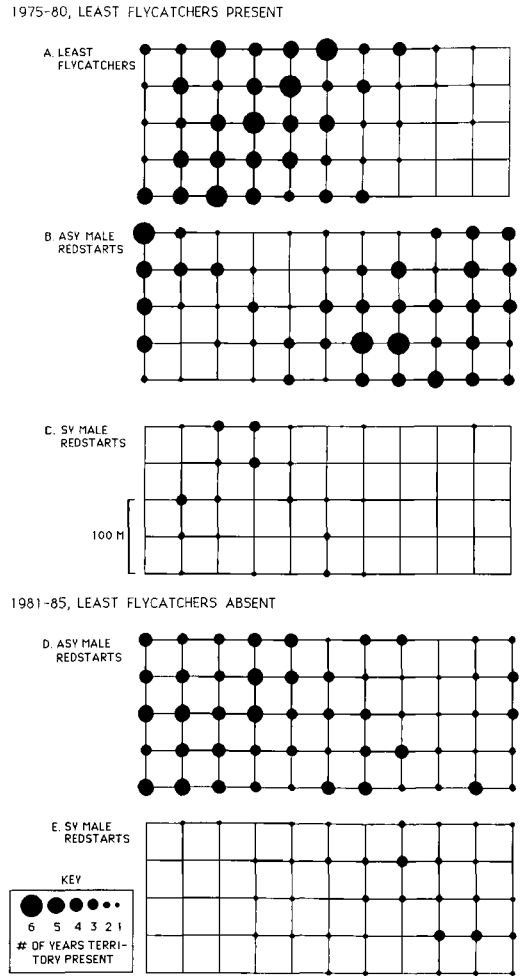

Fig. 2. Distribution of Least Flycatcher and American Redstart males on 10-ha site G. (A) Least Flycatchers, (B) ASY redstarts, and (C) SY redstarts during 1975–1980, when flycatchers were present; (D) ASY redstarts and (E) SY redstarts during 1981–1985, when flycatchers were absent. The circles indicate by size (see key) how many breeding seasons each grid intersection point overlapped a territory of the designated species or age class.

settling in otherwise preferred habitat, and that behaviorally subordinate SY redstarts in turn settled wherever ASY redstarts were absent.

Absolute abundances of the two species did not show as clear a pattern as the spatial distribution patterns on site G. During 1975–1985 the total number of territories of redstarts on the site fluctuated dramatically (range = 7–22), but with little net decline, whereas Least Flycatchers declined to near zero by 1981 and were
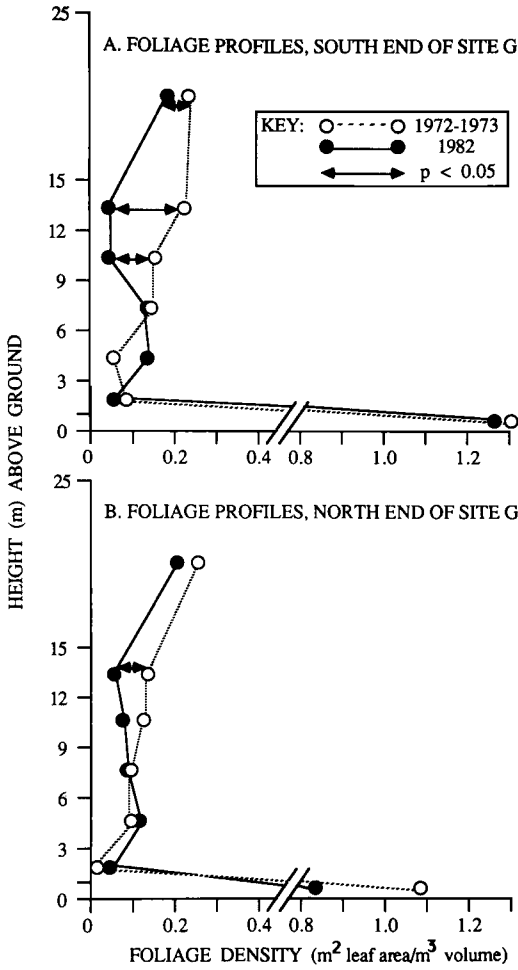
Fig. 3. Foliage profiles (foliage density as a function of height above ground) measured in 1972–1973 and again in 1982 in the northern (flycatcher-preferred) sector and southern (ASY redstart-preferred) sector of site G. "Preferred" sites were defined as grid intersections overlapped in at least 5 seasons by territories of flycatchers or ASY redstarts during 1975–1980 (based on Fig. 2).

Fig. 4. Temporal changes in occupancy of site G by Least Flycatchers and American Redstarts, 1975–1985, given by percentage of preferred grid intersections (see legend of Fig. 3) overlapped by flycatcher or redstart territories.

absent thereafter (see data of Holmes et al. 1986 for abundances on this site through 1984; in 1985, 13.5 redstarts held territories, but no Least Flycatchers).

An alternative explanation for the observed shifts in redstart distribution patterns on site G is that redstarts were responding to vegetation changes, and not to the sudden loss of flycatchers. If this occurred, then redstart settlement patterns should have paralleled vegetation changes both spatially and temporally. Subtle
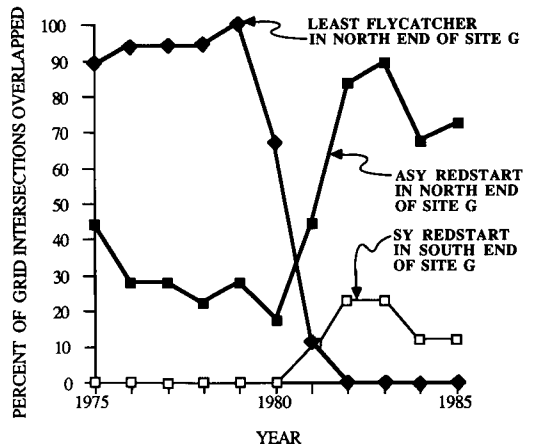
vegetation changes have occurred on site G since the early 1970's (Holmes et al. 1986). Specifically, foliage density decreased slightly in the canopy and increased in the understory primarily as a result of large treefalls. Such treefalls are a normal part of late successional processes that tend to equalize leaf densities over all foliage layers in northern hardwood forests (Aber 1979). These vegetation changes occurred over the entire site, however, and not just in the northern sector (Fig. 3), as would be required to explain why ASY abundance increased there at the same time as it decreased elsewhere in the area. Moreover, these vegetation changes were gradual, and not abrupt between 1980 and 1981 (Holmes and Sherry pers. obs.). By contrast, distribution patterns of flycatchers and redstarts changed abruptly and synchronously on flycatcher- and ASY redstart-preferred parts of the area (Fig. 4). Between 1980 and 1982 ASY redstarts increased dramatically in the area previously occupied by flycatchers. At the same time, SY redstarts began to occupy the area that ASY redstarts had preferred before 1980 (Fig. 4). We conclude that vegetation changes had less effect than did Least Flycatchers on ASY (and indirectly on SY) redstart settlement patterns on this site.

Population changes on 4-ha sites.—Between 1981 and 1984 Least Flycatcher densities on the 4-ha sites (A–F) ranged from 0 to 13 (Table 1). The sites without flycatchers were chosen to be that

TABLE 1. Numbers of male Least Flycatcher and American Redstart (after-second-year [ASY], second-year [SY], and total males, see Methods) territories on 6 4-ha sites, 1981–1984. Total male redstarts exceed the sum of ASY + SY males in 1981 on several sites because not all males were identified by age in that season.

Year	Site					
	A	B	C	D	E	F
Least Flycatchers						
1981	8.5	13.0	6.0	6.0	10.5	0
1982	0	0	9.0	0	8.0	0
1983	0	0	6.0	0	2.0	0
1984	0	0	3.0	0	0	0
Total redstarts						
1981	2.7	5.5	2.5	3.5	4.5	6.0
1982	2.9	5.5	4.5	7.5	3.0	5.5
1983	4.8	5.25	3.5	5.0	6.75	4.75
1984	3.7	5.0	3.5	5.0	2.5	3.5
ASY redstarts						
1981	2.1	2.5	1.0	3.5	2.5	3.0
1982	1.9	5.5	2.5	7.0	3.0	5.5
1983	3.7	5.25	1.0	5.0	4.5	3.5
1984	3.2	4.25	3.5	5.0	2.5	2.5
SY redstarts						
1981	0.5	1.75	0	0	1.0	2.0
1982	1.1	0	2.0	0.5	0	0
1983	1.1	0	2.5	0	2.25	1.25
1984	0.5	0.75	0	0	0	1.0

Fig. 5. Mean abundance ± 1 SE (box) and range (vertical line) of redstarts for combinations of all 4-ha sites and years ($n = 24$) in the presence or absence of Least Flycatchers. (A) ASY males, (B) SY males, and (C) total (ASY + SY) males.

way (site F), were made that way by flycatcher removals (sites A and B), or resulted from natural flycatcher declines (sites C–E). We removed 5 flycatchers from site A and 14 from site B in 1982, and 1 flycatcher from each of these sites in 1983. Local extinction of Least Flycatchers occurred on site D between 1981 and 1982 and on E between 1983 and 1984. Flycatchers also declined in abundance on site C between 1981 and 1984 (Table 1).

We quantified how Least Flycatcher and redstart abundances on the 4-ha sites were related in two ways. First, we compared the abundance of redstarts for sites and years with and without any flycatchers. Second, we plotted redstart abundance as a function of flycatcher abundance. We did not test any of these results statistically because there were too few sites, and because different abundances of birds on the same site in different years cannot be assumed to be statistically independent (cf. "temporal pseudoreplication"; Hurlbert 1984). The trends, however, provide insight into the dynamics of the interaction. ASY male redstarts were more
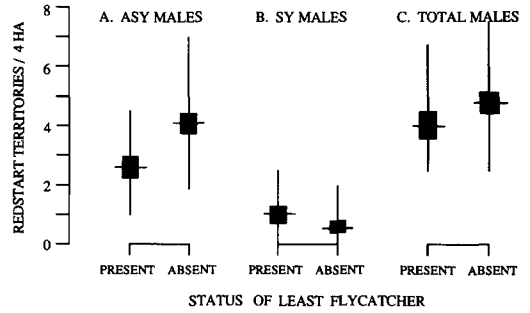
abundant in the absence of flycatchers (Fig. 5A), as expected if flycatchers competed directly with ASY redstarts for habitat, and total redstart males (ASY + SY) were slightly more abundant when flycatchers were absent (Fig. 5C). SY redstarts were slightly less abundant on these sites when flycatchers were absent (Fig. 5B). From the abundances of the 6 plots (data in Table 1), we generated regression equations for ASY redstarts, ($y = 4.07 - 0.19x$), SY redstarts ($y = 0.60 + 0.06x$), and total redstarts ($y = 4.68 - 0.08x$), where y and x are redstart and Least Flycatcher territory abundances, respectively. Thus, ASY redstart abundance increased with declining Least Flycatcher abundance, but both SY and total redstart abundances changed little as flycatcher abundance changed. The slope for ASY redstarts (-0.19) means that a site gained 1 redstart territory, on average, for every 5 flycatchers lost.

Data from individual sites showed that ASY redstart males consistently increased following flycatcher declines over the same period that ASY redstarts declined on control areas. Specifically, on 4 of the 5 4-ha sites with flycatcher removals or declines (B–E), ASY redstart abundance increased in the same season Least Flycatchers declined (Table 1). On the fifth site (A), from which we removed flycatchers in May 1982, ASY redstarts did not increase until the following summer (Table 1). However, ASY redstarts also increased on control areas between 1981 and 1983 (Fig. 6A), and did not decline to 1981 levels again on all three control areas until 1984. We thus asked what was the net redstart (i.e. abundance in 1981 minus that in 1984) on the
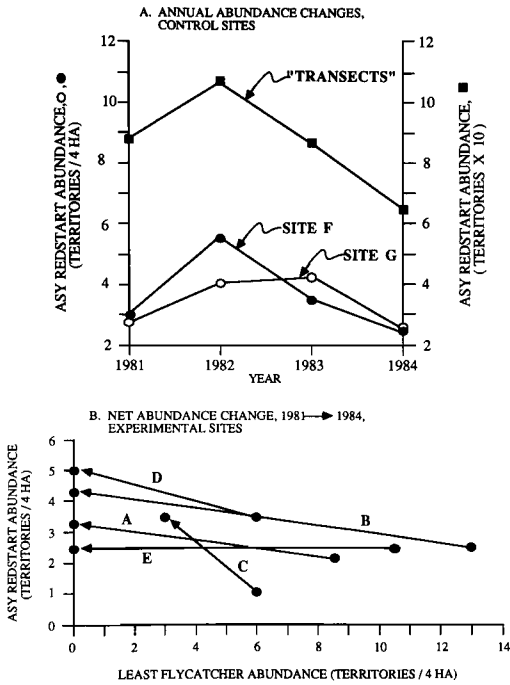
Fig. 6. Changes in abundance of ASY redstarts between 1981 and 1984 on 6 4-ha sites (A–F), a 10-ha site (G), and along the entire area traversed by four transect lines (labeled "transects") shown in Fig. 1. (A) Annual abundances of ASY redstarts on control areas where Least Flycatchers were absent (sites F and G), or where they occupied a small percentage of the total area ("transects"). (B) Net changes in ASY abundance between 1981 and 1984 on 5 4-ha sites (A–E) from which Least Flycatchers either were experimentally removed (sites A and B) or declined independently of our activities (sites C–E). Arrows point from 1981 abundance to 1984 abundance (see also Table 1).

experimental sites. ASY redstarts either increased (sites A–D) over this period or stayed the same (site E; Fig. 6B), in contrast to ASY declines over this same period on control areas (Fig. 6A).

Redstart response to flycatcher recolonization.— In addition to removal manipulations, one would ideally want to perform the converse manipulation, i.e. add flycatchers to an area inhabited by ASY redstarts. We observed the results of one such event when Least Flycatchers recolonized one manipulation site (B) in 1985 and subsequently. We observed 5.75, 4, and 6.25 Least Flycatcher territories on this site during the 1985, 1986, and 1987 breeding seasons, respectively. ASY redstart abundance declined

steadily on this site from 1985 to 1987, with 3.75, 3.25, and 1.5 territories, respectively (there were 1.75 SY redstart territories in 1985, none in 1986, and 1.25 in 1987). Thus, by 1987 ASY redstarts had declined on site B to an abundance below that in 1981. At the same time Least Flycatchers recolonized the site. Territory distributions provided more striking evidence than abundances that Least Flycatchers constrained ASY redstart settlement on this site (Fig. 7). Between 1982 and 1984 ASY redstarts spread dramatically onto the northern corner of the site, previously occupied predominantly by Least Flycatchers (Fig. 7). This showed clearly that in the absence of flycatchers the entire site was acceptable to ASY redstarts. Beginning in 1985 flycatchers recolonized the part of the site from which they had been absent since May 1982. Over the next 2 yr ASY redstarts gradually disappeared from this region, and by 1986 their distribution returned to a pattern similar to that in 1981. Least Flycatchers had the least effect on ASY redstarts in 1985, the first summer of their recolonization.

Redstart age-specific habitat differences.—SY males tended not to settle where ASY males were most concentrated. On site G SY males tended to segregate from ASY males (Figs. 2 and 4) and to shift territory locations abruptly when ASY males shifted (Fig. 4). The abundances of SY and ASY males on site G between 1972 and 1985 were negatively correlated ($r = -0.26$). Finally, SY and ASY densities on the 4-ha sites considered over 4 yr were negatively correlated ($r = -0.38$, $n = 24$). Statistical tests of these relationships are inappropriate because of too few (statistically independent) plots.

Least Flycatchers indirectly affected SY patterns by directly altering settlement patterns of ASY male redstarts (Figs. 2, 4, and 5), and ASY males directly influenced where SY males settled. In contrast to the complete territorial separation of individual SY and ASY males, both age classes of redstarts occasionally overlapped Least Flycatcher territories. SY males often overlapped flycatchers, leading to the positive association observed (Figs. 2 and 4), whereas ASY males occasionally overlapped flycatcher territories (e.g. Fig. 7; see also Sherry 1979).

DISCUSSION

The major question motivating our study was whether or not Least Flycatchers directly restrict redstart habitat use, i.e. whether the two

species compete for habitat (Sherry 1979). The results, showing changes in settlement patterns of redstarts when flycatcher distribution and abundance changed, provide compelling evidence of both direct and indirect effects of Least Flycatchers on redstart habitat use. Thus, competition-mediated habitat selection appears to occur in this situation.

Three observations appear to contradict the competition hypothesis. First, the response of redstarts to the disappearance of Least Flycatchers on some of the 4-ha sites was weak. This may be due to a variety of factors, including (1) insufficient replication of treatments and controls on independent sites, (2) the much larger territories of redstarts than flycatchers (Sherry 1979, Sherry and Holmes 1985), with the consequence that five flycatchers were necessary to affect one redstart territory (see Results), (3) few flycatcher territories per aggregation in the first year of study, and aggregations generally too small to cover the entire experimental site, (4) a regionally declining flycatcher population (see Methods), with the consequence that the fewer flycatchers outside of our intensive study sites may have provided decreasing pressure on ASY redstarts to move onto the removal sites, (5) net declines in redstarts, especially between 1981 and 1984, and declining intraspecific pressure from the redstart population to settle in particular habitats, and (6) a large potential "edge effect" resulting from the few (generally 5 or fewer, and never more than 7.5) redstart territories on these 4-ha sites in any one season. Thus, the considerable spatial and temporal variation documented for both redstarts and Least Flycatchers probably increased the difficulty of detecting any putative competitive effect of flycatchers. For this reason we think the striking results from site G, where a larger area was under study over a longer time, and from site B, where both removal and subsequent return of flycatchers occurred, provide particularly convincing evidence for a flycatcher effect.

A second potential problem concerns the fact that the species' territories often overlapped. The situation does not fit the classical description of exclusive interspecific territoriality. "Partial interspecific territoriality" is not uncommon in birds (Cody 1974), however, and most examples of exclusive interspecific territoriality involve closely related species, especially congeners (Cody 1985), that would be likely to share some vocal or plumage signals
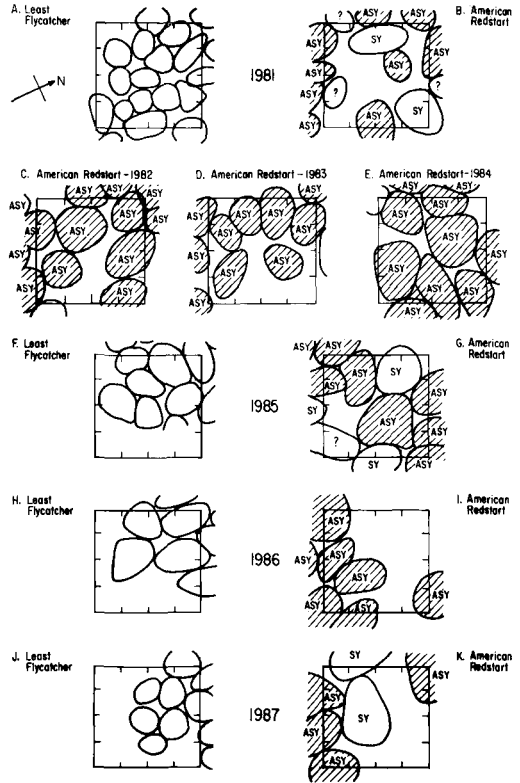

Fig. 7. Changes in the distribution of ASY redstart territories (shaded) and of Least Flycatcher and SY redstart territories (unshaded) on the 4-ha site B, 1981–1987. Least Flycatchers were removed from this site in May 1982 and were absent until they recolonized in May 1985. Question marks refer to territories for which we did not record the male's age.

(Murray 1971). Redstarts and Least Flycatchers share no obvious similarities in their plumages or vocalizations. Moreover, some spatial overlap of ASY redstarts with Least Flycatchers may result if flycatcher avoidance is a learned response, and if naive redstarts are the ones that tend to overlap flycatchers. The fact that the greatest overlap of ASY redstarts and flycatchers on site B occurred in 1985 (Fig. 7), the first year flycatchers recolonized the site, is consistent with this hypothesis. ASY redstarts that returned that year might not have encountered flycatchers previously.

A third finding that appears to contradict the competition hypothesis is the overall positive, albeit not statistically significant, correlation in total abundances of the two species over time on site G. Positive correlation in species abun-

dances are expected when species compete asymmetrically for mutually preferred habitats, as we discuss below.

Thus, from all observations taken together, the most parsimonious explanation for the local habitat distributions of these two species at Hubbard Brook is that Least Flycatchers influenced redstart habitat use.

Sherry (1979) provided circumstantial evidence that Least, Flycatchers compete with American Redstarts, but showed that vegetation between 12 and 15 m above ground was significantly less dense where Least Flycatchers occurred most frequently than where ASY redstarts tended to settle. He could not reject the alternative hypothesis that the two species independently preferred different habitats (e.g. Cody and Walter 1976, Collins et al. 1982). Data collected in this study cause us to reject the latter hypothesis. Results from both the 10-ha site (G) and the 4-ha sites showed that ASY redstart abundance increased after flycatchers disappeared (Figs. 2 and 5), and that these changes occurred quickly (Fig. 4). Furthermore, the results from site G showed that when flycatchers were absent, redstarts occupied areas previously settled by flycatchers and preferred them when flycatchers were absent. Although subtle vegetation changes occurred on this site between the early 1970's and 1980's, they took place gradually and across the entire site and had little net effect on redstarts, whose abundance did not decline dramatically between 1969 and 1985 (see above). The only major change in redstart distribution on the site occurred rapidly, between 1980 and 1982, when Least Flycatchers disappeared (Fig. 4). Finally, reversible changes in ASY redstart use of site B, upon removal and later recolonization by flycatchers (Fig. 7), cannot be explained by vegetation dynamics.

The American Redstart and Least Flycatcher could interact competitively on a broad spatial scale, judging from their geographic and habitat distribution patterns beyond Hubbard Brook. They co-occur in deciduous forests over much of their breeding ranges in the northeastern and north-central United States and southern Canada (Results; see also Sherry 1979). Although redstarts breed farther south and west of Least Flycatchers, they reach their greatest densities in the northeastern parts of the breeding range where they overlap frequently with Least Flycatchers. Both species prefer deciduous

over coniferous vegetation (Sherry and Holmes 1985) as well as middle stages of a vegetation continuum (corresponding with mid-to-late stages of forest succession; Bond 1957, Capen et al. 1986; see Collins et al. 1982 for redstarts). In New England both species also occur along forest-edge and fence-row habitats, where overt aggressive interactions occur (Sherry unpubl. data). Both species are distributed patchily in the 6-km² transect study area at Hubbard Brook and tend to settle disproportionately in relatively deciduous rather than coniferous forest stands (Sherry and Holmes 1985). Furthermore, both species prefer the same patches (as shown on Site G), which concentrates the competitive interaction locally within a habitat. The competitive effects of Least Flycatchers are superimposed locally onto the broad-scale response of redstarts to forest physiognomy and floristic composition.

Ultimate cause of interspecific interference.—Presumably, interspecific aggression, involving chases and attacks (Holmes et al. 1978, Sherry 1979, Procter-Gray and Holmes 1981), is the mechanism by which Least Flycatchers exclude redstarts from particular habitats, although exploitative competition may also occur (see below). Where territories overlap, flycatchers attack redstarts many times per day during the nestling phase of the nesting cycle (Holmes et al. 1978, Sherry 1979), but also throughout the breeding season (Sherry unpubl. data). We have observed flycatchers attack both female and male redstarts. We have not yet determined whether flycatchers are more likely to attack ASY or SY redstarts, although the greater overlap of the flycatcher and SY redstart territories (see Results) suggests that SY males may receive the brunt of the aggression. The redstart–Least Flycatcher interaction is clearly asymmetrical, insofar as the flycatcher is socially dominant over the redstart. Both interference and asymmetry, which characterize this species interaction, are widespread, if not predominant, characteristics of interspecific competition (Lawton and Hassell 1981, Connell 1983, Schoener 1983).

Questions then arise as to why Least Flycatchers chase redstarts, and why both species prefer the same habitat. At least four hypotheses can be proposed. The first is that interspecific aggressive behavior is adaptive for the Least Flycatcher by increasing net food availability, i.e. interference reduces competition for food resources. As Brown (1964) and others have ar-

gued for intraspecific territoriality, and as demonstrated experimentally in Bell Miners (*Manorina melanophrys*; Loyn et al. 1983), we assume that the benefits of chases and attacks to Least Flycatchers exceed the costs. If food is sufficiently limiting for aggressive competition to be adaptive, the benefits to individual Least Flycatchers, the aggressors, should be proportional to dietary similarity and spatial overlap between the two species. Both species are obligate insectivores, as well as behaviorally and morphologically convergent "flycatchers" (Sherry 1979, 1985; Bennett 1980). They forage similarly with respect to heights above ground, prey-capture tactics and substrata, and insects selected (Holmes et al. 1979a, Sherry 1979, Robinson and Holmes 1982), although they differ in some aspects of food-searching behavior (Robinson and Holmes 1982). Their spatial overlap is assured by their preference for similar habitats of comparable successional age. Ecological requirements of the two species overlap considerably, and one might expect them to respond similarly to spatially patchy food resources or other habitat characteristics that influence foraging behavior.

Food for insectivorous birds at Hubbard Brook appears to be limited in abundance, at least during some summers. This increases the likelihood that redstarts and Least Flycatchers might compete for food. As a group, birds significantly reduce insect abundance (Holmes et al. 1979b), particularly Lepidoptera larvae, which are an important food for breeding birds, indicating the potential for food limitation. Recent studies at Hubbard Brook have documented reduced nestling growth and nestling starvation in several species, including redstarts, during summers when food is scarce (Rodenhouse 1986, Sherry and Holmes unpubl. data). Recently, Martin (1987) reviewed evidence for food limitation from a wide variety of studies and concluded that food often may be limiting for Temperate Zone birds.

There are at least three other explanations for why Least Flycatchers chase redstarts. First, many cases of interspecific aggression involve mistaken identities, often among closely related species (Murray 1971). We consider this alternative unlikely here because redstart plumage and vocalizations are so unlike those of Least Flycatchers that the two species should not be easily mistaken (see also Lyon et al. 1977). Moreover, our demonstration that the Least Flycatch-

er excludes the behaviorally subordinate redstart from mutually preferred habitat satisfied Murray's (1971) criterion for "adaptive" interspecific territoriality. Second, redstarts may be attacked disproportionately more often than other species of similar size (Sherry 1979) because they nest and forage in the same strata as Least Flycatchers (Sherry 1979), or because they make frequent aerial attacks on insects and rapid movement rates (Robinson and Holmes 1982, Sherry 1985), which make them conspicuous, or both. Maurer (1984, pers. comm.) argued that resources could be so abundant and concentrated that exploitation competition is undetectable, but interference occurs because the species have a high encounter frequency, resulting in turn from independently evolved autecologies. This seems wasteful of energy, and would not apply if food is regularly limiting in these forests (see above). A third explanation for the interspecific aggression is that Least Flycatchers might chase other small passerine birds to reduce the total density of nests and thereby discourage nest predators. Nest predation at Hubbard Brook is considerable (often >50%) for many open-cup nesters (Holmes and Sherry unpubl. data), and many Tyrannidae, including the Least Flycatcher, aggressively chase nest predators (Murphy 1983). Higher nest-predation rates with greater nest density, both within and between nesting species (Fretwell 1972, Dunn 1977), make this hypothesis plausible, although untested.

We submit that competition for food explains ultimately why Least Flycatchers chase American Redstarts, but alternative hypotheses have not been eliminated. We do not know why particular patches of forest are preferred by both flycatchers and redstarts, although examination of reproduction and survivorship across these patches would provide clues. Whatever the ultimate explanation, we found that flycatchers effectively excluded redstarts from mutually preferred patches of forest at Hubbard Brook via interspecific aggression, leading to partial interspecific territoriality.

Redstart intraspecific interactions.—The evidence for intraspecific competition is scant and largely inferential for redstarts (Ficken and Ficken 1967; Howe 1974a, c; Figs. 2 and 4) and most other paruline warblers (Morse 1985). ASY male redstarts appear to dominate SY males, based on indirect evidence that older males arrive on breeding sites 1–2 weeks earlier on av-

erage than SY males (Ficken and Ficken 1967, Francis and Cooke 1986). Although this dominance effect has yet to be tested experimentally, SY males arrive later and tend to segregate spatially from ASY males both within (Fig. 2; Sherry and Holmes unpubl. data) and between habitats (Ficken and Ficken 1967, Morse 1973, Howe 1974b). SY males probably settle in poorer habitats than ASY males (Ficken and Ficken 1967, Morse 1973, Sherry and Holmes 1985). In our study area the presence of pugnacious Least Flycatchers (Sherry 1979, Procter-Gray and Holmes 1981, this study) could be a factor that decreases habitat quality for redstarts. SY males might be less likely than ASY males to avoid flycatchers (Figs. 2, 3, and 5) because either SY males use only vegetation cues in choosing habitat, before aversive experience with flycatchers, or flycatcher patches are the best available habitat not already saturated with ASY males.

For perspective, we note that the strength and even the sign of this correlation in ASY and SY distribution must be related to the scale of examination. At the scale of individual territories, for example, the correlation will approach -1 simply because strong territoriality by definition reduces spatial overlap, regardless of male age. At increasingly larger scales, SY and ASY breeding distributions will become increasingly positively correlated. The species as a whole selects habitats that are relatively similar ecologically, and the best chance for yearlings to obtain mates and reproduce successfully is to settle in habitats similar to those selected by the older, more experienced males.

Interspecific interactions and habitat use.—Some ecologists deemphasize the effects of competition, implicitly if not explicitly, by emphasizing that species are distributed along habitat gradients independently of one another (see references in introductory paragraphs). We believe that bird species often influence habitat selection by guild members. The frequency of studies documenting interference as the mechanism of interaction (Morse 1974, Colwell and Fuentes 1975, Schoener 1983) corroborates this conclusion. What is not clear is how frequently and by what mechanisms distributions of one species are influenced by the presence of other species in nature.

Our results are unexpected from traditional explanations of how interspecific competition shapes a species' niche or pattern of habitat use. Changes in Least Flycatcher abundance and distribution, in combination with our manipulations, showed that this species affected habitat use by American Redstarts. At the same time, we found no significant inverse relationship in abundance of the two species at any spatial scale, except when we considered very local scale (territory-by-territory) distributions of just older (ASY) male redstarts and Least Flycatchers. Instead, total abundances of the two species tended to covary positively, both on a local scale and on the scale of North American states and provinces examined in the Results. This paradox—that the species compete for habitat despite no obvious evidence from correlations in their abundance—is resolved if we recognize that competition for habitat can affect species distributions in contrasting ways, depending on the form of competition.

Graphical isoleg models (Rosenzweig 1981, 1985; Pimm et al. 1985), which explicitly incorporate effects of inter- and intraspecific competitor abundance, clarify how one species can either narrow or broaden the habitat niche of another species. When each species prefers a different habitat, the appropriate model predicts that both species should *narrow* their habitat range in the presence of the other, leading to negative correlations in abundance, a pattern that many ecologists believe to be the only result of interspecific competition. When two species compete asymmetrically for mutually preferred habitat—conditions we documented for the Least Flycatcher and American Redstart—then one species can *broaden* rather than narrow the range of habitats selected by the other, subordinate competitor. This latter model can explain the inclusive-niche pattern, based on the widespread empirical observation that subordinate species have a broader fundamental niche than dominant ones (Miller 1967, Morse 1974, Colwell and Fuentes 1975, Black 1979, Sherry 1979).

Rosenzweig's and Pimm's graphical models depict isolegs, i.e. lines of points at which individuals of a species switch how they use the habitats, in the two-dimensional state-space of species abundances. The crucial result of their asymmetry model, for present purposes, is that the isoleg along which subordinates switch from selector (of preferred habitat) to opportunist has a negative slope, i.e. subordinates become opportunists sooner when dominants (occupying just the preferred habitat) are added to the system. Their models predict that interspecific

competition should cause the inclusive-niche pattern specifically when (1) two or more interacting species prefer the same habitat; (2) the dominant species effectively (but not completely) restricts access by the subordinate to preferred habitat(s), but not vice versa; (3) intraspecific competition constrains habitat selection at least within the subordinate species; and (4) the dominant species' carrying capacity is below the level at which intraspecific competition causes it to cross its own isoleg from selector to opportunist.

This model also explains how two competing species could have no, or even positive, correlations in their abundances over time, a condition we report here for the redstart and Least Flycatcher. Specifically, the model shows how the abundance of the subordinate species could increase in both habitats, because of favorable conditions in nonpreferred habitat, without causing any change in the abundance of the dominant species occupying just preferred habitat. Population abundances of the two species could be positively correlated if food resources covaried positively in the two habitats. Furthermore, the preference for the same habitat locally by two species means that they probably would respond similarly to environmental perturbations over time, and that they would co-occur geographically if their mutually preferred habitat were broadly distributed. Our study was not designed to test the isoleg models, but we find them compelling because they predict several results we observed that were not predicted by alternative models for competition. Further, they explicitly predict a variety of often contrasting responses of species to competition.

To summarize this species interaction as we currently envision it, Least Flycatchers locally exclude ASY redstarts from the best patches of habitat within a heterogeneous array of such patches, and ASY redstarts settle preferentially near areas occupied by the flycatcher because they are probably most similar in quality. Given the broad sympatry of these two species and possible interaction on a broad geographic scale, we hypothesize that Least Flycatchers over time might have forced redstarts to broaden or to maintain broader habitat tolerances, and perhaps greater feeding flexibility than the flycatchers, which are more specialized in habitat and feeding requirements (see Sherry 1979). Thus, the inclusive-niche pattern exhibited by

these two species may be viewed as the outcome of asymmetric competition for mutually preferred habitat. We do not pretend that these two species are tightly linked coevolutionarily, nor do we argue that Least Flycatchers were the only, or even the dominant, ecological factor that shaped the redstart habitat niche. We know, for example, that redstarts respond to the deciduous-coniferous habitat gradient in our study areas whether or not flycatchers are present (Sherry and Holmes 1985, unpubl. data). Thus, redstart habitat choice is influenced by multiple ecological factors, as in birds in general (Cody 1981). Moreover, any species that is socially dominant to redstarts could reinforce the effect that we believe Least Flycatchers have had.

Detecting interspecific interactions in the field.— The interspecific interaction we documented could easily be overlooked. Neither a spatially nor temporally inverse correlation in abundances of the two species was evident at any spatial scale. Even at a local (territory-by-territory) scale, where competitive interactions should be most intense (Martin 1986), abundances of the two species were inversely related only when one age class (ASY) of male redstarts was considered. Ontogenetic (age-related) ecological changes are important in indeterminate growers (e.g. Werner and Gilliam 1984, Werner 1986) but can also be important in determinate growers such as birds, as our study shows. Two other characteristics of the redstart–Least Flycatcher interaction further complicated detecting competition in the field. The first characteristic was partial overlap of Least Flycatcher territories with those of redstarts, particularly SY males. In some years we observed no clean transition between territories of Least Flycatchers and ASY redstarts, and a threshold of approximately five flycatcher territories may be necessary to exclude ASY territories noticeably from a particular patch of forest habitat (see Results). The interaction between these two species is subtle enough that we did not observe interspecific aggression or suspect an interaction until we had begun intensive behavioral studies of redstarts in 1973. The second characteristic was patchy spatial distribution of both species, particularly flycatchers, in continuous northern hardwoods forest. In particular, we found that the intensity of the competitive interaction is proportional to the quality of the habitat contested, and quality habitat is probably very patchily distributed. We do not yet

know what characteristics of the habitat are most important to these species, but food availability, vegetation structure that affects foraging ability, and safety from nest predators are possible factors.

Cases of interspecific interaction may be easily overlooked for any of the above reasons. In general, demonstration of the absence of competition may be as difficult as the demonstration of its presence. Thus, we urge caution in concluding that competition does or does not occur solely on the basis of habitat-use patterns or simple covariation in abundances. We also urge greater attention to spatial and temporal scale, and to mechanisms, in studies of competition and habitat use.

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