HABITAT SELECTION BY AMERICAN REDSTARTS ALONG A SUCCESSIONAL GRADIENT IN NORTHERN HARDWOODS FOREST: EVALUATION OF HABITAT QUALITY

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ABSTRACT.—To investigate the possible relationship between habitat changes and population declines in the American Redstart (*Setophaga ruticilla*), I studied redstart population structure in habitats spanning a successional gradient in northern hardwoods forests of the White Mountains, New Hampshire during the summers of 1992 to 1994. Early successional stands, in general, supported higher densities and a greater percentage of older (ASY) males than did mature stands. Among mature forests, redstart densities and proportions of ASY males were lower in stands with greater representation of conifers. Mating success varied among habitats, primarily for yearling males, which were more likely to obtain a mate in the early successional habitats and less likely to do so in coniferous habitats. Territories were significantly smaller in early successional habitats. The combination of high densities, high proportions of older males, high mating success in yearlings, and small territory size supports the hypothesis that early successional habitats are more suitable for redstarts than are older forests. Early successional habitats may be more suitable due to higher prey availability and/or reduced predation on nests, although conclusive data are not available for either of these variables. If reproductive success follows a similar pattern, then the loss of early successional habitats as a result of reforestation in the breeding areas could be a major cause of population declines of American Redstarts in New England. *Received 18 December 1995, accepted 8 May 1996.*

RECENT DECLINES in populations of Nearctic-Neotropical migratory birds have raised concerns about habitat alteration on both the breeding and wintering grounds of these species (Robbins et al. 1989, Askins et al. 1990, Hagan and Johnston 1992). Habitat alteration can involve deforestation, resulting in net habitat loss and the fragmentation of remaining habitat, as well as natural changes in plant communities through vegetative succession. These types of habitat changes can affect regional or local bird abundance if species experience higher fecundity and survival in some habitats than in others. Evidence from the breeding grounds suggests that fragmentation of forest habitats can lead to low reproductive success through increased nest predation (Wilcove 1985, Small and Hunter 1988), increased brood parasitism (Brittingham and Temple 1983, Robinson 1992), or a combination of the two (Robinson et al. 1995b). Although changes in bird community composition that accompany vegetative succession are well documented (Johnston and Odum 1956,

Bond 1957, Karr 1968, Morgan and Freedman 1986, Holmes 1990), few data are available on population structure and reproductive success in those species that occupy a range of successional stages (but see Probst and Hayes 1987). If one assumes that a species is rare or absent from certain stages because it experiences low fitness there, changes in the availability of the preferred stage may result in regional population changes. An understanding of a species' habitat distribution, defined as its pattern of abundance across habitats, thus is critical for evaluating the potential effects of landscape change on avian populations.

The American Redstart (*Setophaga ruticilla*) is widely distributed in eastern and north-central North America, where it occurs in deciduous and deciduous/coniferous habitats. Recent data suggest that redstart populations are declining in northeastern North America (Holmes and Sherry 1988, Witham and Hunter 1992, Peterjohn and Sauer 1994). Litvaitis (1993) proposed that this decline is related to regional reforestation and loss of early successional habitat. With respect to plant succession, studies of redstart habitat selection have come to contradictory conclusions. Some studies have found that red-

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starts reach maximum densities in early succes-
sional (DeGraaf 1991, Westworth and Telfer
1993) or intermediate-aged forests (Bond 1957),
or in forests with smaller trees (DeGraaf and
Chadwick 1987), which may approximate early
to mid-successional habitats. Others have char-
acterized redstart habitat as primarily shrub and
forest edge (Martin 1960, Collins et al. 1982). In
some areas, redstarts are more abundant in areas
with a mixture of stand ages than in nearby
areas containing only mature forest (Welsh and
Healy 1993). At the other extreme, some authors
have found maximum redstart densities in more
mature forests (Ficken and Ficken 1967, Craw-
ford et al. 1981, Morgan and Freedman 1986,
Thompson and Capen 1988). Within mature for-
ests, considerable evidence suggests that red-
starts are less common in areas with higher den-
sities of conifers (Martin 1960, Sabo 1980, Sher-
ry and Holmes 1985, DeGraaf and Chadwick
1987). Given that 7 of these 11 studies found
higher redstart densities in early to middle stages
of succession, or in habitats that were structur-
ally similar to these stages, I hypothesized that
early successional habitats were more suitable
for redstarts than were mature forests.

If early successional habitats are of higher
quality, then they should support higher red-
start densities, have higher percentages of older
males, and be settled earlier in the season. The
latter predictions stem from observations that
older males arrive earlier on the breeding
grounds (Francis and Cooke 1986) and are able
to exclude yearlings from "preferred" territo-
ries (Ficken and Ficken 1967, Sherry and Holmes
1989), suggesting that the older birds choose
higher-quality habitats. In addition, because
some yearlings are unable to obtain mates (Proc-
ter-Gray and Holmes 1981, Sherry and Holmes
1989), mating success also may vary among hab-
itats, leading to the prediction that a greater
proportion of males should be mated in early
successional habitats. Finally, Smith and Shu-
gart (1987) showed that territory size can reflect
habitat quality because prey abundance varies
with habitat, leading to the prediction that red-
start territories should be smaller in early suc-
cessional habitats if these habitats are more suit-
able. I tested the hypothesis that early succes-
sional habitats are more suitable for American
Redstarts by measuring a suite of population
parameters that can reflect habitat suitability,
namely density, age ratio, mating success, ar-
rival time, and territory size. Data on habitat

quality across a variety of habitats are needed
before hypothesized relationships between
habitat changes and population declines can be
evaluated.

METHODS

Study sites.—This study was conducted on 44 forest
stands in the Pemigewasset Ranger District of the
White Mountain National Forest, New Hampshire.
Sites were selected from U. S. Forest Service (USFS)
stand records, based on the following criteria: (1) the
vegetation of the stand was classified by the USFS as
"northern hardwoods association;" (2) the stand was
at least 10 ha in size; (3) the stand was accessible; and
(4) the stand was at least four years old (time since
last harvest). All stands harvested since the 1940s had
been clearcut, and I presumed that most of the older
ones were as well, although information on harvest
methodology was not available for all older sites. The
sites sampled represented a broad range of stand ages,
spanning 4 to 122 years, and thus encompassed a
broad range of possible habitats within a heavily for-
ested region. Although some information on land-
scape characteristics was available for each stand (e.g.
distance to other stands, size and age of adjoining
stands, etc.), it was not considered when choosing
sites or used in any analyses because of potential re-
ductions in sample sizes.

Vegetation sampling.—Habitat characteristics at the
44 census sites were measured using a point-centered
quarter method (Cottam and Curtis 1956), with 10
points per stand. In each quadrant around points, I
measured the distance from the point to the nearest
stem >3 cm dbh, and then recorded the species of
tree and its dbh. Numbers of shrubs and saplings were
counted within a 2-m radius of each point. The veg-
etation points were not necessarily the same as the
redstart census points (see below) but were located
in the same part of the stand and reflected the habitat
characteristics of the area censused as a whole. The
distances and tree sizes at each point were used to
calculate densities, basal areas, and relative impor-
tance values for the common tree species in each stand.

Bird censusing.—Numbers of territorial male red-
starts at each census site were determined using a
playback-based point count technique, modified from
Sliwa and Sherry (1992). When stand size and shape
allowed, I censused 10 points per site, all spaced at
least 100 m apart and usually along a transect or grid
line. To minimize detection of birds from different
habitats, points were at least 50 m from the edge of
the stand. At each point I spent 6 min listening and
watching for redstarts; during the last 3 min I used a
portable tape recorder to broadcast redstart song. The
recording consisted of repeat-mode singing (Mac-
Nally and Lemon 1985) by a male redstart recorded
in a previous year in Woodstock, New Hampshire.

The playback protocol was designed to attract males so that I could observe their plumage and determine their age (Johnson et al. 1981). Throughout the 6-min period, I noted the song types of all redstarts heard (MacNally and Lemon 1985) and determined the age class (SY for yearling birds and ASY for birds at least two years old, distinguished by plumage) of all males seen. When possible, I sketched breast patterns of males (see Lemon et al. 1992) to distinguish among individuals. If the same bird was detected at more than one point, this was also noted. Censusing activity occurred between 8 June and 1 July in 1992 (44 sites), 16 June and 1 July in 1993 (35 sites), and 5 June and 2 July in 1994 (26 sites). All censuses were conducted between 0500 and 1030 EST, and each site was censused only once a year.

Data were summarized by counting the minimum number of territorial males on each census. At three sites where fewer than 10 points were censused (two sites with 9 points, and one site with 7 points in one year and 10 points in the other two years), the number of males was adjusted to represent "males per 10 points," the measure used in subsequent analyses and hereafter referred to as "redstart abundance." The number of ASY males seen during a census was divided by the total number of males seen to give "% ASY." Only sites at which at least 50% of the males were observed were used in analysis of this variable.

Mating success.—Seventeen of the 44 stands were intensively surveyed in 1994 in an attempt to measure the number of males with mates (i.e. mating success). Sites were chosen based on results of vegetation ordination (see below) and represented three habitat types: early successional forest (six sites), mature deciduous forest (seven sites), and mature deciduous/coniferous forest (four sites; see Results for habitat definitions). After each census, I spent the remainder of the day observing individual males to determine whether each was successfully mated with a female. If a female was not observed with a given male during the census, that male was monitored for up to 60 min (Villard et al. 1993) or until he was seen associating with a female. If I was unable to monitor all males at a site on the first day, that site was revisited on subsequent days until each male had been observed for a cumulative total of 60 min (if necessary). When a female was seen in a territory, but the male continued singing or otherwise showed no interest in her, the female was assumed to be wandering from a neighboring territory, and observation of the focal male was continued. In addition, I recorded song types (repeat vs. serial mode; MacNally and Lemon 1985) and rates (for at least 5 min, when possible) for all males for which a female had not yet been detected, because singing behavior is a good indicator of mating status (C. Staicer pers. comm.). Unmated males repeat the same song type at a rapid rate (8/min), whereas this rate is significantly slower in mated males (5/min). Mated males also switch among several song types within a singing bout (serial song), a behavior almost never observed in unmated birds (C. Staicer pers. comm.). A male was considered mated if: (1) he was seen associating with a female, or (2) his singing behavior suggested that he was mated. In the process of collecting mating-success data, I also was able to obtain more accurate measures of density and age ratios, data which later were used to assess the accuracy of the census methodology.

Arrival time.—In 1994, I systematically surveyed 13 of the 44 stands in May and early June to determine arrival times and changes in abundance in different habitats. Sites again represented the three habitat types: (1) early successional forest ($n = 5$), (2) mature deciduous forest ($n = 5$), and (3) mature deciduous/coniferous forest ($n = 3$). Each of these sites was visited, weather permitting, once every three days from 7 May to 3 June, between 0530 and 1330 (five to seven visits per site). The order in which sites were visited within a day, and to a lesser extent within a three-day period, was varied as much as possible within the logistical constraints of time of day and distance between sites. Two to six sites were visited each day. During each visit, I spent one hour systematically searching for redstarts, and recorded the number seen and their age, sex, distinguishing markings, behavior, and general location. The same area of each site was covered in each visit, and corresponded roughly with the area used in later censusing.

Territory size.—I measured territory size on three plots within the Hubbard Brook Experimental Forest, White Mountain National Forest, New Hampshire. One 5-ha plot was located within each of two experimental clearcuts, Watersheds 101 and 5, which were harvested in 1970 and 1984, respectively. The third plot was a 20-ha portion of the study area used by Sherry and Holmes (1985, 1992) in their studies of redstarts. This was situated within a large, contiguous mature forest (over 80 years since last harvest). Each plot was marked in a 25-m grid to facilitate territory mapping.

Territory boundaries on the Hubbard Brook plots were determined by mapping locations and movements of individual males (identified by color bands or plumage variation) and recording counter-singing and boundary disputes among males. The plots were visited from mid-May to early July in 1992 and 1993 (only 1993 on Watershed 101), with visits lasting from 5 to 8 h. Territory data from the mature forest were collected as part of an ongoing study of the redstart population at Hubbard Brook (T. W. Sherry and R. T. Holmes unpubl. data). All locations of each bird were transferred to a transparent overlay and territory boundaries approximated by drawing a convex polygon around the area where roughly 90% of the observations were concentrated. Areas were estimated by overlaying each territory polygon on graph paper and counting the number of squares within its borders, with each square scaled to represent 40 m².

TABLE 1. Results of principal components analysis of relative densities of common tree species on 44 forest stands in White Mountain National Forest, New Hampshire.

	Loadings	
Variable	PC1	PC2
Sugar maple (*Acer saccharum*), <10 cm dbh	0.07	−0.19
Sugar maple, ≥10 cm dbh	0.22	−0.30
Red and striped maple (*A. pensylvanicum* and *A. rubrum*)	0.09	0.35
American beech (*Fagus grandifolia*)	0.44	−0.55
Birches (*Betula alleghaniensis, B. papyrifera*), <10 cm dbh	−0.23	0.14
Birches, ≥10 cm dbh	0.18	0.41
Pin cherry (*Prunus pensylvanica*)	−0.81	−0.28
Conifers (*Tsuga canadensis, Abies balsamea, Picea rubens*)	0.06	0.42
Variance explained (%)	59	17

Data analyses.—Principal components analysis (PCA) was used to determine relationships among the vegetation variables, resulting in components that were useful descriptors of habitat gradients. The PCA was based on the densities of seven common tree species and the combined densities of three uncommon conifer species (Table 1), all expressed as relative densities (actual density divided by total tree density). Two taxa (sugar maple and yellow birch; scientific names in Table 1) showed considerable variation in size-class distributions among study sites, and I included this variation in the PCA by using two densities for each taxa (i.e. trees <10 cm dbh and trees ≥10 cm dbh). To determine broad habitat categories, I clustered sites based on the calculated values of the first two principal components. The clustering algorithm used average linkage and Euclidean distances to compare each variable among all 44 sites.

Variation in redstart population variables along the vegetation gradients was analyzed in two major ways. For patterns across all sites, I used multiple regression to examine the relationships between the vegetation gradients (scores on PC1 and PC2) and redstart abundance and age ratios. Differences in redstart abundance, age ratio, and mating success among distinct habitats (based on clustering analysis of vegetation characteristics) were compared using ANOVA and *t*-tests (or Kruskal-Wallis and Wilcoxon tests when sample sizes were small). All analyses were performed on each year's data separately, as well as on means for sites that were censused in all three years. Means for age ratios are based on sites for which I had at least two years of data, because the sample that met acceptance criteria (at least 50% of males seen) in all three years was small.

For arrival times, I determined the first date on which each resident male (i.e. males detected on mating-success surveys) appeared at each site. I then determined the number of resident males present during each subsequent three-day period. Data for each site were summarized as the number of resident males present during each three-day period. Mean numbers per habitat were compared in each three-day period using either Wilcoxon or Kruskal-Wallis tests.

RESULTS

Vegetation characteristics of the study sites.—Sites occupied by redstarts initially were characterized using principal components analysis based on densities of common tree species. The first two principal components collectively explained 76% of the variation (Table 1). Principal component one (PC1) explained 59%, with high negative loadings for pin cherry and small birches and high positive loadings for sugar maple and American beech (Table 1). This pattern is consistent with a successional gradient in northern hardwoods forest in which pin cherry and small birches are common in early stages, but eventually are replaced by large beech, sugar maple, and yellow birch (Marks 1974). PC1 scores also were highly correlated with forest age ($r = 0.8, n = 44, P < 0.001$). The second principal component (PC2) explained 17% of the variance and had positive loadings for conifers, large birch, and red and striped maples, and negative loadings for pin cherry, beech, and sugar maple (Table 1). A similar component (i.e. a gradient from red maple/birch/conifer to sugar maple/beech) was reported by Sherry and Holmes (1985) within mature forest at Hubbard Brook, and was interpreted as reflecting increasing conifer density in response to changes in moisture and other physical factors. Hereafter, I refer to PC1 and PC2 as the successional gradient and the conifer gradient, respectively.

Cluster analysis based on the vegetation gradients revealed an initial separation of the 44 sites into two large groups, with the larger group further divisible into two major subgroups. When PC1 was plotted against PC2, stands younger than 30 years separated from those >30 years old along the successional gradient (Fig.

1). A similar separation of early successional and mature stands was reported by Aber (1979), based on foliage height profiles. Within the mature forest cluster, two smaller clusters corresponded to sites that separated along PC2, thus representing habitats with relatively high or low conifer densities (Fig. 1). All further references to the results of the cluster analysis will refer to the habitat types as "early successional" and "mature" along the age gradient, and as "deciduous" and "coniferous" when the mature habitats are delineated along the coniferous gradient. Sites classified as early successional ranged in age from 4 to 22 years, with a mean of 10.8 years since harvest ($\pm$ SE of 5.6). Mature deciduous stands ranged from 20 to 122 years old ($\bar{x} = 72.4 \pm 5.4$ years), and mature coniferous stands ranged from 36 to 102 years old ($\bar{x} = 73 \pm 7.1$ years).

Redstart abundance.—To assess the reliability of the census methodology, numbers of redstarts detected on censuses were compared with numbers of redstarts detected during mating-success surveys at the same sites. The two measures were positively correlated ($r = 0.96$, $P < 0.001$, $n = 17$), indicating that the playback census was a reliable method for estimating redstart abundance. Therefore, I used the playback census data for assessing redstart abundance, because it was available for all years and covered a larger geographic area.

When all three years were analyzed together, mean redstart abundance declined significantly along the coniferous gradient (PC2; $F = 6.89$, $P = 0.01$) but did not vary along the successional gradient (PC1; $F = 2.75$, $P = 0.11$; $R^2 = 0.29$, df $= 2$ and 24 for both). The lack of significance of PC1 probably resulted from the 1993 data, in which redstart abundance in mature deciduous habitats did not differ from that in early successional habitats. When the same regression model was applied to each year's data individually, redstart abundance declined as forest age increased in 1992 ($F = 5.66$, df $= 2$ and 42, $P = 0.02$, $R^2 = 0.24$) and 1994 ($F = 10.85$, df $= 2$ and 24, $P = 0.003$, $R^2 = 0.44$) but not in 1993 ($F = 0.43$, df $= 2$ and 33, $P = 0.5$, $R^2 = 0.18$). Redstart abundance declined along the coniferous gradient in each of the three years.

An alternative means of investigating the effects of habitat on redstart populations is to group sites into the three habitat clusters (early successional, deciduous, and coniferous) described earlier. When habitat-specific abundances were compared in this way, the results
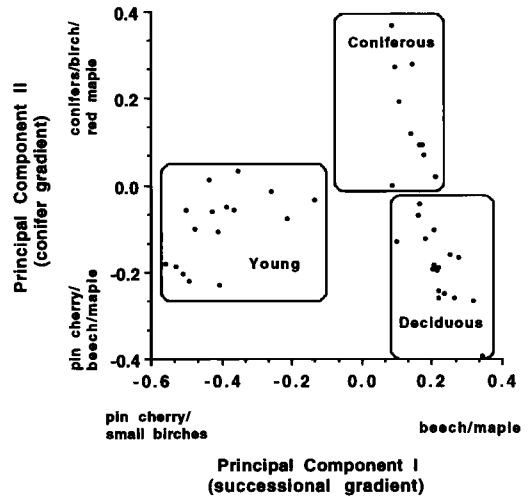

FIG. 1. Distribution of 44 study sites along two major vegetation gradients, showing the locations of the three habitat clusters.

(Fig. 2A) corroborated the regression analyses above. At sites censused in all three years, mean redstart abundance was high in early successional stands, high to intermediate in deciduous stands, and low in coniferous stands ($F = 4.96$, df $= 2$ and 23, $P = 0.016$). Similar patterns were observed when all sites were included and within years. Differences between early successional and coniferous habitats were significant in all cases.

Age ratios of male redstarts.—I used multiple regression to test for relationships between age ratios and the habitat gradients, as represented by the first two vegetation-based principal components. Across years, mean % ASY declined along the successional gradient (PC1; $F = 5.19$, $P = 0.04$) but not along the coniferous gradient (PC2; $F = 2.21$, $P = 0.16$; $R^2 = 0.34$, df $= 2$ and 16 for both). For the 1992 data, % ASY declined significantly along both the successional (PC1; $F = 14.73$, $P = 0.001$) and coniferous gradients (PC2; $F = 4.41$, $P = 0.05$; $R^2 = 0.46$, df $= 2$ and 24 for both). This analysis was not performed for the other years owing to small sample sizes and the fact that most of the sites that met analysis criteria (at least 50% of males were seen) were in early successional habitats.

Age ratios also were examined with respect to the three habitat clusters. Mean % ASY (across years) declined from early successional to mature deciduous to mature coniferous stands ($F = 3.56$, df $= 2$ and 15, $P = 0.054$; Fig. 2B). These differences were most apparent in 1992, when
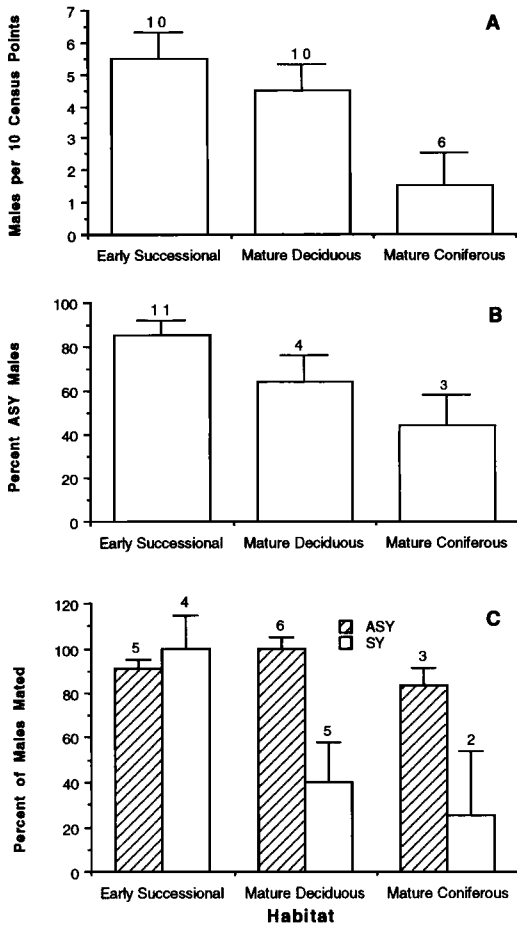
FIG. 2. Characteristics of American Redstart populations in three habitats (mean ± SE). (A) Male abundance, based on sites with three years of data; (B) male age ratio, based on sites with two or three years of data; and (C) male mating success in 1994. Numerals above error bars indicate number of sites in each habitat.

early successional habitats had a significantly higher % ASY than both mature habitats ($F = 8.37$, df = 2 and 23, $P = 0.002$). Percent ASY was uniformly high across all sites in 1993, so no significant differences were detected ($F = 0.38$, df = 2 and 19, $P = 0.69$), although the general trend resembled that of 1992. Too few sites met analysis criteria in 1994, although the trend was again toward more older males in early successional stands and fewer in coniferous stands, based on sites visited for mating-success surveys.

Mating success.—Mating success of ASY males was uniformly high and did not vary signifi-

cantly among habitats (Kruskal-Wallis test, $\chi^2 = 3.96$, df = 2, $P = 0.14$; Fig. 2C). Although the percentage of SY males that obtained mates was highest in early successional stands, intermediate in deciduous stands, and lowest in coniferous stands (Fig. 2C), these differences were not statistically significant ($\chi^2 = 4.71$, df = 2, $P = 0.10$). However, yearling mating success was significantly higher in early successional habitats when compared to the two mature habitats combined ($\chi^2 = 4.49$, df = 1, $P = 0.03$). When both age classes are combined, there were no significant differences among the three habitats ($\chi^2 = 4.0$, df = 2, $P = 0.14$), although the differences between early successional and coniferous stands were significant when compared directly ($\chi^2 = 5.06$, df = 1, $P = 0.025$). Within habitats, there was no significant difference between ASY and SY mating success in early successional stands ($\chi^2 = 3.05$, df = 1, $P = 0.08$), whereas significantly more ASYs than SYs were mated in mature habitats (Wilcoxon test, $\chi^2 = 6.67$, df = 1, $P = 0.01$).

Relationships between density and other population parameters.—To determine if density, age ratio, and mating success showed comparable trends across all sites, I performed regressions using mean redstart abundance (i.e. mean of all three years) as the independent variable. Sites with higher redstart abundance had both higher % ASY ($r^2 = 0.48$, $P = 0.004$; Fig. 3A) and higher 1994 mating success ($r^2 = 0.30$, $P = 0.04$; Fig. 3B). These results indicate that high-density sites also were characterized by high proportions of ASY males and high mating success, rather than these three variables showing inconsistent patterns on a site-by-site basis (e.g. a high-density site dominated by SY males).

Arrival time.—Between 7 and 24 May 1994, the numbers of males settling in early successional and deciduous stands did not differ, although there were slightly more in early successional stands during the third survey period (Wilcoxon test, $\chi^2 = 3.43$, df = 1, $P = 0.06$; Fig. 4). After 24 May, populations in deciduous stands remained stable, whereas those in early successional habitats continued to increase into June, eventually reaching significantly higher levels in the last sampling period ($\chi^2 = 4.58$, df = 1, $P = 0.03$; Fig. 4). This increase was due in part to later-arriving yearlings, which arrived at mature forest sites at the end of May and at early successional sites in early June (pers. obs.). If only ASY birds are used in analysis of arrival
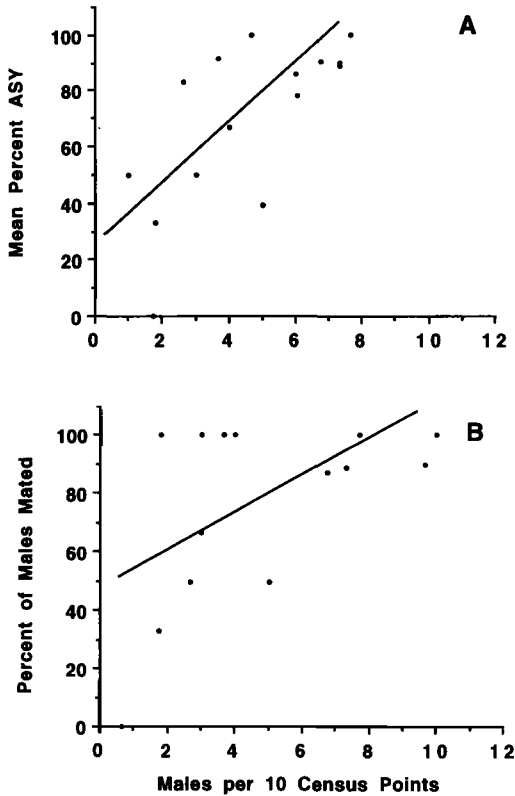
FIG. 3. Relationships between abundance (three-year mean) and (A) age ratios and (B) mating success of male American Redstarts at sites spanning all three habitat types. Differences in point locations between (A) and (B) result from different sites being used in each analysis. Age ratios are from sites censused in two or three years, whereas mating success is from 1994 only.

FIG. 4. Arrival schedules of male American Red-starts (mean ± SE) by habitat between 7 May and 3 June 1994, and breeding densities in mid-June. Sample sizes: early successional ($n = 3$ stands), mature deciduous ($n = 4$), and mature coniferous ($n = 2$). Only sites that supported three or more breeding males were included in analysis.

time, the divergent pattern is retained, but the final difference between habitats is not significant ($\chi^2 = 2.58$, df $= 1$, $P = 0.11$). All but one of the yearlings residing on early successional and mature deciduous sites arrived after all the ASYs had established territories, and many were not recorded until after the arrival-time surveys (i.e. during the playback census or mating-success survey in June). Coniferous stands were not occupied until 28 May, and they gradually filled to a level similar to that of the deciduous stands ($\chi^2 = 2.18$, df $= 1$, $P = 0.14$; Fig. 4). Only two of the birds settling in coniferous sites were ASYs, and these were not detected until early June, after or at the same time as the resident yearlings. There were too few females detected during the arrival surveys to determine their arrival patterns.
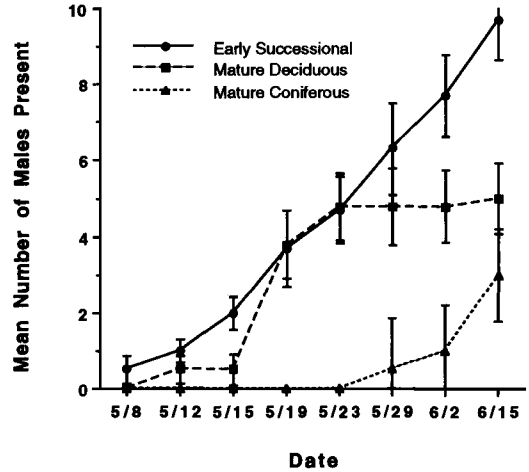
Territory size.—Territory sizes averaged 0.17 ha in Watersheds 5 (8-year-old early successional site; SE $= 0.02$, $n = 21$) and 101 (22-year-old mid-succession site; SE $= 0.037$, $n = 6$), and 0.54 ha in the mature forest (>80 years old; SE $= 0.017$, $n = 27$; Fig. 5) and were significantly smaller in the two younger sites ($F = 116.4$, df $= 2$ and 51, $P < 0.001$). Territory size did not vary between years within either Watershed 5 ($t = 1.26$, df $= 19$, $P = 0.22$) or the mature forest ($t = 0.04$, df $= 25$, $P = 0.96$). Territory size did not differ between ASY and SY redstarts within Watershed 5 ($t = 0.54$, df $= 26$, $P = 0.59$). There were too few SY territories in Watershed 101 and the mature forest plot to compare territory size between age classes.

DISCUSSION

Variation in redstart populations among habitats.—Redstart densities were highest in early successional habitats and lowest in mature coniferous forest (Table 2). The traditional interpretation of such a pattern is that densities are highest in habitats that are most suitable, in part because resource levels must be high enough to support the additional individuals (Brown 1969, Fretwell and Lucas 1969). However, high densities also could result from large numbers
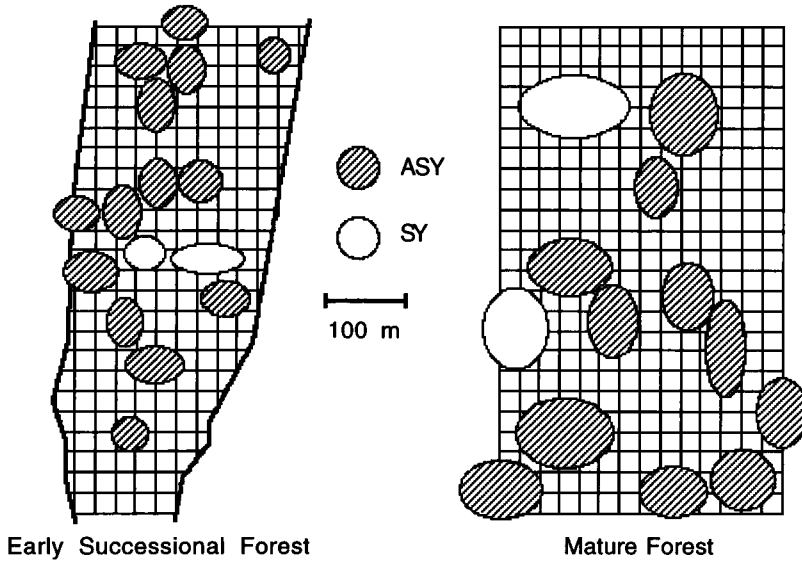
FIG. 5. Locations and approximate sizes of American Redstart territories on an early successional plot (Watershed 5; 8 years post harvest) and a mature forest plot (>80 years post harvest) at Hubbard Brook in 1992.

of subordinate individuals being forced into less suitable, resource-poor habitats (Van Horne 1983, Vickery et al. 1992). Thus, it is important to consider variables other than density when assessing habitat quality.

A better indicator of habitat suitability is reproductive success, with high-quality habitats defined as those where individuals produce the most young. Measuring reproductive success in a variety of habitats was not attempted in this study due to the intensive effort needed to obtain sufficient sample sizes. However, a number of other variables (including age class distributions and mating success) that are positively correlated with reproductive output can be used as surrogate measures of habitat suitability (Lundberg et al. 1981, Alatalo et al. 1985, Van Balen and Potting 1990, Steele 1992, Holmes et al. 1996). In the American Redstart, ASY males are dominant over SY males, and they actively exclude them from supposedly more suitable habitats (Ficken and Ficken 1967, Sherry and Holmes 1989). As a result, the relative abundance of these two age classes serves as a second measure of habitat suitability, with better habitats dominated by older birds and poorer habitats occupied more by yearlings. In this study, redstart age ratios supported density assessments: older males predominated in habitats with high redstart densities (Fig. 3A, Table 2).

This is contrary to the hypothesis that high-density habitats are occupied primarily by subordinate, in this case yearling, individuals.

Habitat quality also may vary in terms of the likelihood that a male will obtain a mate and thus potentially produce young (Gibbs and Faaborg 1990, Holmes et al. 1996). Variation in mating success thus can serve as a third measure of habitat quality in that reproductive success should be higher in habitats where a greater proportion of males are mated (assuming other factors, such as predation, do not vary across habitats). Mating success in American Redstarts varied with both habitat and age class: older males almost always were mated irrespective of habitat, whereas yearlings usually were mated in early successional habitats and often were unmated in mature forest habitats (Table 2; see also Procter-Gray and Holmes 1981, Sherry and Holmes 1989). These findings suggest that more females are settling in early successional habitats, resulting in female densities that are high enough to allow most males to obtain a mate. In mature forest, successfully mated SY males produce the same number of young as mated ASYs (Procter-Gray and Holmes 1981, T. W. Sherry pers. comm.). Thus, when combined with the higher redstart densities in early successional habitats, higher mating success should result in greater productivity per unit area, sup-

TABLE 2. Summary of habitat suitability measures for male American Redstarts in three habitats within northern hardwoods forest.

	Habitat			
Variable	Early successional	Mature deciduous	Mature coniferous	More suitable habitat[a]
Density	High	High-med.	Low	E-S or M-D
Predominant age class	ASY	Variable	SY	E-S
ASY mating success	High	High	High	All equal
SY mating success	High	Low	Low	E-S
Territory size	Small	Large	No data	E-S
Arrival time	Early	Early	Late	E-S or M-D
Nest predation	High	Low	Low	M-D or M-C

[a] More suitable habitat defined as that leading to greater reproductive output, either per individual or on habitat-wide basis. E-S = early successional; M-D = mature deciduous; M-C = mature coniferous.

porting the hypothesis that high-density habitats are more productive. Data on per capita reproductive success in these different habitats are needed to confirm these interpretations and to provide an ultimate assessment of habitat suitability.

Another measure that may reflect habitat quality is territory size, which often is assumed to reflect underlying resource levels (Smith and Shugart 1987). Specifically, birds in habitats with more concentrated or higher-quality food may not need as much space to meet their resource needs, defending smaller territories as a result (although experimental food manipulations have failed to achieve this result; see Franzblau and Collins 1980). Because some evidence suggests that insects are more abundant in early successional habitats (Edwards-Jones and Brown 1993), the finding that redstart territories were significantly smaller in early successional habitats than in mature forest (Fig. 5, Table 2) is consistent with the hypothesis that territories may be smaller in resource-rich habitats. Alternatively, reduced territory size may result from high redstart densities rather than being a consequence of higher resource levels. In extreme cases, it is possible that such reduced territories may not contain enough food to support reproduction, as might be the case if high-density habitats are primarily overflow areas for individuals excluded from more suitable habitats. Although densities in this study were higher in the habitats with smaller territories, there were always unoccupied areas of habitat (Fig. 5), suggesting that territories were not being compressed or constrained by the presence of neighboring birds. In addition, there were no detectable differences in vegetation between redstart territories and unoccupied areas in ear-

ly successional habitats (Hunt 1995), implying that most of the available area was equally suitable. These data strongly suggest that territory size, at least in early successional habitats, is not affected by redstart density (acting through territory compression) or by intra-habitat vegetation differences (as measured by Hunt 1995), leaving resource quality as a likely possibility.

If birds can accurately assess habitat quality, they might be expected to arrive at and establish territories in high-quality habitats before low-quality habitats, as predicted by the ideal free and ideal despotic distributions (Fretwell and Lucas 1969). The despotic model predicts that, as successively poorer habitats become filled, additional settlers will be forced into habitats where they cannot reproduce, or where they experience lowered reproductive success (Brown 1969). Data on arrival times for American Redstarts in my study support the conclusion that mature coniferous habitats were relatively unsuitable, in that such habitats were not settled until late in the arrival period.

The distinction between early successional and mature deciduous habitats, however, is not clear. Both habitats filled at equal rates early in the arrival period, suggesting that redstarts were not distinguishing between them at this time. Later in the season, however, densities in mature habitats leveled off, while densities in early successional habitats continued to increase. These late-settling individuals could be choosing early successional habitat for one of two reasons: (1) this habitat was of higher quality; or (2) these individuals were excluded from other, presumably more suitable habitats. If the birds settling in early successional habitats late in the arrival period were being excluded from more suitable habitats, then I would have ex-

pected them to be primarily subordinate birds, particularly SY males. Although SY males were the late arrivals in early successional habitats, their exclusion from the arrival analysis did not eliminate the divergent pattern mentioned above, although the differences between habitats were less extreme. In addition, uniformly high mating success for both age classes in early successional habitats is inconsistent with SYs being excluded from more suitable habitats. In contrast, although SYs actually arrived slightly earlier in mature habitats, they often were unmated. Late-arriving ASYs in mature habitats, even at more coniferous sites, obtained mates even when SYs that already were present did not obtain mates. The latter suggests mate choice by females, a subject that is beyond the scope of this study (but see Procter-Gray and Holmes 1981, Morris and Lemon 1988, Lemon et al. 1992). Finally, the last "arrival period" in these analyses represents a much broader range of dates (from census and mate survey data), and as such lacks the temporal resolution of the actual arrival surveys. As a result, I do not know when the last males on each site actually arrived. It is possible that some of these males dispersed into my sites after experiencing nest failure elsewhere, further confounding analysis of arrival time. Overall, I believe that the arrival data are not sufficient to distinguish differences between early successional and mature deciduous habitats. Thus, additional study of arrival patterns and within-site habitat selection are needed to clarify the possible relationships among habitat quality, territory selection, and arrival time.

Environmental factors influencing habitat suitability.—Two broad classes of environmental variables potentially can influence habitat suitability: predation pressure and resource characteristics (Smith and Shugart 1987, Martin 1995, Robinson et al. 1995b). Nest predation, in particular, can have a major effect on reproductive success. If nest predation varies consistently among habitats, then habitats with lower predation risk could be considered more suitable. I am aware of no data comparing predator abundances across successional stages. Experiments using artificial nests generally have shown that predation on shrub and sapling nests tends to be higher in early successional than in mature habitats (Yahner and Cypher 1987, Seitz and Zegers 1993, Hunt 1995), suggesting that nest predation in early successional habitats could

be relatively high (making these habitats less suitable for redstarts). However, reported predation rates may be misleading because artificial nest experiments are not always accurate measures of natural predation rates (Storaas 1988, Willebrand and Marcstrom 1988, Haskell 1995), especially when structurally different habitats are being compared (Hunt 1995). Thus, the possibility exists that predation rates estimated in these studies do not reflect real differences between early successional and mature forest habitats. If this is the case, then the role of nest predation in determining habitat quality for American Redstarts must be evaluated with further experimentation or with studies of predation on real redstart nests across an array of habitats.

Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) is analogous to nest predation because it reduces the likelihood that a nest will produce young. Parasitism also shows patterns similar to those recorded for nest predation; i.e. higher rates near edges and in habitat fragments (Robinson 1992; Robinson et al. 1995a, b). Although early successional habitats appear suitable for cowbirds, cowbirds were not detected at any of the sites surveyed in this study, probably because the surrounding forest landscape was poor feeding habitat for cowbirds. As a result, it is unlikely that brood parasitism is an important component of habitat suitability in my study area, and perhaps in most heavily forested areas in northern New England.

Like predation, resource abundance can affect habitat suitability by influencing reproductive output (Holmes et al. 1991, Rodenhouse and Holmes 1992), although the importance of such effects in maintaining population levels remains to be tested (Martin 1991). Food resources also may affect population density. If birds occupying habitats with more abundant food defend smaller territories, then these habitats will support higher densities. All else being equal, if an individual's territory has sufficient resources for reproduction, then per capita reproductive output may not vary among habitats. In such cases, redstarts would not necessarily choose one habitat over another, and high-density habitats would be considered more suitable simply because they support a greater proportion of the population. The initial similarity in redstart arrival patterns, where birds appeared to settle evenly between early successional and mature deciduous habitats, is con-

sistent with this latter possibility. In addition, even if resources are equally abundant in all habitats, qualitative differences (e.g. insect phenologies or growth rates) could affect reproductive success and thus the habitats selected by individual birds.

Measurements of several variables indicate that early successional forest habitats are more suitable for American Redstarts than are later seral stages. In particular, redstarts in early successional habitats are characterized by high densities, high proportions of ASY males, and high mating success among yearling males. My results do not support the hypothesis that high-density habitats are dominated by nonbreeding subordinates, and they also contradict previous studies that found higher redstart densities in mature forest (e.g. Morgan and Freedman 1986, Thompson and Capen 1988). The latter differences may be due in part to differences in sampling effort, based on my observation that densities in both early successional and mature deciduous habitats vary over roughly the same range. If relatively few sites are investigated, there is a greater chance of choosing sites that do not contain representative densities for a given habitat. It also is important to consider interannual variation in the relationship between habitat use patterns and density. For example, if only the 1993 data were considered, my conclusions would have been very different. With respect to redstarts, 1993 was an outlier, probably because of regionally high rates of nest predation in 1992 resulting in low yearling recruitment (see Sherry and Holmes 1992), low redstart densities, and high proportions of ASY males. The latter observation also points out the need to measure other important indicators of suitability such as age ratios, mating success, and arrival time—variables that have been neglected in previous studies of redstart habitat selection.

Higher redstart densities in early successional habitats may result largely from smaller territories, possibly because resources are more abundant in such habitats. Thus, if territory size reflects minimum resource needs, habitats with more territories will produce more young per unit area, making them more suitable in terms of their contribution to regional population dynamics. In a related study, output from mathematical models incorporating such variation in carrying capacity showed that redstart populations declined as early successional habitats

matured (Hunt 1995). In addition, these simulated populations showed trends very similar to those of redstart populations in northern New England (Breeding Bird Survey data) when historical data on vegetation changes were included in the model. It is thus possible that, as early successional forests mature into less-suitable habitats, redstart populations may decline as a result of decreasing regional productivity. Further research on redstart populations in early versus late successional habitats is needed to determine the relationships among resource levels, nest predation, and reproductive success. Such research also could lead to a better understanding of the relationships between habitat selection and population changes in migratory birds.

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