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A Foraging Time-Activity Study of Breeding Songbirds

in a Successional White Spruce Community

**A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science in the Department of Biology**

by

Thomas S. H. Baxter ©

Lakehead University

Thunder Bay, Ontario

March 1999



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Abstract

I investigated the amount of time spent on foraging by birds in a successional white spruce community, during semi-monthly time blocks, in the context of flying, singing and other activities. Five hypotheses were tested: 1) cumulative amounts of time spent on foraging and other activities by birds vary throughout the breeding season and among species; 2) bird species differ in the mean amount of time spent per event on different activities; 3) birds spend more cumulative time in the study area foraging on spruce than on other plants; 4) birds capture more prey on spruce than on other substrates; and 5) prey capture rates differ among species. All bird actions on the study area that were observed with binoculars were counted, timed and recorded. Data for White-throated Sparrow, Song Sparrow, Lincoln's Sparrow, Clay-coloured Sparrow and Savannah Sparrow were analysed. Cumulative foraging times among periods were not significantly different in 1991, but differed for White-throated Sparrow in 1992. Mean foraging times differed only in late July 1992 for White-throated Sparrow and Clay-coloured Sparrow. Foraging, except for Savannah Sparrow, occurred mostly on white spruce, but use of tree species differed among periods in both years. Spruce budworms were most commonly taken between 15 June and 15 July in 1991 and 1992. Prey capture rates differed significantly among bird species in late June 1991, in late June 1992 and early July 1992. Therefore, each hypothesis was supported, but not in each time period. Such variations in bird activities during the breeding season reflect breeding stage and changing ecological conditions. I concluded that sparrows foraged similarly when spruce budworm was most easily obtained. These results were obtained only by the method of dividing the breeding season into time blocks, and by recording time durations rather than counts of events. I recommend that including variables in time as well as space be the new norm in studies of avian life history dynamics.

Introduction

The roles of birds in natural communities have sparked much debate in ecology. Resources required by birds, such as habitat and food, are used to support life and may limit fitness or may affect population dynamics (Andrewartha and Birch 1984; Wiens 1989a). Food acquisition and use by birds, therefore, must be important in defining their ecology (Wiens 1989a,b). Studies of food resources have focussed on diet, food abundance, food availability, and amount consumed (cf. Morris et al. 1958; Busby and Sealy 1979; Robinson and Holmes 1982). Bird collectors in the 19th and early 20th centuries confirmed that birds have varied plant and animal diets (Bent 1968 a,b). How food is obtained has been one of the prime reasons for studying foraging (Holmes 1990a, Wiens 1989a). One might expect that foraging rates (numbers of specific manoeuvres per unit time) and prey capture rates (prey numbers consumed in time) would yield comparable, quantified estimates of total prey consumption, but methods conflict.

MacArthur (1958) used both numbers of observations and duration of foraging time in different tree heights and branch positions to estimate resource partitioning of spruce crowns by warblers, evidence for his paradigm of competition-driven ecological processes. Root (1967) had suggested that organisms belong to guilds, which employ similar ways to exploit the resources of their environment, a concept that fits well with resource partitioning.

MacArthur and MacArthur (1961) investigated the relationship of bird species diversity to "foliage height diversity" and "plant species diversity" indices, which led to investigations by others of correlations between bird species abundance and physiognomy of habitats (collectively referred to as "structural variables") (MacArthur 1972; Cody 1974). More recently, however, Rotenberry (1985) found that structural variables accounted for only one third of the variation in bird abundance in habitats, whereas floristic composition was most significant. Earlier,

Rotenberry (1980a) had found that shrubsteppe birds had similar diets at any given time, but diet composition varied throughout the season, indicating opportunistic feeding. Later, Rotenberry (1985) speculated that response to floristics equated to specific food resources on plants.

Morse (1968, 1976a,b, 1978, 1980, 1989) found that male spruce-woods warblers foraged at greater heights than females, although there was much overlap. Types of foraging behaviour, and capture rates in relation to time of day and prey availability, have been studied in detail in northern hardwoods at Hubbard Brook Experimental Forest, N.H. (Holmes et al. 1978; Holmes, et al. 1979a,b; Robinson and Holmes 1982; Holmes et al. 1986; Holmes and Shultz 1988). Fitzpatrick (1980), studying neotropical tyrant flycatchers, and then Robinson and Holmes (1982) in New Hampshire, established that passerine birds forage at different rates (smaller birds like warblers usually moving more rapidly) in the crowns of different tree species, using various foraging tactics (glean, hover, hanging, flush-chase (tumble), hawk) with varying degrees of skill. Some, but not all birds forage in response to available prey, especially outbreaks of Lepidoptera (Busby and Sealy 1979; Holmes and Schultz 1988).

Most foraging studies of North American birds have been done in the eastern United States, where hardwood (deciduous) forests predominate (Holmes et al. 1986) and in prairie, shrubsteppe habitats of the west (Wiens and Rotenberry 1980, 1981). A few, like Arcese and Smith (1988), have been done on the Pacific coast. In general, these studies have concluded that, 1) prey species usually occur in low numbers (abundance); 2) songbirds exploit a wide range of taxa in their diets, which may vary from year to year; 3) prey outbreaks are uncommon, and occur with great variation in frequency, magnitude and duration; 4) food supply is usually limited (availability), and limiting to bird survival (Busby and Sealy 1979; Arcese and Smith

1988; Holmes 1990b; Rodenhouse and Holmes 1992). In eastern deciduous forests some bird species showed tree species preferences for foraging, choosing leaf surfaces, whereas others foraged on the petioles (Holmes and Robinson 1981; Robinson and Holmes 1984).

The literature has presumed that ecological communities function at or close to an equilibrium driven by resource limitation (Wiens 1989a). Wiens and Rotenberry (1979) found among shrubsteppe birds that dietary overlap among species was substantial, even though there were annual differences among individuals and species. Food supplies did not appear to be limiting. Wiens (1984) concluded that natural systems are non-equilibrial and non-competitive. More recently Wiens et al. (1991), found, after defaunation of shrubs by fumigation, that numbers of some bird species remained relatively unchanged in the first year, and prey of many types (but not Lepidoptera) recovered within a year. They concluded that ecological theory does not yet reflect the diversity of conditions occurring, and that research on arthropod and bird effects on plants requires a narrower focus on resource use.

Alternatively, avian energy budget estimates have also been made (Holmes and Sturges 1973, 1975; Rotenberry 1980b). Laboratory studies have shown that birds consume prey in proportion to energy needs, but it has been problematic to establish in the field the relationship between amount of food consumed and avian energetic demands during breeding, migration or wintering (Paynter 1974; Pinowski and Kendeigh 1977; Walsberg 1983; Ettinger and King 1980; Weathers and Nagy 1980; Williams and Nagy 1984; Weathers et al. 1984). King (1974) attributed lack of compatibility between laboratory energetic studies and avian activities in the field to the cursory attention given by researchers to the income side (food acquisition, prey identification and capture rate estimation) of the energy budget. He believed time and energy

budgets form the only common denominator for analysing life history dynamics.

Numerous methods have been devised to determine time budgets and foraging rates. Time budgets have been used to arrive at estimates of average amounts of time spent on specific activities like food acquisition, nest building or incubation. Foraging rates reveal how birds of different species forage, quantifying type of prey consumed per unit of time (Robinson and Holmes 1982). Studies on both of these topics have recorded the total number of seconds of activity, but have compared foraging activities by ranking foraging times into intervals arbitrarily chosen by the researcher (Altmann 1974; Morse 1976a; Tyler 1979; East 1982), or, by counting numbers of observations in a given period (Holmes et al. 1978). Actual time durations have not been used as the prime data for analysis.

In a totally different approach, estimates of insect consumption by birds have been made on a per-unit-area (per ha) basis (Morris 1963; Gage et al. 1970). That way, prey found in stomach samples of birds were used to determine a capture rate for the sample individuals, and then extrapolated to the population on a given study site during a season. Consequently, the methods of collecting foraging data (by direct observation in the field) have been separated from the methods of determining consumption rates (mostly lab work on collected stomachs). Both methods, though, have been used to speculate on avian impacts on insect populations.

Presumably, a link exists between foraging rates of individuals and total quantities consumed by a species in a given area. Any method that purports to estimate the impact of birds on forest ecosystems should provide a way to estimate the quantity of food taken by an individual of a given species, and then use that value to estimate total consumption by that species in a given area. Obtaining reliable estimates of the quantities of food taken by birds has been difficult

(Morris 1963; Crawford and Jennings 1989; Royama 1984, 1992). Early in this century scientists assumed that birds take enough insects to control insect numbers, keeping them below levels that cause economic damage to agricultural or forest crops (Beebe 1906; McAtee 1915, 1926; Allen 1925). Then, early studies of spruce budworm (*Choristoneura fumiferana*) determined that the sixth (final) instar larva (L_6) was the key factor responsible for 75% of defoliation and bud loss in host trees, balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*), and these same large instar larvae (from L_4 to L_6) and pupae were the life stages of budworm commonly found in avian stomachs (Dowden and Carolin 1950; Mitchell 1952; Dowden et al. 1953). Consumption estimates made from birds' stomach contents collected in New Brunswick (1945 - 1972) did not corroborate expectations of significant budworm population reductions at epidemic ($> 1\ 000\ 000\ L_4/ha$) levels (Morris et al. 1958; Morris 1963).

Consumption rate estimates, made on a quantity/ha basis, obtained from stomach content analyses have come from birds taken on separate sites away from study plots (Mitchell 1952; Dowden et al. 1953; Morris et al. 1958; Crawford and Jennings 1989). Invasive techniques (shooting or emetics (Robinson and Holmes 1982; Prys-Jones et al. 1974)) may disrupt avian territoriality and breeding through death or impairment of individuals (Stewart and Aldrich 1950), a fact only acknowledged as a methodological problem by a few (Dowden et al. 1953; Zach and Falls 1976). Recognizing the inherent difficulties in many currently used methodologies, a need has developed for foraging studies based on real-time measurements (simultaneous recording of the type and quantity of prey taken with the actual time taken to carry out the activity). The timing of events permits the direct, accurate estimation of rates of insect consumption by birds, since it is based on duration of foraging within the total time spent on all

activities (i.e. "absolute time" estimates), not just frequencies (Wiens 1969; King 1974), and it eliminates the use of invasive techniques.

Cumulative amounts of time show clearly the total proportion of time spent on each activity, which may have predictive value in identifying the extent to which bird activities reflect stresses on life history events (equilibrical or non-equilibrical processes). Mean times, by comparison, reveal variability within the data, and allow comparisons of the amount of time per event spent on each type of activity both among species, and on different substrates.

Morse (1990) and Wiens (1989a,b) have argued that foraging studies must measure what birds actually do, not impose constraints based on a researcher's perceptions, and should measure within-breeding-season differences in activity levels. This method is suited first to a single small site that favours concentration of effort so as to collect necessary fine, activity-time details, a case that I believe fits Wiens' (1989b) argument that using localized sites is the only way to answer some questions. The small, local site approach stresses learning, in some detail, how a community of birds uses one area, before making comparisons among sites (cf. Wiens 1989a).

The study reported here was designed to investigate, in real time, the absolute, cumulative time taken by different species of passerine birds in a young, white spruce-dominated community for foraging, flying, singing, and other activities like perching. It also investigated the mean amount of time spent by different species on each of those activities. In addition, this study investigated the type and quantity of prey taken by birds, including capture rates, in real time, which ultimately may permit estimation of total insect consumption by birds.

The hypotheses tested were: 1) cumulative amounts of time spent on foraging and other activities by birds vary throughout the breeding season, and among species; 2) bird species differ

in the mean amount of time spent per event on different activities; 3) birds spend more cumulative time in the study area foraging on spruce than on other plants; 4) birds capture more prey on spruce than on other substrates, and 5) prey capture rates differ among species.

Study area

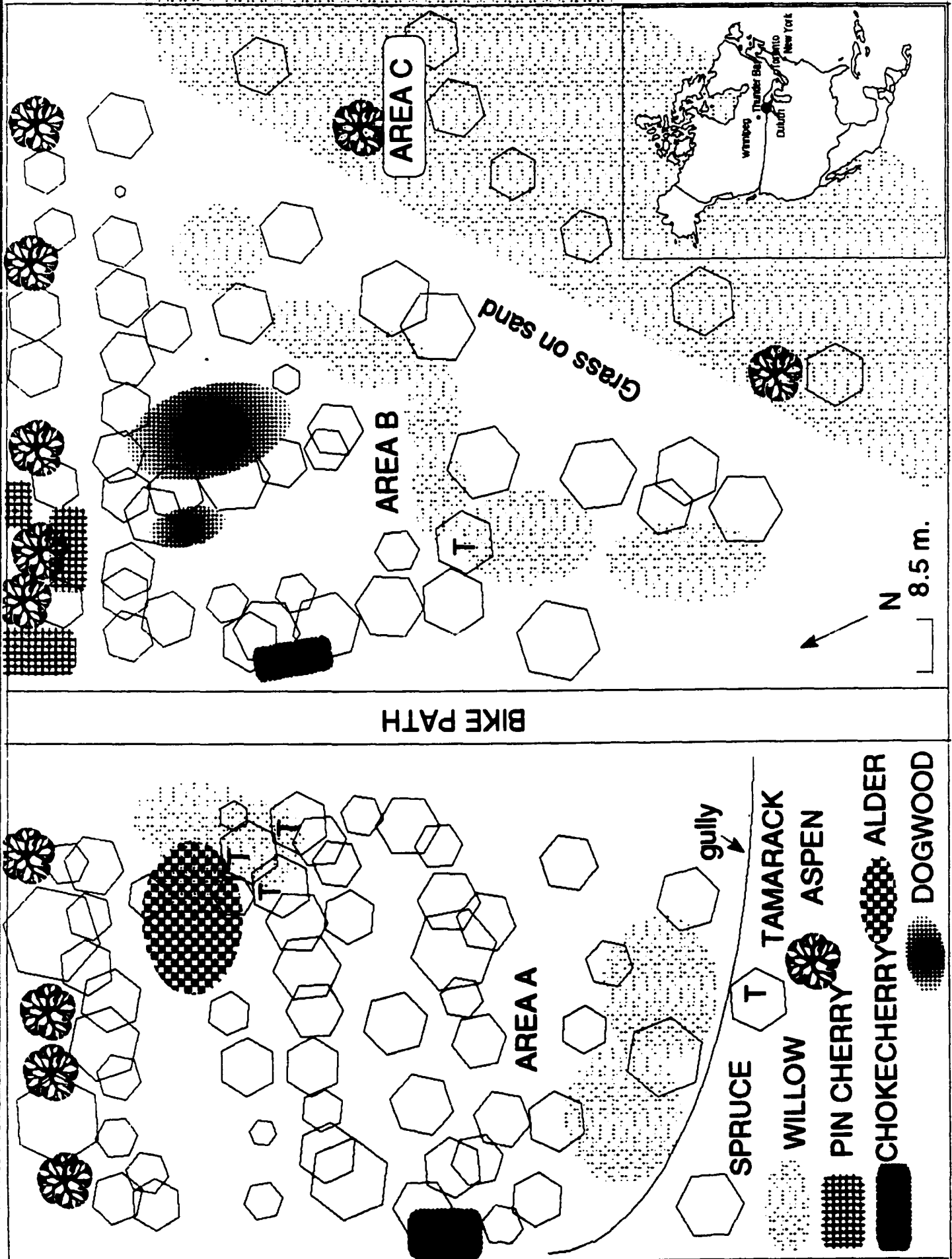
A small study plot (2.5 ha) was chosen, part of a 25-ha, mostly forested, area which was located adjacent to the campus of Lakehead University, Thunder Bay, Ontario (48°25'N; 89°15'W). It provided convenient access, making possible an early start to field studies each day and yielding long blocks of time on most days to closely monitor avian activities, including identification of prey taken and use of the available plant groups (Fig. 1).

The plot consisted of a clearing (former farmland) with white spruce (*Picea glauca*: 333 trees over 3.5 m high) at the thicket stage of succession (clumps of spruce with branches interconnecting (Sutton 1992)), plus large clumps of deciduous shrubs (especially willows, *Salix* spp., up to 3 m high, and red-osier dogwood, *Cornus stolonifera*, about 1.5 m high). Pin cherry (*Prunus pensylvanica*), and choke cherry (*Prunus virginiana*) occurred in small patches and serviceberry (*Amelanchier* spp.) was scattered throughout the study area.

A paved city bike path running north to south bisected the plot into approximately two-fifths on the west side (called Area A) of the path and three-fifths on the east side (Area B). Herbs, grasses and sedges grew throughout the plot. To the north was a more mature, second-growth forest stand of trembling aspen (*Populus tremuloides*) (ca 8 m) and white spruce (ca 14 m). Willow thickets, with spruce and aspen, dominated the eastern edge of the plot (Area C). Locations of dominant trees were plotted by compass angles, and measured (in m).

Fig. 1: The study area

.



Methods

Observation of the avian community: identification of individuals, territories and nests

All individuals of each bird species seen within the study area were identified by species, and by sex where possible, and counted. In the absence of colour-marking, which was not used, males using the same song posts in the same area, while also driving other males away, were considered territory holders (Kendeigh 1944; Knapton 1979). Paired females of the monomorphic species were identified by consistent, non-aggressive interactions with males within specific territories. Attempting to identify the sexes, and to define mated pairs in their territories, were important efforts in helping to relate activity (especially foraging) levels to demands for food.

Nests were found by chance, or by following birds carrying nesting materials or food. Active nest searches were not undertaken after mid-summer 1991 when a bold red fox (*Vulpes fulva*) was discovered following me to nest sites and consuming their contents. Nests that were found, and observation of copulatory activities, were used as an indication of stage of breeding.

Time-based observations: counting and timing of activities; foraging details and diets

Behavioural observations of birds were undertaken in 1991 from 8 June until 31 July, and in 1992 from the onset of territoriality of the earliest males to arrive (ca. 10 May) until 15 August. Several vantage points were used repeatedly for observing birds, collectively permitting sampling of avian activities over the whole site. The activities of all bird species seen on the study site were recorded in order to determine the extent to which each bird used spruce. All activities of an individual bird, observed from one vantage point on each occasion, were recorded, counted and timed (duration) with reference to four categories: foraging, flight, song and other (mostly perching). An activity sequence might include any, some, or all of the activity

types. A foraging sequence (or event) could occur alone or as part of a sequence of activities. Both a tape recorder and a field notebook (using a "shorthand" notation) were used for records.

As plant foliage was the substrate for all but isolated cases of foraging, plants were grouped into four categories: spruce, deciduous trees, shrubs and ground (the latter composed of grasses, sedges and herbs). Numbers of perch changes, type of perch change (after Robinson and Holmes 1982), plant group (e.g. *Salix* sp.), number of plants used, prey attacks (jabs made), prey captures (a prey item was seen to be seized with the bill), and prey type (identified with 9-power binoculars to the finest taxonomic category possible (e.g. spruce budworm was recognized by its distinctive colouring, whereas most caterpillars were only distinguishable as Lepidoptera)), were recorded for each foraging sequence. Unidentifiable insects were simply "other insects."

The total time of all songs in an activity sequence was recorded. Other time was dominated by perching, but included vigilance (in males, recognized by peering around during perching), incubation (where females could be seen on the nest from a specific vantage point), preening and copulations. Observation sessions were conducted daily, weather permitting. They were not less than two hours in length and not more than six hours, with most occurring between 0600 and 1500 hours Eastern Daylight Time (EDT). Although some observations were made as late as 2300 hours, efforts were focussed on mornings. Temperatures ($^{\circ}\text{C}$) were recorded in each outing with a hand-held thermometer at the start, middle and end of observations.

To compare differences in foraging times over the breeding season, data were grouped into semi-monthly time blocks (01-15 May, 16-31 May, 01-15 June, 16-30 June, 01-15 July, 16-31 July, 01-15 August) and treated as independent data sets. Time blocks in May and early June yielded insufficient data for analysis and were not used again. Semi-monthly time blocks were

chosen because passerine birds incubate for about two weeks, followed by about two more weeks from hatching to independence (Bent 1968a,b). Robinson and Holmes (1982) and Holmes et al. (1986) stated that the main breeding period, when most nesting occurs, for passerines at 45-49° N latitude, is 15 June to 15 July. Time blocks defined as semi-monthly periods, therefore, may have been somewhat arbitrary, but served as suitable references for studying bird activities, an approach which is not new. Guinan and Sealy (1987) used 12-day sampling periods.

Each day's observations began by locating singing males, and by watching for movement or activity of any bird. Male territories were compared with those identified the previous day to confirm occupation of the same area. A "focal animal" (Altmann 1974) was selected that was easy to see and usually within close range (or clearly discernible in binoculars). All activities that occurred from the time an individual came into view until it went out of sight were recorded and timed; if the individual changed plant substrates during the sequence then a new sequence was considered to have begun. Most observations were under five minutes in length. A new sequence was started with the same or a different individual as events dictated, as was done by Robinson and Holmes (1982). Some individuals were observed for more than 5 minutes. Due to the openness of the site, long departure flights were often witnessed. No birds were followed.

Birds were considered to be foraging when they made deliberate movements along a branch or hopped from branch to branch, usually accompanied by head and eye movements up, down or to the side, directed at different portions of foliage. Wing-assisted hops across branches in adjoining tree crowns were considered foraging rather than search flights, whereas flights to other trees nearby were counted as actual flights (Robinson and Holmes 1982).

Estimation of foliage surface area as an index of relative abundance of insects

A preliminary count of insects on 30 branch tips of no fewer than four spruce trees was made in early June of both years, but was not extended to other plants, nor continued through the season, due to the time commitment required for avian observations. During observations of birds, however, inspections of plants were made after birds captured insects on them, to find insects matching the same size, shape and colours as observed. Insects observed were identified in the field using Rose and Lindquist (1977, 1982) and Ives and Wong (1988).

The heights, determined with a Suunto™ clinometer, and the crown diameters (measured at the ground with a tape measure) of 21 spruce trees distributed throughout the site were taken each September. As an index of relative insect abundance, foliage surface area was calculated, by treating each spruce tree as a cone (assuming that spaces between branches were balanced by multiple shoots per branch). Mean height and diameter of the sample of trees was used to determine the surface area. Shrubs were treated as spheres for estimating surface area. Obtaining an absolute insect population estimate would have been preferable (Southwood 1978), but this relative method avoided potential bias to sampling avian foraging by destructive methods.

Data analysis: calculation of cumulative totals, means, and tests

The cumulative totals of time spent on each activity and on different substrates were integer data so they were treated as counts (i.e. of time). As such, however, they were unsuitable for contingency table analysis because total amounts of time recorded differed in each semi-monthly period. Consequently, cumulative amounts of time spent on various activities (foraging, flight, song and other activities) were converted to percentages of total recorded observation time. Each set of percentage time data spent on foraging, for the whole bird community, and for

species yielding sufficient data, in all semi-monthly time periods, was converted by arcsine transformation and tested by χ^2 contingency table analysis for independence (Sokal and Rohlf 1981). Expected frequencies, computed from within the data, assumed that foraging times should be equal in all time periods. Due to the number of tests run, significance was accepted only at the $P < 0.001$ level to minimize Type I error (Rohlf and Sokal 1981; Holmes and Shultz 1988).

All time-duration data were inherently asymmetrical about the mean with the standard deviation coupled to the mean (increasing or decreasing with the mean). To uncouple the deviation from the mean and for normalization, these data were transformed to natural logarithms (Sokal and Rohlf 1981). Tests on the variability about the mean of each group of transformed data (e.g. foraging, flight, song or other) among species were made by determining mean and standard deviations, computing 95% confidence intervals, and then back-transforming to report geometric mean and confidence limits in seconds (Sokal and Rohlf 1981). Back-transformed data remained somewhat heteroscedastic since there were commonly occurring activity times (e.g. 10, 20, 30, 60, 120, 150 sec) and, occasionally, very long activity sequences. Geometric means underestimate the true (*sic* arithmetic) mean, but transformation has merit in normalizing data, allowing statistical testing of variability (Sokal and Rohlf 1981; Zar 1984). Southwood (1978) also pointed out that whenever data is transformed the reader should have access to a summary of the raw data in order to make comparisons. Each set of activity time data (natural-log-transformed) in each period was tested by Kruskal-Wallis tests to compare means among species; Kruskal-Wallis tests are less sensitive to heteroscedasticity than ANOVA (Sokal and Rohlf 1981).

Multivariate analyses were not considered seriously for either cumulative time data or mean time data because multivariate statistics characteristically change the data structure (through

calculation of eigenvalues and other tools; and some considerably greater time investment than already invested would have had to be devoted exclusively to a variety of exploratory techniques to find a multivariate distribution that might work on the data: cf. Seber 1984). I was seeking to retain the original time structure of the data as much as possible. Statistical calculations were performed on SPSS (Norusis 1993).

For each species, and for the entire avian community, foraging time data, as a percentage of total activity time (arcsine-transformed), on spruce versus deciduous shrubs and trees, were tested against the percentage surface area of foliage of that group on the site by χ^2 .

To test whether or not prey were taken in proportion to the availability of substrates, the percentages (arcsine-transformed) of total prey captures on spruce and on deciduous plants were tested by χ^2 against the percentage (arcsine-transformed) of available foliage surface area for these plant groups on the site.

Two ways of determining prey capture rates were employed. Firstly, "capture rates," in real time, were derived by dividing cumulative totals of spruce budworm captured on spruce, and of all prey captured from all substrates, by the cumulative total of time spent on all activities. A χ^2 -single-classification contingency test for proportions was performed on overall capture rates (total prey / total time spent on all activities); differences among species were detected by a modified Tukey test for multiple comparisons of proportions (Zar 1984).

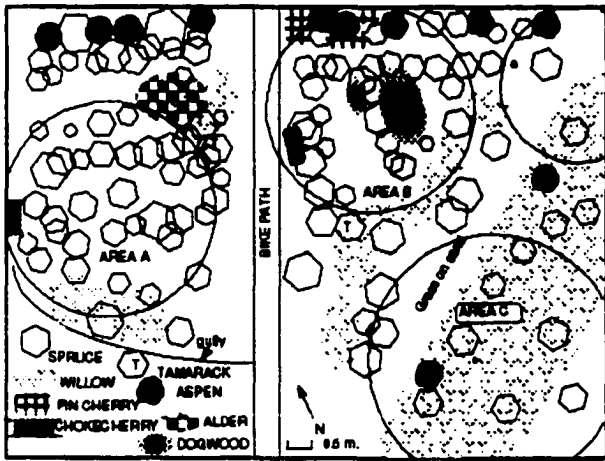
By the second method perch changes, prey attacks and prey captures were calculated on a per-minute basis, and then perch change-to-capture (PC) ratios, and attack-to-capture (AC) ratios were determined pairwise for all foraging sequences. These data were compared by Pearson product-moment correlation analyses (Robinson and Holmes 1982).

In recent years the possibility of data points in a foraging sequence being serially- or auto-correlated (dependent) has become a pre-occupation in the foraging literature (Morrison 1984; Hejl et al. 1990). Foraging data from many individuals has the inherent possibility of containing repeated observations of some individuals, causing loss of independence in the data. Such data are believed to underestimate sample variance (Hejl et al. 1990). Previously, Holmes et al. (1979b) addressed these concerns by testing whether subsets of first manoeuvres among foraging sequences differed from the overall data; they found no significant differences by G-tests ($P < 0.05$). They argued, therefore, that all foraging data should be used to get as complete information as possible (taking advantage of the fact that longer sequences produce more behaviours or extensions of behaviours), rather than being biased towards conspicuous behaviours as the first ones might be. I followed the example of Robinson and Holmes (1982) and Holmes and Schultz (1988) by using all observational data collected to obtain the largest possible cumulative sample size, but I focussed on time durations rather than counts.

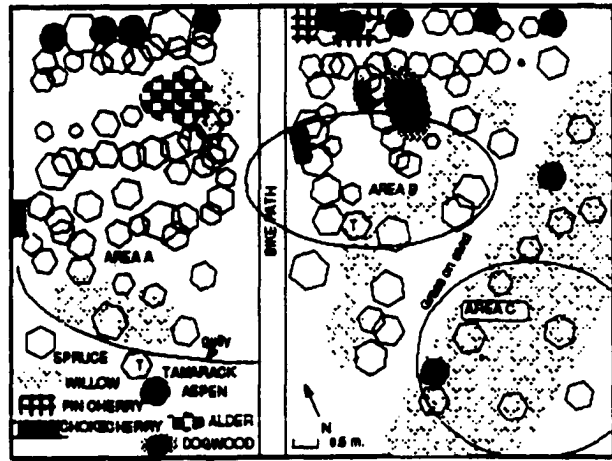
Results

In 1991 and 1992, 63 bird species (the same ones in both years) used the plot (App. A1). Territories were established by White-throated Sparrow (*Zonotrichia albicollis*), Lincoln's Sparrow (*Melospiza lincolni*), Song Sparrow (*M. melodia*), Clay-coloured Sparrow (*Spizella pallida*), Chipping Sparrow (*S. passerina*), and Savannah Sparrow (*Passerculus sandwichensis*) (Figs. 2, 3). Magnolia Warbler (*Dendroica magnolia*), Yellow-rumped Warbler, (*D. coronata*), American Redstart, (*Setophaga ruticilla*), Alder Flycatcher (*Empidonax alnorum*), Cedar Waxwing (*Bombycilla cedrorum*), and Veery (*Catharus fuscescens*) established territories that

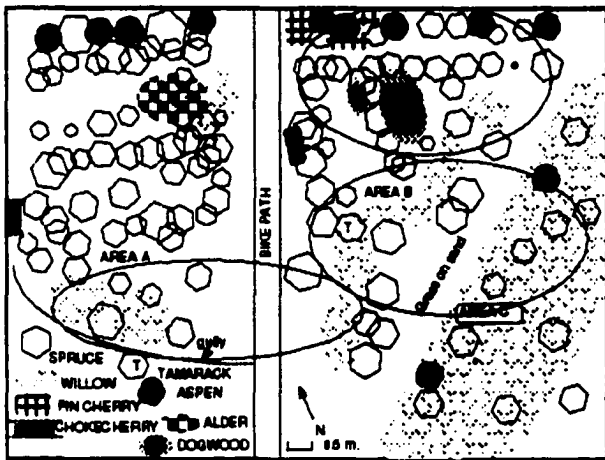
Fig. 2. Territories of sparrows on the study plot, 1991. (territories are defined by circles or ellipses that represent the areas of most concentrated activity; symbols for trees represent a prominent clump, not a single tree; individual small trees are not depicted; only major patches of shrubbery are shown: almost all spruce trees had shrubbery growing up around the base.)



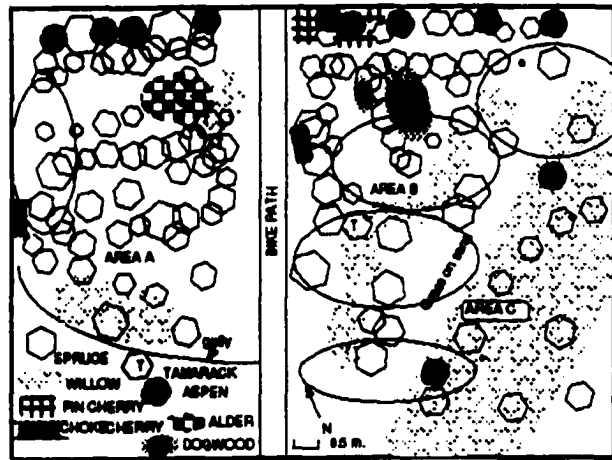
a) White-throated Sparrow



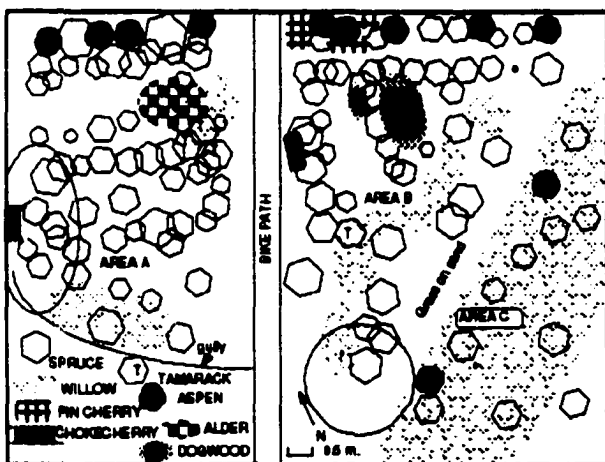
b) Lincoln's Sparrow



c) Song Sparrow



d) Clay-coloured Sparrow

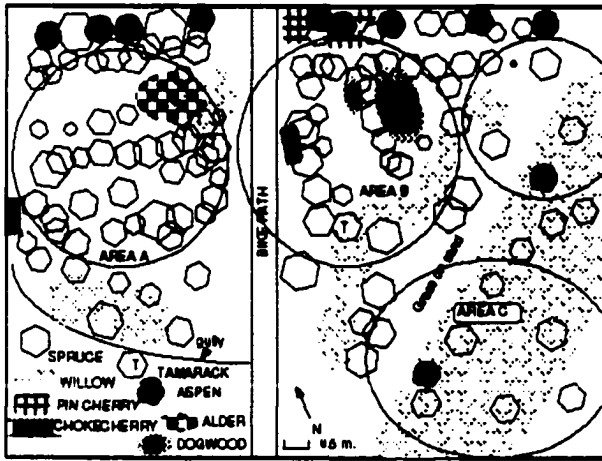


e) Savannah Sparrow

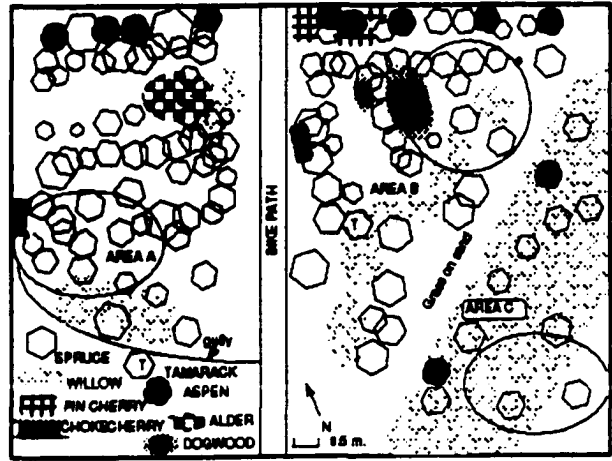


f) Chipping Sparrow

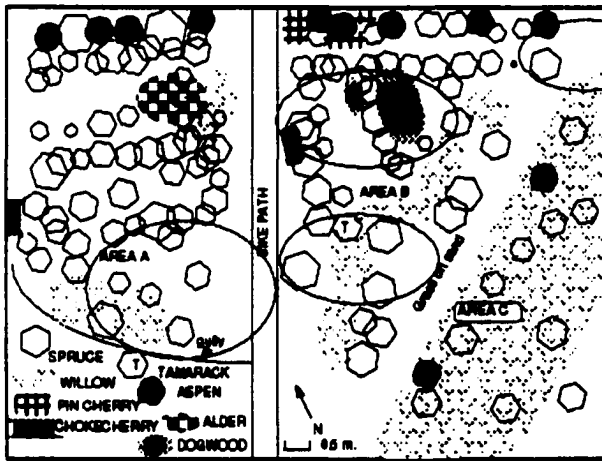
Fig. 3. Territories of sparrows on the study plot, 1992 (definitions as in Fig. 2).



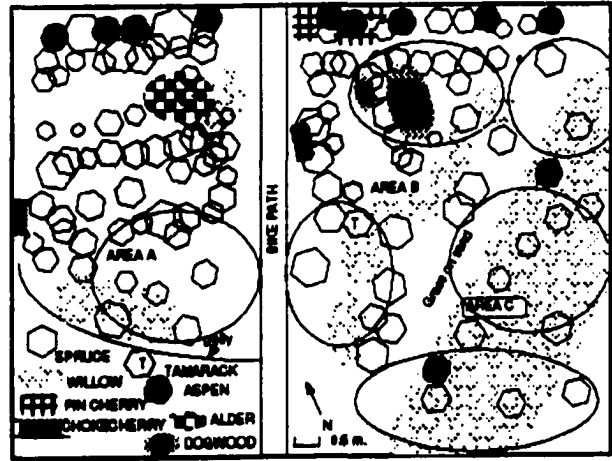
a) White-throated Sparrow



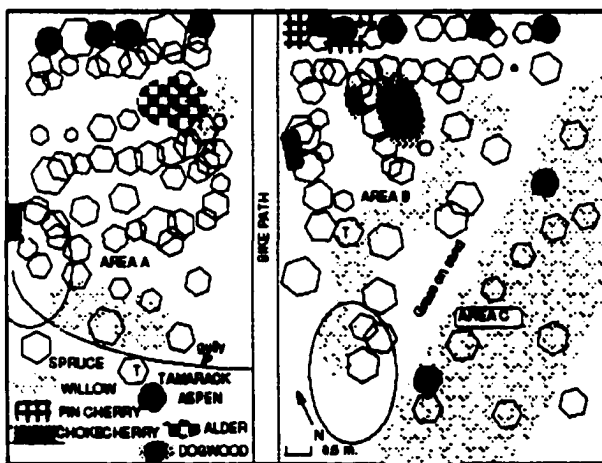
b) Lincoln's Sparrow



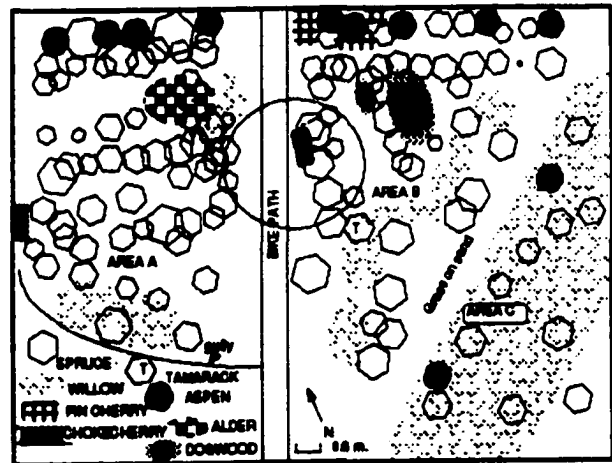
c) Song Sparrow



d) Clay-coloured Sparrow



e) Savannah Sparrow



f) Chipping Sparrow

were mostly or wholly within the plot in 1991 (App.A2); five of those species were present in 1992 (App.A3). Individual males of resident species, though unmarked, consistently occupied, sang in, and defended identifiable territorial boundaries from 15 June to late July, 1991, and to early August in 1992. Other species were seen and heard on adjacent sites; some were migrants.

Black-capped Chickadee (*Parus atricapillus*), Red-eyed Vireo (*Vireo olivaceus*), and Chestnut-sided Warbler (*Dendroica pensylvanica*) held territories just outside the study plot but used the plot regularly for foraging. One pair of American Robin (*Turdus migratorius*) nested within the plot in July 1991. A male Yellow-rumped Warbler (*Dendroica coronata*) had two mates, each of which attempted two nests in the plot in 1991; only one clutch survived to hatching. American Goldfinch (*Carduelis tristis*), which was not territorial during most of the season, was present on the plot regularly. A Magnolia Warbler pair raised a Brown-headed Cowbird (*Molothrus ater*) chick on the site in 1991. Consequently, the study plot supported territories, or parts of territories, for 12 species. Individuals of these species gave the most data.

Most resident passerine species, except Red-eyed Vireo and Chestnut-sided Warbler, were observed consuming budworms and other defoliators on spruce at some time during each summer. The Chipping Sparrow excepted, only data for the sparrows were available in contiguous semi-monthly periods, permitting separate analysis. Observational data on sparrows were gathered from individuals of White-throated Sparrow (1991: 4 ♂♂; 3 ♀♀; 1992: 4 ♂♂; 4 ♀♀), Lincoln's Sparrow (1991: 2 ♂♂; 1 ♀♀; 1992: 2 ♂♂; 2 ♀♀), Song Sparrow (1991: 3 ♂♂; 1 ♀; 1992: 3 ♂♂; 1 ♀), Clay-coloured Sparrow (1991: 5 ♂♂; 5 ♀♀; 1992: 5 ♂♂; 4 ♀♀), and Savannah Sparrow (1991: 2 ♂♂; 2 ♀♀; 1992: 2 ♂♂; 2 ♀♀). Insufficient behavioural data were available for individuals or for females alone for comparisons between sexes, within and among

species, except for White-throated Sparrow, so analyses by individual and by sex were not completed. Behavioural data on other species were retained in avian community data sets.

Nests were established by White-throated Sparrow and Song Sparrow around 20 May, but these nests were abandoned or destroyed by predators before 1 June in both years. All pairs re-nested. Copulations and carrying of nesting materials were observed in all species from the first week of June onwards. Copulations were observed commonly from sunrise until about 0800, but they occurred at other times of the day, too. Sparrows copulated in early June, and again in the last week of June or first week of July. Except for a few that started early nests, other species copulated and carried nesting materials in mid-June and mid-July. Copulation and nest-building began about one week later in 1992 than in 1991. Nests of White-throated Sparrow, Clay-coloured Sparrow, and Chipping Sparrow were found. Males sang and perched while females incubated. For Lincoln's Sparrow, Song Sparrow and Savannah Sparrow, approximate locations of nests (identified by food-carrying or flushed individuals in alarm), but not nests themselves, were found. Fledged young of all species were seen in late June and in late July in both years.

Males of all sparrow species were observed off territory with young but without females in late June or early July of both years. Females were assumed to be incubating a second set of eggs; where nests were known this was confirmed. Family groups (both male and female with young) were seen off territory in late July and early August in both years, during territorial breakdown. Therefore, two periods of nesting occurred, the first beginning in early June and extending until the first week of July, and the second from early July to early August. Most pairs of sparrows, therefore, seemed to be double-brooded.

Hypothesis 1: no difference in cumulative time invested in all activities

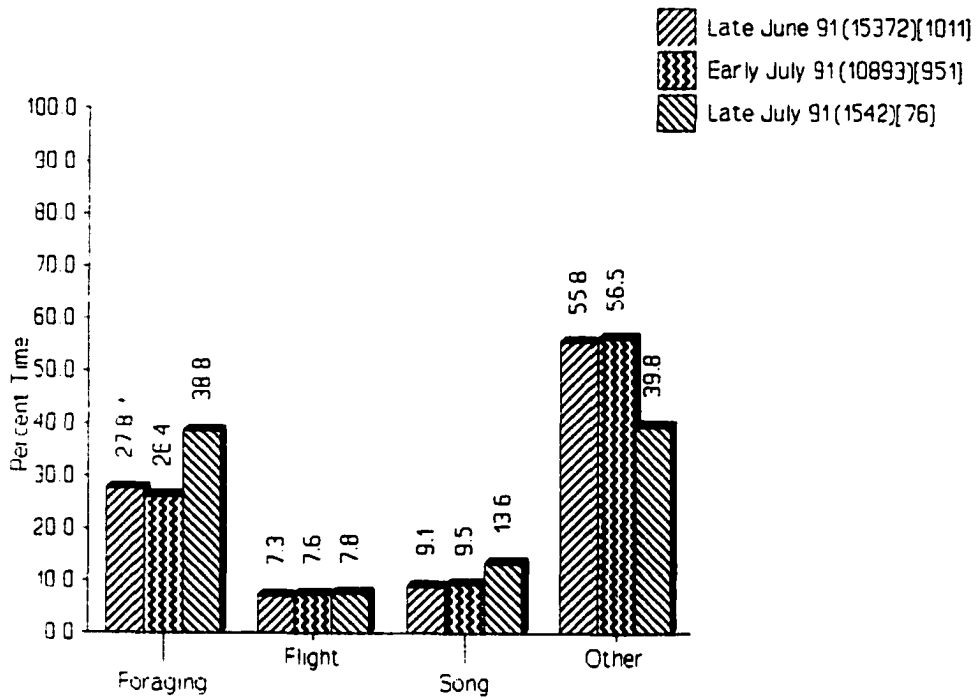
Activity levels of the entire bird community were similar, but not the same, in all semi-monthly periods in 1991 (Fig. 4a) and 1992 (Fig. 4b). Collectively the avian community foraged about 27% of the time between 15 June and 15 July in both 1991 (Fig. 4a) and 1992 (Fig. 4b), but increased towards the end of July, 1991 (Fig. 4a), and after mid-July, 1992 (Fig. 4b). Flight and song consumed small amounts of time (Fig. 4). The whole avian community showed almost constant cumulative song time throughout the study period in 1991 (Fig. 4a), but declined through 1992 (Fig. 4b; Table 1). Other time (mostly male perching with some female incubation), fluctuated in relation to foraging, flying and singing (Fig. 4).

Time proportions devoted to each activity differed among species (Fig. 5). In general, time spent foraging among semi-monthly periods in 1991 was more consistent within species than in 1992 (Fig. 5). Two nesting periods with lower foraging times, followed by increased foraging activity as young fledged, were observed for all species in 1992, but were distinguished quantitatively only for White-throated Sparrow (Fig. 5b), and Savannah Sparrow (Fig. 5j). Lincoln's Sparrow foraging times were almost constant (Fig. 5d); those of Song Sparrow declined (Fig. 5f); Clay-coloured Sparrow foraging increased (Fig. 5j).

Single-classification goodness-of-fit tests among different time periods detected no differences in foraging times among species in 1991 (Table 1). In 1992 foraging times (Fig. 4, 5) differed significantly at the $P < 0.001$ level only for White-throated Sparrow (Table 1, Fig. 5b). Savannah Sparrow foraging times would also have differed significantly had a $P < 0.005$ level been used (Table 1). No differences were detected by contingency table analysis in cumulative foraging times among all five sparrow species, for all time periods (Table 1).

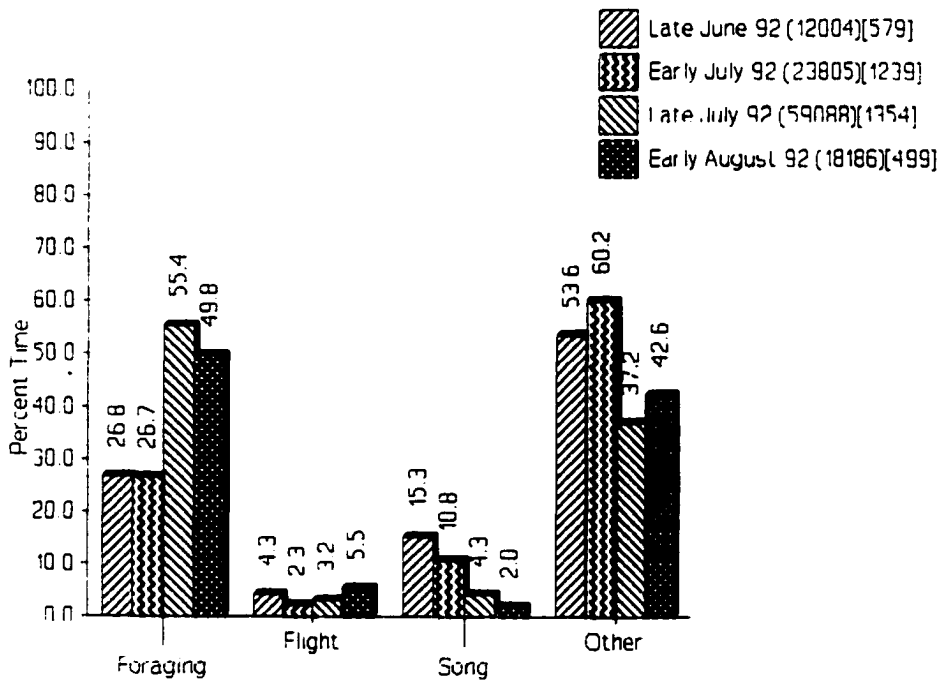
Fig. 4: Percentage of time devoted by all species to foraging, flight, song, and other behaviours by semi-monthly time period, in 1991 (a) and 1992 (b). Numbers in parentheses are the total numbers of seconds (cumulative time) invested in all activities during the respective period; numbers in square brackets are the total number of observations.

1991



a)



1992

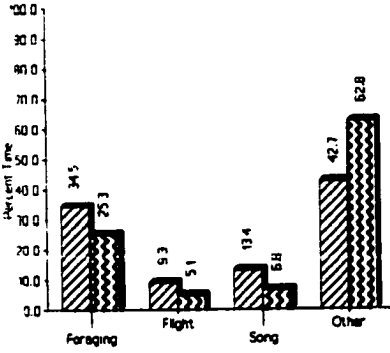


b)




Fig. 5: Percentage of time spent by sparrows on activities by semi-monthly time period in 1991 (a,c,e,g) and 1992 (b,d,f,h). Numbers in brackets are those defined in Fig. 4.

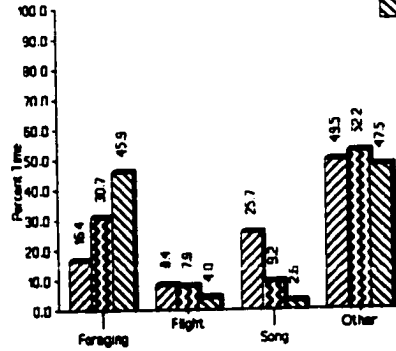
1991

 Late June 91 (730)(77)
 Early July 91 (1006)(77)



1992



 Late June 92 (657)(67)
 Early July 92 (1323)(86)
 Late July 92 (2979)(105)

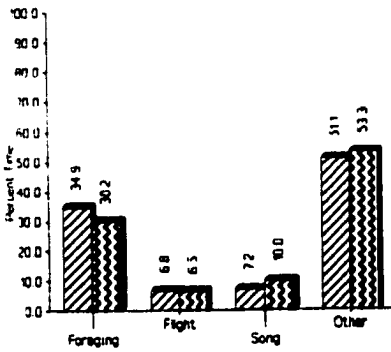





g)

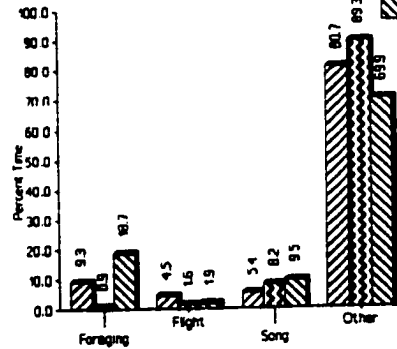
Clay-coloured Sparrow

h)

 Late June 91 (1402)(96)
 Early July 91 (739)(56)



 Late June 92 (1402)(62)
 Early July 92 (328)(62)
 Late July 92 (2305)(70)



i)

Savannah Sparrow

j)

Table 1: Chi-squared tests of avian foraging levels against the null hypothesis of no differences among time periods for the avian community and for each of the five common sparrow species, 1991 and 1992, and by contingency table analysis for all five sparrow species in all semi-monthly time periods in 1991 and 1992.

Species	1991		1992	
	df	X ²	df	X ²
All Species†	2	1.024	3	6.201
WTSP‡	1	0.001	2	17.197*
LISP	1	1.166	2	0.000
SOSP	1	2.844	2	4.702
CCSP	1	0.499	2	5.261
SASP	1	0.119	2	12.641
Five Sparrows	3	1.562	6	13.241

† All Species Observations Pooled

‡ Abbreviations of Species Names: White-throated Sparrow (WTSP); Lincoln's Sparrow (LISP); Song Sparrow (SOSP); Clay-coloured Sparrow (CCSP); Savannah Sparrow (SASP).

* $P < 0.001$.

Hypothesis 2: mean amounts of time spent on foraging differed only in one period

Geometric means of activities and their confidence limits are shown in Tables 2 and 3 (raw data summaries in Apps. B1, B2). There were no extreme limits (a value of the limit deviating from the mean by more than the size of the mean itself) calculated for 1991 data (Table 2). Several extreme limits were calculated for 1992 (Table 3). Confidence limits tended to encompass very narrow ranges if there were many observations, and extreme ranges if there were only a few observations (Tables 2, 3). In 1991, most observations were under 120 seconds, whereas, in 1992, time durations varied widely.

Data with wide confidence limits included some observation periods in excess of 200 seconds. For instance, in late June 1992, 5 observations of foraging in the Song Sparrow totalling 359 seconds were marked by extremely wide confidence limits, while 5 foraging observations for Clay-coloured Sparrow amounting to only 107 seconds, produced upper and lower confidence limits each less than the size of the mean (Table 3). Similar contrasts were evident in July 1992 (Table 3). Wide confidence intervals were common in foraging and other activity data (Table 3).

The mean amount of time invested per foraging event (the part of an activity sequence which involved foraging) by the five species of sparrows was significantly different only in late July 1992 (Table 4). In that time period differences among sparrows in mean foraging times occurred on spruce (Table 4), due to different mean foraging times of White-throated Sparrow (44.4 s) and Clay-coloured Sparrow (16.6 s) (Tukey's honestly significant difference test, alternate procedure for unequal sample sizes: $q_{(207)(5)} = 36.64$, $P < 0.001$; Zar 1984).

Table 2: Mean and 95% confidence limits for activity times (seconds) of the avian community and five common sparrow species, 1991.

Particulars	Foraging				Flying				Singing				Other				Total of All Activities				
	#obs	L ₁	mean	L ₂	#obs	L ₁	mean	L ₂	#obs	L ₁	mean	L ₂	#obs	L ₁	mean	L ₂	#obs	L ₁	mean	L ₂	
All Species																					
16-30 June '91	111	16.1	18.9	22.1	318	3.2	3.3	3.5	515	2.6	2.6	2.6	352	10.8	12.2	13.8	1011	6.3	6.8	7.3	
01-15 July '91	101	16.1	18.5	21.2	244	3.1	3.3	3.4	388	2.6	2.6	2.7	417	10.5	11.3	12.1	951	6.5	6.9	7.4	
16-31 July '91	20	18.4	23.5	30.0	19	3.3	4.0	4.7	77	2.5	2.7	2.8	32	7.9	10.0	12.7	160	4.9	5.7	6.6	
White-throated Sparrow																					
16-30 June '91	27	12.4	15.7	19.9	51	2.5	2.8	3.1	49	2.9	2.9	3.0	65	9.4	12.4	16.3	139	8.3	9.8	11.6	
01-15 July '91	11	12.4	21.1	35.4	13	2.4	2.9	3.9	36	2.8	2.9	3.0	34	9.3	11.9	15.4	80	6.1	7.7	9.5	
Lincoln's Sparrow																					
16-30 June '91	16	15.6	21.7	30.0	22	2.4	3.1	3.9	33	2.8	3.0	3.2	34	15.9	21.4	28.7	79	8.6	11.2	14.5	
01-15 July '91	7	14.3	18.6	23.9	9	2.8	2.7	3.8	13	2.6	2.8	3.1	24	9.5	14.7	22.5	38	7.5	10.9	15.5	
Song Sparrow																					
16-30 June '91	8	9.3	13.2	18.6	11	1.5	2.2	3.0	31	2.7	3.0	3.3	12	7.4	11.9	18.6	51	5.3	6.8	8.7	
01-15 July '91	4	4.2	10.5	24.2	3	2.0	2.0	2.0	20	2.8	2.9	3.1	10	7.1	12.9	22.9	34	5.2	5.7	7.7	
Clay-coloured Sparrow																					
16-30 June '91	9	9.9	15.5	24.1	19	2.5	3.2	4.1	49	2.0	2.0	2.0	22	6.5	9.8	14.6	77	3.8	4.9	6.3	
01-15 July '91	9	8.9	12.9	18.5	16	2.5	3.0	3.6	32	2.0	2.1	2.2	36	5.7	7.2	9.1	77	5.7	7.2	9.1	
Savannah Sparrow																					
16-30 June '91	10	17.1	21.2	28.2	31	2.6	3.0	3.4	37	2.5	2.7	2.9	34	9.0	12.8	19.0	86	7.1	9.1	11.6	
01-15 July '91	8	11.6	17.5	28.2	14	2.6	3.5	4.5	26	2.7	2.8	3.0	24	6.2	8.0	10.4	56	6.2	8.0	10.4	

#obs: number of observations; L₁: lower limit; L₂: upper limit

* Extreme high or low confidence limits: the limit exceeds the size of the mean

Table 3: Geometric mean and 95% confidence limits for activity times (seconds) of the avian community and five common sparrow species, 1992.

Particulars	Foraging				Flying				Singing				Other				Total of All Activities				
	All Species	#obs	L ₁	mean	L ₂	#obs	L ₁	mean	L ₂	#obs	L ₁	mean	L ₂	#obs	L ₁	mean	L ₂	#obs	L ₁	mean	L ₂
16-30 June '92	59	19.5	25.4	33.1	93	3.6	4.3	5.0	421	2.9	3.1	3.3	99	14.9	20.3	27.5	579	5.6	6.2	7.0	
01-15 July '92	65	18.0	23.3	31.8	125	3.3	3.7	4.1	430	3.1	3.3	3.6	206	16.9	20.8	25.5	1239	7.1	7.7	8.4	
16-31 July '92	296	30.4	34.9	39.9	365	3.1	3.4	3.7	486	3.2	3.4	3.7	659	14.3	15.6	17.1	1354	12.2	13.1	14.1	
01-15 August '92	137	25.1	30.9	39.0	182	3.7	4.2	4.6	125	2.5	2.7	3.9	196	17.9	21.0	24.4	499	11.7	13.2	15.0	
White-throated Sparrow																					
16-30 June '92	21	24.4	34.8	49.5	21	2.4	3.3	4.7	66	2.7	3.0	3.4	20	10.3	18.4	28.7	99	7.1	9.4	12.4	
01-15 July '92	13	13.7	17.0	22.8	17	2.6	3.4	4.5	87	3.0	3.6	4.4	38	15.9	27.7	44.2	116	6.7	8.7	11.2	
16-31 July '92	89	35.5	42.2	50.1	77	2.1	2.3	2.6	126	3.3	3.8	4.4	101	17.6	23.3	28.1	264	16.4	19.1	22.3	
Lincoln's Sparrow																					
16-30 June '92	8	18.3	39.1	81.5*	13	2.1	3.2	4.9	62	3.0	3.5	4.1	20	9.2	21.0	46.4*	81	5.2	7.3	10.1	
01-15 July '92	6	8.3	21.8	54.9*	2	2.0	2.0	2.0	55	2.7	3.0	3.3	12	7.8	22.0	58.6*	65	3.6	4.9	7.7	
16-31 July '92	10	14.7	22.6	34.6	14	2.5	3.0	3.7	23	2.4	3.8	5.9	44	15.0	23.6	36.8	73	11.0	15.3	21.3	
Song Sparrow																					
16-30 June '92	5	21.0	57.9	156.5*	5	1.0	2.4	4.6	45	2.7	4.4	4.3	4	1.3	39.9	702.7*	49	3.7	5.5	8.1	
01-15 July '92	7	7.4	20.6	55.0*	19	2.3	3.3	4.5	31	2.6	3.3	4.0	16	21.3	45.4	95.5*	53	7.0	9.6	15.0	
16-31 July '92	2	0.6	20.2	739.7*	2	0.2	4.3	184.2*	49	2.7	3.2	3.7	11	10.7	17.4	27.8	57	7.8	9.7	12.1	
Clay-coloured Sparrow																					
16-30 June '92	5	8.5	12.4	18.0	12	2.2	3.6	5.6	57	2.2	2.5	2.9	7	3.5	17.3	72.4*	67	3.0	4.0	5.3	
01-15 July '92	10	9.9	16.8	28.1	28	2.9	3.5	4.2	44	2.0	2.3	2.7	29	8.1	12.7	19.8	86	4.8	6.3	8.1	
16-31 July '92	15	12.9	20.4	31.9	33	2.3	2.9	3.7	32	2.1	2.3	2.6	59	8.3	11.1	14.6	105	7.8	9.7	12.1	
Savannah Sparrow																					
16-30 June '92	10	9.9	20.0	39.6	20	4.1	5.9	8.2	41	2.8	3.4	4.4	21	22.5	49.3	106.8*	62	8.1	12.8	19.8	
01-15 July '92	3	10.0	10.0	10.0	12	2.4	3.6	4.2	42	2.6	3.4	4.4	29	24.2	43.3	76.9	62	7.6	11.9	18.6	
16-31 July '92	7	17.2	32.2	59.8	14	2.4	3.1	3.9	46	3.0	3.6	4.4	33	14.0	23.1	34.8	78	7.5	10.3	14.0	

#obs: number of observations;

L₁: lower limit; L₂ upper limit; * Extreme high or low confidence limits: the limit exceeds the size of the mean

Time spent singing, however, differed significantly among species in all semi-monthly time periods in both 1991 and 1992 (Table 4). Actual mean time spent singing differed little among species (Tables 2 and 3), but within the data there were wide ranges in amounts of singing from individual songs, to extended periods of songs delivered continuously when males were perched for a longer time. Also, significant effects were found in most semi-monthly time periods in both 1991 and 1992, for mean total activity times (Table 4).

Hypothesis 3: birds accumulated foraging times mostly on spruce

The foliage surface area of spruce in 1991 was 5 576.8 m² (34.8% of total foliage surface area) and for deciduous woody shrubs: 10 449.5 m² (65.2% foliage surface area). In 1992, values were: spruce (6 894.2 m², 30.1%); woody shrubs (15 985.5 m², 69.9%).

Cumulative time data showed that the bird community (Fig. 6), including sparrows (Fig. 7), foraged mostly on spruce in 1991 and 1992, although this varied with time period (Table 5). Savannah Sparrow divided its time almost evenly among substrates (Fig. 7h), with frequent trips to chokecherry between 15 June and 15 July 1991 and 1992 (Table 5).

Hypothesis 4: spruce budworm was the most common item in the diet

When birds were foraging spruce budworm was taken readily, and its distinctive markings were clearly visible in binoculars; all available life stages (larvae, pupae, moth) of spruce budworm were consumed (Table 6, 7). When foraging for prey to feed the young, adults sometimes consumed every second or third larva taken. Pupae were flipped up, and turned head-first before being swallowed. For carrying, larvae were loaded, two at a time, into the angulated commissure of the bill and then two or three more larvae were held in anteriormost positions before going to the nest. Mixed loads of larvae, pupae and moths were observed during changes

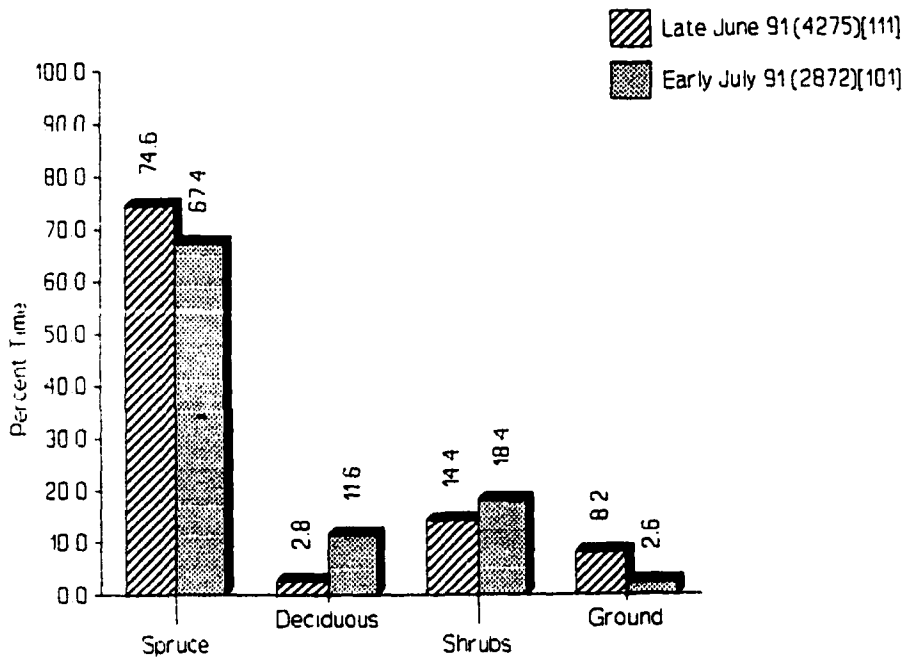
Table 4: Kruskal-Wallis analysis of variance tests of differences in mean activity time data (natural log-transformed) among the five common sparrow species.

Year	Activity	16-30 June		01-15 July		16-31 July	
		n \parallel	H \S	n	H	n	H
1991	Foraging	129	7.85	53	5.33		
	On Spruce	110	4.51	40	7.61		
	On Others	20	4.19	14	2.37		
	Flight	134	6.53	53	8.64		
	Song	199	127.15*	127	65.02*		
	Other	167	12.62	129	0.33		
	Total	481	46.37*	303	8.03		
1992	Foraging	64	12.87	60	2.06	233	14.93
	On Spruce	56	9.72	51	1.34	212	19.07*
	On Others	9	2.89	10	3.09	30	1.75
	Flight	70	14.34	78	3.83	140	15.77
	Song	270	41.21*	259	39.98*	275	31.19*
	Other	72	4.75	124	13.06	249	14.85
	Total	364	33.63*	402	11.82	701	56.01*

\parallel n: number of cases from all five sparrow species pooled;
 \S : Kruskal-Wallis H statistic;
 * significant ($P < 0.001$).

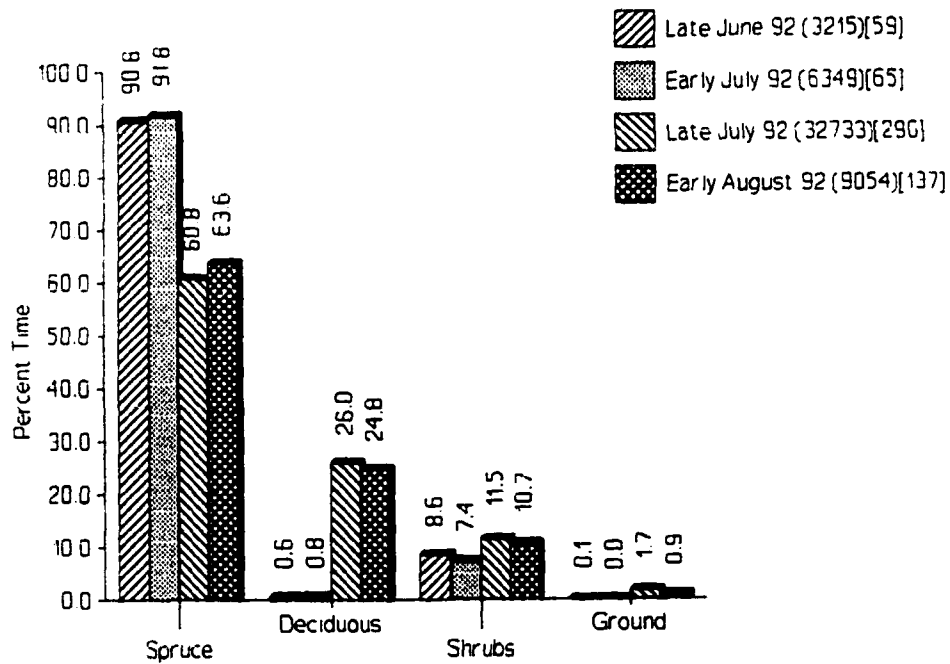
Fig. 6: Substrate use (% time) of the entire avian community (all species). Numbers in brackets were defined in Fig. 4.

1991



a)

1992

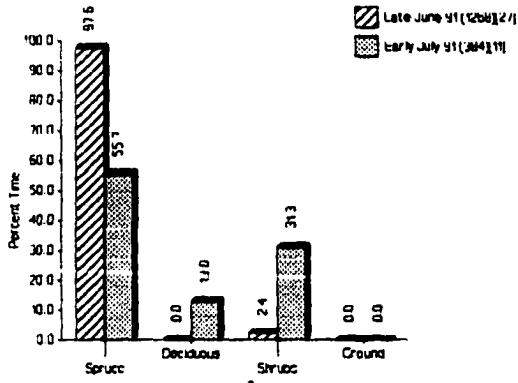


b)

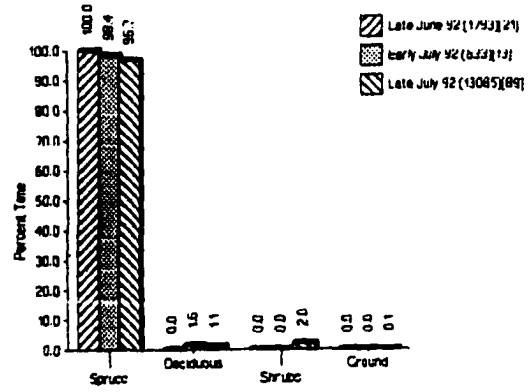
Fig. 7: Substrate use (% time) of sparrows. Numbers in brackets were defined in Fig. 4.

1

1991



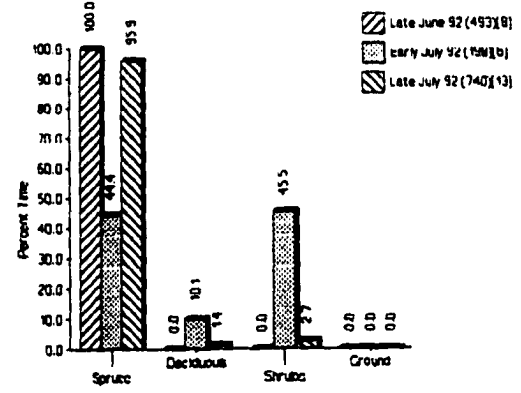
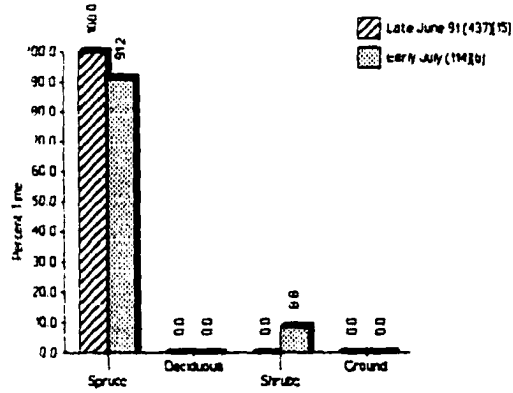
1992



a)

White-throated Sparrow

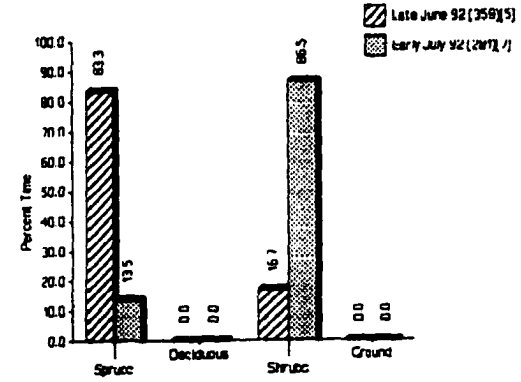
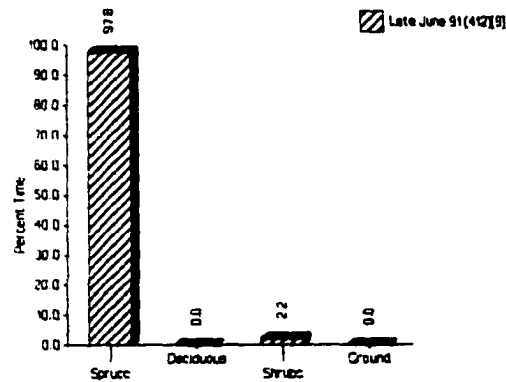
b)



c)

Lincoln's Sparrow

d)

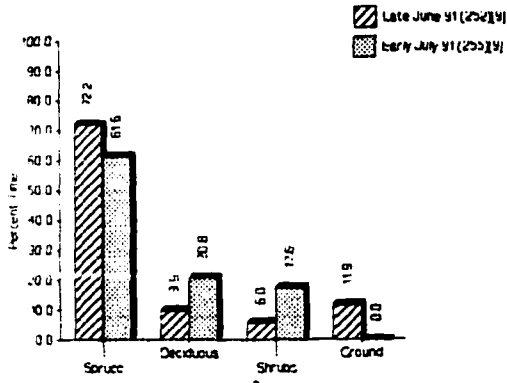


e)

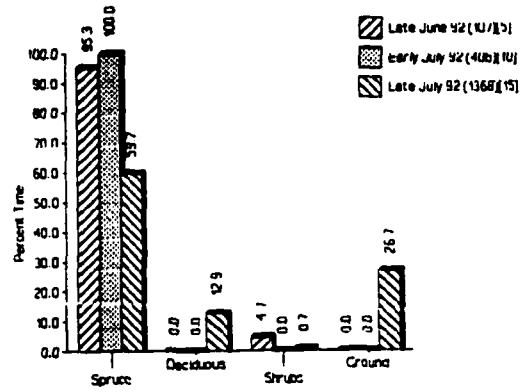
Song Sparrow

f)

1991



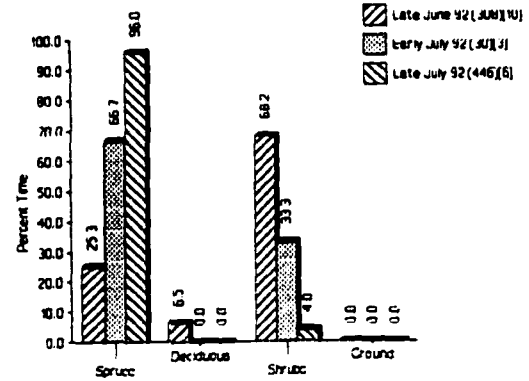
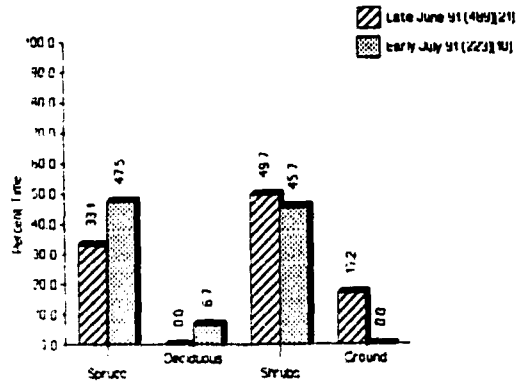
1992



g)

Clay-coloured Sparrow

h)



i)

Savannah Sparrow

j)

Table 5: Chi-squared contingency table tests of percentage foraging time spent on each plant type, versus percentage total plant foliage surface area occupied by the foliage surface area of the designated substrates (spruce and deciduous woody plants), for each time period recorded in 1991 and 1992. †

Species	1991		1992			
	Late June	Early July	Late June	Early July	Late July	Early August
	X ²	X ²	X ²	X ²	X ²	X ²
All	12.414	8.051	34.843*	36.973*	7.198	8.568
WTSP	49.061*	3.278	49.911*	53.757*	45.824*	nd
LISP	49.911*	31.128*	54.467*	1.655	47.842*	nd
SOSP	50.387*	49.911*	23.873*	3.600	nd	nd
CCSP	10.809	5.381	45.864*	54.467*	6.697	nd
SASP	0.025	1.247	0.230	10.260	48.191*	nd

† Abbreviations as in Table 1; all percentages were arcsine transformed.

* significant at $P < 0.001$; $df=1$.

nd: insufficient data for testing.

in life stages. Smaller insects were taken in smaller proportions but identification was difficult, so that some remained unidentified (Table 6, 7).

The diets of the sparrows, and much of the avian community, were dominated by spruce budworm until late July in both years, except for the Savannah Sparrow, which foraged a lot on chokecherry (especially in late June) for several types of leafrollers (particularly the oblique-banded leafroller, *Choristoneura rosaceana*) (Tables 6, 7).

When the percentage of prey taken by each species on spruce versus other substrates was tested in relation to the proportions of foliage surface area on the respective substrates, White-throated Sparrow, Lincoln's Sparrow and Song Sparrow foraged on spruce and took spruce budworm most frequently (Table 6) in both late June and early July 1991. The Clay-coloured Sparrow showed significantly more captures of budworm and other prey on spruce in late June, but not in early July, 1991 (Table 6). No bias in insect captures by substrate was found for Savannah Sparrow in 1991 (Table 6). Ground foraging was only recorded for Clay-coloured Sparrow (Fig. 7g,h) and Savannah Sparrow (Fig. 7i).

The findings were similar in 1992 (Table 7) with some important exceptions. Insignificant tests were obtained in at least one time period for each of Lincoln's Sparrow and Song Sparrow (Table 7). The Savannah Sparrow showed a bias in captures of other insects on spruce over spruce budworms in late July 1992 (Table 7).

Table 6: Diet selections and prey capture rates of sparrows and all species of the bird community combined, 1991

Particulars/prey type	WTSP†		LISP		SOSP		CCSP		SASP		All Species	
	1§	2§	1	2	1	2	1	2	1	2	1	2
Spruce budworm larvae	0	0	0	0	0	0	0	0	5	0	6	0
pupae	12	0	5	0	1	0	7	1	0	0	33	5
moths	10	7	12	2	13	2	4	1	0	3	39	35
budworm sub-total	22	7	17	2	14	2	11	2	5	3	78	40
Lepidoptera on spruce	1	0	0	4	0	0	0	1	0	0	1	7
Other prey on spruce	1	0	0	1	0	0	0	1	0	0	4	9
Total insects on spruce	24	7	17	7	14	2	11	4	5	3	83	56
Foraging time: spruce (sec)	1238	214	437	104	403	105	182	157	162	106	3189	1937
Capture rate: spruce (no./sec act)¶	0.007	0.007	0.011	0.009	0.020	0.006	0.015	0.004	0.004	0.004	0.005	0.005
Foraging events on spruce	25	7	16	6	8	4	6	6	7	4	80	62
Lepidoptera on deciduous	0	1	0	0	1	0	2	2	7	2	11	11
Other prey	0	0	0	0	0	0	0	3	0	0	83	27
Total insects	24	6	17	7	15	2	13	9	12	5	177	94
Total foraging time (sec)	1268	384	437	114	412	105	252	255	489	223	4275	2872
Total activity time (sec)	3369	1033	1595	803	709	332	730	1006	1402	739	15372	10893
Overall capture rate (no./sec act)¶	0.007	0.008	0.011	0.009	0.021	0.006	0.018	0.009	0.009	0.007	0.012	0.009
Total foraging events	27	11	16	7	8	4	9	9	10	8	111	101
χ² values: prey by substrates‡	49.911*	25.153*	49.911*	49.911*	35.496*	49.911*	21.454*	0.725	0.377	4.754	1.127	4.604

†Species codes: WTSP: White-throated Sparrow; LISP: Lincoln's Sparrow; SOSP: Song Sparrow; CCSP: Clay-coloured Sparrow; SASP: Savannah Sparrow

§Semi-monthly time blocks (periods): 1. 16-30 June 1991; 2. 1-15 July 1991.

¶ the number of insects captured on the specified substrate(s) divided by the total time (in seconds) of all activities.

‡df = 1; * P < 0.001;

Table 7: Diet selections and prey capture rates by sparrows and all species of the bird community combined, 1992

Particulars	WTSP†			LISP			SOSP		CCSP			SASP			All Species		
	1§	2§	3§	1	2	3	1	2	1	2	3	1	2	3	1	2	3
Budworm																	
larvae	26	17	1	3	2	0	5	1	4	14	1	4	2	0	44	52	5
pupae	1	2	16	0	0	0	0	0	0	0	2	0	0	0	10	3	21
moths	0	0	4	0	1	0	0	0	0	0	1	0	0	0	0	1	54
budworm sub-total	27	19	21	3	3	0	5	1	4	14	4	4	2	0	54	56	80
Lepidoptera on spruce	0	0	7	0	0	1	0	0	0	0	0	0	0	0	0	1	19
Other prey on spruce	0	0	17	0	0	13	0	0	0	0	5	0	0	8	0	4	96
Total insects on spruce	27	19	45	3	3	14	5	1	4	14	9	4	2	8	54	61	195
Spruce foraging time (sec)	1793	623	12658	493	88	710	299	38	102	406	817	78	20	428	2918	5830	19889
Capture rate on spruce (no./sec act)‡	0.010	0.004	0.002	0.001	0.003	0.004	0.004	0.000	0.006	0.011	0.003	0.001	0.001	0.003	0.004	0.003	0.003
Foraging events on spruce	21	12	72	8	3	10	4	2	4	10	7	3	2	6	49	47	194

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Table 7
(continued)

	WTSP	LISP	SOSP	CCSP	SASP	ALL SPECIES
Lepidoptera: deciduous.	0	0	0	0	1	15
Other prey	0	0	0	0	0	1
Total insects	27	19	53	3	6	77
Total foraging time (sec)	1793	633	13065	493	198	740
Total activity time (sec)	2663	4452	18578	2483	1049	3712
Overall capture rate (no./sec act) [†]	0.010	0.004	0.003	0.001	0.006	0.005
Total foraging events	21	13	89	8	6	13
X [‡] : prey by substrate	54.47	54.47	25.82	54.47	54.47	3.11
						22.85
						3.18
						54.47
						54.47
						22.19
						0.87
						10.26
						31.55
						17.64*
						19.55*
						0.21

†Species codes: WTSP: White-throated Sparrow; LISP: Lincoln's Sparrow; SOSP: Song Sparrow; CCSP: Clay-coloured Sparrow; SASP: Savannah Sparrow

‡Two-week time blocks (periods): 1. 16-30 June 1982; 2. 1-15 July 1982; 3. 16-31 July 1982.

§ The number of insects captured on the specified substrate(s) divided by the total time (in seconds) of all activities.

* df = 1; * P < 0.001;

All sparrows foraged on or around the vicinity of the territories, but also moved around extensively over the whole plot, especially as the season progressed. Also, in late July 1992, as the numbers of budworm captured declined, sparrows were observed leaving territories on the plot, flying to another patch of spruce about 100 metres north of the study area, foraging, and returning with a bill full of insects. Some also began consuming serviceberries.

Before budworm captures declined the birds landed on spruce trees at various crown positions, hopping across several branches, while working outwards towards the tip from mid-branch, or occasionally they worked in along the branch instead. Branches appeared to be chosen randomly. After budworm captures declined in mid-July of 1991 (reflected in bird foraging, Table 6) and in the latter half of July 1992 (Table 7) all birds foraging on spruce changed their actions dramatically. All species began foraging at a branch base low in the crown. Then they worked upwards, going counter-clockwise away from the trunk. Occasionally they crossed branches to another crown, starting low in the crown again. Captures of unidentifiable small insects then became common (Tables 6,7).

Although not statistically significant, mid-day temperatures in late June 1992 were slightly lower than in 1991 (16.3 vs. 17.8 °C, $t = 0.44$, $df = 9$, $P = 0.672$); there was no significant difference between early July temperatures either (1992: 17.5 vs. 1991: 20.3, $t = 0.95$, $df = 7$, $P = 0.373$). In the field the same number of days with rain was recorded in both years in late June (4) and early July (7).

Hypothesis 5: prey capture rates differed among species only in some time periods

Overall prey capture rates, based on absolute data (total captures / total recorded times) did not vary among species in late June ($X^2 = 15.882$, $P > 0.001$, $df = 4$) and in early July ($X^2 = 0.481$, $df = 4$), 1991. In 1992 overall prey capture rates differed significantly in late June ($X^2 = 19.22$, $df = 4$) and early July ($X^2 = 23.06$, $df = 4$), but not in late July ($X^2 = 3.31$, $df = 3$). The modified Tukey test for multiple comparisons detected differences between Lincoln's Sparrow and the rates of the other sparrows ($q_{0.001,0.5}$: WTSP \neq LISP \neq SOSP = CCSP = SASP) for late June 1992.

Relative foraging rates obtained by adaptation of the method of Robinson and Holmes (1982) are shown in Tables 8 and 9. Kruskal-Wallis tests detected no differences among the five sparrow species for prey captures per minute in late June ($n = 62$, $H = 8.198$, $P = 0.0846$) and in early July, 1991 ($n = 19$, $H = 8.503$, $P = 0.0748$). In 1992, rates were not different in late June ($n = 32$, $H = 7.284$, $P = 0.1216$) and early July ($n = 27$, $H = .5859$, $P = 0.9646$), but significantly different in late July ($n = 61$, $H = 12.0465$, $P = 0.0170$).

Perch changes per minute varied among species and changed throughout the season with no clear-cut pattern (Tables 8, 9). Perch change-to-capture ratios increased through the season (Tables 8, 9). The attack-to-capture ratio (AC ratio) was close to 1.0 for the whole community and for all species in 1991 (Table 8); in 1992 that ratio was more variable among species, and generally higher than in 1991 (Table 9). Numbers of prey attacks were found by direct observation to be dependent on whether or not the prey was resting in the open on the foliage or concealed inside some type of feeding refugium. Prey found loose on leaves of plants or needles of spruce were easily plucked without further handling. Sewn refugia had to be opened.

Table 8: Relative foraging rates on spruce of all passerine species compared to the five common sparrow species, 1991.

Species, period	Perch changes per min.			Prey attacks per min.			Prey captures per min.			PC ratio††		AC ratio††		Times § seconds
	n†	Mean	±SE*	n	Mean	±SE	n	Mean	±SE	n	PC (r)††	n	AC (r)††	
All Species														
16-30 June	135	15.7	0.9	73	5.4	0.5	73	5.0	0.5	73	3.6(0.62**)	73	1.1(0.91**)	3189
01-15 July	84	22.2	1.6	47	4.0	0.3	46	3.9	0.3	46	5.3(0.12)	46	1.1(0.90**)	1937
White-throated Sparrow														
16-30 June	52	18.7	1.9	22	5.9	0.9	22	5.8	1.0	22	4.1(0.72**)	22	1.1(0.99**)	1238
01-15 July	9	14.7	1.5	6	2.7	0.4	6	2.7	0.4	6	5.3(0.32)	6	1.0(1.00**)	214
Lincoln's Sparrow														
16-30 June	17	10.2	2.2	15	3.7	0.7	15	3.7	0.7	15	2.9(0.14)	15	1.0(1.00**)	437
01-15 July	6	26.6	7.9	6	3.6	0.3	6	4.3	0.8	6	7.2(-0.26**)	6	0.9(0.59)	104
Song Sparrow														
16-30 June	23	18.0	2.4	12	5.8	1.1	12	5.7	1.1	12	3.4(0.83**)	12	1.0(0.99**)	403
01-15 July	7	40.9	8.3	1	6.0	0.0	1	6.0	0.0	1	2.5	1	1.0	105
Clay-coloured Sparrow														
16-30 June	11	19.2	2.9	8	7.3	1.4	8	7.3	1.4	8	4.4(-0.49**)	1	1.0(1.00**)	182
01-15 July	13	22.9	2.8	3	2.8	0.8	3	2.8	0.8	3	3.7(0.68)	3	1.0(1.00**)	157
Savannah Sparrow														
16-30 June	7	13.2	3.1	5	4.8	1.9	5	3.6	0.8	5	3.0(0.78)	5	1.0(1.00**)	162
01-15 July	5	20.5	1.9	4	4.6	1.4	3	4.1	1.0	3	5.3(0.63)	3	1.3(1.00**)	106

† no. observations;

*SE: standard error;

††: Perch Change-to-Capture Ratio; Attack-to-Capture Ratio;

r = Correlation Coefficient;

§ foraging;

|| not testable;

** P < 0.001.

Table 9: Relative foraging rates on spruce of all passerine species compared to the five common sparrow species, 1992.

Species, period	Perch changes per min.			Prey attacks per min.			Prey captures per min.			PC ratio††		AC ratio††		Time§ seconds
	n†	Mean	±SE*	n	Mean	±SE	n	Mean	±SE	n	PC (r)††	n	AC (r)††	
All Species														
16-30 June	67	12.6	1.2	43	4.5	0.5	41	3.8	0.5	41	4.4(0.73**)	41	1.5(0.89**)	2918
01-15 July	82	15.2	1.5	51	7.1	0.9	44	5.2	0.7	44	4.1(0.50**)	44	1.3(0.89**)	5830
16-31 July	331	13.1	0.6	131	4	0.5	115	3.5	0.6	115	7.6(0.80**)	115	1.2(0.99**)	19889
White-throated Sparrow														
16-30 June	32	10.5	1.3	21	2.7	0.4	21	2.2	0.3	21	5.5(0.67**)	21	1.6(0.80**)	1793
01-15 July	27	15.4	2.2	13	7.6	1.3	12	5.7	1.4	12	3.5((0.13)	12	1.5(0.82**)	623
16-31 July	158	11.1	0.7	48	2.8	0.5	40	2.2	0.5	40	10.8(0.6**)	40	1.3(0.94**)	12658
Lincoln's Sparrow														
16-30 June	9	19.7	5.6	2	6.8	5.2	2	6.8	5.2	2	7.5	2	1.0	493
01-15 July	4	11.1	1.3	2	10.6	9.4	2	7.3	6.0	2	3.5	2	1.3	88
16-31 July	18	16.7	3.3	10	3.7	0.7	9	3.7	0.7	9	5.2(0.81)	9	1.1(0.94**)	710
Song Sparrow														
16-30 June	5	6.4	0.7	2	6.0	0.7	2	3.1	1.3	2	2.4	2	2.3	299
01-15 July	2	7.7	3.2	1	5.5		1	5.5		1	2.0	1	2.0	38
16-31 July	2	16.7	3.3	1	4.4		1	4.4		1	3.0	1	1.0	42
Clay-coloured Sparrow														
16-30 June	7	10.1	1.1	6	4.2	0.5	4	4.5	0.6	4	2.5(0.65)	4	1.0(1.00**)	102
01-15 July	16	15.6	2.6	12	8.6	2.2	10	6.2	1.9	10	2.9(0.95**)	10	1.4(0.89**)	406
16-31 July	25	10.9	1.3	6	3.7	0.9	6	3.2	0.9	6	4.3(0.75)	6	1.3(0.91)	817
Savannah Sparrow														
16-30 June	3	11.4	4.2	3	6.3	2.6	3	6.3	2.6	3	2.2(0.96)	3	1.0(1.00**)	78
01-15 July	2	12.0	0.0	2	6.0	0.0	2	6.0	0.0	2	2.0	2	1.0	20
16-31 July	9	10.9	1.9	7	3.6	0.6	5	3.5	0.8	5	4.9(0.28)	5	1.3(0.83)	428

† no. observations; *SE: standard error;

††: Perch Change-to-Capture Ratio; Attack-to-Capture Ratio; r = Correlation Coefficient; § foraging;

|| not testable; ** P < 0.001.

All sparrows were adept at tearing apart the silk feeding cocoons made by budworm larvae to hold spruce shoots together. Equally, they did not exhibit any problems in tearing open curled leaves that had been tied together by leafrollers. Whenever larvae backed out of feeding cocoons or curled leaves, or when moths fluttered downwards to escape predation, all birds showed great skill at a "tumble-flycatching" manoeuvre (cf. Robinson and Holmes 1982) in which the bird flipped over downwards in a rolling motion, catching the prey, and landing on another branch. In only one case, involving a juvenile bird, was prey loss observed during this manoeuvre. In 1992, the number of prey attacks required before capture was greater than 1991 (Tables 8, 9).

Discussion

Ecological community dynamics (Wiens 1989a) was evident in this study. I found within-season temporal variation in activity levels (Figs. 4, 5) and in diet selection (Tables 6, 7) among bird species. There was constancy in the activities of the whole avian community from 15 June to 15 July in both years. These findings may be interpreted as evidence of a form of equilibrium.

Interpreting ecological data, however, has long sparked disputes with regard to whether or not species compete for limited resources, what constitutes equilibrium in natural communities, how one would identify equilibrium, and the problems of not including all species in a community in the study. Wiens (1989a: 15) said: "temporal variation in resource levels ... may affect the degree to which a community matches the equilibrium assumptions of theory." In the same section he said that a species is not an ecological constant; determining its community role or position by averaging over samples that are geographically widespread may

obscure this important variation. My findings, therefore, and the methods that revealed them, warrant discussion, especially as they offer alternative interpretations to an established paradigm that competition drives ecological processes.

My use of one site removed the opportunity for inter-site comparison but also removed the risk of smoothing out variation by merging data, thus meeting one of Wiens' (1989a) concerns. By including all species in the observations several species were eliminated from study by directing their activities outside the plot. Therefore, species were not removed from consideration by any *a priori* design of mine, but by sheer limitations in the size of data sets. As great care was taken to carry out a disciplined set of observations at defined locations throughout the plot I am confident that the data remaining reflect avian activities on the plot much more than any bias on my part.

After elimination of small data sets a guild (Root 1967) of sparrows remained for study. Hespenheide (1975) argued that birds that forage in different ways on the same insects take different proportions of them, so that the composition of the diet relates to foraging behaviour. On the other hand, sparrows are considered a guild of birds that shows little variability in foraging behaviour or prey selection among species (Wiens and Rotenberry 1980, 1981). Perhaps that lack of variability is an adaption to their habitats, or a reflection of opportunism.

Temporal variation in foraging and other activities

This study showed that there was within-season variation in all types of cumulative activity time among the five sparrow species (Figs. 4, 5), but that the differences among their cumulative foraging times were often not statistically significant (Table 1). The first hypothesis was not supported in 1991, but it was supported in 1992 only by the White-throated Sparrow

(Fig. 5b, Table 1). If the statistical criterion used for rejection of the null hypothesis had not been made so strict, to overcome the risk of type I error, then activity levels of Savannah Sparrow also would have been significantly different (Table 1). Either one significant test is aberrant or it reflects a more complex process with slight adjustments between 1991 and 1992.

The paradigm founded by MacArthur and his colleagues (MacArthur 1972; Cody and Diamond 1975) viewed competition as the driving force in proximate ecological processes, and ultimately in evolutionary ones. Similar species living in the same areas should partition resources to diminish competition (MacArthur 1958). Differences in body size, bill length and limbs are believed to confer adaptations on birds for a time to exploit specific habitat conditions, prey types, or variations in resource abundance while reducing competition (Karr and James 1975; Wiens 1989a). Closely related species have not shown rapid morphological change in response to proximal environmental conditions (Root 1967; Wiens and Rotenberry 1980; Wiens 1989a). In 1992 significant differences in foraging time for the White-throated Sparrow (Table 1) suggested a temporal response to changed food resources and breeding demands. The habitat seemed unchanged, but the diet shifted from mostly spruce budworm to other prey (Tables 6, 7).

The second hypothesis that mean times spent foraging differ among species was supported, but was not supported when just two species of similar size (Godfrey 1966) and habits (Bent 1968b) like White-throated Sparrow and Song Sparrow (Table 4) were compared. Mean data displayed the great variability in lengths of foraging events during late June and late July 1992 (though it was not evident in Tables 2 and 3), when field observations showed that young were out of the nest and being fed by parents. Tests on mean data also confirmed that the larger White-throated Sparrow had longer mean foraging events than the smaller Clay-coloured

Sparrow, yet birds intermediate in size did not have significantly different mean foraging events. Such mean foraging time differences support the concept of varied strategies for foraging among species. Robinson and Holmes (1982), for example, found that species at Hubbard Brook could be grouped according to differences in their foraging rates. Some were physically separated when foraging by preferences for various plant species (Robinson and Holmes 1984).

Mean foraging time differences among species may have been driven by energetic differences associated with body size (Calder 1974, 1984). For example, the Clay-coloured Sparrow must have had shorter intervals between foraging events than larger species due to the limited time it could afford to be away from its young per trip (pointing to metabolic rates). Otherwise, if the length of foraging events occurred about equally among species of different size, larger sparrows would have loaded more prey into their bills per trip than the small one, but that was not the case. These findings suggest that conditions, like relationship of food supply to nest site location, as well as species differences in feeding habits like multiple-prey loading (Stephens and Krebs 1986), influence both cumulative time structure and mean times. These relationships warrant closer scrutiny with further studies.

Initially it seemed surprising that the cumulative time spent foraging was not greatest during the main breeding period from mid-June to mid-July (Fig. 4, 5), but in retrospect this finding makes sense. The consistent cumulative proportion of 27% time spent on foraging in late June and early July in two summers (Fig. 4), and the constancy of spruce budworm acquisition during the same periods (Tables 6, 7), suggest that the resources necessary to support breeding (nest sites, food supply) were relatively constant during the peak period of the breeding season in both years. Even without a separate measure of prey availability the distribution of prey types

taken in relation to substrates and composition of total diets shows clearly in Tables 6 and 7.

In addition, as reported, pairs of each species carried on periods of intense foraging to feed their young, while others spent prolonged periods perching or incubating; species differences in activity levels were also great (Fig. 5). Therefore, asynchrony in breeding activities among different pairs of each species is the most likely explanation for constant overall levels of foraging for the entire community (Fig. 4), since extreme periods of low foraging due to perching or incubating by some individuals would be balanced by extreme periods of intense foraging among those raising nestlings. Nolan (1978) documented many such cases of asynchronous breeding and feeding in his study of the Prairie Warbler (*Dendroica discolor*). Expansion of time data collection using marked individuals, while trying to increase sample sizes, would be a logical extension beyond my study.

Foraging studies done elsewhere, often in conjunction with energy budget estimation, have produced widely varied amounts of time for inactive periods like perching and incubation, and for foraging (Holmes et al. 1979a; Ettinger and King 1980; Weathers et al. 1984). Robinson and Holmes (1982) and Holmes et al. (1979a) stated that passerine birds in the Hubbard Brook Forest spent most of their time foraging during nestling and fledging periods. Therefore, extremes in foraging time versus perching or incubating may be common from year to year, in order to create a common, community value of 27% foraging time. The value of 27% cumulative foraging time, however, may have been site-specific, and peculiar to 1991 and 1992, since spruce budworm were taken most commonly (Tables 6, 7), but budworm populations are known to go through great extremes in population size over local and large areas of scale; their populations even collapse (Blais 1954; Hardy et al. 1987). If the study had been done in years

in which budworm populations were low perhaps less profitable prey would have been encountered, and cumulative foraging times would have been greater. This is only speculation at this point, but forms a basis for a new hypothesis. More universal biological significance, however, might emerge in association with the 27% time value if multiple studies employing similar methods were to show consistently that cumulative foraging times approximated 27% during the height of the breeding season in similar habitats.

Breeding has been recognised for a long time as the process that drives other activities (Murton and Westwood 1977). A range of foraging activity levels probably reflects significant change in energy demands, especially to feed the young (Kluyver 1950; Royama 1966; Verner 1965). Observed differences in foraging time patterns among species are consistent with the expectation that although individuals in a population have been shown to come into physiological preparation for breeding by synchrony with sun light-dark cycles (Murton and Westwood 1977), stochastic processes (e.g. predation of one nest but not another; differences among males in territorial placement; differences among females in receptiveness) alone would mean that not all pairs of a species would be likely to be at the same point in the breeding cycle at the same time. Both between-year and within-year conditions, as well as species differences, must be taken into account. Little variability in 1991 among activities and among species (Figs. 4, 5), yet increased variability in 1992, suggest that circumstances governing breeding and survival (like habitat conditions, cover or weather), or food supply, differed in each year. Temporal variation, within and among species, in the percentage of time spent foraging (Fig. 4, 5), gives support for the long-held belief, widely speculated in the literature, that birds change their activity levels, including foraging times, during the breeding season, in response to changing conditions (Wiens

1989a). Numerous studies have been done at the nest that confirmed differences in feeding activities in response to different growth stages of the young (Bierman and Sealy 1982; Knapton 1980, 1984; Knapton and Falls 1983; Meunier and Bédard 1984; Nolan 1978; Royama 1966; Van Horne and Bader 1990), but those studies did not relate activity at the nest to the total or mean time spent on foraging and other activities throughout the habitat during the breeding season. Busby and Sealy (1979) showed that Chironomidae were taken in proportion to availability in most but not all time periods, whose unequal lengths reflected stages in the breeding cycle. Guinan and Sealy (1987), using 12-day sampling periods, found that Chironomidae were taken in greatest quantities in most periods, but overall correlated best with their proportion of the total biomass in sweep-net samples. Arthropod sampling in defined time periods is a common entomological practice now used to show insect availability to birds (Holmes and Schultz 1988; Rodenhouse and Holmes 1992).

I reported prolonged periods of perching, especially among males, of all species. Based on my observations, I agree with Ettinger and King (1980) that the breeding season in northern habitats seems to be marked by large amounts of "loafing time" ("other" time in Fig. 5). Ettinger and King (1980) suggested that such large amounts of time free to perch may provide the energetic leeway necessary to deal with crises (like reductions in food supply, nest predation, or disruption of nesting due to weather events) when they come. "Loafing" by males in this study may have been due in part to the ease of acquisition of budworm and other defoliators (ease of acquisition implies ready availability) during the peak nestling and fledging periods (Tables 6, 7). Martin (1987) suggested that perching time may not be "loafing" but an important part of commitment to reproductive success.

Time spent perching ("loafing") as identified by Ettinger and King (1980), and the "commitment to reproductive success" noted by Martin (1987), must work together. I found that most of the time spent perching (by males) (Fig. 5) occurred during the long periods when females were out of sight incubating. In other periods (especially clear in White-throated Sparrow, Fig. 5b) they were very busy foraging to feed young (Fig. 5). As reported, only the data for White-throated Sparrow were significant (Table 1), but perching by males of the other species made up most of their other time data, too (Fig. 5). My inability to detect differences for those species may have been due to small sample size or to conformity in levels of activity from period to period. It has been established previously that during such long periods of inactivity males and females maintain energetic levels only slightly above basal metabolism (King 1974; Holmes et al. 1979a; Kendeigh et al. 1977; Ettinger and King 1980). Therefore, "loafing" time can serve to save energy while allowing males to maintain vigilance over both their territories and nest sites.

Foraging substrates, diet selection and prey capture rates

There are only three possible reasons for foraging on one substrate more than others: it is the most abundant substrate, it has the most readily available (possibly most abundant) prey, or it is the most nutritionally or energetically profitable (Stephens and Krebs 1986). With the high metabolic rates of passerine birds there would be little surplus time, without survival risk, available to forage on plants yielding very few prey items, so a plant on which frequent foraging occurred must have had prey. The bias in favour of foraging on spruce, despite a greater amount of deciduous (shrub) foliage available (Table 5), helps support the conclusion that birds chose white spruce over other plants as a source of prey. The hypothesis that birds foraged mostly on

white spruce was supported.

This study confirmed that a steady diet of insects, largely spruce budworm, was taken on spruce (Tables 6, 7), and low attack-to-capture ratios on spruce confirmed success (i.e. efficiency) at capturing prey (Tables 8, 9). It was also shown that as budworm captures declined on spruce, even though foraging there continued, prey from other plants was obtained that had not been taken earlier in each season, especially in 1992 (Tables 6, 7). These observations are consistent with the within-season variability in availability of insect prey reported by Holmes and Schultz (1988). Insect captures by birds on spruce reflected at least easy access to prey (mostly budworm) if not also greater insect availability on spruce (Tables 6, 7). More insects were taken on spruce by sparrows in most time periods, so the hypothesis that birds capture more insects on spruce than other plants was supported.

Repeated foraging by birds on spruce indicated knowledge of food supply, certainly while spruce budworm larvae and pupae were available. Subsequently sparrows took budworm from an adjacent site before altering their foraging tactics on spruce crowns. These facts are evidence of opportunistic feeding so as to choose larger, more profitable prey (budworm, being Lepidoptera), giving them the greatest energy return for the foraging time investment (optimality: Stephens and Krebs 1986). Flying to an adjacent site was more "profitable" than altering foraging technique. Subsequently, failure to obtain budworm or other Lepidoptera easily on adjoining sites, led to the change of foraging strategy that I reported, which involved a very orderly, counter-clockwise route of travel upwards through the tree, accompanied by a change in diet mix (see late July 1992, especially for all species (Table 7)). The change in foraging technique suggests that the birds on the site were running a thorough search pattern in order to

turn up smaller insects, and throughout the season were tracking their resources through a learning mechanism that allowed them to recall past measures of success at given locations.

Equally important, the results of this study show that prey capture rates based on absolute time measurements differed among sparrow species in some but not all time periods (Tables 8, 9), so the results generally support the fifth hypothesis that prey capture rates differ among species. The fact that the hypothesis was not supported in all time periods raises the possibility that prey captures rates are not just a function of bird species differences but also of prey availability. The most likely reason for common rates in some time periods was the combination of easy prey captures (Tables 8, 9) combined with common level of demand (Fig. 4), as induced by breeding. Sample size, however, must also be considered a factor, since rates calculated from smaller sample sizes may have been biased.

Recent ecological literature continues the debate over food limitation. At Hubbard Brook, insect populations were low during most years of their studies, and foraging time was believed to account for most avian activity time (Holmes et al. 1979a,b; Robinson and Holmes 1982, 1984; Holmes and Schultz 1988; Rodenhouse and Holmes 1992). Food limitation has been seen as a factor that limits reproductive success, causing trade-offs between annual fecundity and adult survival (Martin 1987, 1995). Conversely, Martin (1995) concluded that differences in fecundity were not due to food abundance but to different tactics in partitioning similar levels of food abundance. He reasoned that variation in fecundity and adult survival had more to do with nest sites and their vulnerability to predation. By comparison Arcese and Smith (1988) found that adult Song Sparrows given supplemental food had lower survival rates than control birds, and spent less time foraging. In my study I found no evidence that birds were under a food shortage,

and saw no acts of aggression. Any territorial displacements after nesting failure pointed to fox predation, not competition among species.

Access to prey on spruce in 1991 and 1992 was easy and the rate of insect captures was lower in 1992 (Table 7) than in 1991 (Table 6). Capture of spruce budworm extended for a longer period of time in 1992 (Table 7), than in 1991 (Table 6), attributable to the delayed season. In comparison, higher capture rates in absolute time on spruce (Tables 6, 7), and lower attack-to-capture ratios in 1991 (Table 8) than in 1992 (Table 9) confirmed greater ease of prey acquisition in 1991. Increase in the total length of time spent on foraging in late July 1992 (Figs. 4, 5), and concurrent reduction in consumption of spruce budworm (Table 7) shows adaptive changes of the sparrows in response to changed food supplies. I conclude, therefore, that spruce budworm represented a readily available source of food that required minimum capture and handling time, i.e easy prey, supporting the idea of easy availability even in the absence of an abundance measure.

The sparrows observed in this study were clearly multiple-prey loading, central-place foragers, with the territories being the central location for their activities (Fig. 2, 3) (Krebs et al. 1983; Krebs and McCleery 1984), since for all except observations in early August 1992 they foraged within or close to territories marked by the actions of singing males. Birds' foraging actions and diet selection suggested that the study area was suitably supplied with profitable prey in late June to late July, since they confined their foraging there, and obtained mostly spruce budworm (Tables 6, 7). There were no acts of overt aggression, or of sudden changes in numbers of any species, that might have indicated competition, so competition probably was not occurring. Unlike the case that Knapton (1980) reported for the Clay-coloured Sparrow, the birds

nested and foraged in the same area. The return of resident sparrows from an adjacent site, with bills fully loaded, maximized energy return per trip (Stephens and Krebs 1986). These findings raise the prospects that birds in boreal habitats may not suffer from food limitation during the breeding season. High species diversity of songbirds in the boreal forest (Erskine 1977; Robbins et al. 1986), therefore, may be due to abundant food supply, and ample habitat for nest sites. Further work on quantifying the timing of food acquisition in relation to breeding activities may reveal more clearly relationships between competition for resources and equilibrium theory (Wiens 1977, 1989b).

On the use of time-based methods to study avian ecology

Division of the breeding season into time periods made it possible to detect changes in activities during the season that would normally be missed by pooling data. Recording cumulative time durations, rather than counts, gave a real-time context to avian activities. Inclusion of all activities demonstrated the changing importance of foraging in different time periods during the breeding season. This technique is versatile, adaptable and expandable.

The need for new approaches has been recognized for some time, but a consensus has not yet emerged (Morrison et al. 1990). Methods aimed at ensuring statistical independence distort the time structure by mathematical manipulations of the data (Hejl et al. 1990). Wiens et al. (1986) used an approach similar to mine where all activities were recorded. In that study, though, percentages in time were calculated for each activity as a proportion of the sequence in which it occurred. Mean proportions, including zero values in the calculation, were reported for each activity. The sums of these proportions exceeded 100%. All proportions were arcsine-transformed (Wiens et al. 1986). That method, similar to mine, is good for determining

variability within the data. Calculating mean proportions, though, to use in a time budget distorts the time structure of the data. My method retains the real time structure of the original data.

Real-time data, if analysed as raw data, which they must be to retain the connection between events and their context in absolute time, do not conform to conventional statistical methods. Transformation normalizes such data but distorts the real-time context, causing the researcher to overlook important real trends during the season (such as the true magnitude of arithmetic means, and of their respective differences between 1991 and 1992: App. B1, B2). Validity of sample sizes in cases where confidence limits were wide, is a concern, primarily because of the statistical requirement to weight limits by number of observations. Some of the time samples, though, that were considered unreliable on the strength of calculated confidence limits were as large as or larger than ones that were accepted. Had the events followed some clear oscillation in time, and had samples been available on perfectly regular sample dates (e.g. every second day), then time series analysis methods would have permitted the fitting of a periodic function to the data. Expansion of the field time investment could achieve this.

My time-based techniques should be integrated with conventional and non-destructive methods in long-term, interdisciplinary studies on the same plots, measuring plant and animal population growth parameters, including measures of abundance. It is especially important to link these methods with measures of avian fecundity, survival and productivity, and with research in nutrition and energetics, since debate in community ecology centres on relationships between resource use and species fitness. Application to long-term budworm research will finally delineate the role of predators in time and space (Royama 1992). Addition of my time-based methods to conventional (spatial) ones will permit investigation of causal ecological processes.

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Appendices

Appendix A1: Species Recorded on the Study Area, 1991 and 1992.

Accipitridae

Sharp-shinned Hawk, *Accipiter striatus*
Cooper's Hawk, *Accipiter cooperii*
Broad-winged Hawk, *Buteo platypterus*

Falconidae

American Kestrel, *Falco sparverius*
Merlin, *Falco columbarius*

Phasianidae

Ruffed Grouse, *Bonasa umbellus*

Cuculidae

Black-billed Cuckoo, *Coccyzus erythrophthalmus*

Trochilidae

Ruby-throated Hummingbird, *Archilochus colubris*

Picidae

Yellow-bellied Sapsucker, *Sphyrapicus varius*
Downy Woodpecker, *Picoides pubescens*
Hairy Woodpecker, *Picoides villosus*
Northern Flicker, *Colaptes auratus*
Pileated Woodpecker, *Dryocopus pileatus*

Tyrannidae

Eastern Wood-Pewee, *Contopus virens*
Yellow-bellied Flycatcher, *Empidonax flaviventris*
Alder Flycatcher, *Empidonax alnorum*
Least Flycatcher, *Empidonax minimus*

Hirundinidae

Tree Swallow, *Tachycineta bicolor*

Corvidae

Gray (Canada) Jay, *Perisoreus canadensis*
Blue Jay, *Cyanocitta cristata*
American Crow, *Corvus brachyrhynchos*
Common Raven, *Corvus corax*

Paridae

Black-capped Chickadee, *Parus atricapillus*

Sittidae

Red-breasted Nuthatch, *Sitta canadensis*
White-breasted Nuthatch, *Sitta carolinensis*

Mucicapidae: Sylviinae

Golden-crowned Kinglet, *Regulus satrapa*
Ruby-crowned Kinglet, *Regulus calendula*

: Turdinae

Veery, *Catharus fuscescens*
Swainson's Thrush, *Catharus ustulatus*
American Robin, *Turdus migratorius*

Bombycillidae

Cedar Waxwing, *Bombycilla cedrorum*

Vireonidae

Solitary Vireo, *Vireo solitarius*
Philadelphia Vireo, *Vireo philadelphicus*
Red-eyed Vireo, *Vireo olivaceus*

Emberizidae: Parulinae

Tennessee Warbler, *Vermivora peregrina*
Nashville Warbler, *Vermivora ruficapilla*
Yellow Warbler, *Dendroica petechia*
Chestnut-sided Warbler, *Dendroica pensylvanica*
Magnolia Warbler, *Dendroica magnolia*
Cape May Warbler, *Dendroica tigrina*
Yellow-rumped Warbler, *Dendroica coronata*
Black-throated Green Warbler, *Dendroica virens*
Blackburnian Warbler, *Dendroica fusca*
Black-and-White Warbler, *Mniotilta varia*
American Redstart, *Setophaga ruticilla*
Ovenbird, *Seiurus aurocapillus*
Mourning Warbler, *Oporornis philadelphia*
Common Yellowthroat, *Geothlypis trichas*
Wilson's Warbler, *Wilsonia pusilla*
Canada Warbler, *Wilsonia canadensis*

: Emberizinae

Chipping Sparrow, *Spizella passerina*
Clay-coloured Sparrow, *Spizella pallida*
Savannah Sparrow, *Passerculus sandwichensis*
LeConte's Sparrow, *Ammodramus lecontei*
Song Sparrow, *Melospiza melodia*
Lincoln's Sparrow, *Melospiza lincolni*
White-throated Sparrow, *Zonotrichia albicollis*

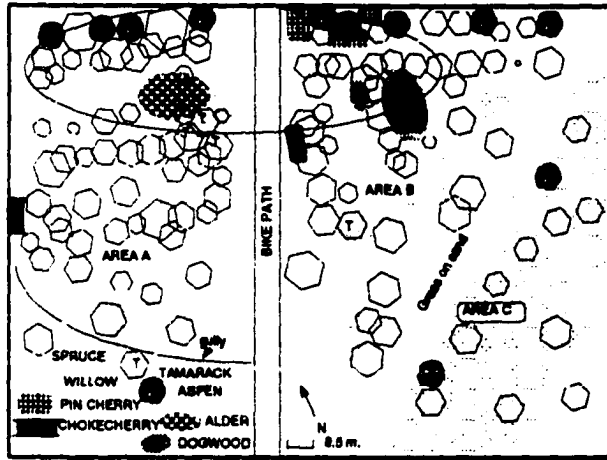
: Icterinae

Red-winged Blackbird, *Agelaius phoeniceus*
Common Grackle, *Quiscalus quiscula*
Brown-headed Cowbird, *Molothrus ater*

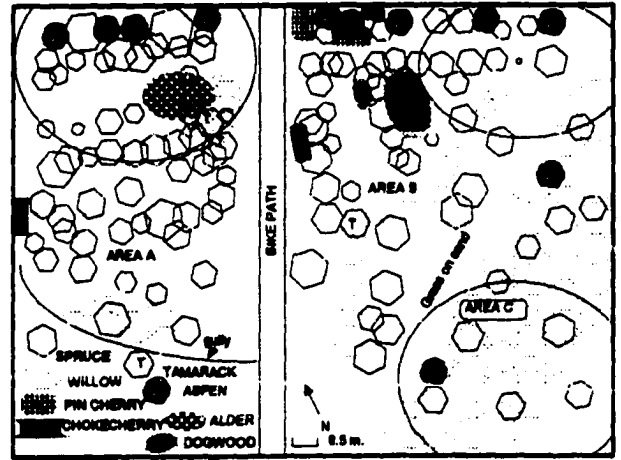
Fringillidae

Purple Finch, *Carpodacus purpureus*
American Goldfinch, *Carduelis tristis*
Evening Grosbeak, *Coccothraustes vespertinus*

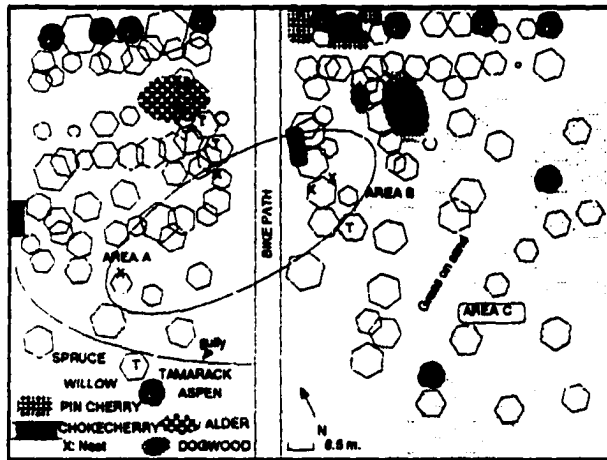
Appendix A2: Territories of resident passerines other than sparrows, 1991.



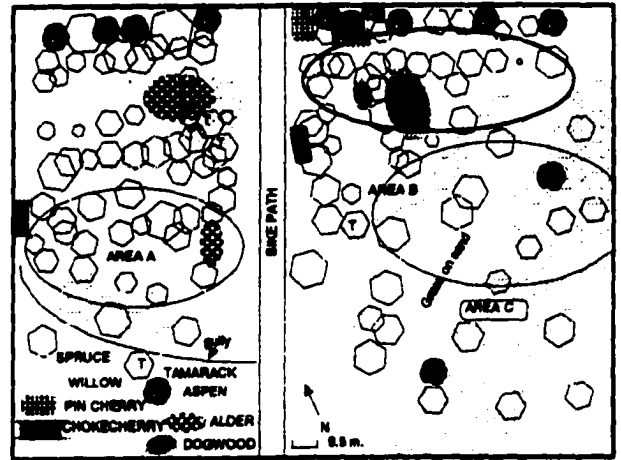
a) Magnolia Warbler



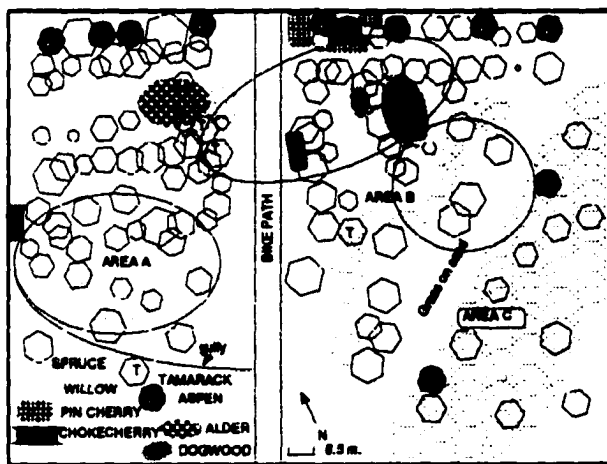
b) American Redstart



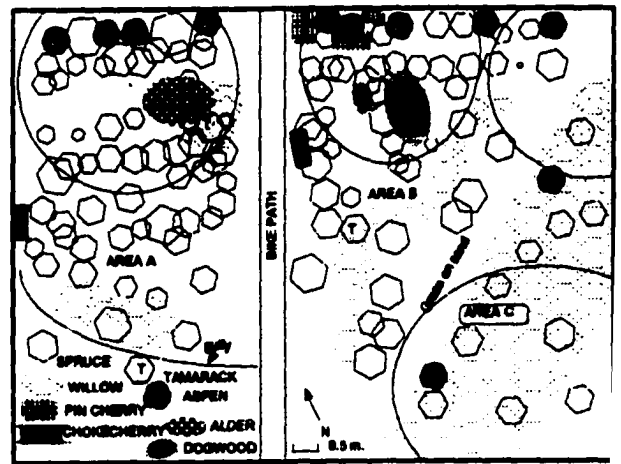
c) Yellow-rumped Warbler



d) Alder Flycatcher

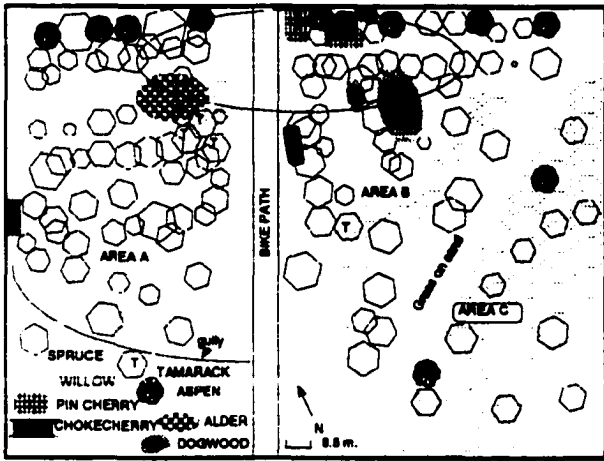


e) Cedar Waxwing

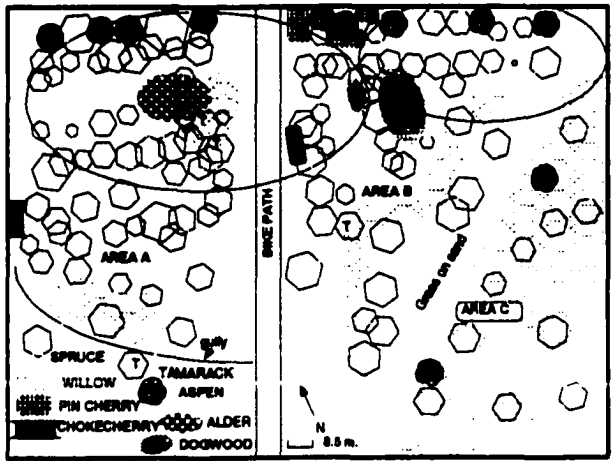


f) Veery

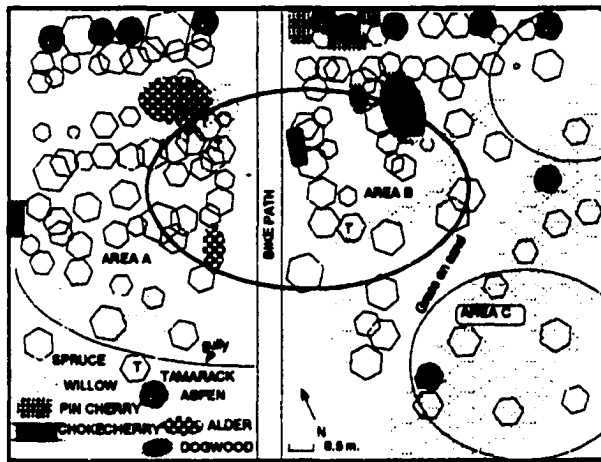
Appendix A3: Territories of resident passerines other than sparrows, 1992.



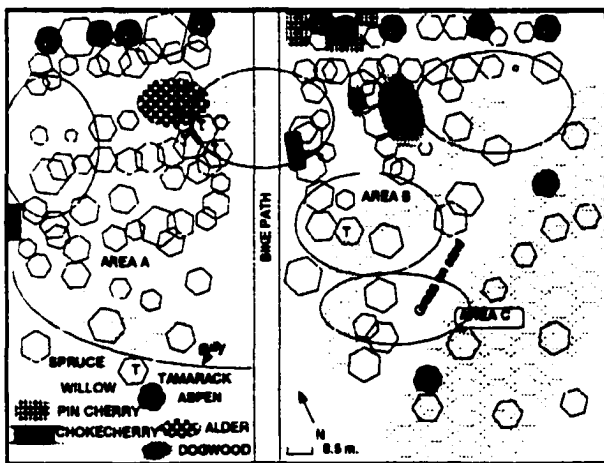
a) Magnolia Warbler



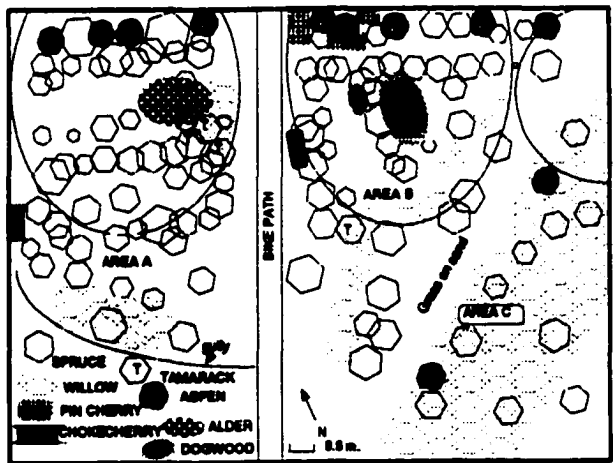
b) American Redstart



c) Alder Flycatcher



e) Cedar Waxwing



f) Veery

Appendix B1: Means (\pm SD) for actual activity times (seconds) of the avian community and sparrows, 1991.

Particulars	Foraging			Flying			Singing			Other			Total of All Activities			
	All Species	#obs	mean	SD†	#obs	mean	SD†	#obs	mean	SD†	#obs	mean	SD†	#obs	mean	SD†
16-30 June '91		111	25.9	27.7	318	3.6	1.7	515	2.7	1.2	352	24.4	44.2	1011	11.4	26.8
01-15 July '91		101	23.2	20.6	244	3.5	1.6	388	2.7	0.8	417	14.8	14.8	951	9.4	13.3
16-31 July '91		20	28.5	19.8	19	4.2	1.8	77	2.7	1.1	32	11.2	6	160	9.5	14
White-throated Sparrow																
16-30 June '91		27	23.9	31.0	51	3.0	1.2	49	2.9	0.2	65	27.8	64.2	139	15.5	39.8
01-15 July '91		11	29.5	29.9	13	3.0	0.9	36	2.9	0.3	34	14.9	10.6	80	10.9	14.5
Lincoln's Sparrow																
16-30 June '91		16	25.7	15.9	22	3.4	1.9	33	3.1	0.9	34	28.9	21.3	79	19.7	20.6
01-15 July '91		7	19.0	4.6	9	2.9	1.5	13	2.8	0.4	24	25.4	36.5	38	20.3	31.1
Song Sparrow																
16-30 June '91		8	17.4	12.9	11	2.4	1.4	31	3.1	0.9	12	14.7	11.3	51	10.8	12.0
01-15 July '91		4	15.0	15.0	3	2.0	0.0	20	2.9	0.2	10	16.2	10.4	34	8.8	10.6
Clay-coloured Sparrow																
16-30 June '91		9	19.4	14.2	19	3.8	2.4	49	2.0	0.0	22	14.2	14.9	77	8.9	12.8
01-15 July '91		9	15.9	11.6	16	3.2	1.4	32	2.1	0.5	36	17.6	15.8	77	12.0	14.2
Savannah Sparrow																
16-30 June '91		10	23.3	10.8	31	3.1	1.1	37	2.7	0.5	34	21.1	26.7	86	16.3	21.0
01-15 July '91		8	20.3	11.5	14	3.7	1.5	26	2.8	0.4	24	16.4	12.4	56	16.4	12.4

#obs: number of observations;
 † standard deviation

Particulars	Foraging			Flying			Singing			Other			Total of All Activities			
	All Species	#obs	mean	SD†	#obs	mean	SD†	#obs	mean	SD†	#obs	mean	SD†	#obs	mean	SD†
16-30 June '92	59	41.8	49.4	93	5.6	5.4	421	4.4	9.9	99	65.0	120.5	579	17.4	54.0	
01-15 July '92	65	63.5	133.5	125	4.4	3.9	430	6.0	21.0	206	69.5	170.1	1239	27.6	100.3	
16-31 July '92	296	75.8	221.8	365	5.1	14.1	486	5.2	12.3	659	33.3	59.4	1354	30.4	113.8	
01-15 August '92	137	62.0	90.6	182	5.5	6.9	125	3.0	2.2	196	39.6	68.0	499	28.0	61.7	
White-throated Sparrow																
16-30 June '92	21	56.0	63.4	21	4.2	3.7	66	3.4	3.5	20	28.1	27.7	99	19.3	38.8	
01-15 July '92	13	22.6	20.3	17	3.8	2.2	87	7.0	22.1	38	82.8	173.5	116	26.2	88.7	
16-31 July '92	89	74.8	98.7	77	2.6	2.0	126	5.3	7.0	101	45.8	61.1	264	38.9	73.1	
Lincoln's Sparrow																
16-30 June '92	8	54.8	42.8	13	4.0	3.7	62	3.2	5.8	20	82.8	144.3	81	30.7	81.9	
01-15 July '92	6	33.0	41.8	2	2.0	0.0	55	3.3	2.1	12	49.4	59.1	65	14.2	34.4	
16-31 July '92	10	35.2	41.7	14	3.1	1.2	23	8.8	25.0	44	63.3	104.7	73	46.3	90.4	
Song Sparrow																
16-30 June '92	5	71.8	43.7	5	2.6	1.5	45	5.5	18.8	4	158.0	284.7	49	25.7	103.2	
01-15 July '92	7	40.1	66.4	19	4.2	5.2	31	4.0	4.7	16	97.4	115.9	53	39.3	81.2	
16-31 July '92	2	21.0	8.5	2	4.5	2.1	49	3.9	5.2	11	20.9	13.1	57	8.3	13.9	
Clay-coloured Sparrow																
16-30 June '92	5	13.4	5.2	12	4.6	4.4	57	2.2	3.0	7	46.0	66.5	67	9.4	25.9	
01-15 July '92	10	25.4	25.1	28	3.9	2.0	44	2.8	3.8	29	27.1	40.7	86	15.7	32.9	
16-31 July '92	15	44.1	66.6	33	3.6	3.3	32	2.4	0.9	59	24.0	63.5	105	24.2	57.3	
Savannah Sparrow																
16-30 June '92	10	30.8	35.0	20	7.5	6.4	41	2.5	4.6	21	127.0	158.3	62	54.1	109.7	
01-15 July '92	3	10.0	0.0	12	4.3	3.6	42	6.4	19.7	29	101.0	111.4	62	52.9	95.2	
16-31 July '92	7	44.6	37.7	14	3.3	1.5	46	5.0	8.7	33	50.5	73.9	78	29.8	56.1	

#obs: number of observations; † standard deviation