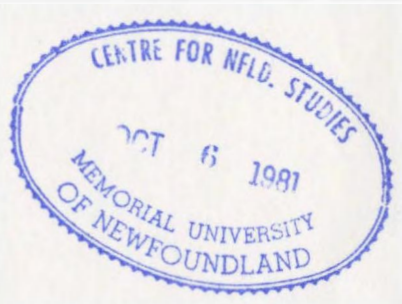
SOME ASPECTS OF THE BREEDING BIOLOGY AND VOCALIZATIONS OF THE FOX SPARROW (PASSERELLA ILIACA MERREM) IN NEWFOUNDLAND

JOSEPH RICHARD BLACQUIERE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Some aspects of the breeding biology and vocalizations of the Fox Sparrow (*Passerella iliaca* Merrem) in Newfoundland

A thesis

presented to

The Department of Biology

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In partial fulfillment

of the requirements for the degree

Master of Science

by

Joseph Richard Blacquiere

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Abstract

The breeding biology and vocalizations of the Fox Sparrow (Passerella iliaca Merrem) was studied during the 1977 and 1978 breeding season in Newfoundland.

The early spring migration, territory establishment, and nesting activities are discussed. Analysis of nest record cards indicated nest height was significantly correlated ($r = -.600$) with advance of the breeding season. Incubation and nestling periods were found to be just over 12 days and 9 days respectively. Nestling growth was rapid, $k = 0.566$, and the relative growth of body parts showed a differential in favour of early development of legs and feet.

Nestling call notes, adult call notes, and presumed female song are described and discussed. The male primary song is described and variation analyzed. The repertoire size of 96.4% of the birds recorded was one song, and only 3.6% sang two songs. Song structure was constant through the breeding season. Analysis of variance of basic song parameters showed some variation between localities but no trends were detected. Cluster analysis showed substantial sharing of syllables within a locality but differences were only apparent in sample that were separated by long distances in continuous breeding habitat or a geographic barrier. The last six syllables of the song were shown to be most closely associated with locality. Song correspond to geographical variation rather than a system of dialects. Preliminary evidence suggests that Fox Sparrows do not discriminate between songs of their own and other, even very distant, localities.

Acknowledgements

First, I would like to thank my supervisor, Dr. William Threfall, who suggested the study. His advice, criticism, and confidence through the course of the work are very much appreciated. Drs. G.F. Bennett and J. Rice, the other members of my committee, provided additional help and advice during the study and immeasureably improved the manuscript with their criticism of the first draft. Dr. Rice was of great assistance in suggesting and interpreting the statistical tests used herein.

Several other people also contributed in various ways to this study. Dr. Jon Lien freely provided his sound recording and analysis equipment for my use during the 1978 field season. He also spent many hours of his time discussing with me various aspects of sound, communication, and bird vocalizations.

I also want to mention Randy Dodge and Bob Church of Computer Services and Mrs. Ruth Cornish of the Statistical Consulting Lab for their patient help and advice in the analysis of the data. Drs. L.M. Tuck, Howard Clase, and Mr. Bernard Jackson provided much useful information about local distribution and habits of the Fox Sparrow. Dr. Tuck allowed me to see some information he is preparing for publication. Mr. Jackson arranged for permission for me to work in Oxen Pond Botanic Park.

Mr. Bruce Johnson, Canadian Wildlife Service, permitted access to Fox Sparrow nest record cards which are kept in his office. Mr. Bursey and Mr. Blackmore of the Atmospheric Environment Service gave me information on local weather conditions.

Dr. D.J. Martin provided a recording of Fox Sparrows from western North America. Dr. E. McClure found a very important Fox Sparrow nest for me in 1977. Mr. Larry Smith allowed access to the Crown Voice Analyzer.

Mr. Eric Blundon took me to Baccalieu Island and Dr. W. Montevecchi provided for my accomodations there. Shane Mahoney provided transportation to Gull Island and generously allowed me to share the facilities there.

Mr. Wayne Lundrigan did some of the drafting. Mrs. Raske deserves much credit for the trying job typing the greater part of the first draft of this thesis. Ms. Carol Butler ablely accomplished the remainder. Ms. Carol Duncan typed the final copy.

To all these people I extend my sincerest thanks.

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Introduction

The Fox Sparrow, Passerella iliaca (Merrem) (Family: Fringillidae; Subfamily: Emberizinae) (A.O.U. Checklist 1957) is a widely distributed North American sparrow. It breeds throughout the northern boreal region from Newfoundland to Alaska and extends south into western United States in the Rocky, Cascade, and Sierra Nevada mountain ranges (Godfrey 1966). The winter range is from southern Canada to southern United States, excluding most of the Great Plains.

At present in the genus Passerella there is a single species, P. iliaca, with 18 subspecies recognized in the A.O.U. Checklist (1957). The limits of member genera of the Emberizinae are obscure (Linsdale 1928a,b; Paynter 1964; Mayr and Short 1970; Short and Simon 1965) and the exact taxonomic relationships of Passerella to its close relatives must await further clarification of their phylogenetic affinities.

This study, which deals with the eastern subspecies of the Fox Sparrow P. i. iliaca, is composed of two parts: a breeding biology study and a study of the vocalizations. Very little work on either aspect has been done in eastern North America. Breeding biology proved difficult to research given the secretive nature of the species and the problems experienced in locating nests. This is probably the reason no intensive work had been carried out prior to this study (Austin 1968). Despite these difficulties descriptive information on nesting activities and quantitative data on the growth of nestlings were obtained for a small number of birds. Nestling development is an important aspect of the breeding strategy adopted by the species (Ricklefs 1969a; O'Connor 1978) and the growth rate of the Fox Sparrow was compared with other

emberizids where similar data were available.

An analysis of the vocalizations of the Fox Sparrow was also undertaken. Males are loud and persistent singers from their arrival on the breeding grounds in early April till the young hatched. They also called readily if a taped song of a Fox Sparrow was played in a territory or if the nest was approached. Females also vocalized frequently in the latter case. Therefore a catalogue of vocalizations was easily compiled. The primary song of the males was analyzed in detail, especially with respect to geographic variations. The Fox Sparrow has a high morphological variability even within subspecies (Swarth 1920; Linsdale 1928a) which indicates some degree of isolation of breeding populations. Isolation in populations of some fringillids may be reinforced by a system of dialects (Lemon 1975; Baker 1975) perhaps through assortive mating based on the song type prefered by the female. Given the morphological variability dialects might be expected in Fox Sparrows. A possible prediction from this hypothesis would be that, given dialects, there should be a differential aggressive response of male birds to the same and different dialects. Preliminary information was gathered on this point. Organization of the repertoire and constancy of the song of individuals through the breeding season was also examined.

Materials and Methods

Investigations into the breeding biology and vocalizations of the Fox Sparrow were carried out during the spring and summer of 1977 and 1978. Fox Sparrows are common throughout most of insular Newfoundland. Several locations were sampled with respect to vocalizations (Figures 1 and 2) while the breeding biology was studied only in the St. John's area.

Nine nests were found during the two breeding seasons. Of these three were located by observing adults carrying materials to the nests in the last stages of construction. The other six were found, by systematic searching or by accident, at a stage when the nest already contained eggs or young. Some additional nest information was gathered from the cards in the Newfoundland Nest Record Scheme.

Eggs were weighed using a Pesola spring scale (50 g: estimation to 0.1 g) and measured at the longest and widest point with Vernier calipers (estimation to 0.1 mm). Five eggs (3 deserted, 2 broken shells found in nests) were collected and their color values determined using the Munsell color scheme. After hatching nestlings were weighed and measured daily with the same scales and calipers. Day of hatching was considered Day 0. Mensural data recorded included tarsus, culmen, rectrix, and wing chord as defined by Godfrey (1966) as well as the inner and outer primaries and the hallux plus claw. The primaries were measured from the point the feather sheath emerged from the skin to the tip of the feather. The hallux plus claw was taken from the joint where the hind toe articulates with the accessory metatarsals to the tip of the claw. Seven nestlings were banded with standard numbered aluminum

Figure 1. Map of Newfoundland showing locations where adult male Fox Sparrow primary songs were sampled except for the area between Cape St. Francis and St. John's. Number of songs recorded at each location are circled.

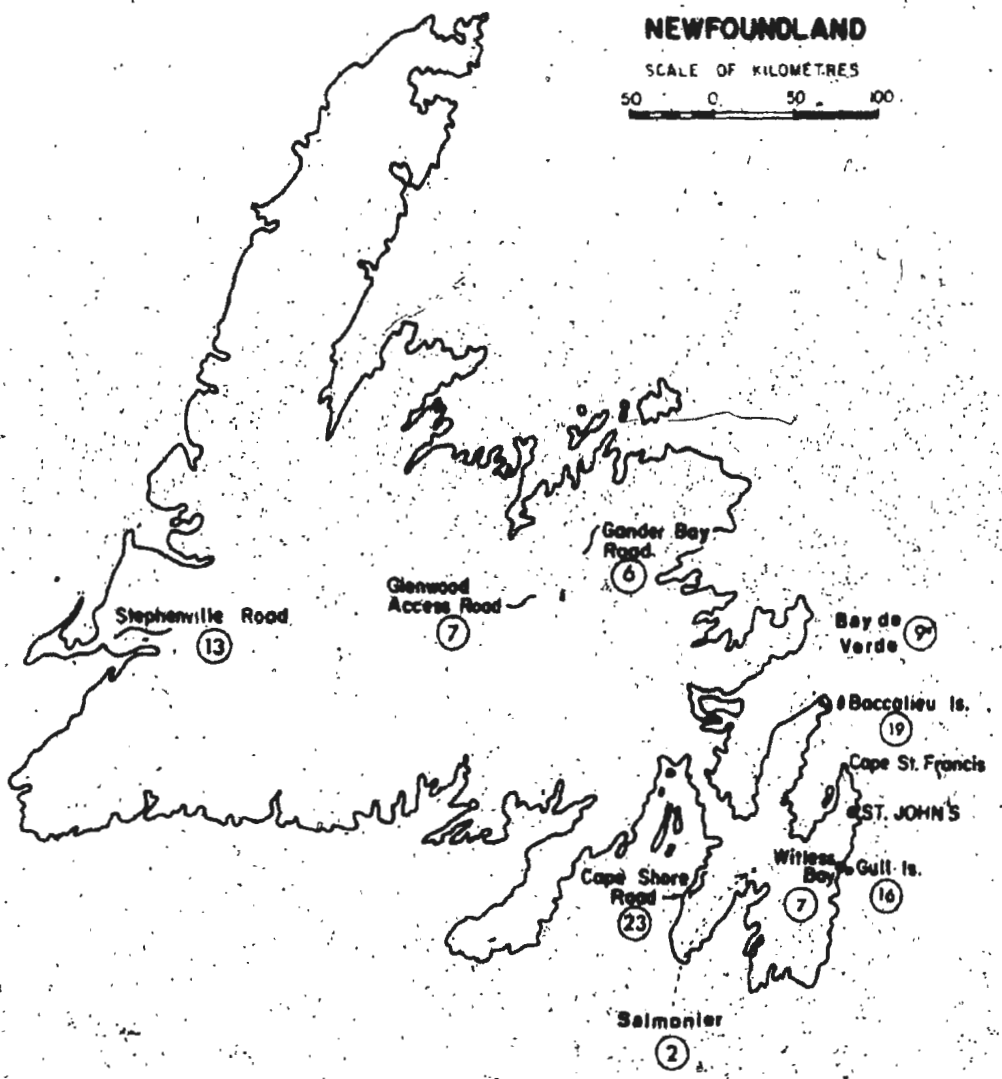
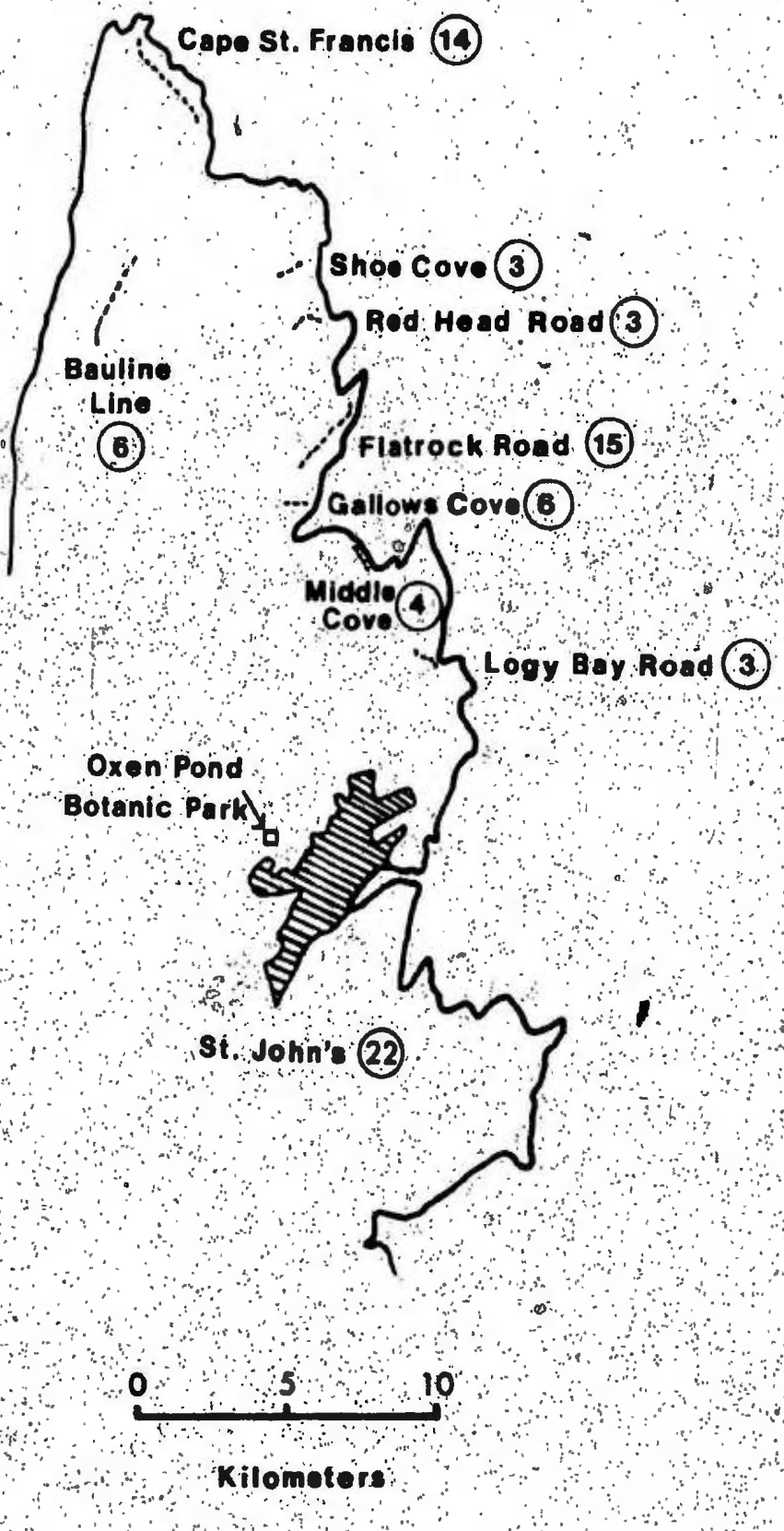

NEWFOUNDLAND
SCALE OF KILOMETRES
50 0 50 100
Gander Bay Road
6
Glenwood Access Road
7
Stephenville Road
13
Bay de Verde
9
Baccalieu Is.
19
Cape St. Francis
ST. JOHN'S
Witless Bay
7
Gull Is.
16
Cape Shore Road
23
Salmonier
2

Figure 2. Map of the Cape St. Francis to St. John's area showing locations where adult male Fox Sparrow primary songs were sampled. Number of songs recorded at each location are circled. Birds recorded in Oxen Pond Botanic Park were included in the St. John's group.


Cape St. Francis 14
Shoe Cove 3
Red Head Road 3
Bauline Line 6
Flatrock Road 15
Gallows Cove 6
Middle Cove 4
Logy Bay Road 3
Oxen Pond Botanic Park
St. John's 22
0 5 10
Kilometers

bands supplied by the Canadian Wildlife Service and colored leg bands, at about 6-7 days old.

A total of 31 adults were mist-netted, banded, weighed, and measured. Two other birds were found dead after they had struck windows and their measurements are included in the Results. The seasonal distribution of these captured and dead birds were as follows: 5 birds in June, 6 in July, and 22 in October. In addition to weight measurements taken on the adult birds included tarsus, culmen, rectrix, and wing chord. Two specimens of adult Fox Sparrows in the Memorial University museum collection were measured with respect to inner and outer primaries and hallux plus claw.

The vocalizations of the Fox Sparrow were recorded on a Uher 4400 IC tape recorder at a tape speed of 9 cm/sec. Scotch Brand, Ampex, or Sony audio recording tape was used. Songs and calls of the adults wre recorded with a Dan Gibson Model P-200 Parabolic Microphone while a Uher M517 interviewer style microphone was used for nestling calls. A captive male Fox Sparrow being held for another study was recorded with the interviewers' microphone and a sound activated relay device so the observer did not have to be present to operate the tape recorder. The adults were recorded mainly from highways, roads, or along existing woods trails generally after a prerecorded tape of a primary song of a Fox Sparrow had been played to stimulate singing and calling.

Analysis of the recorded sounds were carried out on either a Kay Elemetrics Corporation Sound Spectrograph (7030A) or a Crown Voice Analyser 700 series. Sonagrams of adult call notes, female songs, and nestling calls were made on the Kay. Two samples of the primary song(s) of each individual male were rerecorded on a summary tape on another

identical Uher from which a second summary tape was produced on the internal recorder of the Crown. The Crown was used because it was a more efficient machine for the production of large numbers of sonagrams. The second rerecording was necessary because the head configuration of the Uher and Crown recorders were incompatible and therefore the first summary tape could not be used. Though the multiple transfers of the sounds did introduce some extraneous noise this did not have an appreciable effect on the characteristics examined in the sonagrams. Sonagrams of certain songs obscured by background noise were produced on the Kay from the original tape. In all cases the high shaping settling was used and sonagrams were made on both wide and narrow bandpass filter settings.

One-way analysis of variance was used to test for seasonal differences in weights of adult Fox Sparrows and for differences in simple parameters in the Fox Sparrow song including song duration, highest and lowest frequencies, and number of syllables between localities. Variability of syllable and between syllable duration for one day compared to the season was examined in three birds with a paired t-test of the variances. Correlation and replicated goodness-of-fit (G-test) was used to test for a relationship between height of nest and the time of laying within the breeding season. All statistical tests were set at the 95% level of confidence.

All 175 songs recorded were examined with regard to their constituent syllables. Each unique syllable type was given a numerical label. Cluster analysis of songs by syllables was carried out using Memorial University computing services programs entitled Braycurt, Jaccard, and SMC. Songs were then clustered together hierarchically

using the group average method (see Sneath and Sokal, 1973) and dendograms plotted. In this way it could be determined if songs of Fox Sparrows in one locality were distinct from other localities on the basis of shared syllable types.

Results

Part I -- Breeding Biology

In eastern Newfoundland the Fox Sparrow is one of the earliest spring migrants to return from its wintering grounds. Records kept for the St. John's area from 1973 to 1978 (B. Jackson, unpublished data) indicate the mean annual date is about 9 April with a range from 4 April to 19 April. These birds apparently migrate at night and regularly cross large expanses of water (Terrill 1968). They also seem to migrate rapidly in a more or less discrete wave but can be delayed by inclement weather (Terrill 1968). Storms may therefore account for some of the variability in arrival dates in Newfoundland by forcing migrating birds to linger south of their destinations.

Establishment of territories began almost immediately on arrival in the breeding areas. In 1977 the return date was 4 April and Fox Sparrows in Oxen Pond Botanic Park appeared to be well advanced in the process of taking up territories by the next day. This was determined by observing a singing bird consistently at the same singing post. The snow melt in early April that year was far advanced and the ground was bare in several places. In 1978 Fox Sparrows delayed arrival in the St. John's area until 19 April. Once they did arrive, however, territory establishment seemed to take place almost as rapidly as in 1977. Deep snow remained almost until the end of April in 1978 and frequent sightings of birds at feeders suggests that snow deterred some birds from occupying breeding habitat immediately. Bare ground may be a prerequisite in territory establishment because Fox Sparrows forage primarily in the leaf litter in the shrub understory.

The Fox Sparrow inhabits a wide range of habitats. Although no measurements have been done highest densities probably occur in the tuckamoor (clumps of wind dwarfed conifers on barrens) and scrub forest areas (L.M. Tuck, pers. comm.) but, too, can be commonly found in successional old fields, and cut-over and burned-over areas. They can also be found in the continuous coniferous forest and the rocky alpine and coastal barrens as well but are much less numerous in these areas of apparently marginal habitat. This distribution pattern contrasts with the western races which seem to select deciduous shrubs (Linsdale 1928a). In both cases, however, the preference seems to be for dense tangles of low growing vegetation. Actual density of breeding pairs as well as territory size is generally unknown but probably depends on the productivity of the habitat (Hinde 1956). The territory size of 3 individual Fox Sparrows in Oxen Pond Botanic Park in an area of regenerating forest after a fire was roughly estimated to be about 1 ha by maping singing posts and activity ranges.

Function of territory in Fox Sparrows is similar to that in other small passerines being areas where most breeding and feeding activities were confined (Type A territores (Nice 1941)). The degree of territory fidelity between seasons is unknown but unpublished data for Gull Island, Witless Bay and the St. John's area (W. Threlfall and G.F. Bennett respectively, pers. comm.) indicates that it may be high. Fox Sparrows mist-netted and banded in an area in one season were recaptured in the same area the nest season if they were recaptured at all.

The role of vocalizations in territorial behaviour will be discussed in Part II of the results.

Fox Sparrow behaviours other than singing were difficult to observe because they generally occured in dense undergrowth. Very few interactions between individual Fox Sparrows were observed for that reason. Only four chases were seen in the two years of study. The bird doing the chasing was taken to be the male, the holder of the territory, but because the sexes are monomorphic it could never be determined whether the bird being chased was male or female. One chase was observed in Oxen Pond Botanic Park where two birds were involved in a chase in the underbrush. They were visible for only about 2 seconds. Two other chases took place on Gull Island. Those interactions were probably boundary disputes between two neighbouring territorial males. The fourth interaction involving three adult birds was observed on May 1, 1977. These birds were observed for approximately 10 minutes in a single encounter session which included singing by one bird from a perch near the ground and chases involving various combinations of the three birds. A typical sequence of behaviours was for one Fox Sparrow to sing 3-4 times from a perch about 1 m off the ground and then fly at and chase one or both of the other birds which were on the ground. Less frequently a non-singer would fly at the singer. One of the Fox Sparrows eventually flew off leaving the singer and one other which continued the sequence of singing and chases. The chases consisted of fluttering and running about on the ground or hopping from perch to perch among the branches in the dense undergrowth until the non-singer flew a short distance away. The singer would then sing again from a low perch while the other scratched and pecked at the ground. Those birds, too, eventually left the area. Unlike the other three occasions where the bird being chased was probably an intruding male there was no

indication of the sex of these birds other than that the singer was probably a male.

Because Fox Sparrows seem to migrate in a single wave, females probably arrived on the breeding grounds as soon as the males. The process of mate selection is not known. No courtship behaviour other than singing has been reported from migrating birds (Terrill 1968). Site fidelity may suggest that selection is partly for site as well as for mate. Pairing occurred soon after territories were established and birds assumed to be male-female pairs were observed together frequently within a week of the spring arrival.

Apart from singing other courtship and copulatory behaviour was observed only once, during late nest building. On May 29, 1978 in Oxen Pond Botanic Park a male Fox Sparrow was observed singing its primary song from an unusual location, low in the underbrush. A second Fox Sparrow, the female, flew in carrying several pieces of dead grass in its beak. Singing frequently the male approached the female which was also perched in the underbrush, about 1 meter above the ground. When it was within 0.5 meter of the female the male began a wing droop and wing quiver display which lasted through the last stage of the approach. The male then mounted the female with both fluttering their wings. It appeared that the wing fluttering was to maintain balance on the perch. During the copulation, which lasted only 2-3 seconds, the female dropped some of the grass she was holding. The male repeated the wing droop and quiver display again 3-4 times after dismounting but this did not again result in copulation. Within about one minute the female flew down to where the grass had fallen, retrieved most of it, and flew into the underbrush. Watching the female revealed the location of the partially

constructed nest which was about 3 meters away from where the copulation occurred.

Of the eight nests found during the study seven were closely associated with coniferous trees. Five were built in conifers while two were placed on the substrate under conifer trees. In those 7 nests there were overhanging branches which afforded some cover to the nests. The eighth nest was placed behind the trunk of an alder (Alnus sp.) on a slope and supported on the open side by dead branches. In this case the trunk of the tree provided the overhanging protecting. Peters and Burleigh (1951) report a similar preference for coniferous trees though they report one built in a large Yellow Birch (Betula alleghaniensis).

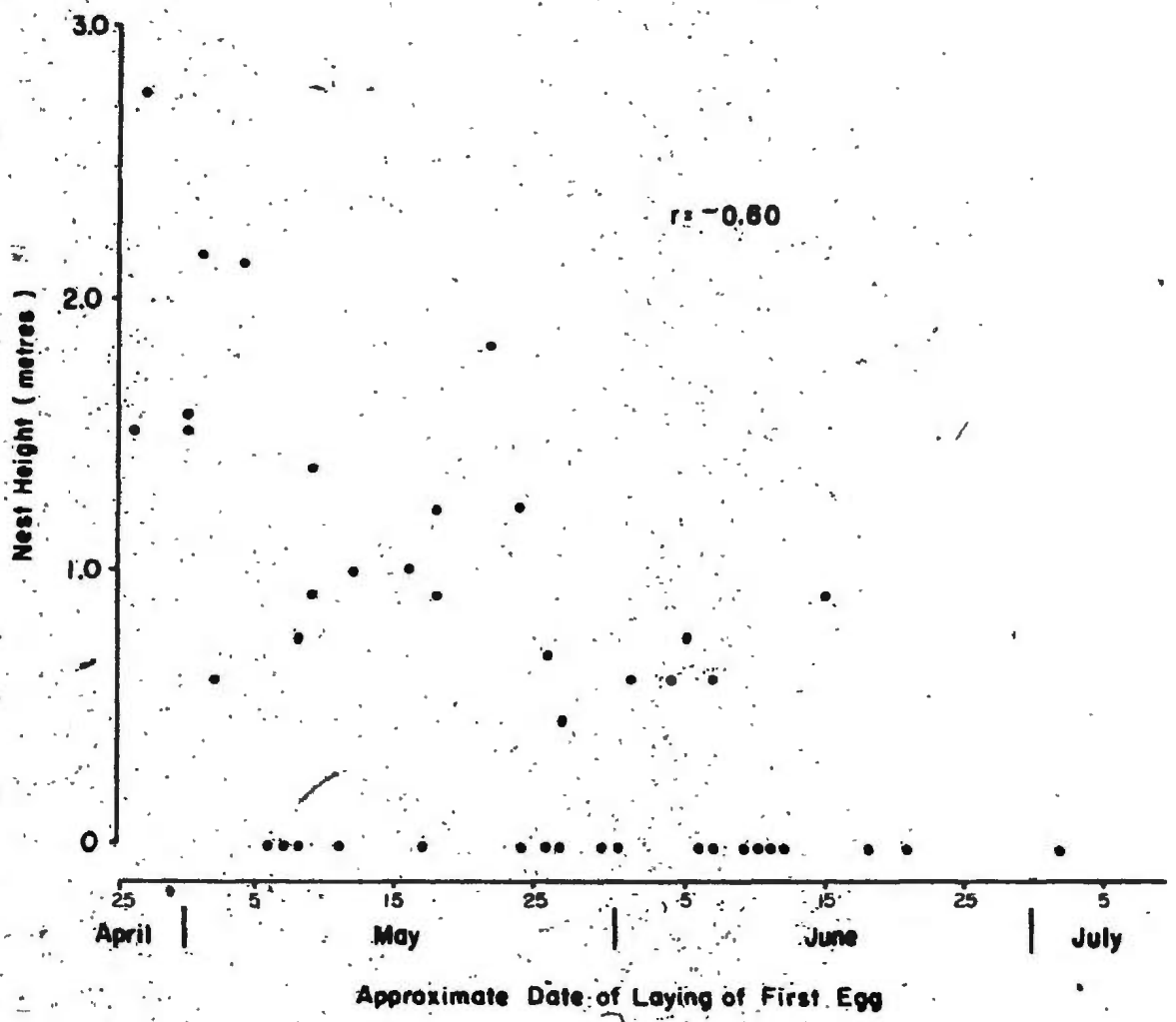
Nests were constructed from a variety of materials and differed on whether they were on the ground or in a tree. Seven nests were collected after they cased to be used by the Fox Sparrows, air dried, and weighed. The average weight of 5 tree nests was 49.6 g (range 39.0 g – 59.7 g) while the 2 ground nests were much smaller at 9.8 g and 15.2 g. Ground nests were constructed from dried grasses and placed in a depression in the ground which supported the sides. Tree nests were more bulky being composed of an outer wall of twigs of black spruce (Picea mariana), rotting wood, lichens (Alectoria sp., Usnea sp.), and moss (Polytrichum sp.) supporting an inner nest cup of dead grasses (Graminae). In both ground and tree nests the lining was primarily fine grass but hair, Alectoria lichens, feathers, and even green monofiliament fishing line was also found. The size of the cup could not be measured accurately because handling the nest deformed the cup to some degree. One nest collected on May 31, 1977 from a tree in Oxen Pond Botanic Park which remained relatively intact had a cup measuring

about 55 mm deep by about 65 mm across at the inner rim. The other nests had cups of approximately this size.

Both Philipp (1925) and L.M. Tuck (pers. comm.) noted the tendency for early season nests to be placed in trees while later ones were generally on the ground. An examination of Fox Sparrow nest record cards in the Newfoundland Nest Record Scheme yielded 46 records with nest height data. One of these was rejected for analysis because of its unusual height, over 6 meters, while all the other nests were less than 3 meters from the ground. The nests reported were found at a variety of points of the nesting cycle so a series of criteria were established to estimate the day of laying of the first egg for all the nests. Except when that day was known exactly the data were subject to those criteria given in Appendix 1. Because the time required to build a nest is not known the date of the start of nest building could not be estimated. In all cases the year and geographic location of the nest were ignored. The latter variable may have introduced some bias because there is a variation in the development of environmental conditions suitable for nesting. Generally it is warmer in the western part of the province earlier than the east. Similarly the variation between year may also have introduced extra variance into the results but no satisfactory way could be found to control for either of those variables.

Egg laying starts covered a period of 68 days from 27 April to 3 July. Nest heights ranged from ground level to 2.7 meters. A scatter diagram of nest height versus the dates of onset of laying is shown in Figure 3. There was a significant negative correlation between nest height and egg laying ($r = -0.60$). There is then a decrease in nest height with the advance of the breeding season. The frequency of nests

Figure 3. Scatter diagram of Fox Sparrow nest height verses date of laying of the first egg in that nest.


3.0
2.0
1.0
0
Nest Height (metres)
r = −0.60
25
5
15
25
5
15
25
5
April
May
June
July
Approximate Date of Laying of First Egg

on and above the ground broken down into four 17-day periods of the 68-day time span is shown in Table 1. A G-test for homogenity in replicates, considering the 4 time periods as replicates, showed a significant difference in frequencies of nest height over time (G = 10.673, df = 3).

Morton (1978) noted a similar trend in nest sites of the White-crowned Sparrow in the mountains of California and attributes this to snow conditions, primarily the depth of the snow pack. This is probably also the major factor affecting Fox Sparrows in Newfoundland because they often begin nesting when there is still snow on the ground. Ground temperatures and water content may also be contributing factors.

The onset of laying began soon after nest contruction ended. One nest in Oxen Pond Botanic Park was found in the last stages of construction on 25 April and contained the first egg on 28 April. The weekly frequency distribution of onset of laying through the breeding season (Table 2) is relatively even from late April to mid June and then drops off to no starts after early July. Eggs were laid at a rate of one per day. The approximate time of laying, known for 3 eggs, was early in the morning, within 2 hours of sunrise. This was determined simply by flushing females off the nest and counting the eggs at various times during the day. The mean clutch size is 3.24 eggs (L.M. Tuck, unpublished data based on 34 nest record cards).

Twenty-one eggs were weighed and 20 were measured. (One egg was accidentally broken after weighing and could not be measured.) Mean values plus or minus one standard deviation were as follows: weight = 3.5 g $\pm$ 0.20; length = 23.5 mm $\pm$ 0.84; width 17.1 mm $\pm$ 0.50. Values given in the literature for water filled egg weight, 3.89 g (Long 1973),

Table 1. Frequencies of ground and tree nests in four 17-day periods during the breeding season. Data from nest record cards using standardizing criterion (Appendix 1)

	Nest Location		
	Ground	Tree	Total
27 April - 13 May	4	12	16
14 May - 30 May	4	7	11
31 May - 16 June	10	5	15
17 June - 3 July	3	0	3
Total	21	24	45

Table 2. Weekly frequency distribution of onset of laying. Date from nest record cards using standardizing criterion (Appendix 1)

Week	Number of Nests
April 27 - May 3	6
May 4 - May 10	8
May 11 - May 17	3
May 18 - May 24	4
May 25 - May 31	7
June 1 - June 7	6
June 8 - June 14	7
June 15 - June 21	2
June 22 - June 28	1
June 29 - July 5	1

and mean length and width measurements 22.7 mm and 16.3 mm respectively (Terrill 1968), were not statistically different from those found in this study. An approximation of egg volume was made using a formula given by Preston (1974): Volume = 11/21 (length) $(width)^2$. The volume of each of the 20 eggs was found and the mean of these volumes was 3584.4 mm^3. A second calculation of egg volume from the relationships described by Paganelli et al. (1974) based on the high correlations of weight, area, and volume was made for comparison. Using the equation Area = 4.835 $weight^{0.662}$ and Area = 4.951 $volume^{0.666}$ and given the mean weight was 3.5 g, area was found to be 11.08 cm^2 and volume was 3352.1 mm^3. These two calculations of egg volume, one based on the relationship of length and width to volume and the other on weight to area and volume gave results within 7% of each other.

Five egg shells were collected with the nests. Three were abandoned eggs, one was an egg damaged while in the nest and did not hatch, and the fifth was a shell of a bird that hatched successfully. They had a background color of light blue (Munsell notation 7.5 BG 9/2) and more or less heavily spotted with browns (Munsell notation 7.5 YR 5/4 to 3/4). The density and size of spots was variable but there was a tendency for the spots to become more concentrated on the large end. The eggs were slightly glossy when laid but the gloss faded with time.

Eox Sparrows seem to, at least occasionally, build more than one nest before laying the first clutch. In an established territory in Oxen Pond Botanic Park a nest was observed under construction on 24 and 25 April 1977. A storm on the night of 25 April filled the nest with snow. The birds were never seen near that nest again. On 3 May a second nest containing 3 eggs was found about 5 meters from the first.

From the approximate hatching date, 13 May, the day the first egg was laid was about 27 April. The second nest was a bulky tree nest and it is unlikely that it could have been built in 1-2 days after the first was abandoned. Fox Sparrows will also renest if the first clutch is destroyed. In a second territory a nest found on 25 April was almost completely built. The nest was checked daily through egg laying and early incubation until 8 May when all 3 eggs disappeared. A second nest containing 4 young a few days old was found in the same territory on 2 June. Backdating to time of laying of the first egg of second clutch using standardizing criteria placed it at about 10-12 May. Peters and Burleigh (1951) and Philipp (1925) suggest that two broods may be raised in a year if the first brood is started early enough. There was no evidence of double broodedness found in this study.

Incubation of the eggs and brooding of the chicks appeared to be accomplished by the female, an observation supported by Philipp (1923) and Mailliard (1921). Evidence for this statement lies in the observation that frequently when nests were checked the male was heard singing from the top of a tree while its mate was found on the nest.

Ryan (1974) found the incubation perod for a clutch of 3 eggs begun on 23 May was 14 days. A nest found in Oxen Pond Botanic Park on 29 May 1978 was followed through incubation. The last egg of the clutch was laid at about 600 hr on 4 June and hatched at 1000 hr on 16 June. Using an incubation period defined as "the time from laying of the last egg of a clutch to the hatching of that egg" (Thompson 1964) the incubation was approximately 12 days, 4 hours. Ryan (1974) also states that "there was no evidence of incubation before the third egg was laid" and hatching was relatively synchronous within a 12-18 hour period. In the Oxen Pond

Botanic Park nest the female was twice observed sitting on the incomplete clutch at midday. The first egg hatched sometime on 14 June and the last at 1000 hr on 16 June giving a time span of at least 36 hours. In this case the last one to hatch was much smaller and weaker than its nest mates and remained in the nest for only 2 days. It was thought that this nestling died and was removed from the nest by the adults between Days 2 and 3.

The following description of hatching is a composite made from observations on several eggs during the study. In the late stages of incubation scraping on the inside of the egg shell could be heard. A small area of the shell was eventually cracked and pipped. Weak vocalizations could be heard once the opening was made. Hatching was accomplished by the chick breaking the egg with the egg tooth in a narrow line around the larger end of the egg just above the equator. The top of the egg eventually broke off and the chick emerged. The adults apparently quickly remove the shells because none were ever found even when the nestlings were still damp.

Nesting period for the Fox Sparrow defined as "the interval between the hatching of the young bird and its departure from the nest" (Skutch 1945) was found by Ryan (1974) to be about 10.5 days for one nest. In this study the young of two nests left after 9 days.

Growth measurements were taken of nestling Fox Sparrows of the two nests whose histories were known from incubation to fledging. Measurements were taken daily beginning at the day of hatching (Day 0) to fledging (Day 9). Sample sizes were small, varying between 3 and 8 nestlings. An equation approximating the daily change in weight was derived using the graphical procedure described be Ricklefs (1967). The

growth constant, k, was found to be 0.566. The asymptotic weight used in the calculation was 27.3 g. The point of inflection was 3.7 days. The logistic equation for the growth of nestling Fox Sparrows based on trends exhibited in the first 9 days after hatching was

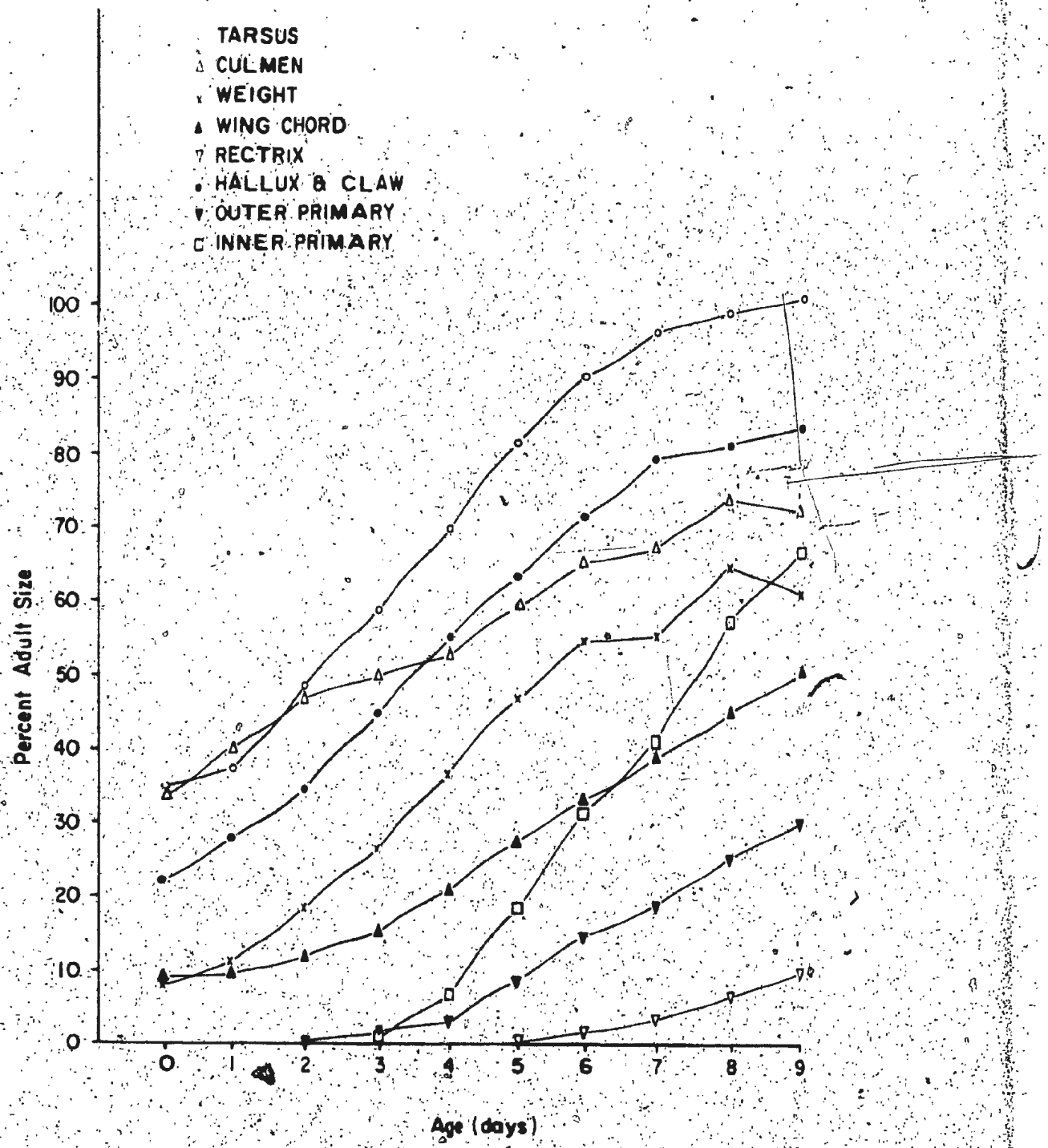
$$W = \frac{27.3\ g}{1 + e^{-.566\ (t-3.7)}}$$

where W is weight in grams at t days. Nestling weight at fledging was about 25-26 g or approximately 64% of adult weight. No fledgings were weighed after they left the nest at sometime between Day 9 and Day 10.

The other 7 body parameters measured in this study are given as daily mean values with standard deviations in Appendix 2. Adult means for the same parameters from captured birds or museum specimens are given in Appendix 3. Daily change in means of all 8 body parameters from hatching to fledging expressed as percent adult size is shown in Figure 4. Only the tarsus reached full adult size prior to fledging. The second largest body part at fledging was the hallus plus claw which was 83% of adult size. All other body parameters measured were less than 75% of adult size at fledging and the rectrix slightly over 10% adult size at fledging, was the smallest relative to all the other.

Both adults fed the nestlings, as was also noted by Philipp (1925). Food is gathered from the forest floor litter by a method known as bilateral scratching. The general characteristics of this foraging behaviour have been described in detail by Greenlaw (1976). Food items and season relative proportions of plant and animal material were discussed by Terrill (1968) which varies from almost entirely animal

Figure 4. Growth of Fox Sparrow nestlings expressed in percent of adult body size.


TARSUS
CULMEN
WEIGHT
WING CHORD
RECTRIX
HALLUX & CLAW
OUTER PRIMARY
INNER PRIMARY
Percent Adult Size
0
10
20
30
40
50
60
70
80
90
100
0
1
2
3
4
5
6
7
8
9
Age (days)

material in the summer to primarily plant in the winter. Adults were twice observed carrying long, brown larva-like organisms to the nest.

The adults were aggressive when the nest was being disturbed giving the loud 'chek' call note frequently. As the vocal powers of the young developed the reactions of the adults to the louder calls of the young also became more intense as evidenced by the adult calling more rapidly and sometimes approached to within 0.5 meters of the observer. The adults accompany the young for a period of time once they leave the nest. A color banded adult male still on its territory was observed 21 days after its offspring had fledged feeding one of its young (also color banded). The fledgling could fly but begged for food by using wing quivering and gaping.

Small groups of Fox Sparrows of generally 2-6 individuals were seen in the late summer. Fully grown immature birds were included in these groups with the adults. The degree of territory fidelity after the young became independent is not known. Fox Sparrows observed in the breeding habitat seemed to decrease in numbers gradually through the fall till they became uncommon in November having migrated south. Some birds have attempted to overwinter in the St. John's area in the past several years. A few appeared to have been successful if a regular food supply was available at feeders when snow conditions prevented normal foraging (B. Jackson, H. Clase, pers. comm.).

Part 2 — Vocalizations

A variety of vocalizations given by Fox Sparrows were recorded in the 1978 breeding season. These were divided into four categories as follows: adult cal notes, nestling call notes, female song, and male

primary song. The division of songs and call notes generally follows Pettingill (1970) who defined song as "a vocal display in which one or more sounds are consistently repeated in a specific pattern" and "all other vocalizations are collectively termed call notes." In the Fox Sparrow song is a well developed sequence of notes with a musical quality easily distinguished from the single- or multi-noted calls.

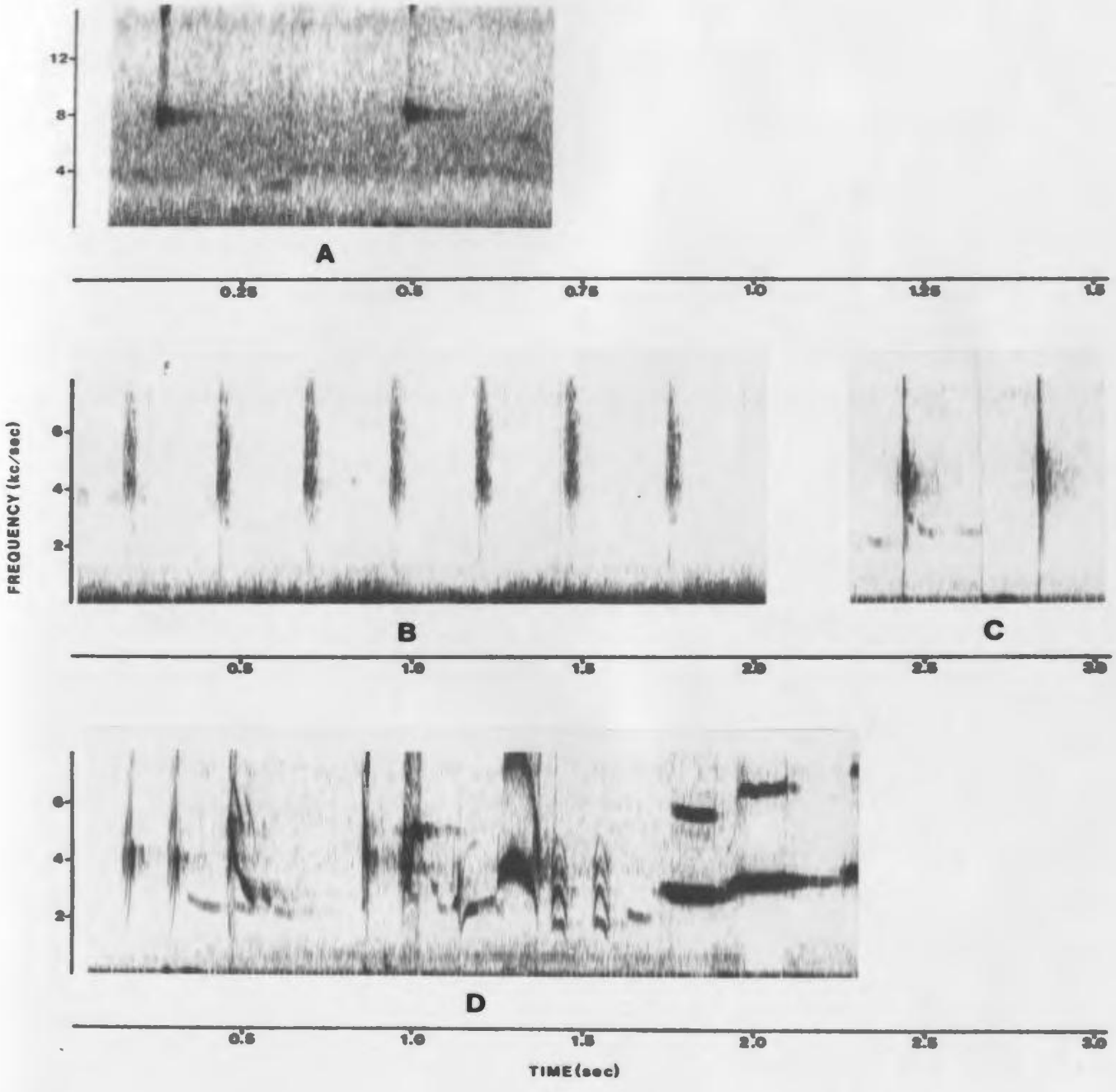
In the following descriptions the calls of both the adults and young are illustrated by representative samples only. due to the infrequent recording of most of the call notes no statistical analysis could be undertaken.

Adult call notes

Four types of adult Fox Sparrow call notes were recorded. The most frequently heard note was a loud, harsh "check". It was a short burst of sound approximately 20 msec. duration with a frequency centered at about 4 kc/set. (Figure 5C). This note was described by Moore (1913) as "an explosive aspirate, which may be indicated by the syllable "check". Townsend and Allen (1907) called it "the usual alarm note, a loud "smack".

In this study the note was almost always heard from the resident male after a prerecorded Fox Sparrow song was played in an established territory. The resident male, and sometimes also the female, would approach the speaker giving a rapid succession of "check" notes but generally stayed hidden in the underbrush. When the tape was stopped the resident male would continue calling at a reduced rate for a period of time (usually 1-2 minutes) then fly up to a perch and begin to sing. It could not be ascertained for those females that did not react if the

Figure 5. Adult Fox Sparrow call notes. See Text for explanation of the 4 types.


12
8
4
A
0.25
0.5
0.75
1.0
1.25
1.5
FREQUENCY (kc/sec)
6
4
2
B
C
0.5
1.0
1.5
2.0
2.5
3.0
6
4
2
D
0.5
1.0
1.5
2.0
2.5
3.0
TIME (sec)

reaction was due to the stimulation by the intruder's song, or the vigorous response to the song by its mate. The note was also used by both males and females when the nest was approached. This note was also heard given during the few encounteres of territorial males that were observed.

The second call note type recorded was a low, sharp "sip". Like the "check" note it was of short duration, about 20 msec., but was centered at a much higher frequency, about 8 kc/sec. (Figure 5A). This note was heard on fewer than ten different occasions, and recorded only twice. Only males in an apparent state of extreme agitation were seen to give the note. The note was a highly directional signal and could only be recorded when the parabola was pointed directly at the bird. This was probably due to the acoustical phenomenon of beaming (Witkin 1977) by which high frequency sounds have a much narrower cone of dispersion from the source than lower frequency sounds.

A third type of call note was a rapidly repeated "chu-chu-..." heard and recorded only once, during a prerecorded Fox Sparrow song playback. These sounds appeared to be approximately 50 msec. bursts of noise, similar to white noise between about 3 and 7 kc/sec. and repeated every 250 msec. (White noise is continuous random sound of an extremely wide frequency bandwidth.) The sequence shown in Figure 5B consisted of seven "chu" notes and the entire sequence lasted about 1.5 sec. During the recording session the sequence was repeated about 6 times. Because a male was calling and eventually sang nearby it was thought that the bird emitting the call note was a female. During the production of the sound the bird was making up and down motions of the head and stayed perched on the same branch, partially hidden by vegetation. Townsend

and Allen (1907) report a similar observation of "one individual who was 'smacking' in a fir tree emitted faint sneezy notes with motions of swallowing between the smacks". No function could be ascribed to this call note.

A fourth type of call note was really a series of notes which a male would sometimes produce immediately prior to singing the primary song. They were an unstructured series of syllable like notes of varying frequency and duration (Figure 5D). They were similar to the series of notes given between male primary songs for a short period just after arrival on the breeding grounds in the spring (see Figures 9A, 9B) and perhaps remnants of the subsong. Like the three note types discussed above this note series was given in response to a prerecorded Fox Sparrow song. Its function could not be determined.

Logistic problems prevented the recording of Fox Sparrow call notes not elicited by a prerecorded song stimulation. One note heard in late summer of both years, and which differed from the four described above, was a faint "tsip". A similar note, rendered "stssp", was described by Townsend and Allen (1907) as being commonly heard in migrating birds but rarely on the breeding grounds. In this study it was heard coming from a group of about 5 Fox Sparrows perched in dense vegetation. It was not clear whether they were using the call as a contact or warning note or for some othr function. Because the observer found the note difficult to localize the warning note function is suggested (Marler 1955).

Two other notes have been described. Terrill (1968) described a call as "a modified form of the alarm "tchek..."" which "... serves as a communal call when migrating fox sparrows are going to roost...". White (1937, in Terrill (1968)) mentions a "...peculiar note, shrill,

prolonged--a kind of squeal" heard from birds fighting among themselves during an interruption in migration caused by a blizzard. I observed neither of these vocalizations during this study.

Nestling call notes

Nestlings produced two basic types of vocalizations. One was a continuous frequency modulated sound ranging between 6 and 10 kc/sec. and lasting about 250 to 750 msec. (Figure 6A, 6B, 6C). It could be rendered phonetically as a high, thin "seep". The modulating frequency of the notes ranged from 30 to 50 cycles/sec. and seemed to be emitted when there was some movement near and/or of the nest.

As the young grew older they became more vocal and called readily when handled. These were louder, lower frequency bursts of sound given in rapid succession. Each burst lasted from 60 to 100 msec. with a repetition rate of about 6-7 bursts per second (Figure 6D, 6E). Each sequence of sound bursts lasted about 1 sec. The modulating frequency of the sound bursts ranged from about 20 to 90 cycles/sec. They appeared to be distress calls and evoked in the adults a vigorous reaction of "check" calls, short rapid flights, and fluttering from branch to branch.

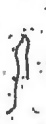
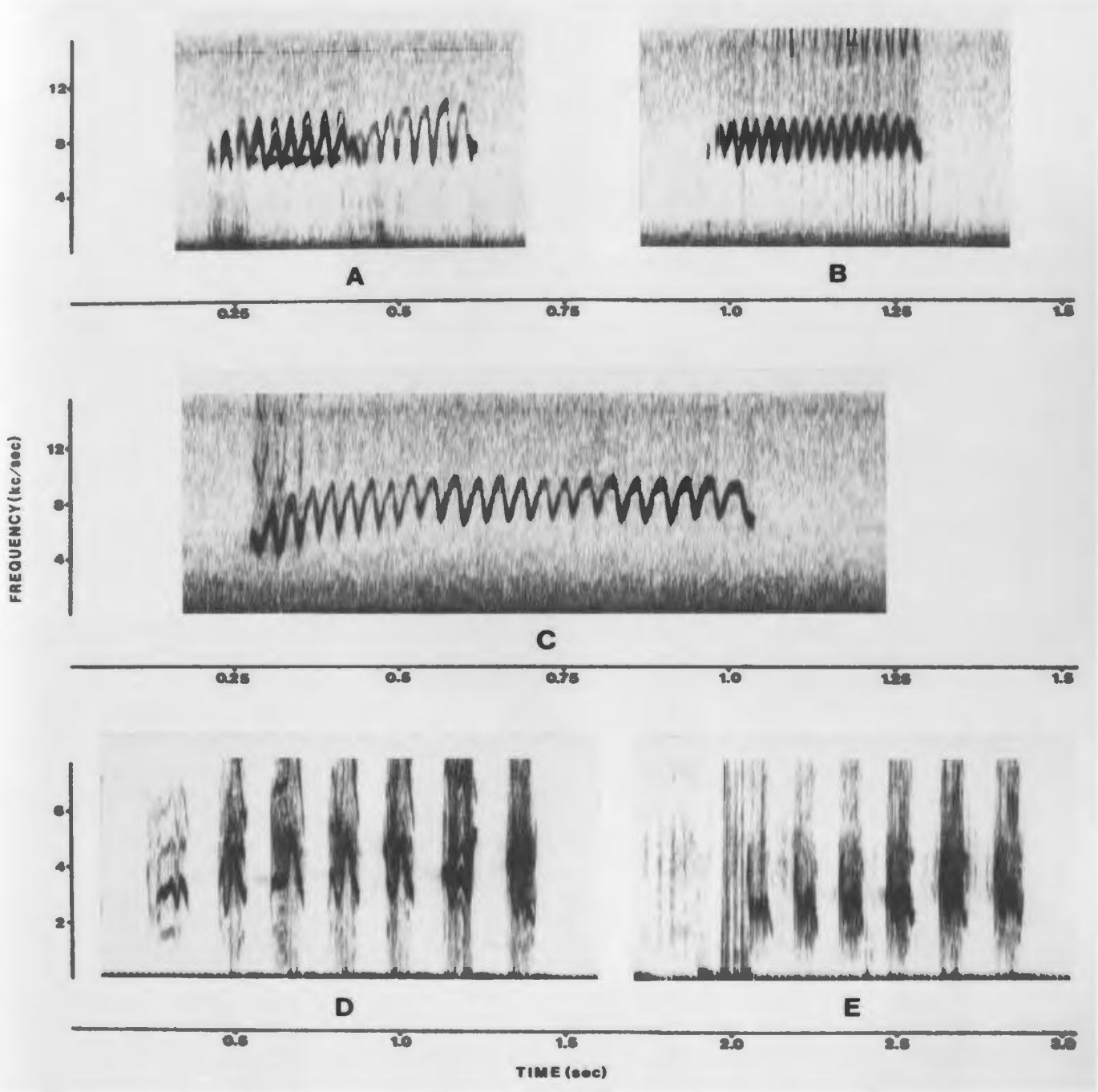


Figure 6. Nestling Fox Sparrow call notes. Five to 6 days of age (A, B, and C) and 7-8 days (D and E).


FREQUENCY (kc/sec)
12
8
4
A
B
0.25
0.5
0.75
1.0
1.25
1.5
C
6
4
2
D
E
0.5
1.0
1.5
2.0
2.5
3.0
TIME (sec)

Female song

Both Saunders (1910) and Martin (1977) state that the female Fox Sparrow will sing. This song is of reduced amplitude and complexity and is rarely heard. On two occasions in 1978 just after spring migration was complete a Fox Sparrow was heard to sing a weak, simple song in a territory already occupied by a male. Figure 7 shows a series of Fox Sparrow vocalizations recorded while two birds were perched in a tree within 1 meter of each other. The presumed female song of one bird is shown in Figure 7A, the normal male primary song of the other bird song is in Figure 7B, and Figure 7C shows an overlapping of the two sounds perhaps indicating that the both sounds were not produced by the same bird. Those birds did not show any agonistic behaviour toward each other but they were not collected to make a positive identification of sex. Female song is also known in the Song Sparrow, Melospiza melodia (Nolan 1968) and the White-throated Sparrow, Zonotrichia albicollis (Lowther and Falls 1968).

The function of the female song in the Fox Sparrow is not known. It may serve to strengthen the pair bond or be used to signal to the male that the female is willing to proceed with courtship. Alternatively it may serve no primary function but simply indicate a female with a hormonal unbalance.

Male primary song

The primary song of the adult male Fox Sparrow was a complex series of syllables of varying frequency and amplitude. Syllables were defined as single- or multi-noted sounds, a note being a single continuous sound (terminology follows Martin (1977)). Examples of 3 songs are shown in

Figure 7. Possible female song (A), male primary song (B), and overlap of the two (C) in a presumed Fox Sparrow pair.

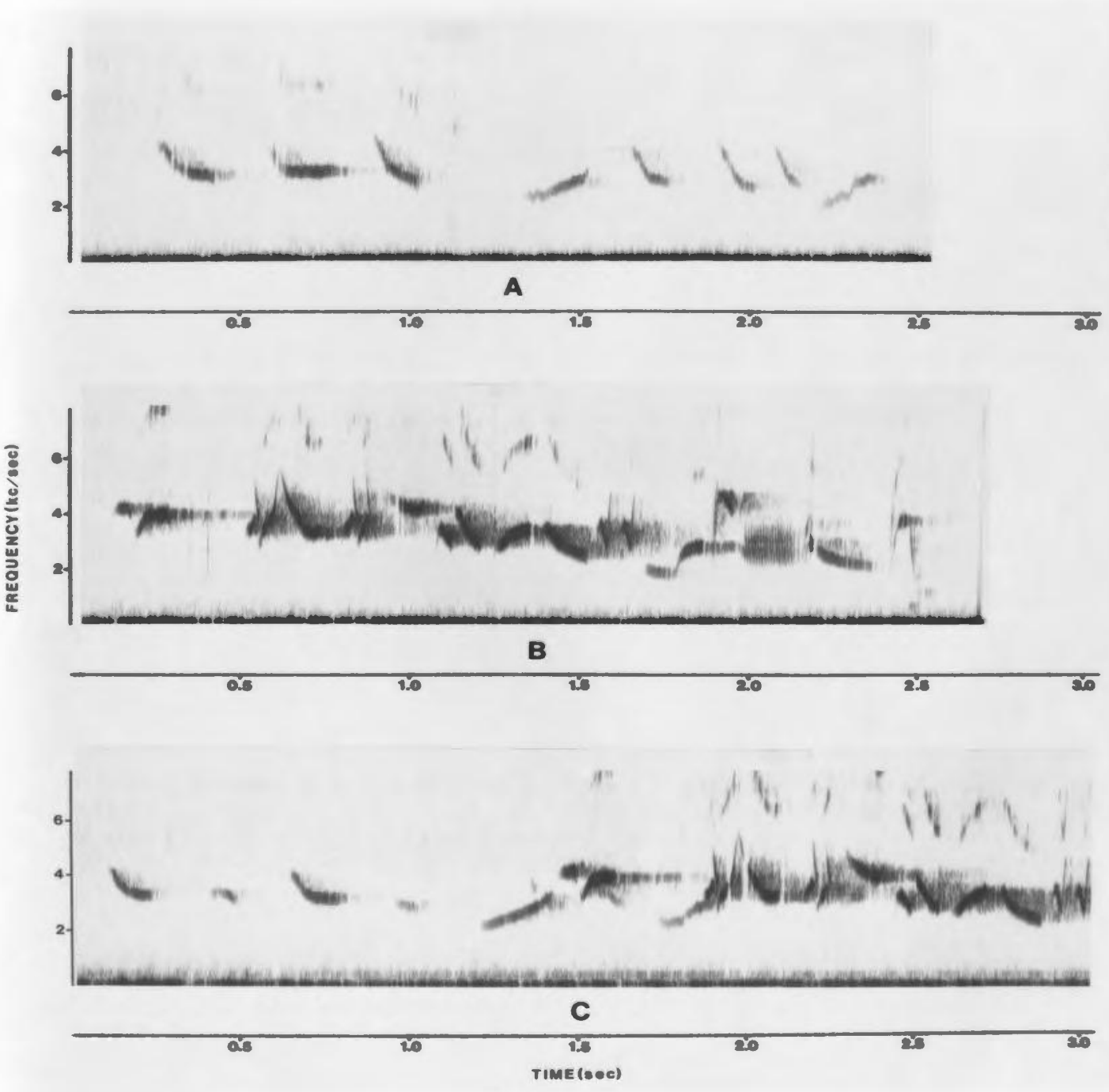

FREQUENCY (kc/sec)
6
4
2
A
0.5
1.0
1.5
2.0
2.5
3.0
B
C
TIME (sec)

Figure 8. Martin (1977) suggested, in the Fox Sparrow, songs probably serve as a distant threat in territory maintenance but reproductive stimulus to the female in addition to location and identity of individual males may also be important functions of the song (Mulligan 1966).

Fox Sparrow singing during spring migration is well known (Terrill 1968). The full song is apparently not sung during the first part of the spring migration but is in the form of a subsong which is characterized by reduced amplitude and complexity of syllables. By the time they reach the breeding grounds the full song has usually developed. Martin (1977) recorded only one bird still in the subsong stage on the breeding grounds but it had developed the fullsong within three days. In this study 4-5 Fox Sparrows were heard singing a subsong.

In the early part of the breeding season just after the spring arrival Fox Sparrows often emitted a series of notes between the song. Figure 9A and 9B show a continuous singing period from the beginning of a full normal primary song through the unstructured notes to the first half of the following primary song. The unstructured notes were considered to be the subsong. These notes are similar to those described in the section on adult call notes (Figure 5D) but because they were recorded in different situations (playback stimulation of the call note verses unstimulated natural song in this case) they are treated separately.

In two different locations songs, believed to be from males, were recorded that were unusually simple in structure. An example is shown in Figure 9C. These two birds reacted to a playback as a male with a

Figure 8. Primary song of three adult male Fox Sparrows from Oxen Pond Botanic Park.

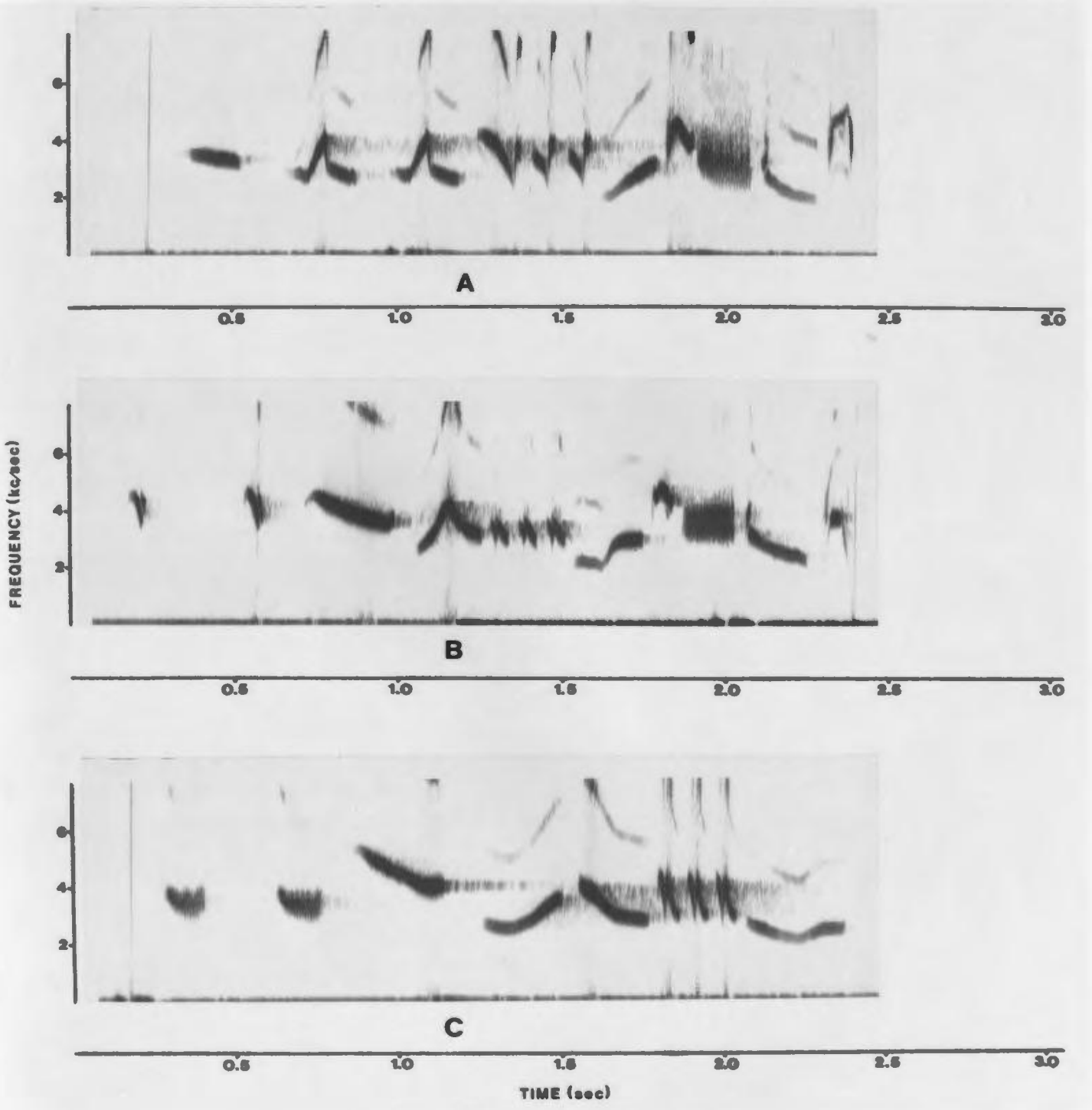
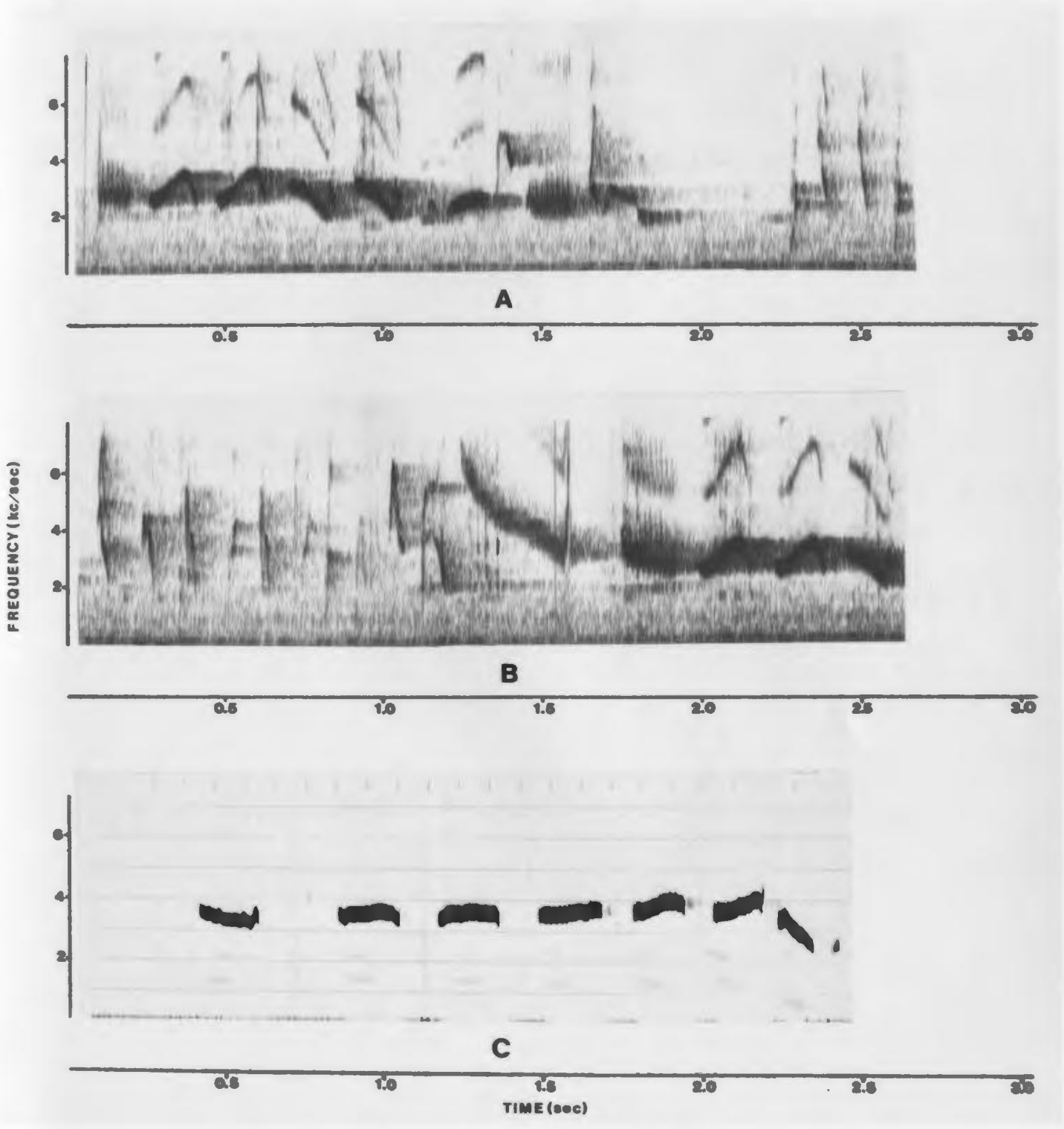

FREQUENCY (kc/sec)
6
4
2
A
0.5
1.0
1.5
2.0
2.5
3.0
B
C
TIME (sec)

Figure 9. Continuous vocal sequence of song-subsong-song of an adult male Fox Sparrow in early spring (A and B) and an unusually simple song of a second Fox Sparrow later in the breeding season.


FREQUENCY (kc/sec)
6
4
2
A
0.5
1.0
1.5
2.0
2.5
3.0
B
C
TIME (sec)

normal song would and otherwise seemed to defend a territory in the usual manner. The significance of those songs of reduced complexity is not known. The reaction of neighbouring males to these birds was not observed because no interactions took place during the time recording was taking place.

There were generally 2 or 3 song perches regularly used by the males, usually in the tallest trees in the territory, within one meter of the top and close to the trunk. Both Moore (1913) and Townsend and Allen (1907) describe similar locations of preferred singing posts. The latter authors noted the tendency of the song to appear ventriloquial, an observation also made in this study. The selection of a high perch is probably related to overcoming sound shadow effects caused by temperature and wind gradients and sound attenuation by boundary (ground) interference (Wiley and Richards 1978; Morton 1975). Ventriloquialism in the song is more difficult to explain. It may be due to scattering of sound waves in the environment causing unexpected interference patterns which might alter the perception of time differences in the observer which are used in the location of a sound source (Marler 1955). Or ventriloquialism may have survival value in that a singing bird perched in the open may be more difficult to locate by a potential predator.

Fox Sparrows participated in the early morning chorus and began singing just after it began to get light prior to dawn. The Fox Sparrow participation in the chorus lasted for about 3-4 hours after dawn. There was a reduction of singing during mid-day though Fox Sparrows could occasionally be heard singing at any time during this period. There was no definite pattern to resurgence of song activity in the

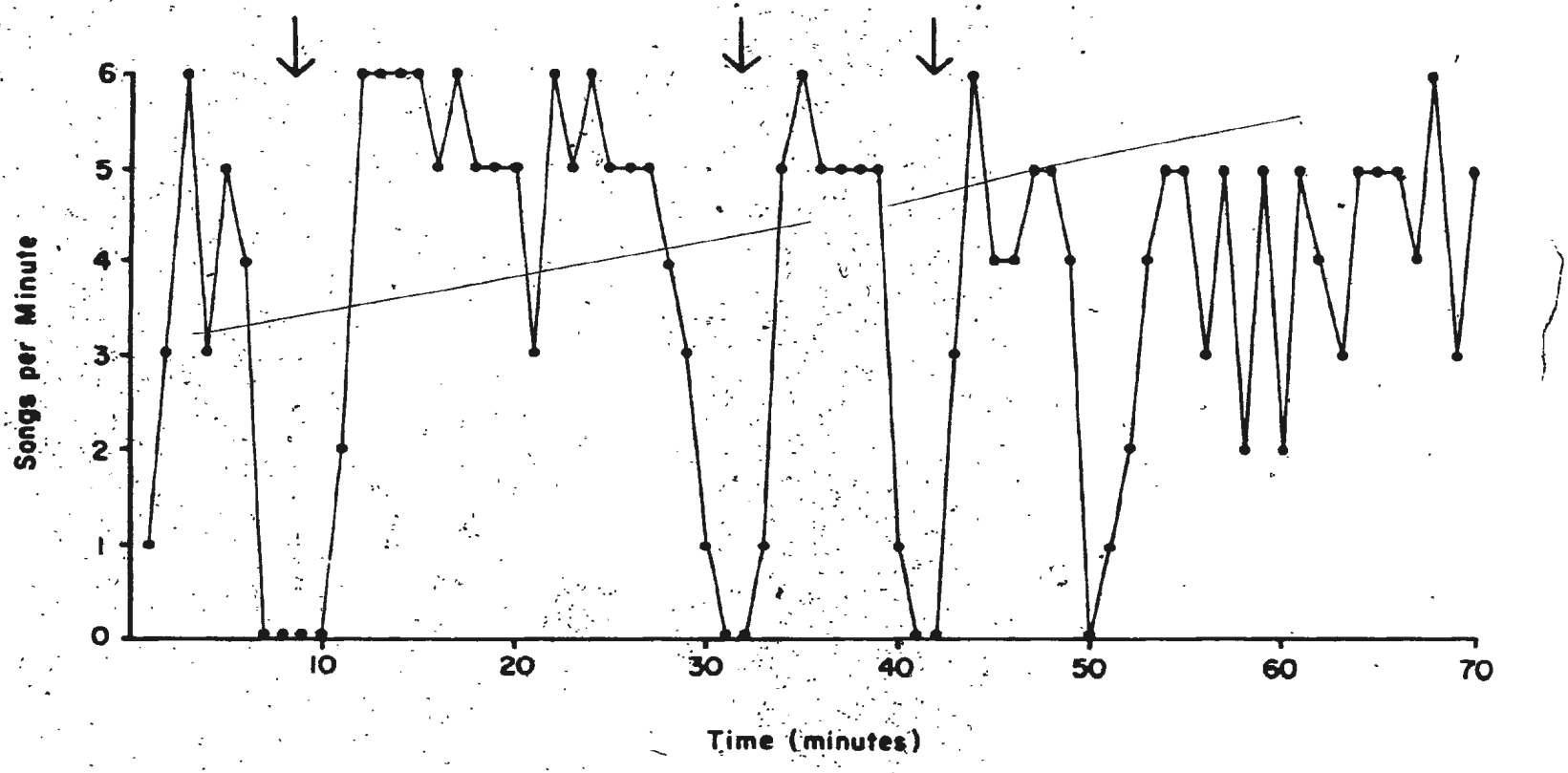
evening; generally songs became more frequent but never reached the level of song activity of the early morning. Moore (1913) found that singing by a single individual would often stimulate other Fox Sparrows in the area to sing.

During the morning chorus Fox Sparrows did not sing constantly but in bouts of varying lengths. The term bout is used here to describe a period of song activity not interrupted by a prolonged period of silence. During the bout the bird generally remained on the same perch but in the between bout period the bird may either stay perched or leave. The singing pattern of one Fox Sparrow in Oxen Pond Botanic Park over a 70 minute period in the early morning chorus on 28 April 1977 is shown in Figure 10. It was a "natural" singing period in that it was unstimulated by a playback. In 3 out of the 4 breaks in singing the Fox Sparrow flew down to the lower vegetation and out of sight. The other time he remained perched but silent. Song delivery within a bout ranged from 1 to 6 songs/min. and bouts ranged from about 10 to 20 minutes in duration.

The seasonal pattern of singing generally followed the breeding cycle. Male Fox Sparrows sang vigorously as soon as they arrived on the breeding grounds and contnued through the nest building and incubation stages. Song activity in terms of numbers of songs delivered per unit time dropped when the young hatched. A slight resurgence of song activity again in the early fall after the postnuptial molt has been reported (Saunders 1948; Martin 1977; L.M. Tuck, pers. comm.).

The primary songs of 169 individual Fox Sparrows were recorded from twenty-two localities in insular Newfoundland. Of these recorded 163 (96.4%) sang a single song. Only 6 (3.6%) sang two songs. Five of

Figure 10. Pattern of singing by an adult male Fox Sparrow in a 70 minute period during the early morning chorus on 28 April 1977. Arrows indicate instances when the bird left the perch.


Songs per Minute
0
1
2
3
4
5
6
10
20
30
40
50
60
70
Time (minutes)

those six birds were found between Cape St. Francis and St. John's and three of the five occupied neighbouring territories. The sixth bird was found on the Cape Shore Road. Those birds with two songs were found to sing them alternately (i.e. ABABAB...) in a singing bout. No birds were found to have more than two different songs. Therefore a total of 175 songs were recorded and treated as individual entities in the analysis of song parameters and geographic location. Martin (1976, 1977) found Fox Sparrows from the Utah-Idaho border area had a mean repertoire of 3.1 and 3.2 songs per individual in 1973 and 1974 respectively. Those songs were sung in a usually unvarying sequence rather than in bouts of a single song type.

The basic parameters measured in each Fox Sparrow song were duration, highest and lowest frequency, and number of syllables types (Table 3). It was found tht syllable types were not unique to each individual bird but were shared to some extent. A total of 91 syllable types were identified (Figure 11). There was some variation within syllable types and therefore the limits of variability of some of the types was arbitrary. But this method, used previously by Martin (1976, 1977) and Thompson (1970), was found to be adequate for this study. The distribution of a particular syllable type through all the songs recorded is shown in Table 4. Martin (1976, 1977) in a study of 133 Fox Sparrows over two years identified 49 syllable types.

The ordering of the syllables in any song was extremely constant. Only two types of exceptions were noted. In the first the final syllable in a number of songs was frequently excluded. The syllable seemed to be present in over half of the songs any individual sang in the early part of the year or if singing had been stimulated by a

Table 3. Fox Sparrow song parameters.

Parameter	n	Mean	S.D.	S.E.	Range
Duration (sec)	175	2.54	0.27	0.02	1.93-3.44
Highest Freq. (kc/sec)	175	5.8	0.5	0.04	4.2-6.9
Lowest Freq. (kc/sec)	175	2.2	0.2	0.02	1.7-2.7
Number of Syllables	175	11.7	2.0	0.15	7-22

Figure 11. Syllable types identified from adult male Fox Sparrow primary songs: types 1 through 28.

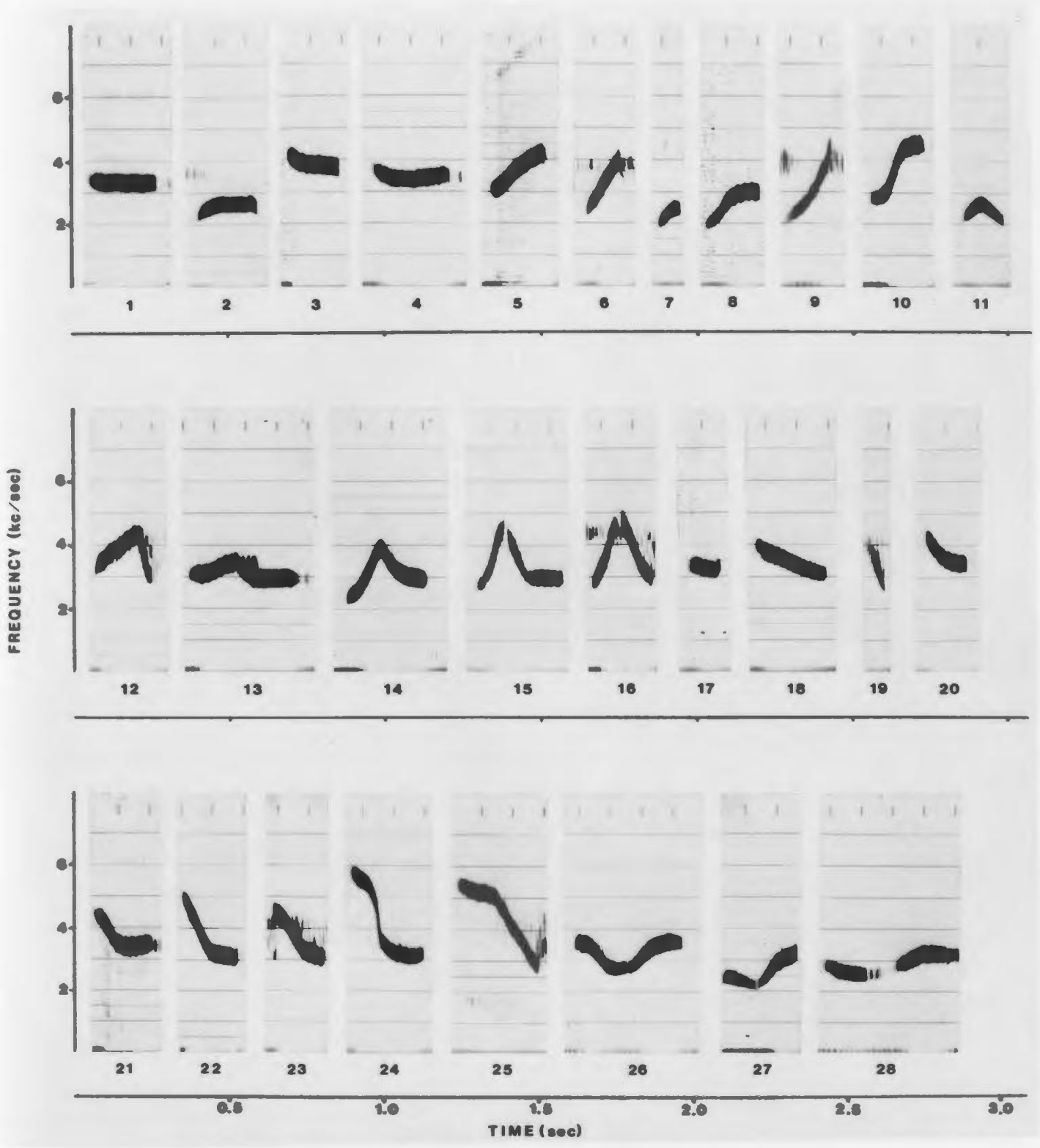

FREQUENCY (kc/sec)
6
4
2
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
0.5
1.0
1.5
2.0
2.5
3.0
TIME (sec)

Figure 11 (continued). Syllable types identified from adult male Fox Sparrow primary songs : types 29 through 61.

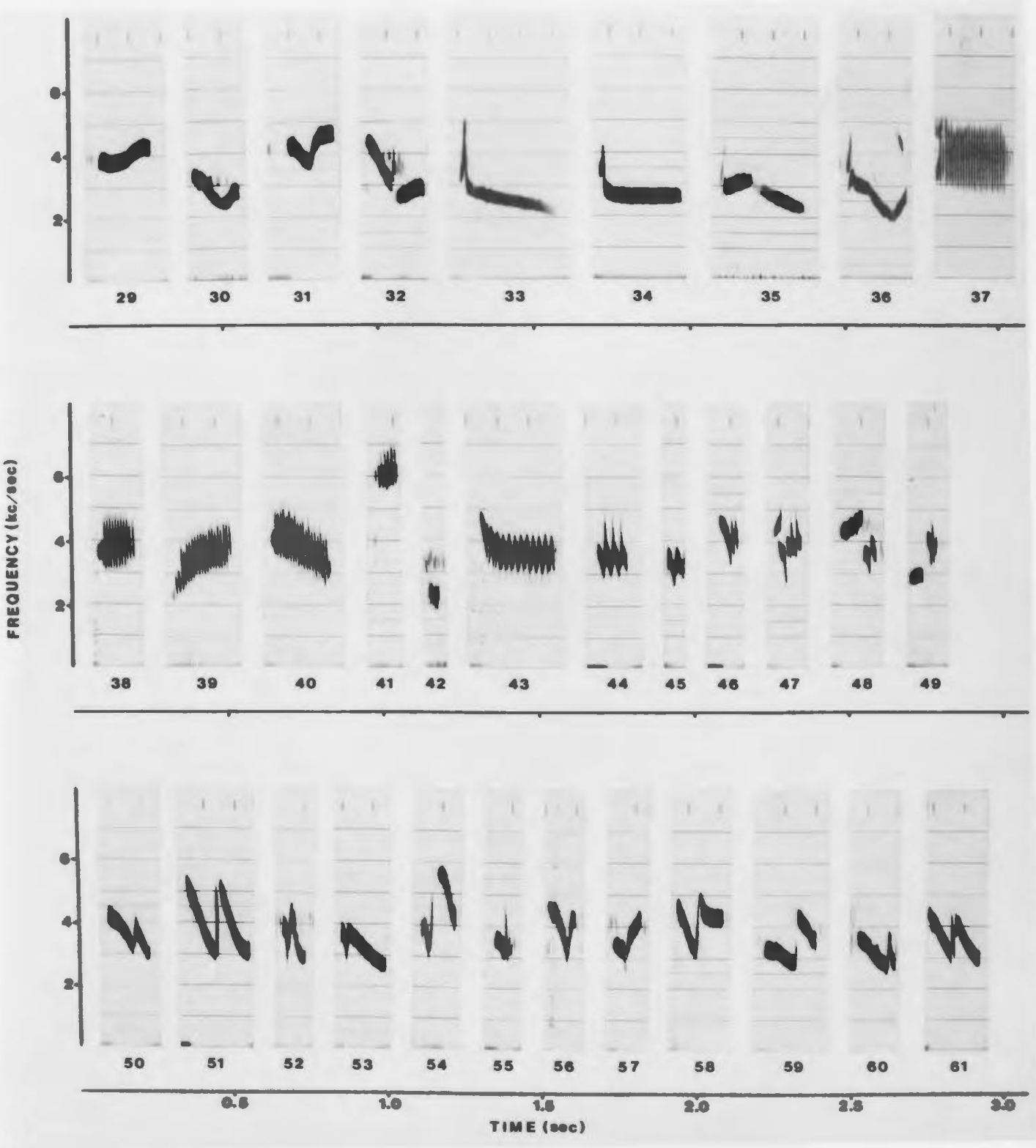

FREQUENCY (kc/sec)
6
4
2
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
0.5
1.0
1.5
2.0
2.5
3.0
TIME (sec)

Figure 11 (continued). Syllable types identified from adult male Fos Sparrow primary songs : types 62 through 91.

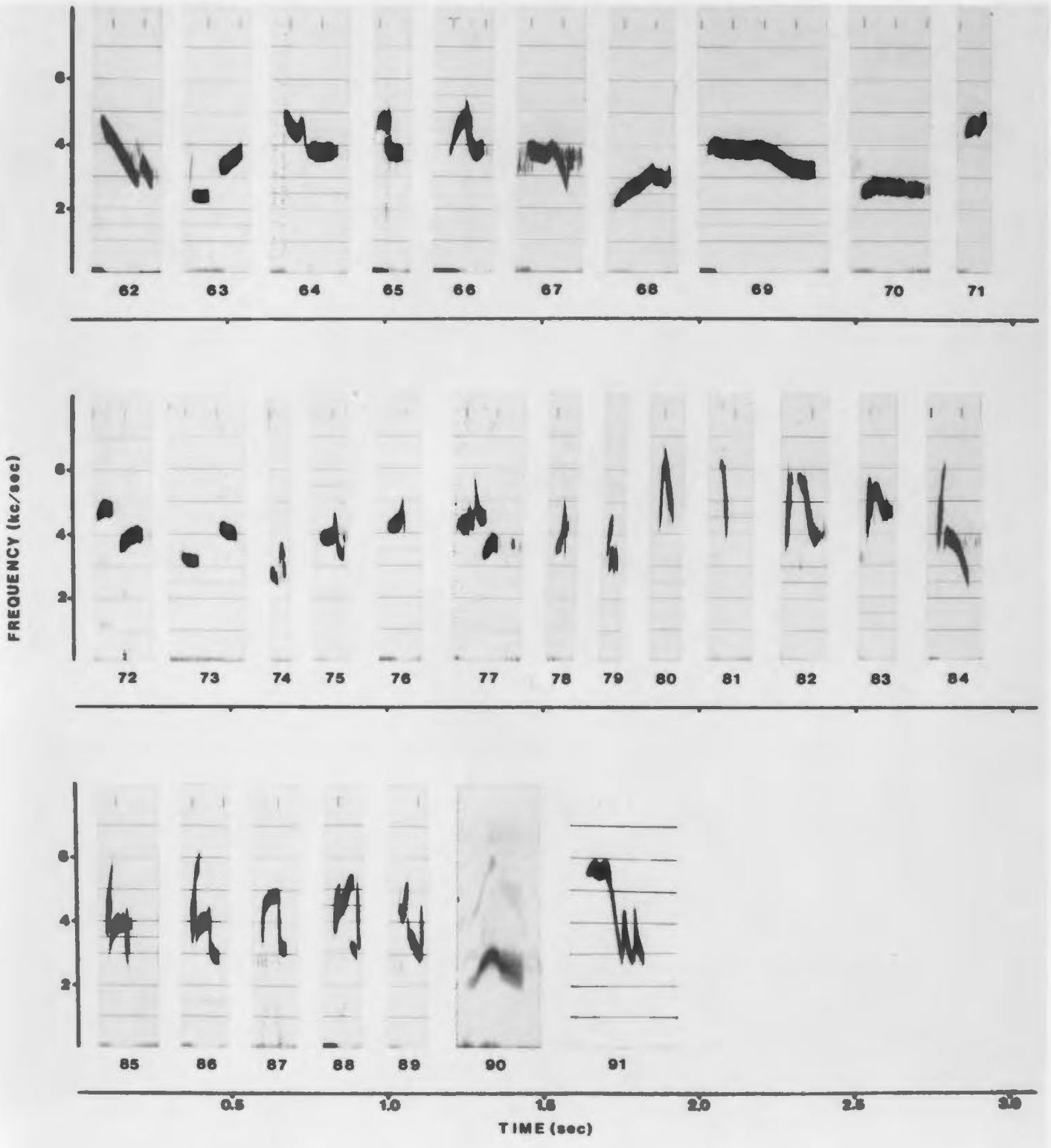

FREQUENCY (kc/sec)
6
4
2
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91
0.5
1.0
1.5
2.0
2.5
3.0
TIME (sec)

Table 4. Percent of Fox Sparrow songs that contained a particular syllable type.

Syllable type	% of songs	Syllable type	% of songs	Syllable type	% of songs
1	45.0	32	3.6	62	18.9
2	20.1	33	39.6	63	1.8
3	33.7	34	13.0	64	4.1
4	7.7	35	11.2	65	1.8
5	29.0	36	0.6	66	0.6
6	5.9	37	70.4	67	1.8
7	24.3	38	10.1	68	1.2
8	25.4	39	13.6	69	4.7
9	10.1	40	4.1	70	0.6
10	10.1	41	13.6	71	3.6
11	10.7	42	4.1	72	2.4
12	3.6	43	3.6	73	2.4
13	5.3	44	1.2	74	1.8
14	11.2	45	7.7	75	2.4
15	5.3	46	17.8	76	1.8
16	4.1	47	1.2	77	1.2
17	14.2	48	1.2	78	0.6
18	32.5	49	0.6	79	8.3
19	17.2	50	4.7	80	32.5
20	27.2	51	9.5	81	16.0
21	5.9	52	14.2	82	13.0
22	11.8	53	3.6	83	20.1
23	27.8	54	3.6	84	3.0
24	5.9	55	10.7	85	4.3
25	1.2	56	4.7	86	7.7
26	4.7	57	1.2	87	10.7
27	14.8	58	4.1	88	2.4
28	5.9	59	9.5	89	3.0
29	1.2	60	22.5	90	1.2
30	4.1	61	6.5	91	0.6
31	1.8				

prerecorded Fox Sparrow song. Inclusion of the syllable in the song seemed to decline toward the latter part of the breeding season. But even within these broad generalizations there was much variability. The second kind of exception was rare and recorded only twice, from different birds. In one it was found that an extra syllable had been inserted into the middle portion of one song and in the other a syllable was deleted from one song. Those were single observations from a series of normal songs from both birds. The alteration of the normal syllable sequence in those birds occurred only when a prerecorded Fox Sparrow song had been played in their respective territories. The birds appeared extremely agitated when the alteration in their song occurred. The change may have been due to upsetting the normal activity patterns by the stimulus.

Amplitude variation among songs from the same bird over all the birds recorded also appeared to be very constant. Absolute sound pressure levels at or near the source are difficult to measure and no data was taken on this aspect. But the relative variation as shown by the intensity of burn on successive sonagrams seemed uniform for each bird. The only exception noted was when one individual sang a series of about six songs at a much reduced volume and then reverted to the normal amplitude. This occurred during a prerecorded song playback. The so-called "whisper" song was noted by Terrill (1968) for migrating Fox Sparrows.

The variability of the temporal aspects of the song through the breeding season was examined in three birds in neighbouring territories in Oxen Pond Botanic Park. (Sonagrams of those three birds are shown in Figure 8.) Recordings were made at 1-2 week intervals through the

breeding season. The untransformed variances of both syllable and between syllable durations, one song from each recording day, were compared to those from a number of songs from a single day by a paired t-test. Of the three birds tested two (birds A and C in Figure 8) showed a significant difference in seasonal variance compared to a single day (Table 5). From an inspection of the variance values it appeared that most of the difference between day and season occured in the opening syllables of the song (Appendix 4). When the first two syllable and between syllable duration variances (four values in total) were deleted from analysis in those two songs the difference became non-significant (Table 5). Therefore the timing and duration of the syllables in the song was uniform through the breeding season the introductory syllables being the most variable.

There seemed to be no trend in the changing variance values over the season for the two birds which initially showed a significant difference. There are two possible explanations for this. First the nature of the recording conditions and equipment makes the recording of long duration, frequency constant notes difficult if they are at low amplitude. The resulting sonagrams are therefore difficult to measure. Second there may be variation with the level of stimulation of the bird. The introductory notes may be used by the bird to convey information on its motivational state. The recordings through the season may have, by chance, sampled a variety of levels to compare with the daily variation recorded at the same level of stimulation. Therefore the seasonal difference shown by the paired t-test for birds A and C (Figure 8) may not be real but may well result from poor quality recordings and differences a bird would normally exhibit through a day at various levels of stimulation.

Table 5. Summary table of paired t-test values of syllable and between syllable duration variances for 3 Fox Sparrows in Oxen Pond Botanic Park.

Bird	t-value	df	t-value**	df
A	2.582*	20	2.066	16
B	1.775	22		
C	2.610*	16	2.027	12

* Significant at the 95% level of confidence.

** Recalculated t-value after first 4 pairs were deleted.

Geographic variation in Fox Sparrow song was examined by one-way analysis of variance for each of the four song parameters (Table 3). Only 9 locations of the 18 locations were used, based on the criteria of having 9 or more song samples from each location. Only the variable number of syllables per song showed no geographic variation (Table 6). For the four variables the means and 95% confidence intervals are plotted for each variable in order of increasing mean in Figure 12. The range of the confidence intervals for the variable duration showed no overlap in cofidence intervals between Bacclieu Island and Cape St. Francis. The variable low frequency showed a difference for Gander and Cape St. Francis birds. High frequency showed much variability in Gull Island which did not overlap with Flatrock Road, St. John's, Cape St. Francis, and Bay de Verde birds in addition to Cape shore Road and Baccalieu Island birds not overlapping with Cape St. Francis. Though the number of syllables per song was not significantly different by location Gull Island and Cape St. Francis again showed no overlap of confidence intervals. Therefore though geographic variation was detected by analysis of variance it was difficult to specify the localities contributing to the variance and general trends could not readily be seen.

Cluster analysis provided a technique of examining geographic variation in Fox Sparrow song on the basis of syllable types. Briefly, cluster analysis seeks to group operational taxonomic units (OTU's) together on the basis of a measure of similarity over a number of variables. In this case each of the 175 songs was considered on OTU to be cluster on the basis of similarity of 91 variables, the syllable types.

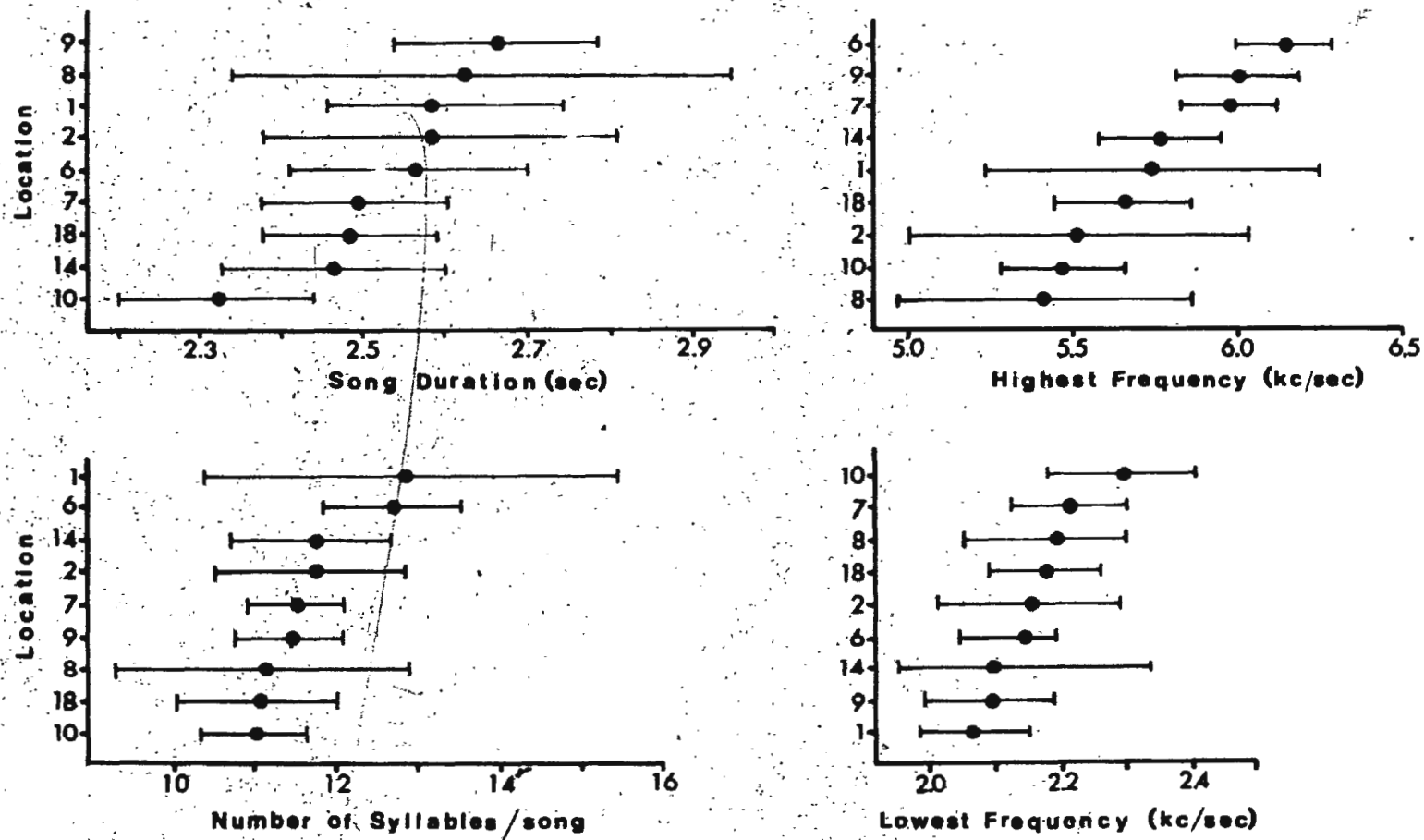
Table 6. Summary table for one-way analysis of variance of each song parameter by nine localities which had sample sizes of 9 or more songs.

Parameter	Source of Variation	df	Mean Square	F ratio	F prob.
Song Duration	Among	8	1638.7	2.289	0.0250
	Between	132	715.8		
High Frequency	Among	8	0.9450	4.020	0.0003
	Between	132	0.2349		
Low Frequency	Among	8	0.0819	2.136	0.0366
	Between	132	0.0383		
Number of Notes/song	Among	8	7.0454	1.633	0.1213
	Between	132	4.3152		

Figure 12. Means and 95% confidence intervals of basic song parameters from 9 localities* with sample sizes of nine or more.

* Localities are as follows :

1 - Gander
2 - Stephenville
6 - Gull Island
7 - Cape Shore Road
8 - Bay de Verde
9 - Baccalieu Island
10 - Cape St. Francis
14 - Flatrock Road
18 - St. John's


Location
9
8
1
2
6
7
18
14
10
2.3
2.5
2.7
2.9
Song Duration (sec)
6
9
7
14
1
18
2
10
8
5.0
5.5
6.0
6.5
Highest Frequency (kc/sec)
Location
1
6
14
2
7
9
8
18
10
10
12
14
16
Number of Syllables / song
10
7
8
18
2
6
14
9
1
2.0
2.2
2.4
Lowest Frequency (kc/sec)

Cluster analysis was performed by calculating similarity coefficients between each pair of OTU's based on the sharing of syllable types. The syllable type variables were measured as either present (1) or absent (0) or frequency of occurrence in a song. Three similarity coefficients Braycurt, Jaccard, and SMC (simple matching coefficient) which treat the data in different ways were initially tested in this study. Braycurt considered, and was very sensitive to, the frequency of occurrence of each syllable type in each song. Jaccard and SMC used presence and absence of syllable types but Jaccard did not recognize 0-0 matches. Sneath and Sokal (1973) discuss the derivation of the similarity coefficient formulas. The similarity coefficients resulting from the formula calculation were entered into a resemblance matrix and subject to cluster analysis by successively pooling of the most similar OTU pairs. The hierarchical agglomerative group average method (Sneath and Sokal 1973; Everitt 1974) was used in forming clusters.

Fox Sparrows from three locations, Gander Bay Road, Glenwood Access Road and Stephenville, were initially subject to cluster analysis using all the three association coefficients. This was done to determine if there were groupings of songs corresponding to location and, if so, which association coefficient grouped the birds most accurately. It was found that there was a separation of Stephenville birds from the other two areas but there was no differentiation of the Gander Bay and Glenwood Access Roads Fox Sparrows. Therefore those latter two areas were combined in a single group called Gander. The three similarity coefficients showed very similar groupings of Gander and Stephenville birds which corresponded to geographic location to a high degree (Figures 13, 14, 15). All three coefficients also consistently

Figure 13. Dendrogram of songs from the Gander and Stephenville areas clustered using Braycurt similarity coefficient.

GANDER - G

STEPHENVILLE - S

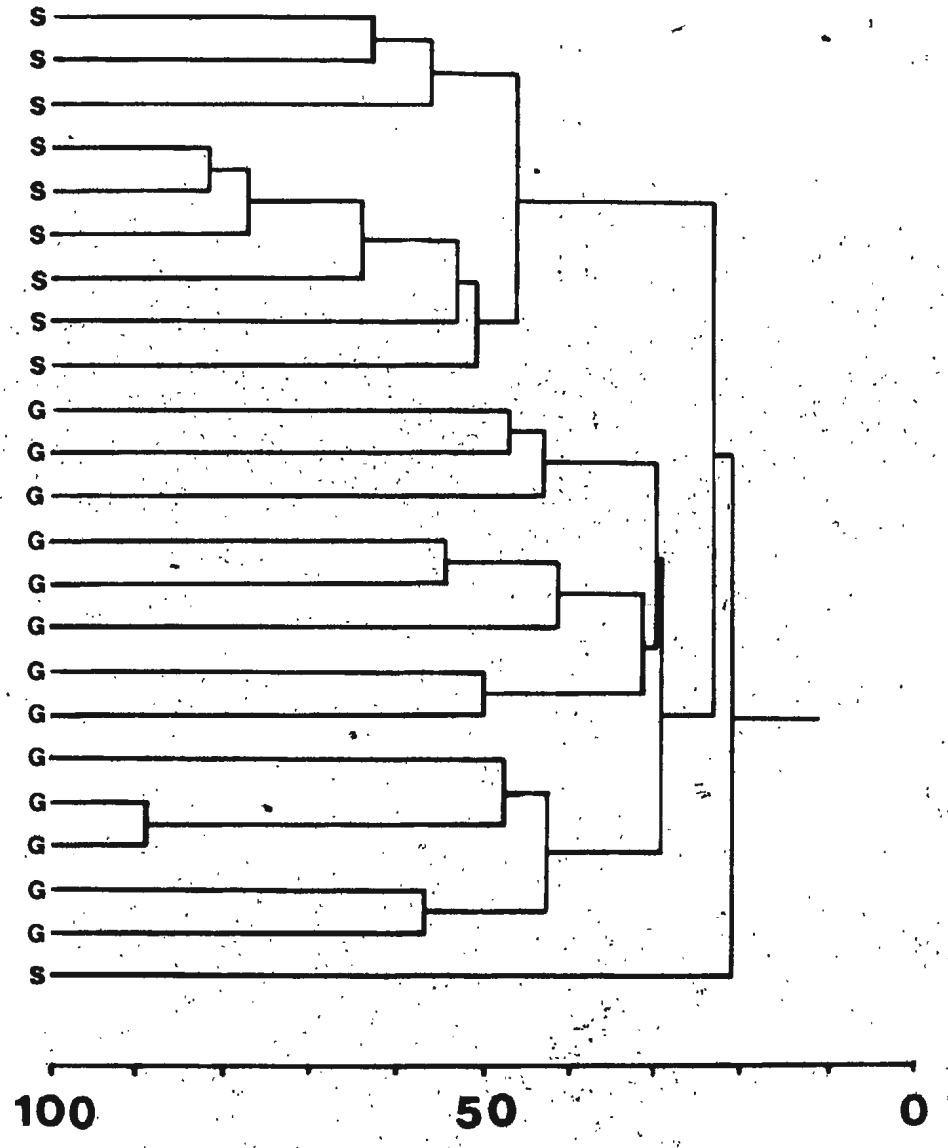


Figure 14. Dendrogram of songs from the Gander and Stephenville areas clustered using Jaccard similarity coefficient.

GANDER - G

STEPHENVILLE - S

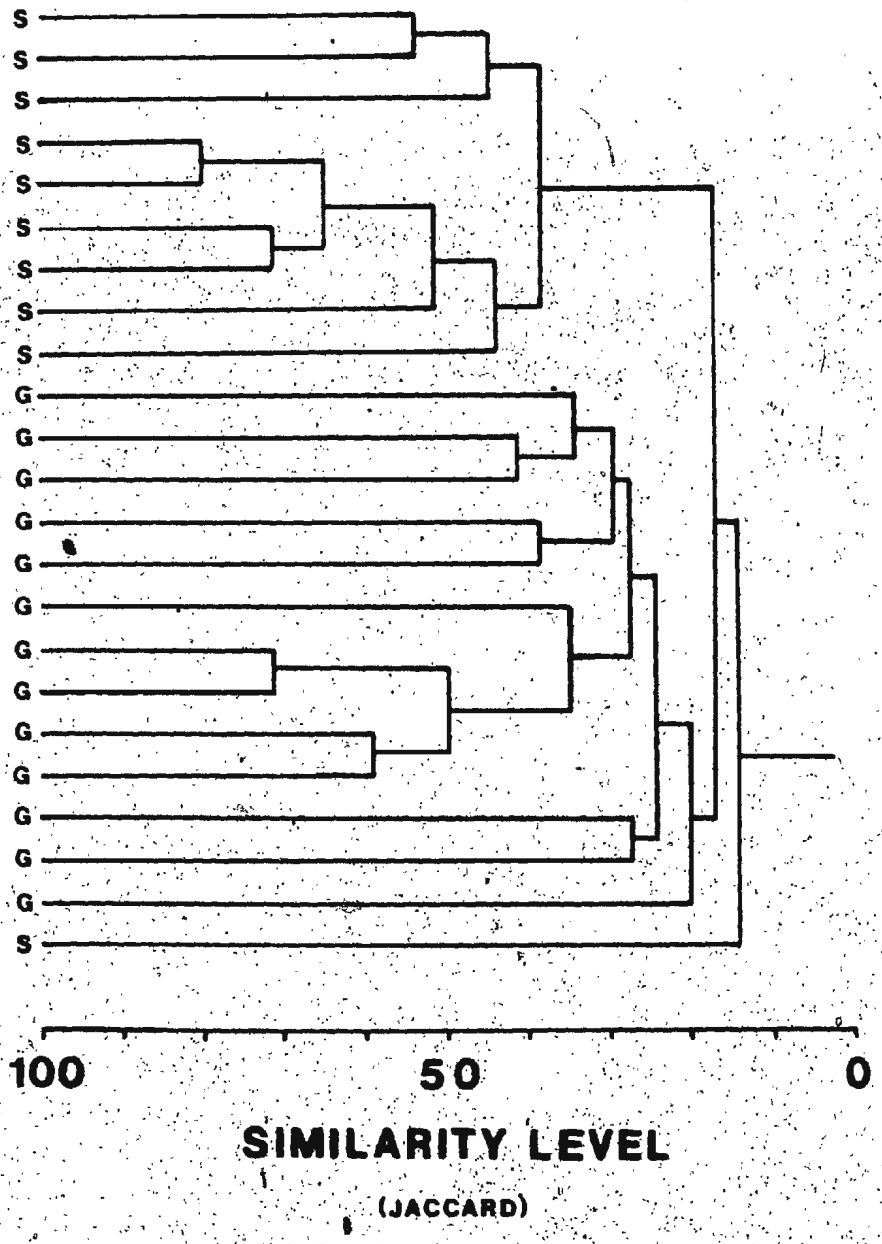
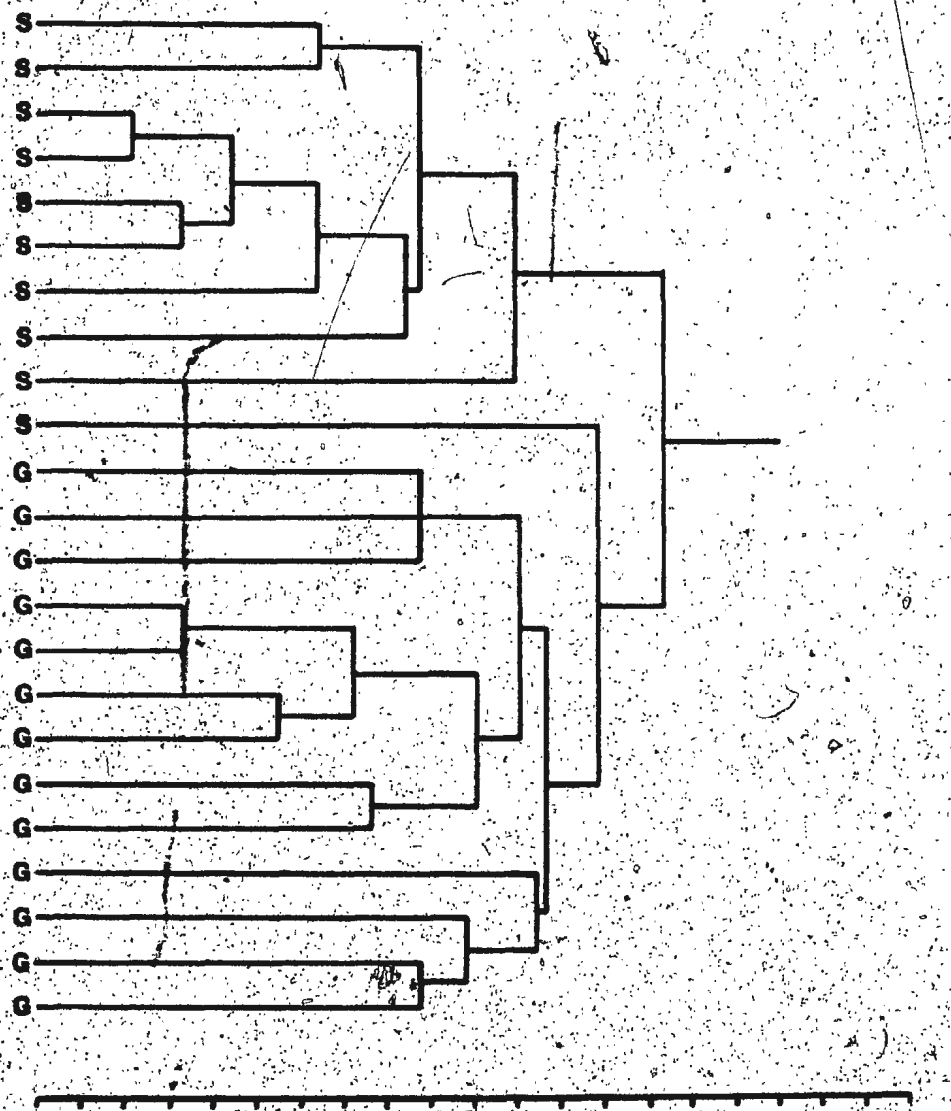


Figure 15. Dendrogram of songs from the Gander and Stephenville areas clustered using SMC similarity coefficient.

GANDER - G

STEPHENVILLE - S



separated out a single Stephenville bird which did not combine closely with either group. Syllable sequences of all songs are listed in Appendix 5.

Martin (1976) found, compared with Jaccard only, SMC to be the most accurate in clustering songs by location. No such decision could be made in this study on the basis of the preliminary trials and Braycurt was chosen for the remaining analyses with a view to providing a limited comparison of the two methods. With 91 possible syllable types but only a mean 11.7 syllables per song the 0-0 matches of SMC would heavily influence the clustering results. Martin (1976) considered 0-0 matches, or the absence of a syllable in each song, an important comparison.

The grouping of 23 songs, 13 from Gander and 10 from Stephenville, about 250 km apart, showed a separation corresponding to geographic location. The addition of a third group of 23 additional birds from the Cape Shore Road, about 200 km from Gander and 300 km from Stephenville, produced a third distinct group by cluster analysis (Figure 16). However, some overlap with the other localities did occur and two Cape Shore Road birds clustered out with Gander and two with Stephenville. It was also noted that two Cape Shore Road birds clustered out at a similarity level of 100, or complete similarity. This means that in terms of the numbers of a particular syllable type present in the two songs were identical. It should be noted that the ordering of the syllables in the song did not have to be the same for such a similarity level to occur although they were in this case.

A total of 76 songs were recorded in 9 localities in the 25 km distance between Cape St. Francis and St. John's. Cluster analysis of these songs produced no distinction of locality by song (Figure 17).

Figure 16. Dendrogram of songs from Gander, Stephenville, and Cape Shore Road on the basis of all syllable types in each song.

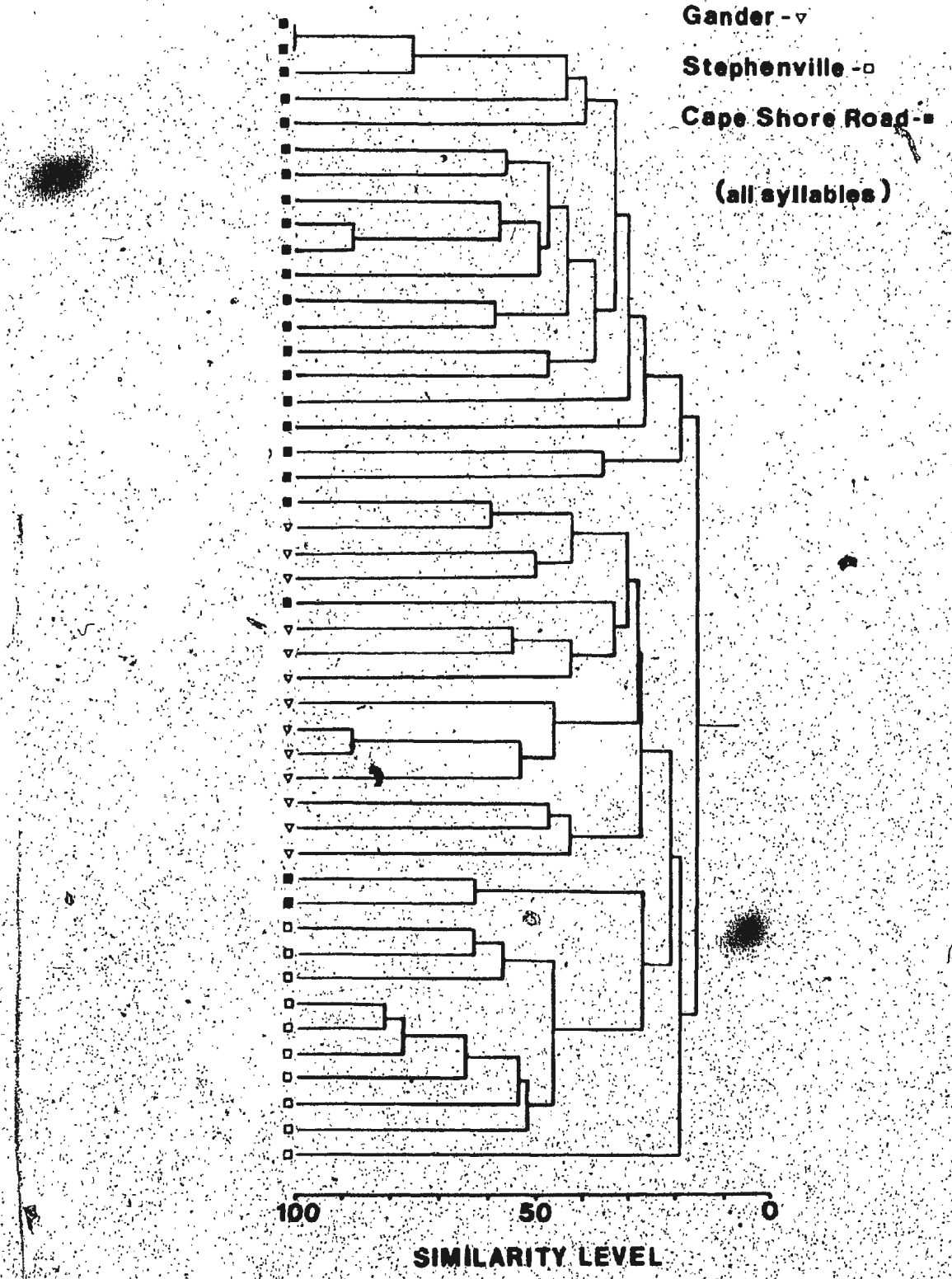
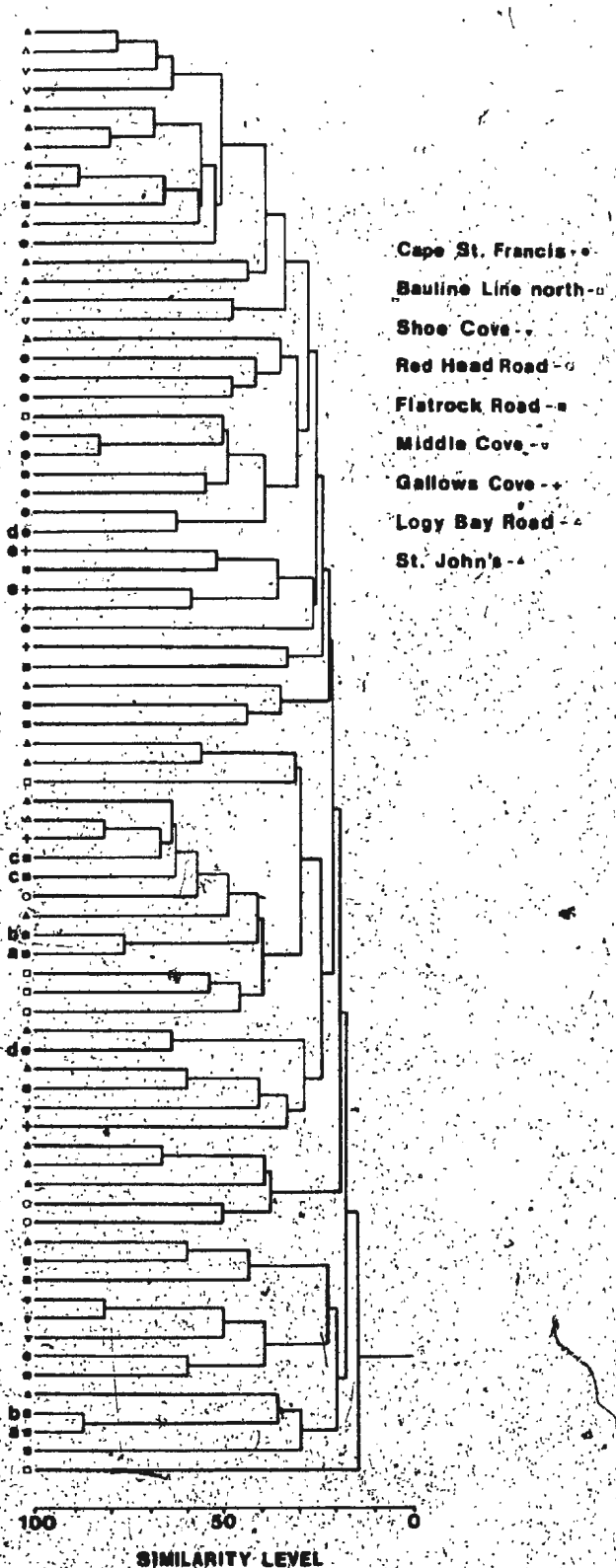

Gander - ▽
Stephenville - □
Cape Shore Road - ■
(all syllables)
100
50
0
SIMILARITY LEVEL

Figure 17. Dendrogram of songs from sample areas between Cape St. Francis and St. John's.*

* Five birds in this area had a repertoire of 2 songs which are indicated by letter pairs.


Cape St. Francis
Bauline Line north
Shoe Cove
Red Head Road
Flatrock Road
Middle Cove
Gallows Cove
Logy Bay Road
St. John's
d
c
b
100
50
0
SIMILARITY LEVEL

Two island and adjacent mainland locations were also sampled. A total of 19 songs were recorded on Baccalieu Island and 9 on the mainland (Bay de Verde). Similarily 16 songs were recorded on Gull Island and 7 on the mainland (Witless Bay). The islands, Baccalieu and Gull, were a minimum of 4 km and 2 km from the mainland, respectively. Cluster analysis of Baccalieu Island Bay de Verde songs showed only one case of overlap (Figure 18). Separation was not clear in the Gull Island and Witless Bay songs but the island songs generally grouped out by themselves (Figure 19).

A cluster analysis of all 175 songs recorded produced groupings generally similar to those discussed above but overlaps became more frequent and the groupings less distinct. (A dendogram of this cluster analysis proved impossible to include to illustrate the groupings.) It seemed that the addition of more songs complicated the analysis by recognizing overlap in syllable types. A process that takes into account ordering of the syllables as patterns might be more successful at differentiating songs by locality rather than simple frequency of syllables in the cases of a large number of songs.

During the field recording sessions it was noticed that the last portion of the song seemed to sound the same within a locality. This observation was tested in the Gander-Stephenville-Cape Shore Road groups which previously showed clear differences on the basis of all the syllable types in the song. The song was divided into two portions comprising the first six and last six syllables of each of the songs. Six syllables were chosen because the mean number of syllables/song was 11.7 and therefore 6 syllables would approximately represent the first and half of each song. Cluster analysis of these areas on each 6

Figure 18. Dendrogram of songs from Baccalieu Island and Bay de Verde.

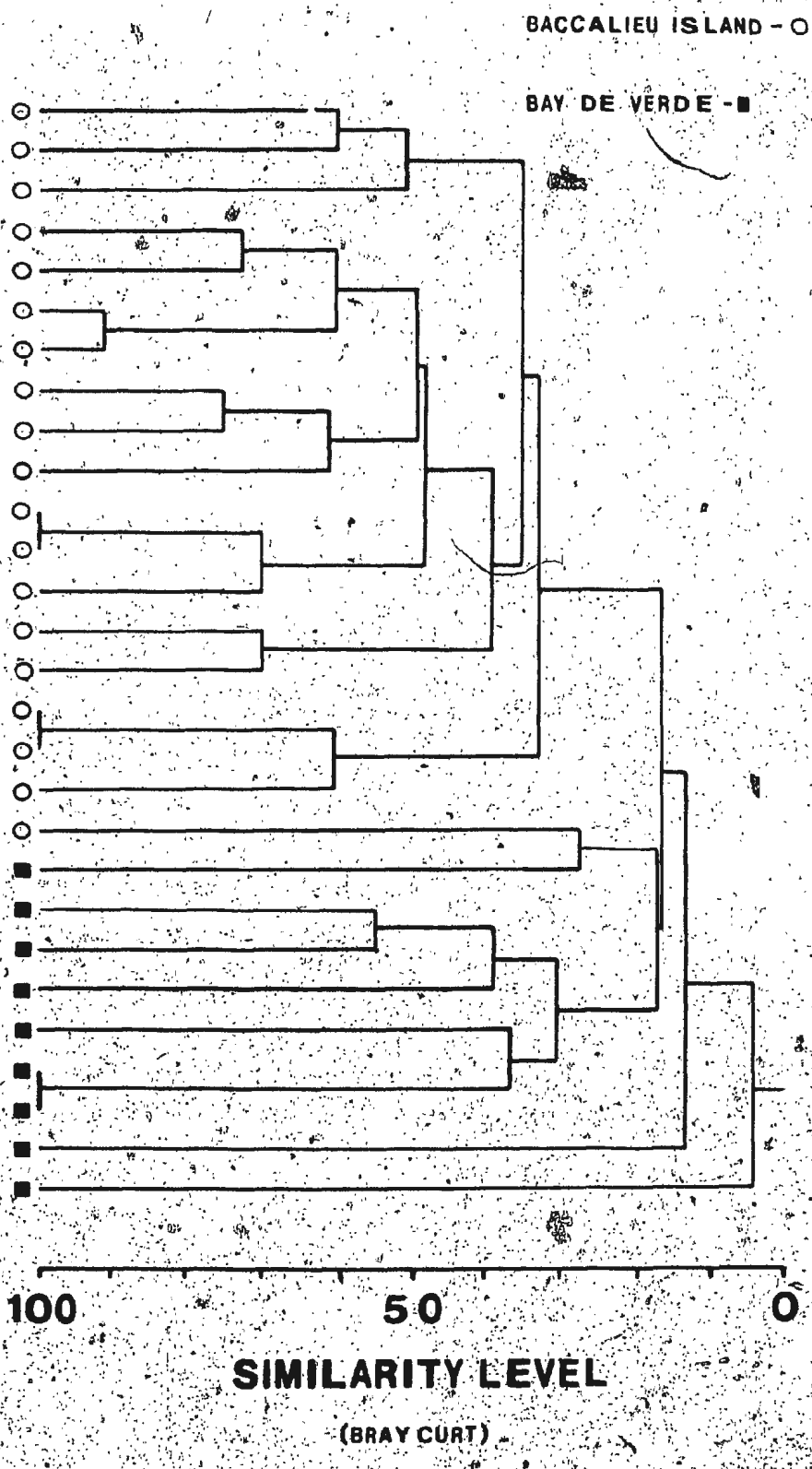
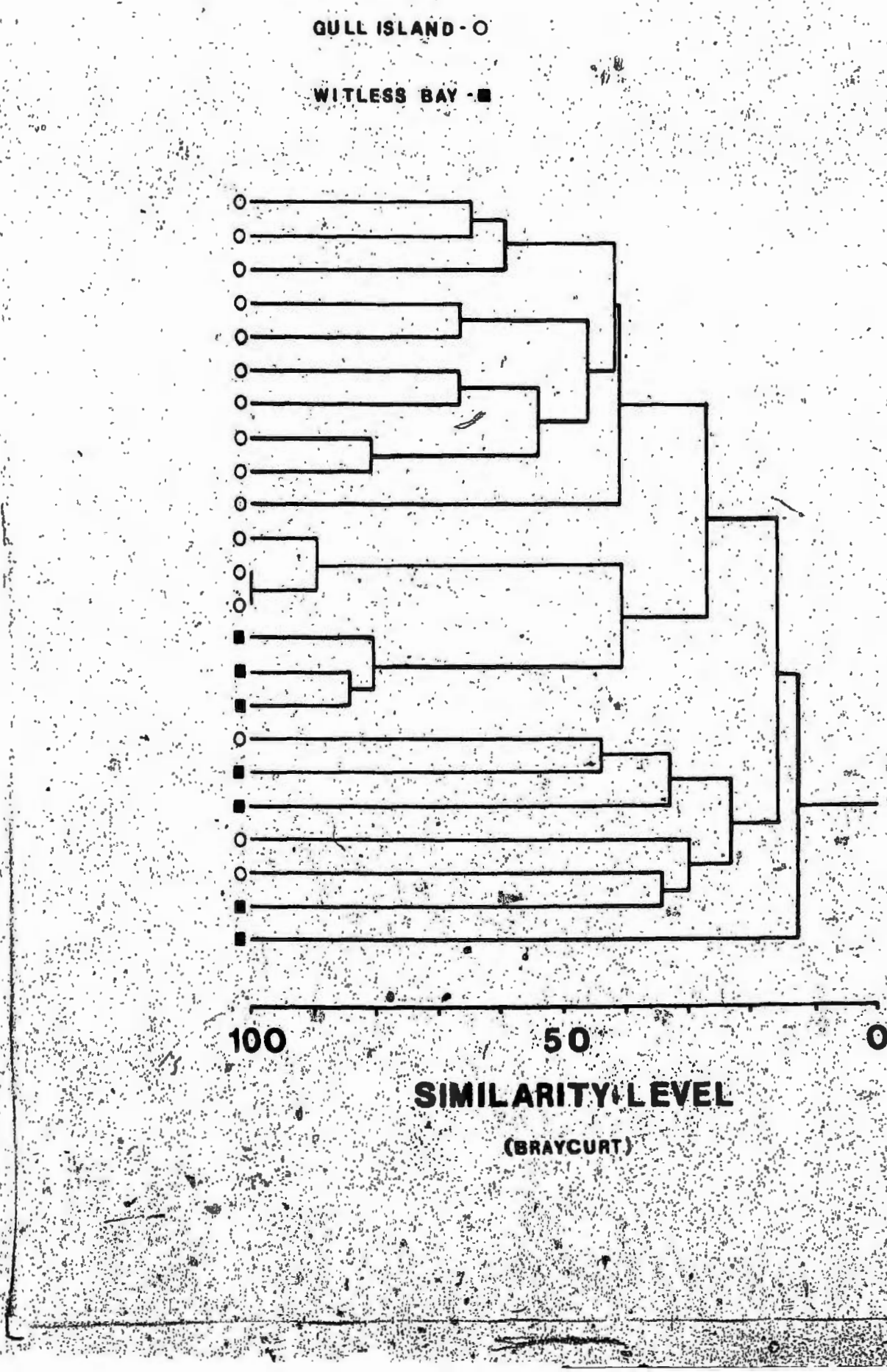

BACCALIEU ISLAND - O
BAY DE VERDE - ■
100
50
0
SIMILARITY LEVEL
(BRAY CURT)

Figure 19. Dendrogram of songs from Gull Island and Witless Bay.


GULL ISLAND - O
WITLESS BAY - ■
100
50
0
SIMILARITY LEVEL
(BRAYCURT)

syllable portion showed that the last six syllables showed more clearly grouped songs by locality than the first six (Figures 20, 21).

In summary, cluster analysis of songs of the Fox Sparrows based on frequency of occurrence of syllable types within a certain geographic location showed a higher similarity to each other than to songs from a long distance away (Gander-Stephenville-Cape Shore Road). In more restricted, continuous areas geographic variation could not be demonstrated (nine localities between Cape St. Francis and St. John's). Over short distances where some object such as open water could act as a geographical barrier differences in song with respect to locality again became apparent (Baccalieu Island-Bay de Verde and Gull Island - Witless Bay).

Figure 20. Dendrogram of songs from Gander, Stephenville, and Cape Shore Road on the basis of the first 6 syllable types in each song.

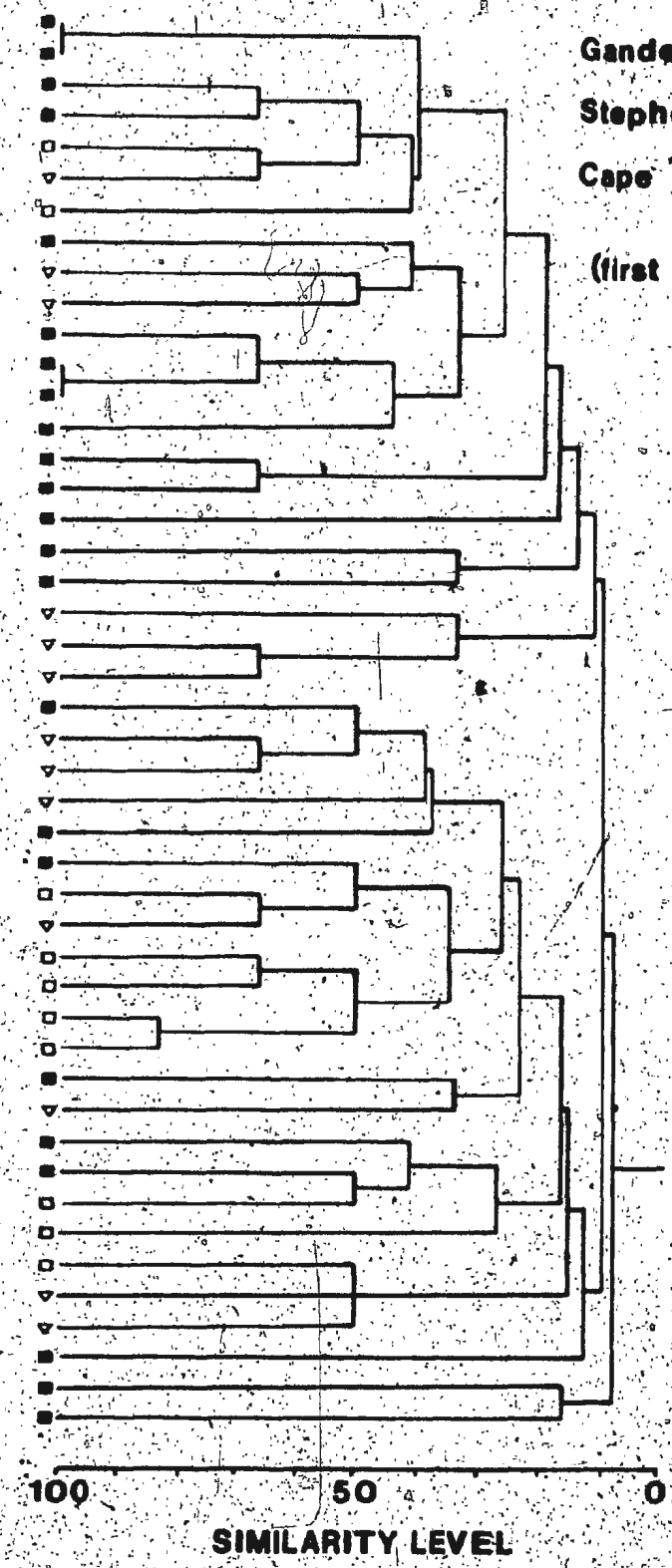
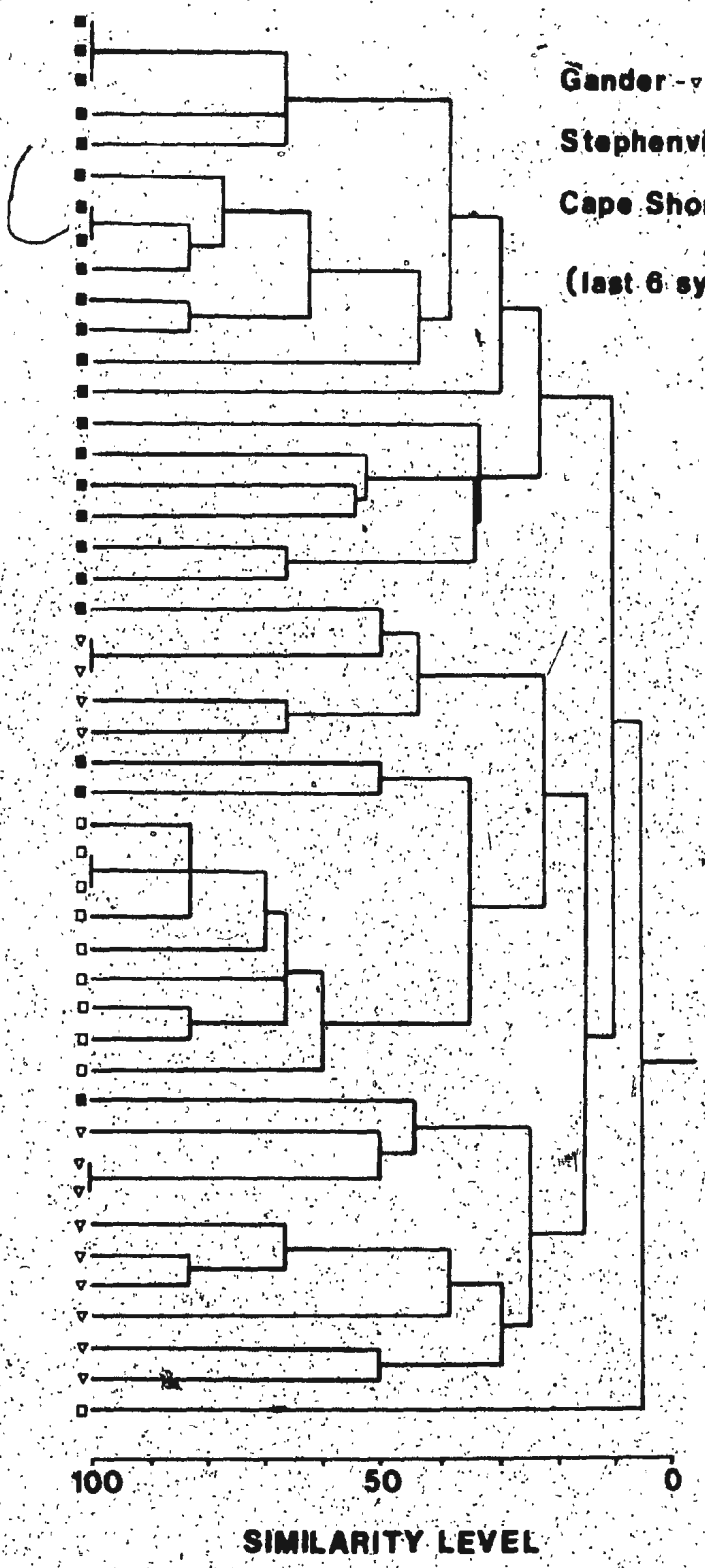

Gander - ▽
Stephenville - □
Cape Shore Road - ■
(first 6 syllables)
100
50
0
SIMILARITY LEVEL

Figure 21. Dendrogram of songs from Gander, Stephenville, and Cape Shore Road on the basis of the last 6 syllable types in each song.


Gander - ▽
Stephenville - □
Cape Shore Road - ■
(last 6 syllables)
100
50
0
SIMILARITY LEVEL

Discussion

Breeding Biology

In general the breeding biology of the Fox Sparrow is similar to other emberizid species inhabiting the boreal zone. A migratory species, it returns to its breeding areas in early spring, attempts to establish a territory, mate, raise young, and return south again, prior to the onset of winter.

The Fox Sparrow does, however, show certain noteworthy characteristics. One is the early arrival date. Fox Sparrows are one of the first migratory species to return to Newfoundland in the spring, sometimes when the snow is still quite deep. Such a situation occurred in the second year of this study. Storms may present additional difficulties; Tuck (in Terrill 1968) reported heavy losses after a storm when freezing rain coated the ground with ice. Because the Fox Sparrow is primarily a ground feeder, an early arrival could increase the risk of having the food supply covered by snow. This might be critical, especially after a long migration. The conflict may be more apparent than real, however, because late snow and severe storms are not common and their effects not long lasting. A more "typical" spring would probably be more like the one experienced in 1977 (C. Blackmoor, pers. comm.). In that year the ground was bare in many places by the time Fox Sparrows returned from the south. Though snow and cold weather did occur subsequent to arrival that year conditions never seemed severe, and the birds appeared to have no trouble in finding an adequate food supply.

Apart from the unpredictable hazards of the environment, arriving

on the breeding grounds early in the season may confer an advantage with respect to reproduction. Fox Sparrows begin nesting early, before their potential competitors (e.g. Northern Waterthrust Seiurus noveboracensis, White-throated Sparrow Zonatrichia albicollis, and Dark-eyed Junco Junco hyelmalis). All four species feed their young animal matter, primarily arthropods (see reviews in: Bent 1963; Lowther and Falls 1968; Eaton 1968; Terrill 1968). The early onset of breeding by the Fox Sparrow may reduce the competition for nestling food. Experiments in manipulating brood size and food supply suggest that food supply is linked to brood size (e.g. Crossner (1977)). Therefore reproductive success may be enhanced by a separation of species' nesting periods. This idea would apply only to the early Fox Sparrow nests and does not explain the range of first egg laying dates shown in Table 2. The range may be the result of renestings due to early nest loss or an inability to nest due to environmental conditions. The data provided on the nest record cards was insufficient to determine if there was a within year synchrony which was masked by a variability of conditions among years.

Fox Sparrows appeared to show specificity in nest site selection, which was generally correlated with time of year, and by inference, to snow depth, ground moisture, or ground temperature. Early nests are usually built in trees and later nests are placed on the ground. Tree nests are large and bulky and probably represent a considerable energy investment early in the year when food may be scarce. Ground nests are of simple construction and would probably require less energy to build. In addition to requiring less energy for construction, ground nests may have enhanced thermal properties by being in contact with the ground. The high specific heat of the ground compared with the air would reduce

the effect of fluctuation of ambient air temperature. Nests with better heat retention capabilities would also free the incubating bird for longer periods for other activities such as feeding (White and Kinny 1974). The data (Table 1) show a seasonal shift from tree to ground nests. The fact that the ground is used later in the season when tree sites are still available suggest a preference for ground nests. Ricklefs (1969b) found that egg and nestling mortality was substantially higher for ground nesting birds than for birds nesting in trees and was due, presumably, to the nest being out of reach of ground dwelling predators. Because the birds continue to nest on the ground suggests that the benefits may outweigh risks. Nest temperature considerations, rather than predation, may be the prime factor.

Growth rates of birds have been the subject of much attention in recent years (Ricklefs 1968, 1973, 1975; Austin and Ricklefs 1977; O'Connor 1977; Tiainen 1978). All passerine growth curves seem to conform to the logistic curve (Ricklefs 1968). The Fox Sparrow had not previously been examined but it was found also to be logistic. The growth rate constant of 0.566 indicates very rapid growth. Although there are no data to compare with Fox Sparrows from other localities the rate is within the range expected from the adult body size (e.g. about 40 g) (Ricklefs 1969a). Growth rate constants for the Rufous-winged Sparrow (Aimophilia carpalis), a species with the same nestling period (9 days) but an adult weight of only 15 g, was even higher at 0.576 (Austin and Ricklefs 1977). The White-crowned Sparrow (Zonotrichia leucophrys) and Song Sparrow (Melospiza melodia), species with an adult weight intermediate between the Rufous-winged Sparrow and Fox Sparrow, were found to have growth rate constants of 0.512 and 0.484,

respectively (Ricklefs 1968). It must be borne in mind, however, when comparing growth rates that the values are not absolute constants. They have been shown to vary intraspecifically among broods (Tiainen 1978) and between years (Maher 1972).

Ricklefs (1969a) proposed a model of growth of altricial birds which was based on the assumption that growth rates have been maximized to some physiological limit. This was attributed to selection to reduce the high mortality of eggs and young in the nest. The longer a nestling bird remains in the nest the longer it will be exposed to the hazards of predation and inclement weather. Any strategy which would reduce the length of the nestling period would thus be selected. Rapid growth seems to be the parameter selected for in passerine species, especially those with open nests on the ground. A comparison of differential development of various body parts at fledging (Figure 4) showed the feet and legs were the most highly developed. This feature, which is correlated with early fledging (Austin and Ricklefs 1977) is an additional part of the reduced nestling period strategy (O'Connor 1978).

Vocalizations

Variation of the song shown by cluster analysis of syllable types was evident when populations were separated by long distances (200-300 km) or when a geographic barrier intervened. Over short distances (25-30 km) separation of populations was not shown. Martin (1976) when analyzing syllable types by cluster analysis also found no clear separation of populations in areas less than 50 km apart. Analysis of variance of basic song parameters did show a significant difference between localities. A plot of means and 95% confidence intervals,

however, indicated consistent geographic trends in the variation and no pattern of discontinuities emerged. The song, then, seemed to vary rather continuously in all directions over several variables and no distinct localized groups except for island populations were formed. Geographic variation in song has been defined as differences between distinct populations which do not normally interbreed, and dialects refer to differences in neighbouring populations (Nottebohm 1969). There are no data available on the genetic integrity of Fox Sparrow populations but given the site fidelity exhibited by Fox Sparrows this may be expected, at least to some degree. Song variation in Fox Sparrows from Newfoundland as in Utah and Idaho (Martin 1976), then, probably more closely corresponds to the definition of geographic variation than to dialects. Variation in the song of this species has been known for some time (Linsdale 1928a; Peyton 1971; Austin 1968) but prior to Martin (1976) it was unclear whether this reflected geographic variation or a system of dialects.

The significance of dialects has been subject to much speculation (Nottebohm 1972; Lemon 1975; Jenkins 1977; Treisman 1978) but geographic variation has been neglected. An assortive mating system appears to be the most widely accepted reason for the presence of dialects by preferred mating, or avoidance, of progeny of a dialect population. Its value would lay in the preservation of locally adapted populations (Nottebohm 1972) perhaps by the female recognizing and prefering to mate with males of her home dialect. Or, it may help prevent excessive inbreeding in a highly static population (Jenkins 1977) by a recognition and avoidance of the parental dialects so as not to mate with siblings or close cousins. A similar explanation could be advanced for

geographic variation by considering songs which vary only over long distances as a "super dialect". In this case local adaptation may act on a much larger scale.

Three other explanations of the phenomenon of geographic variation can be considered in the case of the Fox Sparrow. First, it is possible that dialects do exist but the scale of measurement used was not fine enough to detect them. It was found that geographic variation corresponded to the terminal portion of the song. But it could be that certain syllables within the terminal portion carry more weight than others. A different clustering algorithm might be of use in deciding exactly which syllable type(s) were most important at different levels of the clustering process. One could then trace back through the songs and identify dialects on the basis of these few syllables. Dialects may not be based just on presence or absence of particular syllables, but on the patterns of sound itself. Syllable types and their ordering in the song probably would not have to be identical to produce similar sound patterns in the song. Given that the avian ear is about 10-100 times as acute, in time discrimination as the human ear (Greenwalt 1968) slight variation in the song delivery may be important.

The second explanation involves the degree of genetic variability of populations. Species forming distinct dialects may be inherently more variable than those species showing only geographic variation. The designation of the Fox Sparrows breeding in the area east of northern Manitoba as one subspecies (P. i. iliaca) may indicate a lower variability than more western forms where many subspecies have been described (Austin 1968). In the eastern race, then, locally adapted, partially genetically isolated, populations may not readily form and

dialects would therefore be of no selective advantage. The songs may just vary as an epiphenomenon of vocal learning. Added support for this view comes from playback experiment trials which suggested that Fox Sparrows will respond just as strongly to songs of birds from close locations as to songs from far away. Indeed playback of songs from Utah-Idaho birds elicited a response as or nearly as strong as local songs. Differential response to unfamiliar dialects has been shown in the White-crowned Sparrow (Milligan and Verner 1971) and Song Sparrow (Harris and Lemon 1974) both species in which dialects have been described. It must be stressed that the tests with the Fox Sparrow were preliminary and no quantitative data was taken. However the trend shown initially would be expected if dialects were not a strong feature in the species.

Third, the suggestion that song variation may correspond to the structure of the habitat, and therefore its acoustic properties, has been advanced by Nottebohm (1975). Vocal information is transmitted via frequency and temporal features of the sounds which are affected by noise in the environment (Wiley and Richards 1978). It is not known whether these aspects of Fox Sparrow song are adjusted in each habitat to produce the highest possible signal to noise ratio but it seems an area worthy of investigation.

Summary

Breeding Biology

1. Fox Sparrows returned to the breeding grounds early in the spring (mean arrival date is 9 April) and usually established territories within a week, depending on snow cover.
2. Territory size in a burned forest regeneration area was about 1 ha. Site fidelity within and between years was thought to be high.
3. Nest building was accomplished by the female and nest height was significantly correlated ($r = -0.600$) with advance of the breeding season. Possible factors for this are discussed.
4. Nest site preference seems to be for the ground.
5. Distribution of the dates of onset of laying was relatively even through the season.
6. Clutch size was 3-4 eggs which were laid early in the morning at a rate of 1 per day.
7. Incubation was thought to be entirely by the female and apparently in one case began before the last egg was laid.
8. Incubation period for one nest was just over 12 days but there was an at least 36 hour hatching asynchrony. A comparison of these data was made to published reports.
9. Nestlings were brooded by the female but fed by both adults.
10. Nestlings were probably fed primarily or entirely on animal matter.
11. Nestlings grew rapidly ($k = 0.566$) and showed a differential growth pattern favouring early development of the legs and feet. This pattern was similar to published data on other similar species.

12. Nestlings fledged at 9 days but were unable to fly. They were attended by the adults at least another 21 days.

Vocalizations

13. Nestling call notes, adult call notes, and female song are described and discussed with respect to physical characteristics, context in which they were given, and possible functions.
14. The male primary song was recorded from various localities in Newfoundland.
15. Fox Sparrows begin their daily singing pattern just after first light in the morning, participate in the morning chorus, sing at a much reduced rate through the day, and sing again more frequently before sunset. Songs are delivered in a series of bouts of varying lengths.
16. A total of 169 birds were recorded, six (3.4%) of which had 2 songs giving a total of 175 songs. The significance of repertoire size was discussed.
17. Song parameters were analyzed by one-way analysis of variance. Although significant differences among location were found no trends were detected.
18. Cluster analysis of songs by syllable type showed definite groupings of songs by locality based on frequency of the syllables.
19. Songs seem to vary gradually over long distances. This only became apparent when widely separated localities were sampled and compared to samples from close localities.
20. A geographic barrier (open water) between localities again produced groups separable by cluster analysis.

21. The variation exhibited by the song more closely resembles geographic variation than dialects (in the sense of Nottebohm (1969)).

22. The terminal six syllables of the song was more closely associated with locality than the beginning six syllables.

23. Preliminary tests indicates that Fox Sparrows may not respond differentially to songs from different localities.

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Appendix 1. Rules used to estimate the date of laying of the first egg from Fox Sparrow nest record card data.

The rules are based on the following data :

a) incubation period is 14 days (Ryan 1974)

b) nestling period is 10 days (Ryan 1974)

c) eggs are laid 1 per day (this study)

Rules to estimate date of laying of first egg :

1) Nest abandoned in last stages of construction - add 3 days to the date the adults were last seen at the nest.

2) Nest with eggs (stage unknown) with one visit - assume incubation is 1/2 complete and subtract (7 + 1 day/egg) days from date.

3) Nest with eggs (stage unknown) with multiple visits - assume hatching is 2 days from latest date and subtract (12 + 1 day/egg) days from that date.

4) Nest with incomplete clutch (less than 3 eggs) with one or multiple visits - subtract 1 day/egg from first date.

5) Nest with eggs and young on the same day with one visit - assume that day is day of hatching and subtract (14 + 1 day/egg) days from that date.

6) Nest with eggs and young on different days with multiple visits - assume hatching is mid-point between last egg and first nestling dates and subtract (14 + 1 day/egg) days from that date.

7) Nest with young (age unknown) with one visit - assume nestling period is 1/2 complete and subtract (14 + 5 + 1 day/young) days from that date.

8) Nest with young (age unknown) with multiple visits - assume fledging is 2 days from latest date and subtract (14 + 8 + 1 day/young) days from that date.

9) Nest with young that leave the nest when found - assume nestling period is complete and subtract (14 + 10 + 1 day/young) days from that date.

Appendix 2. Fox Sparrow nesting growth data. Age in days. Sample size in parentheses.

Age		0 (4)	1 (8)	2 (7)	3 (7)	4 (7)	5 (7)	6 (7)	7 (7)	8 (6)	9 (3)
Weight (g)	$\bar{x}$	3.2	4.54	7.34	10.56	14.56	18.69	21.64	22.6	25.65	24.43
	S.D.	0.38	1.06	1.26	1.63	2.06	2.44	1.88	1.72	1.08	0.93
	S.E.	0.19	0.38	0.48	0.62	0.78	0.92	0.71	0.65	0.44	0.54
	R*	2.9-3.7	3.1-6.0	4.8-8.7	7.2-12.1	10.6-16.2	14.1-21.4	18.2-24.1	20.7-24.7	23.9-26.7	23.4-25.2
Tarsus (mm)	$\bar{x}$	8.83	9.43	12.19	14.83	17.63	20.69	22.73	24.31	24.93	25.73
	S.D.	1.04	0.60	0.74	1.30	1.39	0.80	1.37	1.38	0.85	0.45
	S.E.	0.52	0.21	0.28	0.49	0.52	0.30	0.52	0.52	0.34	0.26
	R*	7.9-10.0	8.5-10.4	10.9-13.1	12.4-16.4	15.3-19.0	19.6-21.9	21.3-24.8	22.9-25.9	23.8-26.0	25.3-26.2
Rectrix (mm)	$\bar{x}$	0	0	0	0	0	0.37	1.34	2.71	4.85	7.27
	S.D.	-	-	-	-	-	0.19	0.62	0.72	1.26	2.00
	S.E.	-	-	-	-	-	0.07	0.23	0.27	0.52	1.16
	R*	-	-	-	-	-	0.0-0.5	0.2-2.0	1.6-3.5	2.8-6.0	5.0-8.8
Wing Chord (mm)	$\bar{x}$	7.25	8.19	10.41	13.37	17.83	23.49	28.67	33.52	39.23	43.60
	S.D.	0.52	0.63	0.72	1.46	1.69	2.01	1.95	2.19	1.85	0.99
	S.E.	0.26	0.22	0.27	0.55	0.64	0.76	0.72	0.83	0.76	0.57
	R*	6.9-8.0	7.3-9.0	9.4-11.2	10.6-15.0	14.4-19.8	19.5-25.3	25.2-30.5	30.4-35.8	36.8-41.0	42.5-44.4

Appendix 2. (continued) Fox Sparrow nesting growth data. Age in days. Sample size in parentheses.

Age		0 (4)	1 (8)	2 (7)	3 (7)	4 (7)	5 (7)	6 (7)	7 (7)	8 (6)	9 (3)
Hallux plus claw (mm)	$\bar{x}$	3.75	4.74	5.86	7.51	9.27	10.90	12.10	13.30	13.72	14.03
	S.D.	0.10	0.99	0.48	0.95	0.65	0.59	0.46	0.77	0.64	0.35
	S.E.	0.05	0.35	0.18	0.36	0.25	0.22	0.17	0.29	0.26	0.20
	R*	3.7-3.9	3.3-5.9	4.9-6.4	5.6-8.4	8.2-10.0	9.8-11.6	11.4-12.7	12.4-14.2	12.9-14.4	13.7-14.4
Culmen (mm)	$\bar{x}$	4.08	4.69	5.54	5.87	6.19	6.99	7.66	7.91	8.73	8.50
	S.D.	0.64	0.72	0.59	0.50	0.74	0.46	0.36	0.55	0.46	0.20
	S.E.	0.32	0.25	0.22	0.19	0.28	0.17	0.14	0.21	0.19	0.12
	R*	3.2-4.6	3.9-5.8	4.9-6.4	5.3-66	5.2-7.0	6.2-7.7	7.3-8.1	7.0-8.6	8.4-9.6	8.3-8.7
Outer Primary (mm)	$\bar{x}$	0	0	0.14	0.86	2.46	5.73	9.56	12.46	16.95	20.40
	S.D.	-	-	0.24	0.53	0.78	1.37	1.66	1.83	1.60	2.16
	S.E.	-	-	0.09	0.20	0.29	0.52	0.63	0.69	0.65	1.25
	R*	-	-	0.0-0.5	0.0-1.4	1.0-3.2	3.1-7.0	6.2-10.9	10.2-15.0	14.7-19.0	18.0-22.2
Inner Primary (mm)	$\bar{x}$	0	0	0	0.39	2.81	7.17	12.56	16.33	22.32	26.40
	S.D.	-	-	-	0.32	1.31	1.84	2.24	2.54	2.24	2.33
	S.E.	-	-	-	0.12	0.50	0.70	0.85	0.96	0.91	1.34
	R*	-	-	-	0.0-0.9	0.5-4.5	3.5-9.0	8.3-15.2	12.8-19.5	18.2-24.1	23.9-28.5

* R - Range

Appendix 3. Adult Fox Sparrow measurement data.

Variable	n	$\bar{x}$	S.D.	S.E.	Range
Weight (g)	33	40.0	3.2	0.56	31.5 - 46.6
Tarsus (mm)	33	25.3	0.8	0.15	23.9 - 27.4
Rectrix (mm)	33	72.3	3.1	0.54	63.5 - 79.0
Wing Chord (mm)	33	86.3	2.8	0.49	81.0 - 91.0
Culmen (mm)	33	11.8	1.0	0.17	10.4 - 14.4
Hallux plus Claw (mm)	2	16.9	-	-	(16.3 - 17.3)
Inner Primary (mm)	2	39.6	-	-	(38.2 - 41.0)
Outer Primary (mm)	2	67.0	-	-	(65.3 - 68.7)

Appendix 4. Variances of syllable (odd numbers) and between syllable (even numbers) durations in one day and over the whole season.

Duration Period	Bird A Variation		Bird B Variation		Bird C Variation	
	Day	Season	Day	Season	Day	Season
1	6.03	9.92	0.09	0.61	0.86	5.88
2	0.76	20.61	34.80	71.28	14.29	15.92
3	0.20	3.42	0.15	0.11	1.10	0.36
4	0.56	3.88	1.24	16.86	3.50	5.06
5	0.99	0.88	0.88	6.90	0.49	2.46
6	0.09	2.66	0.58	2.60	3.35	2.12
7	0.17	13.99	0.18	0.27	0.24	1.10
8	0.21	0.50	0.21	0.23	0.20	2.26
9	0.08	0.10	0.12	0.21	0.28	3.52
10	0.19	0.28	0.56	0.17	0,14	1.49
11	0.09	0.08	0.11	0.11	0.09	0.42
12	0.34	0.49	0.14	0.11	0.08	0.60
13	0.39	0.49	0.16	0.08	0.10	0.15
14	0.07	1.14	0.08	0.10	0.16	0.17
15	0.10	0.10	0.20	0.65	0.27	0.22
16	0.31	0.77	0.16	0.47	0.23	0.11
17	0.68	2.13	0.52	0.11	1.56	9.48
18	0.11	1.06	0.11	0.35		
19	0.27	4.28	0.41	2.80		
20	0.28	2.82	0.13	0.33		
21	0.14	0.88	1.89	6.21		
22			0.28	0.74		
23			0.22	0.18		

Appendix 5 . Location and syllable sequence of all 175 Fox Sparrow songs recorded in the 1978 field season.

Song No.	Loc.*	Syllable Sequence
1	GBR	20,18,5,67,67,18,37,63,63,79,87
2	"	1,2,1,2,5,18,67,18,8,37,6,6,41,87
3	"	3,2,69,32,32,18,37,63,63,41,79
4	"	17,3,5,67,67,18,6,6,87
5	"	18,5,64,64,32,37,19,2,87,79
6	"	20,1,20,23,8,8,87,18,8,37,6,6,41,87
7	GAR	6,22,6,22,19,8,19,8,18,8,37,19,7,19,41,79,79,41,79, 79,41,87
8	"	18,28,62,62,18,83,37,6,6,79
9	"	6,23,6,23,19,8,19,8,18,8,37,19,19,41,79,79,41,79,79, 41,87
10	"	20,4,18,32,32,30,37,9,9,41,79
11	"	17,18,62,62,23,8,37,9,9
12	"	20,2,69,19,8,19,8,23,37,10,10,79,41,79
13	"	17,5,18,19,7,19,7,30,37,63,63,79
14	STE	2,3,16,16,3,5,17,19,18,80,41,45
15	"	5,1,23,23,2,2,39,18,80,41,45
16	"	3,59,59,2,2,19,19,19,22,1,37
17	"	59,59,16,16,16,5,23,59,59,2,37,18,80,41,45,42
18	"	5,18,18,1,59,8,8,80,41,45,42
19	"	5,18,16,16,59,59,18,80,41,45,42
20	"	23,5,18,1,59,59,18,80,41,45,42
21	"	20,28,23,32,32,3,17,38,18,80,41,45
22	"	28,1,23,8,8,37,18,80,41,45
23	"	28,23,19,3,1,61,61,18,80,41,45,42
24	SAM	1,13,32,62,5,37,50,50,60,81,37
25	"	38,38,14,10,5,40,50,60,80,37,33
26	WTB	59,20,2,20,2,20,1,51,2,1,81,33,85
27	"	66,14,14,5,20,53,5,80,33,37,33,7,85
28	"	17,1,30,21,23,21,17,8,54,54,5
29	"	1,3,19,21,20,20,18,8,54,54,5,80,33,85

Appendix 5 (continued). Location and syllable sequence of all 175 Fox Sparrow songs recorded in the 1978 field season.

Song No.	Loc.*	Syllable Sequence
30	WTB	65,14,14,5,23,53,5,80,33,37,33,7,85
31	"	14,14,14,10,23,53,5,80,33,37,33,7,85
32	"	46,46,69,1,8,52,52,37,17,7,5
33	GIS	46,46,23,17,2,62,62,62,37,72,86,11,24
34	"	46,23,3,54,54,8,80,33,37,33,86,7,86,11
35	"	46,23,3,54,54,8,80,33,37,33,86,7,86,11
36	"	46,46,23,22,18,52,52,52,7,86,11,24
37	"	46,46,23,22,18,52,52,31,83,37,33,7,86,11,24
38	"	37,4,37,23,22,18,19,52,20,37,7,86,11
39	"	46,46,21,20,60,60,19,7,86,11,24
40	"	37,1,37,20,22,3,62,62,37,33,7,86,11,24
41	"	46,46,20,18,51,51,52,7,86,11,24
42	"	14,4,2,51,51,52,7,86,11,24
43	"	40,40,13,12,12,52,52,1,8,82,33,85
44	"	46,46,12,12,20,1,80,43,60,80,37,62
45	"	1,1,20,8,18,50,50,27,80,37,79,11,85
46	"	46,1,1,60,60,73,7,86,11,24
47	"	37,23,03,54,54,8,80,33,38,33,86,7,86,11,24
48	"	37,1,38,23,22,18,62,74,18,37,7,86,11,24
49	CSR	37,3,1,60,60,27,81,79,79,79,11,85
50	"	37,37,5,2,51,51,5,3,81,18,8,41,85
51	"	15,26,23,62,62,45,39,27,41,85
52	"	1,1,18,3,8,62,62,60,81,1,33
53	"	15,26,23,50,50,45,80,39,27
54	"	13,16,18,16,2,62,62,52,80,33,
55	"	46,75,71,1,29,2,62,62,60,60,81,39,41,85
56	"	38,38,14,14,2,50,50,60,80,33
57	"	74,17,18,31,20,20,2,62,62,60,60,81,33
58	"	75,75,1,3,62,62,60,80,18,5,5,41,85
59	"	75,75,1,3,62,62,60,81,18,5,5,85
60	"	3,3,3,3,2,62,62,60,60,81,33

Appendix 5 (continued). Location and syllable sequence of all 175 Fox Sparrow songs recorded in the 1978 field season.

Song No.	Loc.	Syllable Sequence
61	CSR	75,75,3,20,2,62,62,60,80,33
62	"	1,5,18,61,61,1,3,80,18,6,6,41,85
63	"	1,1,1,56,56,60,60,80,39,33,85
64	"	47,47,13,12,8,62,62,60,60,80,33
65	"	19,20,23,1,8,62,62,60,81,33,9,9,41,85
66	"	77,77,10,18,38,18,38,8,8,80,39,33
67	"	20,18,5,20,18,60,60,80,39,28
68	"	7,17,43,1,62,62,81,38,4,85
69	"	65,78,20,1,23,62,62,60,80,39,28,85
70	"	72,72,1,23,16,62,62,60,80,39,28,85
71	"	72,72,1,23,16,62,62,60,80,39,28,85
72	BDV	73,1,15,43,51,51,8,83,39,33,85
73	"	73,1,15,43,51,51,8,83,39,33,85
74	"	1,17,3,14,51,59,82,39,33,85
75	"	17,3,60,60,17,20,80,18,6,6,40,85
76	"	20,20,18,18,83,9,9,64,9,20,62,8,80,39,33,85
77	"	19,11,22,1,61,61,58,83,37,36,85
78	"	46,46,14,62,59,68,83,37,33,85
79	"	49,49,49,3,13,5,51,59,82,37,33,85
80	"	4,2,2,4,2,2,18
81	BIS	40,40,26,58,58,59,83,37,69,84,84
82	"	3,3,2,8,18,20,20,29,82,37,35,84,84,7
83	"	1,1,37,20,20,2,82,37,35
84	"	1,25,19,18,10,82,37,35,84,84
85	"	37,20,20,3,5,22,61,8,82,37,35,84,84,7
86	"	3,25,19,69,8,82,37,35,84,84
87	"	39,1,1,2,5,20,61,5,82,37,35
88	"	39,1,1,2,5,20,61,5,82,37,35
89	"	1,3,5,22,51,1,82,37,35,88,88,7
90	"	1,3,5,22,51,2,82,37,35,88,88,7
91	"	23,23,23,60,60,18,82,37,35,85,89,7

Appendix 5 (continued). Location and syllable sequence of all 175 Fox Sparrow songs recorded in the 1978 field season.

Song No.	Loc.*	Syllable Sequence
92	BIS	39,20,3,1,10,23,51,7,82,37,35
93	"	20,20,3,5,23,61,7,82,37,35
94	"	38,38,15,1,51,51,10,82,37,35
95	"	39,21,3,4,10,22,51,7,82,37,35
96	"	5,5,18,55,55,5,82,37,35,89,89,7
97	"	38,38,15,1,61,61,10,80,37,35,89,89,7
98	"	38,38,15,1,61,61,10,80,37,35,89,89,7
99	"	22,22,60,60,59,82,37,35,89,89,7
100	CSF	1,4,3,4,55,55,8,83,37,34
101	"	38,1,3,14,62,62,60,80,37,34
102	"	46,46,1,12,12,8,50,10,80,37,34
103	"	76,7,76,7,17,8,58,58,37,34,85
104	"	73,17,7,1,5,58,58,37,34
105	"	46,13,1,37,62,62,62,27,82,37,34
106	"	55,20,37,3,9,57,57,8,81,37,34,85
107	"	38,55,20,68,3,8,55,55,30,81,37,34
108	"	55,17,37,3,9,57,57,8,81,39,34,85
109	"	59,1,76,3,76,56,56,8,81,37,34,85
110	"	39,18,39,4,14,45,45,45,27,81,37,34,85
111	"	59,1,59,59,59,8,80,37,34,85
112	"	37,59,3,56,56,1,1,83,37,34
113	"	69,5,5,52,52,52,8,80,37,34,85
114	BLN	59,59,10,20,50,50,70,80,37
115	"	20,3,55,22,62,62,27,81,37,34
116	"	77,74,64,3,6,18,52,52,52,27,81,39,34
117	"	46,46,18,20,5,22,52,8,83,38,34
118	"	46,19,1,20,9,23,52,52,27,81,37,34
119	"	46,64,46,64,4,9,22,52,52,52,27,80,37,34
120	SCO	71,37,58,58,3,5,53,53,7,83,37
121	"	48,47,3,58,8,61,61,7,83,37,13
122	"	48,58,58,3,5,53,53,7,83,37,33

Appendix 5 (continued). Location and syllable sequence of all 175 Fox Sparrow songs recorded in the 1978 field season.

Song No.	Loc.*	Syllable Sequence
123	RHR	55,23,55,23,14,55,22,44,28,82,37,33
124	"	46,46,3,14,17,52,17,52,27,82,37,33,85
125	"	55,22,55,22,12,19,22,44,27,83,37,33
126	FLR	40,23,14,80,22,8,79,39,79,1,87,85,87
127	"	15,15,5,6,56,56,17,37,19
128	"	23,18,2,32,32,27,81,37,33
129	"	20,20,10,18,10,62,62,60,80,37,33,85
130	"	14,20,3,20,1,56,56,27,81,37,33,87
131	"	79,19,79,19,4,5,23,56,56,18,2,83,37,33,87
132	"	38,38,3,20,5,23,52,52,27,83
133	"	37,7,19,90,8,11,21,11,2,38,33,87
134	"	7,19,7,19,90,8,11,21,11,2,38,33,87
135	"	38,38,20,20,10,23,52,52,52,27,83
136	"	13,5,5,19,52,52,27,83,37,33,87
137	"	46,46,19,17,1,27,52,52,27,83,37,33,87
138	"	65,65,1,14,14,60,60,8,81,37,33
139	"	87,87,87,87,3,21,3,21,20,19,21,19,17,2,81
140	"	14,1,56,56,60,80,39,2,19,85
141	MDC	46,46,1,1,9,1,62,62,20,80,37,33
142	"	55,20,3,23,43,20,5,5,80,37,33
143	"	46,46,1,4,9,3,62,62,23,81,37,33
144	"	30,30,18,3,23,46,7,7,83,37,33,88
145	GAC	13,13,51,59,23,37,33,88,88
146	"	46,46,3,5,52,52,27,83,37,33
147	"	37,37,3,31,31,5,5,80,37,33,87
148	"	46,37,3,37,17,30,30,10,10,80,37,33,87
149	"	46,46,1,20,91,91,27,80,37,33,87
150	"	71,72,71,72,1,3,14,5,60,83,7,43,33
151	LOB	69,69,2,1,62,62,20,37,9,9
152	"	46,46,20,62,5,20,52,52,27,83,37,33
153	"	46,46,3,9,9,62,62,60,80,37,33,85

Appendix 5 (continued). Location and syllable sequence of all 175 Fox Sparrow songs recorded in the 1978 field season.

Song No.	Loc.*	Syllable Sequence
154	STJ	55,55,1,62,62,60,83,37,34,85
155	"	51,55,1,62,62,60,81,37,34,85
156	"	26,23,5,5,62,62,60,80,37,79
157	"	71,1,62,62,60,83,40,33,85
158	"	55,1,62,62,60,80,37,33,85
159	"	55,12,50,52,52,52,1,83,37,33,85
160	"	55,4,62,62,60,80,37,33,85
161	"	17,1,20,5,18,52,52,27,83,37,33,85
162	"	37,9,23,2,71,18,30,81,37,33,85
163	"	64,64,4,19,19,55,55,55,42,42,33,85
164	"	64,64,37,1,22,22,28,83,37,33
165	"	10,3,14,23,51,51,2,80,37,35,85
166	"	46,1,55,23,55,17,55,17,8,62,62,60,83,37,34,85
167	"	71,8,76,16,76,76,21,17,19,7,20,55,55,27,83,37,33,85
168	"	64,64,1,19,19,55,55,37,33,85
169	"	19,41,19,41,1,27,62,62,2,2,81,37,33
170	"	40,40,18,10,23,52,52,52,26
171	"	3,15,15,56,56,56,5,83,37,33,85
172	"	46,46,18,14,45,45,45,27,83,37,33,85
173	"	37,37,21,9,23,52,52,52,26
174	"	1,1,20,20,53,8,17,37,69,85
175	"	46,1,3,9,62,62,60,83,37,33,85

* Location abbreviations are as follows :

GBR - Gander Bay Road
GAR - Glenwood Access Road
STE - Stehpenville Road
SAM - Salmonier
WTB - Witless Bay
GIS - Gull Island
CSF - Cape St. Francis
CSR - Cape Shore Road
STJ - St. John's
BDV - Bay de Verde
BIS - Baccalieu Island
BLN - Bauline Line
SCO - Shoe Cove
RHR - Red Head Road
FLR - Flatrock Road
MDC - Middle Cove
GAC - Gallows Cove