

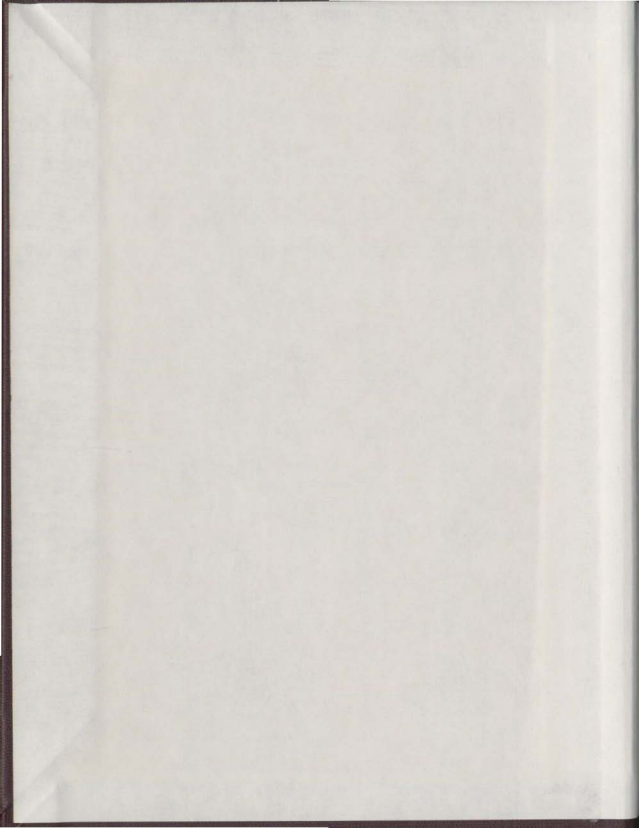
SONG DIALECTS, AND VOCAL DEVELOPMENT
OF SAVANNAH SPARROWS (*PASSERCULUS*
SANDWICHENSIS LABRADORIUS, HOWE)
BREEDING IN NEWFOUNDLAND AND THE ST.
PIERRE ET MIQUELON ISLANDS

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Song dialects, and vocal development of Savannah Sparrows
(Passerculus sandwichensis labradorius, Howe) breeding in
Newfoundland and the St. Pierre et Miquelon Islands.

by



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A Thesis submitted in partial fulfillment
of the requirements for the degree of
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Dialect differences were found in primary song of male Savannah Sparrows (P. s. labradorius) from 10 different breeding localities in Newfoundland and the St. Pierre et Miquelon Islands. Sonograph analysis reproduced note types comprising primary song which were entered into a cluster analysis to determine similarity in song amongst different breeding localities. Sonographs of vocalizations from nestlings and fledglings reveal that some note types comprising primary song and male aggressive notes develop from contact and begging notes of juvenile birds. Homology of breeding display and accompanying flight song of male Savannah Sparrows within the Emberizinae are also discussed.

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Introduction

Communication as defined by Green and Marler (1979), is a "social event," consisting of "the transmission of information from one animal to another." Animals have evolved displays that maximize the probability that information would be sent, received and processed by conspecifics. These displays being clearly distinguishable from each other and from extraneous stimuli, have provided a mechanism for "ethological isolation" (Konishi 1970). Behavioural isolation on a reproductive level has restricted gene flow to those members of a population that are able to transmit and decode information about species' identity, sex, sexual readiness, etc.... (Emlen 1971, Green and Marler 1979). Many male passerines resemble the females of their species and rely more on vocal displays than other forms of communication (Pettingill 1970). While conducting an intensive 10 year study of Myiarchus systematics, Lanyon (1963; 1978) found that visual cues played little if any role in species recognition.

Bird song is produced by the syrinxal components of the avian respiratory apparatus (Greenwalt 1969) which are innervated by the hypoglossus nerve (Nottebohm and Nottebohm 1976; Nottebohm et al. 1979). Dialects describe consistent structural similarities in primary song among conspecifics in separate breeding localities with potential to interbreed

(Marler and Tamura 1962; Nottebohm 1969; Lemon 1975). When these localities are distant enough to prevent interbreeding, geographic variation is used to explain song differences (Nottebohm 1969). The existence of both forms of song variation has been documented in many North American species (Lemon 1974; Baker 1975; Kroodsma 1975; Mundinger 1975; Avery and Oring 1977; Baptista 1977; Bradley 1977; Baptista and King 1980; and South America (Nottebohm 1969; 1975; King 1972), European (Hunter and Krebs 1979; Slater and Ince 1979), African (Payne 1978) and New Zealand birds (Jenkins 1977). Dialect variation has also been documented in the mechanically produced wing-song of the Flappet Lark (Mirafra rufocinnamomea) (Bertram 1977).

There has been much discussion about the reproductive significance of regional variation in primary song. Consistent similarities among song patterns of individuals within a given breeding locality which are different from conspecifics of other breeding localities may serve as an intraspecific isolating mechanism allowing rapid colonization of different habitats (Nottebohm 1969). Treisman (1978) argues that song dialects serve as a genetic marker signalling kin association and possible reduced aggressive tendencies between neighbours. Females might "maximize outcrossing" if they were to select males with foreign dialects and emigrate from their home dialect locale (Baker 1975). Saddleback males (Philesturnus carunculatus)

have been observed by Jenkins (1977) to emigrate from their birthplace which would minimize breeding with close relatives.

Dialect differences may not affect female choice but rather arise as a result of intrasexual selection such that the ability to hold a territory is enhanced by song conformity (Baker 1975). Hansen (1979) proposed that a native song pattern could be the song pattern which suffers the least attenuation from flora comprising breeding habitat and provides the best song model for juveniles to copy. It is also conceivable that dialects may be an epiphenomenon of song learning. The dialect phenomenon is widespread among birds. Its role in reproductive behaviour differs among species and, its function may depend upon species specific breeding and dispersal strategies (Kroodsma 1974, Jenkins 1977).

Systematists normally rely on morphological characters in classifying organisms into taxonomic groupings. In five North American flycatchers of the genus Empidonax, plumage and body size are so similar not only between sexes but among species as well, that primary song is the diagnostic field character (Peterson 1980), and differences among songs of these species played a vital role in causing their present isolation (Stein 1963). Where morphology is similar characters is very high, additional criteria are provided in

the form of vocal characters (Lanyon 1969). The importance of vocal characters in taxonomy has been amply demonstrated by Lanyon's (1978) revision of the Myiarchus flycatchers. Winkler and Short (1978) have also employed vocal behaviour in their study of Pied Woodpecker systematics. Baptista and King (1980) have recently used song dialects of White-crowned Sparrows (Zonotrichia leucophrys ssp.) in postulating the evolution of present subspecies from four refugia isolated during Pleistocene glaciation. The study of dialect systems in migratory species can be employed to trace the origin of invading populations (King 1972; Mundinger 1975; Baptista 1977) and identify wintering grounds of breeding populations (Baptista 1977).

In the present study song dialects in Savannah Sparrows (Passerculus sandwichensis labradorius) were investigated and compared with those of other related subspecies from an evolutionary perspective to generate a hypothetical ancestral song.

Krebs and Kroodama (1980) point out that a number of migratory subspecies east of the Rocky Mountains lack song dialects which are evident in their sedentary western relatives. P. sandwichensis is classified into 18 subspecies (A.O.U. Checklist, 1957, Auk Supplement 1973). Bradley (1977) has reported song dialects in Belding's Savannah Sparrow (P. s. beldingi), a sedentary

subspecies (P. s. ssp.) in Ontario and Nova Scotia. While Chew (1981) did not specify the subspecies he studied, the breeding range of these animals fits the description for P. s. savanna described by Baird (in Bent 1968) and will be referred to as such when compared to the other subspecies. P. s. labradorius is a migratory "dark race" breeding in eastern Quebec, Labrador, Newfoundland and the St. Pierre et Miquelon Islands (Peters and Burleigh 1951). The primary concern of this study was to assay dialect differences in Savannah Sparrows from 10 different breeding communities in Newfoundland, St. Pierre and Miquelon Islands and then compare dialect behaviour between migratory versus sedentary P. s. ssp.

Singing males were recorded on farmland on the Avalon Peninsula and nearby islands in Newfoundland, Isle de Grand Miquelon and Isle de St Pierre. Sonographs were reproduced from field recordings and individual note types were assigned letters of the alphabet. Scores on the absence or presence of note types between songsters were entered into a cluster analysis which produced clusters of individuals similar to each other and different from members of other clusters.

Other components of the vocal repertoire (e.g., whisper song, call notes) and their ontogeny were studied under natural conditions. Juvenile birds were recorded in the

nest at different ages along with fledglings found feeding in family groups. Multiple functions of the "chip" note of labradorius were analyzed and variables discerning its context-specific nature are discussed and compared with three other Emberizine sparrows (Dark-eyed Junco, Junco hyemalis; Fox Sparrow, Passerella iliaca; White-crowned Sparrow, Zonotrichia leucophrys) and one Tyrannid flycatcher (Dusky Flycatcher, Empidonax oberholseri). Reproductive displays and other vocal traits of P. s. labradorius and its homologues within the Emberizinae are discussed.

Table I - Number of male songsters and songs per breeding locale.

Map Code	Geographic Location	Lat.	Long.	# males	# songs
A	Baccalieu Island	48 07	52 47	10	150
B	Bell Island	47 38	52 58	4	47
C	Cape St. Mary's	46 49	54 12	1	4
D	Chamberlains	47 32	52 57	3	27
E	Flatrock	47 42	52 42	1	5
F	Kilbride	47 32	52 45	15	148
G	Little Bell Island	47 34	52 58	1	4
H	Miqueon	47 02	56 20	4	75
I	St. Pierre	46 47	56 11	15	160
J	Trinity	48 22	53 55	2	20
Total		10		58	640

Methods

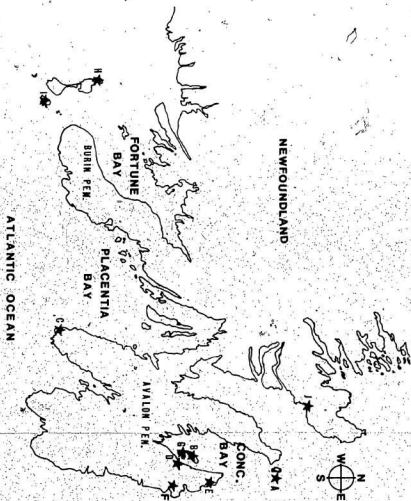
Study Areas

Male Savannah Sparrows were recorded singing at the following locations in Newfoundland: Baccalieu Island (4807N, 5247W), Bell Island (4738N, 5258W), Cape St. Mary's (4649N, 5412W), Chamberlains (4732N, 5257W), Flatrock (4742N, 5242W), Kilbride (4732N, 5245W), Little Bell Island (4734N, 5258W), and Trinity (4822N, 5355W) and from Isle de Grand Miquelon (4702N, 5620W), and Isle de St. Pierre (4647N, 5611W) (Figure 1). The number of males and songs recorded per region are listed in Table I.

Data Collection and Analysis

Vocal behaviour was recorded from May through August (see appendix A), 1980 with a Uher 4400 Report Stereo at 19cm/sec using a Dan Gibson Electronic Parabolic Microphone 200. Samples of primary song were recorded from males in the 10 locations listed above during early morning (0400-0700 hr), when singing intensity was at its peak.

Figure 1. -- Map of Savannah Sparrow breeding localities where song sampling took place: A -- Bacallieu Island, B -- Bell Island, C -- Cape St. Mary's, D -- Chamberlains, E -- Flatrock, F -- Kilbride, G -- Little Bell Island, H -- Miquelon, I -- St. Pierre, J -- Trinity.



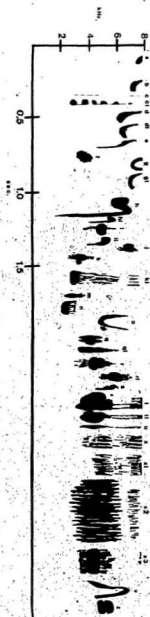
Other components of the adults' vocal repertoire were monitored throughout the breeding season (i.e., call notes, flight song). Two groups of four nestlings each were recorded at 1-3 days old and a group of four 6 day old nestlings, sometimes artificially stimulated by depressing the nest in order to elicit food begging was recorded also. The vocalizations of two age groups of fledglings, 10-15 days old and 15 days plus, totaling 9 individuals were also catalogued. Age determinations were based on individual observations and growth measurements from Threlfall and Cannings (1979). Ten to 15 day old fledglings lacked rectrices and were incapable of sustained flight. Recordings of a Dark-eyed Junco (Junco hyemalis) also lacking rectrices, were made and compared with similar aged P. s. labradorius. Sound spectrograms of song and call notes were produced by Kay Elemetrics Sound Spectrograph (7030A), wide band setting.

The terminology describing bird song employed by Baptista (1977), Bradley (1977), Williams and MacRoberts (1977), Lanyon (1979) and Baptista and King (1980), (Lemon, personal communication) has been condensed into the following terms which will describe and illustrate differences in Savannah Sparrow song. Note - smallest unit of song. Phone - note variant which differs from the basic structure of a song note but is distinctive enough to carry the weight of a separate note type in cluster

analysis. Buzz - longest note in song appearing towards end of song, precedes terminal phrase. Phrase - defined series of notes forming a section of song (i.e., introductory, middle, buzz, terminal trill). Song - temporal grouping of notes always uttered together with a distinguishable superior melodic quality uttered in bouts. Song type - permutations and combinations of notes within a song that make it different from other songs.

A song note catalogue was developed with different song note types assigned letters of the alphabet. (All song note types, regardless of geographic origin, are shown in Figure 2). Patterns of note types within songs were then translated into alphabetical formulae, and three cluster analyses were then performed on the resulting formulae to determine clustering of note types in the areas examined. In an agglomerative cluster analysis, individuals are rated on the presence (1) or absence (0) of prescribed variables (Everitt 1974). Presence or absence of song note types were variables in this analysis. They are assigned clusters based on similarity coefficients which measure relationships between individuals based on scores for each of the designated variables. A distance or similarity matrix contains similarity measurements for all pairs of individuals.

Figure 2 — Song note catalogue, tracings of different song notes "a...z" from all songs sampled. The harmonics of some song notes with frequencies above 8000 Hz are not shown in this figure but they were not judged to be crucial for song note identification.



The group average method was selected from other agglomerative clustering techniques because it computes distance between all pairs of individuals of different clusters (Everitt 1974). The scores "a,b,c,d" reflect four possible comparisons between songs of two males for each note type (or variable) within their respective songs. These scores were then entered into coefficient formulae. The coefficients used were Jaccard, Cezanowski-Dice and Correlation. The formulae for each coefficient are in Appendix B. Jaccard's coefficient ignores negative matches (absence of notes in both individuals) as does Cezanowski-Dice coefficient. The latter coefficient doubles the weight of positive matches (notes common to both individuals). The resulting tree diagram or dendrogram represents fusions of sampled males into alike clusters over successive similarity measurements (1.00=100% similarity).

Signal differences can be illustrated by comparing designated parameters of birdsong (Green and Marler 1979). Five metric parameters used by Baptista (1977) were: 1) total notes per song; 2) total different note types per song; 3) song duration; 4) minimum frequency and 5) maximum frequency were used in conjunction with cluster analysis to assay dialect differences.

Song Perch Selection

Data on substrate type and height (mm) of song perch were taken for each male recorded. If a male used more than one perch, each perch was measured and included in the analysis. Forty-five male Savannah Sparrows sang from 70 perches. Substrates used included spruce, bullrushes, fenceposts, rock, ground, tussocks etc. Use of particular substrates is described in percentages. Per cent use of a particular substrate was calculated by dividing the incidence of substrate usage by the total 70 song perches. Different substrates were treated individually for average height analysis. The average height per substrate was calculated by summing perch heights for a given substrate and dividing the ensuing total by the incidence of perches.

Results

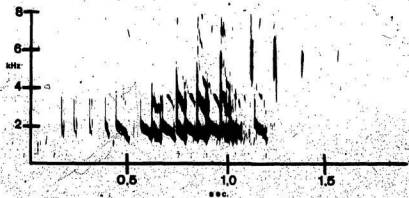
The vocal repertoire of the Savannah Sparrow is divided into two major groups, "song" and "call." The essential difference separating songs from calls is complexity, song being much more elaborate than the simple and often monotypic call display (Thorpe 1961).

Adult Call Repertoire

Territorial Calling -- Confrontations between territorial males usually involved at least one (and more often two) of three different vocalizations (Figures 3, 4). All three calls were observed during interactions involving the expelling of an intruding conspecific from a previously held territory. 1) Gobel (1970) described a "flight song" in P. s. savanna, which Bradley (1977) also found in P. s. beldingi. Bradley (1977) referred to this complex sequencing of call notes a "flight slur" which was also accompanied by a visual display in flight. Newfoundland males gave a similar call (Figure 3) which was accompanied by bilateral and unilateral wing displays in

Figure 3. — Note slur of Savannah Sparrow and Dark-eyed Junco.

DARK-EYED JUNCO



SAVANNAH SPARROW

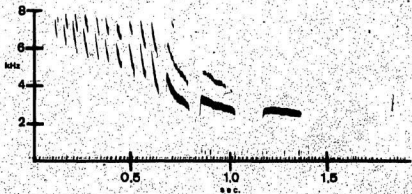
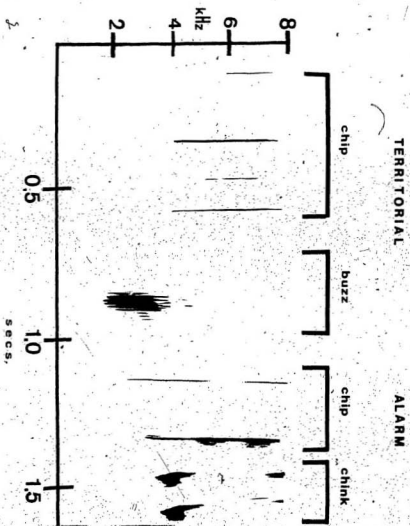


Figure 4 -- Adult call note of Savannah Sparrow:
territorial (chip, buzz) and alarm (chip, chink) calls.



flight and also from song perches. The frequency range of the Newfoundland male is highest in the beginning at 9000 Hz terminating at 2000 Hz. The duration of this vocal display in Figure 4 is 1334 msec. This varied among birds, probably reflecting different levels of individual motivation. 2) The "past" of "buzt" (Figure 4) note, observed by both Gobel (1970) and Bradley (1977), was given and directed by the territory holder at conspecific intruders into the holder's territory. The duration of this call was 144 msec with a low frequency range of 1700 Hz to 4000 Hz. 3) The buzz note was often given in conjunction with a "chip" call (Figure 4). Gobel (1970) described this call as a "tsip" note which was vocalized less frequently than the buzz call. The stick-like structure of this note covers a frequency range of 4000 Hz to 8100 Hz and a variable duration lasting 10-46 msec.

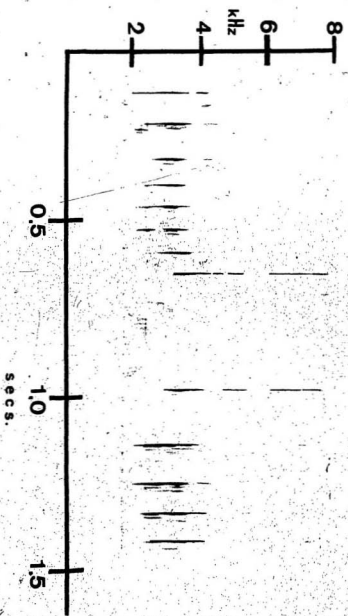
Alarm Calling -- Two different call notes were recorded upon approaching either an active nest or a group of fledglings. Figure 4 contains the harsh "chip" note also observed by Gobel (1970) and Bradley (1977) and a softer "chink" note. The former call is identical to the aggressive "chip" call observed during territorial confrontations. Bradley (1977) commented that this note occurred in a variety of different behavioural contexts and was also given by both sexes. Bradley (1977) suggests that

this call signals to other conspecifics close proximity of a predator which concurs with observations from P. s. labradorius. Unlike the "chip" note, the "chink" call was given only during nest approach (see Figure 4). This call is probably directed towards the young nestlings, signaling approaching danger. Nestlings could not be recorded and remained motionless when adults gave this call, but nestlings could be artificially stimulated to food beg by vibrating the nest and were easily recorded when the adults were chipping nearby. The "chink" call had a "v" structure with a small frequency range of 3700 Hz to 4900 Hz and duration of 46 msec.

Female Soliciting Call -- A series of rapid "chip" notes were recorded from a Chamberlains preceeding copulation (Figure 5). This call resulted in four mounts by her mate and sustained mounting of this nature occurred only after the female gave this call. This rapid burst of "chips" by the female solicits copulation from the male. Individual notes are short at 5 msec and range from 1900 Hz to 8000 Hz.

Figure 5. -- Pre-ovulatory call of Savannah Sparrow female.

♀ PRE-COPULATORY NOTES



Calls of Three Other Emberizine Sparrows

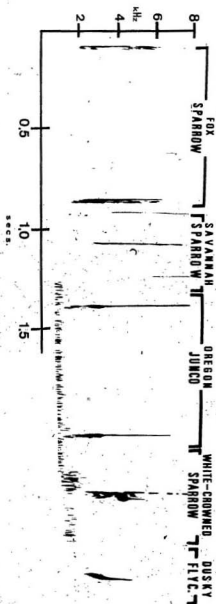
Vocalizations of three other Emberizine sparrows, Dark-eyed Junco, White-crowned Sparrow and Fox Sparrow and a Tyrannid flycatcher, Dusky Flycatcher, were recorded during behavioural contexts similar to Savannah Sparrow recordings. The purpose of this was to determine similarity in structure between vocal displays with the same behavioural function among closely and distantly allied passerines.

A vocalization resembling the flight slur of the Savannah Sparrow was given by a territorial Dark-eyed Junco male during a territorial confrontation with one of its neighbours (Figure 3). The flight slur of the junco lasted 1455 msec with a frequency range of 986 Hz to 9000 Hz, which was 1093 Hz greater (in range) than that of the Savannah Sparrow. However, the junco vocalization was not accompanied by the visual wing display observed in Savannah Sparrow males.

Blacquiére (1979) recorded "check" calls from Fox Sparrows which were employed in various behavioural contexts and serving different behavioural functions, e.g. territorial aggression and alarm (nest approach).

Figure 6. -- Alarm "chip" of four Emberizine Sparrows (Fox Sparrow, Savannah Sparrow, Dark-eyed Junco, White-crowned Sparrow) and one Tyrannid Flycatcher (Dusky Flycatcher) upon approaching a nest.

CHIP NOTES



The "check" call (Figure 6) has a frequency range of 1300-8200 Hz, lasting 23 msec. Approaching the nest of Junco and White-crowned Sparrow induced vigorous alarm chipping from nearby adults in both species (Figure 6). These calls also function to warn conspecifics of predators and are similar in structure to their counterparts in Savannah and Fox Sparrow call repertoire. Duration of this alarm note was longest for White-crowned Sparrow, 48 msec, followed by Fox Sparrow, 23 msec, Dark-eyed Junco, and Savannah Sparrow, 9 msec. The duration of the Savannah Sparrow "chip" can last as long as 46 msec and probably varies with the emotional state of the bird. The frequency ranges of the Dark-eyed Junco and White-crowned Sparrow were 2000-8000 Hz and 2500-8100 Hz, respectively. Ranges of Savannah Sparrow "chip" notes have been recorded at 3100 and 4400-8000 Hz.

Vocal Development

Nestling Call Repertoire -- Nestlings 1-3 days old were artificially induced to food beg by gently vibrating the nest in order to mimic alighting of a feeding adult. Figure 7 contains sonographs of the first "peet-peet"

Figure 7. -- Vocal development of Savannah Sparrow from
nestling to fledgling: 3, 6, 10-15, 15+ days.



(Gobiel 1970) of 1-3 day old nestlings. Individual notes had the highest frequency range of any within the species' repertoire at 8000-11000 Hz. The duration of a single note lasted 8 msec. These call notes were given in conjunction with food-begging posture, gaping, and probably enhances the red mouth lining as a "food target" (Pettingill 1970) for feeding adults.

Nestlings 6-8 days old were similarly stimulated and the resulting vocalizations are shown in figure 7. Two different beg calls are evident in Figure 7 for 6-8 day old nestlings. Type "a" ranges from 8000-10000 Hz with a duration of 38 msec. These same "a" notes are coupled together in a slur forming a "b" note of similar frequency range but lasting three times longer, 121 msec.

Fledgling Call Repertoire -- The vocalizations of two groups of fledglings, 10-15 days old and 15+ days old, were recorded (Figure 7). A "buzz" and "chip" call quite similar to those of adults were given by 10-15 day old fledglings while in filial feeding groups. The fledgling "buzz" call is a food beg note which attracts feeding adults. This note had a wide frequency range of 3000-9200 Hz and lasted 186 msec. The fledgling "chip" may maintain filial contact in feeding and other contexts. This note lasted 21 msec with a range of 3000-8000 Hz.

A soft "chip" call was recorded from 15+ day old fledglings (Figure 7). Gobiell (1970) described a softer variant of his "tsip" note which was given by fledglings and adults. Quay (1957) and Gobiell (1970) both suggested that this note serves to maintain filial contact and later loose flock contact in wintering migrants. This note had a small range of 7000-8000 Hz, lasting 47 msec in P. g. labradorius. Close inspection of the structure of this note reveals that it is song note "b", common to all males sampled.

Vocalizations of another ground-nesting species, Dark-eyed Junco, were also recorded for comparison with a 10-15 day old Savannah Sparrow fledgling (Figure 8). The junco fledgling lacked rectrices as did the fledgling Savannah Sparrows. The junco gave two calls, a "buzz" and "chip" which were both quite similar in structure to its Savannah counterpart. The "buzz" and "chip" calls also served to maintain filial contact in junco family groups. The "buzz" note ranged from 4000-9000 Hz, however it was of shorter duration (138 msec) than the Savannah Sparrow "buzz" (186 msec). The junco "chip" lasted 18 msec with a wide frequency range of 1200-8000 Hz.

Figure 8. -- Calls of two Emberizine fledglings, Savannah Sparrow and Dark-eyed Junco.

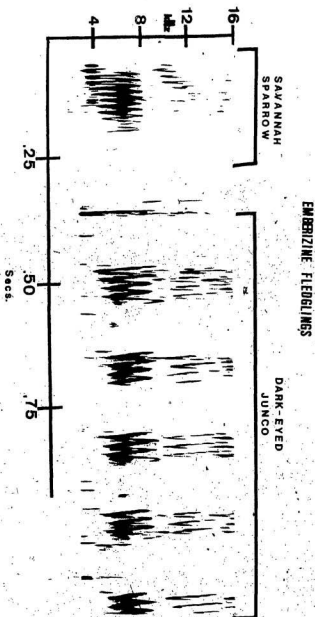


Table II - Percentage occurrence of note and phone types across all individuals sampled.

Note type	% Occurrence	Phone type	% Occurrence	Buzz type	% Occurrence
b	100.0	BK1	1.8	BK1	26.8
c	100.0			BSP	26.8
d	62.4	c1	3.6	BGM	3.6
e	30.3	d1	1.8	BBB1	7.1
f	1.8			BCH	5.4
g	1.8			BCSM	1.8
h	64.8	g1	1.8	PB1	16.1
i	12.5	h1	5.4	BFL	1.8
j	26.8	i1	28.5	BIR	3.6
k	89.3				
l	94.6	k1	1.8		
m	1.6				
n	3.6				
o	9.4	q1	1.8		
p	3.6	r1	1.8		
q	3.6				
r	14.3				
s	1.8				
t	26.8				
u	30.4				
v					
w					
x					
y	1.8				
z	1.8				

Primary Song

Primary and secondary song are two types of singing behaviour described by Van Tyne and Berger (1976). Information encoded in primary song includes sex, territorial status, reproductive state, probability of responding aggressively or sexually to conspecifics (Emlen, 1971). Analysis of primary song samples from 10 breeding communities around eastern Newfoundland revealed song structure varied among these areas.

These data show continuity in song structure within a geographic region which differs from song structure shared by singing males of a different breeding community. Typical primary song of P. s. labradorius is divided into four phrases: 1) introductory, 2) middle, 3) buzz and 4) terminal trill (Figure 9). Table II contains a distribution of the note types within the song samples. The greatest number of different note and phone types (23) occurred in the middle phrase; the least variation occurred in the terminal trill with a maximum of 6 different note types. Secondary song of Savannah Sparrow males will be discussed later in this section.

Figure 9 -- Example of four phrases of Savannah Sparrow
primary song: introductory, middle, buzz, terminal
trill.

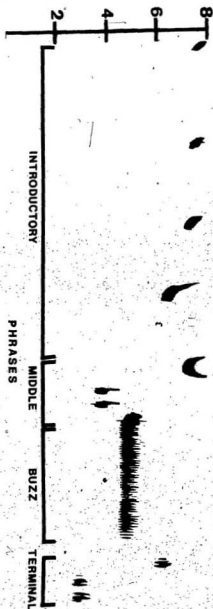


Table III - Individuals singing different song types per area.

Location	Song type per area		
	1	2	3
Baccalieu Isl. (A)	1,3,4,5,6,7,8,9	10	2
Bell Isl. (B)	2,3	1	4
C. St. Mary's (C)	1*	---	---
Chamberslains (D)	1	2	3
Flatrock (E)	1*	---	---
Kilbride (F)	1,3,4,5,6,10,13,14	2,7,8,9	11,12,15
Little Bell Isl. (G)	1*	---	---
Miquelon (H)	1,2,3,4	---	---
St. Pierre (I)	1-15*	---	---
Trinity (J)	1,2	---	---

* only one song type recorded for that area

Individual Variation -- A maximum of three different song types were found in a sampled breeding sub-population. All males recorded had a single song repertoire. The song type shared by a majority of the individuals for any given community was considered the dominant pattern for that region.

Table III lists the different song types for all study areas and the individuals singing those song types. Representative sonographs are found in Figures 10 (Baccalieu Island), 11 (Bell Island), 12 (Chamberlains), 13 (Kilbride), 14 (Cape St. Mary's, Little Bell Island, Flatrock), 15 (Miquelon, St. Pierre, Trinity). Individual variation usually involved addition and/or omission of notes from the dominant song pattern.

An illustration of individual variation within a subpopulation can be seen in Kilbride males (Figure 13, A1,A2,A3). The greatest variation occurred in the middle phrase of the song with "gh", "qqqq", and "rs" sequences for song types 1, 2, 3, respectively. Baccalieu Island, Bell Island and Chamberlains, are three other study areas where more than one song pattern could be identified.

Dialect Variation -- Dialect variation was similar to individual variation and most note variance occurred in the middle phrase of the song. Note types common to different communities often varied in their repetition within a song.

Table IV - Song formulas for all males according to geographic location.

Location	Individual	Introductory	Middle	Qua	Terminal Trill
Macaulay Island	1	ab	rua	DBI	djwaka
	2	abcb	's	DBI	djak
	3	ab	rua	DBI	djak
	4	ab-	rd	DBI	djak
	5	ab	ru	DBI	djak
	6	abdb	ru	DBI	djak
	7	ab	ru	DBI	djak
	8	ab	rua	DBI	djak
	9	ab	rua	DBI	djak
	10	abababab	qiaqiaqia	DBI	dja
Bell Island	1	abab	er	DBBI	jak
	2	ababab	ga3h1	DBBI	jak
	3	abababab	ga3h1	DBBI	jak
	4	abababab	ga3h1	DBBI	jak
Cape St. Mary's	1	abab	atx2	DCM	jamama
Chamberlains	1	ababababab	v	DCH	djak
	2	abababab	ga3h1	DCH	jak
	3	abababab	ka	DCH	a
Flatrock	1	abababab	gr1	DFL	ka
Kilbride	1	abababab	gh1	DBI	jak
	2	abababab	ga3h1	DBI	jak
	3	abababab	gh1	DBI	jak
	4	abababab	gh1	DBI	jak
	5	abababab	gh1	DBI	jak
	6	abababab	gh1	DBI	jak
	7	abababab	ga3h1	DBI	jak
	8	abababab	ga3h1	DBI	jak
	9	abababab	ga3h1	DBI	jak
	10	abababab	ga3h1	DBI	jak
	11	abababab	gr	DBI	jak
	12	abababab	gr	DBI	jak
	13	abababab	gh1	DBI	jak
	14	abababab	ga3h1	DBI	jak
	15	abababab	gr	DBI	jak
Little Bell Island	1	abab	lit	DBI	ki
Miquelon	1	ababab		DCH	jak
	2	ababab		DCH	jak
	3	abab		DCH	jak
	4	abab		DCH	jak
St. Pierre	1	ababababab	g11	DBI	ka
	2	ababababab	g11	DBI	ka
	3	ababababab	g11	DBI	ka
	4	ababababab	g11	DBI	ka
	5	ababababab	g11	DBI	ka
	6	ababababab	g11	DBI	ka
	7	ababababab	g11	DBI	ka
	8	ababababab	g11	DBI	ka
	9	ababababab	g11	DBI	ka
	10	ababababab	g11	DBI	ka
	11	ababababab	g11	DBI	ka
	12	ababababab	g11	DBI	ka
	13	ababababab	g11	DBI	ka
	14	ababababab	g11	DBI	ka
	15	ababababab	g11	DBI	ka
Trinity	1	abab	lit	DBI	oka
	2	abab	lit	DBI	oka

Song formulae for each individual recorded are listed in Table IV. Data for the physical parameters described by Baptista (1977) were taken from the clearest sonograph reproduction for each male as were notes translated into song formulae. The means $\pm$ sd for each of the five parameters are listed in Table V. Dominant song patterns were song by a majority of individuals in an area, variants being sung by an individual or minority of individuals.

The dominant song pattern of Baccalieu Island was "acbdrud/BBI/djkk" containing 9 different note types and 12 notes total (Figure 10, A1). This was sung by eight males (Table III). Two variants of this song type were "babbbx1bq1q1q1/BKI/djk" (Figure 10, A2) and "abcdbdz/BBI/djkk" (Figure 10, A3) sung by birds ten and two respectively.

Two of four birds sang the same song type, "acbcgh3h1/BBBI/jkk" (Figure 11, B1), on Bell Island while two others sang different songs (Figure 11, B2,3). Three separate song types were sung by three Chamberlains males (Figure 12, D1,2,3). Birds D1 and D3 both lack the common "j" note of the terminal trill. Of the 15 Kilbride males, seven sang song type F1 "abbobxbx1bghi/BKI/jkk" (Figure 13), which was the dominant theme for the area. Five sang F2,

Table V - Descriptive statistics for five parameters of Savannah Sparrow Song.

Location (n)	# Notes	# Note Types	Duration	Max. Freq.	Min. Freq.
Bacallau Isl. (10)	11.5 ± 1.43	8.3 ± 0.67	2.15 ± 0.45	8030 ± 48.3	2342 ± 589.2
Bell Island (4)	14.0 ± 4.24	7.5 ± 1.00	1.94 ± 0.43	8050 ± 57.7	2698 ± 325.7
Cape St. Mary's (1)	15.0	9.0	2.46	8000	2456
Chamberlains (3)	14.7 ± 1.53	2.5 ± 0.36	2.50 ± 0.36	8050 ± 50.0	2828 ± 492.8
Flatrock (1)	13.0	8.0	2.27	8050	3403
Kilbride (15)	14.5 ± 1.00	11.3 ± 0.98	2.67 ± 0.20	8043 ± 59.4	2590 ± 292.3
Little Bell Isl. (1)	8.0	6.0	1.59	8100	3004
Miquelon (4)	9.5 ± 0.58	5.5 ± 0.58	2.17 ± 0.13	8000 ± 0.00	3036 ± 453.9
St. Pierre (15)	13.1 ± 1.10	8.0 ± 0.00	2.61 ± 0.32	7986 ± 255.3	2848 ± 389.3
Trinity (2)	10.0 ± 0.00	8.0 ± 0.00	2.2 ± 0.50	8000 ± 00.0	2108 ± 348.0

Figure 10. — Three song types from Baccalieu Island, A1,
A2, A3.

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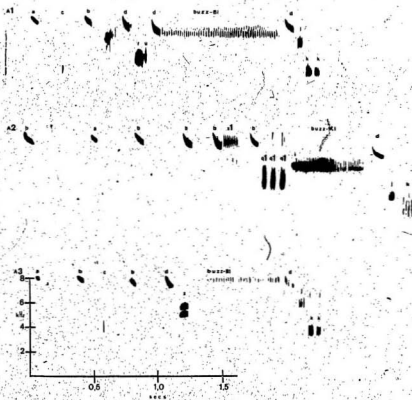


Figure 11. -- Three song types from Bell Island, B1, B2, B3.

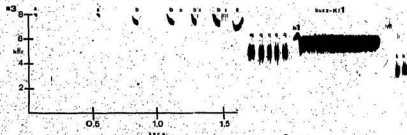


Figure 12. -- Three song types from Chamberlains, D1, D2,
D3.

Figure 13. -- Three song types from Kilbride, F1, F2, F3.

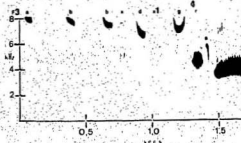
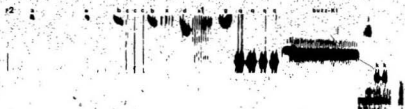


Figure 14. -- One song type from Cape St. Mary's, C; Little
Bell Island, E; Flatrock, G.

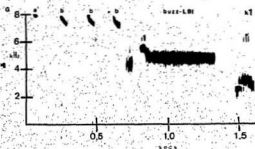


Figure 15. -- One song type from Miquelon, H; St. Pierre,
I; Trinity, J.

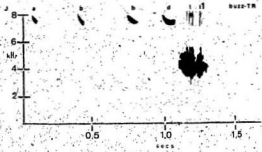
BUZZ-GM



BUZZ-SP



BUZZ-TM



"aabcccbxdxlgqqqqi/BKI/jkk". The "q" notes give the song a bubbly quality, and birds singing with "q" notes or "q1" phones were labeled bubblers. The least common song type for Kilbride was "abbxdxlg/BKI/jkk" sung by three males.

A single male was recorded from each of the following areas, Cape St. Mary's (Figure 14, C), Flatrock (Figure 14, E) and Little Bell Island (Figure 14, G). The Cape St. Mary's male sang "abcbjg1x2/BCSM/jxxxxxx" which contains a seven note terminal trill, the longest for any bird sampled. A male from Flatrock sang "acbcbbx1gr1/BFL/kk" which was similar to Kilbride males, excepting the omission of a "j" note in the terminal trill. The only available song recorded from Little Bell Island, "abbbj1/BLBI/k1" was a post-copulatory whisper song which is a less audible rendering of primary song (Van Tyne and Berger, 1976).

Extreme stereotypy in song structure within a sub-population occurred on Miquelon: "abbc1b/BQM/jkk" (Figure 15, H) for males one and two with birds three and four lacking the "c1" phone. Introductory phrases of Miquelon song contained four "b" notes which was more than Kilbride (3), Flatrock (3) but the same number as Bell Island, Chamberlains and Little Bell Island. St. Pierre males also showed extreme stereotypy with all 15 individuals singing a dominant song pattern "abbbxbxx1g11/BSP/kk" (Figure 15, I) with two individuals replacing "x1" with "x2".

Table VI. - Note and phone types peculiar to breeding communities.

Location (map code)	Introductory	Middle	Buzz	Terminal Trill
Bacoufen Isl. (A)	3 "q" notes per song	q', u, z,	EBI	
Bell Isl. (B)		h', x, j*	BBBI	
C. St. Mary's (C)		x2, 81	BCSH	m
Chamberlains (D)	d1	x3, y	BCH	n
Flatrock (E)		r1	BFL	
Kilbride (F)		h', i, q', r', s	BKI	
Little Bell Isl. (G)		11**	BLBI	k1
Miqueon (H)	4 "p" notes per song, d1		BCM	
St. Pierre (I)	2 "q" notes per song, 6 "p" notes per song	11	BSP	missing "j" note
Trinity (J)		l, l1	BTR	o

* shared with one bird from Chamberlains
 ** shared with all birds from St. Pierre

Table VII - Results of cluster analysis for three different similarity coefficients.

JACCARD COEFFICIENT = .417

cluster #	individuals	misclassified ind.'s
1	KI 1-15, FL 1, BI 10	FL 1, BI 10
2	SP 1-15	-----
3	BI 1-10, GM 1-4, CH 2	GM 1-4, CH 2
4	BBI 1-4	-----
5	CH 1,3	-----
6	TR 1,2	-----
7	CSM 1	-----
8	LBI 1	-----

87.5% CLASSIFIED ACCORDING TO GEOGRAPHIC LOCATION

12.5% MISCLASSIFIED

CEZAROWSKI-DICE COEFFICIENT = .589

cluster #	individuals	misclassified ind.'s
1	KI 1-15, FL 1, BI 10	FL 1, BI 10
2	SP 1-15	-----
3	BI 1-10, GM 1-4, CH 2	GM 1-4, CH 2
4	BBI 1-4	-----
5	CH 1,3	-----
6	TR 1,2	-----
7	CSM 1	-----
8	LBI 1	-----

87.5% CLASSIFIED ACCORDING TO GEOGRAPHIC LOCATION

12.5% MISCLASSIFIED

CORRELATION COEFFICIENT = .514

cluster #	individuals	misclassified ind.'s
1	KI 1-15, FL 1, BI 10	FL 1, BI 10
2	SP 1-15	-----
3	BI 1-10, GM 1-4, CH 2	GM 1-4, CH 2
4	BBI 1-4	-----
5	CH 1,3	-----
6	TR 1,2	-----
7	CSM 1	-----
8	LBI 1	-----

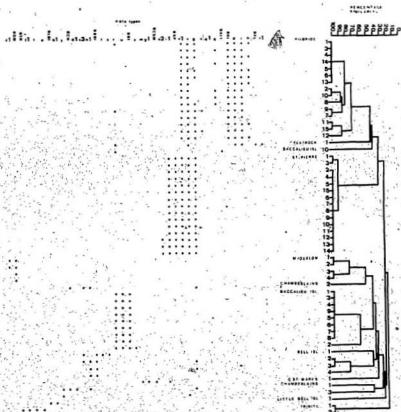
87.5% CLASSIFIED ACCORDING TO GEOGRAPHIC LOCATION

12.5% MISCLASSIFIED

phones. Two males sang the same song in Trinity, "abddtt1/BTR/okk" (Figure 15,J), replacing the traditional "j" note in the terminal trill with an "o" and adding unique "t" note and "t1" phone. Table VI lists song note and phone types peculiar to a breeding community and according to their phrase position in song.

A cluster analysis was performed upon the song formulae in Table IV. Individuals were clustered together on the basis of presence or absence of note types within their individual song structure. Also included were repetition scores for certain note types. Cluster analysis employing Jaccard coefficients yielded a dendrogram which provided an illustration of the groupings (Figure 16). In Figure 16 each individual's song (abscissa) is plotted in terms of percentage similarity (ordinate). A sample of those notes which amplified the pooling of note types within a geographic region are below the males. Three similarity coefficients (Jaccard, Czezanowski-Dice, and Correlation) were used to reclassify males on the basis of similarity of note structure. A Jaccard Coefficient .417 or 41.7% similarity yielded 8 clusters and the members of each cluster are listed in Table VII. The Czezanowski-Dice and Correlation coefficients produced similar results at .589 and .514, respectively. Clusters formed at 41.7%, 58.9% and

Figure 16. — Dendrogram and note pooling from songs
sampled.



51.4% similarity for the three coefficients were considered to be the most ecologically interpretable. Application of cluster analysis interpretation in this fashion has been used by Martin (1977 in Blaquiere 1979) and Blaquiere (1979). True classifications were defined as all birds forming a cluster A that were recorded from study area A. All three coefficients correctly classified 87.5% of the individuals and 12.5% incorrectly. Males from Bell Island, Cape St. Mary's, Chamberlains (males 1,3), Little Bell Island, St. Pierre, and Trinity were classified into true clusters.

Although three different song patterns could be identified from Bell Island and Kilbride, these different themes were still similar enough to the other song types so as to be clustered with them forming a heterogeneous dialect system. Four Miquelon males, one Chamberlains male and one Baccalieu Island male were classified. The Chamberlains male and the four Miquelon males were grouped in with Baccalieu Island males, while the Baccalieu Island male was classified in with Kilbride males.

Secondary Song

Van Tyne and Berger (1976) define four types of secondary song of which one will be discussed here. Whisper

Table VIII - Descriptive statistics of male song perch selection.

	Substrate						
	Spruce	Fencepost	Rock	Willow	Tussock	Bullrush	Other
% usage	41.4	15.7	11.4	11.4	10.0	7.1	2.9
Mean height (n)	215.8cm (29)	114.5 (11)	19.1 (8)	58.1 (8)	31.6 (7)	60.4 (5)	111.8 (2)
SD	151.9	42.9	24.6	25.5	35.3	37.7	14.3

song is "a rendering of primary song with a low audibility limit of about twenty yards" (Van Tyne and Berger, 1976). The sonograph of Little Bell Island song was a whisper song given by the male after dismounting the female (Figure 14,G). Similar post-copulatory singing was observed from Bacallieu Island and Chamberlains males. The Bacallieu Island observation was in July 1980, when other pairs were know to be initiating new broods. Whisper song may play a role in cementing pair bonds.

Song Perch Selection

Seven different strata were employed as song perches by 56 males. Data from the 70 perches analysed (Table VIII) show that males utilized spruce, 41.4% followed by fencepost, 15.7%, rock, 13.4%, tussock, 10.0%, bulrush, 7.1% and other 2.9%. The mean height $\pm$ sd for each substrate is given in Table VIII. The tallest song perch was in spruce at 609.6 cm and the greatest average height, 215.8 ± 151.9 cm was in spruce. The lowest song perches were either on the ground or on rocks at 0.0 cm. These data suggest that males prefer the highest perch available in a territory which concurs with findings of Zimmerman (1971) and Wiens (1973). Although males sang from some low perches as well as in spruce, perches were always at a height range above

Table IX - Color Band Recovery Data for Baccallee Island.

Color Sequence (ad.)	Date Recovered	Date Banded	% Recovered
o o o *	13/5/81	23/6/80	21.7%
bl wildl	13/5/81	5/7/80	
lb g*	16/5/81	9/7/80	
lb wildl g*	18/5/81	7/7/80	
o bl lb*	20/5/81	21/6/80	
Color Sequence (Juv.)	Date Recovered	Date Banded	% Recovered
W g lb	13/5/81	30/6/80	26.7%
o W bl**	14/5/81	17/6/80	
W lb bl	18/5/81	25/6/80	
o lb W	19/5/81	17/6/80	

* recovered on same territory where it was banded the previous summer.

** singing male.

acoustically impeding vegetation described in greater detail by Morton (1970;1975) and Marten and Marler (1977).

Color Band Recovery Data

A total of 38 birds were color banded during summer 1980, composed of 23 adults and 15 juveniles (i.e., nestlings and fledglings). During a 10 day return trip to Baccalieu Island (13/5-23/5/81) five of 23 adults (21.7%) and 4 of 15 juveniles (26.7%) were recovered (see Table IX).

Discussion

Song Dialects

Extreme stereotypy in song structure peculiar to a breeding community was exemplified by males from Baccalieu Island, Kilbride, Miquelon, St. Pierre and Trinity (Table V) where different individuals sang identical song patterns, the dominant theme. Individual variation appeared in metric measurements of song parameters, i.e., maximum frequency, minimum frequency, duration (see Table V). Individuality may be encoded in song by varying physical parameters of a dominant song pattern while still reaping benefits from any reproductive advantages attributed to song conformity. Another form of individual variation was the inclusion of new notes, not included in the dominant pattern, creating new song types. Dialects with a single dominant song pattern are homogeneous while those areas with more than one dominant pattern are heterogeneous.

Homogeneous dialects existed in Miquelon, St. Pierre, and Trinity while heterogeneous dialects were sung by males from Baccalieu Island, Bell Island, Chamberlains, and Kilbride (Table III). For instance, the Kilbride dialect had three song types of which "abbcdxigh1BKIjkk" was the

dominant song pattern. The two variant themes replaced "hi" with "rs" or the bubbler prototype "qqqq." Baccalieu Island and Bell Island males also interchanged notes in the middle phrase creating the three themes recorded there.

Songsters were clustered into dialects according to differences in song structure, i.e., presence and absence of note types. Results of playback experiments involving primary song (Lemon 1967; 1974; Milligan and Verner, 1971) led Lemon (1977) to conclude that dialect differences are embodied in "details of particular syllables." Songsters were clustered into dialects according to differences in song structure. At Jaccard similarity coefficient .417 or an average difference in song structure of 41.7% between clusters, 87.5% of 56 males were clustered accurately according to geographic origin (Table VII). Members of six of eight clusters representing Bell Island, Cape St. Mary's, Chamberlains, and Little Bell Island were clustered according to study area. Nine of ten Baccalieu Island males sang two themes which were similar enough in note structure to be classed as the same dialect. Two of three song types from Baccalieu Island also formed a heterogeneous dialect. In most subpopulations, different song themes were not divergent enough from the dominant theme to be considered a foreign dialect. However, members of two larger clusters composed primarily of Baccalieu Island (Table VII, cluster 4) and Kilbride males (cluster 1) each had males not

recorded in either of the study areas. The Kilbride cluster contained two extra males from Baccalieu Island (male 10, Figure 10,A2) and Flatrock (male 1, Figure 14,E), while the Baccalieu Island cluster included four males from Miquelon (Figure 15,H) and one Chamberlains male (male 2, Figure 12,D2).

All 15 Kilbride males were clustered together before the addition of Baccalieu Island 10 and Flatrock 1 meaning that these latter two additions were more similar to the entire Baccalieu Island subpopulation compared to average differences with clusters representing other dialects. There is a continuous connection of farm habitat between Kilbride and Flatrock and other bubbler males were heard in the immediate singing vicinity of Flatrock 1. This implies a Kilbride dialect which stretches 12-15 km north to Flatrock. Baccalieu Island 10 (Figure 10, A2) was a bubbler which raised a brood of four young. The bubbler song type was common to Kilbride males, although this male's song did have some Baccalieu Island traits, like the "d" note included in the terminal trill. Bubbler males are predominant in Kilbride and appear rarely in other dialect areas like Baccalieu Island and Bell Island (Figures 10, 11 respectively). Dialects can be used as a tool for tracing the origin of invading populations (Baptista 1975; Mundinger 1975). The occurrence of bubbler males in other dialect areas suggest an emigration from Kilbride where bubbler

males predominate. This would mean that Conception Bay dialects have evolved from birds emigrating from Kilbride in an east--west fashion.

The Miquelon dialect was the simplest song pattern with a mean $\pm$ sd of 5.50 ± 0.58 different notes and phone types (Table V). It lacked a middle phrase between introductory and buzz phrases, the only song type recorded that did (Table IV, Figure 15,H). The simpler song type was subsumed by the more complex Baccalieu Island dialect with which it had the greatest average similarity. Inspection of physical parameters of song (Table V) describing Baccalieu Island song and Miquelon song reveal strong contrast in number of song notes, number of different note types and minimum frequency. Therefore, Miquelon males clustered inaccurately with Baccalieu Island males is an artifact of the clustering technique. The same explanation applies to the misclassification of Chamberlains 2 with the Miquelon cluster. The terminal trill of both dialects share the more traditional "jkk" sequence which is the only real similarity they share. The fact that this Chamberlains male shared terminal trills with Miquelon males while Chamberlains 1 and 3 possessed terminal trills of "d|kk" and "n" respectively, supports the contention that these misclassifications are due to the clustering technique.

Primary song of P. s. labradorius varies among breeding

locations. These differences occur among populations separated by physical barriers in the form of large bodies of water, like Baccalieu, Bell and Little Bell Islands, and St. Pierre et Miquelon. Dialect differences also were found between Chamberlains and Kilbride males which were not separated by geographical barriers, though there is no pasture or other farmland connecting the two areas as there is the between Flatrock and Kilbride. Breeding habitat of labradorius is restricted largely to pasture habitat in Newfoundland and St. Pierre et Miquelon which means that its distribution on these islands can be considered patchy. Odum (1971) described these areas as having biomes composed primarily of taiga and tundra habitat, which is unsuitable breeding habitat for labradorius. This patchy aspect of suitable breeding habitat is similar to a condition of ecological islands described by Baker (1975) and Orejuela and Morton (1975) for migratory subspecies of White-crowned Sparrow (Zonotrichia leucophrys oriantha), which possessed dialects corresponding to these islands. This could explain the difference between Chamberlains and Kilbride song dialects and the absence of differences with Flatrock males for which there was a continuous connection between breeding habitats.

According to Alcock (1979), characters common to related species are usually older in evolutionary time than distinctive and rare characters which are "recent

modifications of ancestral behavior." In an analysis of parameters eliciting species recognition in Indigo Buntings, Passerina cyanea, Emlen (1972) concluded that "species-specific traits" of bird song are those notes having the highest probability of being shared by all songsters.

The seven most common song notes found in this study were "a" 100%, "b" 100, "j" 94.6%, "k" 89.3%, "g" 64.8%, "c" 62.4% and "x1" 53.6%. Buzz notes of varying structure were included in all songs recorded. These notes were probably the main constituents of a simple four part song from which today's present dialects arose. A close representation of what ancestral song might have looked like is evident in the simple Miquelon pattern (Table IV). Miquelon is one of the few islands between Newfoundland and the mainland (Nova Scotia). Its geographic location and simple song structure may be evidence that labradorius may have begun its colonization of Newfoundland from Miquelon. Comparison with Nova Scotia songsters would be necessary to confirm this assumption.

Comparison of vocal behaviour between P. s. labradorius, P. s. beldingi (Bradley 1977) and P. s. savanna (Chew 1981) indicate that vocal divergence occurs in primary song notes (see Figure 2, Bradley 1977, Figures 1,2 in Chew 1981, and Figure 2, this study) with each subspecies.

possessing note types unique to their breeding range. Gross examination of labradorius and savanna songs show less song note divergence, especially notes of the introductory phrase. From this comparison it has also been shown that six basic similarities exist between the two species' singing behaviour. 1) Like beldingi, labradorius has a single song repertoire, each song composed of four phrases, a simple introductory phrase with three different note types or less, a highly variable middle phrase followed by the main buzz section which is in turn followed by the terminal trill which is least resistant to variability. Chew (1981) described five phrases for savanna song but little difference existed between A and B phrases of Chew's schema. Considered as a single phrase giving this song a four part structure, this subspecies' skeletal makeup closely resembled those of the other subspecies. 2) Although shorter variations of the main buzz note occurred in the introductory and middle phrases (parts 1 and 2 of Bradley's schema), the third phrase was reserved for the longest buzz note in both subspecies. 3) Bradley (1977) described the terminal flourish of beldingi as the most traditional and least variable of song phrases which was also observed for labradorius in this study. Labradorius males had a characteristic "jkk" sequence with either or both "j" and "k" notes found in the terminal trill of most birds sampled. 4) Song duration ranged from 1.7--3.1 sec for beldingi

Table X - Characteristics of *P. sandwichensis* ancestral song *

Phrases			
Introductory	Middle	Buzz	Terminal Trill
1-3 note types 5-8 total notes	highly variable	main buzz note location	1-6 notes, fixed phrase duration

* proposed duration of 1.5-3.0 sec

(Bradley, 1977), 1.85--2.65 sec for savanna (Chew 1981) and 1.59 to 2.60 sec for labradorius showing some overlap in song length. 5) Bradley (1977) noted extreme stereotypy in song structure within breeding subpopulations. Song pattern ABO1, the dominant song pattern for Anaheim Bay (Bradley, 1977) was sung identically by 18 males. This phenomenon of theme dominance within a subpopulation was also observed in labradorius subpopulations from Bacallieu Island, Kilbride, Miquelon, St. Pierre, Trinity, where 8/10, 6/15, 4/4, 15/15 respectively, sang dominant themes peculiar to their respective communities. Kilbride males sang two dominant patterns 1 and 2 consisting of six "ghi" and six bubblers "qqqq", respectively. 6) Another important feature shared by labradorius and beldingii is that the phrase of greatest note variance is the middle phrase for both individual and dialect variation. Results of principle components analysis of savanna song parameters also indicated dialectal variance in this phrase (Chew 1981).

Provided that commonality of a behavioural character indicates it is more primitive than other species-specific traits, combination of these similarities shared between these three subspecies yield a crude description of ancestral song. From the results of the above comparison, a crude description of what characteristics ancestral P. sandwichensis song might have had is given in Table X. If behaviour is shaped by natural selection and has a genetic

component, then species of common ancestry should have similar behavioural traits (Alcock 1979). Therefore it is not surprising that these two subspecies should have extremely similar vocal behaviour.

The buzz note was the longest song note for all males recorded and bears close morphological similarity to hostile buzz calling recorded during territorial confrontations. This study has shown that separate components of the call repertoire of labradorius fledglings and adults can be clearly identified as song notes (see Figure 2, "b", "c"; Figure 4, "buzz"; Figure 7, 15+ days old). This has lead me to hypothesize that ancestral song probably evolved from a crude incorporation of call repertoire components which were ritualized into primary song.

Subspecific comparisons of vocal characters are important as a means assaying what role dialect differences might play in species radiation. The two subspecies dealt with here share common ancestry with 15 other subspecies of P. sandwichensis in North America, and Bradley (1977) believes that this is indicative of rapid speciation of many coastal Emberizine species. Analysis of song samples from the other 15 subspecies would firm up this preliminary description of ancestral song and provide further criteria for detecting origin and radiation of P. sandwichensis ssp. in North America in a manner similar to that which Baptista

and King (1980) did with White-crowned Sparrow subspecies.

Dialect differences in single song repertoire of P. sandwichensis resemble the same phenomena studied extensively in White-crowned Sparrows (Milligan and Verner 1971; Baker 1975; Orejuela and Morton 1975; Baptista 1977; Baptista and King 1980). The findings that metric parameters and song morphology (note types) do not covary in Z. leucophrys (Baptista 1977) have also been observed in P. s. labradorius dialect behaviour. Apparently, selection pressures promoting individuality versus dialect conformity act on song in the same manner in both species producing similar modes of song variance.

Another similarity between the two species is presence of dialect differences in both sedentary and migratory subspecies. Dialects in the two migratory subspecies, P. s. labradorius and Z. l. oriantha, was mentioned earlier, and also dialects were probably enhanced by patchy distribution of breeding habitat distribution. Pettingill (1970) and Krebs and Kroodsma (1980) remarked that dialects were less readily developed in migratory subspecies. Perhaps ecological constraints in the form of patchy breeding habitat distribution may be a form of intraspecific allopatry enhancing dialect propagation. Kroodsma (1972; 1974) observed identical singing behaviour among neighbouring Bewick Wren (Thyromanes bewickii) songsters

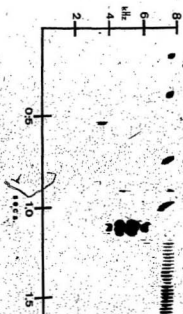
with large song repertoires and Baptista (1977) and Bradley (1977) have noted this phenomenon in single song repertoire species Z. leucophrys and P. s. beldingii respectively.

In view of laboratory work on social isolates, Krebs and Kroodsma (1980) suggest that 1) a single song repertoire species which sings dialects of primary song and 2) males within a dialect which sing identical song patterns (dominant themes) infer a learning mechanism underlying song transmission. Song learning in Z. leucophrys has been demonstrated by Marler (1970) and expounded on by Nottebohm (1976). Kroodsma (1972) also noted song learning as the mechanism of transmission. Song learning was also documented by Konishi (1964) in two junco species, implying a wider distribution of song learning in the Emberizinae. A single song repertoire and neighboring males singing identical song patterns has been demonstrated in P. sandwichensis beldingii and P. s. labradorius. Of the 38 color banded birds for Baccalieu Island during 1980, 23.7% were recovered in 1981 during a 10 day interval. Four of five returning male adults were recovered on the same territory that they were banded on in 1980 (see Table IX). Intense site tenacity exemplified by the birds above and four returning first year birds fledged in 1980 provides potential for cultural transmission of song patterns. Song recorded in 1981 from a 1980 fledgling and 1980 song of its father show similar patterns (Figure 17, A-Son, B-Father).

The fledgling was from an early brood (before known second broods were initiated) enabling it exposure to territorial singing preceeding the second nesting. Kroodsmma and Pickert (1980) have shown that the amount of adult singing heard and photoperiod influence the ability nestlings to learn adult song in Marsh Wrens (Cistothorus palustris). In my study fledglings from second broods were not banded, and I am not aware of any such study on Savannah Sparrows. Occurrence of song learning in other Emberizine sparrows and similarity in dialect behaviour discussed above between Z. leucophrys, T. bewickii and P. sandwichensis clearly implies a learning mechanism for the latter species, but work on socially isolated Savannah Sparrows must be completed to confirm this assumption.

The fact that labrdorius exhibits dialect behaviour raises many questions as to its behavioural significance. Further research along the lines of Emlen (1971) must be conducted to evaluate the effect of dialect differences on the ability to hold a territory within a breeding community. Environmental factors might also select for the formation of dialects. Dialect differences could be related to specific habitat differences and should be studied further along the lines of Morton (1970) and Hunter and Krebs (1979).

Figure 17. -- Father - Son comparison of song structure from
BacCalieu Island, A-Son, B-Father.



Vocal Development

The food target for feeding parents is the red, mouth lining of gaping nestlings (Pettingill 1970). The food beg notes of gaping 1-3 day old and 6-8 day-old nestlings have the highest frequency of all components of labradorius vocal repertoire and are directed at the feeding parent. Directional beaming^u of messages towards a receiver conspecific was observed in chickadees by Witkin (1977). Food begging posture consisted of gaping skyward by nestlings and can be artificially elicited by gently vibrating the nest. As the parents face downward towards the food begging nestlings, they become a target of nestling vocal beaming. The gaping mouth becomes the "acoustical horn" discussed by Witkin (1977) which focuses the sound beam on the parent target. Directional beaming of high frequency food beg notes which have low transmission distance because of habitat attenuation (thereby reducing predator detection), should be selected for among nestlings.

Studies of vocal development showed that call notes of juvenile (nestlings and fledglings) birds are precursors of some of the adult call repertoire and are also incorporated as song notes. Similar vocal development has been documented for chaffinches by Marler (1955; 1957) and Nottebohm (1972). According to Marler and Mundinger (1971),

development of call notes is independent of song learning for most species excepting Chaffinches raised in social isolation which depended upon adult tutoring for proper "chink" call development (Marler 1956).

The adult derivative of the nestling "chip" call was first observed in 1-3 day old nestlings (Figure 7). The two notes of lowest frequency at the .25 sec mark of Figure 7 are the rudimentary "chip" notes and form part of the first beg calls. The "chip" call was also recorded through fledgling and adult ages. This call is also incorporated into primary song where it has been identified as the "c" note (Figure 2). Rudimentary form of the buzz note is a loose aggregation of high frequency beg notes of 1-3 day old nestlings in Figure 7. At 6 days old these notes are more rapidly modulated, attaining crude adult form by 10-15 days. The ability to modulate food begging vocalizations by 6 days illustrates growth of syringeal musculature and syringeal innervation enabling greater vocal control (Nottebohm 1972). Buzz phones "x, x1, x2, x3" (Figure 2) and the main buzz note of primary song are adult versions of the fledgling buzz note. This call is a refined version of the nestling buzz call, a reflection of improved vocal ability due to better developed musculature also. Fledglings 15 days or older and adults gave a soft contact note (Figure 7) which also can be found in primary song as the common "b" note of the introductory phrase (Figure 2).

Table XI - Contextual variables defining message of "chip" call in different contexts.

Behavior	Variables defining contextual conditions									
	Seasonal timing	Age of sender	Age of receiver	Receiver species	conspecific	other	territorial	non-territ.	nest approach	
Code	present post-fledge	ad	TL	ad	TL					
1	-	+	-	+	+	+	-	-	+	-
2	+	-	+	-	+	+	-	-	-	-
3	-	-	-	-	-	-	-	-	+	-
4	-	-	-	-	-	-	-	-	-	-

• Variable present during context

• Variable absent during context

1. Feeding context (filling)

2. Intra-specific territorial hostility

3. Alarm note (predator approaching)

4. Adult conspecific soliciting (female)

TL - fledgling

Multiple Functions of a Vocal Display

Beer (1975) described three different gull displays, "crooning", "facing away", and "long call" which occurred in variety of contexts. Manley (1960, cited in Beer 1975) proposed that ubiquitous displays of a message sender conveying different information to conspecific receivers is influenced by the context in which the display is given. According to Manley common displays are "context determined" and "context interpreted" by Black-headed Gulls (Larus ridibundus) Smith (1965) also noted that signal meaning included "accompaniment" and it was the accompaniment which changed the nature of the message so that it conveyed the intended message of the sender to the receiver.

As was noted earlier, the "chip" call was observed in four different contexts: 1) filial contact of 10-15 day old fledglings; 2) intraspecific territoriality; 3) alarm and 4) precopulatory soliciting of females. Variables present or absent during these contexts are listed in Table XI. The proposed functions of the "chip" call have been dealt with earlier.

It is the presence or absence of these variables which aid in defining the intended message of the sender. Multiple functions have also been assigned "chip" calls of Passerella iliaca iliaca (Blacquiére 1979), Junco hyemalis

(Pitocchelli unpublished data). Post and Greenlaw (1975) described a "tuck" call for which they proposed multiple functions. Contextual interpretations of vocal displays in Emberizines may be a reflection of the same phenomena in gulls. Colonial breeding gulls rely on visual and vocal means of communication whereas the passerine ground-nesting sparrows occupying dense vegetation rely primarily on vocal communication. If context interpretation is fundamental to animal communication it might be profitable to study those communication pathways which a species relies on most heavily to transmit information.

Evolution of Emberizine Vocal Behaviour

Lanyon (1978) documented vocal character displacement and divergence in Myiarchus flycatchers which could be used in conjunction with anatomical measurements in further understanding taxonomic relationships among these birds. Character divergence was found in both song and territorial calls. Homologous alarm calls of four Emberizine sparrows and one Empidonax flycatcher alarm call are shown in Figure 6. From Figure 6 it can be seen that Emberizine character displacement in call morphology is greatest in White-crowned Sparrow, although the stick-like structure still persists. Figure 5 of Post and Greenlaw (1975) depicts the "tuck" call of Ammodramus maritima which shares similar stick-like

morphology with its fellow Emberizines. Lanyon (1969) argued that "highly adaptive nature" of alarm calls showing convergence in unrelated avian species (Marler, 1955; 1957) and more recently between marmosets (Sanguinus fuscicollis illigeri) and birds (Vencel, 1977) and "hence have no taxonomic value." The call of Z. leucophrys is more similar to the distantly related Dusky Flycatcher than its closer Emberizine relatives (see Figure 6).

Beecher (1955) hypothesized that North American Ammodramus species arose from P. s. ssp. stock, evolving "attenuate tails and slender, insectivorous bills" and restricted to salt marsh habitat. This division was thought to have occurred after Pleistocene glaciation entered its recessive stages, retreating northward. Ancestral P. sandwichensis stock followed the glacial retreat leaving behind coastal seaside stock restricted to salt marsh habitat out of which Ammodramus evolved (Beecher 1955). A number of vocal characters recorded by Bradley (1977) and in this study for P. sandwichensis strongly resemble Ammodramus maritima vocalizations. Previously mentioned are the "tuck" and "chip" alarm calls which have multiple functions in both species and are likely to be homologous.

The "zuck" call of A. maritima is a "low pitched growling" sound (Post and Greenlaw 1975). The "zuck" call is likely to be homologous to the low frequency buzz note of P.

sandwichensis, similarly observed in hostile interactions between territorial males. A J. hyemalis fledgling was (Figure 8) recorded giving "chip" and buzz notes nearly identical to P. s. labradorius fledglings 10-15 days old. I have observed adult buzz calls in the former species but was not able to record them or their contexts. I have observed the same buzz notes given by male Swamp Sparrows (Melospiza georgiana), but these buzzes were observed primarily during territorial encounters. The incorporation of buzz notes in primary song by A. maritima and P. sandwichensis suggests closer taxonomic affinity between these species. The buzzy nature of Emberizine sparrow vocal repertoires, i.e., presence of buzz notes in fledgling and adult repertoires could be considered a primitive trait evolved from ground-nesting Emberizine ancestors. A. maritima's "tchi" vocalization (Figure 5A, in Post and Greenlaw 1975) accompanied wing raise displays (Figure 6, in Post and Greenlaw 1975) during territorial confrontations. This is probably homologous to the note slur of P. sandwichensis and J. hyemalis (Figure 3). The note slur accompanies bilateral and unilateral wing raise displays in territorial P. sandwichensis males but not in J. hyemalis. M. georgiana breeding in Newfoundland used bilateral and unilateral wing-raise displays in response to primary song playback but the wing-raise was accompanied by primary song (Pitocchelli unpublished data). Character displacement involves

"displacement" of characters (morphological, physiological, behavioural and ecological) in two sympatric species (Brown and Wilson, 1955) and best describes the asymmetry of wing raise displays accompanied by flight slurs. Similarities between vocal characters of A. maritime and P. sandwichensis support Beecher's (1955) hypothesis that seaside Sparrows evolved from ancestral Savannah Sparrow stock.

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Appendix A

Location and Dates of P. s. labradorius
recordings (1980, 1981)

Location	Dates
Beccalieu Island	12/6-28/7/80,
13-23/5/81	
Bell Island	26/5/80
Cape St. Mary's	29/5/80
Chamberlains	28/5/80
Flatrock	23/7/80
Kilbride	13-15/5/80
Little Bell Island	21/7/80
Miquelon	22,23/5/80
St. Pierre	17-20/5/80
Trinity	1/8/80

Location and Dates of Other Avian Recordings

Location	Dates	Species
California	2/7/79	Dusky Flycatcher
California	2/7/79	White-crowned Sparrow
California	2/7/79	Oregon Junco
Newfoundland	30/7/81	Dark-eyed Junco
Newfoundland	3/5/81	Fox Sparrow

Appendix B'

Frequency Scores for Presence and or
Absence of Song Notes Between Two Individuals

song notes	
Songster	w x y z
individual male 1	1 0 1 0
individual male 2	1 1 0 0
Frequency	a b c d

1=presence, 0=absence of song note

Similarity Coefficient and Formulae

Jaccard

a

a + b + c

Cezanowski-Dice

$$2a$$

$$2a + b + c$$

Correlation

$$(ad-bc)(ad-bc)$$

$$(a+b)(a+c)(b+d)(c+d)$$

